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# Cosmopolitan Distribution of the Spitting Spider *Scytodes thoracica* Latreille, 1802 (Aranei, Scytodidae) and Its New Findings in the Northern Parts of the Range

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**Abstract**—We have compiled data on the distribution of spitting spider *Scytodes thoracica* Latreille, 1802 throughout the world and discussed our original findings of the spider in the northern part of its Eurasian range. This cosmopolitan species has a Mediterranean origin; the only place where it has not been found is Antarctica. The wide distribution of this species is due to the anthropogenic factor. However, *S. thoracica* demonstrates synanthropic behavior outside its natural range. Based on the published data of studies in the Mediterranean region, we describe the range of this species as a synanthrope; there lies the northern border of its range. We also determine the northern border of the range in natural areas (including agricultural landscapes). The southern region of the Middle Volga is the northernmost location of *S. thoracica* in the natural ecosystems of Eastern Europe and the easternmost location in the natural ecosystems of northern Eurasia.

*Keywords:* Aranei, Scytodidae, *Scytodes thoracica*, spitting spider, range, synanthrope, cosmopolitan, dispersal, anthropochory, colonization, July isotherm, Mediterranean, Europe, Middle Volga region, Samara oblast

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Like most animal species, spiders are capable of active distribution. Their distribution across large areas and the expansion or their range is partially provided by passive ways of dispersal, such as anemochory (dispersal by air flows) and biochory (dispersal by vertebrates, including birds and large mammals). The distance and direction of spider dispersal by wind depends on the local features of the wind rose. The dispersal by vertebrates depends on their motor activity and migration routes. Independent dispersal (autochory) depends on the presence of suitable habitats. All three types of dispersal are constantly used by spiders. These types of dispersal are limited by geographic barriers, such as high mountains, deserts, oceans, and huge areas without suitable habitats.

Over the last few centuries, the biochoric type of species dispersal has included dispersal resulting from anthropogenic activity, i.e., anthropochoric. Nowadays humans inhabit all the continents, and people can move in all directions regardless of climatic conditions. Some species can be transported by people at huge distances accidentally or on purpose. Thus, transported species can survive in a suitable habitat, reproduce, occupy an ecological niche, and form a sustainable population.

*Scytodes thoracica* (Latreille 1802) has become a cosmopolitan species due to the anthropogenic factor.

The family of Scytodidae includes 5 genera and 239 species; the genus of *Scytodes* includes 228 species (World Spider Catalog, 2017). In the area of the former Soviet Union, five species of two genera can be found; four of them belong to the genus *Scytodes*. The only species that has been found in Russia is *S. thoracica* (Mikhailov, 2013).

This is a small and slow spider with a size of 3 to 6 mm (3–5 mm for males and 4–6 mm for females) (Roberts, 1995). It is mainly active at night. The species can be relatively easily distinguished from other spider species inhabiting middle latitudes using the following anatomical features. The cephalothorax is wide, oval-shaped, with a pattern and without medial or radial fissure, and with 6 eyes (Dunin, 1992). The chelicerae have short claws. Poison glands are large and divided into two sections. The anterior section has its own muscles and produces the poison. The posterior section is larger and serves as a kind of a spinning gland. When a spider sees a prey at a distance of 1–2 cm, it sprinkles the poison from chelicerae. The liquid poison is rapidly solidified in the air and forms a zigzag

web, which glues the prey to the substrate; the web also has a toxic effect. Then the spider approaches the prey and kills it by sticking it with the claws of chelicerae and administering the poison from the anterior parts of poison glands (Ivanov, 1965; Tyshchenko, 1971). The period of seasonal activity is from April (males) or May (females) until September (males) or October (females) (Le Peru, 2011). Copulation is not accompanied by a mating display. Cocoons are round and brownish and can contain 4 to 44 (22–25 on average) eggs. Females protect the cocoons and carry them in chelicerae (Tyshchenko, 1971; Roberts, 1995). It has been found that cocoons are only formed once a year (Bristowe, 1958). Females live 2–3 years; males live 1.5–2 years (Roberts, 1995). This species usually lives under stones, in soil splits, detritis, soil litter, burrows of rodents, moss, under the bark of trees (Dunin, 1992), in stony littoral areas and solochak zones (Le Peru, 2011), and sometimes in caves (Di Caporiacco, 1936; Ruffo, 1938; Kekenbosch, 1955; Brignoli, 1969; Zhu and Zhang, 2011).

The purpose of this study is to discuss the northernmost findings of *S. thoracica* in its Eurasian range, including original findings, with respect to the literature data on its worldwide distribution. Synanthropic conditions of the range of this species, i.e., places with central heating during the winter, are contrasted with its natural environment, i.e., natural habitats and habitats located in suburban green areas and agricultural landscapes (fields, plantations, pastures, etc.) with open land.

### *Findings of S. thoracica in the Northern Volga Region*

There have been new findings of *S. thoracica* in the northern Volga region: 1♀ (Figs. 1a, 1b)—Samara oblast, Samara, Krasnoglinsky raion, Kuznetsov Mountain, southern slope, broad-leaved forest, May 25, 2003, A.V. Lyulina; 1♀ (Figs. 1c, 1d)—Samara oblast, Samara, Kirovsky district, Stara-Zagora street, second floor of a five-story house, ceiling of a flat, December 6, 2015, D.V. Varenov; 1♀, the same place, wall of bathroom, July 9, 2017, D.V. Varenov; 1♀, the same place, July 19, 2017, D.V. Varenov. The species had been previously found in a natural habitat (Krasnobaev, 2003; this article mistakenly states that *S. thoracica* was found by E.A. Belosludtsev on August 28, 1999; it was actually found by V.V. Gasilin in Samara oblast, Kranoyarsky raion, pasture near the settlement of Lopatino, June 3, 1999). Thus, five samples of *S. thoracica* have been found in Samara oblast over the last 15 years; two of them were found in natural conditions.

The first sample was found in the natural environment of secondary forest at a distance of 0.5–1.0 km from residential buildings. Apart from this species, 52 other spider species were collected by soil traps in the periods from May 23, 2003, to August 14, 2003, and from May 10, 2004, to September 20, 2004. The number of species in our sample reaches 13.8% of total species composition of spider fauna in Samara bend (377 species) and 10.8% of spider fauna in Samara oblast (480 species) (Krasnobaev, 2004, 2007; Kuz'min, 2013; Dedyukhin et al., 2015; Marusik et al., 2015). The incidence of some species calculated based on the data of two seasons is presented in the table. The relative structure of dominance of spider species is discussed in a corresponding section.

The analysis of world literature data on the distribution of *S. thoracica* helped determine the boundaries of its historic range and the external boundaries depending on synanthropy. It also provided a conclusion on the main limiting factors of distribution, which can explain the findings described above.

### *European Northern Boundary of the Range of S. thoracica outside Residential Buildings*

The northern boundaries of the range of this species in Eastern Europe and the easternmost findings in Northern Europe are described below. The findings of *S. thoracica* closest to our points are situated in Astrakhan oblast, where it was found inside and outside residential buildings (Boroznov, 2010) and in Kalmykia near the boundary with Dagestan (in plant detritus on the border of the floodplain of Kuma river and semidesert (Minoranskii et al., 1980). More southern findings of the species in the natural environment have been recorded in Dagestan (Ponomarev et al., 2008; Abdurakhmanov and Alieva, 2011; Abdurakhmanov et al., 2012), Chechnya, Ingushetia, Abkhazia, Georgia, Armenia, Azerbaijan (Dunin, 1989, 1992; Dunin and Mamedov, 1992; Ponomarev et al., 2008; Alieva, 2010; Kovblyuk et al., 2011), Iran (Kashefi et al., 2013; Zamani, 2014; Malek-Hosseini et al., 2015), Pakistan (Perveen and Jamal, 2012; Khan and Zaman, 2015), Turkey (Kunt et al., 2012; Özkütük et al., 2013), and Syria (Brignoli, 1969). Findings in the natural environment to the west of the Caspian Depression have been recorded in Krasnodar krai on the Black Sea coast (Ponomarev and Mikhailov, 2007; Ponomarev and Volkova, 2013) (the species most probably also inhabits Stavropol krai, at least in the southwestern region adjacent to Abkhazia); the Donetsk People's Republic (Dunin, 1992; Polchaninova, 2006); Crimea (Kovblyuk, 2003, 2012; Kovblyuk et al., 2008, 2015); Moldova (Karpenko and Legotaj, 1980); Romania (Duma, 2007), and in all countries of Southern Europe, including Portugal (Dabelow, 1958; Brignoli, 1969; Blick, 1989; Komnenov, 2002, 2009, 2013; Le Peru, 2011). Findings of this species in the natural environment north of Southern Europe are very rare.

The empirical northern boundary of its range outside residential buildings in this part of the world can be set approximately at 46.19° N, 48.1° E (Astrakhan, Russia) in the Caspian Depression, at 44.44° N,

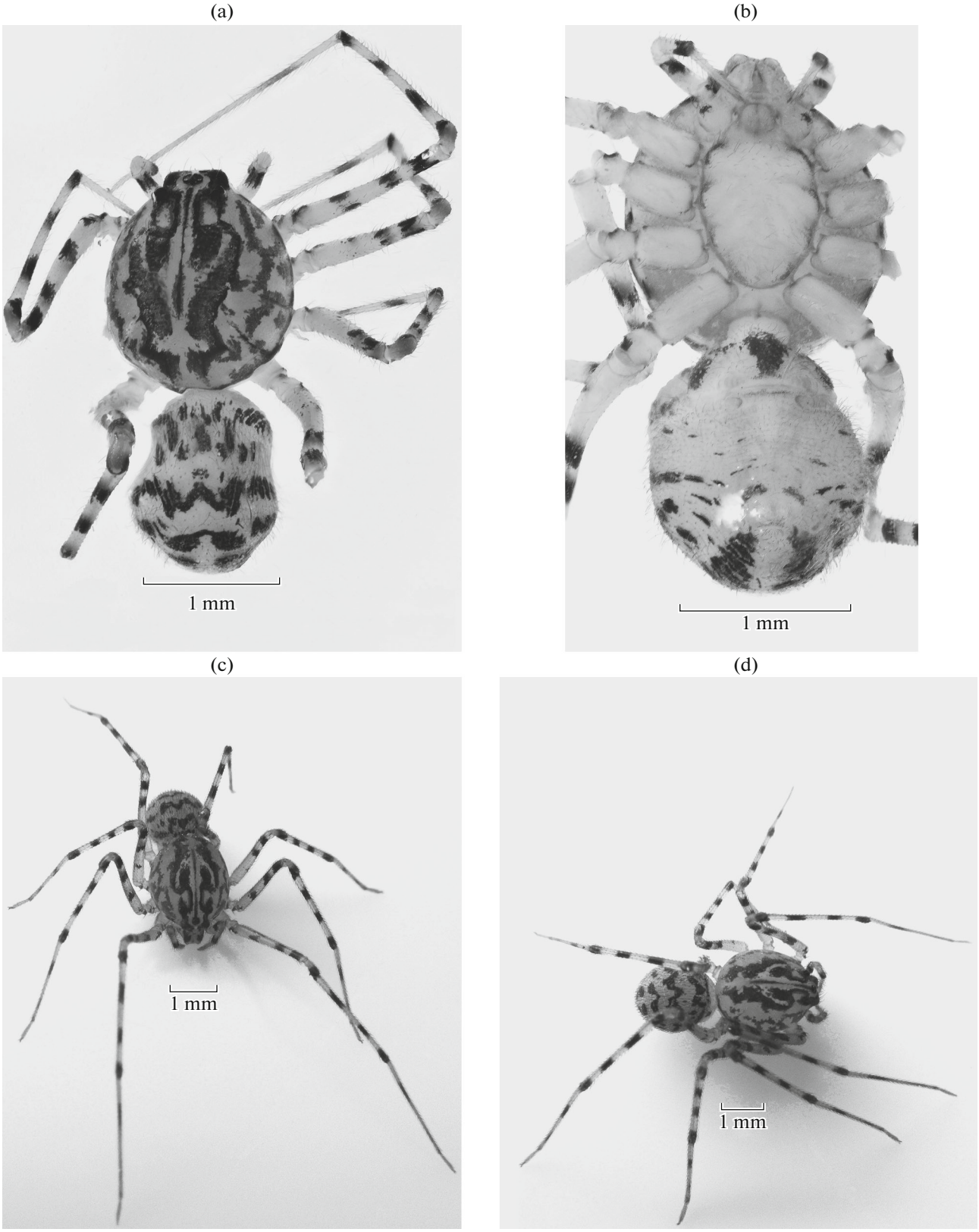


**Fig. 1.** External morphology of *Scytodes thoracica* (Latreille, 1802): (a) ♀, Samara, Krasnoglinsky raion, Kuznetsov Mountain, southern slope, broad-leaved forest, May 25, 2003, A.V. Lyulina, dorsal view; (b) the same sample, ventral view; photo by A.S. Tilli; (c) ♀, Samara, Kirovsky raion, Stara-Zagora ul., second floor of a five-story house, ceiling of a flat, December 6, 2015, D.V. Varenov, frontal view; (d) same sample, dorsal view; photo by D.V. Varenov.

37.25° E (Bolshoy Utrish, Krasnodarsk Krai, Russia) in northern Black Sea region, at 45.8° N, 33.35° E (Saki) in the Crimean region, at 47.0° N, 28.51° E (Kishinev, Moldova) in the Trans-Dniester region, at 45.15° N, 22.35° E in Southern Karpaty (Tyrgu mountains, Romania), and at 48.45°, 16.52° E (Breclav, Czech Republic) in the biosphere reserve Nizhnyaya Morava (Bryja et al., 2005). Then the boundary moves to the south to 46.21° N, 15.53° E (Spodn'ye-Prapreche, Slovenia) (Candek et al., 2013). Another finding in this region was recorded at 45.35° N, 13.51° E (Osp, Slovenia) (Candek et al., 2013). Then the boundary reaches the northern coast of Lake Garda in northern Italy (Thaler, 1966). It has been recorded that *S. thoracica* has not been found in the natural environment in Austria, and that the coast of Lake Garda is the closest point it was found outside residential areas (Thaler, 1966). There have been three findings of this species in the natural environment in Germany: in the valley of the Rhine (Blick, 1989) and near the cities of Eifel (Wiehle, 1953) and Mainz (Braun, 1955). *S. thoracica* has been found in natural environment in southern France (Brignoli, 1969; Le Peru, 2011). Moreover, there have been two findings on the Mediterranean coast: at 43.36° N, 3.52° E and at 43.42° N, 7.18° E (Montpellier and Villefranche-sur-Mer, France) (Dabelow, 1958). The western part of this boundary is from 45.38° N, 10.40° E (Lake Garda, Italy) to 50.0° N, 8.16° E (Mainz, Germany) and supposedly reaches the southwestern coast of France at 45.37° N, 1.1° W (Royan, France) (Fig. 2). In the southern Mediterranean region, the species has been found in the high northwest of Africa (Keer van and Bosmans, 2014).

The species is also common in residential areas in these areas.

### *Northern Boundary of the Range in Europe*

According to literature data, *S. thoracica* in northern regions is a totally synanthropic species. For example, it has been found in residential buildings in Rostov oblast in Russia (Minoranskii et al., 1980); Kharkiv, Poltava, Chernihiv, Kiev, Ternopil, and Lviv oblasts and more southern areas, including Odessa, in Ukraine (Evtushenko and Singaevskii, 2008; Fomichev, 2008; Polchaninova, 2009; Fedoryak and Rudenko, 2009; Prokopenko et al., 2010); southern and central Poland (Rozwałka et al., 2013, 2016); northern Czech Republic (Bryja et al., 2005; Šefrova and Laštůvka, 2005); northern and central Germany (Platen et al., 1996); Denmark, the Netherlands, and northern France (Dabelow, 1958; Brignoli, 1969; Blick, 1989; Le Peru, 2011); and Great Britain (Roberts, 1995).

*S. thoracica* has also been found in Belgorod oblast in Russia, in southern areas of Donetsk People's Republic, western Germany, Belgium, and Scotland as a synanthrope (Ponomarev and Polchaninova, 2006; Bosmans, 2009) and in the natural environment of nature reserves (Wiehle, 1953; Berezantseva, 2000; Baattrup-Pedersen et al., 2015), as well as in urban and suburban green areas (Bosmans, 2009); these findings are exceptions for Eastern Europe and continental and insular Western Europe, respectively.

In Great Britain the species has only been found as a synanthrope in southern areas; the northernmost findings were situated in the Midlands (Roberts, 1985). *S. thoracica* has also been found in Scotland (Baattrup-Pedersen et al., 2015), which means that its range is extended in northern direction, and the species can inhabit the whole archipelago, including Ireland. The authors of the latter study did not discuss the significance of this finding. At the same time, according to our data, this is the northernmost finding of *S. thoracica* in Eurasia with a known location and habitat description; the species has been found in Denmark (Le Peru, 2011; Lissner, 2011), but the location of this finding was not described.

*S. thoracica* has not been found in Belarus or northwestern areas of Ukraine. We cannot exclude that this results from the low number of studies and data collected in these regions. For example, 474 spider species have been recorded in Belarus (Ivanov, 2013), which is 58% of the species composition recorded in Poland (819 species) (Cera, 2009; Biteniekyte and Relys, 2011). Similar proportions were observed in Lithuania, Latvia, and Estonia, which are all smaller countries when compared with Poland and Belarus (54, 56, and 64% of the total species composition in Poland) (Cera, 2009; Biteniekyte and Relys, 2011). Notably, although Estonia is situated to the north of countries listed above, the number of spider species per unit area there is highest; thus, the spider fauna of Estonia is studied to the highest extent.

As for Poland, *S. thoracica* has not been included in spider fauna for the whole century. At the end of the 20th century, the species was found near Wrocław (southwestern Poland), and this was considered as the first finding in Poland (Woźny and Mizera, 1999). Then a second finding was reported in the same region (Król and Mąkol, 2012). Actually, the species was found as early as in 1896 in the historic area of Silesia (Rozwałka et al., 2013), which is situated in the same southwestern region of Poland. Now the boundary of the range in Poland has moved to the north and the range now includes Warsaw (Król and Mąkol, 2012).

According to the literature data on the range of *S. thoracica*, its northern boundary in Europe lies from 46.19° N, 48.1° E (Astrakhan, Russia) to the northwest at 47.13° N, 39.43° E (Rostov-on-Don, Russia), then to 50.36° N, 36.34° E (Belgorod, Russia), then to the west at 49.44° N, 24.0° E (Lviv, Ukraine), and then to the northwest again 52.13° N, 21.0° E (Warsaw, Poland). Then the boundary probably goes to the west along this latitude to the border of Germany, reaches the coast of the Baltic Sea, surrounds Denmark (Le Peru, 2011;

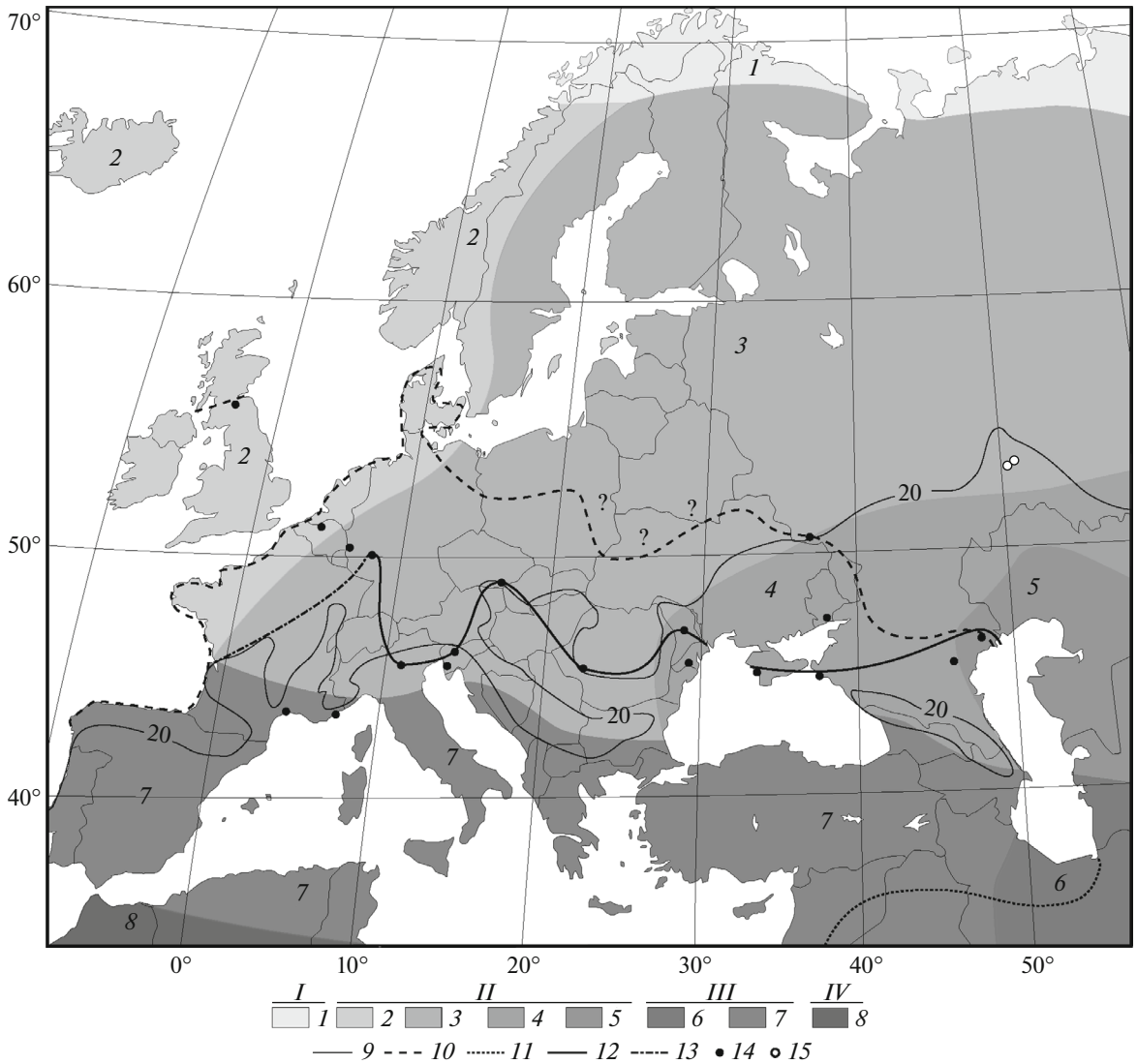


**Fig. 2.** Climatic zones and areas (Climatic zones..., 1964) and distribution of *S. thoracica* on the border of Europe, Asia, and Africa: (I) subarctic zone, (II) temperate zone, (III) subtropical zone, and (IV) tropical zone. (*1*) Area with cool and humid summer and windy and humid winter; (*2*) area with relatively warm winter, unstable weather conditions and strong wind, and relatively cool summer with homogenous and sometimes excessive humidity; (*3*) area with transitional (oceanic to continental) climate with excessive (Polar region) or sufficient humidity; (*4*) area with transitional (oceanic to continental) climate with low humidity; (*5*) area with continental climate, dry zone; (*6*) area with dry hot summer and relatively cold winter; (*7*) area with dry summer and humid winter (Mediterranean climate); (*8*) dry hot area with very high daily amplitude of temperatures; (*9*) July isotherm of 20°C (Air temperature..., 1964); (*10*) boundary of range in continental Europe and on the British Archipelago (based on the findings in housings with heating systems); (*11*) boundary of range in Western Asia; (*12*) northern boundary of common findings in natural habitats (on open soil surfaces); (*13*) supposed northern boundary of common findings in natural habitats in Western Europe; (*14*) points of findings in natural habitats in northern parts of the European range; (*15*) points of findings in Samara oblast, Russia.

Lissner, 2011), and goes across localities along the northern coast of Europe to Portugal (Fig. 2). *S. thoracica* is a synanthropic species in Great Britain. In addition, populations of this species can probably be found in some localities of southern Sweden, at least on its western coast.

Thus, the ecological niche of the species in the European part of its range grows narrower in the northern direction: the species inhabits natural and synanthropic habitats in southern regions, then becomes an obligate synanthrope and inhabits synanthropic habitats only in more northern regions and is not common to the north and east of this zone (Fig. 2).

### *Worldwide Distribution and Restored Historic Center of the Range of S. thoracica*

Other points of findings of *S. thoracica* are situated at significant distances from the Mediterranean region. For example, the species has been found in spi-

der fauna of Central Asia (Minoranskii et al., 1980; Dunin, 1992), India (Tikader, 1977; Chetia and Kalita, 2012; Nikunj, 2014), eleven provinces of China—both continental and coastal (Zhu et al., 1985; *Farm Spiders*..., 1987; Song et al., 1999; Zhu and Zhang, 2011; Yin et al., 2012), South Korea (Paik, 1978; Kim and Cho, 2002; Namkung, 2003), Japan (Ono, 2009), and the Philippines (Barrion and Litsinger, 1995). *S. thoracica* has also been found in Australia (World Spider Catalog, 2017) and New Zealand and (Paquin et al., 2010) and has not been found in Indonesia (Stenchly, 2011). In North and South America, it is an eusynanthropic species in the United States and Canada (Suman, 1966; Kaston, 1976; Paquin and Dupérré, 2003) and Argentina (Brand, 2013).

Notably, *S. thoracica* is rare in natural habitats outside the Mediterranean and nearby regions. Moreover, we suppose that most of the reports on findings in natural habitats (in soil splits and soil litter and under stones) in other regions are associated with places situated near residential areas, as was recorded, for example, for findings in the United States and Canada (Emerton, 1902). The species is cosmopolitan (Suman, 1966; Barrion and Litsinger, 1995; Özütük et al., 2013) but synanthropic, and can only be found in certain habitats. This proves that the Mediterranean region and Macaronesia are the historic range of this species and the center of its dispersal (Wiehle, 1953; Dabelow, 1958; Brignoli, 1976; Blick, 1989; Le Peru, 2011). Moreover, we suppose that Caucasus, southwestern Caspian region, and the whole Black Sea region are also included in this area. Thus, *S. thoracica* occupies the area of the ancient Mediterranean region (Kryzhanovskii, 2002).

The Mediterranean and adjacent regions were populated by humans relatively early. In the second half of the Middle Holocene (the Bronze Age), i.e., about 4000 years ago, the first processes of state formation began in Ancient Greece. In the beginning of the Late Holocene (the Iron Age), i.e., about 2500 years ago, subtropical forests surrounding the Mediterranean Sea were destroyed due to agriculture, animal husbandry, metal industry, ship building, and urban development in many coastal regions (Blavatskii, 1976; Sadori, 2007; Knipping et al., 2008). This process continued in the Roman Empire (Jahns, 1993); by now the zone of subtropical forests in the Mediterranean region no longer exists. Thus, the original habitats of *S. thoracica* have changed significantly over the last few millennia. It is hard to say whether the species has mainly remained in open or closed landscapes, whether the destruction of forests was a favorable condition, or whether the species preferably inhabits stony coastal areas with a high amount of sunlight (where it is usually found now) or soil litter in rare forest stations (restored after continuous forest felling) and the shrubs which substituted forests. Anyway, the history of this species started with the development of ancient civilization, which helped extend its range.

Obviously, such a narrow range (the ancient Mediterranean region) is a refugium of some species that had been more abundant. Thus, some points of findings in the natural environment at huge distances from the center of the range can also be refugiums, albeit smaller ones. For example, some authors suppose that the populations of *S. thoracica* in Japan can be relic (Brignoli, 1976).

By now the species can be found in almost all regions of the world. Such a wide distribution is associated with the effect of anthropogenic factor over the last few centuries, probably since the Age of Discovery. However, *S. thoracica* is still of great interest, since natural limiting factors have a significant influence on its dispersal, despite the "protective" anthropogenic impact, and the ancient Mediterranean region remains the largest favorable area for this species. The boundary of the range of this species, at least in Central Europe, is relatively constant, which is proven, for example, by the location of almost all samples found in Poland in southern regions of the country, where it was first found more than 100 years ago.

### *Physical and Geographical Conditions and the Range of S. thoracica in Europe*

The range of *S. thoracica* in Europe and Western Asia is situated in the southern part of temperate and subtropical zones. The climate of the southern part of the temperate zone is affected by the air masses coming from southern latitudes. The summer period here is longer than in the northern part of the temperate zone, and the temperatures are higher (on average lower than 20°C); tropical air masses often come here during the summer period (Aleksandrovskaya et al., 1963). The subtropical zone covers almost all of southern Europe and the northern part of Western Asia (Fig. 2). The western European part of this zone has a Mediterranean type of climate. Mean monthly temperatures during the summer in this type exceed 20°C and positive temperatures in winter exceed 4°C; there is no constant snow cover in plain areas (Aleksandrovskaya et al., 1963). The most typical feature of this type of climate is a minimal precipitation rate in summer and maximal precipitation rate in winter. Stable dry and sunny weather is typical of the summer period.

The northern boundary of the range of *S. thoracica* in natural habitats, which was proposed in this article based on literature data and our data, can be explained by the July isotherm of 20°C (Fig. 2). This boundary crosses the border of climatic zones several times in Western Europe, while it only lies in the southern part of temperate zone in Eastern Europe. It also surrounds the Greater Caucasus; the isotherms of this mountain range decrease starting from 20°C as the height increases. We suppose that the July isotherm of 20°C should be considered the hypothetical border of maximal distribution of *S. thoracica* in open landscapes in

the northern direction in Southern Europe and Western Asia until any contradictory data are reported. It should also be noted that all isotherms have moved to the north over the last few decades (Beniston, 2013).

The predictability of isotherm in Eastern Europe, which has been moving to higher latitudes from 30° E, has become lower, since it can no longer explain the absence of *S. thoracica* in the spider fauna of natural habitats of Ukraine, the Don region, and the steppe zone of the Lower Volga region. We suppose that the distribution of this species in natural habitats in southern regions of Eastern Europe is affected by one of the complexes of transitional climate conditions: the areas adjacent to the Black and Azov seas from north has low humidity. This may be why most northern findings of *S. thoracica* in natural habitats are associated with coastal areas (Fig. 2). The northern and western adjacent climatic zones have higher humidity. There has been a finding of this species on the border of these zones and almost on the July isotherm of 20°C in a natural habitat near Belgorod (Fig. 2). Our samples were collected to the south of this isotherm in the zone of transitional (oceanic to continental) climate with sufficient humidity level, i.e., in climatic conditions similar to those in northern natural habitats of Western Europe, where other samples were found (Fig. 2). In addition to other factors, the location of our findings in open landscapes can also be affected by the influence of Saratov and Kuybyshev water reservoirs, which attenuates a continental climate.

Thus, it is unclear why the range of *S. thoracica* as a synanthropic species is limited in the northern direction and why it has not inhabited residential areas in northern parts of Western Europe and in Eastern Europe to the north of Ukraine and regions of Russia, including the Lower Don region. The limitation of dispersal by low minimal temperatures in the winter period could be a possible explanation if this species spent the winter in places with low temperatures, i.e., if it left human houses. However, such behavior has never been described for arthropods. Synanthropic spider species are active throughout the year in normal conditions of residential houses. *S. thoracica* is not an exception; it can be found in human houses during the heating season (see above; Szinetár et al., 1999; Schmidt, 2016). This biological feature can be considered an advantage over autochtonous species, which spend the winter in natural habitats.

We think that the tapering of the ecological niche of this species in northern direction can result from the gradient of nocturnal temperatures on soil surface and the gradient of humidity in the summer. The species is rather small and slow; it is only active during the night and at lower daily temperatures. In the southern parts of its range, *S. thoracica*, as a poikilothermic species, obtains a sufficient amount of energy from heated soil during the night; therefore, the species is common both in natural habitats and in residential areas. Due to dry weather in the summer period, *S. thoracica* can easily shelter in soil splits and under stones. In the northern parts of its range, nocturnal temperatures are lower and humidity is higher, which prevents the dispersal of this species in its typical habitats but does not prevent its active dispersal. As a result, the stable habitats of the species are human houses with constant conditions. The findings of *S. thoracica* outside residential areas in northern parts of its range, such as city gardens of various areas in Belgium (Keer van et al., 2010), suburban areas in western Germany (Wiehle, 1953), and even conservation areas in Scotland (Baattrup-Pedersen et al., 2010) and Belgorod oblast in Russia (Berezantseva, 2000) illustrate that this species is capable of active dispersal in synanthropic zones and can probably sometimes colonize urban and suburban green areas. Finally, the species is absent in areas with low temperatures, where it cannot actively move on soil surface.

Therefore, we can conclude that this species needs active dispersal, at least during the summer, for retaining its range. Passive dispersal, such as anthropochory, which moves separate individuals of *S. thoracica* huge distances from the center of its range in favorable conditions (even in the case of multiple anthropochory of individuals of both sexes and similar age), e.g., in residential areas, cannot guarantee their further distribution if active dispersal is impossible. The sporadic dispersal of *S. thoracica* in Scandinavia, Baltic countries, Belarus, and other countries with the opportunity to inhabit residential houses with constant conditions cannot be excluded. Passive dispersal in such areas, obviously, does not provide a sufficient number of individuals for the formation of stable populations in localities. Isolation by climatic factors prevents possible distribution.

The demographic factor, i.e., differences in the population density in different regions, can also affect the distribution of *S. thoracica* as a synanthropic species if local conditions provide the active nocturnal dispersal of individuals on soil surface. We can suppose that the northern boundary of the range of this species in Great Britain corresponds with the southern boundary of the coniferous forest zone; in Eastern Europe, it corresponds with the southern boundary of the mixed forest zone (Fig. 3). The complex of conditions typical of these and more northern zones is apparently unfavorable for *S. thoracica* on open soil surface even in urban areas, where the mean temperature is usually higher than in natural habitats (Odum, 1986).

The use of July isotherm as the northern boundary of the range, as proposed in this article, is certainly a provisional method, since the species can be found in natural habitats all across its range, as wass mentioned above. The boundary is dynamical and can only be estimated with higher accuracy based on the threshold values of the abundance gradient, since the role of

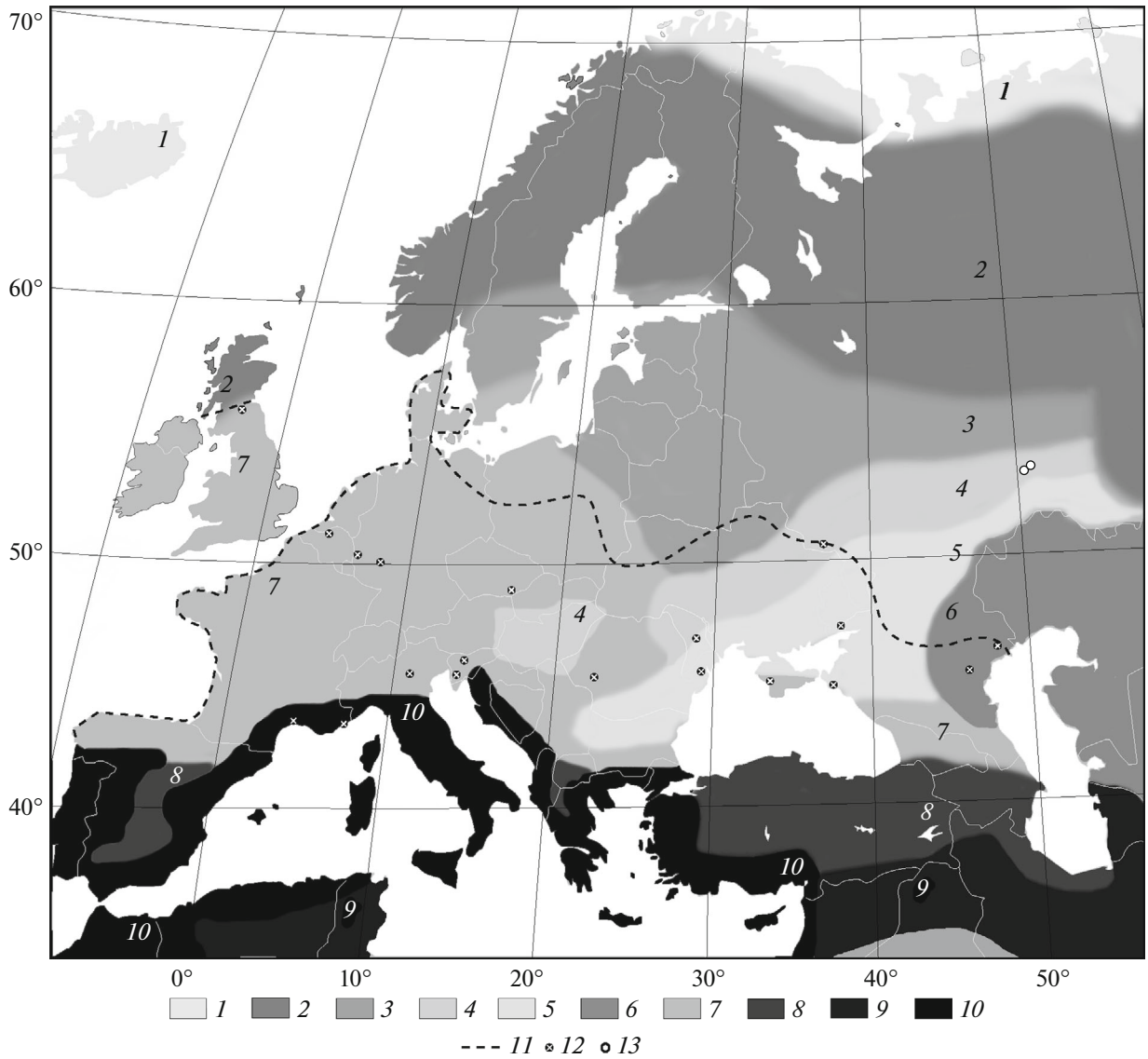


**Fig. 3.** Vegetation zones (Geographical belt..., 1981) and the northern boundary of the range of *S. thoracica* on the border of Europe, Asia, and Africa: (*1*) tundra zone, (*2*) coniferous forests, (*3*) mixed forests, (*4*) forest steppe zone, (*5*) steppe zone, (*6*) semideserts and deserts, (*7*) broad-leaved forests, (*8*) shrubby steppes, (*9*) semideserts and deserts, (*10*) sclerophyllous forests and shrubberies (Mediterranean type), (*11*) boundary of range in continental Europe and on the British Archipelago (based on findings in housings with heating systems), (*12*) points of findings in natural habitats in northern parts of the European range, and (*13*) points of findings in Samara oblast in Russia.

human housings as the reservoir of populations increases in efferent direction, while the dependence between the abundance on open soil surface and weather conditions grows more significant.

Apart from climatic and zone- and landscape-related preferences of the *S. thoracica*, the availability of prey, the presence of concurrent species, and other limiting factors certainly play a crucial role in its survival outside the center of its range and eventually determine the pattern of its distribution.

The points of our findings are situated at similar distances from Astrakhan (about 800 km), where this species inhabits natural habitats, and from Belgorod (about 970 km) and Rostov-on-Don (about 990 km), i.e., the northernmost points of findings in synanthropic areas only. Animals cannot cover such huge distances without humans, i.e., human transport facilities. The version of anthropochory and colonization is only suitable until the species is found in more southern regions between the Middle Volga region and the rest of the range.

We cannot be sure that single findings of *S. thoracica* indicate the presence of this species in spider fauna of Samara and nearest settlements. These populations can be spatially and temporally isolated; their founders

could be transferred independently from different places. However, the presence of separate individuals at relatively significant distances from human housings (on pastures and in forests) leads to two correlating conclusions. Firstly, these findings indicate that factors favorable for the species coincide in this area during a time period sufficient for the dispersal of individuals from housings in the spring. Secondly, they indirectly prove that the abundance of this species in this area is relatively high for species with such a level of abundance even in the center of its range. Anyway, the appearance of *S. thoracica* in natural habitats in the studied area should be considered secondary. The centers of dispersal are residential and household buildings of settlements with heating systems.

### *Faunistic Surroundings of S. thoracica in Natural Habitats: Place of the Species in Relative Dominance Structure*

We collected the samples of spider faunas in natural habitat associated with the first finding of *S. thoracica* described in this article in two seasons. We have collected 1068 pubescent individuals of 52 species. For further comparison we also used the representative data obtained in natural habitats with the presence of *S. thoracica* in the northern part of its European range (Scotland, Czech Republic, and Serbia). The Scottish sample includes data obtained on six inundated islands on the Yorn River in 2010–2011 (Baattrup-Pedersen et al., 2015). The Czech sample includes data obtained on a river island in the Nizhnyaya Morava biosphere reserve in 1996–1998 (Bryja et al., 2005). The Serbian sample was collected in a waterlogged area of the Zasavitsa nature reserve in an inundated forest (Gajić, I. and Grbić, G., 2016). A complete list of spider fauna including *S. thoracica* (according to our data) was compared with the lists of Scottish ($K_j$ = 0.06), Czech ($K_j$ = 0.09), and Serbian ($K_j$ = 0.10) populations using the Jaccard index. The values of the index show that the similarity of faunistic compositions is very low. The similarity of faunas of Scotland and Serbia ($K_j$ = 0.11) and of Serbia and Czech Republic ($K_j$ = 0.12) is also low. The faunas of Scotland and the Czech Republic are more similar ($K_j$ = 0.18). The species found in three out of four samples (see Table 1) include *Bathyphantes nigrinus*, *Diplostyla concolor*, *Erigone dentipalpis*, *Linyphia triangularis*, *Pardosa amentata*, *P. lugubris*, *Ero furcata*, *Pachygnatha clercki*, and *P. degeeri*. *S. thoracica* was the only species found in all samples.

The analysis of the relative abundance of species estimated based on the samples of different years is provided below. The parameters of faunas for quantitative analysis are presented in Table 1.

The dominant species in our sample is *Pardosa lugubris*, which is rare in the samples of Czech Republic and absent in the Scottish sample (Table 1). Other species in our sample can be considered rare or very rare. *S. thoracica* is very rare in all studied samples. The dominant species in the Serbian sample is *Diplostyla concolor* (Linyphiidae), which is absent in the Scottish sample and very rare in the other two samples. A species of the same family, *Oedothorax apicatus*, is dominant in the Czech sample, common in the Scottish sample, and absent in the other two samples. *P. amentata* was found in all samples except for our sample; it is most abundant in the Scottish sample (Table 1). The pattern of distribution of proportions of species in our sample is similar to that in the Serbian (and partially Czech) sample: the share of dominant species is much higher that the share of second species. In the Scottish sample, which has the lowest species diversity, the shares of species are more similar, which probably results from the heterogeneity of habitats in the studies areas.

The diversity of spider faunas in the studied samples reflects the multiple influence of ecological factors and the parameters of survival for each species. The presence of *S. thoracica*, which is rare in the center of its range (Serbia) and in adjacent areas with synanthropic distribution (Scotland and the Czech Republic), as well as distant areas (Samara, Russia, and others), indicates that this species successfully occupies its ecological niche.

### *European Spider Species with Northern Range Extension*

Another species, *Oecobius navus* (Blackwall 1859) (Oecobiidae), is similar to *S. thoracica* in a number of biological parameters, such as size of body, diagnostic morphological properties, the use of stones and soil splits as preferable shelters, subtropical and tropical origin, and cosmopolitan distribution. Like *S. thoracica*, *Oecobius navus* is a synanthropic species in Central and Northern Europe. The dispersal of this species in northern direction has been observed in synanthropic spider fauna in Finland (Fritzen, 2013). These two species have zones of sympatry in Europe, the Caucasus, and other parts of the world and can coexist in one human housing. Since *O. navus* as a tropical species can inhabit areas to the north of the range of *S. thoracica* (such as Baltic countries), the temperature-, humidity- and dispersal-related reaction norm of *O. navus* is wider, but this species has not been found in Russia (Mikhailov, 2013).

Another European species with a tendency of dispersal to the northern direction is *Argiope bruennichi* (Scopoli 1772) (Araneidae), a transpalearctic species common in forest steppe, steppe, and semidesert zones of Eurasia (Mikhailov et al., 2011; Mikhailov and Borisova, 2013; Mikhailov and Panov, 2014), including the southern parts of the Middle Volga Region (Krasnobaev, 2004). The northern boundary of its range in Western Europe and then in the central part of Eastern Europe has been moving in the north-

**Table 1.** Proportion of pubescent spiders in field samples collected in northern parts of the European range of *S. thoracica* according to original and literature data (Krasnobaev, 2004; Bryja et al., 2005; Baattrup-Pedersen et al., 2015; Gajić, I. and Grbić, G., 2016); the table contains the most abundant species and species present at least in two spider fauna, %

| Species | Scotland | Czech Republic | Serbia | Russia | |
|---|---|---|---|---|---|
| | | | | Samara | Samara oblast |
| Gnaphosidae | | | | | |
| *Zelotes latreillei* (Simon 1878) | 0 | 0 | 0.29 | 0.09 | + |
| Linyphiidae | | | | | |
| *Bathyphantes gracilis* (Blackwall 1841) | 3.64 | 1.16 | 0 | 0 | + |
| *Bathyphantes nigrinus* (Westring 1851) | 0.91 | 6.94 | 0 | 0.28 | + |
| *Diplostyla concolor* (Wider 1834) | 0 | 0.46 | 55.79 | 0.19 | + |
| *Erigone atra* (Blackwall 1833) | 6.01 | 2.38 | 0 | 0 | + |
| *Erigone dentipalpis* (Wider 1834) | 6.10 | 1.92 | 1.29 | 0 | + |
| *Gongylidiellum vivum* (O. P.-Cambridge 1875) | 0.18 | 0.05 | 0 | 0 | – |
| *Leptorhoptrum robustum* (Westring 1851) | 19.95 | 0 | 0 | 0 | + |
| *Linyphia triangularis* (Clerck 1757) | 0.18 | 0 | 0.14 | 5.06 | + |
| *Neriene clathrata* (Sundevall 1830) | 0 | 0 | 1.29 | 0.47 | + |
| *Oedothorax apicatus* (Blackwall 1850) | 12.20 | 55.95 | 0 | 0 | + |
| *Tenuiphantes flavipes* (Blackwall 1854) | 0 | 0.05 | 0 | 0.47 | + |
| *Tenuiphantes tenuis* (Blackwall 1852) | 3.01 | 0.25 | 0 | 0 | – |
| Liocranidae | | | | | |
| *Agroeca brunnea* (Blackwall 1833) | 0 | 0.30 | 0 | 0.09 | + |
| Lycosidae | | | | | |
| *Pardosa agricola* (Thorell 1856) | 0 | 10.28 | 0 | 0 | + |
| *Pardosa amentata* (Clerck 1757) | 29.60 | 0.25 | 1.72 | 0 | + |
| *Pardosa lugubris* (Walckenaer 1802) | 0 | 0.35 | 0.14 | 71.25 | + |
| *Trochosa ruricola* (De Geer 1778) | 0.82 | 0.41 | 0 | 0 | + |
| *Trochosa terricola* (Thorell 1856) | 0 | 0.05 | 0 | 1.03 | + |
| Mimetidae | | | | | |
| *Ero furcata* (Villers 1789) | 0 | 0.10 | 0.29 | 0.09 | + |
| Pisauridae | | | | | |
| *Pisaura mirabilis* (Clerck 1757) | 0 | 0 | 0.14 | 0.09 | + |
| Scytodidae | | | | | |
| *Scytodes thoracica* (Latreille 1802) | 0.09 | 0.05 | 0.14 | 0.09 | + |
| Tetragnathidae | | | | | |
| *Metellina segmentata* (Clerck 1757) | 0 | 0.05 | 0 | 3.65 | + |
| *Pachygnatha clercki* (Sundevall 1823) | 0.46 | 7.04 | 0.14 | 0 | + |
| *Pachygnatha degeeri* (Sundevall 1830) | 1.82 | 0.15 | 1.14 | 0 | + |
| Thomisidae | | | | | |
| *Xysticus kochi* (Thorell 1872) | 0 | 0 | 0.29 | 0.09 | + |
| Proportion of individuals of species found in one spider fauna only | 15.03 | 11.80 | 37.2 | 17.04 | |
| The range of proportions of individuals of species found in one spider fauna only | 0.09-7.56 | 0.05–1.16 | 0.14– 7.73 | 0.09–3.18 | |
| Amount of species found in one spider fauna only | 11 | 34 | 33 | 36 | |
| Amount if pubescent individuals | 1098 | 1975 | 699 | 1068 | |

+ Designates present species; – designates that the species is absent.

ern direction for about 25 years. Now the species can be found there in southern parts of the forest zone; it has reached the Baltic States and Finland (Mikhailov and Borisova, 2013; Mikhailov and Panov, 2014).

Examples presented above illustrate that the negative effect of the main limiting factors on the dispersal of spider species in northern regions has been reduced over the latest years. These factors most probably include temperature and humidity. Mean temperatures are known to increase over the last 2–3 decades when compared with earlier years, while humidity in northern regions has decreased. Although we suppose that the appearance of *S. thoracica* in the Middle Volga region is a colonization caused by anthropogenic impact, the conditions of this region have become favorable for this species (maybe due to the anthropogenic factor, i.e., the consequences of global warming). Our findings illustrate the expansion of a subtropical spider species in the northern direction.

## CONCLUSIONS

Based on the data on the largest area of continuous distribution of *S. thoracica* (the Mediterranean region, Western Europe, the southern parts of Eastern Europe, and the northern part of Western Asia), we determined possible factors that limit the distribution of this species. We found that climatic conditions limit dispersal due to their effect on groups of spiders inhabiting open soil surfaces. Such groups play an important role in the dispersal of the species. Synanthropic individuals play another role: they serve as a basic reservoir, which provides the regeneration of the first group if the conditions are not favorable enough. A July isotherm of 20°C can be considered the northern boundary of areas with favorable conditions, i.e., the center of its range. In neighboring areas with lower summer temperatures, the species can rarely be found on an open soil surface, but is still common in synanthropic fauna. The species cannot be found to the north (from the zone mixed and coniferous forests) and to the east of these areas (the zone of transitional [oceanic to continental] climate with low humidity, the zone of continental climate, and the subarctic zone).

The findings of *S. thoracica*, as a species native to the Mediterranean regions, at significant distances from the center of its range can be considered a biological indicator of changes in local climate. The dispersal of *S. thoracica* as a cosmopolitan species is extensive: its abundance is relatively low both in the center of its range and in suitable habitats in distant areas, but it can constantly remain a component of local spider fauna, since it mainly inhabits human housings, where interspecies competition is limited by a small number of synanthropic spider species.

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