

Review articles

The role of particular tick developmental stages in the circulation of tick-borne pathogens affecting humans in Central Europe. 3. Rickettsiae.

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ABSTRACT. *Ixodes ricinus*, *Dermacentor reticulatus* and *D. marginatus* ticks are the most important vector for *Rickettsia* spp. in Central Europe. Ticks sustain rickettsial transmission cycles transovarially and transstadially, it makes enable the rickettsial circulation in the tick population in the absence of vertebrate competent reservoir. *Rickettsia helvetica* is transmitted by *I. ricinus* tick; the highest rates of infection are noted in adult females, lower in males and in nymphs. All tick developmental stages apart males are able to infect mammal hosts and humans. The potential animal reservoir could be wild boar, the role of deer is unclear; small rodents maintain the tick population. *Rickettsia slovaca* is transmitted by *D. marginatus* and *D. reticulatus* ticks. The available data suggest the role of wild boars and *Apodemus* mice as animal reservoir. The ticks able to infect human are adults *D. marginatus*. *Rickettsia raoultii* is transmitted by *D. marginatus* and *D. reticulatus*. The infections of mammals are not recorded. As in *Rickettsia slovaca*, human can be infected by adults *D. marginatus*. *Rickettsia monacensis* is transmitted in Central Europe by *I. ricinus* tick (apart males), although there is a documented infection of *Dermacentor* ticks. The differences in the infection rates of tick's larvae, nymphs and adults suggest the limited role of transovarial transmission, and the participation of mammals in the zoonotic cycle, being the source of infection for larvae and nymphs.

Key words: SFG, *Rickettsia slovaca*, *Rickettsia helvetica*, *Rickettsia raoultii*, *Rickettsia monacensis*, ticks

Introduction

Rickettsia is a genus of Gram-negative bacteria belonging to the Rickettsiaceae family, order Rickettsiales. They are rod shaped, with dimensions about 0.3–0.45×0.8–1.2 μm [1,2]. Rickettsiae are obligatory, intracellular parasites of many mammal species, among others humans, and cause the diseases called rickettsioses. Rickettsioses are divided into three groups, according to vector specificity – the typhoid group (TG, flea-borne rickettsioses), spotted fever group (SFG, tick-borne rickettsioses), and unclassified *Rickettsia* parasitizing insects [3–5]. The SFG *Rickettsia* transmitted by ticks contain over 25 species, among them 16 associated with human disease. Although different

species within SF group may share certain common features of ecologic interest (e.g., geographic distribution, common arthropod vectors, mammal hosts), the life cycles of most tick-borne rickettsiae are incompletely known. It seems that development and transmission cycle of all species of rickettsiae is in a general way similar, however, can differ in the details. Some species, such as *R. rickettsii*, may be associated with several different ticks' vectors, belonging to different genera. This contrasts with other rickettsiae, such as *R. conorii*, which appear to be associated with only one tick vector. Between these extremes, there are certain rickettsiae which are associated within the same genus with several tick species, such as *R. slovaca* [2,6].

According to the available data, among 13 SFG *Rickettsia* species which affect or are potentially able to affect humans in Europe [7], four occur in Middle European countries: *Rickettsia helvetica*, *R. slovacica*, *R. raoultii*, and *R. monacensis*. Other species (*R. conorii*, *R. aeschlimannii*, *R. sibirica*, and *R. massiliae*) were recorded indirectly in human sera, using serodiagnostic tests [8]. Due to the possibility of cross reactions between several *Rickettsia* species [9,10] these records, however, need confirmation and their presence in the environment has been not yet demonstrated. Although the general circulation routes of several *Rickettsia* species in the environment are similar, they are associated with different vectors and animals being their vertebrate reservoir.

The ways of transmission

Ticks sustain rickettsial transmission cycles transovarially and transstadially as well as passing on the rickettsiae to vertebrate hosts during feeding when their salivary glands are infected. *Rickettsia* multiplies in almost all organs and fluids of its tick host, particularly in the salivary glands and ovaries of adult females [1,6]. The transovarial and transstadial transmission of *Rickettsia* in vector population make the ticks being simultaneously vectors and reservoirs of the pathogen [3,5]. It was demonstrated for *R. helvetica* and *R. slovacica* under laboratory conditions that the transovarial transmission rate (TOT), i.e., proportion of infected *I. ricinus* and *D. marginatus* females giving rise to at least one positive egg or larva, may reach 100% [6].

Ticks may also acquire infection with rickettsiae by co-feeding, when several ticks feed closely to each other on the same host specimen. In this case the *Rickettsia* from an infected tick spread to a non-infected, even in the case of non-infected host. Co-feeding transmission was demonstrated in the case of *R. massiliae* and *R. rickettsii* [6]; however, such possibility cannot be excluded in the case of other species.

The pathogenicity of rickettsia to the tick host may vary. For *R. slovacica* parasitizing in *D. marginatus* maintenance of rickettsiae via transovarial transmission has no effect on the reproductive fitness and viability of the tick host. In contrast, *R. rickettsii* in *Dermacentor andersoni* diminishes survival and reproduction capacity of tick [2].

There are the records about the infection of mesostigmatid and trombiculid mites with *Rickettsia* spp, mainly from the genera *Laelaps*, *Haemogamasus*, *Hirsutiella*, *Chelodonta*, *Neotrombicula* [11,12]; however, most of them are collected from possibly infected hosts, and the presence of pathogen in their organism is not the irrefutable argument of the transmission possibility.

Because ticks serve as a reservoir of the bacteria, the distribution of the rickettsiae will be identical to that of its tick's area occurrence [7]. In the case of some rickettsia species, such as *R. monacensis*, the described occurrence area is discontinuous; however, it may be caused by the lack of official records, not their absence in the environment. The strong association of pathogen with vector cause the potential changes of endemic area with the changed occurrence area of ticks [13] or the cases of import of the disease outside the endemic area [14].

The competitive vectors and animal reservoir of Central European rickettsiae

Rickettsia helvetica

This species has been isolated for the first time from *Ixodes ricinus* tick in Switzerland in 1979, and initially presumed to be non-pathogenic. Afterwards, the infections have been noted in people with a non-specific fever, meningitis and perimyocarditis, mainly in Sweden [15–18] and France [19]. *R. helvetica* is noted in ticks in many European countries, along strip from Great Britain and France, across Denmark, Germany, Poland to Belarus and Ukraine, in the north to Sweden and Baltic countries, and to the south to Mediterranean beach countries and Bulgaria [2,5,9,20–24]. On middle-European latitude *I. ricinus* tick is recognized as the most important vector for *R. helvetica* [9,25–28]. The prevalence of infected ticks varies from 4.7% in Slovakia [29] up to 17.4% in Sweden [30]; transitional prevalence was noted in Belarus (10.0%) [22], Poland (11.4%) [20], Germany (13.3%) [31].

Most of the available data concern adult females mainly collected from vegetation as well from the hosts. Because in the latter case the source of infection is questionable, to the construction of circulation scheme only the infected questing ticks are useful.

The variability of rickettsial infection in different developmental stages of ticks collected from vegetation and hosts was noted by Stańczak [32]

Table 1. The prevalence of infection *Ixodes ricinus* ticks with *Rickettsia helvetica* and *R. monacensis* in particular tick developmental stages (%)

Larvae	Nymphs	Females	Males	References
nd	1.6	10.5	11.8	[70]
nd	4.6 (0.0–13.0) ^a	10.6 (0.0–18.0)	5.1 (0.0–17.0)	[20]
nd	4.9 ^{a b}	7.8 ^{a b}	2.8 ^{a b}	[33]
nd	1.2 ^c	7.5 ^c	7.2 ^c	[34]
nd	12.3–30.1 ^a	11.7 (0.0–22.2)	13.7 (0.0–50.0)	[31]
1.0–17.2	1.6–18	0	2.6–10	[30]
0.6 ^d	0.3 ^d		0.3 ^d	[76]

Explanations: ^a tick infection rate; ^b *R. helvetica* (n=70) and *R. monacensis* (n=1) together; ^c *R. helvetica* (91.4%) and *R. monacensis* (8.6%) nymphs, females and males together; ^d *R. monacensis* only

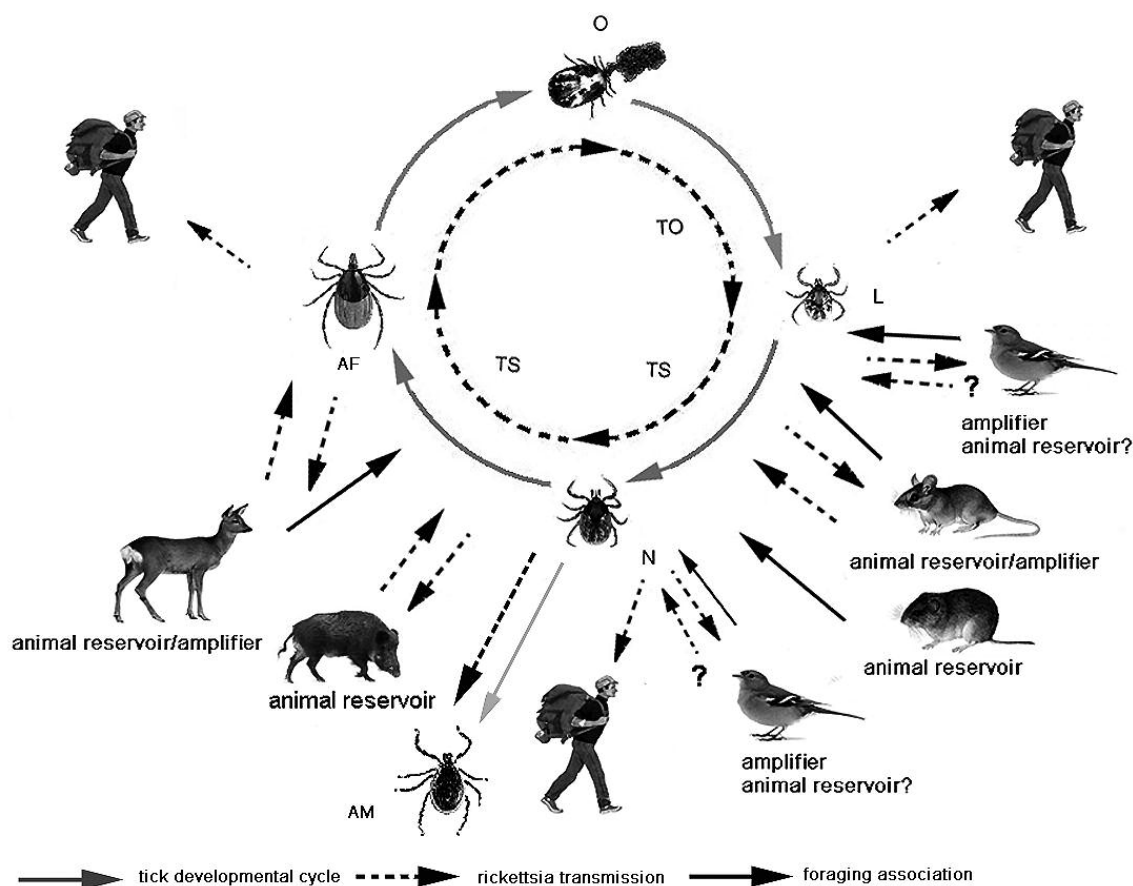
and Stańczak et al. [20] – the highest prevalence rate of infection was in adult females (10.5–10.6%), equal or lower in males (5.1–11.5) and lower in nymphs (1.6–4.6); similar results were obtained by Reye et al. [33] and Silaghi et al. [31,34]. Different data origins from Sweden where Severinsson et al. [30] recorded the similar infection rate in adult males, nymphs and larvae (2.6–10.0, 1.6–18.0, 1.0–17.2) and the lack of infection in adult females (Table 1).

The animal reservoir of *R. helvetica* needs follow study. During field investigations, *R. helvetica* was detected in wild boar in Holland with the prevalence 6.9% [35]. Equally possible (potential) reservoir can be roe deer, the infections were recorded in Slovakia and Holland, with prevalence 6.5% and 19.0% respectively [35,36], although some authors call in question roe deer to be reservoir hosts for *R. helvetica* [27]. The counterargument can be that the direct transmission of *Rickettsia* from wild boar and deer to ticks has not been documented yet. The trace evidence can be the differences in prevalence infections between ticks collected from hosts and vegetation, from not statistically significant [27] to quite noticeable [37]. According to Nielsen et al. [38], the presence of *R. helvetica* was the highest in adult ticks collected from dogs and roe deer.

The role of rodents in *R. helvetica* circulation remains unknown. After some authors, these rickettsiae are not able to infect Murinae and Microtinae rodents being the most important hosts for immature stages of ticks [37,39,40]. Biernat et al. [41] collected larvae and nymphs of *I. ricinus*

infected with *R. helvetica* from non-infected rodents. On the other hand, *R. helvetica* was detected in *Apodemus* mice and voles in Bayern, Germany, however, in single specimens only [42]. The reservoir role of rodents for *R. helvetica* suggests Burri et al. [40], using xenodiagnosis test. This author showed that *A. sylvaticus* and *M. glareolus* did not transmit *R. helvetica* to ticks feeding on them, whereas *A. flavicollis* transmitted it very rarely, probably due to a very fast and intense immune answer. It seems that the infections observed in larvae fed on captured rodents was most probably the result of either an extremely short rickettsiemia, or of transovarial transmission. Due to high transovarial transmission of *R. helvetica*, the tick itself is most probably the main reservoir host for this pathogen, as also suggested Sprong et al. [35].

The open question is the role of birds as animal reservoir of *R. helvetica*. Tick *I. ricinus* belongs to parasites having the great spectrum of hosts, so birds are often affected by larvae and nymphs [43]. Hornok et al. [44] noted bacteraemia with *R. helvetica* in *Erithacus rubecula* and *Prunella modularis*, while Berthová et al. [45] recorded the infection of ground-feeding Passeriformes birds, as *Parus major*, *Cyanistes caeruleus*, *Sylvia atricapilla*, *Fringilla coelebs* in Slovakia. Although ticks are only one source of infections with *Rickettsia* for birds, there is no evidence that birds can infect ticks. The authors suggested that rickettsiemia may last after detachment of the vector tick in relevant birds and rickettsiemic hosts may

Fig. 1. The proposed scheme of zoonotic cycle of *Rickettsia helvetica* (orig.)

Ixodes ricinus tick is the most important vector in the maintenance of the circulation of *R. helvetica* in the environment. The potential animal reservoir should be wild boar, the role of roe deer is unclear, but it has important participation as amplifier. Small rodents, as hosts for larvae, maintain the tick population, Murinae rodents by some authors also may serve as animal reservoir. Birds are hosts of larvae and nymphs, and possibly play the role in the spreading of *Rickettsia* spp., but their role as the source of infection for ticks needs confirmation. Transovarial and transstadial transmission enables the rickettsia circulation in the tick population also in the absence of competent reservoirs and makes the presence of infection in larvae possible. All tick developmental stages are able to be the source of infection to their hosts, and effectively infect human; however, because males do not feed not participate in the follow *Rickettsia* transmission.

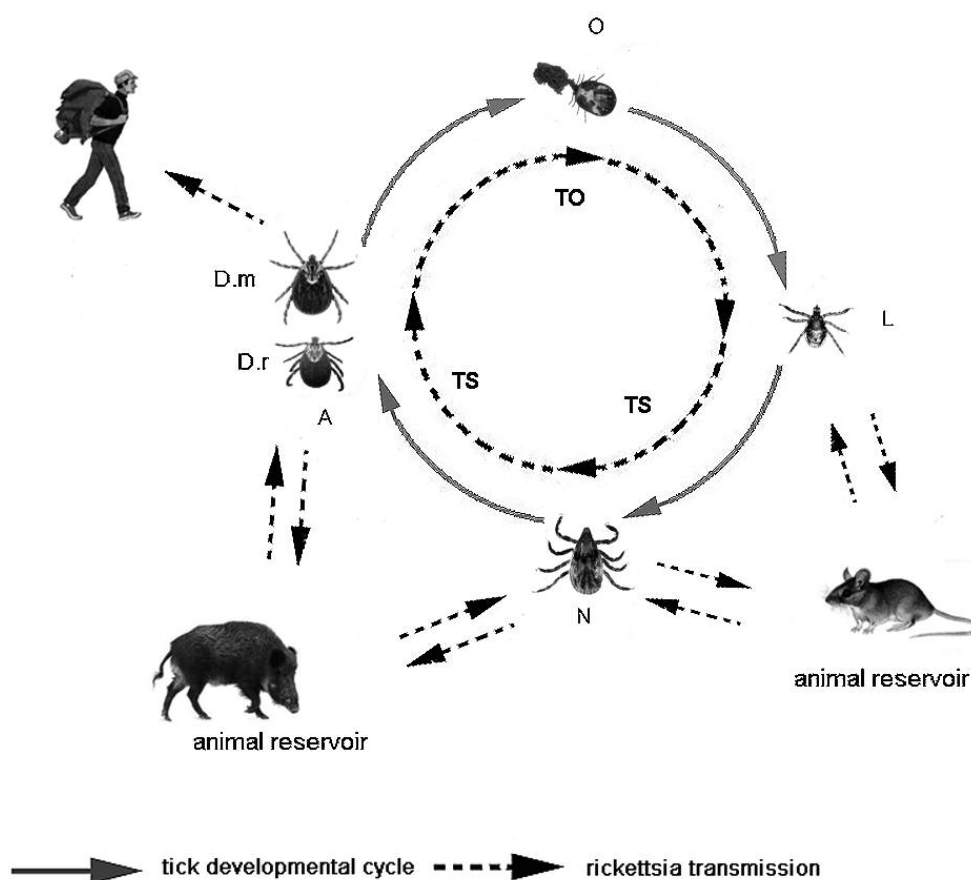
TO – transovarial transmission; TS – transstadial transmission; L – larva; N – nymph; AF – adult female; AM – adult male; O – eggs

provide a source of infection for *I. ricinus*, but efficacy of transmission is low. However, birds could play a role of carrier of infected ticks to great distances and ensure the distribution and maintenance of *Rickettsia* spp. in nature [45]. The proposed scheme of *R. helvetica* circulation in environment is presented in the Fig. 1.

Rickettsia slovaca

This bacteria was first isolated in 1968 from *Dermacentor marginatus* tick in Slovakia [46,47]. To 1997 this species has been concerned as non-pathogenic for human, until stay associated with

diseases concerned so far as atypical cases of *Borrelia burgdorferi* infections. The first correct diagnosis has been made in Hungary in 90. of XX century [48] and the disease has been named TIBOLA (Tick-borne lymphadenopathy). In Spain the disease is called DEBONEL (*Dermacentor*-borne necrosis-erythema-lymphadenopathy) [49]. This syndrome is defined as the association of a tick bite, an inoculation eschar on the scalp, and cervical lymphadenopathies. It is common in Southern and part of Central Europe and central Asia. The endemic areas are recognized in many European countries, the majority in Hungary, Spain and

Fig. 2. The possible zoonotic cycle of *Rickettsia slovaca* (orig.)

Dermacentor marginatus and *D. reticulatus* ticks play role in the maintenance of the circulation of *R. slovaca* in the environment. The potential animal reservoir are probably wild boar and *Apodemus* mice. Transovarial and transstadial transmission enable the rickettsial circulation in the tick population also in the absence of competent reservoirs and make possible the presence of infection in small percent of larvae. Small mammals are hosts and source of infection for larvae and nymphs of ticks. The possibility of rodents to infect larvae and nymphs, and the transstadial transmission make possible the maintenance of *R. slovaca* cycle in environment, also in the absence of competent large mammals. Wild boar can be infected by nymphs and adult ticks. The tick able to effectively infect human is *D. marginatus*; tick *D. reticulatus* does not attack human, but participates in the circulation of the virus in the environment.

TO – transovarial transmission; TS – transstadial transmission; L – larva; N – nymph; A – adult; O – eggs; D.m – *Dermacentor marginatus*; D.r – *Dermacentor reticulatus*

France [5,50,51] to the south the endemic area reaches Mediterranean Sea coast and Mediterranean islands [52], to the east *R. slovaca* is recorded from Ukraine and Armenia [7]. Presently it was noted in other countries, i.e. Poland [53].

The role of *D. marginatus* as efficient vector for *R. slovaca* has been considered, however, later studies indicate also on the role of *D. reticulatus* ticks. It seems that due to the different occurrence area, the role of *D. marginatus* and *D. reticulatus* ticks is variable in southern and northern parts of Europe. The *D. marginatus* occurrence area extends more to the south than *D. reticulatus*, and this tick is rare or absent in the north from Carpathian

Mountains [14,43]. Moreover, *D. marginatus* is more competent to infect human than *D. reticulatus*, thus it has bigger epidemiological significance in southern Europe [54]. Nevertheless, on the area where *D. marginatus* is absent, *D. reticulatus* tick stays the most important factor in *R. slovaca* circulation in environment. The competence to transmission *R. slovaca* by this tick species was demonstrated in Germany (prevalence 5%) [39], Slovakia (prevalence 1.7–3.4%) [47], and Poland (40.7%) [21,53]. Because the developmental cycles of *D. reticulatus* and *D. marginatus* are similar [43,56,57], their participation in *R. slovaca* circulation in the environment should be

comparable. Unfortunately, due to the lack of data about the infection of immature tick stages with *R. slovaca*, the finding of possible differences of larvae and nymphs in participation in zoonotic cycle is impossible.

The identified vectors are, apart from *Dermacentor* ticks, also *I. ricinus*, *Haemaphysalis punctata* and *H. sulcata*, however, are infected in lower prevalence [57]. Moreover, in Central Europe *Haemaphysalis* ticks are not such common [14] and their role in *Rickettsia* circulation could be marginal only.

The animal reservoir for this rickettsia is poorly known. Řeháček [46,57] showed the laboratory possibility of infection *Apodemus flavicollis* with *R. slovaca*, and demonstrated the antibodies in dogs, wild boars and roe deer. In last decade, the presence of *R. slovaca* was noted on the base of PCR in wild boar from Spain [5,58]. Due to the ability of Murinae rodents and wild boars to be infected with *R. slovaca*, they can simultaneously play the role of the animal reservoirs as amplifiers for the rickettsia. The competence of other wild mammals, being the hosts for *Dermacentor* ticks (deer, carnivores, Microtinae rodents) to be hosts for *R. slovaca* is not known, thus their role in rickettsia circulation in environment cannot be established. The proposed scheme of *R. slovaca* circulation in environment is presented in the Fig. 2.

Rickettsia raoultii

This bacteria has been isolated for the first time from Asiatic species of *Dermacentor* ticks [59,60], and since 1999 has been detected also in Europe, i.e., European part of Russia [61], throughout Middle-European countries, along the countries of Carpathian Mountain Range from Atlantic coast (Spain, France) to Poland [21,23,47,62–65]. It is also noted in Great Britain [25]. The pathogenicity of this species for human has been demonstrated in France and China [51]. In France the cases of *R. raoultii* infection were confirmed by positive culture [6,7]. In Poland the presence of *R. raoultii* is noted in *D. reticulatus* ticks in the area of Białowieża Primeval Forest and in central and southern regions predominate over other SFG rickettsiae [21,67], and one suspected case of human infection confirmed by serologic test was noted [68].

As a strain of *R. raoultii* is presently considered also RpA4 strain. This rickettsia was described in Russia, as genospecies of *R. massiliae* and it was

isolated from *Rhipicephalus* ticks in Astrakhan region. Presently, this pathogen was detected in *D. reticulatus* tick collected from deer and dogs in Germany and ticks collected from vegetation in Poland [32,62].

As first vector for *R. raoultii* was considered tick *D. marginatus*. The infections were noted in Great Britain, Slovakia and Germany, the prevalence was 6.5%, 8.09% and 31.0%, respectively [25,47,69]. However, there is the documented competence of *D. reticulatus* tick as vector for *R. raoultii*, independently from *D. marginatus* tick. Moreover, as in the case of *R. slovaca*, the big importance has the question of different occurrence of *D. marginatus* and *D. reticulatus* ticks. *Dermacentor marginatus* is the main vector in the south from Carpathian Mountains, and *D. reticulatus* can spread *R. raoultii* in the north from the occurrence range of *D. marginatus*. The infection of *D. reticulatus* with *R. raoultii* was demonstrated in Great Britain, Germany, Slovakia, Poland, Belarus; the prevalence of infection was relatively high, from 22.3 to 56.7% [21,25,32,39,47,67]. There are also known the cases of *I. ricinus* tick infection with this rickettsia, the prevalence was about 20.0–23.0% of *I. ricinus* [20,53,67,70]. As in the case of *R. slovaca*, there is no data about the prevalence of immature tick stages infection with this, and the finding of possible differences of larvae and nymphs in participation in zoonotic cycle is impossible.

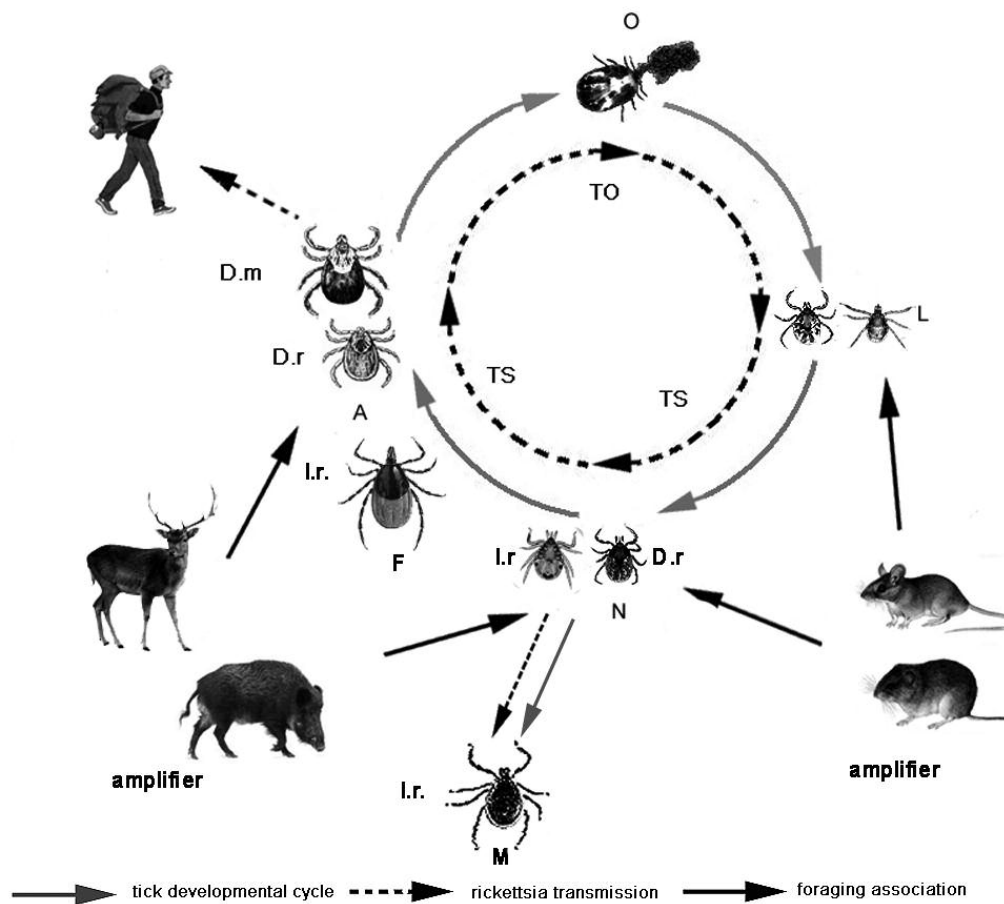
The infections of mammals with *R. raoultii* are not recorded yet. Possibly, there is no animal reservoir of this species, and in their circulation and zoonotic cycle participate ticks only; however, the finding of this rickettsia in wild animals cannot be excluded in the future.

The proposed scheme of *R. raoultii* circulation in environment is presented in the Fig. 3.

Rickettsia monacensis

This species was described for the first time in Switzerland [37,71] where it was isolated from *I. ricinus* ticks. Recently the presence of this rickettsia has been noted also in Bayern in Germany, Hungary, Slovakia, Poland and Eastern Ukraine [12,23,28,34,72] the foci are also recorded from north-African populations of *I. ricinus* in Algeria [73]. There are the described human cases of disease, caused by this species in Spain and Italy [74,75]. New reports show the role of *I. ricinus* tick in transmission of *R. monacensis* [33,73], the prevalence of infection seems to be relatively low. By Socolovschi et al.

Fig. 3. The possible zoonotic cycle of *Rickettsia raoultii* (orig.)



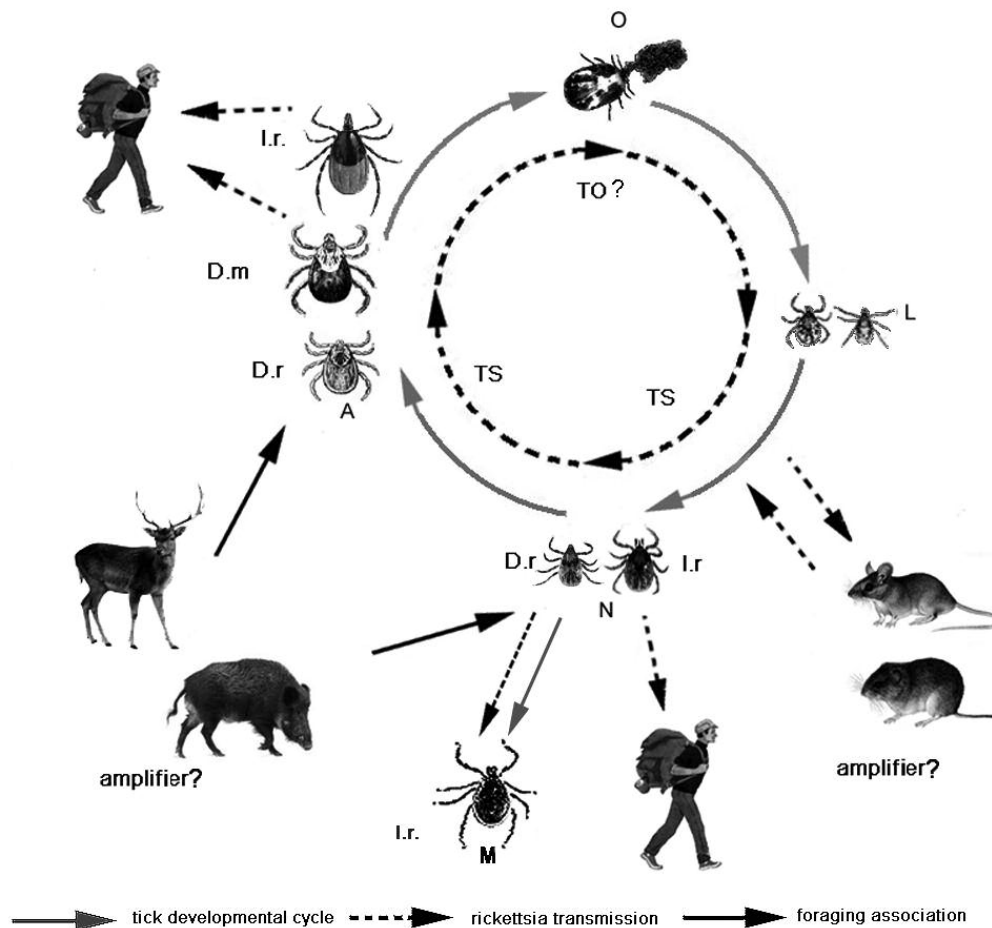
Ticks *Dermacentor marginatus* and *D. reticulatus* are the most important vectors in the maintenance of the circulation of *R. raoultii* in the environment, with participation of *Ixodes ricinus* larvae, nymphs and females. *I. ricinus* males do not feed, thus not participate in the follow *Rickettsia* transmission. The animal reservoir is not confirmed; possibly wild mammals play the role of amplifier mainly, in maintenance of the tick population. Transovarial and transstadial transmission protect the rickettsia circulation in the tick population. The ticks able to effectively infect human are *I. ricinus* and adult *D. marginatus*; tick *D. reticulatus* doesn't attack human, but participates in the circulation of the bacteria in the environment.

A – adult; TO – transovarial transmission; TS – transstadial transmission; L – larva; N – nymph; D.m – *Dermacentor marginatus*; D.r – *Dermacentor reticulatus*; F – female; I.r – *Ixodes ricinus*; M – male; O – eggs

[6,7] infection rate in questing ticks varied between 2.4% and 8.6% in Spain and Germany, respectively, to 12.2% and 52.9% in Slovakia and Bulgaria. Schorn et al. [76] present the prevalence of adult ticks, nymphs and larvae 0.3%, 0.3% and 0.6%, respectively. By fact that it is transmitted by *I. ricinus* ticks and has been found on the same latitude, their presence in other Middle-European countries cannot be excluded.

Because the animal reservoir of this *Rickettsia* species is practically unknown, therefore it is difficult to make the scheme of their zoonotic foci, consider the routes of pathogens circulation and the influence of biotic and abiotic external factors on

the rickettsial presence in the environment. The documented vectors – *Ixodes ricinus*, *D. marginatus* and *D. reticulatus* both attack rodents, carnivores, wild boars and cervids, thus these animals are exposed to the infections with rickettsiae and, in the case of competence, can be the source of infection to tick's population. The transfer of rickettsia within the tick population takes place similarly as in the case of viruses. The differences in the infection rates of larvae, nymphs and adults (Table 1) suggest the limited role of transovarial transmission, and the participation of mammals in the zoonotic cycle being the source of infection for larvae and nymphs and in result the highest infection prevalence in

Fig. 4. The possible zoonotic cycle of *Rickettsia monacensis* (orig.)

Dermacentor marginatus and *D. reticulatus* ticks are the most important vectors in the maintenance of the circulation of *R. monacensis* in the environment, with big participation of *Ixodes ricinus*. The animal reservoir is not confirmed; possibly large wild mammals play the role of amplifier mainly, in maintenance of the tick population, and rodents the role of amplifier and animal reservoir. Transovarial transmission needs confirmation or exception; transstadial transmission protects the rickettsia circulation in the tick population. In this case, larvae could be the stage which acquires infections from rodents, while nymphs and adults would be able to infect mammal hosts. The ticks able to effectively infect human are adults and nymphs of *I. ricinus* and adult *D. marginatus*; *D. reticulatus* ticks rarely attack human, but participate in the circulation of the rickettsiae in the environment.

A – adults; TO – transovarial transmission; TS – transstadial transmission; L – larva; N – nymph; D.m – *Dermacentor marginatus*; D.r – *Dermacentor reticulatus*; I.r – *Ixodes ricinus*; M – male; O – eggs

adults. Ticks can be infected with rickettsiae in every active developmental stage, from the infected host, and follow, due to the transstadial and transovarial transmission, the next developmental stage succeeds the pathogen. The possible circulation scheme of *R. monacensis* can be similar to *R. raoultii* (Fig. 4) with the bigger participation of *I. ricinus* tick.

Conclusions

The presence of transstadial and transovarial routes of *Rickettsia* transmission in tick's

population results in the participation of all active developmental stages of ticks in the circulation of these bacteria in the environmental and enzootic cycle. Adults, as well as immature stages both are able to be infected by rickettsiae, and afterwards infect mammal hosts. The facility of *R. helvetica* and *R. monacensis* to *I. ricinus* tick causes that great range of mammal hosts can be infected, as well as many bird species. It is secured by the great host range of larvae, nymphs and adult females of *I. ricinus* tick. This way, also human can be affected by every three active tick's stages; this is the reason why the number of young stages and their

prevalence of infection with rickettsiae should be calculated in the epidemiological estimations of risk infection with *Rickettsia helvetica*.

Ticks *D. reticulatus* and *D. marginatus* have a wide range of hosts, but their developmental stages differ in the host's preferences. Larvae and nymphs prefer small rodents and insectivores as hosts, adults medium sized and large animals. Moreover, adult *D. reticulatus* tick generally does not affect human. Thus, in the area of *D. marginatus* occurrence has place the threat of infection with *R. slovaca*, and only adult ticks are the threat for human; immature stages participate only in the circulation of pathogen in the environment. In the area where *D. reticulatus* predominates, the possibility of infection is insignificant, although *Rickettsia* commonly occurs in the environment.

Due to poor knowledge about the infections of mammals and birds with SFG rickettsias in central Europe, presented schemes are still the propositions, possibly to verification according to new records.

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