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Zoogeography of the genus *Lepthyphantes* in the USSR (Araneae, Linyphiidae)

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Composition and peculiarities in the distribution of the USSR fauna of *Lepthyphantes* are dealt with in the five major regions delimited: the European part, the Caucasus, Siberia (western, central, eastern, and southern), Middle Asia, and the Far East. The faunal relationships are discussed between the regions concerned and some other Holarctic territories. All the regions are characterised by a rich and conspicuous fauna, but the highest degree of endemism is observed in the mountainous systems of the southern Palaearctic: Middle Asia (85%), the Caucasus (51%), the Far East (42%), Siberia (38%), and the European part (28%).

1. Introduction

The present paper is the first in a prospective series concerning the zoogeography of *Lepthyphantes* Menge, 1866, the largest genus in the spider family Linyphiidae. This genus, encompassing over 400 species, is widespread within the Holarctic, but not restricted to it. The latest studies of the mountains of eastern and central Africa have revealed a rather rich and very conspicuous fauna of *Lepthyphantes*. It is noteworthy, however, that a considerable number of the Afrotropical species referred to as *Lepthyphantes* seems to belong in fact to other genera. The discoveries of a few species in the Australian (New Zealand), Neotropical (Chile) and Oriental (Sri Lanka) realms are obviously due to either introductions (as in the case of *L. tenuis* (Blackwall)), or incorrect generic allocations.

The data accumulated in recent years on the distribution of *Lepthyphantes* in various regions of the Palaearctic (in particular within the USSR which includes the greater part of its area), are in need of an up-to-date review and analysis (Eskov 1986, Tanasevitch 1986, 1987a, b, c, 1988, 1989, Tanasevitch & Eskov 1987).

Peculiarities in the distribution of any taxon can be assessed in two ways. The first one implies the superimposition of a general regioning scheme on the distribution pattern of a group studied, with a subsequent analysis of the significance of various borders/limits. The second involves a particular zoogeographical regioning, based on sufficiently known distributions of the constituent subtaxa. In the latter case, borders between the different regions reflect the areas of maximum condensation of range limits. As regards the USSR fauna of *Lepthyphantes*, it is sufficiently well

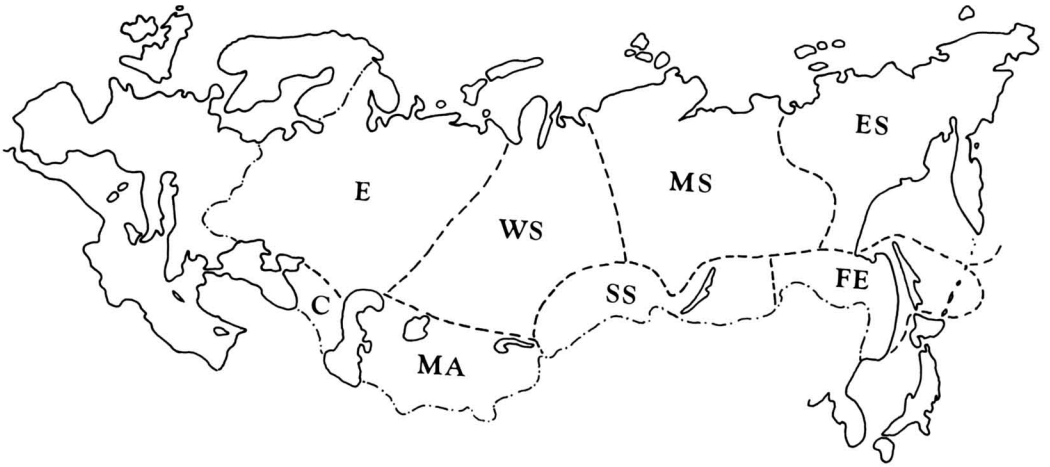

Fig. 1. USSR regions: E – European part, C – Caucasus, WS – Western Siberia, MS – Central Siberia, ES – Eastern Siberia, SS – Southern Siberia, MA – Middle Asia, FE – Far East.

explored (124 species, of which 9 are still undescribed) to allow preliminary zoogeographical conclusions to be made, but not sufficiently enough to attempt a detailed regioning. Therefore, being limited by the material to the first approach, I am bound to consider mainly the regional structure of the fauna, giving emphasis to its degree of endemism and correspondence to various zoogeographical units. When drawing the borders, I was forced to compromise on the physico-geographical regioning of the USSR territory in order to avoid "neutral" or additional a priori, insufficiently explored areas.

Five regions are distinguished within the USSR: the European part, the Caucasus, Siberia (subdivided into western, eastern, central and southern areas), the Far East, and Middle Asia (Fig. 1).

2. The fauna of the USSR

2.1. The Caucasus

The fauna of the Caucasus comprises 23 *Lepthyphantes*, of which 12 (51%) are unknown beyond the region and may be considered as Caucasian endemics. However, since the Near Eastern fauna has been relatively poorly explored, there is a chance that some of these species are actually Caucaso-Anatolian, Caucaso-Turanian or of another kind of east (Ancient) Mediterranean pattern. The relationships with the European fauna are due to both widespread and European species. As regards the widespread elements, the Caucasus also has connections with Siberia, Middle Asia and the Far East. No actual specific relations to these three regions are evident, but a couple of Caucasian *Lepthyphantes*, shortly to be described, are obviously Asian in origin. One of these species belongs in the Siberian *incestus*-group and seems to be especially close to the montane *L. frigidus* Simon known in the Alps and the Balkans. The second is a member of the *nebulosus*-group and is distinctly close to both Middle Asian *L. kronebergi* Tanasevitch and *L. turkestanicus* Tanasevitch: this trio forms a clear-cut monophyletic subgroup.

2.2. Middle Asia

The Middle Asian fauna is rich and extremely conspicuous (Fig. 2A). Out of a total of 40 *Lepthyphantes* reported from this region, with four of them undescribed, only six are known beyond it: *L. tenuis* (Blackwall) is Holarctic, *L. mengei* Kulczynski is Palaearctic, *L. pinicola* Simon is Euro-Ancient Mediterranean, *L. spasskyi* Tanasevitch is Central Ancient Mediterranean, *L. nebulosoides* Wunderlich and *L. pepticus* Tanasevitch demonstrate evident relationships with Central Asia (the latter species has recently been collected

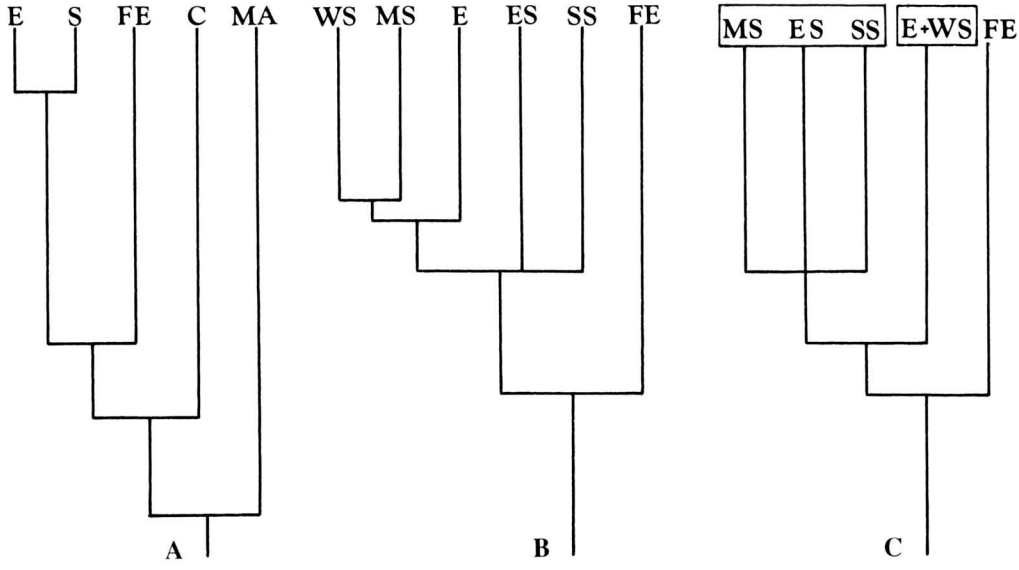

Fig. 2. Dendrograms showing three regional faunal relationships, based on Sokal's & Sneath's similarity index: E – European part, S – Siberia, FE – Far East, C – Caucasus, MA – Middle Asia, WS – Western Siberia, MS – Central Siberia, ES – Eastern Siberia, SS – Southern Siberia.

also in the USSR: ♂♂ and ♀♀ from Alma-Ata and Taldy-Kurgan Areas of Kazakhstan, V. 1988, leg. Ch. Tarabaev, A. Zyuzin & M. Zarko). The remaining 34 species (85%) are regional endemics. A further contribution to the Middle Asian fauna may be expected due to both endemic and Central Asian species. No actual specific relationships with either Siberia or the Far East are evident, although two species (i.e. *L. cruciformis* Tanasevitch and *L. palaeformis* Tanasevitch) inhabiting the coniferous forests of the northern Tien-Shang, display obvious Siberian roots.

2.3. The European part of the USSR

The regional fauna encompasses at present 40 *Lepthyphantes* and comprises, with a few exceptions only, almost all the species known outside the Alps and the eastern Mediterranean, i.e. common European species. Out of these 40 species, 11 (28%) are European (s.lat.) endemics: *L. collinus* (L. Koch), *L. decolor* (Westring), *L. insignis* (O.P.-Cambridge), *L. keyserlingi* (Ausserer), *L. lephthyphantiformis* (Strand), *L. mansuetus* (Thorell), *L. monticola* (Kulczynski), *L. mughi* (Fickert), *L. nitidus* (Thorell), *L. whymperi* (F.O.P.-Cambridge), *L. zimmermanni* (Bertkau). Besides, 8 species (20%) are subendemics: *L. angulatus* (O.P.-Cambridge), *L. angulipalpis* (Westring), *L. antroniensis* (Schenkel), *L. cristatus* (Menge), *L. pallidus* (O.P.-Cambridge), *L. tenebricola* (Wider), *L. flavipes* (Blackwall), and *L. quadrimaculatus* (Kulczynski). The range of the last two species comprises the Caucasus, the remaining cross the Urals, but they fail to extend beyond western Siberia. The relationships with both Middle Asia and the Far East are due to widespread elements, only *L. spasskyi* demonstrates a specific connection between Europe and Middle Asia.

2.4. Siberia

This vast region has traditionally been subdivided into western, central, eastern and southern parts. The border between western and central Siberia lies along the western edge of the Central-Siberian

Upland, forming the so-called Yenisei zoogeographical barrier separating the European and Siberian faunas. The border between central and eastern Siberia, as defined by me, follows the Ob River. Southern Siberia comprises the mountainous lands bordering the USSR adjacent to China and Mongolia.

If the total fauna of Siberia is considered, its 45 constituent species comprise 17 (38%) endemics and 13 (29%) subendemics. Of the latter, 7 species are also met with in the Far East: *L. dybowskii* (O.P.-Cambridge), *L. karpinskii* (O.P.-Cambridge), *L. taczanowskii* (O.P.-Cambridge), *L.* sp., *L. abiskoensis* Holm, *L. nigriventris* (L. Koch), *L. suffusus* Strand. The last three species, as well as *L. bergstroemi* Schenkel, *L. decipiens* (L. Koch), *L. punctulatus* Holm, *L. sobrius* Thorell, *L. geminus* Tanasevitch and *L. laricetorum* Tanasevich & Eskov, occur in the northern part of Europe in addition to Siberia. If the western border of the range of the last two species lies apparently at the latitude of Kanin Peninsula or the Pechora River, the remaining *L. abiskoensis*, *L. bergstroemi*, *L.decipiens*, *L. nigriventris*, *L. punctulatus*, *L.sobrius* and *L. suffusus* reach as far as Fennoscandia where, together with some other Siberian elements, they constitute the kernel of the Siberian fauna (Eskov 1986). In other words, an irregular interpenetration of both European and Siberian faunas is noted. While the Siberian elements manage to reach as far west as Fennoscandia, the representation of European species beyond the Urals is poor and seems to be restricted to western Siberia (*L. angulatus*, *L. angulipalpis*, *L. antroniensis*, *L. cristatus*, *L. tenebricola*), and to a lesser extent to southern Siberia (*L. pallidus*). A similar pattern is observed when the faunas of both Siberia and the Far East are dealt with.

The fauna of eastern Siberia comprises more conspicuous elements than any other Siberian subregion: 7 endemics (22%). The poorest in this respect are Middle and western subregions since neither has any endemics. The latter part's fauna is closer to the European (s.lat. & s.str.), being not only the easternmost area for the distribution of European species (see above), but it also lacks some purely Siberian elements, such as *L. karpinskii*, *L. flexilis* Tanasevitch, *L. incestoides* Tanasevitch & Eskov, *L. nenilini* Tanasevitch, *L. sibiricus* Tanasevitch. The central Siberian fauna consists of 19 species (obviously an underestimate due to insufficient data) and is closer to both the southern and the eastern rather than the western fauna. A number of specific components relate the central Siberian fauna to the adjacent ones: *L. sibiricus* to the southern, *L. nenilini* to the eastern, and *L. flexilis* to both the southern and eastern. In the mountains of southern Siberia, 24 *Lepthyphantes* are known, of these, two do not occur beyond the subregion (*L. distichus* Tanasevitch and *L. cerinus* (L.Koch)), and a few are closer to eastern Siberian species than to central Siberian species (*L. flagellifer* Tanasevitch, *L. incestoides*, *L. unicornis* (O.P.-Cambridge)). The relationships between the faunas of Siberia and North America are surprisingly weak, this is probably due to insufficient data from the latter. Such connections are demonstrated by the widespread *L. leprosus* (Ohlert) and *L. nebulosus* (Sundevall) (both *L. minutus* (Blackwall) and *L.tenuis* often referred to as Holarctic, are not known within Siberia, the first being Euro-American and the second, Euro-Ancient Mediterraneo-American), circumpolar boreo-hypoarctic *L. complicatus* (Emerton) and *L. alpinus* (Emerton) (the latter being new to the USSR fauna; ♂♂, Chukotka, Anguem & Vulvyveem River, 22.VII.1988, leg. Yu. Marusik; this species is an American vicariant of the Siberian *L. nenilini*).

Cases of vicariance of East Palaearctic *Lepthyphantes* are noteworthy. The vicariant complex *angulatus-geminus*- cf. *angulatus-bipilis*, encompassing taxonomically closely-related species, is particularly interesting. The range of the former comprises northern Europe (up to the arctic coast of Fennoscandia) and reaches as far as western Siberia. Already in the European part of its range, in the tundra and forest-tundra belts east of Kanin Peninsula, it is substituted by the Siberian *L. geminus*. In western Siberia both species apparently occur sympatrically, whereas in both southern and central Siberia only *L.geminus* is present. In its turn, in the Far East it gives way to *L.* cf. *angulatus*, which in eastern Siberia is substituted by *L. bipilis* Kulczynski. The other vicariant complexes are represented by species pairs. *L. bergstroemi* widespread in the northern part of Europe, in western and central Siberia, gives way, in both southern and eastern Siberia to the very closely-related *L. flagellifer* Tanasevitch. The

European *L. angulipalpis* reaches as far eastward as western Siberia, but further eastward it is replaced by the close relative *L. karpinskii*. The Holarctic *L. nebulosus* (Sundevall) is substituted in central Asia by *L. nebulosoides* Wunderlich.

2.5. The Far East

The fauna of the Far East (24 species) consists of one Holarctic (*L. nebulosus*), three Palaearctic (*L. mengei*, *L. obscurus* (Blackwall), *L. alacris* (Blackwall)), one Manchurian (*L. nigromaculatus* Zhu & Wen), comb. nov. ex *Bolyphantes*[1]) and one Japanese species (*L. cericeus* (Saito)[2]), 8 species (33%) are Siberian and Euro-Siberian (see above), 10 species (42%) have not yet been found outside this region, mainly representing perhaps the largely unexplored Manchurian fauna. The discovery of two, as yet, undescribed species in Kedrovaya Pad State Reserve, southern Primorye, is highly interesting and at the same time very characteristic and these form, together with the Japanese *L. cericeus*, a highly homogenous group close to the *martensi*-group recently established for three *Lepthyphantes* in the Himalayas (Tanasevitch 1987b).

3. Discussion

The Caucasian fauna of *Lepthyphantes* is very different from the European one (s.lat.), although, in general, the regional Linyphiidae are mainly European in their origin (Tanasevitch 1987c). This witnesses to the fact that this mountaineous land is either an independent origin centre of the genus concerned, or constitutes part of a Near Eastern one, or even part of an East Mediterranean centre. In any case, the Caucasus should not be considered as a subordinate unit within the European realm.

The Middle Asian fauna, which is practically that of the region's mountain systems to which *Lepthyphantes* are mainly confined, is highly conspicuous and seems to be part of the great Central Asian centre, more exactly of a whole "set" of Central Asian centres. This is obvious, at least, from a comparison between the absolutely different faunas of both Middle Asia and the Himalayas (Tanasevitch 1987b).

The Far Eastern fauna, displaying a mixed Siberio-Manchurian character, may be regarded as peripheral to the Sino-Manchurian realm, or as a transitional zone between the latter and the Siberian regions. Earlier a Manchurian centre of faunogenesis in *Lepthyphantes* was believed to be expressed very weakly (Tanasevitch & Eskov 1987), but recent discoveries of a good number of highly conspicuous species, obviously restricted to this area, witness to an underestimation of the role of the Manchurian centre. In this respect, the poor representation of *Lepthyphantes* in Japan, which cannot be accounted for by insufficient data, remains to be explained.

The USSR's territory occupies a considerable part of the European, and all the Siberian part of the Palaearctic. The Yenisei barrier serves as the border between both of these. Against the background of the unity of the faunas of Middle, eastern and southern Siberia, that of western Siberia stands somewhat apart. It displays (Fig. 2B) a more pronounced relationship to the central Siberian one, this being, in my opinion, the result of insufficient exploration of the latter. Western Siberia together with the European part, forms a pair easily opposed to central, eastern, and southern Siberia which represent a clear (relative) unity (Fig. 2C). Such a scheme corresponds perfectly to the traditional division of the European and the Siberian realms. Western Siberia can apparently be regarded as a transitional zone between both regions, including the parts of Europe with a pronounced influence from the Siberian fauna.

In conclusion, let me note that despite the presence among *Lepthyphantes* of a considerable number of widespread species, the genus as a whole displays a pronounced tendency towards the formation of high-level endemic regional faunas. The most proliferic centers of speciation are mainly confined to the mountainous systems

[1]This is a species new to the USSR fauna: ♀♀, Amursk Area, Arkhara, 12.VIII.1983, leg. Yu. Marusik; ♀, Vladivostok, Artem, 3.VI.1981, leg. P. Dunin.

[2]This species is new to the USSR fauna: ♂♂ and ♀♀, Kuril Islands, Kunashir Island, Otradnoye, VIII.1987, leg. A. Basarukin.

of the southern and, to a lesser extent, northeastern Palaearctic.

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