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Soft Ticks as Pathogen Vectors: Distribution, Surveillance and Control

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1. Introduction

Ticks are highly specialized obligate haematophagous ectoparasites of mammals, birds and reptiles. Ticks are distributed worldwide and are of enormous medical and veterinary relevance owing to the direct damage they cause to their hosts and, especially, because they are vectors of a large variety of human and animal pathogens. In fact, ticks are second to mosquitoes as vectors of human pathogens and the most important vectors of pathogens affecting cattle worldwide (Peter et al., 2005). In humans, tick infestations typically involve few specimens and the greatest risk for people bitten by a tick lies in infection due to a tick-borne pathogen (Parola & Raoul, 2001). Such pathogens are diverse and include viruses, bacteria, and protozoa (Jongejan & Uilenberg, 2004; de la Fuente et al., 2008a). In animals, tick infestations are much more severe than in humans. Animals can be parasitized by hundreds or even thousands of ticks, which obviously multiplies the effect on the host, either by direct injuries or disease transmission. Direct injuries to animals can be very serious, especially in tropical climates, and are mainly observed in infestations with ixodid ticks but also in infestations with some argasid ticks as *Ornithodoros lahorensis* and *O. savignyi* (Hoogstraal, 1985). The most frequent of these direct forms of damage include: (i) tissue destruction caused by the tick mouth parts and by the local inflammatory reaction of host to tick saliva; (ii) loss of blood, which in massive infestations can cause acute anaemia; (iii) paralyses caused by salivary toxins, such as the holocyclotoxin from the Australian tick *Ixodes holocyclus*, a tick species that can paralyze and kill a young animal with only one female bite; (iv) toxicoses, such as the Sweating sickness caused by the African *Hyalomma truncatum*; in ruminants this disease elicits eczematous skin lesions, hyperexcretion of exudates and more than 75% mortality in young animals, and (v) immunosuppression, which renders animals more susceptible to pathogen transmission (Mans et al., 2008a). All these direct forms of damage together with tick-transmitted diseases (including Babesiosis, Theileriosis, Anaplasmosis and Cowdriosis) cause important economic losses to the livestock industry, mainly affecting tropical and subtropical countries, where ticks constitute one of the main difficulties for the development of the livestock breeding industry (Jongejan and Uilenberg, 2004; Rajput et al., 2006).

Tick species can be grouped in two main families, the Argasidae or soft ticks, and the Ixodidae or hard ticks. A third tick family, Nuttalliellidae, only has one species, *Nuttalliella namaqua*. These three families share common basic properties that are modified distinctively inside each family according to their particular behaviour patterns and life-style (Hoogstraal, 1985).

The family Argasidae includes some 193 species, but their phylogeny and taxonomy is as yet controversial, the genus-level classification of the family Argasidae being much less settled than that of the Ixodidae (Estrada-Peña et al., 2010), and most species of Argasidae can be assigned to more than one genus. A discussion of these issues is out of the scope of this review and the reader is referred to recent papers addressing them (Nava et al., 2009a; Guglielmone et al., 2010).

Argasid ticks differ from ixodids in a range of morphological and biological characteristics. Typically, argasids do not possess a dorsal shield or scutum; their capitulum is less prominent and ventrally -instead anteriorly- located; their coxae are unarmed (without spurs), and their spiracular plates are small. In Argasidae, there are more than four developmental stages in the life cycle: egg, larva, several nymphal stages, and adult. Nymphs have from two to eight separate instars. The exact number of instars varies according to the species and its future sex when adult. It is also influenced by the individual's state of nutrition. Argasids tend to be endophilic/nidicolous parasites that colonize the nests and burrows of their hosts and feed when the host arrives. In contrast, ixodids are mostly exophilic ticks that actively seek hosts when the seasons are suitable, although examples of nidicolous ixodid ticks also exist, especially among species of the genus *Ixodes*.

Some soft tick species exhibit extremely rigid host specificity. However, it has been suggested that most soft ticks show indiscriminate host feeding and such apparent variation in host preference probably reflects microhabitat preference and host availability within the microhabitat (Vial, 2009). Most argasids are fast feeders, ingesting a relatively small amount of blood per meal and adult specimens can feed and reproduce repeatedly. Argasids are very resistant to starvation and can survive for several years without feeding (Sonenshine, 1992). This, and their diapause periods, affords them great flexibility in their developmental cycles (Vial, 2009).

Argasid distribution can be considered cosmopolitan since they can be found throughout the world with the exception of places showing extreme conditions, although specimens have been found in Sub-Antarctic biogeographical regions (Estrada-Peña et al., 2003). The distribution of each particular species is more limited, but it may be very extensive, depending on factors such as the adaptability of each particular species to new ecological environments, the dissemination of immature phases by migratory birds, and the ability of adult specimens to infest different host species. It is therefore possible that species that have never been identified on one continent can be imported from different continents, and that new species can be identified in different parts of the world, contributing to a geographic distribution of soft tick species in constant evolution. Changes in argasid distribution are more difficult to predict than those of ixodids and currently no distribution models have yet been published for them. However, investigations are in progress, suggesting that soft tick distribution modelling is also possible. This modelling is based on the natural niche concept and takes into account the influence of climatic factors and the particularities of soft ticks, including their nidicolous lifestyle, indiscriminate host feeding, and a flexible developmental cycle along diapause periods (Vial, 2009). In this context, the development of

new methods for systematic soft tick surveillance, i.e. serological methods, would help to monitor soft tick occurrence and the prediction of their distribution and its evolution. Table 1 offers information about the known distribution of a number of argasid species grouped by biogeographical regions (Udvardy, 1975). It should be noted that this table does not aim to be exhaustive but simply illustrative and that it might contain unconfirmed reports and some controversial species names.

Species	Localization	Hosts	References
Paleartic region			
Argas abdussalami	Pakistan	Birds	Ghosh et al. (2007)
Argas arboreus	Israel	Cattle, birds	Belozerov et al. (2003)
Argas assimilis	China	Livestock	Chen et al. (2010)
Argas beijingensis	China	Livestock	Chen et al. (2010)
Argas miniatus	Portugal	Poultry	Lisbôa et al. (2009),
Argas japonicus	China, Japan	Livestock, poultry	Chen et al. (2010), Yamaguti et al. (1968)
Argas persicus	Spain, Italy, Iran, Pakistan, China, Russian Federation	Birds, poultry, livestock	Cordero del Campillo et al. (1994), Pantaleoni et al. (2010), Ntiamoa-Baidu et al. (2004), Keirans & Durden (2001), Ghosh et al. (2007), Chen et al. (2010), Dikaev (1981)
Argas polonicus	Poland	Birds	Siuda (1996)
Argas pusillus	Tadzhikistan, Kyrgyzstan, Turkmenistan	Bats, humans	Gavrilovskaya (2001), de la Fuente et al. (2008a)
Argas reflexus	Poland, Italy, France, Spain, Iran, Pakistan, Russian Federation	Humans, birds	Karbowiak & Supergan (2007), Poggiato (2008), Gilot & Pautou (1982), Cordero del Campillo et al. (1994), Ntiamoa-Baidu et al. (2004), Siuda (1996), Ghosh et al. (2007), Dikaev (1981)
Argas robertsi	China	Birds	Chen et al. (2010)
Argas vespertilionis	Sweden, Portugal, Great Britain, Germany, Pakistan, Tadzhikistan, Kyrgyzstan, Turkmenistan, Russian Federation	Bats, humans, livestock	Jaenson et al. (1994), Caeiro (1999), Hubbard et al. (1998), Gavrilovskaya (2001), de la Fuente et al. (2008a), Cornely & Schultz (1992), Ghosh et al. (2007), Dikaev (1981)
Argas vulgaris	China, Russian Federation	Livestock	Chen et al. (2010), Dikaev (1981)
Carios capensis	Great Britain, Croatia, Spain, China, Torishima Island, Japan	Seabirds	Converse et al. (1975), Reeves et al. (2006), Ushijima et al. (2003), Chen et al. (2010)

Species	Localization	Hosts	References
Carios pusillus	China	Livestock	Chen et al. (2010)
Carios sinensis	China	Livestock	Chen et al. (2010)
Carios vespertilionis	China	Livestock	Chen et al. (2010)
Ornithodoros alactagalis	Armenia, Azerbaijan, Georgia, Iran, Northern Caucasus, Transcaucasia, Turkey	NR	Filippova (1966)
Ornithodoros asperus	Caucasus, Iraq	Humans, rodents	Assous and Wilamowski (2009), Parola & Raoult (2001)
Ornithodoros coniceps	Italy, France, Spain, Israel, Jordan, Egypt, Afghanistan, Ukraine,	Pigeons	Hoogstraal et al. (1979), Khoury et al. (2011), Ghosh et al. (2007)
Ornithodoros erraticus	Portugal, Spain, Greece, Italy, Cyprus, Algeria, Egypt, Tunisia, Morocco, Iraq, Iran	Humans, pigs	Caeiro (1999), Oleaga-Pérez et al (1990), Parola & Raoult (2001), EFSA (2010a)
Ornithodoros lahorensis	Armenia, Kazakhstan, Russian Federation, Kosovo, Syria, Turkey, Iran, China	Cattle	Moemenbellah-Fard et al (2009), Ahmed et al. (2007), Chen et al. (2010), Ghosh et al. (2007), Aydin & Bakirci (2007), EFSA (2010c), Dikaev (1981)
Ornithodoros maritimus	Portugal, Italy	Seabirds	Caeiro (1999), Manilla (1990)
Ornithodoros pavlovsky	Kazakhstan, Kirghizia, Tajikistan, Turkmenistan, Uzbekistan	Mammals	Filippova (1966)
Ornithodoros savignyi	Egypt	Camel, sheep, goat, cow, buffalo	Helmy (2000)
Ornithodoros sonrai	Morocco, Libya, Egypt, Turkey , Iran	Domestic and sylvatic pigs	Vial et al. (2006), Vial (2009)
Ornithodoros tartakowskyi	Iran, central Asia, China	Humans	Parola & Raoult (2001), Chen et al. (2010)
Ornithodoros tholozani	Cyprus, Daghestan, Egypt, Iraq, Iran, China, Israel, Jordan, Kazakhstan, Kyrgyzstan, Lebanon, Libya, Syria, Turkey, Ukraine, USSR	Humans, livestock	Moemenbellah-Fard et al. (2009), Assous et al. (2009), Chen et al. (2010)
Ornithodoros verrucosus	Armenia, Georgia, Russian Federation	NR	Maruashvili (1965), Gugushvili (1972), Dikaev (1981)

Species	Localization	Hosts	References
Afrotropical region			
Argas africolumbae	Kenya, Tanzania, South and South-West Africa	Birds	Hoogstraal et al. (1977)
Argas arboreus	South Africa	Cattle, birds	Mumcuoglu et al. (2005)
Argas persicus	Ghana	Poultry	Ntiamoa-Baidu et al. (2004), Jongejan & Uilenberg (2004)
Argas reflexus	Ghana	Humans, poultry	Ntiamoa-Baidu et al. (2004), Siuda (1996), Jongejan & Uilenberg (2004)
Argas walkerae	South Africa	Poultry	Nyangiwe et al. (2008)
Argas vespertilionis	Ghana	Bats	Ntiamoa-Baidu et al. (2004)
Carios capensis	Indic ocean islands	Seabirds	Converse et al. (1975)
Ornithodoros compactus	South Africa	Tortoises	Horak et al. (2006)
Ornithodoros coniceps	Kenya	Pigeons	Hoogstraal et al. (1979)
Ornithodoros coriaceus	Africa	Domestic and sylvatic pigs	Labuda & Nuttall (2004), de la Fuente et al. (2008a)
Ornithodoros graingeri	Africa	Humans	Parola & Raoult (2001)
Ornithodoros moubata	Central and South Africa	Humans, domestic and sylvatic pigs	Ntiamoa-Baidu et al. (2004), Parola & Raoult (2001)
Ornithodoros porcinus	Southern and East Africa	Humans, domestic and sylvatic pigs	Bastos et al. (2009), Mitani et al. (2004)
Ornithodoros savignyi	Kenya, Central and South Africa	Livestock, humans	Walton (1951), Howell (1966), Hoogstraal (1985)
Ornithodoros sonrai	Kenya, Mauritania, Senegal, Mali, Gambia	Domestic and sylvatic pigs	Vial et al. (2006), Vial (2009)
Ornithodoros turicata	Africa	Domestic and sylvatic pigs	Labuda & Nuttall (2004), de la Fuente et al. (2008a)
Ornithodoros zumpti	Africa	Humans	Rebaudet & Parola (2006)
Neartic region			
Argas cooleyi	USA	Humans	Calisher et al. (1988)
Argas monolakensis	Mono Lake (USA)	Humans	Schwan et al. (1992)
Argas persicus	USA	Poultry	Keirans et al. (2001)
Carios capensis	Hawaii, South Carolina, and Texas (USA)	Seabirds	Reeves et al. (2006), Rawlings (1995)
Ornithodoros coriaceus	California, Oregon and Nevada (USA)	Cattle	Teglas et al. (2006), Failing et al. (1972)

Species	Localization	Hosts	References
Ornithodoros hermsi	USA, Canada	Humans	Dana (2009), Schwan et al. (2007), Parola & Raoult (2001)
Ornithodoros kelleyi	USA	Bats, humans	Cilek & Knapp (1992)
Ornithodoros parkeri	USA, Canada	Human	Dana (2009), Dworkin et al. (2002)
Ornithodoros puertoricensis	USA	Reptiles	Venzal et al. (2006, 2008), Bermúdez et al. (2010)
Ornithodoros rossi	USA	Bats	Steinlein et al. (2001)
Ornithodoros talaje	USA	Rodents, domestic animals, humans	Parola & Raoult (2001)
Ornithodoros turicata	USA, Canada	Humans, dogs, tortoises	Dana (2009), Dworkin et al. (2008), Whitney et al. (2007), Adeyeye et al. (1989)
Otobius megnini	USA	Humans, cattle	Nava et al. (2006, 2009b)
Neotropical region			
Antricola delacruzi	Brazil	Bats	Labruna et al. (2008)
Antricola guglielmonei	Brazil	Bats	Labruna et al. (2008)
Argas dulus	Dominican Republic	Birds	Keirans et al. (1971)
Argas keiransi	Chile	Birds	Estrada-Peña et al. (2003, 2006)
Argas persicus	Paraguay	Poultry, birds, livestock	Nava et al. (2007)
Argas miniatus	Paraguay, Chile, Brazil	Pultry	González-Acuña & Guglielmone (2005), Nava et al. (2007), Ataliba et al. (2007)
Argas monachus	Argentina, Paraguay	Birds	Keirans et al. (1973), Nava et al. (2007)
Argas neghmei	Argentina, Chile	Poultry, humans	Di Iorio et al. (2010)
Carios mimon	Bolivia, Uruguay, Brazil	Bats, humans	Barros-Battesti et al. (2011)
Nothoaspis amazoniensis	Brazil	Bats	Nava et al. (2010)
Ornithodoros rioplatensis	Uruguay, Argentina, Chile	NR	Venzal et al. (2008)
Ornithodoros amblus	Peru, Chile	Birds	Clifford et al. (1980), Need et al. (1991)
Ornithodoros brasiliensis	Brazil	Humans	Martins et al. (2011)
Ornithodoros coriaceus	Mexico	Humans	Failing et al. (1972)

Species	Localization	Hosts	References
Ornithodoros hasei	Paraguay	NR	Nava et al. (2007)
Ornithodoros hermsi	Mexico	Humans	Dana (2009), Schwan et al. (2007), Parola & Raoult (2001)
Ornithodoros marinkellei	Colombia, Panama, Venezuela, Guyana, Brazil	Bats	Labruna et al. (2011)
Ornithodoros parkeri	Mexico	Humans	Dana (2009), Dworkin et al. (2002)
Ornithodoros puertoricensis	México, Guatemala, Nicaragua, Panama, Colombia, Venezuela, Paraguay , Jamaica, Dominican Republic, Puerto Rico, Haiti	Reptiles	Nava et al. (2007), Venzal et al. (2006, 2008), Bermúdez et al. (2010), Endris et al. (1989)
Ornithodoros rondoniensis	Brazil	Bats	Labruna et al. (2008)
Ornithodoros rostratus	Paraguay, Brazil, Argentina	Reptiles	Venzal et al. (2006), Martins et al. (2011), Guglielmone et al. (2003)
Ornithodoros rudis	Paraguay	Humans	Parola & Raoult (2001)
Ornithodoros spheniscus	Chile	Penguins	González-Acuña & Guglielmone (2005)
Ornithodoros talaje	México, Brazil, Chile[1]	Rodents, domestic animals, humans	Tizu et al. (1995), Parola & Raoult (2001), González-Acuña & Guglielmone (2005)
Ornithodoros turicata	Mexico	Human	Dana (2009)
Ornithodoros yunkeri	Galapagos Islands	Seabirds	Keirans et al. (1984)
Otobius megnini	Argentina, Chile	Humans, cattle	Nava et al. (2006, 2009b)
Oriental region (Indomalayan)			
Argas abdussalami[1]	India	Livestock	Ghosh et al. (2007)
Argas gujaratensis[1,2]	India	Bats	Ghosh et al. (2007)
Argas hermanni	India	Birds	Ghosh et al. (2007)
Argas hoogstraali[1]	India	Bats, wild mammals	Ghosh et al. (2007)
Argas indicus[1,2]	India	Bats, wild mammals	Ghosh et al. (2007)
Argas japonicus	China, Korea	Livestock, poultry	Chen et al. (2010), Yamaguti et al. (1968)
Argas persicus	India, Bangladesh	Poultry, birds, livestock	Keirans et al. (2001), Ntiamoa-Baidu et al. (2004), Ghosh et al. (2007)

Species	Localization	Hosts	References
Argas robertsi	Taiwan, Thailand, India, Indonesia, Sri Lanka	Birds	Hoogstraal et al. (1975), Ghosh et al. (2007)
Argas soneshinei[1,2]	India	Livestock	Ghosh et al. (2007)
Argas vespertilionis	India	Livestock, bats, humans	Gavrilovskaya (2001), Ghosh et al. (2007), de la Fuente et al. (2008a)
Argas wilsoni[1,2]	India	Bats	Ghosh et al. (2007)
Carios batuensis	Indonesia	Bats	Durden et al. (2008)
Carios chiropterphila[1,2]	India	Bats	Ghosh et al. (2007)
Carios faini[1]	India	Bats, wild mammals	Ghosh et al. (2007)
Ornithodoros coniceps	India	Pigeons	Hoogstraal et al. (1979), Ghosh et al. (2007)
Ornithodoros crossi[2]	India	Livestock	Ghosh et al. (2007)
Ornithodoros lahorensis	India	Cattle	Moemenbellah-Fard et al. (2009), Ahmed et al. (2007), Ghosh et al. (2007)
Ornithodoros piriformis[1]	India	Bats	Ghosh et al. (2007)
Ornithodoros savignyi	India	Livestock	Ghosh et al. (2007)
Ornithodoros tholozani	India, Kashmir	Human	Moemenbellah-Fard et al . (2009), Assous & Wilamowski (2009)
Otobius megnini	India	Humans, cattle, dogs	Nava et al. (2006, 2009b), Ghosh et al. (2007)
Australian			
Argas persicus	Southern Australia	Poultry	Petney et al. (2004)
Argas robertsi	Australia	Birds	Hoogstraal et al. (1975)
Carios capensis	Heron island, Australia	Humans	Humphery-Smith et al. (1991)

Table 1. Soft tick distribution ordered by biogeographical regions (historical records). [1]Need confirmation; [2]controversial name. NR, not reported.

2. Pathogens and infectious diseases transmitted by soft ticks

Ticks are among the most competent and versatile arthropod vectors of pathogens. Today, most emerging infectious diseases arise from zoonotic pathogens, and many of them are transmitted by arthropod vectors. Tick-borne infectious diseases are a growing and very serious world health problem and a major obstacle for animal health and production (Rajput et al., 2006). For example, in the United States Lyme disease is transmitted by *Ixodes* ticks and it has become the most common arthropod-borne infectious disease in that country (Díaz, 2009). In Europe, important pathogens transmitted by ticks are *Borrelia* spp.,

Anaplasma spp., *Rickettsia* spp., *Babesia* spp., Tick borne Encephalitis Virus (TBEV), and Crimean-Congo Haemorrhagic Fever Virus (CCHFV) (Heyman et al., 2010). In Africa, tick-borne diseases and tick infestations are among the most commonly documented causes of morbidity (Phiri et al., 2010).

Regarding the pathogens transmitted by argasid ticks, they are mainly viruses together with a number of bacterial species, and they cause severe diseases in humans and animals. The currently recognized viral diseases transmitted by soft ticks are shown in Table 2. Among them, African swine fever (ASF) has received particular attention and will be used as a model in this review. The argasid-borne bacteria are almost exclusively borreliae, which cause relapsing fever in humans (Table 3). Other potential argasid-borne pathogens that have been transmitted experimentally are shown in Table 4. Finally, most vector specimens also contain a range of non-pathogenic microorganisms that can also be transmitted to the host in the tick saliva, some of them also being included in Table 4.

2.1 African swine fever virus

The African swine fever virus (ASFV) belongs to the Asfarviridae family of arboviruses and represents the only known DNA arbovirus to date (Kleiboeker & Scoles, 2001; Labuda & Nuttall, 2008). It affects only porcine species and causes African swine fever (ASF), highly lethal to pigs, which is one of the most important viral diseases of swine included in the A list of the OIE (http://www.oie.int/en/animal-health-in-the-world/oie-listed-diseases-2011/).

In nature ASFV circulates in two types of enzootic cycles -sylvatic and domestic- both of which involve porcine hosts and argasid ticks of the genus *Ornithodoros*, including *O. moubata, O. porcinus, O. savignyi*, and *O. sonrai* in Africa; members of the *O. erraticus* complex on the Iberian Peninsula, the trans-Caucasus countries and the Russian Federation, and *O. coriaceus, O. turicata, O. parkeri* and *O. puertoricensis* in North America and the Caribbean (Kleiboeker & Scoles, 2001; Labuda & Nuttall, 2008). The virus replicates in the tissues of these tick species and, depending on the species, can be transmitted transstadially, transovarially and sexually (EFSA panel, 2010c). Among the Old World species, transovarial, transstadial and sexual transmission of ASFV have been described in *O. moubata*; transstadial and sexual transmission have been demonstrated for *O. erraticus* (Endris & Hess, 1994) and only transstadial transmission has been demonstrated for *O. savignyi*. Among the New World species, the transstadial transmission of ASFV has only been demonstrated for *O. coriaceus* and *O. parkeri*, and transovarial transmission has only been demonstrated for *O. puertoricensis* (Kleiboeker & Scoles, 2001). Thus, it can be said that all *Ornithodoros* species investigated so far (i.e., those mentioned above) can become readily infected by ASF, and all of them, except *O. parkeri* (EFSA, 2010c), can also transmit the virus to pigs, thereby playing a potential role not only as reservoirs but also as active biological vectors of ASFV. Interestingly, in spite of evidence suggesting that *O. puertoricensis* could be an efficient vector for ASFV, the presence of this tick in Haiti and the Dominican Republic did not appear to complicate the eradication of ASF from those countries in 1978. This was probably due to a lack of contact between infected pigs and *O. puertoricensis*, since the Dominican Republic II strain of ASFV (one of the strains isolated from that epizootic outbreak) was shown to be capable of infecting and being transmitted by these ticks under experimental conditions (Kleiboeker & Scoles, 2001). Other *Ornithodoros* species remain untested for ASFV infection and transmission and the possibility that they might play some kind of role in the epidemiology of ASF cannot be ruled out.

Soft tick species	Virus	References
Argas robertsi	Kao Shuan virus, Pathum Thani virus, Nyamanini virus, Lake Clarendon virus	Hoogstraal et al. (1975), Hoogstraal (1985), Labuda & Nuttall (2008)
Argas abdussalami	Manawa virus, Bakau virus, Uukuniemi virus	Hoogstraal (1985), Labuda & Nuttall (2008)
Argas africolumbae	Pretoria virus	Labuda & Nuttall (2008)
Argas arboreus	West Nile virus, Quaranfil virus, Nyamanini virus	Hoogstraal (1985), Mumcuoglu et al. (2005)
Argas cooleyi	Mono Lake virus, Sixgun virus, Sapphire II virus, Sunday Canyon virus	Hoogstraal (1985), Calisher et al. (1988), Vermeil et al. (1996), Labuda & Nuttall (2008), de la Fuente et al. (2008a),
Argas hermanni	Chenuda virus, Abu Hammad virus, Royal Farm virus, West Nile virus, Grand Arbaud virus, Nyamanini virus, Quaranfil virus	Hoogstraal (1985), Labuda & Nuttall (2008)
Argas monolakensis	Mono Lake Virus	Schwan et al. (1992), Vermeil et al. (1996), de la Fuente et al. (2008a)
Argas persicus	CCHF virus	Hoogstraal (1985)
Argas pusillus	Issyk-Kul Fever virus	Gavrilovskaya (2001), de la Fuente et al. (2008a)
Argas reflexus	Uukuniemi virus, CCHF virus	Labuda & Nuttall (2008), Tahmasebi et al. (2010)
Argas vespertilionis	Issyk-Kul Fever virus, Sokuluk virus	Hoogstraal (1985), Gavrilovskaya (2001), de la Fuente et al. (2008a)
Carios amblus	Mono lake virus	Labuda & Nuttall (2008)
Carios capensis	Upolu virus, Nyaminini virus, Quaranfil virus, Saumarez Reef vírus, Soldado vírus, Hughes virus	Converse et al. (1975), Hoogstraal (1985), Labuda & Nuttall (2004, 2008)
Carios maritimus	Chenuda virus, West Nile virus	Labuda & Nuttall (2008)
Carios spp.	Chobar Gorge virus	Labuda & Nuttall (2008)
OME/CTVM21 O. moubata cells	Karshi and Langat virus	Bell-Sakyi et al. (2009)
Ornithodoros amblus	Huacho virus, Punta Salinas virus	Hoogstraal (1985)
Ornithodoros coniceps	Baku virus	Hoogstraal et al. (1979)
Ornithodoros coriaceus	ASFV[1], Bluetongue virus	Groocock et al. (1980), Stott et al. (1985), Kleiboeker et al. (1998), Labuda & Nuttall (2004), de la Fuente et al. (2008a)
Ornithodoros denmarki	Soldado virus, Hughes virus, Raza virus, Quaranfil group	Labuda & Nuttall (2004), de la Fuente et al. (2008a)

Soft tick species	Virus	References
Ornithodoros erraticus	Qalyub virus (QYB), ASFV	Miller et al. (1985), Labuda & Nuttall (2004, 2008), Basto et al. (2006), de la Fuente et al. (2008a)
Ornithodoros kohlsi	Matucare virus	Labuda & Nuttall (2008)
Ornithodoros lagophilus	Colorado tick fever virus	Sonenshine et al. (2002)
Ornithodoros lahorensis	CCHF virus	Hoogstraal (1985), Telmadarraiy et al. (2010)
Ornithodoros maritimus	Soldado virus	Labuda & Nuttall (2004), de la Fuente et al. (2008a)
Ornithodoros moubata	ASFV, West Nile virus, HIV[2,3] Hepatitis B virus[1]	Haresnape & Wilkinson (1989), Labuda & Nuttall (2004, 2008), de la Fuente et al. (2008a), Lawrie et al. (2004), Shepherd et al. (1989), Durden et al. (1993), Humphery-Smith et al. (1993), Jupp et al. (1987)
Ornithodoros parkeri	ASFV[1], Karshi and Langat virus	Kleiboeker & Scoles (2001), Turell et al. (1994, 2004)
Ornithodoros porcinus	ASFV	Kleiboeker et al. (1998), Bastos et al. (2009)
Ornithodoros puertoricensis	ASFV[1]	Endris et al. (1991), Kleiboeker et al. (1998), Labuda & Nuttall (2004), de la Fuente et al. (2008a)
Ornithodoros savignyi	AHF virus, Bluetongue virus[1], ASFV[1]	Kleiboeker et al. (1998), Charrel et al. (2007), Bouwknegt et al. (2010)
Ornithodoros sonrai	Karshi and Langat virus, ASFV, Bandia virus	Turell et al. (1994, 2004), Vial et al. (2007), Labuda & Nuttall (2008)
Ornithodoros tadaridae	Estero Real virus	Málková et al. (1985), Labuda & Nuttall (2008)
Ornithodoros tartakovskyi	Karshi and Langat virus	Turell et al. (2004)
Ornithodoros tholozani	Karshi and Langat virus	Labuda & Nuttall (2008)
Ornithodoros turicata	ASFV[1]	Hess et al. (1987), Kleiboeker et al. (1998), Labuda & Nuttall (2004), de la Fuente et al. (2008a)
Otobius lagophilus	Colorado tick fever group	Hoogstraal (1985)

Table 2. Viruses transmitted by or associated to soft ticks. AHF, Alkhurma hemorrhagic fever virus; CCHF, Crimean Congo haemorraghic fever; ASFV, African swine fever virus; QYB, Qalyub virus. [1]Experimental infection; [2]laboratory transmission; [3]mechanical transmission.

The pathogenesis of ASFV in Old World *Ornithodoros* tick species is characterized by a low infectious dose, lifelong infection, and low mortality until after the first oviposition; by contrast, in New World *Ornithodoros* ticks species relatively high nymphal mortality has been reported after infection, and infection does not appear to be lifelong, although it is not known whether the reduction in the number of infected ticks with time is due to differential mortality or to loss of infection (Kleiboeker & Scoles, 2001). In general, *Ornithodoros* ticks have a long life span, and some species can survive up to 15-20 years in their adult stage. Consequently, ASFV-infected soft tick populations can maintain this virus for years, although they do not seem to play an active role in the spreading of the virus over long distances. Recently, *O. erraticus* specimens collected from pig farms in Portugal more than five years after the removal of infectious hosts showed the presence of the virus and the experimental transmissibility of these persistent infections, highlighting the epidemiological role of *O. erraticus* ticks in the persistence of ASFV in the field (Boinas et al., 2011).

The epidemiological role played by soft ticks becomes important when domestic pigs are managed under traditional systems, in which pigs range freely in wild or peridomestic habitats and may enter into contact with ticks. Ticks feed mainly on wild hosts living in burrows and pigs are mostly accidental hosts. The mechanism of ASFV transmission from the sylvatic cycle to domestic pigs is probably through infected ticks feeding on pigs.

ASF affects only porcine species. Wild boars have been shown to be susceptible to ASFV infection in Sardinia (Italy), Spain and Portugal, showing similar clinical signs and case-fatality rates. This was also the case for experimentally infected feral pigs in Florida. The transmission of ASFV between the European wild boar and soft ticks is unlikely to occur since wild boars do not live in burrows; however wild boars and feral pigs can transmit the virus directly to domestic swine as well as between themselves. Whether wild boars have a reservoir role and/or could be infected in areas with outbreaks in domestic pigs remains to be elucidated (McVicar et al., 1981; Sánchez-Vizcaíno, 2006). In Africa, it has been observed that ASFV induces an unapparent infection in three species of wild swine (warthogs, bushpigs and red river hogs); however, current evidence suggests an unlikely role for bushpigs in the maintenance and transmission of ASFV, while the role played by the giant forest hog has not yet been clarified (Jori and Bastos, 2009; Ravaomanana et al., 2011).

The disease is currently endemic in many countries of Africa (mainly located south of the Sahara), Sardinia and the Caucasus. In Africa it is maintained by a cycle of infection between wild suidae and soft ticks. ASFV infection is characterized by low levels of virus in host tissues and low or undetectable levels of viraemia, but this is sufficient to infect soft tick vectors and cause subsequent tick transmission to domestic pigs. In Europe, ASF is still endemic in Sardinia, where wild boars seem to be as susceptible as domestic pigs. Previous studies have failed to find ticks from the *O. erraticus* complex in Sardinia (Encinas-Grandes, pers. com.), but those studies did not rule out the presence of the tick and this aspect deserves further attention. More recently in 2007, ASFV spread to Georgia and later to the Trans-Caucasic countries and the Russian Federation, with devastating effects on pig production (Rowlands et al., 2008). The origin of the outbreak is more probably related to entry through international ports or airports through swine fed with garbage containing ASFV-contaminated wastes. The vector competence of ticks for the ASFV currently circulating in the Caucasus is unknown; however the presence of ticks of the *O. erraticus* group has been reported in the Caucasus (Table 1).

Currently, the eradication of ASF from endemic areas is very difficult to achieve because there is no effective vaccine or treatment and the virus can be transmitted by many other routes besides tick bites. Thus, the prevention of the introduction of the virus into new areas and control of tick populations are of great importance to avoid the risk of ASF spreading from infected areas into new ones, as could be the case of virus spread throughout Europe from the Caucasus. Recommendations based on the development of an integrated strategy involving trans-Caucasus countries, the Russian Federation, and the European Union should facilitate the trans-boundary control of ASF (Wieland et al., 2011). The EFSA Panel on Animal Health and Welfare (EFSA 2010a, b, c) offers more detailed information about ASF, ASFV and its vectors in Europe, also presenting several recommendations regarding the ASFV vectorial ability of soft ticks for effective disease management.

2.2 Other soft tick transmitted viruses

West Nile virus has been isolated from *O. moubata* ticks, suggesting that ticks can become infected after feeding on viremic hosts (Lawrie et al., 2004). The tick maintains the infection through moulting, and can transmit the virus to laboratory rodents during a second blood meal (Lawrie et al., 2004). These findings suggest a potential role for *O. moubata* as a reservoir and vector of West Nile virus.

Ornithodoros ticks can also become infected with the encephalitis-producing Karshi and Langat virus group, and hence they can transmit it vertically and horizontally. These viruses have been passed in *O. moubata* cell lines without changing their biological properties (Bell-Sakyi et al., 2009). Taken together, these observations suggest a potential role for *O. moubata* as a vector of this virus group.

Indirect evidence has shown the presence of RNA from flaviviruses such as Alkhurma virus in *O. savignyi* (Charrel et al., 2007), suggesting the possibility of viral replication in this argasid and, consequently, its potential role as a vector. This possibility should be further investigated.

O. savignyi ticks can also become infected with serotype 8 of the bluetongue virus (BTV8), and this infection has been shown to be transmitted transovarially, suggesting that this soft tick could be a potential vector for bluetongue virus. Although soft ticks do not occur on livestock in Europe, they could play a role in the introduction of bluetongue virus in this region (Bouwknegt et al., 2010).

Several studies have been carried out to determine the presence of Crimean Congo Hemorrhagic Fever (CCHF), hepatitis B and HIV-1 viruses in *O. moubata*, with the conclusion that only the hepatitis B virus could be transmitted mechanically to man by this argasid (Jupp et al., 1987). Later, Shepherd et al. (1989) and Durden et al. (1993) confirmed the absence of laboratory transmission of CCHF virus by *Argas walkerae, O. sonrai, O. porcinus* and *O. savignyi*. Humphery-Smith et al. (1993) confirmed the absence of HIV-1 transmission by *O. moubata,* although these authors commented that this may not be the situation under field conditions.

The absence of CCFH virus in *O. moubata* is in accordance with the notion that the CCFH virus is not associated with argasids. However, two exceptional reports exist of the isolation of

CCHF virus from argasids, although the information should be regarded with caution. The first one reports the isolation of the virus from an *O. lahorensis* larva in Iran (Sureau et al. 1980), although this was not confirmed later; the second report describes the isolation of the virus from *A. persicus* in Uzbeck (Rusia) (Hoogstraal, 1985). Recently, in CCHF endemic areas of Iran *O. lahorensis* and *A. reflexus* ticks collected from infected and non-infected hosts have been found to be infected with the CCHF virus (Telmadarraiy et al., 2010; Tahmasebi et al., 2010). Moreover, in these areas antibodies to the CCHF virus have been found in domestic and wild animals and in birds, in which the virus can replicate and, consequently, be spread over long distances (Chevalier et al., 2004). Although it has not been evaluated whether *O. lahorensis* or *A. reflexus* can transmit the CCHF virus, the above data suggest that these ticks could be real vectors of this virus, reflecting the broad range of animal species that can act as reservoirs for the CCHF virus, and also the varied range of potential animals acting as tick hosts. Should this be confirmed, the real field situation for CCHF could be unexpectedly worrying.

Some arboviruses have been identified in *Argas* spp. ticks such as Kao Shuan, Pathum Thani and Nyamanini viruses (Hoogstraal et al., 1975), the West Nile virus (WNV) (Mumcuoglu et al., 2005), Issyk-Kul Fever virus (Gavrilovskaya, 2001), and Mono Lake virus (Labuda & Nuttall, 2008). Since the main hosts of *Argas* spp. ticks are birds, more research is necessary to know the role of tick-infested migratory birds as distributors of emerging arthropod-borne viral diseases worldwide.

About one fourth of the last pandemics were originated by the spread of vector-borne pathogens (Alcaide et al., 2009). Emerging pathogens are frequently RNA viruses with a broad host range, and tick-borne viruses are found in all the RNA virus families (Labuda and Nuttall, 2004; Reperant, 2010). Since these new pathogens can emerge either through introduction into a new population or when the interaction with the vector changes, it is very important to identify the new vectors and reservoirs of such pathogens.

2.3 Bacteria causing relapsing fevers

The most frequent bacterial disease transmitted by soft ticks is human recurrent (relapsing) fever, causing high fever in patients that abates and then recurs, giving the disease its name. Other argasid-borne bacteria causing disease in animals are less frequent, or simply under-reported.

Human relapsing fever is an arthropod-borne infection caused by *Borrelia* spp. spirochetes, whose reservoir hosts are usually wild rodents (Cutler, 2006, 2009). There are two types of human relapsing fever: the endemic or tick-borne (TBRF) type (Calia & Calia, 2000; Dworkin et al., 2002, 2009), caused by several *Borrelia* species and transmitted mainly -but not only- by ticks of the genus *Ornithodoros* (Table 3), and the epidemic or louse-borne type, caused by *Borrelia recurrentis* and transmitted by the human body louse *Pediculus humanus*; this type is more severe than the tick-borne variety.

Ornithodoros spp. ticks act not only as vectors but also as reservoirs of relapsing fever spirochetes, which seem to be quite vector-specific without crossed infections (Shanbaky & Helmy, 2000). Each *Borrelia* species responsible is identified closely with its tick vector and such species share parallel nomenclature; for example, *Borrelia hermsii* is the agent transmitted by *Ornithodoros hermsii*. Vertebrates and humans become infected during a tick blood meal through contamination of the feeding site by salivary and/or coxal secretions of the tick (Parola & Raoult, 2001). Also, transplacental transmission has been reported (Cutler, 2006).

Soft tick-transmitted *Borrelia* species causing disease in humans			
Soft tick species	**Borrelia species**	**Disease**	**References**
Argas africolumbae	*Borrelia anserina*	TBRF	Gothe et al. (1981)
Argas persicus	*Borrelia anserina*	TBRF	Gothe et al. (1981)
Carios kelleyi	*Borrelia johnsoni*	TBRF	Schwan et al. (2009)
Ornithodoros asperus	*Borrelia caucasica*, *Borrelia microti*, *Borrelia baltazardi*	TBRF	Assous & Wilamowski (2009), Parola & Raoult (2001)
Ornithodoros erraticus	*Borrelia microti*, *Borrelia hispanica*, *Borrelia crocidurae*	TBRF	Gaber et al. (1984), Anda et al. (1996), Masoumi et al. (2009), Cutler (2009)
Ornithodoros graingeri	*Borrellia graingeri*		Parola & Raoult. (2001)
Ornithodoros hermsi	*Borrelia hermsi*	TBRF	Dana (2009), Schwan et al. (2007)
Ornithodoros moubata	*Borrelia duttoni*	TBRF	Cutler (2006), Mans et al. (2008a)
Ornithodoros parkeri	*Borrelia parkeri*	TBRF	Dana (2009), Dworkin et al. (2002)
Ornithodoros porcinus	*Borrelia duttoni*	TBRF	Mitani et al. (2004), Cutler (2006)
Ornithodoros rudis	*Borrelia venezuelensis*	TBRF	Rebaudet & Parola (2006)
Ornithodoros savignyi	*Borrelia crocidurae*	TBRF	Gaber et al. (1984), Helmy (2000), Shanbaky & Helmy (2000)
Ornithodoros sonrai	*Borrelia crocidurae*	TBRF	Vial et al. (2006)
Ornithodoros talaje	*Borrelia mazzottii*	TBRF	Davis (1956), Rebaudet & Parola (2006)
Ornithodoros tartakovskyi	*Borrelia latyschewii*	TBRF	Parola & Raoult (2001), Rebaudet & Parola (2006)
Ornithodoros tholozani	*Borrelia persica*	TBRF	Sidi et al. (2005), Assous & Wilamowski (2009), Moemenbellah-Fard et al. (2009), Masoumi et al. (2009)
Ornithodoros turicata	*Borrelia turicatae*	TBRF	Dana (2009)
Ornithodoros zumpti	*Borrelia tillae*		Rebaudet & Parola (2006)
Soft tick-transmitted *Borrelia* species causing disease in animals			
Species	**Borrelia species**	**Disease**	**References**
Argas spp.	*Borrelia anserina*	Avian spirochetosis	Barbour & Hayes (1986)
Argas miniatus	*Borrelia anserina*[1]	Avian spirochetosis	Lisbôa et al. (2009)
Ornithodoros coriaceus	*Borrelia coraciae*	Bovine epizootic abortion	Hendson & Lane (2000), Barbour & Hayes (1986), Teglas et al. (2006), Chen et al. (2007)

Table 3. Bacteria transmitted by soft ticks. TBRF, tick-borne relapsing fever. [1]Experimental transmission.

At present, TBRF can be considered a zoonotic disease since endemic foci in humans have been detected in zones with high prevalences in animals and high infection rates in ticks (McCall et al., 2007). TBRF is characterized by episodes of recurrent fever and other non-specific symptoms, such as headache and myalgia. If not treated with antibiotics it can be fatal. In Tanzania, TBRF caused by *B. duttoni* is endemic. The infection primarily occurs in children and pregnant women, and is associated with foetal loss and neonatal deaths. Perinatal death ratios of 436/1000 have been reported from disease-endemic regions of the country (Cutler, 2006). The laboratory diagnosis of TBRF is done by detecting the spirochetes in human peripheral blood or, better, by flagelin gene PCR amplification and sequencing (Kawabata et al., 2006; Assous & Wilamowski, 2009). This method can be applied to any infection by *Borrelia* spp. spirochetes and allows the specific identification of the etiologic agent. Currently, any *Borrelia* species could represent a health risk for any country, since an exotic pathogen may be introduced into that country by infected people coming from endemic areas. TBRF is considered an emerging disease and it should be kept in mind by health-care providers, especially when dealing with travellers showing symptoms such as fever and in whom malaria is not detected.

More studies are necessary to determine the geographical distribution of *Borrelia*-infected soft ticks, the prevalences of tick infection, and how these prevalences change, and also to identify any new reservoir.

2.4 Other pathogens transmitted by soft ticks

Soft ticks also transmit other pathogens, most of which are important rickettsiae impacting human and animal health. In addition, some protozoan and filarial species may be also transmitted by argasids (Table 4).

Modern molecular biology techniques have enabled the detection of a large number of rickettsial species in argasids. In many cases, the importance of these rickettsiae as pathogens remains to be determined, as does the epidemiological role played by argasid ticks as their vectors and that of migratory birds as spreaders. As already occurs in ixodids, it is anticipated that increasing numbers of new bacterial species will be detected in argasid ticks.

3. Soft ticks as pathogen vectors in a changing environment

Climate is an important factor in the geographic distribution of arthropod vectors. Environmental and climatic global change is currently exerting a strong impact on the transmission and distribution of tick-borne pathogens (El Kammah et al., 2007). The effect of climate on infectious diseases is largely determined by the unique transmission cycle of each pathogen. Transmission cycles that require a vector are more susceptible to external environmental influences than diseases which include only the pathogen and host (Estrada-Peña, 2009).

Generally, the most significant determinant in the transmission of vector-borne pathogens is the survival rate of the vector involved. Warmer temperatures generally increase the survival and development rates of blood-feeding vectors; however, host availability is more important than climate in determining the abundance and distribution of vector ticks (Patz, et al., 2010). Climatic conditions and the political changes with human biotic, abiotic, and synergistic causal factors mainly affecting agriculture, cover and land properties and their

use, have a strong effect on the structure of the vegetation, favouring tick ecology (Randolph, 2008, 2010) and, probably, the expansion of tick populations from heavily infested areas of the planet –such as Africa- to nearby places such Europe (Gray et al., 2009) and to more distant areas such Australia, Latin America, and parts of Asia. The increase in tick populations can enhance the contact rates between hosts and ticks.

Specie	Pathogen	Disease	References
Argas spp.	*Aegyptianella pullorum*	Aegyptianellosis	El Kammah et al. (2007)
Argas arboreus	*Wolbachia persica*[1]		Noda et al. (1997)
Argas persicus	*Rahnella aquatilis*, *Pseudomonas fluorescens*, *Enterobacter cloacae*, *Chryseomonas luteola*, *Chryseobacterium meningosepticum*		Montasser (2005)
Argas vespertilionis	*Borrelia burgdorferi*	Lyme disease	Hubbard et al. (1998)
Carios capensis	*Rickettsia scc3*, *Rickettsia hoogstraalii*	Spotted fever	Reeves et al. (2005), Kawabata et al. (2006)
Carios kelleyi	*Rickettsia* spp.[2]		Loftis et al. (2005)
	Borrelia spp.[3] *Borrelia lonestari*, *Rickettsia felis*		Schwan et al. (2009) Loftis et al. (2005)
	Two undescribed *Rickettsia* spp.		Reeves et al. (2006)
	Bartonella henselae	Cat scratch disease	Loftis et al. (2005)
Carios sawaii	*Rickettsia scc3*	Spotted fever	Kawabata et al. (2006)
Ornithodoros coriaceus	Deltaproteobacteria	Bovine Epizootic Abortion[4]	Teglas et al. (2006), Chen et al. (2007)
Ornithodoros erraticus	*Babesia meri*		Gunders & Hadani (1973)
Ornithodoros lahorensis	*Coxiella burnetii*[5]	Q-fever	Mishchenko et al. (2010)
Ornithodoros moubata	*Rickettsia* spp.[2]	Q-fever	Cutler et al. (2006)
	Proteobacteria simbiont[6], Another specific simbiont[7]		Noda et al. (1997)
	Babesia equi[5]	Babesiosis	Battsetseg et al. (2007)
	Acanthocheilonema viteae[5]	Filariasis	Lucius & Textor (1995)
Ornithodoros sonrai	*Coxiella burnetii*	Q-fever	Mediannikov et al. (2010)
Ornithodoros tartakowskyi	*Dipetalonema viteae*[5]	Filariasis	Londoño (1976)

Table 4. Other bacteria, protozoa and filariae with medical/veterinary interest harboured or transmitted by argasid ticks. [1]Symbiont; [2]novel rickettsial agent; [3]closely related to *Borrelia turicatae*; [4]likely agent; [5]experimental transmission or infection; [6]gamma subgroup of proteobacteria symbiont monophyletic group with *Coxiella burnetii*; [7]symbiont which form a monophyletic group with *Francisella tularensis* and *Wolbachia persica*. NR, not reported.

Currently, a change is being noted in the epidemiology of tick-borne diseases caused by changes in environmental parameters: i.e., small changes in temperature can account for large variations in the spreading area of infectious diseases. Increasing tick populations can boost contact rates between ticks and pathogens and also contact between ticks and domestic and wild animals, modifying the endemicity of tick-borne diseases with a higher risk of clinical cases (Cumming & van Vuuren, 2006). Interestingly, an epidemiological heterogeneity of tick-borne infectious diseases with periodic epidemics is being observed; i.e., those of CCHF, which is now appearing with increasing frequency in new areas of Europe. These changes in disease distribution and the emergence of tick borne diseases in unexpected areas may be associated with pathogen dissemination caused, among others, by the movements of livestock, wild animals, and migratory birds.

To date it has been accepted that many of the etiologic agents of these diseases are transmitted exclusively by hard ticks. This specificity seems to be determined by molecular factors involving ticks (i.e., the intracellular process of blood meal digestion in ticks) and pathogens (infection, replication, aggregation), which condition pathogen infection and development in vectors and vertebrates. However, it is tempting to speculate that there could be some pathogens not exclusively transmitted by either hard or soft ticks, since new conditions favouring ticks and pathogen dissemination could provide the opportunity for the establishment of new tick-pathogen interactions. An example supporting such an idea is the association observed between the CCHF virus and the soft tick species referred to above. Evidently, confirmation of this issue will require evidence that well-known soft-tick pathogens can be transmitted by an ixodid species or, conversely, the transmission by argasids of pathogens normally transmitted by species of ixodid ticks. This highlights the need for a systematic surveillance for as yet unknown associations between pathogens and competent vectors and the occurrence of new emerging diseases.

4. Soft tick location and surveillance

As mentioned above, each tick species requires optimum environmental conditions and biotopes for its development, which determine their geographic distribution and the pathogens they transmit (Parola & Raoult, 2001). Accurate knowledge of the distribution of ticks and the monitoring of changes in their distribution are important to define risk areas for tick-borne diseases and to establish adequate measures for tick control and the prevention of tick-borne disease. In this context, continuous tick surveillance emerges as a permanent need.

Direct methods for tick surveillance are based on the capture and identification of specimens, either from the vegetation (dragging method) or from animal hosts in the area sampled. While these procedures are useful for the surveillance of ixodid ticks owing to their exophilous lifestyle and long feeding times, they will not work with argasid ticks because they are endophilous/nidicolous and fast feeders. This means that vegetation dragging and the removal from animals are inefficient as direct methods for argasid surveillance; instead it is necessary to explore all possible tick refuges in the area sampled before such an area can be considered tick-free (Oleaga-Pérez et al., 1990; Vial et al., 2006). Evidently, this is an impractical procedure for large-scale studies.

These drawbacks have encouraged the development of serological tests (ELISA) as indirect methods for tick surveillance, especially for argasid ticks. Serological methods are based on the detection of specific antibodies against tick salivary proteins in serum samples taken from animal hosts -or humans- living in the area under study. The development of such methods requires the resolution of several issues such as: 1) the host species to be sampled; these are determined first by the host preference of the tick species investigated, and second by factors such as the availability and ease of management of the different animal hosts. Domestic instead of wild animals are preferred. 2) Demonstration that the tick species investigated induces a humoral immune response. 3) Characterization of the response in terms of how many tick bites are necessary to induce detectable antibody levels, and how long antibodies remain at detectable levels after the last tick-host contact. 4) Which antigen should be used and what its sensitivity and specificity are.

Such tests have been developed for *O. erraticus* in southern Europe and for *O. moubata* in Africa. In Spain and Portugal, *O. erraticus* lives in close association with swine on free-range pig farms, where it can transmit TBRF and ASF. Accordingly, elimination of the tick from pig farms would greatly improve the control of such diseases (Oleaga-Pérez et al., 1990; Manzano-Román et al., 2007). As part of an ASF eradication campaign carried out in the 90's in Spain, an ELISA test was developed to detect specific antibodies against *O. erraticus* in pigs. The authors of the test demonstrated first that *O. erraticus* bites induced detectable humoral responses in pigs, and that after secondary contact antibody levels were detectable for at least 3 months (Canals et al., 1990). Then, the authors analysed the specificity of the antigen used in the test, which was a crude salivary gland extract (SGE) obtained from adult *O. erraticus* ticks, with a composition similar to that of tick saliva (Baranda et al., 1997). The SGE demonstrated 100% sensitivity and specificity with sera from experimentally infected pigs (Pérez-Sánchez et al., 1992) and 90% sensitivity and specificity in field conditions (Oleaga-Pérez et al., 1994). Subsequently the SGE-ELISA test was used to analyse anti-*O. erraticus* antibodies in more than 19,000 samples of pig sera from 3,478 farms located in 234 townships in the province of Salamanca (Spain). This allowed the identification of the farms infested with the argasid in the province, the establishment of a significant association between the presence of the tick and the persistence of ASF cases on such farms (Pérez-Sánchez et al., 1994), and consequently the application of specific control measures to avoid tick-pig contact on the tick-infested farms. Recently, a similar serological study has been done in Madagascar to look for the presence of anti-*O. moubata* ticks in domestic pigs and bushpigs, using as antigen an SGE obtained from adult *O. moubata* in a similar way to that of *O. erraticus* (Ravaomanana et al., 2011). The absence of anti-tick antibodies and anti-ASFV in bushpigs suggested that the latter are unlikely to play a significant role in the maintenance and transmission of ASFV in Madagascar. In addition, the presence of antibodies against *O. moubata* in domestic pigs suggests that soft ticks may be able to maintain ASFV within a domestic pig cycle in areas of Madagascar where they remain present.

The above indicates that the *O. erraticus* and *O. moubata* SGEs are suitable antigens for the serological surveillance of these two ticks by ELISA tests, although SGEs have some drawbacks. Their collection is time-consuming and difficult to standardise, their composition is poorly known and they may contain non-specific antigens, giving rise to unexpected cross-reactivity. The alternative to SGE would be the use of an individual salivary antigen of proven specificity. With this aim, Baranda et al. (2000) purified the four

main antigens from both the *O. erraticus* and *O. moubata* SGE and studied their diagnostic value. Regarding *O. moubata*, the best candidate for the serodiagnosis of infested animals was its 20A1 antigen. This antigen was later identified as a homologue of the TSGP1 salivary lipocalin of *O. savignyi* (Mans et al., 2008b; Oleaga et al., 2007). Recently, this *O. moubata* TSGP1 has been cloned, obtaining the recombinant form (rOmTSGP1), and shown to have a better diagnostic performance (sensitivity and specificity) than SGE (Díaz-Martín et al., 2011), thereby providing a reliable serologic tool for *O. moubata* surveillance.

Regarding the use of anti-tick ELISA tests for ixodid surveillance, only a few studies have been carried out using similar SGEs as antigens and human sera (Schwartz et al., 1993; Lane et al., 1999; Nebreda et al., 2004). These studies also confirmed the suitability of the method to detect anti-ixodid tick antibodies but found a high degree of cross-reactivity among ixodid species. As in the case of *O. moubata*, the use of a specific recombinant antigen would probably solve these problems.

5. Soft tick control

Tick control is an intrinsically difficult task for a number of reasons: ticks produce abundant progeny (they lay many eggs); they usually have more than one developmental stage in nature, and they often parasitize numerous and diverse hosts. Several methods for tick control have been used but none of them has been efficacious against all ticks and the problems they cause.

Chemical control with acaricides (arsenicals, chlorinated hydrocarbons, organophosphates, carbamates and synthetic pyrethroids) was considered the best method but resistant tick strains to these acaricides have been selected (Foil et al., 2004). Furthermore, acaricides may cause toxicity problems and contamination of the environment and animal products, such as milk and meat (George et al., 2008). In addition, owing to the nidicolous life-style of the argasids, their control through the use of acaricides is very difficult to achieve simply because it is not feasible to ensure that the acaricide will reach all places where the parasites hide (Astigarraga et al., 1995).

The problems associated with acaricides have encouraged the development of alternative methods for tick control, such as anti-tick vaccines or bio-control using entomopathogenic organisms, including bacteria, fungi and nematodes. To date, the only bio-control agents tested against soft ticks have been entomopathogenic fungi (Samish et al., 2008). These have been shown to be effective against many ixodid species in different laboratory and field studies. The most pathogenic species were *Beauveria bassiana* and *Metarhizium anisopliae* (Samish et al., 2004; Ostfeld et al., 2006). These two fungal species have received the greatest attention and have been the object of subsequent studies (Fernandes & Bittencourt, 2008; Polar et al., 2008). However, such studies have been focused almost exclusively on the control of ixodid ticks, and have neglected the control of argasid ticks. One exception is the work by Sewify & Habib (2001), which studied the pathogenic effect of *M. anisopliae* on the argasid tick *A. persicus*. These authors sprayed heavily infested poultry houses with a fungal spore suspension and observed that the argasid population disappeared in 3 weeks. More recently, Zabalgogeazcoa et al. (2008) and Herrero et al. (2011) carried out laboratory trials showing that isolates of *B. bassiana* and *Tolypocladium cylindrosporum* caused up to 70% mortality in *O. erraticus* and up to 40% mortality in *O. moubata*. These results justify further

efforts towards the application of entomopathogenic fungal strains as anti-argasid bio-control agents.

Immunological control using anti-tick vaccines offers an attractive alternative to the use of acaricides. In spite of the research efforts invested in this field over the last two decades, only two recombinant anti-hard tick vaccines against *Rhipicephalus (Boophilus)* species have become available commercially (de la Fuente et al., 2007; Willadsen, 2008). The application of these vaccines has shown that it is possible to control tick populations through host vaccination. Nevertheless, the progress in vaccine development against other tick species has been disappointing, and this is especially evident in relation to argasid ticks (de la Fuente & Kocan, 2003; de la Fuente et al., 2008b; Willadsen, 2008). Among other reasons underlying the slow development of new and more effective anti-tick vaccines, the main one is the difficulty involved in identifying tick protective antigens (Willadsen, 2008).

As far as we know, the only attempts to develop anti-argasid vaccines have been those undertaken by our group, which focused on *O. erraticus* and *O. moubata*. We found a concealed antigen from the endothelial gut cells of *O. erraticus*, the so-called Oe45, which induces a protective response in pigs, causing up to 80% mortality in nymphs and a 50% reduction in female fecundity (Manzano-Román et al., 2006, 2007). In *O. moubata*, a salivary anti-haemostatic protein that acts as an antagonist ligand of the host P-selectin molecule has been characterized (García-Varas et al., 2010). This protein, called Om44, does not elicit an immune response in naturally-infected hosts, but when administered as a vaccine in pigs and rabbits it induces a protective immune response that inhibits tick feeding by up to 70%, and the protective response increases with successive infestations. Hence, Om44 is a new example of "silent" salivary antigen according to the new concept introduced for the salivary sialostatin L2 from *I. scapularis* (Kotsyfakis et al., 2008).

Consequently, the search for and identification of new anti-soft tick protective antigens should continue, and tick saliva could be an important antigen source. As demonstrated with Bm86, tick gut proteins may also provide good candidate protective antigens. It would be desirable that the new antigens were shared between soft and hard ticks, since this would allow the development of universal anti-tick vaccines. In the search for protective antigens, new genomic-based experimental approaches, such as Expression Library Immunization (ELI) and RNA interference-based screening of cDNA libraries, have been developed and successfully applied to *Ixodes scapularis* and *Amblyomma americanum* (Almazán et al., 2005, de la Fuente et al., 2010). The results of these studies showed that the use of RNAi gene silencing for the identification of tick protective antigens is a rapid and cost-effective tool for the discovery of candidate vaccine antigens.

6. Conclusions

Soft ticks are distributed worldwide and global climatic changes, along with social factors, influence soft-tick habitats and their hosts. These factors hinder the prediction of the argasid and argasid-borne diseases distribution patterns. Also, several factors could influence the vector competence of soft ticks. A serious swine disease transmitted by argasids is African Swine Fever. This disease jumped between continents in the 60´s and 70´s and recently in the North of Europe, exemplifying the growing possibility that human and animal tick-

borne infectious diseases can emerge and colonize previously uninfected areas because the potential distribution of the infection is transcontinental.

Endemic zones for a specific tick-borne pathogen may serve as the origin for its epidemiological dissemination towards new environments, and this dissemination would probably require the adaptation of both the pathogen and the new vector to each other, implying some kind of genetic evolution. The recent characterization of non-specific viruses in argasid vectors and all the argasid-associated pathogens mentioned in this review suggest the great potential of argasids for viral and bacterial disease transmission in any part of the world owing to their extensive geographical distribution and their relatively indiscriminate host feeding.

Here, we show that soft-tick surveillance by serological methods and control thought vaccination could be possible and this opens new avenues for the development and advance of new tests and further research on other argasid species. The possibility that argasids might serve as vectors for many more pathogens that expected requires a greater effort in implementing control measures, such as the search for new protective antigens to be included in a broad spectrum anti-tick vaccine as well as specific coordinated and urgent epidemiological and parasite-surveillance programs. Since there is no single ideal solution for the control of ticks, an integrated control approach is probably the most effective. Vector and reservoir surveillance is an important component of such a strategy.

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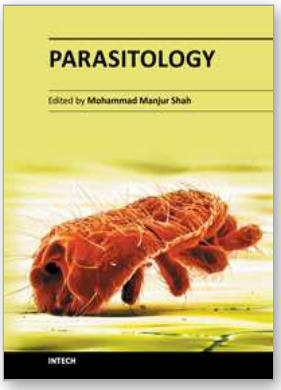

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Parasitology is an established discipline that covers a wide area of subjects, ranging from the basics (study of life cycle, ecology, epidemiology, taxonomy, biodiversity, etc) to the advanced and applied aspects (human and animal related, although control aspect remains the most important task). There is a great scarcity in the amount of available literature that is freely accessible to anyone interested in the subject. This book was conceptualized with this in mind. The entire book is based on the findings of various studies performed by different authors, comprising reviews and original scientific papers. I hope this book will be helpful to diverse audiences like biologists, zoologists, nematologists, parasitologists, microbiologists, medical doctors, pathologists as well as the molecular biologists, by providing them with a better understanding of the subject.

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