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Monograph

# Checklist of hosts, illustrated geographical range, and ecology of tick species from the genus *Ixodes* (Acari, Ixodidae) in Russia and other post-Soviet countries

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## Abstract

Hard ticks (Acari: Ixodidae) are the economically and ecologically most important blood-sucking arthropod vectors that can transmit disease agents under temperate climate. In this group, the highest number of species (currently nearing 270) belongs to the genus *Ixodes*. For this review, more than 400 papers related to this genus in the context of Russia were checked for data on the host records, locations of collection, as well as ecology of assigned tick species. This monograph compensates for the lack of a similarly comprehensive English-language overview of *Ixodes* species in the region of Russia for nearly half century, and also makes a large set of data easily available for international readers, which is especially important if the original source is difficult to access from outside this country. In addition, the data from a significant number of papers on this topic available only in the Russian language are made accessible through this work.

**Key words:** Acari, Aves, Ixodidae, Mammalia, Reptilia, subgenus, taxonomy



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## Introduction

Russia is the largest country of the globe, covering nearly one third of the territory of Eurasia and 1/8$^{th}$ of the entire Earth's landmass. It belongs to the Palearctic Zoogeographic Region (Guglielmone et al. 2023). The ecosystems of Russia are very diverse, including polar deserts, tundra, forest tundra, taiga, mixed and broad-leaved forests, forest steppe, steppe, semi-desert, and subtropics. At least 1100 species of terrestrial vertebrates are known to occur in this country, of which 65% of the territory is considered virtually untouched by economic and other human activities (CBD 2023).

With such a vast area, the broad spectrum of suitable habitats and vertebrate hosts in the background, the tick fauna of Russia was extensively studied. Although there was an enormous collection of data published in English (Anastos 1957), because it is more than half a century old, it is outdated. Moreover, the most well-known source describing the taxonomic diversity of Ixodidae Koch in this country and its nearby regions was compiled decades ago (Filippova 1977;

1997), and is only available in the Russian language. This book on ixodid species in Russia included 34 *Ixodes* Latreille species, which is updated to 37 by adding species with more recent data, as exemplified by *Ixodes prokopjevi* Emelyanova and *I. ghilarovi* Filippova & Panova, as well as *I. turdus* Nakatsudi with its first and single record (Bolotin and Kolonin 1979). Recent work has also been published including a list of hard tick species known to be indigenous in Russia (Guglielmone et al. 2023) with indications of tick species of other post-Soviet countries. However, the latter does not consider their specific locations or host records and various distinctive features of biology relevant to certain regions. Less studied species (some often known exclusively from these territories by single or a limited number of findings) are also reviewed here in more detail, in particular with the addition of precise data on their type specimens.

The need was recognized for a comprehensive work that would contain data and references from the last decades, written in English, which would thus be accessible by experts and anyone interested in the current ixodid fauna and its supportive hosts in the vast geographical and biotope range of Russia, as well as several other post-Soviet territories. In this review the authors tried to compensate for this scarcity of fresh information on hard ticks occurring in Russia and former states of the Soviet Union, targeting the most species-rich genus, *Ixodes*. Although the checklist and georeferenced data might still contain gaps, this work is also intended to be used as baseline data for the unfolding quest to discover and to describe not-yet-known ixodid species in this extensive geographical range.

## Materials and methods

The relevance of publications used in this review was searched in databases using the keywords of *Ixodes* species, their hosts, and locality or region. The following databases were used: Library of the Russian Academy of Sciences (including its department at the Zoological Institute of the Russian Academy of Sciences), Springer Link, Web of Science, Zoological Record, Google Scholar, and CyberLeninka – the Russian scientific electronic library. However, a limited number of works was excluded from consideration and inclusion in the review due to the absence of scientific background and/or indeterminate data. Similarly, papers with repetitive data (i.e., not adding new tick-host associations, geographical locations to existing literature data) are not cited.

The same databases were used for searching and estimating the data on *Ixodes* from the post-Soviet territories, reviewed in this checklist: Russia, Belarus, Ukraine, Moldova, Georgia, Azerbaijan, Armenia, Kazakhstan, Kyrgyzstan, Uzbekistan, Turkmenistan, and Tajikistan. The Baltic states (Estonia, Latvia, and Lithuania) were excluded from the consideration due to the availability of recently updated tick checklists, as well as the well-studied tick fauna (Paulauskas et al. 2010; Kitrytė and Baltrūnaitė 2023), which is also very similar to the tick fauna of neighboring Belarus and northwestern Russia.

Within Prostriata (genus *Ixodes*), tick species names are arranged according to their subgenera and are used sensu Guglielmone et al. (2014). The Latin names of tick species are written according to Guglielmone et al. (2023). The only exception is *Ixodes filippovae* Černý which we consider a synonym of *Ixodes crenulatus* Koch according to Filippova (1958a, 1977). The names of host species are written in accordance with their international English names, as well as the current

Latin names using the online databases, such as ASM Mammal Diversity Database (https://www.mammaldiversity.org/index.html) as well as Avibase (https://avibase.bsc-eoc.org/) and Reptile Database (http://www.reptile-database.org/).

## Systematics

**Class Arachnida**
**Order Ixodida**
**Family Ixodidae Koch, 1844**
**Genus *Ixodes* Latreille, 1795**
**Subgenus *Ceratixodes* Neumann, 1902: 115**

***Ixodes uriae* White, 1852**

*Ixodes uriae* White, 1852: 208.
*Ixodes jacksoni* Hoogstraal, 1967: 37.
*Ixodes fimbriatus* Kramer & Neumann, 1883: 527; Neumann 1911: 29.
*Ixodes borealis* Kramer & Neumann, 1883: 526; Neumann 1911: 29.
*Ixodes hirsutus* Birula, 1895: 353; Arthur 1963: 152.
*Ixodes putus* (Pickard-Cambridge, 1876): 260; Neumann 1899: 125; Schulze 1938: 12.
*Ixodes putus procellariae* Schulze, 1930: 123; Zumpt 1952: 12.

**Recorded hosts. Aves:** auks - birds of the family Alcidae, namely: *Alca torda* Linnaeus (razorbill), *Cepphus grylle* Linnaeus (black guillemot), *Fratercula arctica* Linnaeus (common puffin), *Uria aalge* (Pontoppidan) (common guillemot), *Uria lomvia* Linnaeus (Brünnich's guillemot) (Filippova 1977).

Occasional hosts include *Fratercula cirrhata* (Pallas) (tufted puffin) and also various species of gulls and kittiwakes (Laridae): *Rissa brevirostris* (Bruch) (red-legged kittiwake), *R. tridactyla* (Linnaeus) (black-legged kittiwake) (Karpovich 1970; Dietrich et al. 2012), as well as fulmars (Procellariidae) – *Fulmarus glacialis* Linnaeus (northern fulmar) and cormorants (Phalacrocoracidae) – *Phalacrocorax capillatus* (Temminck and Schlegel) (Japanese cormorant), *Urile pelagicus* (Pallas) (pelagic cormorant), *Urile urile* (Gmelin) (red-faced cormorant) (Lvov et al. 1972b, 1975; Filippova 1977; Dietrich et al. 2012; Duron et al. 2014). A single atypical case of parasitism on *Motacilla alba* Linnaeus (white wagtail) (Motacillidae) was also reported (Karpovich 1970).

**Recorded locations (Fig. 1). Murmansk seacoast (Russia):** islands and seashores of the White Sea and also the Barents Sea (Karpovich 1971), namely: the Kuvshin Island and Kharlov Island (Karpovich 1970), Podpakhta Bay (Beklesheva et al. 1970), Dvorovaya Bay (Flint and Kostryko 1967), Seven Islands Reserve (Belopolskaya 1952; Karpovich 1973). **The Far East (Russia):** Mosolova Bay (the northern coast of the Strait of Tartary) (Savitskaya 1975), Bering Island (Lvov et al. 1975; Dietrich et al. 2012), Ptichy Island and Starichkov Island (Dietrich et al. 2012), Iony Island (Lvov et al. 1975), Kuril Islands (Lvov et al. 1975; Dietrich et al. 2012), Tyuleniy Island (Karpovich 1971; Lvov et al. 1972a; Filippova 1977), Sakhalin (Lvov et al. 1972a), Commander Islands (Dietrich et al. 2012).

**Ecology and other information.** *Ixodes uriae* is the only representative of the subgenus *Ceratixodes* in the tick fauna of Russia and the northern hemisphere


**Figure 1.** Map of Russia and neighboring countries showing the locations where *Ixodes uriae* was reported.

in general. As a nidicolous parasite of seabirds living in colonies, it is a species with a circumpolar distribution, occurring on oceanic coasts and islands of both the northern and southern hemispheres, from the polar regions to the subtropical zone (Wilson 1967; Filippova 1977).

In the northern hemisphere, this tick species is strongly associated with seabirds of the family Alcidae. The high degree of nest conservativity of these birds contributes to supporting a considerable number of ticks in bird colonies, which use the same places for many years (Karpovich 1971). The occasional hosts of *I. uriae* usually become involved in its life cycle in mixed bird colonies, where nests of typical and atypical hosts are located very close to each other (Violovich 1962b). In absence of auks, it may also use, for example, cormorants as exclusive hosts, as reported on the Kuril Islands (Lvov et al. 1975; Dietrich et al. 2012). In the southern hemisphere it was noted that penguins (Spheniscidae) are more typical hosts; this can be explained by similarities in the habits of these birds to those of puffins and guillemots.

There were noted rare records of adults from Carnivora: Mustelidae, and nymphs from Rodentia: Muridae (Eley 1977; Jaenson and Jensen 2007; Baggs et al. 2011; Guglielmone et al. 2020) and even humans (Karpovich 1971; Keirans and Lacombe 1998; Martyn 1998; Smith et al. 2006; Jaenson and Jensen 2007).

### Subgenus *Eschatocephalus* Frauenfeld, 1853: 55

### *Ixodes simplex* Neumann, 1906

*Ixodes simplex* Neumann, 1906: 197.
*Ixodes audyi* Kohls, 1955: 1; Clifford et al. 1973: 489.
*Ixodes spiculae* Arthur, 1956: 180.
*Ixodes pospelovae* Emchuk, 1955: 606; Beaucournu 1966: 495.
*Ixodes chiropterorum* Babos & Janisch, 1958: 389; Beaucournu 1966: 495.


**Figure 2.** Map of Russia and neighboring countries showing the locations where *Ixodes simplex* was reported.

**Recorded hosts. Mammalia:** *Myotis blythii* Tomes (lesser mouse-eared bat), *Miniopterus schreibersii* (Kuhl) (common bent-wing bat), *Nyctalus leisleri* (Kuhl) (lesser noctule) (Filippova 1977).

**Recorded locations (Fig. 2). Russia:** Krasnodar Krai – outskirts of Sochi (Emchuk 1955; Filippova 1972). **Ukraine:** eastern Carpathians – outskirts of Solotvyn and Rakhiv (Emchuk 1955; Filippova 1972). **Azerbaijan:** outskirts of Şahbuz and Hadrut (Emchuk 1955; Filippova 1972).

**Ecology and other information.** *Ixodes simplex* is a tick species specialized for bats as hosts (Filippova 1977). This species is mainly monoxenous and can be found usually on the common bent-wing bat although some other species of the Chiroptera may also act as hosts, especially which share colonies with its main host (Beaucournu 1967). Some rare cases of human infestation are also recorded (Okino et al. 2010; Péter et al. 2021).

### *Ixodes vespertilionis* Koch, 1844

*Ixodes vespertilionis* Koch, 1844b: 232.
*Ixodes longipes* Lucas: Neumann 1901: 249.
*Ixodes pagurus* Neumann, 1911: 28.
*Ixodes nodulipes* (Kolenati): Neumann 1911: 28.
*Ixodes troglodytes* Schmidt in Frauenfeld: Neumann 1901: 249.
*Eschatocephalus gracilipes* Frauenfeld: Estrada-Peña 1989: 165.
*Eschatocephalus nodulipes* Santos Dias: Santos Dias 1961: 229.
*Eschatocephalus seidlitzii* Koch: Neumann 1911: 30.
*Eschatocephalus frauenfeldi* Koch: Neumann 1901: 249.
*Eschatocephalus seidlitzi* Koch: Neumann 1901: 249.
*Eschatocephalus vespertilionis* (Koch): Neumann 1901: 249.
*Eschatocephalus exaratus* (Kolenati): Neumann 1901: Santos Dias 1961: 229.

*Eschatocephalus flavipes* (Koch): Doss and Anastos 1977: 34.

**Recorded hosts. Mammalia:** *Eptesicus serotinus* (Schreber) (serotine bat), *Myotis blythii* (lesser mouse-eared bat) (Filippova 1977), pond bat *Myotis dasycneme* (Boie) (Starikov et al. 2017b), Daubenton's bat *Myotis daubentonii* (Kuhl) (Orlova et al. 2011), *Myotis myotis* (Borkhausen) (greater mouse-eared bat) (Filippova 1977), *Myotis mystacinus* (Kuhl) (whiskered bat) (Bobkova 2003), *Nyctalus noctula* (Schreber) (common noctule), *Pipistrellus pipistrellus* (Schreber) (common pipistrelle), *Rhinolophus ferrumequinum* (Schreber) (greater horseshoe bat), *Rhinolophus hipposideros* (Bechstein) (lesser horseshoe bat), *Rhinolophus mehelyi* Matschie (Mehely's horseshoe bat) (Filippova 1977).

**Recorded locations (Fig. 3). Russia:** Udmurtia (Orlova et al. 2011), Voronezh Oblast (Usmsnskyi pine forest), (Khitsova and Sherstyanykh 2014), Novosibirsk Oblast (resort Lake Karachi) (Fedorov 2016), Khanty-Mansi Autonomous Okrug (outskirts of the urban locality Mortka) (Starikov et al. 2017b), Krasnodar Krai (Sochi National Park) (Romashin 2021), Stavropol Krai (Tsapko 2019). **Ukraine:** Ivano-Frankivsk Oblast, Chernivtsi Oblast, Ternopil Oblast, Zakarpattia Oblast, Crimea (Bobkova 2003). **Moldova:** Codru Reserve (Dniester-Prut interfluve) (Uspenskaya 1987). **Georgia:** Abkhazia (Kerbabaev 2011). **Azerbaijan:** Shusha, Hadrut (Filippova 1972). **Armenia:** Meghri (Ogandzhanyan 1949). **Kyrgyzstan:** Chüy Valley (Fedorova 2012a). Turkmenistan: rural localities Ahcha-Kuima and Mollagara (Dubinin and Bregetova 1952). **Tajikistan:** northern spurs of the Zarafshan Range (Filippova 1972).

**Ecology and other information.** *Ixodes vespertilionis* Koch is a species of ixodid ticks associated with bats as typical hosts (Filippova 1977), mostly from the families Rhinolophidae and Vespertilionidae. Usually, *I. vespertilionis* can be found in caves inhabited by bats. Occasional findings in Central Russia and Siberia are considered to result from accidental transportation.


**Figure 3.** Map of Russia and neighboring countries showing the locations where *Ixodes vespertilionis* was reported.

**Subgenus *Filippoviella* Apanaskevich, Greiman & Fedorov, 2024: 229**

***Ixodes ghilarovi* Filippova & Panova, 1988**

*Ixodes ghilarovi* Filippova & Panova, 1988: 212.

**Recorded hosts. Mammalia:** *Apodemus flavicollis* Melchior (yellow-necked field mouse), *Chionomys gud* Satunin (Caucasian snow vole), *Chionomys nivalis* (Martins) (European snow vole), *Microtus daghestanicus* (Shidlovsky) (Daghestan pine vole), *Nothocricetulus migratorius* (Pallas) (grey dwarf hamster), *Sorex raddei* Satunin (Radde's shrew) (Filippova and Panova 1989; Filippova and Stekol'nikov 2007).

**Recorded locations (Fig. 4). Russia:** Dagestan – the valley of the Akhtychay River which is the right tributary of the Samur River near the confluence of these rivers, ~ 1000 m a.s.l. and at the same location near rural locality Khnov, ~ 1700 m a.s.l.; the valley of the Avar Koysu River, ~ 1000 m a.s.l. (Filippova and Panova 1989); Kabardino-Balkaria, Bezengi gorge – 1550–2500 m a.s.l. and Karachay-Cherkessia – 1900–2200 m a.s.l. (Filippova and Stekol'nikov 2007). **Georgia:** Mtskheta-Mtianeti region, Kazbegi Municipality, outskirts of the hamlet Suatisi, 2200 m a.s.l. (Filippova and Panova 1989).

**Ecology and other information.** *Ixodes ghilarovi* is the second representative of the subgenus *Filippoviella* in the Palearctic tick fauna together with *I. trianguliceps* but known at the current moment exclusively from several locations of the Caucasus (Filippova and Panova 1988). The species was found only in rocky biotopes on the slopes containing xerophilous herbaceous-shrub vegetation consisting of many endemics of Southern Dagestan (Filippova and Panova 1989).

Further investigations of this poorly studied tick species are of undoubted interest. *Ixodes ghilarovi* has certain common structural features with the African


**Figure 4.** Map of Russia and neighboring countries showing the locations where *Ixodes ghilarovi* was reported.

species *I. alluaudi*, for example the presence of auriculae, especially visible in nymphs of both species (Filippova 2010); molecular analysis is also necessary to obtain more data on interspecific connections of these ticks and inside the subgenus in general. The host-parasite relations of *I. ghilarovi* and its distribution and habitats are probably wider than it is known today. The seasonality of *I. ghilarovi* and its role as a vector of tick-borne infections remain unknown.

The type specimens of *I. ghilarovi* are deposited at the Zoological Institute of the Russian Academy of Sciences and include the holotype: nymph; Russia, 25, Daghestan, Samur Mt. Range, near Akhty Village, River Akhtychay valley, ~ 1000 m a. s. l., *Chionomys gud*, Sat., 24.5.1980, coll. I.V. Panova; FBM 610a, 610b and the paratypes: 4 nymphs; FBM I610a, I610b. Description – Filippova and Panova 1989: 419–421 (female, larva; male unknown) (Filippova 2008).

### ***Ixodes trianguliceps* Birula, 1895**

*Ixodes trianguliceps* Birula, 1895: 358.
*Ixodes nivalis* Rondelli, 1928: 85; Pomerantsev 1950: 84.
*Ixodes tenuirostris* Neumann, 1901: 286.
*Endopalpiger heroldi* Schulze, 1939: 35; Černý 1959: 156.

**Recorded hosts. Mammalia:** *Alexandromys oeconomus* (Pallas) (tundra vole), *Apodemus agrarius* (Pallas) (striped field mouse) (dominates as the host in the Udel'ny forest park in St. Petersburg, according to Tretyakov (2009), *Apodemus flavicollis* (yellow-necked field mouse), *Apodemus sylvaticus* (Linnaeus) (wood mouse), *Apodemus uralensis* Pallas (Ural field mouse), *Arvicola amphibius* (Linnaeus) (European water vole), *Chionomys gud* (Caucasian snow vole), *Chionomys nivalis* (European snow vole), *Craseomys rufocanus* (Sundevall) (grey red-backed vole), *Cricetus cricetus* (Linnaeus) (European hamster), *Crocidura leucodon* (Hermann) (bicolored shrew), *Crocidura suaveolens* (Pallas) (lesser white-toothed shrew), *Eutamias sibiricus* (Laxmann) (Siberian chipmunk), *Lasiopodomys gregalis* (Pallas) (narrow-headed vole), *Lepus europaeus* Pallas (European hare), *Lepus timidus* Linnaeus (mountain hare), *Micromys minutus* (Pallas) (harvest mouse), *Microtus agrestris* (Linnaeus) (short-tailed field vole), *Microtus arvalis* (Pallas) (common vole), *Microtus majori* (Thomas) (Major's pine vole), *Microtus socialis* (Pallas) (social vole), *Microtus subterraneus* (de Selys-Longchamps) (European pine vole), *Mus musculus* Linnaeus (house mouse), *Mustela nivalis* Linnaeus (least weasel), *Myodes glareolus* (Schreber) (bank vole), *Myodes rutilus* (Pallas) (northern red-backed vole), *Myopus schisticolor* (Lilljeborg) (wood lemming), *Neomys anomalus* Cabrera (Mediterranean water shrew) (Filippova 1977), *Neomys fodiens* (Pennant) (Eurasian water shrew) (Lutta 1968), *Nyctalus noctula* (common noctule), *Ochotona alpina* (Pallas) (alpine pika), *Prometheomys schaposchnikowi* Satunin (long-clawed mole vole), *Rattus norvegicus* (Berkenhout) (brown rat), *Sciurus vulgaris* Linnaeus (red squirrel), *Sicista betulina* Pallas (northern birch mouse), *Sorex araneus* Linnaeus (common shrew), *Sorex caecutiens* Laxmann (Laxmann's shrew), *Sorex daphaenodon* Thomas (Siberian large-toothed shrew) (Filippova 1977), *Sorex isodon* Turov (taiga shrew) (Sapegina 1980), *Sorex minutus* Linnaeus (Eurasian pygmy shrew), *Sorex minutissimus* Zimmermann (Eurasian least shrew) (Filippova 1977), *Sorex roboratus* Hollister (flat-skulled shrew)

(Shtilmark 1963; Sapegina 1980), *Spermophilus suslicus* (Güldenstädt) (speckled ground squirrel), *Vulpes vulpes* (Linnaeus) (red fox) (Filippova 1977).

**Aves:** *Anthus trivialis* (Linnaeus) (tree pipit), *Carduelis carduelis* (Linnaeus) (European goldfinch), *Dendrocopos major* (Linnaeus) (great spotted woodpecker), *Emberiza citronella* Linnaeus (yellowhammer), *Nucifraga caryocatactes* (Linnaeus) (Eurasian nutcracker), *Strix uralensis* Pallas (Ural owl), *Turdus viscivorus* Linnaeus (mistle thrush) (Filippova 1977).

**Reptilia:** *Zootoca vivipara* (viviparous lizard) (Lichtenstein) (Filippova 1977).

**Recorded locations (Fig. 5). Russia:** North Karelia – Cape Kartesh (Stanyukovich and Fedorov 2022); Karelia (Lutta 1968) including the village Malaya Gomselga (southern Karelia) (Bespyatova and Bugmyrin 2015; Bespyatova et al. 2019), St. Petersburg (Tretyakov 2009), Leningrad Oblast (Sukhomlinova 1977), Novgorod Oblast (Grigoryeva and Tretyakov 1998), Pskov Oblast – the village Gogolevo (own data, unpublished), Kaliningrad Oblast, the Vistula Spit (own data, unpublished); Tver Oblast (Schipanov and Makhanko 2018), Tula Oblast (Kozlova et al. 2014), Perm Oblast (Korenberg et al. 2015), Eastern Upper Volga (Egorov et al. 2016), Krasnodar Krai and the Caucasus (Shatas 1957; Filippova and Stekol'nikov 2007), Kurgan Oblast (Starikov and Starikova 2021), Tyumen Oblast (Bragina et al. 2013), Omsk Oblast (Rar et al. 2014, 2020), Kemerovo Oblast (Kovalevsky et al. 2018), Western Sayan (Shtilmark 1963), Eastern Sayan (Schluger 1961), Khamar-Daban ridge (Vershinina 1988). **Belarus** (Arzamasov 1963). **Ukraine:** Crimea (Filippova 2010), Polesia (Podobivskyi and Fedonyuk 2017). **Moldova:** north and central Moldova (Uspenskaya et al. 2006). **Georgia:** the village Bakuriani and the Roki Tunnel (Djaparidze 1960). **Armenia:** the whole territory (Ogandzhanyan 1960). **Azerbaijan:** the south of the country (Ogandzhanyan 1960).

**Ecology and other information.** *Ixodes trianguliceps* Birula has a wide geographical distribution in the Palaearctic region, occurring from the coast of Lake

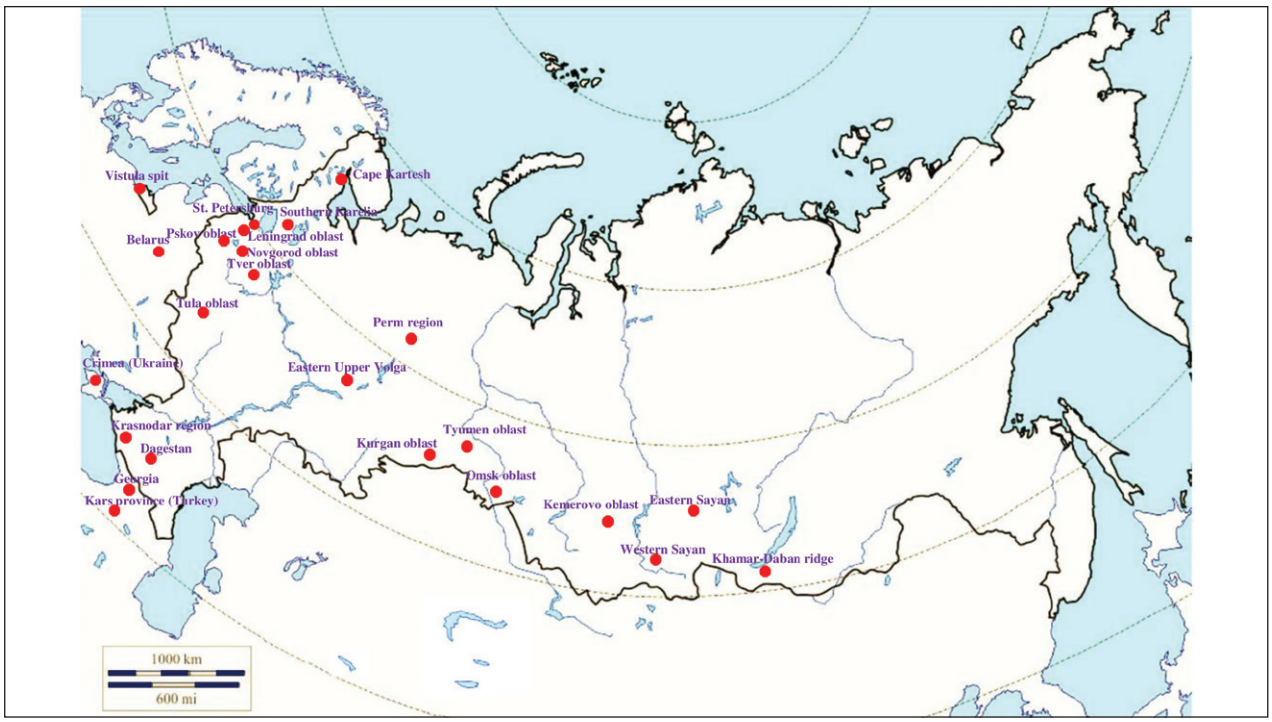


**Figure 5.** Map of Russia and neighboring countries showing the locations where *Ixodes trianguliceps* was reported.

Baikal to Western Europe (Filippova 2010; Estrada-Peña et al. 2018). In the north it reaches northern Karelia and the Scandinavian Peninsula (Fedorov and Leonovich 2021). Also, an isolated southern population of this species was found in the Crimean Peninsula (Filippova 2010) although in other parts of Ukraine it is present in forest zones, such as Polesia (Podobivskyi and Fedonyuk 2017).

The population that was supposed to be isolated in the mountain systems of the Caucasus (Filippova 2010) now seems to be more expanded, as proved by the recent finding in Turkey (Bolu and Kars province, the north of Turkey) (Keskin and Selçuk 2021). The Kars province is located near the border with Georgia, where this species was known before (Djaparidze 1960) and, therefore, the ticks reported from there are probably part of the same Caucasian population.

The map of findings of this tick species in Russia clearly illustrates that it lives in a broad range of forest biotopes throughout a vast territory including the zonal and mountain deciduous and mixed forest of the European type and forests of southern and middle-taiga types. Along the southern border of the largest part of the range in Russia, *I. trianguliceps* occurs in the forest-steppe zone, populating shrubby and forested biotopes. This distinctly correlates with the main habitats of shrews and rodents, because the presence of these small mammals together with well-developed soil litter, plays an important role in the abundance of ticks in the landscape, as it is known that shrews of the genus *Sorex* are the most preferable host for larvae (Randolph 1975).

Interestingly, *I. triangulipeps* was also reported from two bat species (*Myotis myotis* in Poland (Siuda et al. 2009) and *Nyctalus noctula* in Russia, as well as several bird species and one reptile species (Filippova 1977). These animals are non-typical and occasional hosts for this tick species. The single cases of parasitism on these host species can be a clear indication that *I. trianguliceps* is predominantly an exophilic species, because it is unlikely that ticks could contact bats and birds in a burrow. Findings of this tick species in micropores of burrow tunnels in Belarus in winter (Arzamasov 1963) demonstrate only the ability of its larvae to remain active even during winter.

Phylogenetic trees inferred from the concatenated nucleotide sequences of 10 protein-coding genes of the mitochondrial genome of *I. trianguliceps*, together with consideration of its morphology, justified to establish the new subgenus *Filippoviella* and include there *I. trianguliceps* together with aforementioned *I. ghilarovi* (Apanaskevich et al. 2024) both of which used to belong to the subgenus *Exopalpiger*.

**Subgenus *Ixodes* Latreille, 1795: 179**

***Ixodes apronophorus* Schulze, 1924**

*Ixodes apronophorus* Schulze, 1924: 281.
*Ixodes arvicolae* Warburton, 1926: 55; Morel and Pérez 1978: 201.
*Ixodes arvalis* Karpov & Popov, 1944: 75; Morel and Pérez 1978: 201.
*Ixodes dorrien-smilhi* Turk: Morel and Pérez 1978: 201.
*Ixodes dorriensmithi* Turk: Morel and Pérez 1978: 201.

**Recorded hosts. Mammalia:** *Alexandromys oeconomus* (tundra vole), *Apodemus agrarius* (striped field mouse), *Apodemus flavicollis* (yellow-necked field mouse),

*Apodemus sylvaticus* (wood mouse), *Arvicola amphibius* (European water vole), *Cricetus cricetus* (European hamster), *Craseomys rufocanus* (grey red-backed vole), *Erinaceus europaeus* Linnaeus (European hedgehog), *Eutamias sibiricus* (Siberian chipmunk), *Lasiopodomys gregalis* (narrow-headed vole), *Lepus timidus* (mountain hare), *Micromys minutus* (Eurasian harvest mouse), *Microtus arvalis* (common vole), *Microtus agrestis* (Linnaeus) (short-tailed field vole), *Mus musculus* (house mouse), *Mustela nivalis* (least weasel), *Mustela sibirica* Pallas (Siberian weasel), *Myodes glareolus* (bank vole), *Myodes rutilus* (northern red-backed vole), *Myopus schisticolor* (wood lemming), *Neomys fodiens* (Eurasian water shrew), *Nothocricetulus migratorius* (grey dwarf hamster), *Ondatra zibethicus* (Linnaeus) (muskrat), *Rattus rattus* (Linnaeus) (black rat), *Sicista betulina* (northern birch mouse), *Sorex araneus* (common shrew), *Sorex caecutiens* (Laxmann's shrew), *Sorex daphaenodon* (Siberian large-toothed shrew), *Sorex isodon* (taiga shrew), *Sorex minutus* (Eurasian pygmy shrew), *Sorex roboratus* (flat-skulled shrew), *Talpa europaea* Linnaeus (European mole), *Vulpes vulpes* (red fox) (Filippova 1977).

**Aves:** *Anas crecca* Linnaeus (Eurasian teal) (Adamovich 1968), *Gallinula chloropus* (Linnaeus) (common moorhen) (Filippova 1977), *Motacilla alba* (white wagtail), *Turdus merula* Linnaeus (common blackbird) (Adamovich 1968).

**Recorded locations (Fig. 6). Russia:** Arkhangelsk Oblast (Olenev 1931a), Karelia (Lutta 1976), Saint-Petersburg (Tretyakov 2009), Leningrad Oblast (Sukhomlinova 1977), Vologda Oblast, Tver Oblast (Filippova 1977; Belova et al. 2008), Moscow Oblast (Mosolov 1961), the whole territory of the Upper-Volga (Egorov et al. 2016), Samara Oblast (Kirillova and Kirillov 2008a), Bryansk Oblast (Adamovich 1968), Voronezh Oblast, Nyzhny Novgorod Oblast (Solovyov 1966), Chuvash Republic (Petrov et al. 1967), Krasnodar Krai (Kalita and Pelipeychenko 1957; Shevchenko et al. 1960), Kabardino-Balkaria (Bittirova et al. 2019), Dagestan (Aliev et al. 2012), Perm Krai, Chelyabinsk Oblast (Filippova 1958a),


**Figure 6.** Map of Russia and neighboring countries showing the locations where *Ixodes apronophorus* was reported.

Ekaterinburg (Chernousova and Tolkachyov 2009), Omsk Oblast (Znamenskiy district and Bolsheukov district) (Sabitova et al. 2023), Khanty-Mansiysk (Popov 1967), Surgut (Petukhov et al. 2018), Novosibirsk Oblast (Novosibirsk and Toguchinsky District) (Mal'kova and Bogdanov 2004), Tyumen Oblast – Nyzhnevartovsk (Starikov et al. 2017a), Kurgan Oblast (Starikov and Starikova 2021), Salekhard (Starikov et al. 2017a), Tomsk Oblast (Chainsky District) (Mal'kova and Bogdanov 2004), Kemerovo Oblast, Altai Krai, Altai Republic (Bogdanov and Yakimenko 2016), Krasnoyarsk Krai – Podkamennaya Tunguska River and the rural locality Bolshoy Kemchug (Voltsyt 1997). **Ukraine:** Volyn Polesie (Adamovich 1968), outskirts of Kyiv (Akimov and Nebogatkin 2013), Cherkassy Oblast (Nikitchenko 2011), the North-Western seacoast of the Black Sea (Rusev 2009). **Belarus:** throughout the whole territory (Subbotina and Osmolovsky 2022). **Moldova:** reedbeds of the lower reaches of the Prut River (Uspenskaya et al. 1984). **Kazakhstan:** Jambyl Region (Galuzo 1950), Jetisu Region – outskirts of Taldykorgan and Jarkent, Almaty Region – outskirts of Sarkand and Almaty (Golov 1933; Sorokoumov 1937; Ushakova and Fedosenko 1972; Ushakova et al. 1976). **Kyrgyastan:** outskirts of Bishkek, Tokmak Reserve (Grebenyuk 1966), Chuy Valley (Kharadov et al. 2013).

**Ecology and other information.** *Ixodes apronophorus* has a wide distribution in the Northern Palearctic from the Atlantic coast to Eastern Siberia. Its geographical range generally coincides with the distribution of the water vole, its most frequent host, as both the tick and its common host prefer swampy and humid places for living, especially near water bodies.

### *Ixodes eldaricus* Djaparidze, 1950

*Ixodes eldaricus* Dzhaparidze, 1950: 117.
*Ixodes tatei* Arthur, 1959: 108; Clifford et al. 1973: 489.

**Recorded hosts. Aves:** *Alectoris chukar* (Gray) (chukar partridge), *Anthus campestris* (Linnaeus) (tawny pipit), *Athene noctua* (Scopoli) (little owl), *Chroicocephalus ridibundus* (Linnaeus) (black-headed gull), *Coccothraustes coccothraustes* (Linnaeus) (hawfinch), *Coloeus monedula* (Linnaeus) (western jackdaw), *Curruca communis* (Latham) (common whitethroat), *Emberiza bruniceps* Brandt (red-headed bunting), *Galerida cristata* (Linnaeus) (crested lark), *Lullula arborea* (Linnaeus) (woodlark), *Luscinia svecica* (Linnaeus) (bluethroat), *Melanocorypha bimaculata* (Ménétrés) (bimaculated lark), *Monticola solitarius* (Linnaeus) (blue rock thrush), *Oenanthe* sp. (wheatear), *Passer domesticus* (Linnaeus) (house sparrow), *Perdix perdix* (grey partridge), *Petronia petronia* (Linnaeus) (rock sparrow), *Phoenicurus erythronotus* (Eversmann) (Eversmann's redstart), *Phylloscopus griseolus* (Blyth) (sulphur-bellied warbler), *Pica pica* (Linnaeus) (Eurasian magpie), *Sitta tephronota* Sharpe (Eastern rock nuthatch), *Turdus merula* (common blackbird) (Filippova 1977).

**Mammalia:** *Crocidura leucodon* (bicolored shrew), *Meriones persicus* (Blanford) (Persian jird), *Mus musculus* (house mouse), *Nesokia indica* (Gray) (short-tailed bandicoot rat), grey dwarf hamster *Nothocricetulus migratorius* (Pallas), *Rattus pyctoris* (Hodgson) (Turkestan rat), *Rhinolophus mehelyi* (Mehely's horseshoe bat) (Filippova 1977).

**Recorded locations (Fig. 7). Russia:** Dagestan and North Osetia-Alania (Shatas 1957; Filippova 1977). **Ukraine:** Crimean Peninsula, in particular the Tarkhankut Peninsula and the Kara Dag (Filippova 1974). **Georgia:** the Shiraki Plain and the Vashlovani Nature Reserve (Djaparidze 1950, 1960). **Armenia:** Vayots Dzor Province – the rural locality Herher (Ogandzhanyan 1959). **Azerbaijan:** Karabakh Plateau – Lachin District and Hadrut District, Adzhynokhur Steppe (Ogandzhanyan 1959; Filippova 1977). **Kazakhstan:** Dzungarian Alatau (Ushakova et al. 1976) and Trans-Ili Alatau (Filippova 1977). **Kyrgyzstan:** Terskey Ala-too Range (Filippova 1974). **Turkmenistan:** the Kopet Dagh – the valley of the Chandyr River, Magtymguly, Gökdepe District, outskirts of Ashgabad, Köytendag Range, Bayramaly (Kerbabaev 1960; Kochkareva et al. 1971; Berdyev 1973; Scherbinina 1973). **Uzbekistan:** Termez (Filippova 1977). **Tajikistan:** Hisar Range, Varzob gorge, outskirts of Dushanbe (Filippova 1977).

**Ecology and other information.** *Ixodes eldaricus* is a little studied endophilic tick species which is mainly a parasite of ground-feeding birds although nymphs and larvae, besides birds, were also found on small mammals – rodents and shrews. It usually inhabits deciduous mountain forests and shrub thickets in mountain river valleys. The vertical distribution range of its occurrence varies from 300 (Ashgabat) to 1800 m (Terskey Ala-too Range and Hisar Range) a. s. l. (Filippova 1977).

Briefly described by a female from the east of Georgia (type locality: the Shiraki Plain), *I. eldaricus* was later found in Armenia and Azerbaijan, and the male, nymph descriptions were based on the material from Azerbaijan (Ogandzhanyan 1959). The holotype female described from the grey partridge is stored at the Institute of Zoology of Ilia State University. The above findings from post-Soviet territories are known from the Crimea, as well as the Causasus and Central Asia. The majority of samples are stored at the collection of the Zoological Institute of the Russian Academy of Sciences.


**Figure 7.** Map of Russia and neighboring countries showing the locations where *Ixodes eldaricus* was reported.

Additionally, it is important to note that in Crimea this tick species is considered disappearing (Nebogatkin 1998) due to anthropogenic pressure followed by destruction of its habitats and decline in its host populations (Uspensky 2021).

### *Ixodes kashmiricus* Pomerantsev, 1948

*Ixodes kaschmiricus* Pomerantsev, 1948: 132; Filippova 1969: 675.
*Ixodes persulcatus kaschmiricus* Pomerantsev, 1948: 132; Filippova 1969: 675.

**Recorded hosts. Mammalia:** *Apodemus sylvaticus* (wood mouse), *Canis familiaris* Linnaeus (dog), *Ovis aries* Linnaeus (sheep) (Filippova 1977).

**Recorded locations (Fig. 8). Kyrgyzstan:** the Tien Shan – northern and eastern slopes of the Terskey Ala-too range (gorges Ulken-Kokpak and Chon-Dzhargylchak) (Filippova 1969).

**Ecology and other information.** *Ixodes kashmiricus* is a tick species with a disjunctive relict range limited by the Tien Shan in Kyrgyzstan as well as India (Filippova 1977) and Pakistan (Numan et al. 2022). In Kyrgyzstan the tick was found mainly in the mid-altitude vertical zone of the mountains at the lower border of the forest at the altitude of 2000 and 2500 m a. s. l. Cases of parasitism on humans have been recorded (Hoogstraal 1970).

Phylogenetic analysis of mitochondrial and nuclear genes showed that *I. kashmiricus* belongs to the *I. ricinus* group (Kovalev et al. 2018) and clusters with such members of the *I. ricinus* group as *I. apronophorus* and *I. kazakstani* (Numan et al. 2022).

The type specimens are stored at the Zoological Institute of the Russian Academy of Sciences and include the lectotype - female; [India], Kashmir,


**Figure 8.** Map of Russia and neighboring countries showing the locations where *Ixodes kashmiricus* was reported.

Vardvan Maru River, northern tributary of Chinab River, 10–13. V.1910, coll. S.P. Trubetskoi; AL I533, as well as the paralectotype - male; AL 533a. *Ixodes kashmiricus* (see: Filippova 1969: 677). Description – Filippova 1977: 292–296 (female, male, nymph, larva) (Filippova 2008). Originally the tick was named *I. persulcatus kaschmiricus* (lapsus).

### *Ixodes kazakstani* Olenev & Sorokoumov, 1934

**Recoeded hosts. Mammalia:** *Apodemus sylvaticus* (wood mouse) (Filippova 1977), *Canis familiaris* (domestic dog) (Kovalev et al. 2018), *Dryomys nitedula* (Pallas) (forest dormouse), *Lepus tolai* Pallas (tolai hare), *Mus musculus* (house mouse), *Nothocricetulus migratorius* (grey dwarf hamster) (Filippova 1977).

**Aves:** *Phasianus colchicus* Linnaeus (common pheasant) (Filippova 1977).

**Recorded locations (Fig. 9). Kazakhstan:** Betpak-Dala – the valley of the Chu River (Ushakova 1961), Tian Shan – the valley of the Ili River (Ushakova 1958; Kovalev et al. 2018), outskirts of Jarkent (Olenev and Sorokoumov 1934; Pomerantsev 1950). **Kyrgyzstan:** the Issyk-Kul basin (Filippova 1958b; Kovalev et al. 2018), the valley of the Talas River (Olenev and Sorokoumov 1934; Pomerantsev 1950; Grebenyuk 1966; Lyashko 1973; Kovalev et al. 2018).

**Ecology and other information.** *Ixodes kazakstani* is a tick species with a disjunctive relict range limited by Southeastern Kazakhstan and neighboring territories of Kyrgyzstan (Filippova 1977). The patchy arrangement of its range can be explained, above all, by associations of this tick mainly with the animals dwelling in tugai forests which also create humidity conditions in the soil suitable for this tick species (Filippova 1958b). Also, there are some cases of parasitism on livestock and humans (Lyashko 1973; Filippova 1977). On livestock it was found in few numbers among mass parasitism of other tick species.


**Figure 9.** Map of Russia and neighboring countries showing the locations where *Ixodes kazakstani* was reported.

Phylogenetic analysis of mitochondrial and nuclear genes showed that *I. kazakstani* belongs to the *I. ricinus* group (Kovalev et al. 2018) and clusters with such members of the *I. ricinus* group as *I. apronophorus* and *I. kashmiricus* (Numan et al. 2022). *Ixodes kazakstani* can presumably exemplify links between Nearctic and Palearctic species, so further studies of genetic sequences of *I. kazakstani* are necessary to understand better evolutionary connections between more tick species in the *I. ricinus* group.

The type specimens are stored at the Zoological Institute of the Russian Academy of Sciences and include the holotype: female; Kazakhstan, Jarkent, collected from human dress, 20.VI.1932, coll. Kirin; AL I536. Description - Filippova 1977: 283–290 (female, male, nymph, larva) (Filippova 2008).

### *Ixodes laguri* Olenev, 1929

*Ixodes laguri* Olenev, 1929a: 489.
*Ixodes redikorzevi lagurae* Olenev: Olenev 1931b: 62.
*Ixodes laguri armeniacus* Kirshenblat, 1938: 46; Morel and Pérez 1978: 201.
*Ixodes laguri colchicus* Pomerantsev, 1946: 1; Morel and Pérez 1978: 201.
*Ixodes laguri slovacicus* Cerny, 1960: 178; Morel and Pérez 1978: 201.

**Recorded hosts. Mammalia:** *Allactaga major* (Kerr) (great jerboa), *Allocricetulus eversmanni* (Brandt) (Eversmann's hamster), *Apodemus sylvaticus* (wood mouse), *Chionomys nivalis* (European snow vole), *Cricetus cricetus* (European hamster), *Dryomys nitedula* (forest dormouse), *Ellobius talpinus* (Pallas) (northern mole vole), *Erinaceus europaeus* (European hedgehog), *Glis glis* (Linnaeus) (European edible dormouse), *Hemiechinus auratus* (Gmelin) (long-eared hedgehog), *Lagurus lagurus* (Pallas) (steppe lemming), *Marmota bobak* (Müller) (bobak marmot), *Martes martes* (Linnaeus) (European pine marten), *Microtus arvalis* (common vole), *Microtus socialis* (social vole), *Meles meles* (Linnaeus) (European badger), *Meriones meridianus* (Pallas) (midday jird), *Mesocricetus brandti* (Pallas) (Turkish hamster), *Mesocricetus raddei* (Nehring) (Ciscaucasian hamster), *Mus musculus* (house mouse), *Mustela eversmanii* (Lesson) (steppe polecat), *Mustela nivalis* (least weasel), *Nothocricetulus migratorius* (grey dwarf hamster), *Pygeretmus pumilio* (Kerr) (dwarf fat-tailed jerboa), *Rattus rattus* (black rat), *Spalax microphthalmos* Gueldenstaedt (greater blind mole-rat), *Spermophilus citellus* (Linnaeus) (European ground squirrel), *Spermophilus fulvus* (Lichtenstein) (yellow ground squirrel), *Spermophilus pygmaeus* (Pallas) (little ground squirrel), *Spermophilus suslicus* (speckled ground squirrel), *Spermophilus xanthoprymnus* (Bennett) (Asia Minor ground squirrel), *Stylodipus telum* (Lichtenstein) (thick-tailed three-toed jerboa), *Vormela peregusna* (Güldenstädt) (marbled polecat), *Vulpes corsac* (Linnaeus) (Corsac fox), *Vulpes vulpes* (red fox) (Filippova 1977).

**Recorded locations (Fig. 10). Russia:** Samara Oblast (Kirillova and Kirillov 2008b), Rostov Oblast (Stakheev and Panasyuk 2016), Krasnodar Krai (Popov et al. 2019), Stavropol Krai (Tsapko 2019), Volgograd Oblast, Astrakhan Oblast (Nelzina et al. 1955), Kalmyk Republic (Sandzhiev et al. 2006), Chechnya (Baisarova 2021), Dagestan (Musaev et al. 2019) and North Osetia-Alania (Filippova 1977). **Ukraine:** Kyiv (Omeri and Moysak 2013), Odesa Oblast (Rusev 2008), Kherson Oblast, Chernivtsi Oblast, Ternopil Oblast, Luhansk Oblast, Donetsk


**Figure 10.** Map of Russia and neighboring countries showing the locations where *Ixodes laguri* was reported.

Oblast, the Crimean Peninsula, particularly in the Syvash (Filippova 1958a; Emchuk 1960; Sklyar 1970; Andryushchenko et al. 2005; Evstafiev 2017). **Moldova:** Bălți Steppe, Bugeac Steppe (Filippova 1977) and Tiraspol (Kravchenko 2014). **Georgia:** Abkhazia (Shaposhnikova and Sakhno 2012), Imereti (Sukhiashvili et al. 2020), Lagodekhi Nature Reserve (Djaparidze 1960). **Armenia:** Lori Province –Nalband and the valley of the river Hrazdan (Filippova 1977). **Azerbaijan:** Talysh (Pomerantsev 1950), the Nakhchivan Autonomous Republic – the Zangezur Mountains (Kadatskaya and Shirova 1963; Filippova 1977). **Kazakhstan:** West Kazakhstan Region (Pomerantsev 1950; Levit 1957; Filippova 1977), Kyzylorda Region (Loseva 1963), Kostanay Region, Akmola Region (Ushakova 1961, 1962). **Turkmenistan:** the Kopet Dagh (Kerbabaev 1961).

**Ecology and other information.** *Ixodes laguri* is a tick species which is mainly a nidicolous parasite of rodents and small and medium carnivores, first of all ground squirrels. It is present usually in zonal and mountainous steppes at the altitude of 1500 m a.s.l. This tick species is less common in desert and semi-desert biotopes (Filippova 1977).

Filippova (1977) states that the tick has four subspecies – *I. laguri laguri*, *I. l. armeniacus*, *I. l. colchicus* and *I. l. slovacicus*. The differential characters of the female and the male of *I. l. slovacicus* are based on comparison with characters of the other subspecies in Pomerantsev (1950) but some of them, such as the genital aperture and chaetotaxy of the scutum and the hypostome and the coxa 1, are not characterized precisely enough (Filippova 1977).

According to Filippova (1977), *I. laguri laguri* can be found in Moldova, Ukraine, Kazakhstan, as well as in the south of Russia; *I. l. armeniacus* is distributed in the Caucasus – North Osetia-Alania, Dagestan, Georgia, Armenia and Azerbaijan; *I. l. colchicus* is known from the western spurs of the Greater Caucasus, the now abandoned rural locality Babuk-Aul; *I. l. slovacicus* was described from the south-east of Slovakia.

The type specimens of *I. laguri* are deposited at the Zoological Institute of the Russian Academy of Sciences and include *I. l. armeniacus*: the lectotype, female; Armenia, Nalband, from *Mesocricetus brandti* Nehr., 9.9.1936; AL I558 and the paralectotype, male; AL I556, description – Filippova 1977: 384 (female, male, nymph; larva unknown). (Filippova 2008), as well as *I. l. colchicus*: the lectotype, male; Western Caucasus, near Babuk-Aul, *Glis glis* L., 30.9.1935, coll. V. K. Popov, det. B. Pomerantsev: *I. l. colchicus*, type; AL I554a; paralectotypes: 2 females; AL I554a, description – Filippova 1977: 384 (female, male; nymph and larva unknown) (Filippova 2008).

### *Ixodes nipponensis* Kitaoka & Saito, 1967

**Recorded hosts. Mammalia:** *Apodemus agrarius* (striped field mouse), *Craseomys rufocanus* (grey red-backed vole), *Microtus fortis* (Büchner) (reed vole), *Myodes rutilus* (northern red-backed vole) (Filippova 1977).

**Recorded locations (Fig. 11). Russia:** Primorsky Krai – the Lake Khasan, the Poyma River, the Partizansky District, outskirts of urban localities Posyet, Kraskino, Slavyanka and cities Vladivostok and Nakhodka, near the village Rechitsa (Filippova 1969; Filippova and Belyaev 1970; Allenov et al. 2015).

**Ecology and other information.** *Ixodes nipponensis* is a tick species found in Russia in the south and south-west of the Primorsky Krai and also in the Korean peninsula and Japan (Filippova 1977). In Russia it was reported mainly from murine rodents, although in the Republic of Korea it was also observed on lizards (Kim et al. 2018) and cattle, goats, dogs, horses, and birds in Japan (Kitaoka and Saito 1967; Yamaguti et al. 1971).


**Figure 11.** Map of Russia and neighboring countries showing the locations where *Ixodes nipponensis* was reported.

Multiple cases of parasitism on humans have been recorded (Nakatsukase and Hatsushika 1985; Paik et al. 1989; Cho et al. 1995; Chu et al. 1997; Ryu et al. 1998; Ko et al. 2002).

### *Ixodes occultus* Pomerantsev, 1946

**Recorded hosts. Mammalia:** *Crocidura suaveolens* (lesser white-toothed shrew), *Diplomesodon pulchellum* (Lichtenstein) (piebald shrew), *Meriones libycus* Lichtenstein (Libyan jird), *Meriones meridianus* (midday jird), *Meriones persicus* (Persian jird), *Mustela nivalis* (least weasel), *Nothocricetulus migratorius* (grey dwarf hamster), *Rhombomys opimus* (Lichtenstein) (great gerbil), *Spermophilopsis leptodactylus* (Lichtenstein) (long-clawed ground squirrel), *Vormela peregusna* (marbled polecat) (Filippova 1977).

**Reptilia:** *Gloydius halys* (Pallas) (Halys pit viper) (Filippova 1977).

**Recorded locations (Fig. 12). Kazakhstan:** Mangystau Region – the Mangyshlak Peninsula (Kaluzhenkova et al. 1961) and the Ustyurt Plateau; Kyzylorda Region (Filippova 1958a; Loseva 1963; Maslennikova and Ushakova 1971), Jambyl Region – the Moiynkum Desert (Maslennikova and Ushakova 1971), Almaty Region – the foothills of the Dzungarian Alatau: the Sholak and Katutau mountains, the deserts Taukum and Saryesik-Atyrau (Ushakova 1960; Maslennikova et al. 1964; Ushakova et al. 1976). **Turkmenistan:** distributed everywhere – the southern Ustyurt, the Octumkumy Desert, the Üňüzaňyrsy and Türkmenbaşy Plateau, the Meshed and Saynaksan Desert, the Karakum Desert (Pomerantsev 1950; Kerbabaev 1961; Kochkareva et al. 1971); Hojagala (Berdyev and Annaev 1997). **Uzbekistan:** the Pistalitau Ridge and the rural locality Tashrabat (Maslennikova and Ushakova 1971).


**Figure 12.** Map of Russia and neighboring countries showing the locations where *Ixodes occultus* was reported.

**Ecology and other information.** *Ixodes occultus* is a tick species inhabiting deserts. It is mainly a nidicolous parasite of gerbils and jirds (subfamily Gerbillinae), first of all, the great gerbil, as well as of those small mammals which also use long and deep burrows of great gerbils as shelters (Filippova 1977). Some predators which have strong trophic relationships with gerbils and regularly contact with their colonies act as secondary hosts for this tick species.

The type specimen of *I. occultus* is deposited at the Zoological Institute of the Russian Academy of Sciences and includes the holotype: male; Turkmenia, Repetek, *Rhombomys opimus*, 5.10.1937, coll. B.I. Pomerantsev, type; AL I550. Description – Filippova 1977: 365–371 (female, male, nymph, larva) (Filippova 2008).

### *Ixodes pavlovskyi* Pomerantsev, 1946

**Recorded hosts. Aves:** *Acrocephalus dumetorum* Blyth (Blyth's reed warbler), *Acrocephalus schoenobaenus* (Linnaeus) (sedge warbler), *Anas platyrhynchos* Linnaeus (mallard), *Anthus trivialis* (tree pipit), *Calliope calliope* (Pallas) (Siberian rubythroat), *Carduelis carduelis* (European goldfinch), *Carpodacus erythrinus* (Pallas) (common rosefinch), *Chloris chloris* (Linnaeus) (European greenfinch) *Columba livia* Gmelin (rock dove), *Corvus cornix* Linnaeus (hooded crow), *Corvus corone* Linnaeus (carrion crow), *Coturnix coturnix* (Linnaeus) (common quail), *Crex crex* (Linnaeus) (corn crake), *Curruca communis* (Latham) (common whitethroat), *Curruca curruca* (Linnaeus) (lesser whitethroat), *Cyanopica cyanus* Pallas (azure-winged magpie), *Emberiza calandra* Linnaeus (corn bunting), *Emberiza citrinella* Linnaeus (yellowhammer), *Emberiza leucocephalos* Gmelin (pine bunting), *Emberiza spodocephala* Pallas (black-faced bunting), *Ficedula hypoleuca* (Pallas) (European pied flycatcher), *Fringilla coelebs* Linnaeus (Eurasian chaffinch), *Fringilla montifringilla* Linnaeus (brambling), *Lanius collurio* Linnaeus (red-backed shrike), *Locustella lanceolata* (Temminck) (lanceolated warbler), *Luscinia luscinia* (Linnaeus) (thrush nightingale), *Luscinia svecica* (Linnaeus) (bluethroat) *Parus major* Linnaeus (great tit), *Passer montanus* (Linnaeus) (Eurasian tree sparrow), *Pastor roseus* (Linnaeus) (rosy starling), *Phoenicurus phoenicurus* (Linnaeus) (common redstart), *Phylloscopus fuscatus* (Blyth) (dusky warbler), *Phylloscopus trochiloides* (Sundevall) (greenish warbler), *Pica pica* (Eurasian magpie), *Sitta europaea* Linnaeus (Eurasian nuthatch), *Sturnus vulgaris* Linnaeus (common starling), *Sylvia borin* (garden warbler), *Tetrao urogallus* (western capercaillie), *Tetrastes bonasia* (hazel grouse), *Turdus iliacus* Linnaeus (redwing), *Turdus philomelos* Brehm (song thrush), *Turdus pilaris* Linnaeus (fieldfare), *Turdus ruficollis* Pallas (red-throated thrush), *Turdus viscivorus* (mistle thrush) (Filippova 1977; Moskvitina et al. 2014).

**Mammalia:** *Alexandromys oeconomus* (tundra vole), *Apodemus agrarius* (striped field mouse), *Arvicola amphibius* (European water vole), *Craseomys rufocanus* (grey red-backed vole), *Cricetus cricetus* (European hamster), *Eutamias sibiricus* (Siberian chipmunk), *Lepus timidus* (mountain hare), *Microtus agrestis* (short-tailed field vole), *Microtus arvalis* (common vole), *Mus musculus* (house mouse), *Myodes glareolus* (bank vole), *Myodes rutilus* (northern red-backed vole), *Neomys fodiens* (Eurasian water shrew), *Nothocricetulus migratorius* (grey dwarf hamster), *Ochotona alpina* (Alpine pika), *Sciurus vulgaris* (red squirrel), *Sicista betulina* (northern birch mouse), *Sicista subtilis* (Pallas) (southern


**Figure 13.** Map of Russia and neighboring countries showing the locations where *Ixodes pavlovskyi* was reported.

birch mouse), *Sorex araneus* (common shrew), *Sorex minutus* (Eurasian pygmy shrew), *Sorex roboratus* (flat-skulled shrew), *Stenocranius gregalis* (Pallas) (narrow-headed vole) (Filippova 1977).

**Recorded locations (Fig. 13). Russia:** Tomsk Oblast (Kovalev et al. 2015), Novosibirsk Oblast, Altai Republic (Tkachev et al. 2017), Altai Krai, Kemerovo Oblast, Krasnoyarsk Krai, Khakassia, northern spurs of the Western Sayan, Amur Oblast, Khabarovsk, Primorsky Krai – the Sikhote-Alin (Filippova 1969; Sapegina and Ravkin 1969; Filippova and Panova 1998), Russky Island (Nikitin et al. 2021). **Kazakhstan:** East Kazakhstan Region (Tkachev et al. 2017; Perfilyeva et al. 2020), Abai Region, Jetisu Region (Filippova 1977), Tarbagatai Mountains, Dzungarian Alatau, Küngöy Ala-Too Range (Ushakova et al. 1976; Filippova and Panova 1998). **Kyrgyzstan:** Küngöy Ala-Too Range (Filippova and Panova 1998), Terskey Ala-too (Fedorova 2017).

**Ecology and other information.** *Ixodes pavlovskyi* is a tick species distributed in Western Siberia, the Far East, Eastern Kazakhstan, and Kyrgyzstan (Filippova 1977; Fedorova 2017), as well as in China (Guo et el. 2016) and Japan (Nakao et al. 1992; Guglielmone et al. 2023). It more often prefers birds as hosts, as well as small mammals although some cases of human and livestock infestation are also recorded. Its preferred habitats include usually coniferous and deciduous forests, undergrowth, as well as motley grass (Filippova 1977).

Often it can be found in the same biotopes together with *I. persulcatus* with complete coincidence of the seasons of activity of both species at each ontogenetic stage (Filippova 1999) and where their hybridization can also occur (Kovalev et al. 2015; Rar et al. 2019).

In certain areas of Siberia *I. pavlovskyi* outnumbers *I. persulcatus* and also other tick species due to the high abundance of ground-feeding birds, especially in urban landscapes with habitats suitable for ticks like parks and cemeteries. So, for example, in the city of Tomsk in Western Siberia *I. pavlovskyi* dominates

everywhere in the city and its outskirts (Romanenko 2011). Probably eventually over time *I. persulcatus* was gradually replaced by *I. pavlovskyi* because it is too difficult for adult *I. persulcatus* to find its preferred hosts, namely mammals (Romanenko and Leonovich 2015).

Filippova and Panova (1998) recognize two subspecies in Russian populations of this tick, namely *I. pavlovskyi pavlovskyi* and *I. pavlovskyi occidentalis* which differentiation is based on morphological features between western and eastern specimens.

The type specimens of *I. pavlovskyi* are deposited at the Zoological Institute of the Russian Academy of Sciences and include *I. pavlovskyi*, Pomerantsev (Pomerantsev 1946: 11), the holotype: female; [Russia], DVK [Primorskii Terr.], Imanskii Forestry, hazel, 2.9.1932, type; AL I513. Description – Filippova 1977: 305–312 (female, male, nymph, larva); as well as *I. pavlovskyi* subsp. *occidentalis* (Filippova and Panova 1998: 396–411 – female, male, nymph, larva) the holotype: female; Russia, western foothills of Kuznetskii Ala Tau, basin of upper Tom River, environs of Mezhdurechensk, from vegetation, flagging, 24.5.1972, coll. E.D. Chigirik, det. N.A. Filippova; AL I1016 and finally *I. pavlovskyi* subsp. *pavlovskyi* (Filippova and Panova 1998: 396–411, female, male, nymph, larva), the holotype (the same as the holotype of the species): see *I. pavlovskyi* (Filippova 2008).

### ***Ixodes persulcatus* Schulze, 1930**

*Ixodes persulcatus* Schulze, 1930: 294.
*Ixodes ricinus miyazakiensis* Kishida: Morel and Pérez 1978: 201.
*Ixodes persulcatus diversipalpis* Schulze, 1930: 294; Pomerantsev 1950: 43.
*Ixodes persulcatus cornuatus* Olenev: Pomerantsev 1950: 43.
*Ixodes sachalinensis* Filippova: Kolonin 1981: 49.

**Recorded hosts.** The spectrum of hosts of *I. persulcatus* is extremely broad both systematically and ecologically and includes more than 200 species of mammals and 100 species of birds (Shilova and Clabovskii 1968). Rarely it can parasitize reptiles – lizards of the family Lacertidae (Ravkin 1969). Literally almost all mammals and birds inhabiting various types of forests and their derivative biotopes can act as hosts for *I. persulcatus*. Larvae and nymphs parasitize more often small and medium-sized mammals, such as shrews, hedgehogs, rodents, and lagomorphs, as well as ground-feeding and ground-nesting birds. Adults usually feed on large and medium-sized mammals – ungulates, carnivores, lagomorphs. Humans and domestic animals can also be hosts for this tick species (Filippova 1977).

**Distribution in Russia and other post-Soviet countries (Fig. 14).** The range of *I. persulcatus*, like no other Palearctic species, is extended in the latitudinal direction by a continuous strip, covering a significant part of the taiga forest zone in Eurasia between 21°–66° latitude in the northern hemisphere from the Scandinavian Peninsula, the Baltic states, Belarus and Ukraine in the west where it is present sporadically to the east up to the Pacific coast including the Kamchatka Peninsula and the Sakhalin Island and further to the north-east of China, the Korean Peninsula and Japan (Filippova 1977; Wang et al. 2023). This tick belongs to the tick fauna of the next post-Soviet countries: Estonia, Latvia,

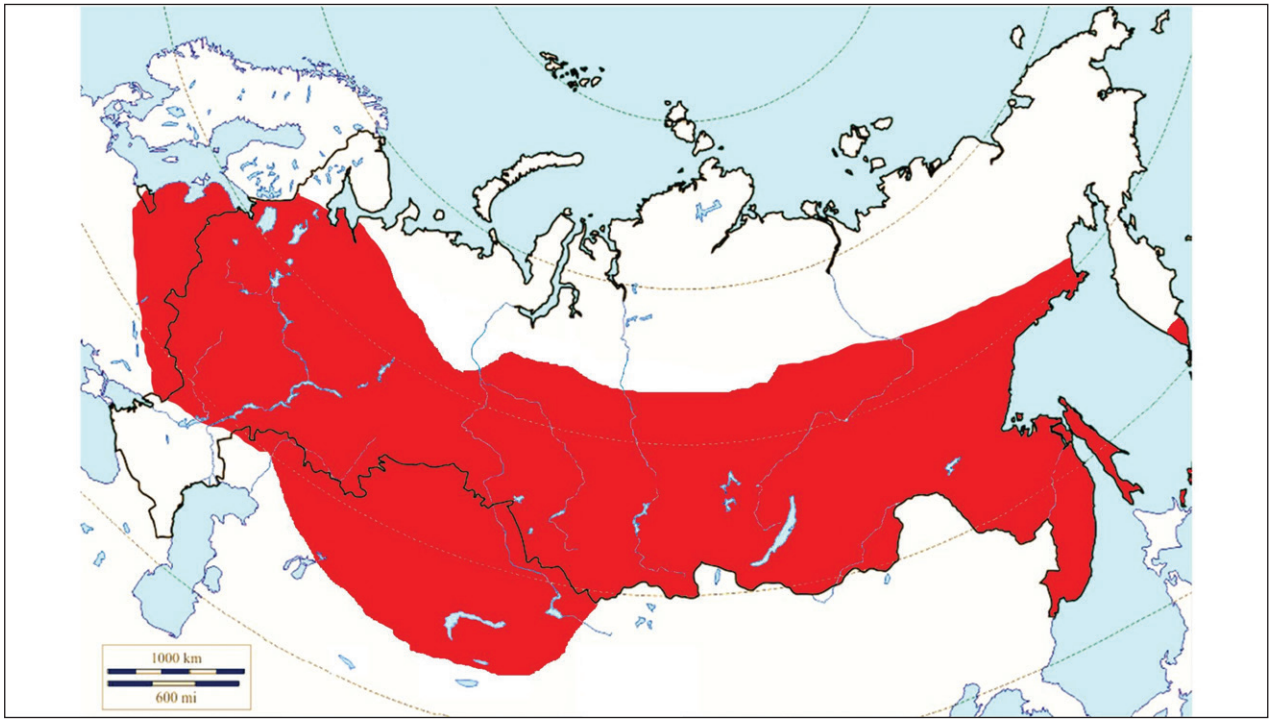


**Figure 14.** Map of Russia and neighboring countries showing the locations where *Ixodes persulcatus* was reported.

Lithuania, Belarus, Russia, Ukraine, Kazakhstan, Kyrgyzstan (Guglielmone et al. 2023). The presence of *I. persulcatus* in Ukraine outside the south-west border of the taiga was mentioned by Filippova (1977), although the possibility of permanent populations existing there was disputed by Nebogatkin (1993). Therefore, this probably exemplifies transportation by migratory birds.

**Ecology and other information.** *Ixodes persulcatus* is an exophilic tick species widely distributed in the northern Palearctic along the forest zone. It may use almost all mammals and birds living in its biotopes; therefore, it is one of the most important vectors of a broad range of tick-borne pathogens. Since it can also transmit tick-borne encephalitis virus, together with *I. ricinus* it has the greatest medical and veterinary significance among other ticks of the genus *Ixodes* in the Palearctic. Another important fact is that *I. persulcatus* is a very aggressive species toward humans (Uspensky 1993) and, therefore, this species represents especially high medical-epidemiological risks.

The most significant part of the range of *I. persulcatus* stretches across the territory of Russia where we can observe the full spectrum of biotopes where *I. persulcatus* can be found. There are a lot of published works about its ecology in different regions which depend on the climatic region and biotic-abiotic conditions in it.

This tick prefers various types of forest and forest-steppe biotopes, especially taiga forests and their derivatives, i.e., mixed forests and bushes (both plain and mountainous), up to 2000 m a.s.l., like in the Tian Shan. In other words, it can inhabit any herbaceous forest and forest-steppe biotope with the level of humidity high enough for reproduction and supporting the life cycle, even in urban landscapes (Filippova 1977). In the Dzungarian Alatau there were some observations of occurring in steppe regions bordering forests and parasitizing the unusual host, namely the grey marmot *Marmota baibacina* Kastschenko (Bibikov et al. 1961). Permanent and stable populations of *I. persulcatus* exist in some areas adjacent

to cities within its range and even inside these cities on condition that the the suitable forest environment together with hosts, such as wild animals of different sizes and stray dogs are present. Examples of such cities are Saint Petersburg, Petrozavodsk, Novosibirsk, Tomsk, Irkutsk, and Vladivostok (Uspensky 2017).

Several studies attest the changing boundaries of the ranges of *I. persulcatus*. It is assumed that ticks of the *I. presulcatus* group appeared and evolved in forest biotopes similar to modern relict forests of the Ussuri type and the taiga of the mountains of Southern Primorye, Southern Siberia, and the Korean Peninsula in the Pliocene. The wide ecological niche of *I. persulcatus* was formed during the formation of the species in the process of its adaptation to various landscape and climatic conditions. This allowed the species to gradually expand its range in the northwestern direction in the Holocene (Filippova 2017). An increase in air temperature by one or several degrees in a particular region near the boundaries of its range was probably the main driver of its expanding distribution. The fact of finding *I. presulcatus* populations in Sweden (Jaenson et al. 2016) and even in the Magadan Oblast in the north-east of Russia where it was absent before (Yamborko et al. 2015) are good examples of the distribution expansion in several directions and confirm the tendency which continues.

In Russia, high numbers of observations show noticeable changes in the distribution of *I. persulcatus* in certain regions. In Karelia the range expansion of *I. persulcatus* to the north is noted in relation to general climate warming (Bugmyrin et al. 2013). A similar observation was also recorded in the Komi Republic (Glushakova et al. 2011). The range expansion of this tick species in Arkhangelsk Oblast and Western and Central Siberia to the north is confirmed both by the results of their records and by the data on tick bites and morbidity in the human population, not only in places which were free from ticks before (Pogodina 2021). Besides that, there are some data about the range expansion of *I. persulcatus* to the north in the Republic of Sakha (Yakutia). The reasons causing these changes are under evaluation but climate change, anthropogenic pressure in natural landscapes as well as the number of vertebrate animals are among the most influential factors. At the same time, it is also possible that inadvertent dispersal of ticks by timber material transported from tick-infested areas may be in part responsible for this phenomenon (Danchinova et al. 2006). Although other factors are not excluded, it is believed that climate changes have made the greatest contribution to the increase in areas primarily for TBE foci in the northern regions of the country. But despite all this, as a result of the same changes, the southwestern part of the range of *I. persulcatus* in Belarus and the Baltic countries has decreased (Pogodina 2021).

Often it can be found in the same biotopes together with *I. ricinus* in Europe and *I. pavlovskyi* in Siberia with complete or partial coincidence of the seasonal activity of these species at each ontogenetic stage (Ushakova and Filippova 1968; Bolotin et al. 1977; Filippova 1999). In zones of sympatry their hybridization can occur, and their hybrids can also transmit tick-borne encephalitis virus and probably other pathogens (Kovalev et al. 2015; Rar et al. 2019; Belova et al. 2023). Under laboratory conditions, interspecific hybridization between *I. ricinus* and *I. persulcatus* was successfully conducted as well. F1 hybrid ticks were completely sterile, as revealed by unsuccessful attempts of their subsequent hybridization with ticks of the parent generation (Balashov et al. 1998). In *I. persulcatus* and *I. ricinus*, any morphological barrier to crossing is undoubdetly

absent and then sterility of the F1 hybrid generation is probably a quite significant factor limiting the population size of both species in their sympatric areas. Hybrid ticks also have morphological features allowing to differentiate them at preimaginal and imaginal stages (Bugmyrin et al. 2015, 2016). Moreover, some studies were conducted in the Southern Primorye (Filippova 2002) in sympatric zones of *I. persulcatus* and *I. pavlovskyi occidentalis*, due to the close cohabitation of both species. These showed that in case of these two species there are distinct morphological barriers which are manifested in the fitting of organs involved in mating, in particular their size proportions. According to the result of the studies, mating and hybridization of different tick species are possible only in the next combination: female *I. pavlovskyi* and male *I. persulcatus*. Whereas in case of the reverse combination, the parameters of the genital aperture of the female exceed those of the largest width of the hypostome in the male.

There is an excellent summary on the questing behavior of *I. persulcatus* in the monograph by Filippova (1985). In brief, the ticks climb onto the vegetation in quest of a host. When the host approaches, the tick spreads its first pair of legs and, upon contact with the host, become attached. From time to time, ticks perform vertical migrations and go even into the soil litter for rehydration. Horizontal movements of ticks towards trails used by potential hosts are also possible, as well as crawling onto a nearby animal. Ticks react to humans by spreading their first legs from distances of ~ 15–20 m. At short distances, ticks also react to a heat source. In general, a similar pattern of questing behavior is used by other exophilic ticks of the genus *Ixodes*.

In *I. persulcatus* there is an important signaling mechanism causing a morphogenetic diapause – a developmental delay which is the response of ticks to the duration of the diurnal photoperiod (Belozerov 1976). Moreover, *I. persulcatus* has a behavioral diapause of non-engorged adult ticks, which is not connected with photoperiodic regulation (Korenberg et al. 2021). But as the studies in the Kirov Oblast and Udmurt Republic showed, in more warmer areas, an increased proportion of engorged larvae and nymphs develop without the diapause and the reason for this is the early activation and, as a result, their mass feeding on hosts in the first half of summer. The factors determining the diapause of engorged larvae and nymphs in the compared regions practically do not differ (Korotkov 2008). The correlation of the tick number varies, depending on the type of biotope, as well as temperature and humidity and also many other abiotic factors. For example, in boreal taiga forests of Karelia mainly *I. persulcatus* dominates (except the southwestern part where the mass species is *I. ricinus*) (Bugmyrin et al. 2013). The beginning of adult *I. persulcatus* activity also differs in different regions depending on the sum of abiotic factors listed above. For example, in the Far East the seasonal peak in the number of larvae is observed in the third decade of May – second decade of July, whereas in the European part of its range in the third decade of July (Belozerov 1976; Filippova 1977; Balashov 1998; Korenberg et al. 2013). In the territory from the Volga River to Primorye the average activity of adult ticks varies from 60 to 140 days (Korenberg et al. 1974). The boundaries of the range of the tick are determined mainly by the combination of photo- and hygrothermal factors. The general indicators of warmth and moisture along the range of this tick species vary widely. The fundamental ecological niche of *I. persulcatus* with the broad scope of its preferred conditions allows it to adapt to the wide diversity of biotopes in the forest zone.

Some type specimens of *I. persulcatus* are deposited at the Zoological Institute of the Russian Academy of Sciences and include *I. persulcatus* subsp. *diversipalpis* (Schulze 1930: 300), lectotype: male; [Russia, Primorskii Terr.], lower Amur River, 8 km of Vyatskoe Vill., 26.VI.1910, coll. Soldatov, det. N.O. Olenev: *I. ricinus ovatus*; AL I266, as well as the paralectotypes: 1 female, 1 male; AL I266a. *I. persulcatus* (see: Filippova 1969: 677). Description – Filippova 1977: 316–327 (female, male, nymph, larva) (Filippova 2008). But Filippova (1969) also states that re-examination of the type material of the above subspecies demonstrated that the specimens used for describing differences of this subspecies are damaged in some morphologically important parts (not noticed before), and the key morphological characters that were previously thought to distinguish the subspecies are not specific enough and can be found in ticks throughout their entire geographical range.

### *Ixodes redikorzevi* Olenev, 1927

*Ixodes redikorzevi* Olenev, 1927: 219.

**Recorded hosts. Mammalia:** *Apodemus agrarius* (striped field mouse), *Apodemus mystacinus* (Danford and Alston) (eastern broad-toothed field mouse), *Apodemus uralensis* (Ural field mouse), *Arvicola amphibius* (European water vole), *Chionomys nivalis* (European snow vole), *Chionomys roberti* (Thomas) (Robert's snow vole), *Cricetus cricetus* (European hamster), *Crocidura leucodon* (bicolored shrew), *Crocidura suaveolens* (lesser white-toothed shrew), *Dryomys nitedula* (forest dormouse), *Erinaceus europaeus* (European hedgehog), *Glis glis* (European edible dormouse), *Hemiechinus auratus* (long-eared hedgehog), *Lepus europaeus* (European hare), *Marmota bobak* (bobak marmot), *Martes martes* (European pine marten), *Meles meles* (European badger), *Meriones libycus* (Libyan jird), *Meriones meridianus* (midday jird), *Meriones persicus* (Persian jird), *Meriones tamariscinus* (Pallas) (tamarisk jird), *Meriones tristrami* Thomas (Tristram's jird), *Mesocricetus auratus* Waterhouse (golden hamster), *Mesocricetus raddei* (Ciscaucasian hamster), *Microtus arvalis* (common vole), *Microtus majori* (Major's pine vole), *Microtus socialis* (social vole), *Mus musculus* (house mouse), *Mustela eversmanii* (steppe polecat), *Mustela nivalis* (least weasel), *Nesokia indica* (short-tailed bandicoot rat), *Nothocricetulus migratorius* (grey dwarf hamster), *Rattus norvegicus* (brown rat), *Rattus pyctoris* (Turkestan rat), *Rattus rattus* (black rat), *Rhombomys opim*us (great gerbil), *Sciurus anomalus* Gmelin (Caucasian squirrel), *Sciurus vulgaris* (red squirrel), *Sicista betulina* (northern birch mouse), *Sicista subtilis* (southern birch mouse) *Spalax giganteus* Nehring (giant blind mole-rat), *Spalax microphthalmos* Gueldenstaedt (greater blind mole-rat), *Spermophilopsis leptodactylus* (long-clawed ground squirrel), *Spermophilus pygmaeus* (little ground squirrel), *Sorex araneus* (common shrew), *Vormela peregusna* (marbled polecat) *Vulpes vulpes* (red fox) (Filippova 1977).

**Aves:** *Alauda arvensis* Linnaeus (Eurasian skylark), *Alectoris chukar* (chukar partridge), *Anthus campestris* (tawny pipit), *Anthus pratensis* (Linnaeus) (meadow pipit), Coccothraustes coccothraustes (hawfinch), *Columba livia* (rock dove), *Emberiza calandra* (corn bunting), *Emberiza schoeniclus* (Linnaeus) (common reed bunting), *Erithacus rubecula* (Linnaeus) (European robin),

*Galerida cristata* (crested lark), *Garrulus glandarius* (Linnaeus) (Eurasian jay), *Lullula arborea* (woodlark), *Melanocorypha calandra* (Linnaeus) (calandra lark), *Mergus serrator* Linnaeus (red-breasted merganser), *Oenanthe hispanica* (Linnaeus) (western black-eared wheatear), *Oenanthe isabellina* (Temminck) (Isabelline wheatear), *Oenanthe lugens* (Lichtenstein) (mourning wheatear), *Oenanthe oenanthe* (Linnaeus) (northern wheatear), *Oenanthe picata* (Blyth) (variable wheatear), *Phylloscopus collybita* (Vieillot) (common chiffchaff), *Phylloscopus fuscatus* (dusky warbler), *Pica pica* (Eurasian magpie), *Pterocles orientalis* (Linnaeus) (black-bellied sandgrouse), *Saxicola torquatus* (Linnaeus) (African stonechat), *Sturnus vulgaris* (common starling), *Turdus merula* (common blackbird), *Turdus philomelos* (song thrush), *Turdus ruficollis* (red-throated thrush) (Filippova 1977).

**Reptilia:** *Darevskia chlorogaster* (Boulenger) (greenbelly lizard) (Orlova et al. 2022), *Lacerta agilis* Linnaeus (sand lizard) (Filippova 1977), *Lacerta strigata* Eichwald (Caucasus emerald lizard) (Orlova et al. 2023), *Pseudopus apodus* (Pallas) (Pallas's glass lizard) (Filippova 1977).

**Recorded locations (Fig. 15). Russia:** Rostov Oblast (Khametova et al. 2018), Krasnodar Krai, Stavropol Krai, Kalmyk Republic, Chechnya, Dagestan, and North Osetia-Alania (Shatas 1957; Shevchenko et al. 1960; Zaytsev and Popova 1967; Tiflova 1974; Filippova 1977; Abdulmagomedov et al. 2017; Zaytseva et al. 2022). **Ukraine:** Odesa Oblast (Bugeac Steppe), Kherson Oblast (Black Sea Biosphere Reserve), Poltava Oblast, Chernivtsi Oblast, Dnipropetrovsk Oblast, Luhansk Oblast, Donetsk Oblast, widely distributed in the Crimean Peninsula (Emchuk 1960; Emchuk 1967; Sklyar 1970; Filippova 1977). **Moldova:** the north of the country (Uspenskaya et al. 2006). **Georgia:** outskirts of Kutaisi and Tbilisi and the Lagodekhi Nature Reserve, as well as the seacoast of the Black Sea (Kirschenblatt 1936; Djaparidze 1960; Filippova 1977). **Armenia:** outskirts of


**Figure 15.** Map of Russia and neighboring countries showing the locations where *Ixodes redikorzevi* was reported.

Yerevan and most of the rest of the territory (Zilfyan et al. 1960; Tiflova 1974). **Azerbaijan:** Zagatala State Reserve, Hadrut District, and the Mil plain (Tiflova 1974), outskirts of the Bilasuvar, the Sara Peninsula (Kirschenblatt 1936), Talysh (Pomerantsev 1950), Nakhchivan Autonomous Republic (Kadatskaya and Shirova 1963; Filippova 1977). **Kazakhstan:** West Kazakhstan Region, Kyzylorda Region, North Kazakhstan Region, Jambyl Region, Turkistan Region, Abai Region (Loseva 1963; Popova and Sokolova 1963). **Kyrgyzstan:** outskirts of Bishkek, Chüy Valley, Talas Valley, Issyk-Kul Basin, Terskey Ala-too Range (Filippova 1958b; Grebenyuk 1966; Filippova 1977). **Turkmenistan:** foothills of the Uly Balkan and the Kopet Dagh; the Kugitangtau Range (Kochkareva et al. 1971; Filippova 1977). **Uzbekistan:** outskirts of Tashkent, foothills of the Chatkal Range, Qurama Mountains, the Hisar Range, the Kugitangtau Range and Karakalpakstan – the Ustyurt Plateau and the lower reaches of the Amu Darya River (Kuklina 1967; Uzakov 1972; Filippova 1977). **Tajikistan:** Hisar Range - Varzob gorge, outskirts of Dushanbe – the Ramit State Nature Reserve, Vakhsh Range, Peter the First Range (Lotozky 1951; Sosnina 1957; Filippova et al. 1966; Kochkareva et al. 1971; Filippova 1977).

**Ecology and other information.** *Ixodes redikorzevi* is a tick species which is mainly a parasite of rodents, shrews, and small carnivores, as well as of dendrophilic ground-feeding birds and rarely reptiles (Filippova 1977). According to Tiflova (1974), this species is considered exophilic and can be found in significant numbers on dendrophilic birds. In the absence of mammalian and avian hosts, *I. redikorzevi* can parasitize lizards in significant numbers (Orlova et al. 2022). It usually inhabits mountain deciduous forests and steppes located nearby.

Beyond the post-Soviet territories considered above, the range of this tick covers also Eastern Europe, Turkey, Israel, as well as Afghanistan (Filippova 1977) and China (Yin et al. 2010).

At the current moment it is still questionable whether *I. redikorzevi* is a synonym of *I. acuminatus* or not. Kolonin (2009) considers this species a synonym of *I. acuminatus*, but Guglielmone et al. (2010) regard it as provisionally valid. As it was fairly noted by Guglielmone et al. (2014) this question can be solved by comparison of the type specimens of both species. Moreover, Pomerantsev (1950) described by females two subspecies: *I. redikorzevi redikorzevi* and *I. redikorzevi emberizae*. Later the other subspecies *I. redikorzevi theodori* was described although Filippova comments (1977) that the authors had quite little material during descriptions but the differences in size and shape of some characters are visible and it is necessary to compare more specimens from more locations of its large area of distribution.

*Ixodes redikorzevi redikorzevi* occurs in Ukraine, the Transcaucasus and Tajikistan according to Pomerantsev (1950); and *I. redikorzevi emberizae* can be found in Lankaran and the Hisar Range in Tajikistan. Later the other subspecies, *I. redikorzevi theodori* was described from the Middle East (Warburton 1927).

The type specimens of *I. redikorzevi* are deposited at the Zoological Institute of the Russian Academy of Sciences and include the holotype: female; [former] Tavricheskaya Province (Crimea), Yaman-Kala, near Baidar, 25.10.1924, coll. V. Shnitnikov, AL I338 and the paralectotype of *I. redikorzevi emberizae* female; AL I522. Description – Pomerantsev 1950: 63 (female; male unknown); Filippova 1977: nymph, larva (Filippova 2008).

### *Ixodes ricinus* (Linnaeus, 1758)

*Acarus ricinus* Linnaeus, 1758: 616.
*Ixodes reduvius* (Linnaeus): Neumann 1911: 12.
*Ixodes sanguisugus* (Linnaeus): Morel and Pérez 1978: 201.
*Ixodes vulgaris* (Fabricius): Neumann 1911: 12.
*Ixodes holsatus* (Fabricius): Nuttall and Warburton 1911: 285.
*Ixodes megathyreus* Leach: Neumann 1911: 12.
*Ixodes bipunctatus* Risso: Neumann 1911: 12.
*Ixodes trabeatus* Audouin: Neumann 1911: 12.
*Ixodes marginalis* Hahn: Oudemans 1896: 191.
*Ixodes sciuri* Koch: Neumann 1911: 12.
*Ixodes fuscus* Koch: Neumann 1911: 12.
*Ixodes sulcatus* Koch: Neumann 1911: 12.
*Ixodes rufus* Koch: Neumann 1901: 249.
*Ixodes lacertae* Koch: Neumann 1911: 12.
*Ixodes pustularum* Mégnin: Neumann 1911: 12.
*Ixodes vicinus* Yerrill: Oudemans 1896: 191.
*Ixodes fodiens* Murray: Neumann 1904: 444.
*Ixodes nigricans* Neumann: Schulze 1939: 1.
*Ixodes areolaris* Olenev: Pomerantsev 1950: 37.

**Recorded hosts.** The host spectrum of *I. ricinus* is extremely broad both systematically and ecologically, including literally almost all mammals and birds of its geographical range, rarely even reptiles inhabiting the same biotopes with the tick. The fact of mass parasitism of immature stages on lizards of the Lacertidae family, in particular species of the genus *Darevskia* in the Caucasus (Kidov et al. 2013; Orlova et al. 2022) in habitats where they outnumber small mammals probably brightly demonstrates that *I. ricinus* is a generalist tick capable to use almost any available terrestrial vertebrates as hosts. Overall, the list of hosts consists of more than 300 species of mammals, birds and reptiles which have been recorded (Gern et al. 2002). Humans and domestic animals can also be hosts for the tick (Filippova 1977).

**Distribution (Fig. 16).** The distribution of *I. ricinus* in Russia includes almost the whole territory of its European part excluding subpolar tundra areas (see the map) (Filippova 1977; Kahl and Gray 2023) and due to climate changes, the distribution of this tick species becomes wider (Gray et al. 2009; Yasyukevich et al. 2009). *Ixodes ricinus* is part of the tick fauna of the following post-Soviet countries: Estonia, Latvia, Lithuania, Belarus, Russia, Ukraine, Moldova, Georgia, Azerbaijan, Armenia, Turkmenistan, and Kazakhstan (Guglielmone et al. 2023). In Kazakhstan a little number of specimens were found in the northern part of West Kazakhstan Oblast (Maikanov 2012). In Turkmenistan the tick was also recorded in few numbers in the western foothills of the Kopet-Dag (Kerbabaev 1960) which probably could be transported there by migratory birds.

**Ecology and other information.** *Ixodes ricinus* is an exophilic tick species widely distributed in Europe, mostly inhabiting deciduous and mixed forest zones in both plain and mountainous areas, as well as forest-steppes bordering them. It also occurs in city parks and gardens (Gray 1998). In addition, it can be found in North Africa (Arthur 1965). In Ukraine *I. ricinus* colonized and reached

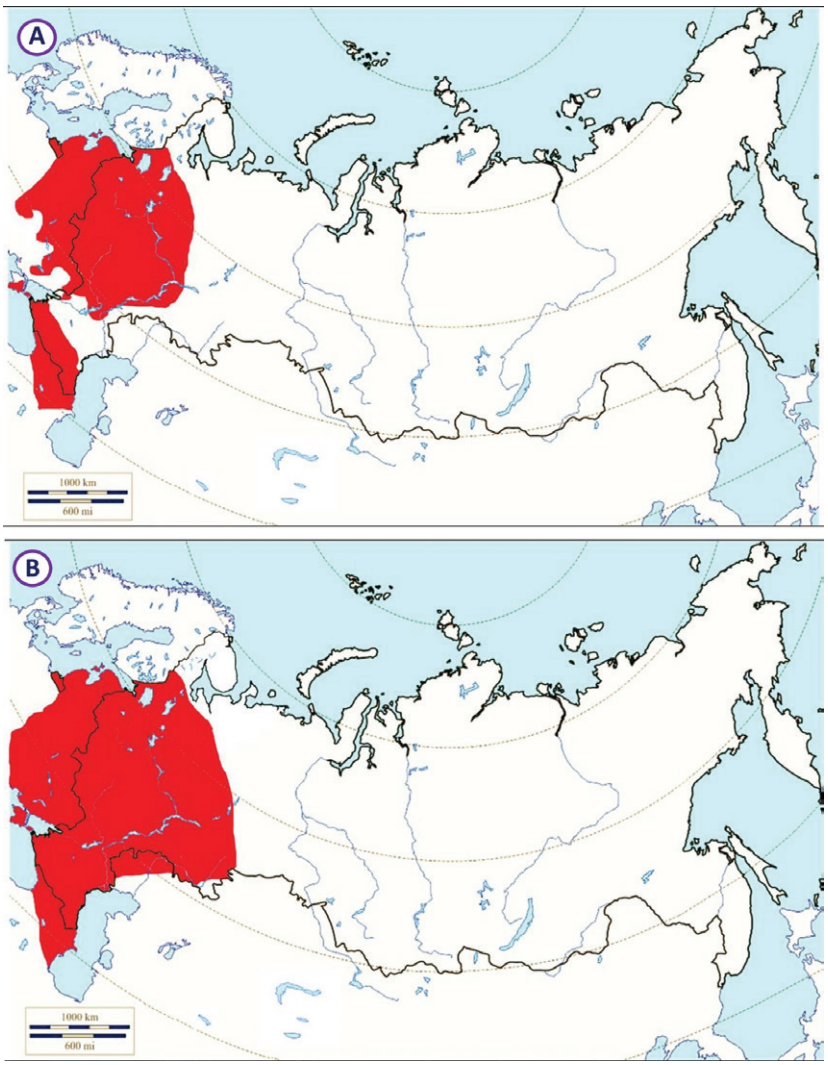


**Figure 16.** Map of Russia and neighboring countries showing the locations where *Ixodes ricinus* was reported: **A** before 1975 **B** from 1976.

a high abundance in artificial forest plantations of the Askania-Nova Nature Reserve surrounded from all sides by steppes for a period of less than 80 years (Emchuk 1972). In urban areas with conditions able to support tick populations, for example, Minsk or Kyiv, *I. ricinus* usually dominates among other tick species, especially among members of the genus *Ixodes* (Uspensky 2017). This tick species uses almost all forest vertebrate animals as hosts and, together with *I. persulcatus*, it is one of the most important vectors of a broad spectrum of tick-borne pathogens, first of all, tick-borne encephalitis virus (Filippova 1977).

Often it can be found in the same biotope with *I. persulcatus*, often exhibiting complete or partial coincidence of seasonal activity at each ontogenetic stage (Filippova 1999). In zones of sympatry their hybridization can occur, and although hybrid offspring are incapable of reproduction (Bugmyrin et al. 2015), they can still transmit tick-borne encephalitis virus and probably other pathogens (Kovalev et al. 2016; Belova et al. 2023). The absence of any morphological barrier for copulation was discovered in geographical points of probably the secondary sympatric zone (Filippova 2002) of *I. persulcatus* and *I. ricinus* in the north-west of the East European Plain (Balashov et al. 1998). However, in some areas of this sympatric zone, for example, in southern Kare-

lia, its slight shrinking has recently been noted due to the withdrawal of *I. ricinus* from territories where it used to live (Bespyatova and Bugmyrin 2021).

Due to the high epidemiological significance and wide distribution of *I. ricinus* and its regular contacts with humans and domestic animals, its biology and life cycle were more extensively studied than in case of any other species of its genus inhabiting the same territories. As a species, *I. ricinus* probably appeared approximately 8–12 thousand years ago when deciduous and mixed forests formed in the southeast of Europe and the Mediterranean, as well as in the northern and northeastern slopes of the Greater Caucasus, when current environmental conditions of these territories have begun to shape. And the climate there was also milder than in Siberian taiga forests where *I. persulcatus* evolved (Filippova 2017).

It was revealed that in a certain region the duration of tick activity period and the number of adult ticks depend on spring and summer temperatures and air humidity (Korotkov et al. 2015; Korenberg et al. 2021). Females and larvae usually attach to hosts when the air near the soil warms up from +2 to +30 °C, and in the case of nymphs from +2 to +22 °C. The relative humidity of the surrounding air has to be higher than 60% for an extended period of time (Sirotkin and Korenberg 2018). It is absolutely important for ticks to receive the necessary amount of warmth to complete their metamorphosis at each stage within a strictly defined period of time (Korenberg et al. 2013). As a consequence, the seasonal activity of all stages of *I. ricinus* is more extended than in the case of *I. persulcatus*, and engorged ticks begin oviposition or metamorphosis without strict dependance on the photoperiod. Therefore, in the southern range of distribution (the Mediterranean, Central Europe, the Caucasus) ticks initiate activity in the end of March – the beginning of April (Korenberg et al. 2021), whereas in Eastern European regions – in April (Medvedev et al. 2016; Korenberg et al. 2021). *Ixodes ricinus* also uses a diapause as a biological mechanism, although due to warmer conditions in the majority of its distribution range, no more than 10–20% of ticks at each stage undergo such an interruption of development (Korenberg and Kovalevsky 1977; Korenberg et al. 2016).

### *Ixodes sachalinensis* Filippova, 1971

*Ixodes sachalinensis* Filippova, 1971: 236; Kolonin 1981: 49.
*Ixodes persulcatus diversipalpis* Schulze, 1930: 294; Pomerantsev 1950: 43.
*Ixodes persulcatus cornuatus* Olenev: Pomerantsev 1950: 43.

**Recorded hosts. Mammalia:** *Lepus timidus* (mountain hare) (Filippova 1977).

**Recorded locations (Fig. 17). Russia:** the Sakhalin Island, Sachalin Oblast, the rural locality Khomutovo (Filippova 1971).

**Ecology and other information.** *Ixodes sachalinensis* is a tick species known only by the single finding from Sakhalin. It was collected from a mountain hare together with 79 females, 15 males and 7 nymphs of *I. persulcatus* (Filippova 1971).

Kolonin (2009) and Camicas et al. (1998) consider *I. sachalinensis* a synonym of *I. persulcatus*, but Barker and Murrell (2004) and Guglielmone et al. (2009, 2010) recognize this species as valid.

The type specimen is deposited at the Zoological Institute of the Russian Academy of Sciences and includes the holotype: female; [Russia], Sakhalin, near Khomutovo Vill., *Lepus timidus*, 27.5.1950, [coll.: unknown]; AL I729 (Filippova 2008).


**Figure 17.** Map of Russia and neighboring countries showing the locations where *Ixodes sachalinensis* was reported.

**Subgenus *Ixodiopsis* Filippova, 1957: 31.**

***Ixodes angustus* Neumann, 1899**

*Ixodes angustus* Neumann, 1899: 136.

**Recorded hosts. Mammalia:** *Alexandromys oeconomus* (tundra vole), *Craseomys rufocanus* (grey red-backed vole), *Eutamias sibiricus* (Siberian chipmunk), *Mus musculus* (house mouse), *Myodes rutilus* (northern red-backed vole), *Ochotona alpina* (alpine pika), *Rattus norvegicus* (brown rat), *Sicista caudata* Thomas (long-tailed birch mouse), *Sorex araneus* (common shrew), *Sorex minutus* (Eurasian pygmy shrew) (Filippova 1977).

**Recorded locations (Fig. 18). Russia:** outskirts of Magadan and the lower reaches of the Kukhtui River, Okhotsky district – the northernmost points of record of *I. angustus* in the Palearctic (Belyaev 1963); Kamchatka Peninsula – outskirts of the villages Tigil and Ust-Khayryuzovo (Pomerantsev 1950), the valley of the Kamchatka River to Ust-Kamchatsk (Serdjukova 1956), the eastern coast of the Kamchatka peninsula to Petropavlovsk-Kamchatsky (Speranskaya 1958), the valley of the rivers Avacha and Pinachevskaya (Paramonov et al. 1966); Middle Outer Manchuria (Filippova 1977); Sovetsko-Gavansky district (Emelyanova and Koshkin 1962); Sikhote-Alin (Belyaev and Filippova 1976); Sakhalin – Novoaleksandrovka (former Konuma), the valley of the Lyutoga River (Pomerantsev 1950) and the Cape Patience (Skrynnik 1950; Asanuma 1951; Violovich 1958, 1960; Savitsky and Okuntsova 1967; Timofeeva and Kon'kova 1971); Kuril Islands – Simushir (Pomerantsev 1950; Violovich 1958, 1960; Timofeeva and Kon'kova 1971).

**Ecology and other information.** *Ixodes angustus* occurs in the Palearctic predominantly on the East Asian coast and also in the Nearctic – Canada and the USA (Filippova 1977). In the Russian Far East in Outer Manchuria, the islands


**Figure 18.** Map of Russia and neighboring countries showing the locations where *Ixodes angustus* was reported.

and along the main ridges of the Sikhote-Alin it inhabits a wide range of biotopes: various types of mixed and broad-leaved forests in mountains and valleys, as well as tundra and rocks, stone outcrops, coastal biotopes, meadow and river valleys (Speranskaya 1958; Violovich 1958; Emelyanova and Koshkin 1962; Belyaev 1963; Paramonov et al. 1966; Savitsky and Okuntsova 1967; Belyaev and Filippova 1976).

*Ixodes angustus* is considered a nidicolous ectoparasite of rodents and shrews because it was found not only on hosts but also in their burrows (Filippova 1977), although there are documented cases on this species biting humans without contacts with burrows (Cooley 1946). As a parasite which is connected with rodents, and, like other rodent ticks, *I. angustus* plays a role in supporting natural foci of tick-borne infections such as anaplasmosis (Yamborko and Eremeeva 2014) and the Lyme disease (Peavey et al. 2000).

Although hyperparasitism is not common in *Ixodes* ticks, *I. angustus* belongs to a small number of species of the genus, in which this phenomenon was recorded (Durden et al. 2018), when a male was feeding from a female attached to a red squirrel *Tamiasciurus hudsonicus*. The other *Ixodes* species in which males have been recorded to attach and feed on engorging conspecific females include *I. holocyclus* in Australia and *I. pilosus* in South Africa (Oliver et al. 1986).

### ***Ixodes pomerantzevi* Serdjukova, 1941**

*Ixodes pomerantzevi* Serdjukova, 1941: 519.

**Recorded hosts. Mammalia:** *Apodemus agrarius* (striped field mouse), *Craseomys rufocanus* (grey red-backed vole), *Erinaceus amurensis* Schrenk (Amur hedgehog), *Eutamias sibiricus* (Siberian chipmunk), *Microtus fortis* (reed vole), *Myodes rutilus*

(northern red-backed vole), *Sorex araneus* (common shrew) (Filippova 1977), *Sorex caecutiens* (Laxmann's shrew), *Sorex unguiculatus* Dobson (long-clawed shrew), (individual specimens ((Okulova et al. 1986), *Rattus norvegicus* (brown rat), *Tscherskia triton* (De Winton) (greater long-tailed hamster) (Filippova 1977).

**Recorded locations (Fig. 19). Russia:** Sikhote-Alin – outskirts of Dal'ny Kut (the northernmost point of finding (Filippova 1977), valley of the Dorozhnaya River, Dalnegorsk, Ussurisky (former Komarovskii) Nature Reserve; coast of the Sea of Japan – outskirts of the villages Terney, Dukhovo, Kamenka, Lazovsky nature reserve, Fokino (former Promyslovka), the bays Razboynik and Linda; the coast of the Peter the Great Gulf: Kedrovaya Pad Nature Reserve, the rural localities Barabash and Posyet (Serdjukova 1941; Pomerantsev 1950; Slonov 1961; Khudyakov 1963; Belyaev and Filippova 1976).

**Ecology and other information.** *Ixodes pomerantzevi* is a relict species occurring on the East Asian coast (Filippova 1977) and in Russia its distribution is limited to a few locations in Outer Manchuria (a.k.a. Primorsky Krai) in the Russian Far East (Tsapko 2020). It is also known to occur in Korea (Kim et al. 2009a, 2010, 2011) and China (Guo et al. 2016). Predominantly it can be found in coniferous and broad-leaf forests, or secondary forests and bush thickets, as well as rock and stone outcrops among trees in the Sikhote-Alin and on the coast of the Sea of Japan (Belyaev and Filippova 1976).

Luh and Woo (1950) supposed that *I. pomerantzevi* is possibly a synonym of *Ixodes angustus*; Filippova (1977) considered it as valid and in the last list of valid tick species names, it is also considered valid (Guglielmone et al. 2020).

*Ixodes pomerantzevi* is a nidicolous tick species, an ectoparasite of rodents, hedgehogs, and shrews (Filippova 1977).

The type specimen of *I. pomerantzevi* is deposited at the Zoological Institute of the Russian Academy of Sciences and include the holotype: female; [Russia], DVK


**Figure 19.** Map of Russia and neighboring countries showing the locations where *Ixodes pomerantzevi* was reported.

[Primorskii Terr.], Suputinskii [Komarovskii or Ussurisky] Nature Reserve, from *Myodes rufocanus*, 9–13.VI.1939, coll. B.I. Pomerantsev; AL I502. Description – Filippova 1977: 128–132 (female, male - unknown, nymph, larva) (Filippova 2008).

### ***Ixodes stromi* Filippova, 1957**

*Ixodes stromi* Filippova, 1957: 864.

**Recorded hosts. Mammalia:** *Alticola argentatus* (Severtzov) (silver mountain vole), *Apodemus agrarius* (striped field mouse), *Craseomys rufocanus* (grey red-backed vole), *Crocidura sp.* (shrew), *Lasiopodomys gregalis* (narrow-headed vole), *Microtus arvalis* (common vole), *Mustela sp.* (weasel), *Myodes centralis* (Miller) (Tien Shan red-backed vole), *Nothocricetulus migratorius* (grey dwarf hamster), *Ochotona macrotis* (Günther) (large-eared pika), *Rattus pyctoris* (Turkestan rat) (Filippova 1977).

**Recorded locations (Fig. 20). Russia:** Western Sayan (Arumova and Dineva 1973). **Kazakhstan:** Tarbagatai Mountains (Afanas'eva 1959), Dzungarian Alatau (Ushakova and Fedosenko 1963; Ushakova et al. 1976), Trans-Ili Alatau (Ushakova and Fedosenko 1963). **Kyrgyzstan:** Kyrgyz Ala-Too Range (Fedorova 2012b), Terskey Alatau (Fedorova 2012b), Chuy Valley – found in 1966 (Grebenyuk 1966), was not found in the same territories in 2018 (Fedorova 2021). **Tajikistan:** Peter the First Range (Filippova 1977), Varzob gorge (Sosnina 1954 – here *I. stromi* was incorrectly identified as *I. trianguliceps* because the new species was described by Filippova in 1957b).

**Ecology and other information.** *Ixodes stromi* is a tick species only indigenous to southern Siberia in Russia (Tsapko 2020). The main part of its distribution spans in Kazakhstan and Middle Asia. In all territories of its range,


**Figure 20.** Map of Russia and neighboring countries showing the locations where *Ixodes stromi* was reported.

it is confined to the forest-meadow and forest-steppe belt of medium-altitude mountains, to stony and rocky habitats, which are insolated and, therefore, have a warmer microclimate (Filippova 1967).

This species is nidicolous and uses rodents, shrews, and small carnivores as hosts at all stages. It is considered a rare species reaching small individual number (Filippova 1977).

The type specimens of *I. stromi* are known from Kyrgyzstan and stored at the Zoological Institute of the Russian Academy of Sciences: the lectotype: the nymph; Kyrgyzstan, Tien Shan, Kungei Ala Tau Mt. Range, Ch-Aksu Canyon, talus, from *Clethrionomys frater* (synonym of *Myodes centralis*), 11.VIII.1953, coll. N.A. Filippova; AL I78. The paralectotypes: 6 larvae; FBM I586, I876; 6 larvae; FBM I873, I875. Description – Filippova 1977: 122–127 (female, nymph, larva; male unknown) (Filippova 2008).

**Subgenus *Monoixodes* Emelyanova & Kozlovskaya, 1967: 489.**

***Ixodes maslovi* Emelyanova & Kozlovskaya, 1967**

*Ixodes maslovi* Emelyanova & Kozlovskaya, 1967: 489.

**Recorded hosts.** To date hosts of this tick species are unknown (Guglielmone et al. 2014).

**Recorded locations (Fig. 21). Russia:** Khabarovsk Krai – Khekhtsir Range and the rural locality Vyatskoye (Emelyanova and Kozlovskaya 1967); Krasnoyarsk Krai – Kozulsky District, the village Bolshoy Kemchug (Voltsyt 1997).

**Ecology and other information.** *Ixodes maslovi* is an almost unstudied tick known and described from two findings of its male and female (Emelyanova and Kozlovskaya 1967), as well as the nymph (Voltsyt 1997).


**Figure 21.** Map of Russia and neighboring countries showing the locations where *Ixodes maslovi* was reported.

Camicas et al. (1998) and Kolonin (2009) regard *I. maslovi* as an abnormal form of *I. persulcatus* although Filippova (1977) and Guglielmone et al. (2020) consider *I. maslovi* a valid taxon.

The type specimens are deposited at the Zoological Institute of the Russian Academy of Sciences – the holotype: male; [Russia], environs of Khabarovsk, Khekhtsir Mt. Range, 12.VI.1964, collected from vegetation by O.L. Kozlovskaya; FBM I1412; the paratype: female; FBM I1413. Description – Filippova 1977: 248–251 (female, male); Voltsit 1997: 265–268 (nymph; larva unknown) (Filippova 2008).

**Subgenus *Pholeoixodes* Schulze, 1942: 630.**

***Ixodes arboricola* Schulze & Schlottke, 1929**

*Ixodes arboricola* Schulze & Schlottke: Morel and Pérez 1973: 275.
*Ixodes arboricola muscicapae* Schulze, 1930: 3; Haarløv 1962: 425.
*Ixodes strigicola* Schulze & Schlottke: Haarløv 1962: 425.
*Ixodes dryadis* Schulze & Schlottke: Haarløv 1962: 425.
*Ixodes passericola* Schulze: Haarløv 1962: 425.
*Ixodes arboricola bogatschevi* Kirshenblat, 1936: 93; Haarløv 1962: 425.
*Ixodes lagodechiensis* Dzhaparidze, 1950: 117; Kolonin 1981: 84.

**Recorded hosts. Aves:** *Accipiter gentilis* (Linnaeus) (northern goshawk), *Acrocephalus scirpaceus* (Hermann) (Eurasian reed warbler), *Aegithalos caudatus* (Linnaeus) (long-tailed tit), *Aegolius funereus* (Linnaeus) (boreal owl), *Athene noctua* (little owl), *Certhia brachydactyla* Brehm (short-toed treecreeper), *Certhia familiaris* Linnaeus (Eurasian treecreeper), *Chloris chloris* (European greenfinch), *Coloeus monedula* (Linnaeus) (western jackdaw), *Columba palumbus* Linnaeus (common wood pigeon), *Coracias garrulus* Linnaeus (European roller), *Corvus frugilegus* Linnaeus (rook), *Curruca communis* (common whitethroat), *Cyanistes caeruleus* (Linnaeus) (Eurasian blue tit), *Dendrocopos major* (great spotted woodpecker), *Emberiza citrinella* (yellowhammer), *Erithacus rubecula* (European robin), *Falco peregrinus* Tunstall (peregrine falcon), *Falco tinnunculus* Linnaeus (common kestrel), *Ficedula albicollis* (Temminck) (collared flycatcher), *Ficedula hypoleuca* (European pied flycatcher), *Garrulus glandarius* (Eurasian jay), *Glaucidium passerinum* (Linnaeus) (Eurasian pygmy owl), *Hirundo rustica* Linnaeus (barn swallow), *Lophophanes cristatus* (Linnaeus) (crested tit), *Motacilla alba* (white wagtail), *Muscicapa striata* (Pallas) (spotted flycatcher), *Parus major* (great tit), *Passer domesticus* (house sparrow), *Passer montanus* (Eurasian tree sparrow), *Periparus ater* (Linnaeus) (coal tit), *Phoenicurus ochruros* (Gmelin) (black redstart), *Phoenicurus phoenicurus* (common redstart), *Phylloscopus trochilus* (Linnaeus) (willow warbler), *Picus canus* Gmelin (grey-headed woodpecker), *Poecile montanus* (Conrad von Baldenstein) (willow tit), *Poecile palustris* (Linnaeus) (marsh tit), *Pyrrhula pyrrhula* (Linnaeus) (Eurasian bullfinch), *Remiz pendulinus* (Linnaeus) (Eurasian penduline tit), *Riparia riparia* (Linnaeus) (sand martin), *Serinus serinus* (Linnaeus) (European serin), *Sitta europaea* (Eurasian nuthatch) (Filippova 1977; Keve et al. 2022), western rock nuthatch *Sitta neumayer* Michahelles (Ogandzhanyan 1984), *Spinus spinus* (Linnaeus) (Eurasian siskin), *Strix aluco* Linnaeus (tawny owl), *Sturnus vulgaris* (common starling), *Troglodytes troglodytes* (Linnaeus) (Eurasian wren),


**Figure 22.** Map of Russia and neighboring countries showing the locations where *Ixodes arboricola* was reported.

*Turdus merula* (common blackbird), *Turdus philomelos* (song thrush), *Tyto alba* (Scopoli) (barn owl), *Upupa epops* Linnaeus (Eurasian hoopoe) (Filippova 1977; Keve et al. 2022).

**Recorded locations (Fig. 22). Russia:** Southern Primorskyi Krai (Pogranichny District, Vladivostok, Nakhodka, Putyatin Island) (Emelyanova and Gordeeva 1969; Emelyanova 1972; Bolotin 2000). **Ukraine:** outskirts of Kyiv (Nebogatkin 2014), Dnipropetrovsk Oblast (the rural locality Andriivka), Crimea (Olenivka and Alushta) (Filippova 1977). **Belarus:** Białowieża Forest, Minsk, Gomel Oblast (the village Markovskoye) (Gembetsky 1966, 1972). **Armenia:** Syunik Province (former Goris Province) (Ogandzhanyan 1984). **Azerbaijan:** Karabakh (Kirschenblatt 1936). **Georgia:** Lagodekhi Nature Reserve (Djaparidze 1960). **Kyrgyzstan** (Fedorova 2012a).

**Ecology and other information.** *Ixodes arboricola* is an endophilic parasite, mainly of birds from ecological groups nesting in tree holes and nest boxes and also even in ground burrows (Filippova 1977). Also, certain cases of this species infesting bats in tree holes have been recorded (Arthur 1963).

The interesting feature of its distribution is the disjunctivity, which is confirmed by the discovery of this species in the areas quite distant from each other – western and central Europe, North Africa, Transcaucasia, western Asia, and the Far East in Russia (Estrada-Peña et al. 2018) and China (Chen et al. 2010).

### *Ixodes cornutus* Lotozky, 1956

*Ixodes cornutus* Lototsky, 1956: 27.
*Ixodes rugicollis* Schulze & Schlottke: Morel and Aubert 1975: 99.

**Recorded hosts. Mammalia:** *Mustela erminea* Linnaeus (stoat) (Filippova 1977).


**Figure 23.** Map of Russia and neighboring countries showing the locations where *Ixodes cornutus* was reported.

**Recorded locations (Fig. 23). Tajikistan:** Peter the First Range, the source of the Divansu River, close to the Oshanin glacier (Filippova 1977).

**Ecology and other information.** *Ixodes cornutus* is a species described from two identical females (Lotozky 1956) that were found in Tajikistan, in the eastern part of Peter the First Range, by the source of the Divansu River (the basin of the Surkhob River), near the Oshanin glacier, on a stoat.

The type specimen of *I. cornutus* is deposited at the Zoological Institute of the Russian Academy of Sciences (Lotozky 1956: 27). Lectotype: female; 38 [Tajikistan, the Peter the First Mt. Range], the source of the Divansu River, the ancient moraine of the Oshanin glacier, *Mustela erminea*, ad.; male; 4.VII.1954; AL I845. Description – Filippova 1977: 178 (female; male, nymph, larva unknown) (Filippova 2008).

### *Ixodes crenulatus* Koch, 1844

*Ixodes crenulatus* Koch, 1844c: 39; Morel and Pérez 1973: 275.

**Note.** Tick names are used sensu Guglielmone et al. (2014) in this review. Thus, this species is not synonymous with *I. canisuga* Johnston as suggested by Filippova (1977) based on their morphological similarities and because the latter is not known to occur in Russia. *Ixodes crenulatus* was erroneously synonymized with *I. kaiseri* Arthur (Sonenshine et al. 1969), as clarified later (Filippova and Uspenskaya 1973).

**Recorded hosts. Mammalia:** *Allactaga major* (Kerr) (great jerboa), *Allactaga sibirica* (Forster) (Mongolian five-toed jerboa), *Allocricetulus eversmanni* (Brandt) (Eversmann's hamster), *Apodemus sylvaticus* (wood mouse), *Canis aureus* Linnaeus (golden jackal), *Canis familiaris* (domestic dog), *Canis lupus* Linnaeus (gray wolf), *Cricetulus barabensis* (Pallas) (Chinese striped hamster),

*Ellobius talpinus* (northern mole vole), *Erinaceus europaeus* (European hedgehog), *Felis catus* Linnaeus (domestic cat), *Felis lybica* Forster (African wildcat), *Hemiechinus auratus* (long-eared hedgehog), *Homo sapiens* Linnaeus (human), *Lasiopodomys gregalis* (narrow-headed vole), *Lepus tolai* (tolai hare), *Marmota baibacina* (gray marmot), *Marmota bobak* (bobak marmot), *Marmota caudata* (Geoffroy) (long-tailed marmot), *Marmota kastschenkoi* Stroganov and Yudin (forest-steppe marmot), *Marmota menzbieri* (Kashkarov) (Menzbier's marmot), *Marmota sibirica* (Tarbagan marmot), *Meles meles* (Eurasian badger), *Microtus arvalis* (common vole), *Mustela eversmanii* (steppe polecat), *Mustela nivalis* (least weasel), *Myodes glareolus* (bank vole), *Myospalax myospalax* (Siberian zokor), *Nothocricetulus migratorius* (grey dwarf hamster), *Nyctereutes procyonoides* (Gray) (common raccoon dog), *Ochotona dauurica* (Pallas) (Daurian pika), *Ochotona pallasi* (Gray) (Pallas's pika), *Otocolobus manul* (Pallas) (Pallas's cat), *Ovis aries* (domestic sheep), *Phodopus sungorus* (Pallas) (winter white dwarf hamster), *Procyon lotor* (Linnaeus) (raccoon), *Spermophilus dauricus* Brandt (Daurian ground squirrel), *Spermophilus pygmaeus* (little ground squirrel), *Spermophilus relictus* (Kashkarov) (relict ground squirrel), *Spermophilus suslicus* (speckled ground squirrel), *Vulpes corsac* (corsac fox), *Vulpes vulpes* (red fox) (Filippova 1977; Litvinov and Sapegina 2003; Kalyagin et al. 2005, 2008).

**Aves:** *Emberiza cia* Linnaeus (rock bunting), *Oenanthe isabellina* (isabelline wheatear) (Filippova 1977).

**Recorded locations (Fig. 24). Russia:** Tula Oblast (Myasnikov and Katelina 1964), Kursk Oblast (Lgovsky District), Voronezh Oblast (Kamennaya Steppe Nature reserve), Rostov Oblast (Aksay), Republic of Kalmykia (Derbetovsky District, Sarpinsky District), Volgograd Oblast (Gorodishchensky, Derbetovsky and Sarpinsky District) (Denisov 2010, 2019), Kabardino-Balkaria


**Figure 24.** Map of Russia and neighboring countries showing the locations where *Ixodes crenulatus* was reported.

(tract Khaimasha) (Bittirova et al. 2019), Dagestan (Aliev et al. 2007), Astrakhan Oblast, Stavropol Krai (Filippova 1977), Saratov Oblast (Turtseva 2007; Denisov 2010, 2019; Porshakov et al. 2020), Yekaterinburg (Milintsevich et al. 2016), Tyumen Oblast (Glazunov and Zotova 2014), Kurgan Oblast (Starikov and Starikova 2021), Novosibirsk Oblast (Suzunsky, Karasuksky and Maslyaninsky District) (Davydova and Lukin 1969), Omsk Oblast (Tarasevich et al. 1971), Kemerovo Oblast (Kalyagin et al. 2005, 2008; Kovalevsky et al. 2018); Altai Krai (Oberth et al. 2015) (Sovetsky District, the village Kokshi) (Filippova 1977), Altai Republic (Shebalinsky District, the village Cherga) (Litvinov and Sapegina 2003), Tuva (Glazunov and Zotova 2014; Filippova 1977), Transbaikal (villages Borgoy, Kyakhta, Selenge and Borzinsky District) (Filippova 1977); Amur Oblast (village Krasny Vostok), Southern Outer Manchuria (Khankaysky District (Kolonin 1986; Bolotin 2000). **Ukraine:** outskirts of Kyiv (Akimov and Nebogatkin 2016), Zakarpattia Oblast and Western Ukraine in general (Podobivskyi and Fedonyuk 2017), Cherkasy Oblast, Dnipropetrovsk Oblast, Askania-Nova Nature Reserve, Striltsivskyi Steppe Nature Reserve, Kharkiv Oblast (Tokarsky and Zorya 2007), Lugansk Oblast (Kuznetsov and Bondarev 2007) (including Khomutovs'kyi Steppe) (Filippova 1977), the north-western sea coast of the Black Sea (Rusev 2009), Crimea (Evstafiev 2017) – plain and mountainous lands (Filippova 1977). **Belarus:** Viciebsk Voblasts (Subbotina and Osmolovsky 2022), Białowieża Forest (Filippova 1977), considered rare (Bychkova et al. 2015). **Moldova:** Lozova, Ivancea, Leova, reedbeds of the low Dniester and Pruth (Filippova 1977; Uspenskaya et al. 2006). **Georgia:** Samegrelo-Zemo Svaneti, Imereti (Sukhiashvili et al. 2020). **Armenia:** Aragats mountain range (Dilbaryan and Poghosyan 2018). **Kazakhstan:** through the whole territory of Kazakhstan (Filippova 1977) and plus recent findings in the next regions: West Kazakhstan Region (Tanitovsky and Maikanov 2018), Almaty Region (Bibikov and Bibikova 2010), Pavlodar Region (Amirova et al. 1989), the north of Betpak-Dala (Rapoport et al. 2017), Jambyl Region (Kyrgyz Ala-Too Range, Talas Alatau) (Sarsenbaeva et al. 2016). **Kyrgyzstan:** Tian Shan in general (Abdikarimov et al. 2018) and its certain ranges and valleys including Kyrgyz Ala-Too Range (Akyshova et al. 2022) and Terskey Ala-too Range (Fedorova 2012b); Chuy Valley (Fedorova 2021). **Turkmenistan:** Krasnovodsk Peninsula, Daşoguz, the foothills of The Köpet Dag, Badhyz State Nature Reserve, Karakum Desert (Kochkareva et al. 1971), Serhetabat (former Kushka) (Filippova 1977). **Uzbekistan:** Tashkent Region (Muratbekov 1954). **Tajikistan:** outskirts of the rural locality Jilikul (Filippova 1977), Tigrovaya Balka (Manilova and Shakhmatov 2008).

**Ecology and other information.** *Ixodes crenulatus* is among the tick species that have the most extensive ranges comparing to other representatives of its family within Russia (Tsapko 2020).

It is a typical nidicolous parasite of mammals and in the Asian part of its range as the main hosts it uses species of marmots of the genus *Marmota* (with a predominance of gray marmot) and such representatives of predatory mammals as badgers, steppe polecats, red and corsac foxes. The composition of the main host spectrum from different orders (rodents and predatory mammals) finds an explanation in close connections of topical and trophic relationships of marmots and predators. All of them have burrows of medium diameter, complex design, with a nesting chamber, remote from the entrance, which

provides the stability of the microclimate, where ticks find suitable conditions. The above species of carnivores often use the burrows of their prey, marmots, and small carnivores, facilitating the exchange of ticks not only between individual burrows, but also between remote host settlements (Filippova 2011).

This tick species is considered rare, for example, only few findings were mentioned in the Astrakhan Oblast (Zimina et al. 1965; Zimina et al. 1996) and Saratov Oblast (Denisov 2019). In most of the recognized range, *I. crenulatus* coexists with the closely related *I. kaiseri*. These species not only inhabit the same territory and the same biotopes but can also parasitize one host individual at the same time (Tsapko 2017). Therefore, it is necessary to consider that accurate identification of these species is required and there is always a chance of their misidentification.

According to some suggestions (Emelyanova 1979), *I. crenulatus* is probably a species group, or at least has remarkable intraspecific variations involving morphotypes (Filippova and Panova 2000).

### *Ixodes hexagonus* Leach, 1815

*Ixodes hexagonus* Leach, 1815: 397; Morel and Pérez 1973: 275.
*Ixodes autumnalis* Leach: Neumann 1911: 17.
*Ixodes erinacei* Audouin: Neumann 1911: 17.
*Ixodes auricularis* Robineau-Desvoidy: Morel and Pérez 1973: 275.
*Ixodes sexpunctatus* Koch: Neumann 1911: 17.
*Ixodes vulpis* Pagenstecher: Neumann 1911: 17.
*Ixodes erinaceus* Audouin: Neumann 1911: 17.

**Recorded hosts. Mammalia:** *Bos taurus* Linnaeus (cattle), *Canis familiaris* (domestic dog), *Erinaceus europaeus* (European hedgehog), *Felis catus* (domestic cat), *Lutra lutra* (Linnaeus) (Eurasian otter), *Meles meles* (Eurasian badger), *Mustela erminea* (stoat), *Mustela nivalis* (least weasel), *Mustela putorius* Linnaeus (European polecat), *Oryctolagus cuniculus* (Linnaeus) (European rabbit), *Ovis aries* (sheep), *Rattus norvegicus* (brown rat), *Vulpes vulpes* (red fox) (Filippova 1977).

**Aves:** *Turdus merula* (common blackbird) (Filippova 1977).

**Recorded locations (Fig. 25). Ukraine:** outskirts of Kyiv, Khmelnytskyi Oblast (Levytska et al. 2021), the North-Western seacoast of the Black Sea (Rusev 2009), Zakarpattia Oblast (the rural locality Malyi Berezny) (Filippova 1961).

**Ecology and other information.** *Ixodes hexagonus* is a typical nidicolous parasite of carnivores and hedgehogs. It has certain morphological similarities to *I. crenulatus* and *I. kaiseri* and has common sympatric zones with this species along its range (Filippova 1999). Ukraine is the only country of the former Soviet Union, on the territory of which this European species is present in the tick fauna (Filippova 1977). In general *I. hexagonus* was detected quite rarely in Ukraine, and almost always in the west of Ukraine and mainly from hedgehogs (Kolonin 2009). Akimov and Nebogatkin (2016) assumed that it can be found in the vicinity of Kyiv, and eventually it was confirmed by Levytska et al. (2021). Rare occasional human bites have been recorded (Rosický and Weiser 1952; Arthur 1963; Bursali et al. 2012).


**Figure 25.** Map of Russia and neighboring countries showing the locations where *Ixodes hexagonus* was reported.

### *Ixodes kaiseri* Arthur, 1957

*Ixodes kaiseri* Arthur, 1957: 578; Morel and Aubert 1975: 99.
*Ixodes bakonyensis* Babos: Morel and Aubert 1975: 99.
*Ixodes vulpinus* Babos: Morel and Aubert 1975: 99.

**Recorded hosts. Mammalia:** *Canis familiaris* (domestic dog), *Erinaceus concolor* Martin (southern white-breasted hedgehog), *Erinaceus europaeus* (European hedgehog), *Erinaceus roumanicus* Barrett-Hamilton (northern white-breasted hedgehog), *Felis chaus* Schreber (jungle cat), *Felis lybica* (African wildcat), *Hyaena hyaena* (Linnaeus) (striped hyena), *Hystrix indica* Kerr (Indian crested porcupine), *Lepus europaeus* (brown hare), *Mustela eversmanii* (steppe polecat), *Meles meles* (Eurasian badger), *Nyctereutes procyonoides* (common raccoon dog), *Vulpes corsac* (corsac fox), *Vulpes vulpes* (red fox) (Filippova 1977; Tsapko 2017).

**Recorded locations (Fig. 26). Russia:** southwestern peripheries of the Central Russian Upland and also Rostov Oblast (Khametova et al. 2018) and Stavropol Krai (Tsapko 2017) and the North Caucasus – the outskirts of Grozny (Chechnya) (Filippova 1977, 1999; Tsapko 2017, 2020) and Nogaysky District (Dagestan) (Tsapko 2017). **Ukraine:** outskirts of Kyiv (Akimov and Nebogatkin 2016) and the south of Ukraine, in particular Askania-Nova Nature Reserve (Filippova 1977), the North-Western seacoast of the Black Sea (Matyukhin 2017), Crimea (Filippova 1977). **Moldova:** Lozova, Ivancea, Doibani, Leova, Etulia, reedbeds of the low Dniester and Pruth (Filippova 1977; Uspenskaya et al. 2006). **Georgia:** the outskirts of Tbilisi, Lagodekhi Nature Reserve (Filippova 1977), Eldari Steppe (Tsapko 2017). **Armenia:** Gegharkunik Province (rural locality Geghamashen) (Tsapko 2017), Aragats


**Figure 26.** Map of Russia and neighboring countries showing the locations where *Ixodes kaiseri* was reported.

mountain range (Dilbaryan and Poghosyan 2018). **Azerbaijan:** Mil plain (Filippova and Uspenskaya 1973), Beylagan District, Zangilan District, Aghjabadi District, Martuni Province, Shaki District (Tsapko 2017). **Kazakhstan:** West Kazakhstan Region, Dzungarian Alatau – outskirts of the rural locality Topolëvka and the Koksu district (Ushakova et al. 1976; Filippova 1999). **Kyrgyzstan** (Fedorova 2012b).

**Ecology and other information.** *Ixodes kaiseri* is a typical nidicolous parasite of carnivores and also hedgehogs and porcupines which is morphologically very similar to *I. crenulatus* and has common sympatric zones with this species along its range (Filippova 1999). Its range itself is patchy and disjunctive areas of sympatry for both of these species are found in southeastern Europe - Romania, Moldova, Ukraine, including the Crimean Peninsula as well as in Russia - the southwestern extremities of the Central Russian Upland and the Northern Caucasus; then after a long gap - in Western Kazakhstan and again after a big gap - in the Dzungarian Alatau (Filippova 1999). Judging by literature, it is also known from Egypt and Israel (Arthur 1957, 1960, 1965). As Filippova and Uspenskaya (1973) assumed, its distribution in the Middle East and also other parts of Asia can be wider than it is known at present, which was already confirmed by the findings of this tick species in Turkey (Orkun and Karaer 2018) and Xinjiang in China (Zhao et al. 2019) near the border with Kazakhstan and the Dzungarian Alatau and hence, it is possible that the sympatry of these two species is more widespread. This is also supported by literature data, because until the 1970s in the territory of the former USSR *I. kaiseri* was not differentiated from *I. hexagonus* and *I. crenulatus* (Emelyanova 1979; Filippova 1999).

These species not only inhabit the same territory and inhabit the same biotopes in some places but can also parasitize one host individual at the same time (Tsapko 2017). It is also important to note that according to Filippova's

opinion (1999), the territorial signs of the ranges of these two species, their biotope and host-parasite relationships indicate that the range of *I. crenulatus* (which is predominantly connected with marmots and their burrows in steppe and forest-steppe zones) over the most part of its distribution has a Central Asian origin, while the range of *I. kaiseri* (mainly the parasite of carnivores and occurring in their burrows) is supposedly of European origin.

### *Ixodes lividus* Koch, 1844

*Ixodes lividus* Koch, 1844: 234; Morel and Pérez 1973: 275.
*Ixodes bavaricus* Schulze & Schlottke, 1929: 95.
*Ixodes plumbeus bavaricus* Schulze & Schlottke: Morel and Pérez 1973: 275.
*Ixodes plumbeus obotriticus* Schulze & Schlottke: Morel and Pérez 1973: 275.
*Ixodes* (*Pholeoixodes*) *hirundinicola* Schulze: Kolonin 1981: 19.

**Recorded hosts. Aves:** *Alauda arvensis* (Eurasian skylark), *Delichon urbicum* (Linnaeus) (common house martin), *Merops apiaster* Linnaeus (European bee-eater), *Passer domesticus* (house sparrow), *Passer montanus* (Eurasian tree sparrow), *Riparia diluta* (Sharpe & Wyatt) (pale martin), *Riparia riparia* (sand martin) (Filippova 1977; Tagiltsev et al. 1984; Rusev 2009; Bolshakova et al. 2019; Kovalevsky et al. 2019).

**Mammalia:** *Mus musculus* (house mouse) (Filippova 1977).

**Recorded locations (Fig. 27). Russia:** Curonian Spit (Kaliningrad Oblast) (Filippova 1961), Karelia (Bobrovskikh 1979), Leningrad Oblast, (Zolotov and Buker 1976), Moscow Oblast (Glashchinskaya-Babenko 1956), Ryazan Oblast (Filippova 1977), Ivanovo Oblast (Mayorova 2004), Saratov Oblast (Korneev


**Figure 27.** Map of Russia and neighboring countries showing the locations where *Ixodes lividus* was reported.

et al. 2018), Kuybyshev Reservoir (Republic of Tatartstan) (Lvov et al. 2014), Voronezh Oblast (Gaponov and Tewelde 2021), Tymen Oblast (Starikov et al. 2017b), Kurgan Oblast (Starikov and Starikova 2021), Omsk Oblast (Tagiltsev et al. 1984; Yakimenko et al. 1991), Tomsk Oblast, Kemerovo Oblast (Kovalevsky et al. 2019), Novosibirsk Oblast (Yakimenko et al. 2013), Irkutsk Oblast (Danchinova et al. 2007), Ikatsky Ridge (Republic of Buryatia), Zabaykalsky Krai (Emelyanova et al. 1963), Republic of Tuva (Kholodilov et al. 2019), Sakha (Yakutia) (Shadrina et al. 2011), Khabarovsk Krai (Volkov and Chernykh 1977). **Ukraine:** Zakarpattia Oblast, Kaniv Nature Reserve (Cherkasy Oblast), (Emchuk 1960), Danube Biosphere Nature Reserve (Odesa Oblast) (Emchuk 1960; Didyk 2013), Kyiv (Akimov and Nebogatkin 2002), delta of the Dniestr River (Rusev 2009). **Belarus:** Gomel Region, Minsk Region (Gembetsky 1972). **Moldova:** banks of the Dniestr River (Movila et al. 2008). **Kazakhstan:** Atyrau Region (Pomerantsev 1950; Levit 1957), Kostanay Region (Makhmetov 1961), Pavlodar Region (Amirova et al. 1989), Akmola Region (Filippova 1961; Ushakova 1962).

**Ecology and other information.** *Ixodes lividus* is a specific nidicolous ectoparasite of the sand martin, *Riparia riparia*. Also, it has been collected from birds and house mice which occasionally could visit sand martin's nests such as house sparrows and common house martins.

Due to the wide distribution of its main host, this tick species also occurs in a vast geographical range and can be characterized by having a trans-Palearctic distribution. The locations of findings in Russia and the neighboring countries listed above reflect the general pattern of its distribution on a map so we can suppose that this tick can be found in the north of the Palearctic almost everywhere in habitats of the sand martin.

### *Ixodes prokopjevi* (Emel´yanova, 1979)

*Pholeoixodes prokopjevi* Emel'yanova, 1979: 14.

**Recorded hosts. Mammalia:** Daurian hedgehog *Mesechinus dauuricus* (Sundevall) (Emelyanova 1979).

**Recorded locations (Fig. 28). Russia:** Transbaikal (Emelyanova 1979).

**Ecology and other information.** *Ixodes prokopjevi* is an extremely poorly studied tick species initially described based on the male holotype from steppes of north-eastern Mongolia; its paratypes, larvae and nymphs, are noted as originating from the outskirts of the lake Baruun Shavart Nuur in Eastern Mongolia, as well as females and nymphs from the south-eastern Transbaikal without any indications of certain points of findings (Emelyanova 1979).

Kolonin (2009) states that this species should be considered a synonym of *I. crenulatus* but Guglielmone et al. (2010, 2014) recognize it as a valid species.

The Daurian hedgehog was recorded as a host, but we can assume that carnivores, lagomorphs, and rodents are also hosts of this tick species, as in case of *I. crenulatus*, another representative of the subgenus *Pholeoixodes* and the most similar species to this tick. The distribution area and ecology of *I. prokopjevi*, as well host-parasite relationships and their role in transmission of vector-borne infections remain unknown.


**Figure 28.** Map of Russia and neighboring countries showing the locations where *Ixodes prokopjevi* was reported.

### ***Ixodes subterraneus* Filippova, 1961**

*Ixodes subterranus* Filippova, 1961: 226. Morel and Pérez 1973: 275.
*Pholeoixodes arboricola koshkinae* Emel'yanova: Kolonin 1981: 20.
*Pholeoixodes arboricola deserta* Emel'yanova: Kolonin 1981: 20.

**Recorded hosts. Aves:** *Athene noctua* (little owl), *Carduelis carduelis* (European goldfinch), *Coracias garrulus* (European roller), *Coturnix coturnix* (common quail), *Galerida cristata* (crested lark), *Falco naumanni* Fleischer (lesser kestrel), *Oenanthe hispanica* (western black-eared wheatear), *Oenanthe isabellina* (isabelline wheatear), *Oenanthe oenanthe* (northern wheatear), *Parus major* (great tit), *Passer ammodendri* Gould (saxaul sparrow), *Passer domesticus* (house sparrow), *Passer montanus* (Eurasian tree sparrow), *Pastor roseus* (rosy starling), *Petronia petronia* (rock sparrow), *Pica pica* (Eurasian magpie), *Sturnus vulgaris* (common starling), *Turdus ruficollis* (red-throated thrush) (Filippova 1977).

**Recorded locations (Fig. 29). Russia:** Transbikalia (Barguzin Valley, Cape Ryty) (Emelyanova 1972, as *I. arboricola*). **Kazakhstan:** Mangyshlak Peninsula (Maslennikova and Ushakova 1971), Jambyl Region (Kokuzek), Trans-Ili Alatau, Syugaty Valley (Maslennikova and Stogov 1974), Almaty Region (lower reaches of the Ili River) (Ushakova 1958, as *Ixodes* sp.), Dzungarian Alatau (Ushakova et al. 1976). **Kyrgyzstan:** Jalal-Abad Region (Bazar-Korgon District), the valley of the river Naryn (Grebenyuk 1966). **Turkmenistan:** Krasnovodsk plateau, outskirts of Geok Tepe, Kara Kala, Ashgabat, Tejen, Baýramaly, highland Badhyz (Filippova 1961; Kochkareva et al. 1971; Scherbinina 1973). **Tajikistan:** southern spurs of the Hisar Range – the vicinity of Hisar (Filippova 1977).

**Ecology and other information.** *Ixodes subterraneus* is a parasite of birds nesting in ground burrows (Filippova 1977). The main part of its distribution


**Figure 29.** Map of Russia and neighboring countries showing the locations where *Ixodes subterraneus* was reported.

lies in Kazakhstan and Middle Asia, the lesser part in Transbaikalia (Russia) (Filippova 1977). This tick species can be found in foothill dry steppes, as well as near and in deserts. This species was originally named *I. subterranus* in Filippova (1961) but amended to *I. subterraneus* in Filippova (1977).

**Subgenus *Scaphixodes* Schulze, 1941: 491**

***Ixodes berlesei* Birula, 1895**

*Ixodes berlesei* Birula, 1895: 353.

**Recorded hosts. Aves:** *Apus pacificus* (Latham) (Pacific swift), *Corvus frugilegus* Linnaeus (rook), *Falco rusticolus* Linnaeus (gyrfalcon), *Falco tinnunculus* Linnaeus (common kestrel), *Monticola solitarius* (blue rock thrush), *Montifringilla nivalis* (Linnaeus) (white-winged snowfinch), *Phoenicurus erythrogastrus* (Güldenstädt) (Güldenstädt's redstart), *Phoenicurus ochruros* (black redstart), *Phoenicurus erythronotus* (Eversmann's redstart), *Plectrophenax nivalis* (Linnaeus) (snow bunting), *Prunella collaris* (Scopoli) (alpine accentor), *Sturnus vulgaris* (common starling), *Tichodroma muraria* (Linnaeus) (wallcreeper) (Filippova 1977; Voltsyt 1997).

**Recorded locations (Fig. 30). Russia:** Dagestan (Filippova 1977), Western Siberia – Salair Ridge, Kuznetsk Alatau (Chunihin 1967), Eastern Siberia – banks of the Angara River (Birula 1895) and Buryatia (Ikatsky Ridge) (Emelyanova et al. 1963), Bering Island (Voltsyt 1997). **Kazakhstan:** Trans-Ili Alatau (Grebenyuk 1966). **Kyrgyzstan:** Aksay Valley (Grebenyuk 1966). **Turkmenistan:** outskirts of Ashgabad (Filippova 1977). **Tajikistan:** Hisar Range, Varzob gorge (Ivanov 1945; Lotozky 1945).

**Ecology and other information.** *Ixodes berlesei* is a little studied nidicolous tick occurring in the Greater Caucasus, as well as in Middle Asia and Siberia.


**Figure 30.** Map of Russia and neighboring countries showing the locations where *Ixodes berlesei* was reported.

There is one report about a finding of this tick on the Bering Island belonging to the Commander Islands in the Bering Sea, a female and three larvae collected 26 August 1990 from a snow bunting and deposited at the collection of the Zoological Museum of Moscow State University (Voltsyt 1997). The author states that the date of the tick collection indicates the presence of a permanent population of this species on the island because in the end of August birds usually already are prepared for the autumn migration after the breeding period, and, therefore, ticks could not have been transported there from the continent. Hence, we could assume that probably the real distribution of this tick is much wider and includes mountainous areas not only in a warmer and temperate climate but also in cooler tundra and other climatically similar landscapes. The snow bunting as a host of this species also was registered for the first time. Overall, its hosts include birds nesting usually in rocks and feeding on the ground and during the flight (Filippova 1977).

The type specimen is deposited at the Zoological Institute of the Russian Academy of Sciences - holotype: female; 683, [Russia, Siberia] Angara, 1867, Chekanovskii, type; AL I528. Description – Filippova 1977: 230–236 (female, nymph, larva; male unknown) (Filippova 2008).

### *Ixodes caledonicus* Nuttall, 1910

*Ixodes caledonicus* Nuttall, 1910: Nuttall 1910: 408.
*Ixodes caledonicus sculpturatus* Schulze, 1929: 60; Arthur 1963: 53.
*Ixodes gussevi* Reznik, 1958: 457; Filippova and Panova 1975: 339.

**Recorded hosts. Aves:** *Apus pacificus* (Pacific swift), *Corvus corax* Linnaeus (common raven), *Corvus cornix* (hooded crow), *Columba livia* (common pigeon),


**Figure 31.** Map of Russia and neighboring countries showing the locations where *Ixodes caledonicus* was reported.

*Coloeus monedula* (western jackdaw), *Falco peregrinus* (peregrine falcon), *Monticola solitarius* (blue rock thrush), *Oenanthe oenanthe* (Northern wheatear), *Petronia petronia* (rock sparrow), *Phoenicurus* sp. (redstart), *Tachymarptis melba* (Linnaeus) (Alpine swift) (Filippova 1977; Bolotin and Kolonin 1979).

**Recorded locations (Fig. 31). Russia:** valley of the Zerkalnaya River (Bolotin and Kolonin 1979). **Ukraine:** Crimean Peninsula, in particular the Tarkhankut Peninsula and the cape Kazantyp (Emchuk 1960; Filippova 1977). **Azerbaijan:** Qabala (Reznik 1958), Julfa (Filippova and Panova 1975). **Tajikistan:** Hisar Range (Filippova and Panova 1975).

**Ecology and other information.** *Ixodes caledonicus* is a little studied nidicolous tick species occurring in Europe as well as Western and Middle Asia. In Crimea this species is very rare and never has been found after 1980 (Nebogatkin 1998). Its hosts are birds that usually nest in rocks, feed on the ground, or feed and drink during flight (Filippova 1977).

### ***Ixodes semenovi* Olenev, 1929**

*Ixodes semenovi* Olenev, 1929: 489.

**Recorded hosts. Aves:** *Prunella collaris* (alpine accentor), *Pyrrhocorax pyrrhocorax* (Linnaeus) (red-billed chough) (Filippova 1977).

**Recorded locations (Fig. 32). Kazakhstan:** Tian Shan – the northern slope of the Kyrgyz Ala-Too Range, the source of the river Merke (Jambyl Region) (Olenev 1929b). **Kyrgyzstan:** Terskey Ala-too Range (Grebenyuk 1961, 1966).

**Ecology and other information.** *Ixodes semenovi* is a very rare species in the post-Soviet territories known only from Kazakhstan and Kyrgyzstan, from


**Figure 32.** Map of Russia and neighboring countries showing the locations where *Ixodes semenovi* was reported.

the Tian Shan, where it inhabits rocks at an altitude of 2000 m a. s. l. (Filippova 1977). The type specimen of *I. semenovi* is deposited at the Zoological Institute of the Russian Academy of Sciences: the holotype - female; Mi[ddle] Asia, Aleksandrovskii Mt. Range [Kirgizskii Ala Tau], source of Merke River, Aral-Tyube, from *Accentor collaris*, 4.VII.1929, coll. I.A. Portenko; AL I549. Description – Filippova 1977: 219–223 (female, male, nymph; larva unknown) (Filippova 2008).

### *Ixodes signatus* Birula, 1895

*Ixodes signatus* Birula, 1895: 353.
*Ixodes arcticus* Osborn: Cooley and Kohls 1945: 201.
*Ixodes parvirostris* Neumann: Neumann 1904: 444.
*Ixodes eudyptidis v. signata* Birula: Neumann 1911: 21.

**Recorded hosts. Aves:** *Phalacrocorax carbo* (Linnaeus) (great cormorant), *Urile pelagicus* (pelagic cormorant), *Urile penicillatus* (Brandt) (Brandt's cormorant), *Urile urile* (red-faced cormorant) (Filippova 1977).

**Recorded locations (Fig. 33). Russia:** islands: Furugelm Island, Tyuleniy Island, the Kuril Islands – Paramushir, Urup and Makanrushi, the Commander Islands – the Kamen Ariy and the Bering Island (Kirschenblatt 1936; Pomerantsev 1950; Violovich 1958, 1962a; Leonova et al. 1971; Timofeeva et al. 1971, 1974; Lvov et al. 2014b); mainland – Primorsky Krai (Lazovsky District) (Kozlovskaya el al. 1968).

**Ecology and other information.** *Ixodes signatus* is a nidicolous tick species occurring in several archipelagos and separate islands of the Russian Far East,


**Figure 33.** Map of Russia and neighboring countries showing the locations where *Ixodes signatus* was reported.

as well as in Japan and the west coast of North America together with the Pacific islands nearby (Filippova 1977). It inhabits mostly coastal rocks being an obligate parasite of cormorants. Other birds, for example the Siberian thrush *Geokichla sibirica* (Pallas), are considered occasional hosts (Violovich 1962a). Findings in the mainland Eurasia are probably occasional cases of transportation (Kozlovskaya et al. 1968).

The type specimens of *I. signatus* are deposited at the Zoological Institute of the Russian Academy of Sciences (Filippova 2008) and include the lectotype: female; [Aleut Islands], Unalashka, 1846, coll. Voznesenskii, type; AL I358; paralectotypes: 8 females, 1 nymph, AL I358a; 2 females; CB I3170, I3171. Description – Filippova 1977: 204–210 (female, male, nymph, larva).

### *Ixodes unicavatus* Neumann, 1908

*Ixodes unicavatus* Neumann, 1908: 109; Schulze 1941: 491.
*Ixodes tauricus* Vshivkov & Filippova, 1957: 553; Gilot and Beaucournu 1973: 131.

**Recorded hosts. Aves:** *Gulosus aristotelis* (European shag) (Linnaeus) (Filippova 1977).

**Recorded locations (Fig. 34). Ukraine:** Crimean Peninsula, in particular the Tarkhankut Peninsula, The Kara Dag, the Kerch Peninsula, the cape Kazantyp (Emchuk 1960; Filippova 1977).

**Ecology and other information.** *Ixodes unicavatus* is an endophilic tick occurring in Europe primarily in coastal areas of the Atlantic Ocean and which can be found in its hosts' nests and under stones near them (Filippova 2007). It uses mostly cormorants - the European shag *Gulosus aristotelis* and the great


**Figure 34.** Map of Russia and neighboring countries showing the locations where *Ixodes unicavatus* was reported.

cormorant *Phalacrocorax carbo* as hosts (Schulze 1932; Arthur 1963; Guiguen et al. 1987; Kolonin 2008). In Crimea, this species has been known from a little number of specimens (Serdjukova 1956; Emchuk 1960).

**Subgenus *Trichotoixodes* Reznik, 1961: 276.**

***Ixodes brunneus* Koch, 1844**

*Ixodes brunneus* Koch, 1844a: 232.
*Ixodes californicus* Banks, 1904: Keirans and Clifford 1978: 54.
*Ixodes kelloggi* Nuttall & Warburton, 1907: Cooley and Kohls 1945: 205.

**Recorded hosts. Aves:** *Lanius collurio* (red-backed shrike) (Filippova 1977)

**Recorded locations (Fig. 35). Ukraine:** Crimea – Sudak City Municipality, the village Perevalivka (Filippova 1977).

**Ecology and other information.** *Ixodes brunneus* is a tick occurring mainly in the Americas being predominantly a parasite of passerine birds (Filippova 1977). The only record in Crimea on a red-backed shrike is considered a case of accidental introduction (Tsapko 2020).

***Ixodes frontalis* (Panzer, 1798)**

*Acarus frontalis* Panzer, 1798: 59, 23; Koch 1844a: 234.
*Ixodes pallipes* (Fabricius): Arthur 1963: 111.
*Ixodes pari* Leach, 1815: 399; Neumann 1911: 18.
*Ixodes sturni* Pagenstecher: Neumann 1901, 249.


**Figure 35.** Map of Russia and neighboring countries showing the locations where *Ixodes brunneus* was reported.

*Ixodes avisugus* Berlese: Neumann 1899: 107.
*Ixodes apronatus* Kirshenblat, 1934: 257; Arthur 1963: 111.
*Ixodes sigalasi* Lamontellerie, 1954: 561; Lamontellerie 1965: 87.

**Recorded hosts. Aves:** *Alectoris chukar* (chukar partridge), *Caprimulgus europaeus* Linnaeus (European nightjar), *Chloris chloris* (European greenfinch), *Corvus frugilegus* (rook), *Curruca communis* (common whitethroat), *Curruca curruca* (lesser whitethroat), *Erithacus rubecula* (European robin), *Falco tinnunculus* (common kestrel), *Fringilla coelebs* (Eurasian chaffinch), *Fringilla montifringilla* (brambling), *Garrulus glandarius* (Eurasian jay), *Hippolais icterina* (Vieillot) (icterine warbler), *Lanius collurio* (red-backed shrike), *Luscinia luscinia* (thrush nightingale), *Luscinia megarhynchos* (Brehm) (common nightingale), *Muscicapa striata* (spotted flycatcher), *Oenanthe hispanica* (western black-eared wheatear), *Oenanthe isabellina* (isabelline wheatear), *Parus major* (great tit), *Passer domesticus* (house sparrow), *Passer montanus* (Eurasian tree sparrow), *Petronia petronia* (rock sparrow), *Phoenicurus phoenicurus* (common redstart), *Phylloscopus trochilus* (willow warbler), *Phasianus colchicus* (common pheasant), *Pica pica* (Eurasian magpie), *Regulus regulus* (Linnaeus) (goldcrest), *Saxicola rubetra* (Linnaeus) (whinchat), *Streptopelia turtur* (Linnaeus) (European turtle dove), *Turdus iliacus* (redwing), *Turdus merula* (common blackbird), *Turdus philomelos* (song thrush), *Turdus torquatus* Linnaeus (ring ouzel), *Turdus viscivorus* (mistle thrush) (Filippova 1977).

**Mammalia:** *Meriones libycus* (Libyan jird) (Tsapko and Kotti 2017).

**Recorded locations (Fig. 36). Russia:** Kurgan Oblast – the rural locality Ketovo (Ruzsky 1929), Stavropol Krai (Reznik 1950; Guseva 1962; Tiflova et al. 1970), Krasnodar Krai; Chechnya (Marutyan 1963; Baisarova 2021), Dagestan (Gusev and Guseva 1960). **Ukraine:** Poltava Oblast (Olenev 1931a), Odesa Oblast, Mykolaiv Oblast, Kherson Oblast (Rusev 2009), Crimea (Filippova 1977). **Belarus:** Pripyatsky National Park (Tsvirko 2008). **Moldova:** Codru (Morozov et al. 2022),


**Figure 36.** Map of Russia and neighboring countries showing the locations where *Ixodes frontalis* was reported.

Olănești (Filippova 1977), Chishinau (Morozov and Proka 2012). **Armenia:** Syunik Province (former Goris Province) (Ogandzhanyan 1984). **Azerbaijan:** Alazani River (Ter-Vartanov et al. 1956), Lankaran (Filippova 1977), Shaki District (Tsapko and Kotti 2017). **Georgia:** Kutaisi, Lagodekhi, Dedoplistsqaro (Kirschenblatt 1936; Djaparidze 1960), Guria (Sukhiashvili et al. 2020). **Turkmenistam:** outskirts of Magtymguly, Aydere (Berdyev and Annaev 1997).

**Ecology and other information.** *Ixodes frontalis* is an exophilic tick species parasitizing primarily dendrophilic birds (Filippova 1977). It is relatively widely distributed throughout Europe, Western Asia, as well as North Africa (Filippova 1977; Estrada-Peña et al. 2018). *Ixodes frontalis* is rare in most of its range. However, the place of mass reproduction of this species was discovered in Dagestan near the Sulak River in a big colony of rooks (Gusev and Guseva 1960). Under the nests in the rookery, a high, uncountable number of larvae of these ticks was observed. Often there were up to 5,000 individuals per $m^2$ (Tsapko 2023).

Single collections of *I. frontalis* from mammals are known as exceptions. In Europe, adults were found on representatives of the mustelid family (Guglielmone et al. 2014). In the Shaki District of Azerbaijan (2 km north of the village of Şirinbulaq, 31 Oct 1956), two nymphs were taken from two Libyan jird *Meriones libycus* (collections of R.B. Kosminsky and R.S. Karandina) (Tsapko and Kotti 2017). In addition, certain cases of attachments to humans are known (Gilot et al. 1997).

### *Ixodes turdus* Nakatsudi, 1942

*Ixodes turdus* Nakatsudi, 1942: 287.

**Recorded hosts. Aves:** *Turdus pallidus* Gmelin (pale thrush) (Bolotin and Kolonin 1979).


**Figure 37.** Map of Russia and neighboring countries showing the locations where *Ixodes turdus* was reported.

**Recorded locations (Fig. 37). Russia:** Primorsky Krai, Nadezhdinsky District, the right shore of the Razdolnaya River (Bolotin and Kolonin 1979).

**Ecology and other information.** *Ixodes turdus* is a bird-associated tick species that can be found usually in East Asia, especially in Nepal, Korea, and Japan (Takahashi and Chunikhin 1972; Clifford et al. 1975; Ishiguro et al. 2000; Kim et al. 2009b; Sato et al. 2021). The single case of finding *I. turdus* in the Far East of Russia is considered a result of transportation (Bolotin and Kolonin 1979). Some occasions of parasitism on humans (Woo et al. 1990; Kadosaka and Hasegawa 1996), as well as on wild boars (Chae et al. 2017) are also recorded.

## Discussion

The territory of Russia and other post-Soviet countries reviewed here occupies a significant part of the Palearctic and its *Ixodes* tick fauna comprises in total approximately 37 species belonging to ten subgenera (Table 1). Some of these species are endemic. A significant ratio of these *Ixodes* species have a broad distribution area, as exemplified by *I. ricinus*, *I. persulcatus*, *I. trianguliceps*, *I. apronophorus*, *I. crenulatus*, *I. kaiseri*, *I. laguri*, *I. redikorzevi*, *I. eldaricus*, *I. frontalis*, and *I. lividus*. Moreover, the geographical range of some of these species also continues further to the west (into Europe) and to the south and east (to other parts of Asia).

Tick species like *I. ricinus* and *I. persulcatus* are able to live in a broad range of forest and forest-steppe biotopes and parasitize literally any vertebrate hosts among mammals, birds, and in some cases reptiles available in their habitats. Further species listed above parasitize species of those ecological groups of higher vertebrates which are widely distributed within the limits of the reviewed territories and even outside of them (like shrews, rodents, carnivores, and passerines), so this could explain the wide distribution of these species together

with the presence of suitable hosts and biotopes. On the other hand, five tick species – *I. stromi*, *I. semenovi*, *I. signatus*, *I. uriae*, *I. occultus* – have more limited distribution areas, occurring only in certain habitats where they are specialized to parasitize an ecologically restricted range of hosts. There are at least five tick species (*I. angustus*, *I. pomerantzevi*, *I. nipponensis*, *I. kashmiricus*, *I. redikorzevi*) which have geographical ranges extending far beyond post-Soviet territories, and these also occur in neighboring and more distant countries sharing a similar fauna. The distribution areas of six further species (*I. berlesei*, *I. caledonicus*, *I. arboricola*, *I. subterraneus*, *I. simplex*, *I. vespertilionis*) cannot be defined more precisely, due to the limited number of their findings in locations distantly separated from each other. It is important to note here that these ticks are nidicolous parasites of birds and bats, therefore can be transported by their hosts to new habitats in other locations during migration, although it is not necessary that they will establish and form sustainable populations there. The distribution area of the tick *I. pavlovskyi* is also disjunct and populated by two different subspecies. Finally, there are four tick species known exclusively from the reviewed territories and certain locations by a very few records and their real distribution areas and biology are poorly studied, namely *I. cornutus*, *I. ghilarovi*, *I. maslovi*, and *I. prokopjevi*.

It is still questionable whether or not *I. brunneus* and *I. turdus* are indigenous in the examined geographical area. There have been no confirmations of stable populations of these two species in the locations where both species were found on migratory birds; both are known from these territories by single specimens outside their main distribution areas. Therefore, we suspect that these two tick species do not belong to the tick fauna of Russia and post-Soviet territories.

Among the reviewed *Ixodes* species, from the point of view of host preferences, there are both generalists and specialists. Rodents of the families Muridae and Cricetidae, as well as passerine birds, harbor the highest number of *Ixodes* species in the reviewed territories (Table 2). All these groups live almost everywhere in a great variety of biotopes, often in significant numbers, therefore playing an important role in diverse ecosystems and also having epidemiological significance as reservoirs of multiple tick-borne pathogens. Among the ticks in this review, 15 species parasitize murine rodents and 14 passerine birds (Table 2). Shrews (family Soricidae) also include a relatively high number of species which are ubiquitous and serve as typical hosts for certain *Ixodes* species, predominantly from the subgenera *Filippoviella* and *Ixodiopsis*.

In general, 18 *Ixodes* species are typically parasites of mammals from various taxonomic and ecological groups, 12 species prefer birds as hosts. Altogether, six species are generalists and therefore can parasitize virtually any available warm-blooded host species. All these species belong to the subgenus *Ixodes*. Ticks from other subgenera can attach to and feed from atypical hosts occasionally. Specific parasites of reptiles among *Ixodes* species are not known to occur in the reviewed territories, but some of the generalist species can parasitize these hosts, especially in the absence of their preferred ones. Sometimes even mass parasitism of *Ixodes* species can be observed on reptiles, as in the case of *I. redikorzevi*. Last, we can note that hosts of *I. maslovi* are still unknown, and the exact host range of *I. cornutus*, *I. ghilarovi*, *I. prokopjevi*, and *I. sachalinensis* also remains to be clarified.

**Table 1.** The list of *Ixodes* subgenera and species according to post-Soviet countries.

| Tick subgenus | Tick species | Russia | Belarus | Ukraine | Moldova | Georgia | Armenia | Azerbaijan | Kazakhstan | Kyrgyzstan | Uzbekistan | Turkmenistan | Tajikistan |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Ceratixodes*** | *I. uriae* | + | | | | | | | | | | | |
| ***Eschatocephalus*** | *I. simplex* | + | | + | | | | + | | | | | |
| | *I. vespertilionis* | + | | + | + | + | + | + | | + | | + | + |
| ***Filippoviella*** | *I. ghilarovi* | + | | | | + | | | | | | | |
| | *I. trianguliceps* | + | + | + | + | + | + | + | | | | | |
| ***Ixodes*** | *I. apronophorus* | + | + | + | + | | | | + | + | | | |
| | *I. eldaricus* | + | | + | | + | + | + | + | + | + | + | + |
| | *I. kazakstani* | | | | | | | | + | + | | | |
| | *I. kashmiricus* | | | | | | | | | + | | | |
| | *I. laguri* | + | | + | + | + | + | + | + | | | + | |
| | *I. nipponensis* | + | | | | | | | | | | | |
| | *I. occultus* | | | | | | | | + | | + | + | |
| | *I. pavlovskyi* | + | | | | | | | + | + | | | |
| | *I. persulcatus* | + | + | + | | | | | + | + | | | |
| | *I. redikorzevi* | + | | + | + | + | + | + | + | + | + | + | + |
| | *I. ricinus* | + | + | + | + | + | + | + | + | | | + | |
| | *I. sachalinensis* | + | | | | | | | | | | | |
| ***Ixodiopsis*** | *I. angustus* | + | | | | | | | | | | | |
| | *I. pomerantzevi* | + | | | | | | | | | | | |
| | *I. stromi* | + | | | | | | | + | + | | | + |
| ***Monoixodes*** | *I. maslovi* | + | | | | | | | | | | | |
| ***Pholeoixodes*** | *I. arboricola* | + | + | + | + | + | + | + | | + | | | |
| | *I. cornutus* | | | | | | | | | | | | + |
| | *I. crenulatus* | + | + | + | + | + | + | | + | + | + | + | + |
| | *I. hexagonus* | | | + | | | | | | | | | |
| | *I. kaiseri* | + | | + | + | + | + | + | + | + | | | |
| | *I. lividus* | + | + | + | + | | | | + | | | | |
| | *I. prokopjevi* | + | | | | | | | | | | | |
| | *I. subterraneus* | + | | | | | | | + | + | | + | + |
| ***Scaphixodes*** | *I. signatus* | + | | | | | | | | | | | |
| | *I. berlesei* | + | | | | | | | + | + | | + | + |
| | *I. caledonicus* | + | | + | | | | + | | | | | + |
| | *I. unicavatus* | | | + | | | | | | | | | |
| | *I. semenovi* | | | | | | | | + | + | | | |
| ***Trichotoixodes*** | *I. brunneus* * | | | + | | | | | | | | | |
| | *I. frontalis* | + | + | + | + | + | + | + | | | | + | |
| | *I. turdus* * | + | | | | | | | | | | | |
| **Total number of species** | | **29** | **8** | **18** | **11** | **11** | **10** | **11** | **16** | **15** | **4** | **10** | **9** |
| **Total number of subgenera** | | **9** | **4** | **6** | **5** | **5** | **5** | **6** | **4** | **5** | **2** | **5** | **5** |

* non-indigenous (transported) tick species in the reviewed territories.

**Table 2.** The list of *Ixodes* tick subgenera and species according to host taxa recorded in post-Soviet countries.

| Tick subgenus | Tick species | Host taxonomic groups |
|---|---|---|
| ***Ceratixodes*** | *I. uriae* | **Aves:** |
| | | Charadriiformes – Alcidae, Laridae; |
| | | Suliformes – Phalacrocoracidae; |
| | | Procellariiformes – Procellariidae |
| ***Eschatocephalus*** | *I. simplex* | **Mammalia**: |
| | | Chiroptera |
| | *I. vespertilionis* | **Mammalia**: |
| | | Chiroptera |
| ***Filippoviella*** | *I. ghilarovi* | **Mammalia**: |
| | | Eulipotyphla – Soricidae; |
| | | Rodentia – Cricetidae, Muridae |
| | *I. trianguliceps* | **Mammalia**: |
| | | Eulipotyphla – Soricidae; |
| | | Rodentia – Cricetidae, Muridae, Sminthidae |
| ***Ixodes*** | *I. apronophorus* | **Mammalia**: |
| | | Eulipotyphla – Erinaceidae, Soricidae, Talpidae; |
| | | Rodentia – Cricetidae, Muridae, Sciuridae, Sminthidae; |
| | | Lagomorpha – Leporidae; |
| | | Carnivora – Canidae, Mustelidae |
| | *I. eldaricus* | **Aves:** |
| | | Galliformes; |
| | | Passeriformes; |
| | | Strigiformes |
| | | **Mammalia**: |
| | | Eulipotyphla – Soricidae; |
| | | Rodentia – Cricetidae, Muridae |
| | *I. kazakstani* | **Aves:** |
| | | Galliformes |
| | | **Mammalia:** |
| | | Lagomorpha – Leporidae; |
| | | Rodentia – Cricetidae, Muridae, Gliridae |
| | *I. kashmiricus* | **Mammalia**: |
| | | Rodentia – Muridae; |
| | | Carnivora – Canidae; |
| | | Artiodactyla – Bovidae |
| | *I. laguri* | **Mammalia:** |
| | | Eulipotyphla – Erinaceidae; |
| | | Rodentia – Cricetidae, Gliridae, Dipodidae, Muridae, Sciuridae, Spalacidae; |
| | | Carnivora – Canidae, Mustelidae |
| | *I. nipponensis* | **Mammalia:** |
| | | Rodentia – Cricetidae, Muridae |
| | *I. occultus* | **Mammalia**: |
| | | Eulipotyphla – Soricidae; |
| | | Rodentia – Cricetidae, Muridae, Sciuridae |
| | *I. pavlovskyi* | **Aves:** |
| | | Anseriformes; |

| Tick subgenus | Tick species | Host taxonomic groups |
|---|---|---|
| ***Ixodes*** | *I. pavlovskyi* | Columbiformes; |
| | | Galliformes; |
| | | Gruiformes; |
| | | Passeriformes |
| | | **Mammalia**: |
| | | Eulipotyphla – Soricidae; |
| | | Lagomorpha – Leporidae, Ochotonidae; |
| | | Rodentia – Cricetidae, Muridae, Sciuridae, Sminthidae |
| | *I. persulcatus* | Any mammalian and avian hosts (rarely reptilian) available |
| | *I. redikorzevi* | **Aves:** |
| | | Anseriformes; |
| | | Columbiformes; |
| | | Galliformes; |
| | | Passeriformes; |
| | | Pterocliformes |
| | | **Mammalia**: |
| | | Eulipotyphla – Erinaceidae, Soricidae; |
| | | Lagomorpha – Leporidae; |
| | | Rodentia – Cricetidae, Gliridae, Muridae, Sciuridae, Sminthidae, Spalacidae |
| | | Carnivora – Canidae, Mustelidae |
| | | **Reptilia:** |
| | | Squamata – Lacertidae |
| | *I. ricinus* | **Mammalia, Aves, Reptilia** |
| | *I. sachalinensis* | **Mammalia**: |
| | | Lagomorpha – Leporidae |
| ***Ixodiopsis*** | *I. angustus* | **Mammalia**: |
| | | Eulipotyphla – Soricidae; |
| | | Rodentia – Cricetidae, Muridae, Sciuridae, Sminthidae; |
| | | Lagomorpha – Ochotonidae |
| | *I. pomerantzevi* | **Mammalia**: |
| | | Eulipotyphla – Erinaceidae, Soricidae; |
| | | Rodentia – Cricetidae, Muridae, Sciuridae |
| | *I. stromi* | **Mammalia**: |
| | | Eulipotyphla – Soricidae; |
| | | Rodentia – Cricetidae, Muridae; |
| | | Lagomorpha – Ochotonidae; |
| | | Carnivora – Mustelidae |
| ***Monoixodes*** | *I. maslovi* | Unknown |
| ***Pholeoixodes*** | *I. arboricola* | **Aves:** |
| | | Accipitriformes; |
| | | Bucerotiformes; |
| | | Columbiformes; |
| | | Passeriformes; |
| | | Piciformes; |
| | | Strigiformes; |
| | | Falconiformes |
| | *I. cornutus* | **Mammalia**: |
| | | Carnivora – Mustelidae |

| Tick subgenus | Tick species | Host taxonomic groups |
|---|---|---|
| ***Pholeoixodes*** | *I. crenulatus* | **Mammalia**: |
| | | Eulipotyphla – Erinaceidae; |
| | | Rodentia – Cricetidae, Muridae, Sciuridae, Pálcaidé; |
| | | Lagomorpha – Ochotonidae, Leporidae; |
| | | Carnivora – Canidae, Felidae, Mustelidae, Procyonidae |
| | *I. hexagonus* | **Mammalia**: |
| | | Eulipotyphla – Erinaceidae; |
| | | Lagomorpha – Leporidae; |
| | | Carnivora – Canidae, Felidae, Mustelidae |
| | *I. kaiseri* | **Mammalia**: |
| | | Eulipotyphla – Erinaceidae; |
| | | Rodentia – Hystricidae; |
| | | Lagomorpha – Leporidae; |
| | | Carnivora – Canidae, Felidae, Hyaenidae, Mustelidae |
| | *I. lividus* | **Aves:** |
| | | Passeriformes; |
| | | Coraciiformes |
| | *I. prokopjevi* | **Mammalia**: |
| | | Eulipotyphla – Erinaceidae |
| | *I. subterraneus* | **Aves:** |
| | | Galliformes; |
| | | Passeriformes; |
| | | Strigiformes; |
| | | Falconiformes |
| ***Scaphixodes*** | *I. signatus* | **Aves:** |
| | | Phalacrocoracidae – Phalacrocoracidae |
| | *I. berlesei* | **Aves:** |
| | | Apodiformes; |
| | | Passeriformes; |
| | | Falconiformes |
| | *I. caledonicus* | **Aves:** |
| | | Apodiformes; |
| | | Columbiformes; |
| | | Passeriformes; |
| | | Falconiformes |
| | *I. unicavatus* | **Aves:** |
| | | Suliformes – Phalacrocoracidae |
| | *I. semenovi* | **Aves:** |
| | | Passeriformes |
| ***Trichotoixodes*** | *I. brunneus* * | **Aves:** |
| | | Passeriformes |
| | *I. frontalis* | **Aves:** |
| | | Caprimulgiformes; |
| | | Columbiformes; |
| | | Galliformes; |
| | | Passeriformes; |
| | | Falconiformes |
| | *I. turdus* * | **Aves:** |
| | | Passeriformes |

* non-indigenous (transported) tick species in the reviewed territories.

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## Additional information

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The authors have declared that no competing interests exist.

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### Author contributions

Denis Fedorov: writing, data curation, methodology. Sándor Hornok: conceptualization, writing, methodology.

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### Data availability

All of the data that support the findings of this study are available in the main text.

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