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REVIEW

Transovarial transmission of pathogenic protozoa and rickettsial organisms in ticks

Reghu Ravindran[1] · Prabodh Kumar Hembram[1] · Gatchanda Shravan Kumar[1] · Karapparambu Gopalan Ajith Kumar[1] · Chundayil Kalarickal Deepa[1] · Anju Varghese[1]

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Abstract

Transovarial transmission (TOT) is an efficient vertical transmission of pathogens that is observed in many arthropod vectors. This method seems to be an evolutionarily unique development observed only in *Babesia* sensu stricto (clade VI) and *Rickettsia* spp., whereas transstadial transmission is the common/default way of transmission. Transovarial transmission does not necessarily contribute to the amplification of tick-borne pathogens but does contribute to the maintenance of disease in the environment. This review aims to provide an updated summary of previous reports on TOT of tick-borne pathogens.

Keywords *Babesia* · *Anaplasma* · *Rickettsia* · Eggs · Larvae · PCR

Abbreviations

TOT	Transovarial transmission
SFG	Spotted fever group
TTBDs	Ticks and tick-borne diseases
PCR	Polymerase chain reaction
nPCR	Nested polymerase chain reaction
RLB	Reverse line blot
qPCR	Quantitative polymerase chain reaction
IFAT	Indirect immunofluorescent antibody test
msp5	Major surface protein 5
msp1α	Major surface protein1α
TBF	Tick-borne fever
B	*Babesia*
A	*Anaplasma*
Th	*Theileria*
Rh	*Rhipicephalus*
Ha	*Haemaphysalis*
Hy	*Hyalomma*
I	*Ixodes*
D	*Dermacentor*
R	*Rickettsia*
NA	Not available
s.s.	sensu stricto
s.l.	sensu lato

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✉ Reghu Ravindran
drreghuravi@yahoo.com; reghu@kvasu.ac.in

[1] Department of Veterinary Parasitology, College of Veterinary and Animal Sciences, Pookode, Wayanad, Kerala 673 576, India

Background

Ticks are obligate hematophagous ectoparasites of mammals, birds, reptiles, and amphibians found worldwide, and have great medical and veterinary importance (Perez-Sautu et al. 2021). Ticks and tick-borne diseases (TTBDs) can reach serious levels resulting in human mortality and significant economic losses in livestock (Jongejan and Uilenberg 2004; Schnittger et al. 2012; Florin-Christensen et al. 2014). To date, there have been ~ 970 species of ticks identified in the order Ixodida with ~ 750 hard tick species (Ixodidae), ~ 218 species of soft ticks (Argasidae), and single species under the family Nuttalliellidae (*Nuttalliella namaqua*) and family Deinocrotonidae (Sonenshine 1991; Dantas-Torres and Otranto 2022).

Tick-borne protozoan pathogens infecting domestic animals are various species under the genera *Babesia*, *Theileria*, *Cytauxzoon*, and *Hepatozoon*. Similarly, many species of *Rickettsia* are infecting domestic animals. Species under each genus have different modes of transmission. To understand the unique transmission methods in each species, knowledge on the phylogeny or evolutionary history is important. Molecular phylogeny using 18S rRNA genes of piroplasmids infecting mammals resulted in the formation of six clades, viz., I (*B. microti* group), II (Western clade), III (*Cytauxzoon* spp.), IV (*T. equi*), V (*Theileria* sensu stricto), and VI (*Babesia* s.s.) (Schnittger et al. 2012, 2022).

Tick-borne pathogens have the potential to be transmitted through horizontal, transstadial, transovarial, venereal, co-feeding, and localized transmission (Parola and Raoult 2001; Turell 2007; Chauvin et al. 2009). During horizontal transmission, parasites are spread from host to tick and vice versa. Transstadial transmission occurs when there is transmission of parasites throughout the development of tick life stages, from the engorgement through moulting into the next unfed stage of the same individual tick. Such transmission may continue through more than one tick stage within a generation (larva to nymph to adult) in the absence of an oral infection (of the nymph) from a vertebrate host, whereas, in the case of transovarial or vertical transmission, the parasite transmission occurs from the female tick to the larvae of the next generation via the eggs (Randolph et al. 1996). The group of true *Babesia* or *Babesia* s.s. (clade VI) is characterized by transstadial and transovarial transmission. In contrast, true *Theileria* or *Theileria* s.s. (clade V) and *T. equi* (clade IV or Equus clade) show transstadial transmission and a schizont parasite stage (Schnittger et al. 2022). However, *Babesia* sensu lato clade I (*B. microti* group), II (Western clade), and III (*Cytauxzoon*) exhibit only transstadial transmission.

During localized transmission, an infected tick transmits the parasite to uninfected ticks feeding at the same skin site (transmission may continue beyond the duration of the blood meal of the infected tick). Whereas during co-feeding, the transmission occurs from infected to uninfected ticks while feeding simultaneously on the same host, but not necessarily at the same skin site, in the absence of a systemic infection in the host (Randolph et al. 1996). Lastly, venereal or sexual transmission occurs during the mating of ticks. For a tick to be considered a competent vector, horizontal transmission and at least one of these other transmission routes must be present (Kahl et al. 2002; Pfaffle et al. 2013; Schnittger et al. 2022).

Among the different transmission mechanisms, transstadial transmission is the key survival strategy for many piroplasms. The lifelong carrier status of the vertebrate host ensures the infection of different lifecycle stages of ticks. In contrast, in the case of transovarial transmission, the parasite will be passed on to the next generation once a tick is infected, without the need for prior feeding on an infected host. Here, the tick functions as a carrier of the pathogen. Hence, a prolonged carrier status of the vertebrate host is not necessary for the transovarial transmission. The transovarial transmission facilitates species diversification by host switching to other vertebrate host species (Schnittger et al. 2022). It is not necessarily contributing to the amplification of tick-borne disease, rather contributes to the maintenance of disease in the environment. Hence, more detailed studies on transovarial transmission are essential. Here, in this review, the updated information on the reports of transovarial transmission of pathogens in ticks is presented.

***Babesia* spp.**

Babesiosis was the first arthropod-borne mammalian disease discovered and has been shown to spread from one generation of a hard tick to the next via a transovarial transmission (Smith and Kilbourne 1893; Demessie and Derso 2015). Ticks become infected with *Babesia* parasites when they ingest blood cells containing gametocytes, which develop into ray bodies or Strahlenkörper (male and female gametes) in their midgut (Uilenberg 2006), which fuse to form a motile zygote (ookinete), that invades the tick gut cells and undergoes meiotic division, resulting in the production of kinetes. Kinetes disseminate via hemolymph to peripheral tick tissues, including ovarian cells leading to the infection of eggs (Jalovecka et al. 2019).

Babesia sensu stricto (clade VI) shows a unique evolutionary pattern because of their ability of transovarial transmission which facilitates the diversification of *Babesia* s.s. species to all groups of vertebrates around the world. All ruminant infecting *Babesia* species (*B. bigemina*, *B. bovis*, *B. divergens*, *B. ovata*, *B. major*, *B. occultans*, *B. orientalis*, *Babesia* sp. Mymensingh nk, *Babesia* sp. Tengchong, *B. ovis*, *B. crassa*, *B. motasi*, *B. motasi*-like, *Babesia* sp. Xinjiang, etc.) belong to the *Babesia* sensu stricto group (clade VI) (Schnittger et al. 2012, 2022), which are characterized by the lack of a schizont stage, asexual reproduction exclusively within red blood cells in vertebrate hosts, and the occurrence of transovarial transmission in the tick vector (Uilenberg 2006; Schnittger et al. 2012; Jalovecka et al. 2019). Ticks belonging to the genera *Rhipicephalus* and *Ixodes* are generally implicated in the transmission of bovine babesiosis.

Babesia spp. that cause infections in dogs are divided into the *Babesia* s.s. clade (clade VI) (*B. vogeli*, *B. canis*, *B. rossi*, *B. gibsoni*, *Rangelia vitalii*, and *Babesia* sp. Coco, *Babesia* sp. Akita610) and two clearly identifiable *Babesia* s.l. clades, namely, the Western clade (clade II) (*B. negevi*, *B. conradae*) and *B. vulpes* group (clade Ib) (*B. vulpes*) (Jalovecka et al. 2019). In horses, only *B. caballi* is recognised as a true *Babesia* species (*Babesia* s.s) (clade VI), while *B. equi* is reclassified as *T. equi* (clade IV). *Babesia caballi* is transmitted transovarially. Among the babesias (*B. trautmanni*, *B. perroncitoi*, *Babesia* sp. Suis) that cause infections in swine, *Babesia* sp. Suis was recently characterized as *Babesia* s.s. (clade VI), based on the molecular phylogeny using 18S rRNA genes (Avenant et al. 2021).

Table 1 lists the reports of transovarial transmission of different *Babesia* spp. In ticks, the transovarial infection rate

Table 1 Transovarial transmission of *Babesia* spp. in ticks

Place	Tick species	Study type, test performed	Transovarial infection rate	Filial infection rate	Reference
***B. bigemina* (bovine)**					
Australia	*Rh. microplus*	Experimental study	NA	NA	Riek (1964)
Brazil	*Rh. microplus*	nPCR	NA	NA	Oliveira-Sequeira et al. (2005)
Brazil	*Rh. microplus*	Microscopic examination	NA	NA	Oliveira et al. (2005)
Brazil	*Rh. microplus*	qPCR	20 to 40%	NA	Giglioti et al. (2018)
Cuba	*Rh. microplus*	qPCR	68%	NA	Obregon et al. (2020)
India	*Rh. microplus*	DNA hybridization with a nonradioactive probe	NA	NA	Ravindran et al. (2006)
India	*Rh. microplus*	nPCR	7.41%	NA	Bhat et al. (2017)
India	*Rh. annulatus*	PCR	38%	NA	Hembram et al. (2022)
Iran	*Rh. annulatus*	PCR	NA	NA	Rajabi et al. (2017)
Israel	*Rh. annulatus*	Nested PCR	NA	NA	Molad et al. (2015)
Kenya	*Rh. decoloratus*	Experimental study	NA	NA	Morzaria et al. (1977)
South Africa	*Rh. decoloratus*	Experimental study	NA	NA	Gray and Potgieter 1982
Turkey	*Rh. annulatus*	Reverse line blot (RLB)	NA	NA	Ica et al. (2007)
Uruguay	*Rh. microplus*	PCR	NA	NA	Gayo et al. (2003)
USA	*Rh. annulatus*	Experimental study	NA	NA	Smith and Kilbourne (1893)
***B. bovis* (bovine)**					
Australia	*Rh. microplus*	Experimental study	NA	NA	Mahoney and Mirre (1979)
Brazil	*Rh. microplus*	nPCR	NA	NA	Oliveira-Sequeira et al. (2005)
Brazil	*Rh. microplus*	Microscopic examination	NA	NA	Oliveira et al. (2005)
Brazil	*Rh. microplus*	qPCR	0.5 to 14.5%	NA	Giglioti et al. (2018)
Cuba	*Rh. microplus*	qPCR	100%	NA	Obregon et al. (2020)
Uruguay	*Rh. microplus*	PCR	NA	NA	Gayo et al. (2003)
USA	*Rh. microplus*	Experimental study	NA	NA	Smith et al. (1978)
USA	*Rh. microplus*	PCR	12% to 48%	NA	Howell et al. (2007)
***B. ovata* (bovine)**					
Japan	*Ha. longicornis*	IFAT	NA	NA	Maeda et al. (2016)
Japan	*Ha. longicornis*	nPCR	NA	NA	Shirafuji et al. (2017)
***B. occultans* (bovine)**					
South Africa	*Hy. rufipes*	Experimental study	NA	NA	Gray and de Vos (1981)
Turkey	*Hy. marginatum*	PCR	22.22%	NA	Aktas et al. (2014)
Turkey	*Rh. turanicus*	PCR	50%	NA	Aktas et al. (2014)
Turkey	*Hy. marginatum*	PCR	NA	NA	Orkun (2019)
Turkey	*Hy. excavatum*	PCR	NA	NA	Orkun (2019)
***B. divergens* (bovine)**					
England	*I. ricinus*	Experimental study	NA	NA	Donnelly and Peirce (1975)
France	*I. ricinus*	PCR	NA	NA	Bonnet et al. (2007)
***B. canis* (canine)**					
England	*Ha. elliptica*	Experimental study	NA	NA	Shortt (1973)
England	*Rh. sanguineus*	Experimental study	NA	NA	Shortt (1973)
Poland	*D. reticulatus*	PCR	100%	NA	Mierzejewska et al. (2018)
West-central Poland	*I. ricinus*	PCR	NA	NA	Liberska et al. (2021)
***B. rossi* (canine)**					
Nigeria, West Africa	*Ha. leachi*	PCR	NA	NA	Kamani (2021)
***B. vogeli* (canine)**					
Taiwan	*Rh. sanguineus*	PCR	NA	NA	Jongejan et al. (2018)
***B. gibsoni* (canine)**					
Japan	*Ha. longicornis*	PCR	NA	NA	Hatta et al. (2012)

Table 1 (continued)

Place	Tick species	Study type, test performed	Transovarial infection rate	Filial infection rate	Reference
Taiwan	*Ha. hystricis*	PCR	NA	NA	Jongejan et al. (2018)
***B. ovis* (ovine)**					
Iran	*Rh. bursa* (two-host tick)	PCR	NA	NA	Esmaeilnejad et al. (2014)
Israel	*Rh. bursa* (two-host tick)	Experimental study	NA	NA	Yeruham et al. (2001)
Israel	*Rh. bursa* (two-host tick)	PCR	NA	NA	Erster et al. (2016)
Turkey	*Rh. bursa* (two-host tick)	PCR	NA	NA	Orkun (2019)
***B. motasi* (ovine)**					
Netherlands	*Ha. punctata*	Experimental study	NA	NA	Uilenberg et al. (1980)
Great Britain	*Ha. punctata*	Experimental study	NA	NA	Alani and Herbert (1988)
***B. caballi* (equine)**					
Americas	*Dermacentor nitens*	PCR	NA	NA	Schwint et al. (2008)
Brazil	*Rh. microplus*	PCR	NA	NA	Battsetseg et al. (2002)
US state, Florida	*Hy. truncatum*	Experimental study	NA	NA	de Waal (1990)
***B. trautmanni* (porcine)**					
South Africa	*Rh. simus*	Experimental study	NA	NA	de Waal et al. (1992)

NA not available

(the percentage of female ticks that pass microorganisms to their progeny) (Burgdorfer and Varma 1967) with different *Babesia* spp. ranged from 0.5 to 100% while the filial infection rate (the percentage of infected progeny derived from an infected female tick) (Burgdorfer and Varma 1967) for the same were not available in the published reports.

Theileria spp.

Theileriosis, (Phylum Apicomplexa; order Piroplasmida; family Theileriidae; genus *Theileria*) remains a burden for millions of livestock in tropical countries, especially crossbreds and exotic cattle annually (Roy et al. 2021). The dominant *Theileria* spp. linked to economic loss and mortality worldwide are *T. annulata* and *T. parva* (Roy et al. 2021). Mild bovine theileriosis is caused by *T. orientalis*, *T. mutans*, *T. velifera*, and *T. taurotragi*. Various genotypes of *T. orientalis* are type 1 (Chitose), type 2 (Ikeda), type 3 (Buffeli), types 4–8, and types N1–N3 (Hammer et al. 2015). Bovine *Theileria* species, which include *T. annulata*, *T. parva*, *T. orientalis* (syn. *T. buffeli*/*T. sergenti*/*T. sinensis*), *T. mutans*, *T. velifera*, and *T. taurotragi*, belong to a monophyletic group corresponding to clade V (*Theileria* sensu stricto group) (Schnittger et al. 2012, 2022). Members of this clade exhibit a schizont stage in the lymphoid cells and piroplasms in the red blood cells of the vertebrate host, as well as exclusive transstadial transmission but not transovarial transmission in the tick (Kiara et al. 2018). *Theileria annulata* (tropical bovine theileriosis) infection is most common in southern Europe, North Africa, the Middle East, and Asia transmitted transstadially by several species of *Hyalomma* ticks, namely, *Hyalomma anatolicum*, *Hy. dromedarii*, *Hy. detritum*, *Hy. scupense*, and *Hy. lusitanicum* (Ali et al. 2013; Jabbar et al. 2015; Gharbi et al. 2020). *Hyalomma* ticks transmit *T. annulata* sporozoites into the host and causes a lymphoproliferative disease similar to cancer (Ghosh et al. 2007; Tretina et al. 2015). In addition to a tick bite, transplacental transmission has been detected for *T. annulata* (Sudan et al. 2015), by PCR analysis. There is no report on the transovarial transmission of *T. annulata* in ticks (Mehlhorn and Schein 1984; Norval et al. 1992).

Theileria parva, transmitted transstadially, most commonly by *Rh. appendiculatus*, is present throughout a large part of eastern and southern Africa (Morrison et al. 2020). These parasites also infect the Asian and African species of buffalo (*Bubalus bubalis* and *Syncerus caffer*, respectively) (Morrison et al. 2020). Based on the available literature, there are no reports on the transovarial transmission of *T. parva* in ticks.

Oriental theileriosis was reported in Asia, New Zealand, Australia, and the USA (Oakes et al. 2019). *Haemaphysalis longicornis* is a known vector tick for *T. orientalis* in different countries (Fujisaki et al.1994; Hammer et al. 2015, Jabbar et al. 2015). Other potential vectors include *Ha. punctata* in France (Uilenberg 2000), *Rh. microplus* in Vietnam and Thailand (Khukhuu et al. 2011; Poolkhetkit et al. 2015), *Rh. decoloratus* and *Rh. evertsi* in Ethiopia (Kumsa et al. 2013), and *Rh. annulatus* in India (Nimisha et al. 2019). Available literature reveals only one report on the detection of the parasite DNA in the eggs of *Rh. microplus* (Kakati et al. 2015) engorged on a parasite-positive animal. *Theileria* *orientalis* can be spread in various ways other than by tick vectors. It has been proven that the infected heifers can transmit the parasite to their foetus or calf (Baek et al. 2003; Lawrence et al. 2016; Swilks et al. 2017; Mekata et al. 2018). Transmission via the transcolostral route is also plausible, but requires more research to confirm this (Emery 2016). In addition, theilerial DNA was detected in mosquitos, lice (*Linognathus vituli*), and other hematophagous insects (Emery 2016; Hammer et al. 2016). *Theileria orientalis* can also be transmitted by transfer of piroplasms when contaminated needles (vaccinations), castration knives, and ear notching equipments are reused. In addition, the injuries sustained during yarding and transport of cattle can also assist in the transmission (Hammer et al. 2016).

Among six *Theileria* species infecting goats, *T. lestoquardi*, *T. luwenshuni*, and *T. uilenbergi* are extremely pathogenic, causing high mortality, and the remaining three, *T. separata*, *T. ovis* and *T. recondite*, are less pathogenic in small ruminants (Islam et al. 2021). It is believed that these infections are transmitted transstadially through multihost ticks and there were no previous reports on transovarial transmission for these parasites.

Babesia equi in horses is reclassified as *T. equi* owing to its extraerythrocytic schizogony, erythrocytic invasion, and transstadial transmission in ticks (Mehlhorn and Schein 1998; Ueti and Knowles 2018). However, there are reports on the occurrence of transovarial transmission of *T. equi* in *Rh. microplus* (Battsetseg et al. 2002) and *Ha. longicornis* tick (Ikadai et al. 2007). Phylogenetic studies proved that *T. equi* does not belong to *Theileria* s.s., but rather represents a unique separate monophyletic clade (clade IV or Equus group) (Schnittger et al. 2012; Jalovecka et al. 2019; Bhoora et al. 2020).

Cytauxzoon (clade III) is characterized by the presence of a schizont stage that infects host cells of the mononuclear reticulohistiocytic system (Schnittger et al. 2022). *Dermacentor variabilis* was initially accepted to be the natural tick vector of *C. felis* (Blouin et al. 1984) while transstadial transmission was experimentally proved recently in *Amblyomma americanum* (Reichard et al. 2009).

Rickettsia spp.

The organisms assigned to the order Rickettsialses were reclassified based on 16S rRNA genes, groESL, and surface protein genes into two families viz., Anaplasmataceae and Rickettsiaceae (Dumler et al. 2001). All the members of the family Rickettsiaceae are slow-growing gram-negative bacteria that are pleomorphic, obligatory intracellular, have a life cycle that involves both an arthropod vector and a vertebrate host (Portillo et al. 2017; Blanda et al. 2020), and grow freely in the cytoplasm of eukaryotic cells. These bacteria can be transmitted to animals and humans by blood-sucking arthropods, causing specific zoonotic diseases termed rickettsioses (Merhej et al. 2014; de Mera et al. 2018). *Rickettsia* and *Orientia* are the two genera causing rickettsioses (Jiang et al. 2021) in animals and man.

Based on the disease presentation, antigenicity, and vectors, rickettsial diseases (and their causative agents) have been traditionally separated into three major groups viz., spotted fever group (SFG), typhus group, and scrub typhus group (Luce-Fedrow et al. 2015; Parola et al. 2013; Abdad et al. 2018; Richards and Jiang 2020). More than 30 species are included in the SFG, with more species being added in each year (https://www.bacterio.net).

Many rickettsial endosymbionts of invertebrates are thought to be vertically transmitted, implying that arthropod vectors serve as reservoirs or amplifiers in nature (Parola et al. 2013). The *Rickettsia* of spotted fever category encompasses a number of human infections, the majority of which are spread by ticks. The *Rickettsia* spp. transmitted transovarially in the ticks are shown in Table 2. In ticks, the transovarial infection rate with different *Rickettsia* spp. ranged from 8 to 100%, while its filial infection rate for the same ranged from 22.7 to 100%.

Anaplasma spp.

The organisms placed under family Anaplasmataceae are obligate intracellular parasites found exclusively within the membrane-bound vacuoles in the host cell cytoplasm. The family Anaplasmataceae include four genera viz., *Anaplasma*, *Ehrlichia*, *Neorickettsia*, and *Wolbachia*. The genus *Anaplasma* include *A. marginale*, *A. marginale* subsp. *centrale*, *A. phagocytophilum*, *A. bovis*, and *A. platys* (Kocan et al. 2010).

A. marginale

Anaplasmosis causes considerable economic loss to beef and dairy industries globally, including those in the America, Europe, Australia, Asia, and Africa (Aubry and Geale 2011; Atif 2015; Kocan et al. 2015). *Anaplasma* spp. can be transmitted biologically by ticks, mechanically by blood-sucking arthropods (blood-contaminated mouthparts of biting flies) or blood-contaminated fomites, i.e., castration and dehorning equipment, needles, and ear tag applicators (Kocan et al. 2015; Battilani et al. 2017).

Many species of ticks are reported to serve as the vectors of *A. marginale* viz., *Argas persicus*, *Dermacentor andersoni*, *D. albipictus*, *D. calcaratus*, *D. variabilis*, *D. occidentalis*, *D. hunteri*, *Hy. excavatum*, *Hy. rufipes*, *I. ricinus*, *I. scapularis*, *Ornithodoros lahorensis*, *Rh. microplus*, *Rh. annulatus*, *Rh. decoloratus*, *Rh. evertsi*, and *Rh. simus*, but the most common vectors throughout tropical and subtropical areas of the world are *Dermacentor*

Table 2 Transovarial transmission of *Rickettsia* spp. in ticks

Place	Tick species	Study type, test performed	Transovarial infection rate	Filial infection rate	Reference
R. rickettsii					
Brazil	*A. aureolatum*	PCR	100%	100%	Labruna et al. (2011)
Brazil	*Rh. sanguineus*	PCR	NA	< 50%	Piranda et al. (2011)
Brazil	*Rh. sanguineus*	PCR	NA	100%	Pacheco et al. (2011)
Brazil	*A. cajennense*	qPCR	< 50%	< 50%	Soares et al. (2012)
Brazil	*A. aureolatum*	qPCR	25%	NA	Binder et al. (2021)
USA	*D. andersoni*	Experimental study	100%	100%	Burgdorfer (1963)
R. conorii conorii					
Algeria	*Rh. sanguineus*	PCR	100%	Up to 99%	Socolovschi et al. (2009a, b)
Algeria	*Rh. sanguineus*	PCR	100%	Up to 99%	Socolovschi et al. (2012)
Thailand	*Rh. sanguineus*	PCR	NA	NA	Matsumoto et al. (2005a, b)
R. raoultii					
India	*Rh. annulatus*	PCR	8%	NA	Hembram et al. (2022)
India	*Ha. bispinosa*	PCR	15%	NA	Hembram et al. (2022)
Netherlands	*D. reticulatus*	PCR	NA	NA	Alberdi et al. (2012)
Northern Mongolia	*D. nuttalli*	nPCR	NA	NA	Moore et al. (2018)
Turkey	*D. marginatus*	PCR	NA	NA	Orkun (2019)
R. slovaca					
Turkey	*D. marginatus*	PCR	NA	NA	Orkun (2019)
USA	*D. variabilis*	PCR	≥ 99%	≥ 99%	Zemtsova et al. (2016)
R. massiliae					
France	*Rh. turanicus*	PCR	100%	98.5%	Matsumoto et al. (2005a, b)
R. africae					
Ivory Coast, Africa	*A. variegatum*	PCR	100%	93.4%	Socolovschi et al. (2009a, b)
R. bellii					
Brazil	*I. loricatus*	PCR	NA	NA	Horta et al. (2006)
R. aeschlimannii					
Turkey	*Hy. marginatum*	PCR	25%	NA	Orkun (2019)
R. amblyommii					
Brazil	*A. auricularium*	PCR	100%	100%	Saraiva et al. (2013)
R. montana					
USA	*D. variabilis*	PCR	NA	NA	Macaluso et al. (2001)
R. rhipicephali					
USA	*D. variabilis*	PCR	NA	NA	Macaluso et al. (2001)
***Rickettsia* spp.**					
Northern Germany	*I. ricinus*	qPCR	NA	22.7%	Hauck et al. (2020)

NA not available

spp. (*D. andersoni*, *D. variabilis*, and *D. albipictus*) and *Rhipicephalus* (*Boophilus*) spp. (*Rh. microplus* and *Rh. annulatus*) (Rar and Golovljova 2011; Kocan et al. 2015). Tick transmission can occur from stage to stage (interstadial or transstadial) or within a stage (intrastadial) (Stich et al. 1989). Interstadial transmission of *A. marginale* has been demonstrated by the 3-host ticks, *D. andersoni*, and *D. variabilis* in the USA (Kocan 1986; Kocan et al. 1981, 1985; Stiller et al. 1989), *Rh. sanguineus* in Israel (Shkap et al. 2009) and by *Rh. simus* in South Africa (Potgieter and Van Rensburg 1980, 1982; Potgieter et al. 1983). Intrastadial transmission of *A. marginale* is caused by male ticks which serve as the reservoir hosts of the organisms, persistently infecting the cattle (Ge et al. 1996; Kocan et al. 1992, 2000; Palmer et al. 2001). The co-feeding of ticks does not appear to influence the dynamics of *A. marginale* transmission (Kocan and de la Fuente 2003). Transplacental transmission of *A. marginale* occurs in cattle, resulting in healthy but persistently infected calves (Grau et al. 2013).

There are very few reports on the occurrence of transovarial transmission of *A. marginale*. Shimada et al. (2004) detected *A. marginale* major surface protein 5 (*msp5*) gene in larvae of *Rh. microplus* by PCR amplification. Amaro Estrada et al. (2020) confirmed the transovarial transmission of *A. marginale* by detecting it in the unfed larvae hatched from the fully engorged *Rh. microplus* by the PCR targeting both *msp5* and *major surface protein1α* (*msp1α*) genes. Kumar et al. (2019) detected this organism in the *Rh. microplus* ticks and their egg masses. Hembram et al. (2022) detected this organism in the *Rh. annulatus* ticks, their egg masses, and unfed larvae.

A. bovis

Anaplasma bovis is a bacterium infecting the circulating monocytes (Sreekumar et al. 1996; Liu et al. 2012) and tissue macrophages of domestic and wild ruminants (Worthington and Bigalke 2001). The infection in cattle is normally asymptomatic, although it can induce a number of clinical symptoms, including decreased body weight, fever, anemia, depression, lymphadenopathy, and in rare cases, abortion, as well as death. *Anaplasma bovis* DNA was detected in the nymphs and larvae of *Ha. megaspinosa* in Japan (Yoshimoto et al. 2010), *Rh. turanicus* in Israel (Harrus et al. 2011), engorged female *Rh. annulatus* in India (Nimisha et al. 2019), and an undescribed tick species in South Africa (Harrison et al. 2011). There are no reports on the transovarial transmission of *A. bovis* in ticks.

A. phagocytophilum

Anaplasma phagocytophilum, an obligate intracellular gram-negative bacterium is the etiological agent of tick-borne fever (TBF) in ruminants (Atif 2015) and of equine, canine, and human granulocytic anaplasmosis (EGA, CGA, and HGA, respectively) (Dumler et al. 2001; Woldehiwet 2010). *Anaplasma phagocytophilum* (Rickettsiales: Anaplasmataceae) has become an important tick-borne pathogen in the USA, Europe, and Asia, with increasing numbers of infected people and animals every year (Bakken and Dumler 2015; Tang et al. 2015)**.** *Anaplasma phagocytophilum* multiplies within a parasitophorous vacuole to form a morula in the cytoplasm of tick and vertebrate host cells (Dumler et al. 2001; Tang et al. 2015; Munderloh et al. 1999). Fatal cases have been reported so far in sheep, cattle, horses, reindeer, roe deer, moose, dogs, and humans (Jenkins et al. 2001; Stuen 2003; Franzen et al. 2007).

The most typical way to spread the *A. phagocytophilum* is through the bite of an infected tick (Jaarsma et al. 2019). Transstadial transmission is essential in maintaining *A. phagocytophilum* within its endemic cycles (Medlock et al. 2013; Jahfari et al. 2014; Krucken et al. 2013). *Ixodes ricinus* (Strle 2004; Parola et al. 2005), *I. scapularis*, and *I. persulcatus* (Alekseev et al. 1998; Woldehiwet 2010) were identified as vectors. *Anaplasma phagocytophilum* has been found in questing ticks belonging to other members of the genus *Ixodes* like *I. trianguliceps* (Ogden et al. 1998), *I. ventalloi* (Santos et al. 2004), *I. hexagonus* (Pfaffle et al. 2011), and *I. nipponensis* (Lee et al. 2020). *Anaplasma phagocytophilum* DNA has also been found in *D. reticulatus* (Karbowiak et al. 2014), *Haemaphysalis punctata*, *Ha. concinna*, and *Rh. bursa* (Barandika et al. 2007).

Although the transovarial transmission has not been shown in *Ixodes* species, it has been demonstrated in moose tick *D. albipictus*, a parasite with a single host life cycle (Baldridge et al. 2009). The presence of *A. phagocytophilum* was confirmed by PCR in unfed larvae of *D. albipictus* (Baldridge et al. 2009) and *I. ricinus* (Hauck et al. 2020). Hembram et al. (2022) detected this organism in the fully repleted *Rh. annulatus* and *Ha. bispinosa* ticks as well as their progenies.

Concluding remarks

Numerous factors have contributed to an increase in the incidence and diversity of tick-borne diseases in both humans and animals in recent years. Global climate change favored the spread of vector populations restricted previously to narrow geo-climatic conditions to new and wider areas, thereby spreading the infections carried by them. Urbanization and habitat encroachment caused increased contact of humans/animals with wildlife and new vectors. Human activities including deforestation, reforestation, and plantation lead to a situation with increased interaction of the host with the widely dispersed blood-feeding ectoparasites, previously restricted only to the forest environments. This resulted in changes in the vector ecology. In addition, the availability of better diagnostic tools and increased awareness among the scientific community, veterinarians, physicians, and public health authorities contributed to significant improvement in the knowledge of TTBDs. Presently, TTBDs are considered to be a major problem for both human and animal populations. There is still a great dearth of knowledge regarding the vector potential of many tick species found throughout the world. In order to elucidate the disease biology of tick-borne diseases, it is essential to understand their transmission mechanisms. Among the different transmission mechanisms, transstadial transmission is the key survival strategy for many piroplasms. The lifelong carrier status of the vertebrate host ensures infection of such organisms infecting different lifecycle stages of ticks. In contrast, in the case of transovarial transmission, the parasite will be passed on into the next generation once a tick is infected, without the need for prior feeding on an infected host. Here, the tick functions as a carrier of the pathogen. Hence, a prolonged carrier status of the vertebrate host is not necessary for transmission. The transovarial transmission facilitates species diversification by host switching to other vertebrate host species. Thus, transovarial transmission plays a role in establishing the endemicity of the infection. Hence, it can affect the control efforts against the pathogen in a particular region. The transovarial transmission results in the formation of infected larvae (more when the transovarial and filial infection rates are high) with greater potential for spreading disease compared to nymphal and adult stages since such larvae are minute and difficult to be detected with the naked eye.

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Declarations

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