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Vicariance in the northern Asian Salticidae (Arachnida, Araneae), with notes on Siberian endemism of the family

Dmitri V. LOGUNOV

Zoological Museum, Institute for Systematics and Ecology of Animals, Frunze Street 11, Novosibirsk, 630091, Russia.

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ABSTRACT

Using the northern Asian Salticidae as an example, it is shown that the faunistic suture zones, where ranges of allopatric species meet or overlap, can be used as 'indicators' of biogeographical boundaries. In northern Asia 16 pairs of allopatric species, divided into 5 groups, characterise the area defined earlier as the Angaran subregion. Additionally 18 endemic/subendemic species (15 % of all northern Asian salticids) are found there. By analysing the habitat preferences of Siberian endemics, it is assumed that they may be traced either to mountain forest-steppe or mountain tundra landscapes, and seem to be of late Pleistocene/Holocene origin.

INTRODUCTION

The problem of vicariance of closely related species is connected with a more general problem, the defining for biogeographical boundaries. For instance, Medvedev and Voronova (1978) reported that the suture zones of allopatric chrysomelid beetles can be used as probable indicators of biogeographical boundaries. The jumping spiders (Salticidae) seem to be such a case as well, illustrating examples of allopatry in northern Asia in relation to biogeographical boundaries defined by e.g. Starobogatov (1970), Eskov (1988), Sergeev (1992), etc. The discussion on the suture zones of vicarious species doesn't substitute the general problem of forming biogeographical regions. To do this other approaches are required, e.g. such as described by Kutcheruk (1979), Kryzhanovskiy (1976a, b), or others.

Particular faunistic regions are e.g. characterized by the degree of species endemism. It is commonly known that there are a lot of Siberian endemics both in plants and animals in northern Asia (Gorodkov 1992). They are either local species inhabiting mountain tundra or semiarid landscapes of Siberia or rather widespread Siberian species. Their extended ranges are often considered as a hallmark of specifically Siberian endemics (Gorodkov 1992).

The problem of Siberian endemism in Salticidae was already discussed by Prószyński (1980, 1986, 1991). The salticid fauna of temperate regions of Eurasia was chiefly formed by the reinvasion of the Holocene colonists from the Mediterranean, Ethiopian and Oriental centres of speciation (10,000-12,000 years BP). Only a few, if any, species survived or originated in the area during the Ice Age. The only exception seems to be the genus *Sitticus*, which, according to Prószyński (1983), could be a real Palaearctic autochtonous that presumably originated and evolved somewhere within the Eurosiberian zone during the Tertiary period.

Thus, the purpose of the present paper is to provide a brief review of all the detected pairs/triads of the vicarious salticid species in the fauna of northern Asia and to develop a list of those northern Asiatic salticids whose ranges and habitat preferences allow us to treat them as Siberian palaeoendemics.

METHODS AND TERMINOLOGY

Ranges of individual taxa have been outlined on maps using the commonly adopted method (e.g. Sergeev 1992). To show the ranges of particular species, maps published by Prószyński (1976, 1983) were used. Nomenclature for range types is largely adopted from Gorodkov (1984, 1992); see also Logunov (1996). In the text, no difference is made between the true allopatry and the parapatry (*sensu* Panov 1989), because up to now nothing is known about interspecific hybridisation between salticid species whose ranges meet or overlap. Most probably, both types of vicariance exist. Therefore, all the detected cases of vicariance are treated as a systematic allopatry (*sensu* Lopatin 1980), i.e. the allopatry of closely related species that in most cases inhabit similar/same biotopes (Tab. 1). Examples of the ecological allopatry in jumping spiders are poorly known (e.g. in some *Chaloscirtus* species, see Marusik 1991), and they are not included in this paper.

RESULTS AND DISCUSSION

I. Salticid suture-zones

Prószyński (1983) was the first to report a few examples of the west-east Palaearctic replacements in the Salticidae, e.g. *Sitticus saxicola* and *Sitticus lineolatus*. Wesołowska and Marusik (1990) reported the vicariance of three *Heliophanus* species (see below, group 3).

The data available suggests that there are at least 16 pairs of vicarious salticid species in northern Asia, which can be divided into 5 groups (Tab. 1).

1. The first, most numerous group (Tab. 1) includes those salticid species whose ranges meet/overlap along a line running roughly from the Bolshoi Khingan Mt. Range in the south-west to the Amur River basin or along Stanovoi Mt. Range in the north-east (Figs. 1-3). This suture zone (Fig. 7: III) occurs along the earlier designated boundary between the Euro-Siberian and Palaearchearctic (= Manchurian) subregions (Semenov-Tien-Shanskij 1936; Lopatin 1980; Sergeev 1992).

Tab. 1 Vicarious species and their habitats in northern Asia

Pairs of vicarious species*		Habitats**
Group 1		
Bianor aurocinctus (Ohlert, 1865); [tE], Fig. 1:1.	*Harmochirus nigriculus* Logunov *et* Wesołowska, 1992; [MJ], Fig. 1: 2.	*B. a.*: birch forest; bushy and spotted tundras; upland meadow. *B. n.*: mixed forest; meadow.
Euophrys erratica (Walckenaer, 1826); [ES], Fig. 1: 4.	*Euophrys iwatensis* Bohdanowicz *et* Prószyński, 1987; [MJ], Fig. 1: 5.	Both species: deciduous and mixed forests (in litter and on trunk).
Euophrys proszynskii Logunov *et al.*, 1993; [Sb], Fig. 2: 7.	*Euophrys sp.* ***; [MJ], Fig. 2: 8.	*E. p.*: sloping stony steppes; mountain stony tundra. *E. sp.*: no data.
Marpissa pomatia (Walckenaer, 1802); [tE], Fig. 3: 1.	*Marpissa dybowskii* (Kulczyński, 1895); [MJ], Fig. 3: 2.	*M. p.*: clearings in deciduous and mixed forests; bushy meadows. *M. d.*: no data.
Group 2		
Sitticus distinguendus (Simon, 1868); [ES], Fig. 3: 3.	*Sitticus avocator* (O.P.-Cambridge, 1885); [DF], Fig. 3: 4.	Both species: talus, screes, open rocks.
Sitticus terebratus (Clerck, 1758); [ES], Fig. 4: 6.	*Sitticus fasciger* (Simon, 1880); [SA], Fig. 4: 7.	Both species: no data.
Evarcha falcata (Clerck, 1758); [ES], Fig. 4: 8.	*Evarcha* sp.****; [SA], Fig. 4: 9.	Both species: bushy clearings in deciduous and mixed forests.
Pellenes tripunctatus (Walckenaer, 1802); [ES], Fig. 8: 8.	*Pellenes sibiricus* Logunov *et* Marusik, 1994; [Sb], Fig. 8: 7.	Both species: as noted for *E. falcata.*
Group 3		
Heliophanus dampfi Schenkel, 1923; [ES], Fig. 5: 1.	*Heliophanus camtschadalicus* Kulczyński, 1895; [Sb], Fig. 5: 2.	*H. d.*: bushy tundra; birch parkland. *H. c.*: valley willow-birch forest, alder thickets
Heliophanus camtschadalicus Kulczyński, 1895; Sb], Fig. 5: 2.	*Heliophanus ussuricus* Kulczyński, 1895; [DF], Fig. 5: 3.	*H. c.*: see above. *H .u.*: clearings in moist deciduous forest; lowland meadow

Tab. 1 continued

Pairs of vicarious species*		Habitats**
Group 4		
Asianellus festivus (C. L. Koch, 1834); [tE], Fig. 6: 7.	*Asianellus potanini* (Schenkel, 1936); [SM], Fig. 6: 8.	*A. f.*: talus; stony sloping steppes; pebble banks of rivers. *A. p.*: no data.
Bianor aurocinctus (Ohlert, 1865); [tE], Fig. 1:1.	*Bianor inexploratus* Logunov, 1991; [KM], Fig. 1: 3.	*B. a.*: see above. *B. i.*: *Lasiagrostis splendens*-stand.
Heliophanus lineiventris Simon, 1868; [tE], Fig. 6: 5.	*Heliophanus chovdensis* Prószyński, 1982; [KM], Fig. 6: 6.	*H. l.*: dry and stony sloping steppes; glades in mixed forest. *H. c.*: no data.
Sitticus finschi (L. Koch, 1879); [SA].	*Sitticus tannuolana* Logunov, 1992; [SM].	Both species: coniferous or mixed forests (on tree trunk).
Group 5		
Sitticus saxicola (C. L. Koch, 1848); [aE].	*Sitticus lineolatus* (Grube, 1861); [SA].	*S. s.*: no data. *S. l.*: mountain tundra
Euophrys frontalis (Walckenaer, 1802); [aE], Fig. 2: 6.	*Euophrys proszynskii* Logunov *et al.*, 1993; [Sb], Fig. 2: 7.	*E. f.*: mixed and deciduous forests (in litter). *E. p.*: see above.

* - Symbols in square brackets reffer to the range pattern of each species: aE - amphi-Eurasian temperate; DF - Dahurian-Far Eastern subboreal; ES - European-Siberian temperate; KM - Kazakhstan-Mongolian subboreal; MJ - Manchurian-Japanese; SA - Siberian-American temperate; Sb- Siberian boreal; SM - S-Siberian-Mongolian, subboreal; tE - trans-Eurasian temperate.

** - Habitat data are compiled from Logunov (1992).

*** - *sensu* Logunov *et al.* (1993).

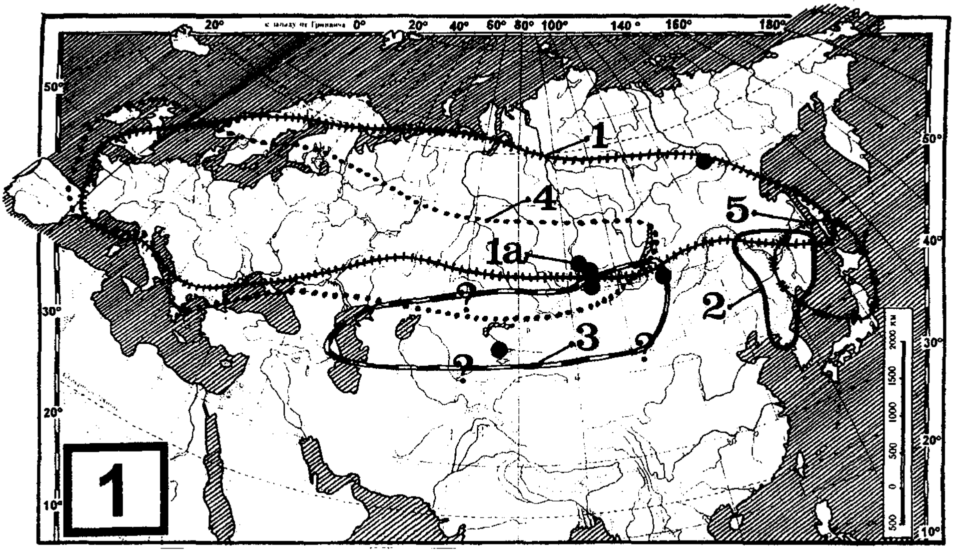
**** - *Evarcha* sp. is a new species that will be described separately.

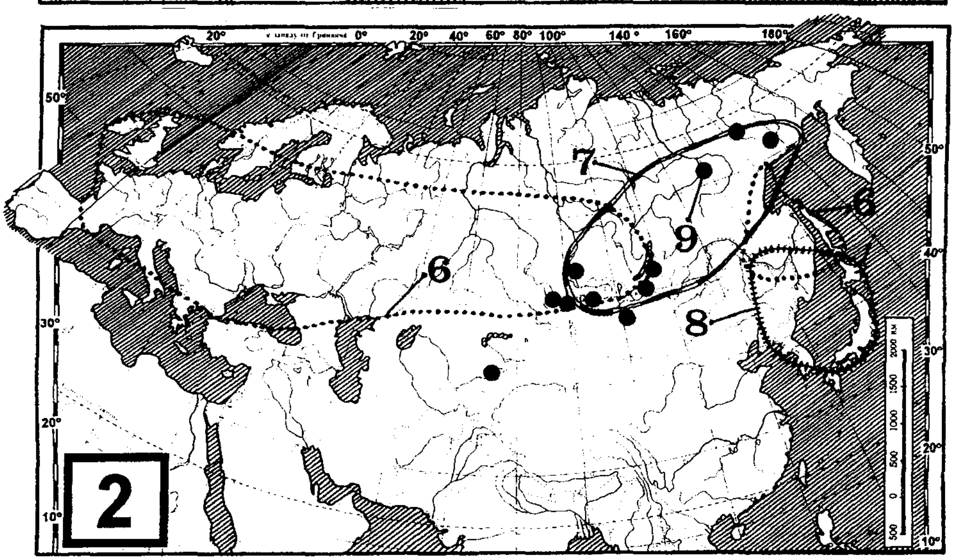
Tab. 2 Siberian (Angaran) endemic and subendemic Salticidae and their habitats

Species	Habitats*
"Bianor" stepposus Logunov, 1991; [se], Fig. 1: 1a.	MSLT: dry steppe; *Lasiagrostis splendens* stand; relic steppe - MFLT: sloping shrub-stony steppe.
Chalcoscirtus glacialis Caporiacco, 1935; [e], Fig. 5: 4.	MSLT: dry steppe; cryo-xerophylous steppe; scree. - GLT: moss-shrub wet tundra.
Chalcoscirtus grishkanae Marusik, 1988; [e], Fig. 7: 1.	GLT: lichen stony tundra.
Chalcoscirtus hyperboreus Marusik 1991; [e], Fig. 8: 5.	GLT: moss-shrub wet tundra.
Dendryphantes biankii Prószyński, 1979; [se], Fig. 8: 2.	MFLT: shruby glades and forest edges. - ILT: urema.
Dendryphantes czekanowskii Prószyński, 1979; [e], Fig. 6: 9.	GLT: moss-shrub wet tundra; larch parkland.
Dendryphantes fusconotatus (Grube, 1861); [e], Fig. 8: 3.	MFLT: sloping meadow shruby steppe.
Euophrys flavoater (Grube, 1861); [se], Fig. 8: 6.	MFLT: glades; larch and mixed forests.
Euophrys proszynskii Logunov *et al.*, 1993; [e], Fig. 2: 7.	MFLT: sloping shrub-stony steppe. - GLT: lichen stony tundra.
Evarcha mongolica Danilov *et* Logunov, 1993; [e], see Danilov & Logunov, 1993.	MFLT: sloping shrub-stony steppe.
Heliophanus baikalensis Kulczyński, 1895; [e], Fig. 4: 10.	MFLT: sloping meadow shruby steppe; glades; larch and mixed forests.
Heliophanus camtschadalicus Kulczyński, 1895; [e], Fig. 5: 2.	MFLT: sloping meadow shruby steppe; larch and mixed forests. - ILT: urema.
Pellenes gobiensis Schenkel, 1936; [se], Fig. 3: 5.	MSLT: dry nanophanerophyte steppe; relic steppe biotops.
Pellenes limbatus Kulczyński, 1895; [se], Fig. 2: 9.	MSLT: cryo-xerophylous steppe; scree.
Pellenes logunovi Marusik *et al.*, 1996; [e], Fig. 8: 4.	GLT: moss-lichen stony tundra.
Pellenes sibiricus Logunov *et* Marusik, 1994; [se], Fig. 8: 7.	MFLT: sloping meadow shruby steppe; shruby glades. - ILT: valley shruby grassland.
Sitticus albolineatus (Kulczyński, 1895); [e], see Prószyński, 1983: Fig. 15.	ILT: Pebble river banks.
Sitticus burjaticus Danilov *et* Logunov, 1993; [e], see Danilov & Logunov, 1993.	MFLT: sloping shrub-stony steppe; crowns of coniferous trees.

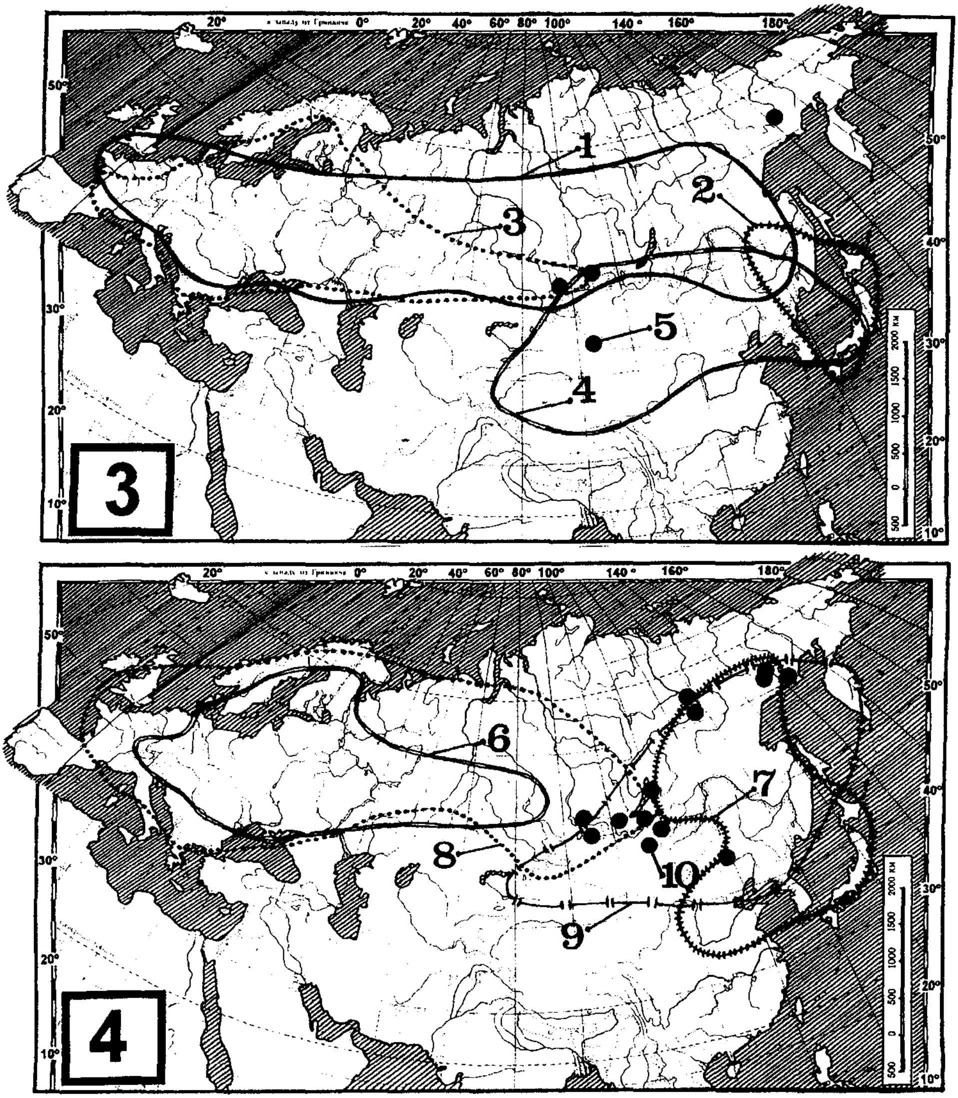
Symbols in square brackets are as follows: e - emdemic; se - sub-endemic. Landscape types: MSLT - mountain steppe langscape; MFLT - mountain forest-steppe landscape; GLT - goltsy (mountain tundra) landscape; ILT - inundated lanscape.

* - Habitat data are compiled from Logunov (1992).

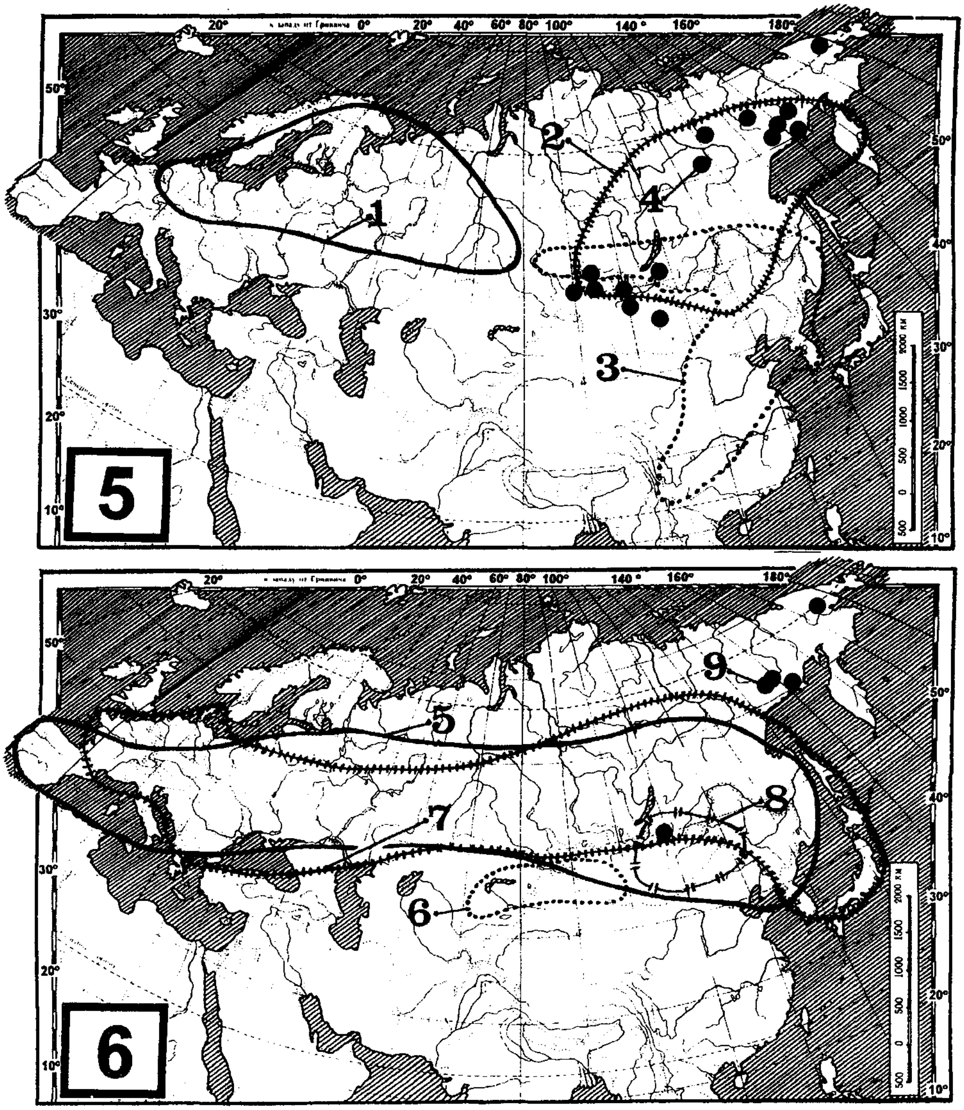




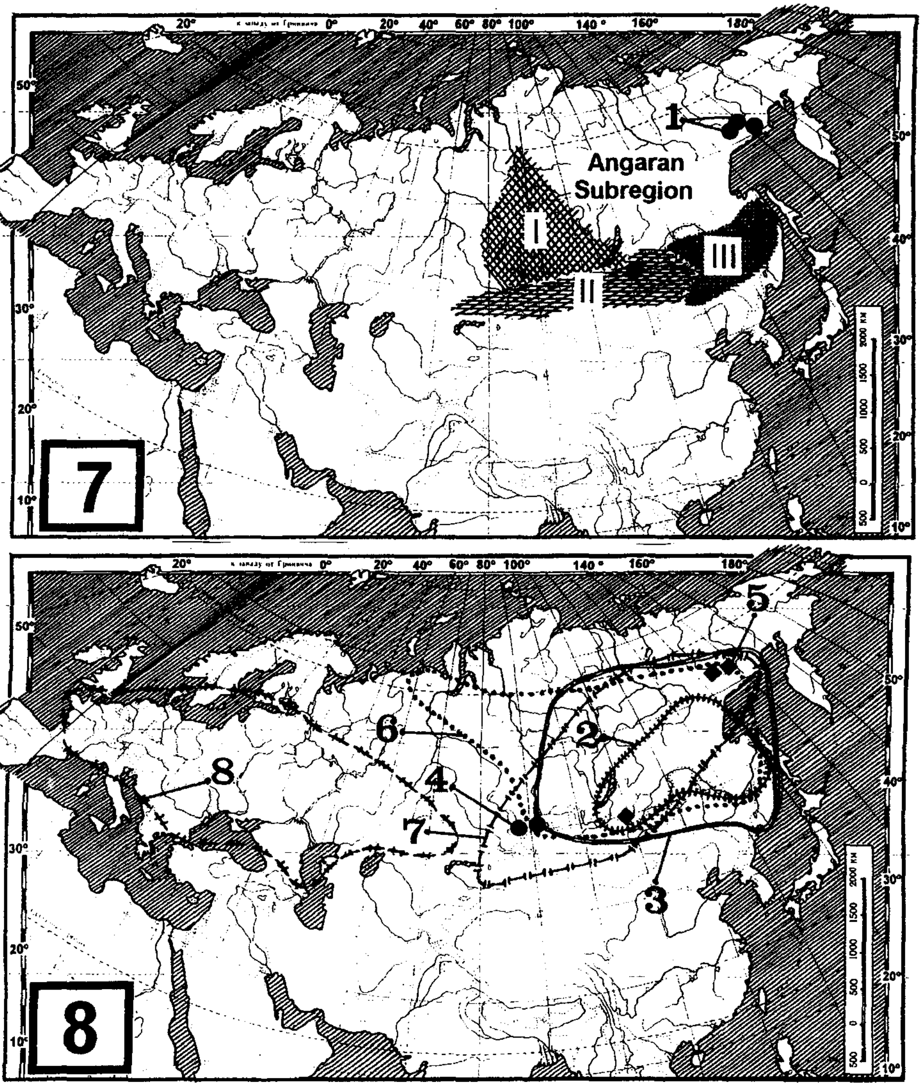
Figs. 1-2. Distribution of *'Bianor' stepposus* (1a), *Bianor aurocinctus* (1), *Harmochirus nigriculus* (2), *Bianor inexploratus* (3), *Euophrys erratica* (4), *Euophrys iwatensis* (5), *Euophrys frontalis* (6), *Euophrys proszynskii* (7), *Euophrys* sp. (8) and *Pellenes limbatus* (9).



Figs. 3-4. Distribution of *Marpissa pomatia* (1), *Marpissa dybowskii* (2), *Sitticus distinguendus* (3), *Sitticus avocator* (4), *Pellenes gobiensis* (5), *Sitticus terebratus* (6), *Sitticus fasciger* (7), *Evarcha falcata* (8), *Evarcha* sp. (9) and *Heliophnaus baikalensis* (10). Distribution of *Sitticus fasciger* and *Evarcha* sp. in N-America is not shown.



Figs. 5-6. Distribution of *Heliophanus dampfi* (1), *Heliophanus camtschadalicus* (2), *Heliophanus ussuricus* (3), *Chalcoscirtus glacialis* (4), *Heliophanus lineiventris* (5), *Heliophanus chovdensis* (6), *Asianellus festivus* (7), *Asianellus potanini* (8), *Dendryphantes czekanowskii* (9).



Figs. 7-8. Three main suture zones in northern Asia based on the Salticidae distribution (Fig. 7: I, II, III; explanations in the text) and distribution of *Chalcoscirtus grishkanae* (1), *Dendryphantes biankii* (2), *Dendryphates fusconotatus* (3), *Pellenes logunovi* (4), *Chalocoscirtus hyperboreus* (5), *Euophrys flavoater* (6) *Pellenes sibiricus* (7) and *Pellenes tripunctatus* (8).

2. The second group consists of the species whose ranges meet approximately along the Yenisei River (Figs. 1-4, 7: I), proving the significance of so-called Johansen's line as biogeographical barrier for spreading from the west to the east (Starobogatov 1970; Chernov 1975; Eskov 1988). For Salticidae, the ranges of the European-Siberian species meet those of the Siberian or Siberian-American species (Tab. 1).

3. Salticid species included in the third group form a triad of species, which alternate in spreading from the north-west to the south-east (Fig. 5). A similar case is also described for three *Araneus* species (Wesołowska & Marusik 1990): *Araneus quadratus* Clerck, 1758 - the W-Palaearctic; *Araneus yukon* Levi, 1971 - E-Siberia and NW-America; and *Araneus pinguis* Karsch, 1879 - China, Mongolia and the Russian Far East. Examples of plants (e.g. *Salix* and *Anemone*) are also well-known (Tolmatchov 1986).

Since the ranges of two or three vicarious species discussed above together yeald a trans-Eurasian or trans-Palaearctic distributional pattern, the existence of allopatry of this kind is commonly considered to be a result of the splitting of the former continuous range of a single species caused by the Pleistocene aridisation and temperature drop (Gorodkov 1979).

4. The fourth group of vicariants (Tab. 1) shows their suture zones running along the latitudinal barrier at the border between Angaran and Central-Asian subregions (Starobogatov 1970) (Fig. 7: II). In this case European-Siberian or Siberian-American salticid species meet or overlap South-Siberian-Mongolian or Kazakhstan-West-Mongolian species (Figs. 1, 3, 6).

5. In this group the range of one allopatric salticid species (Amphi-Eurasian) is divided into two separate areas by the range of another species (Siberian or Siberian-American) (Fig. 2). I.e. Europe and the Russian Far East are occupied by one species, while Siberia - by its close relative. So, there are pairs of suture zones between the ranges of both species corresponding to those of groups 1 and 2 (see above).

As far as the vicariance in the North Asian salticids is concerned, the suture zones of the vicarious species outline the area (Fig. 7) designated hitherto as the Angaran subregion (Starobogatov 1970), where so-called Siberian faunal type predominates (Stegman 1938; Eskov 1988). Among the jumping spiders, there are 16 species that are practically restricted to the Angaran subregion and they can be considered as its endemics or subendemics (Tab. 2).

II. Endemism of Siberian salticids

There are no endemic salticid genera in the fauna of Siberia. For comparison, the linyphiids are known to have no less than 7 endemic and 6 subendemic Siberian genera (Eskov 1986). The genus *Tuvaphantes* comprising two local Tuvan species seems to belong to the centre of endemism restricted by the arid parts of Mongolia and China (*sensu* Sergeev 1992) and hence cannot be considered as a true Siberian endemic.

The salticid species treated here as Siberian (Angaran) endemics (Tab. 2), show mainly Siberian boreal distributional patterns (Figs. 1-8) (see also Logunov 1996: Fig. 5), i.e. they are restricted to the area of so-called Angaran autochtonous faunogenesis complex (*sensu* Eskov 1988). Some of these species, e.g. *Pellenes limbatus* or *Euophrys flavoater*, probably should be considered as subendemics, since their ranges slightly extend over the frontiers of the designated area (Figs. 2, 8). Out of 119 northern Asian Salticid species (29 genera, Logunov 1992) there are 18 endemics (subendemics) (15 %).

Siberian endemics form two distinctive chorological complexes (Tab. 2): (1) dwellers of the mountain-tundra landscape; and (2) those of the mountain forest-steppe landscape (mainly sloping shrub-stony steppes). In both landscapes, the Siberian endemics constitute the main body of inhabitants and, in most cases, are strictly restricted to them (Logunov 1992). Certain species can be found in both landscape types. For example, *Euophrys proszynskii* occurs in mountain lichen-stony tundra and sloping shrub-stony steppe. *Chalcoscirtus glacialis* occurs in both the mountain cryo-xerophylous steppe and the wet mountain moss-shrubby tundra. These facts suggest a specific faunal relationship between the mountain-tundra and mountain-steppe landscapes, and are clear evidence that only the Angaran endemic salticids can be found in both landscape types. Such faunal and floral relationships (Kurentsov 1964; Berman & Alfimov 1984a, b) reflect common Pleistocene-Holocene history of the landscapes considered.

Most mountain steppe dwellers in South Siberia, e.g. *Pellenes gobiensis* or *Chalcoscirtus glacialis*, have also been collected in the relic steppe complexes of north-eastern Siberia (north-eastern Yakutia and the Magadan area) that descended from the so-called Pleistocene tundra-steppe biome (Yurtsev 1981; Kiselev 1981; Sher 1990), with the fauna usually considered as a tundra-steppe relic (Berman & Mordkovitch 1979; Kiselev 1981; Berman & Alfimov 1984a, b). The tundra-steppes are not uniform but make a mosaic of tundra, taiga and steppe components (tundra-forest-steppe) (Kiselev 1981; Golosova *et al.* 1985; etc.) that appeared in the late Pliocene and existed during all the Pleistocene (however, see Sher 1990). In response to climatic changes (humidity vs. cryo-aridity) each of the mosaic components thrived or reduced in turn, but did not disappear totally (Berman & Alfimov 1984a).

Thus the Siberian (Angaran) endemic salticids are the relics of tundra-taiga-steppe landscapes of the Pleistocene/Holocene time, when most modern Siberian landscapes were formed (e.g. Sher 1990) and palaeoendemics, i.e. the species that either originated or at least survived during the Ice Age in the area, being initially Siberian species.

The relationships of pebble shore inhabitant *Sitticus albolineatus* with the Pleistocene tundra-forest-steppe are not so evident. Perhaps it is of another origin and history than the other Siberian endemic salticids.

CONCLUSIONS

1. There are 5 groups of the vicarious salticid species in the fauna of northern Asia, their suture zones characterising the area designated earlier as the Angaran (= eastern Siberian) subregion; the suture-zones can be used as indicators of biogeographical boundaries.
2. The Angaran subregion is characterized by 18 endemic/subendemic species comprising 15 % of the entire salticid fauna of northern Asia; all seem to be palaeoendemics.
3. Chorological analysis of the endemic Salticidae shows the late Pleistocene-Holocene period to be the most important in forming the Angaran autochtonous faunogenesis complex in northern Asia.

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