

## Distribution and assemblage classification of spiders of the East European oak forests (Arachnida Aranei)<sup>1</sup>.

### Распределение и классификация группировок пауков дубрав Восточной Европы (Arachnida Aranei)<sup>1</sup>.

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**КЛЮЧЕВЫЕ СЛОВА:** подстилочные пауки, дубравы, Русская равнина, фауна, группировки, фенология, распределение, классификация, история.

**ABSTRACT:** Based on an analysis of quantitative data on litter-dwelling spiders (124 species) of the East European Plain oak forests (46 sites), 8 groupings are delimited differing in distribution pattern. Two of the groupings reflect a zonal factor, one referring to both western forest and Cisuralian forest-steppe belts, and the other to forest-steppe ranging from Moldavia to the Volga flow. Other three groupings encompass polyzonal species differing either in the presence of centers of maximal abundance (one "northern" and the other "southern") or in their absence. Further three groupings are regional, being restricted to Moldavian, western forest-steppe, and Cisuralian oak forests, respectively. Analysis of large-scale variation in species assemblages allows to distinguish three regional (Cisuralian, Moldavian, central Russian) and one zonal line (between the forest and forest-steppe belts), resulting in the area's araneographic regioning. Classification of the East European Plain oak forests has been proposed as based on the distribution of spider assemblages. Consideration of the main phenological patterns permits discrimination of three main historical components in the region's spider fauna (Fagetal, Betuletal, and Quercetal), neatly corresponding to Kleopov's [1990] respective floral cenotic elements.

**РЕЗЮМЕ:** На основе анализа данных количественных учетов численности подстилочных

пауков (124 вида) дубрав Восточно-Европейской равнины (46 точек сборов) выделено 8 группировок, различающихся по характеру распределения. Две из этих группировок отражают фактор зональности, одна обозначая как западный сектор лесной зоны, так и предуральскую лесостепь, а другая — лесостепь от Молдавии до Поволжья. Еще три группировки включают полизональные виды, отличающиеся либо наличием, либо отсутствием центров наивысшей плотности (один "северный", другой "южный"). Следующие три группировки региональные и соответственно приурочены к молдавским, западным лесостепным и предуральским дубравам. Анализ широкомасштабной изменчивости видовых группировок позволяет очертить три региональные (предуральский, молдавский и центрально-русский) и одну зональную (между зоной лесов и лесостепью) линии, позволяющие провести аранеографические районирование рассматриваемой территории. На основе распределения группировок пауков предложена классификация дубрав Русской равнины. Учитывая основные фенологические типы пауков, в региональной фауне пауков выделяются три главные исторические составляющие (фагетальная, бетулетальная и кверцетальная), хорошо согласующиеся с соответствующими ценотическими флористическими элементами, выделяемыми Клеоповым [1990].

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## 1. Introduction

The importance of investigations dealing with geographic variation in local species assemblages is beyond any doubt [Haila et al., 1987; Brown & Kurzius, 1987]. There are two main approaches in studying this problem. With respect to animals, one is regional historical (or historico-faunistic), i.e. classical historical zoogeography, and the other is landscape-typological, or geozoological [Chernov, 1975, 1984]. Being relative in comparisons between separate communities or ecosystems, differences between both approaches become absolute when typological units are dealt with at the level of macrogeographic regions (e.g. vast heterogeneous areas up to continents) [Chernov, 1975: 197].

The East European, or Russian, Plain is a great and geologically highly heterogeneous area covering most of eastern Europe. It extends from the Baltic and Ciscarpathia in the west to the Ural Mountains in the east (ca. 4,200 km), from Yamal and Kola peninsulas in the north to the Black Sea and Ciscaucasia (= Circassia) in the south (ca. 5,100 km). Being so huge, extremely diverse and displaying a classical pattern of latitudinal nature zonation, with the belts, or zones, of tundra, taiga (= dark-needled coniferous forests), mixed coniferous-broadleaved forests, broadleaved forests, forest-steppe, steppe and even semi-desert regularly succeeding each other from north to south, the Plain has long been known as a highly important arena for historical biogeographic studies.

Unlike our previous paper coping with the spider fauna of the East European Plain's oak forests as an attempted reconstruction of the history of the entire regional nemoral biome [Esjunin et al., 1993], we shall focus here on the geozoological aspect of the distribution of spiders over the Plain. In other words, macrogeographic variation in spider species and species assemblages restricted in the Plain to oak forests is the subject of the present contribution.

Spiders have been chosen as model for such studies due to their high levels of abundance, particular species richness and pronounced importance in soil/litter macrofauna communities virtually everywhere. Oak forests have been chosen as model, for *Quercus robur* L. in the Plain is known to be the main, climax hardwood tree species presumably fully corresponding to macroclimate of the regional nemoral (= broadleaved forest s.l.) biome [Razumovsky, 1981].

## 2. Study area

Our field survey has largely covered the most mature, intact, mainly well-preserved oak stands scattered over the entire Plain (Map 1) (see also Esjunin et al. [1993] and Penev et al. [1994]). The sampling sites were selected so as to be similar with respect to two general aspects: (1) predominance of *Quercus robur* and (2) moderate moisture conditions. The moisture conditions were estimated from the occurrence of a number of dominant mesophilous herb species such as *Aegopodium podagraria* L., *Carex pilosa* Scop., *Asarum europaeum* L., *Stellaria* spp., *Polygonatum multiflorum* L. (All.), *Pulmonaria obscura* Dumort., and *Galium odoratum* (L.) Scop. The state of the forest served as an additional criterion, i.e. we tried to stick to the most mature and well-preserved patches of oak forest in each locality. Despite this, the sites varied considerably in habitat conditions due to their sometimes vast geographic distances or other local factors. To minimize the possible effect of artifacts, we also used collecting techniques identical both in design and in sample size, and restricted the field work to relatively short periods mainly within May-June and from mid-August to early October [Penev et al., 1994].

## 3. Sampling procedure and methods

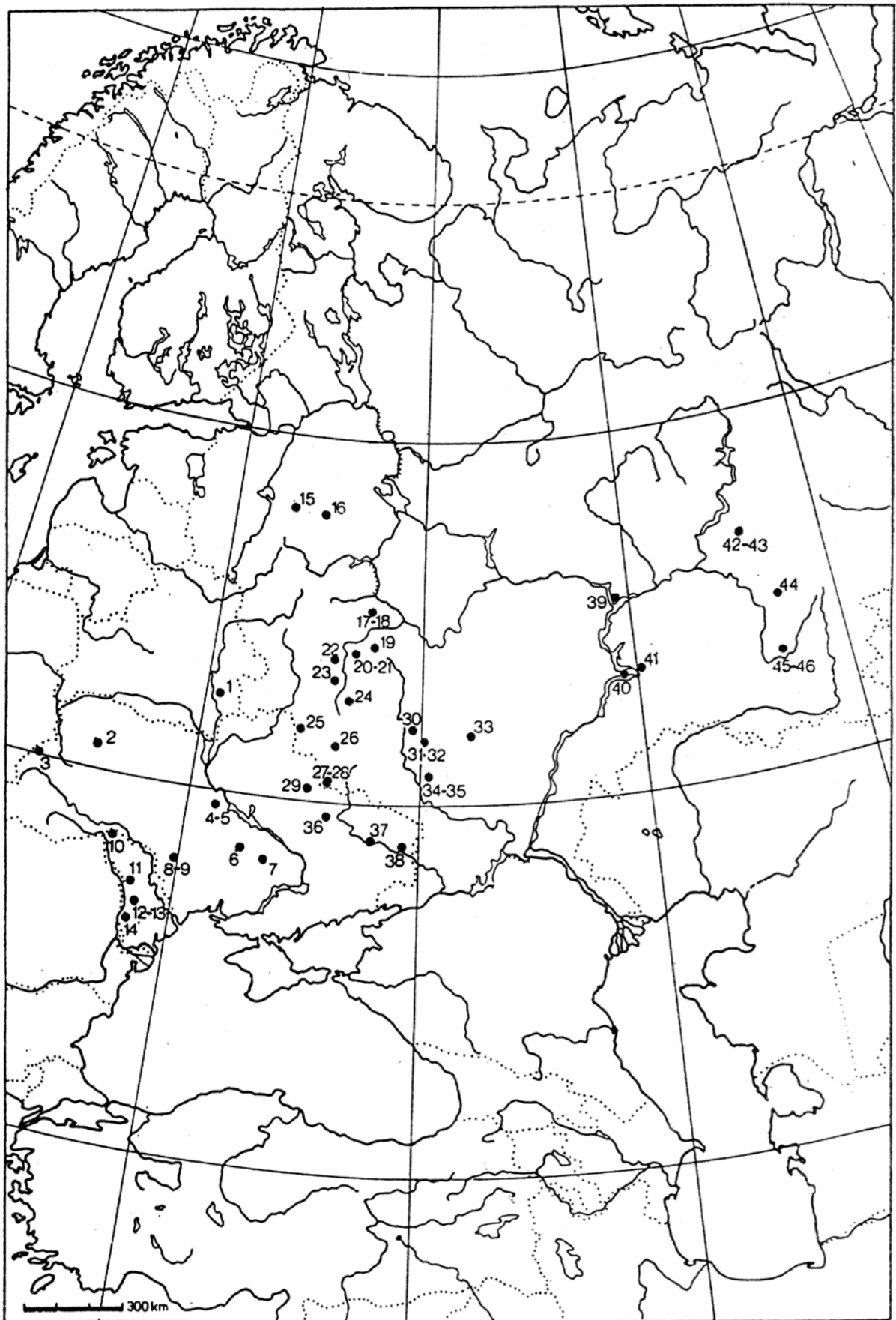
Twenty samples of 25x25 cm each were taken at each site according to the standard methods of soil zoological investigations accepted in Russia [Quantitative methods..., 1987]. Soil macrofauna was sampled from 10 cm thick soil layers on oilskin in the field. However, as regards spiders, they largely occurred in litter, thus making our studies chiefly restricted to the forest litter-dwelling spider complex.

The samples were taken along short transects (200-500 m, as a rule) within homogeneous forest patches. In case of ravines, ten samples were taken on plateau and the remaining ten on the adjacent slopes. To reveal possible microhabitat variation, the samples were taken randomly in consequent series of 3 samples each and systematically within series: the first sample just at an oak tree trunk, the second one between trees under their canopy, and the third one in a small forest "window" (but not in a clearing).

The program BIODIV was used for group average clustering [Baev & Penev, 1991]. The divisive classification procedure was performed with TWIN-

Map 1. Geographical locations of the study sites. Site numbers as in Appendix 1.

Карта 1. Географическое положение изученных точек сборов. Номера точек как в Приложении 1.



SPAN [Hill, 1979]. More information about the sampling sites and the methods of analysis applied is derivable from Esjunin et al. [1993] and Penev et al. [1994].

#### 4. Material

Altogether, 153 spider species were revealed in the litter of the samples in the East European Plain oak forests [cf. Penev et al., 1994]. However, not all of them can be attributed to the litter-dwelling complex known to be well-isolated from spider complexes of other biocenotic strata [Litvinava et al., 1981]. Numerous spider species inhabiting several vegetation strata use the litter as a site for hibernation or occur there accidentally when fallen down or moving between plants. Inclusion of such species taken from the samples into the complex of litter-dwellers is inadequate due to both ecological and biochorological reasons, considerably misrepresenting the general patterns revealed with statistic analyses sensitive to the presence of rare species. Therefore, based on the ecology of separate spider species, particularly with regard to those known from the East European Plain [Pereleshina, 1928; Pichka, 1965, 1974, 1984; Akimtseva, 1979; Sternbergs, 1979; Veselova & Mikhailov, 1986], the following spider taxa/ecological groupings have been excluded from consideration: all orbweaving spiders (Araneidae, Metidae, Tetragnathidae: *Tetragnatha*), as well as horto-, tamno-, and dendrobiontic Linyphiidae (*Drapetisca*, *Linyphia*, *Nerienne*, *Pitiohyphantes*), Theridiidae (*Achaearanea*, *Diplocephalus*, *Steatoda bipunctata*, *Theridion*), Philodromidae, and Thomisidae (*Misumena*). The case of *Enoplognatha ovata* deserves special attention, for its juveniles are sometimes treated as a component of the litter-dwelling spider complex [Stevenson & Dindal, 1982]. However, certain particulars of its ecology on the East European Plain [Pereleshina, 1928; Pichka, 1965, 1974], where its spiderlings are active in the forest litter only during a short period in the autumn, allow us to eliminate this species from further analysis as well. As a result, a list comprising 124 spider species taken from and definitely characteristic of the soil/litter samples in the East European Plain oak forests has been compiled separately for the spring and autumn [Penev et al., 1994, appendices 4 & 5].

Another problem is determined by seasonal changes in the spider population of the oak forest litter stratum. To test the possibility of joint treatment, we have compared spring and autumn samples taken from the same sites (Tab. 1). The significance of the difference in alpha-diversity of

the spring and autumn spider assemblages measured with the Shannon (Sh) index has been evaluated by means of Student's t-criterion [Hutcheson, 1970; Pesenko, 1982]. Besides, the rank distribution of the species in each sample has been carried out using Spearman's rank correlation coefficient ( $r_s$ ).

As regards alpha-diversity, the samples appear to be generally similar. However, in three cases significant differences between autumn and spring samples were found. Spearman's rank correlation coefficient displays quite a contrary pattern, with the values witnessing to that spring and autumn samples were not significantly correlated, except for one case.

The results obtained seem to be biologically explicable. Firstly, when comparing the spring and autumn species lists, only less than a half of the total (53 out of 124) turn out to occur throughout the vegetation season. Whereas the 35 species recorded solely in the spring can be met with in the autumn as well, for the females of spring-breeding forms can last as long as the vegetation season, amongst the 36 species reported solely in the autumn there is a large group in which the adults are restricted to autumn (e.g. *Allomena warburtoni*, *Bolyphantes alticeps*, *Floronina bucculenta*, *Porrhomma pallidum*, *Tapinopa longidens* — see Wiehle [1956]). Secondly, the proportion of species groupings delimited as to the distribution pattern in the East European Plain oak forests (Tab. 2) demonstrates considerable variation in the groupings' faunal composition in the spring and autumn samples. Domination of this or that distribution pattern in the samples cannot fail to affect the similarity between spider assemblages. All this forces us to analyse the spring and autumn samples separately, thus smoothing the effect of seasonality.

#### 5. Results

##### 5.1. Distribution of litter-dwelling spiders in East European Plain oak forests

To obtain a generalized pattern of spider species distributions of the oak forest litter complex, the sum quantitative data were treated with divisive cluster technique [Jongman et al., 1987] by means of the TWINSpan program. Such an analysis allows not only to outline range borders but also the areas where the species are more abundant. The results are presented in a TWINSpan table (Appendix 1). Based on this, 9 conventional species groupings are distinguished.

(1) Species "restricted" to Moldavia (= Moldova) and there displaying high levels of abundance



Table 1.

Таблица 1.

Comparison between spring and autumn samples taken in the same localities as to species diversity and rank distribution.

Сравнение весенних и осенних учетов, проведенных в одних и тех же точках сборов по видовому разнообразию и ранговому распределению.

Sites	Sampling dates		Number of species			$r_s$	tSt
	Spring	Autumn	Spring	Autumn	Total		
4,5	V.88	IX.90	19	11	26	-0.103	3.517**
8,9	V-VI.88	X.89	16	17	22	0.306	0.507
12,13	VI.90	IX.89	12	17	22	0.333	0.648
17,18	V.90	IX.90	12	11	17	0.239	0.270
20,21	V.89	IX.90	14	9	21	-0.535*	1.382
27,28	V.88	IX.90	15	21	26	-0.252	0.465
42,43	VI.91	IX.91	7	17	22	-0.313	2.818**
45,46	VI.91	VIII.88	10	16	21	-0.417	3.855*

Note: one asterisk (\*) —  $P \leq 0.05$ , two asterisks (\*\*) —  $P \leq 0.01$ ,  $r_s$  — Spearman's rank correlation coefficient, tSt — Student's t-criterion of the difference between alpha-diversity of the two sites compared as measured with the Shannon function.

Обозначения: одна звездочка (\*) —  $P \leq 0.05$ , две звездочки (\*\*) —  $P \leq 0.01$ ,  $r_s$  — коэффициент ранговой корреляции Спирмана, tSt — критерий Стьюдента t разности между альфа-разнообразием в обеих сравниваемых точках, оцениваемой с помощью функции Шеннона.

Table 2.

Таблица 2.

Representation of various chorological spider groupings of the East European Plain oak forests in different seasons.

The number of species in the nominator, percentage in the denominator. Abbreviations as in Tab. 1.

Представительство различных хорологических группировок пауков дубрав Восточно-Европейской равнины по разным сезонам. Число видов в числителе, процент в знаменателе. Обозначения как в Табл. 1.

Species groupings	Abbreviation	Spring	Spring-Autumn	Autumn
Moldavian forest-steppe	M	1/3	5/9	2/16
Forest-steppe	S	15/43	4/8	2/16
Western forest-steppe	SC	7/20	3/6	2/6
"Southern" polyzonal	PS	3/9	5/9	-
Polyzonal	P	3/9	14/26	3/8
"Northern" polyzonal	PN	1/3	8/15	-
Forest	NC	3/9	7/13	21/58
Forest & Cisuralian	N	-	5/9	3/8
Cisuralian	U	2/6	2/4	3/8
Total		35/100	53/100	36/100

(**M**, 8 taxa). Within the East European Plain, these have not been found beyond Moldavian oak forests, although some of them are known, e.g., from the Caucasus.

(2) Species widespread within the forest-steppe belt from Moldavia to the Volga River (**S**, 22 taxa). Their maximal numbers are observed either in the western (*Phrurolithus festivus*, Map 2A) or in the central parts of forest-steppe (*Abacoproeces saltuum*, *Panamomops menzei*, Map 2B, C).

(3) Species largely occurring in the western oak forests of the forest-steppe belt (**SC**, 12 taxa). Their maximum abundance is observed in the westernmost sites (*Micragrus herbigradus*, Map 2D).

(4) Polyzonal species with inclination to the southern sites (**PS**, 8 taxa). This group combines the species met with in oak woods of both forest-steppe and coniferous-broadleaved forest belts. Their maximal numbers seem to lie within forest-steppe (*Lepthyphantes flavipes*, *Diplocephalus picinus*, Map 2E, F).

(5) Polyzonal species sensu stricto (**P**, 19 taxa). This seems to be a heterogeneous complex uniting the species displaying various patterns of abundance change in the region's oak forests. The species have been referred here that possess no distinct between-site variation (*Ozyptila praticola*, Map 3A), reach the maximal abundance levels in the western forest-steppe oak stands (*Ballus depressus*, Map 3B), in the belt of mixed coniferous-broadleaved forests (*Microneta viaria*, Map 3C), in central southern forest-steppe and northern steppe (*Lepthyphantes angulipalpis*, Map 3D). Areas of increased numbers can be bipolar (*Ceratinella brevis*, Map 3E) or multipolar, i.e. covering several biomes at once (*Tapinocyba insecta*, Map 3F).

(6) Polyzonal species with inclination to the northern sites (**PN**, 9 taxa). These occur in different zones, but their maximal abundance is observed in oak forests lying within the belt of mixed coniferous-broadleaved forests (*Macragrus rufus*, Map 4A), within the subzone of southern taiga (*Robertus*

*lividus*, Map 4C) or at the border between both biomes (*Gongylidium rufipes*, Map 4D).

(7) Species restricted to or maximally abundant within oak woods of the forest biomes (NC, 31 taxa). Their particularly frequent representatives penetrate the forest-steppe zone through its central regions up to the biome's southern border (*Macragrus multesimus*, *Centromerus sylvaticus*, Map 4E, F).

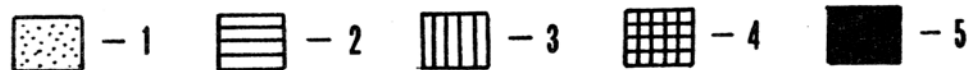
(8) Species occurring in oak woods of both forest biomes and Cisuralian forest-steppe (**N**, 8 taxa). Their maximal numbers are largely either restricted to the Cisuralian sites (*Helophora insignis*, Map 4B; *Bolyphantes alticeps*, *Lepthyphantes nigriventris*, Map 5A, B) or bipolar, with both Cisuralian forest-steppe and western regions of the zone of mixed coniferous broadleaved forests being the areas of their increased abundance (*Lepthyphantes menzei*, *L. tenebricola*, Map 5C, D).

(9) Species recorded solely in Cisuralian oak forests (**U**, 7 taxa). Their majority are known but by a few specimens, with only a *Glyphesis* sp. reaching high levels of abundance.

## 5.2. Classification of species assemblages

There are two main approaches in cluster analysis, agglomerative and divisive [Jongman et al., 1987]. We used both approaches in separate analyses of the spring and autumn samples as based on both qualitative (presence/absence) and quantitative data (species abundance in 20 samples per site). Comparison of the results obtained reveals that divisive methods better reflect the real patterns. This is particularly evident concerning autumn datasets. Agglomerative methods of analysis based on both qualitative and quantitative data fail to fully reveal the true particulars of Ural oak forests, uniting them into a joint cluster with oak woods of the central regions of the East European Plain (sites 40, 41, 45; Fig. 1b). Contrary to that, divisive methods clearly demonstrate their special, isolated

Explanations to the symbols used in Maps 2-5: 1 - 1 ex/m<sup>2</sup>, 2 - 2-3 ex/m<sup>2</sup>, 3 - 4-7 ex/m<sup>2</sup>, 4 - 8-15 ex/m<sup>2</sup>, 5 - 16-24 ex/m<sup>2</sup>.

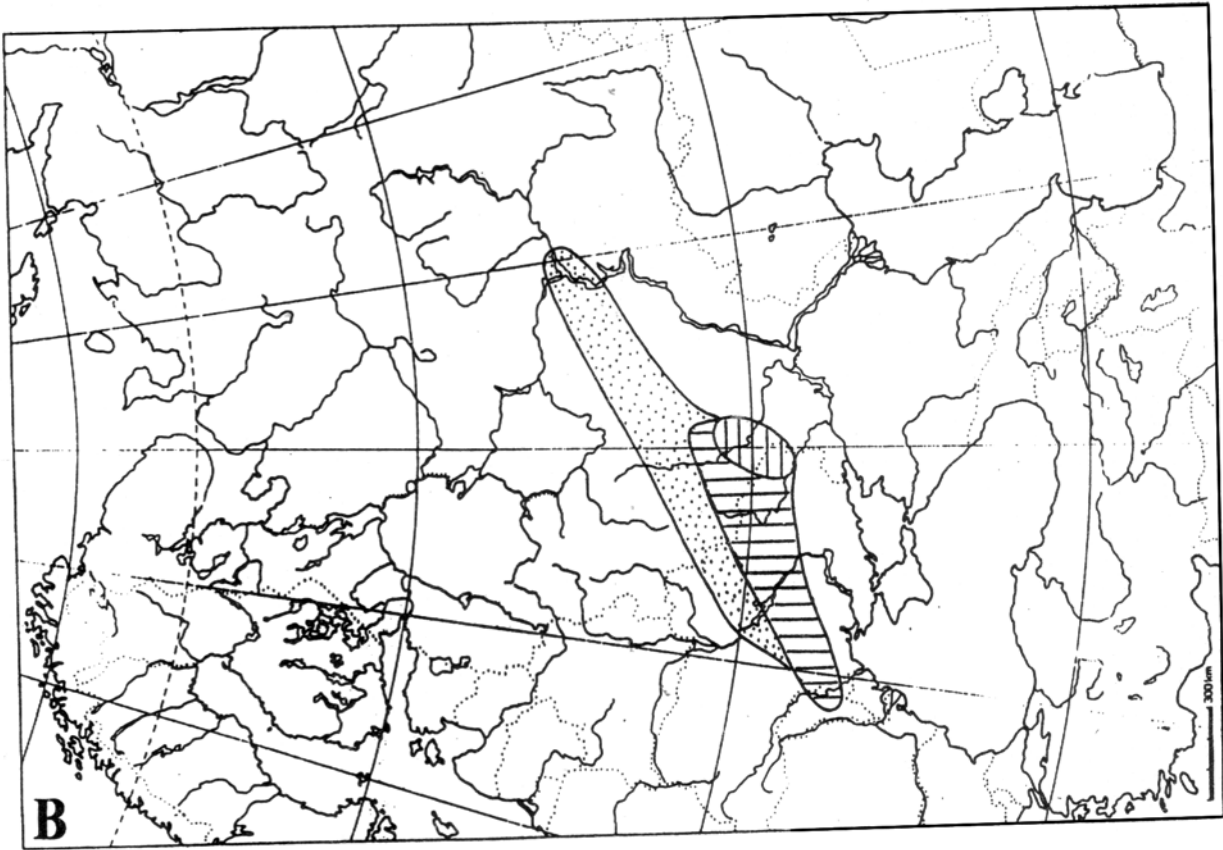
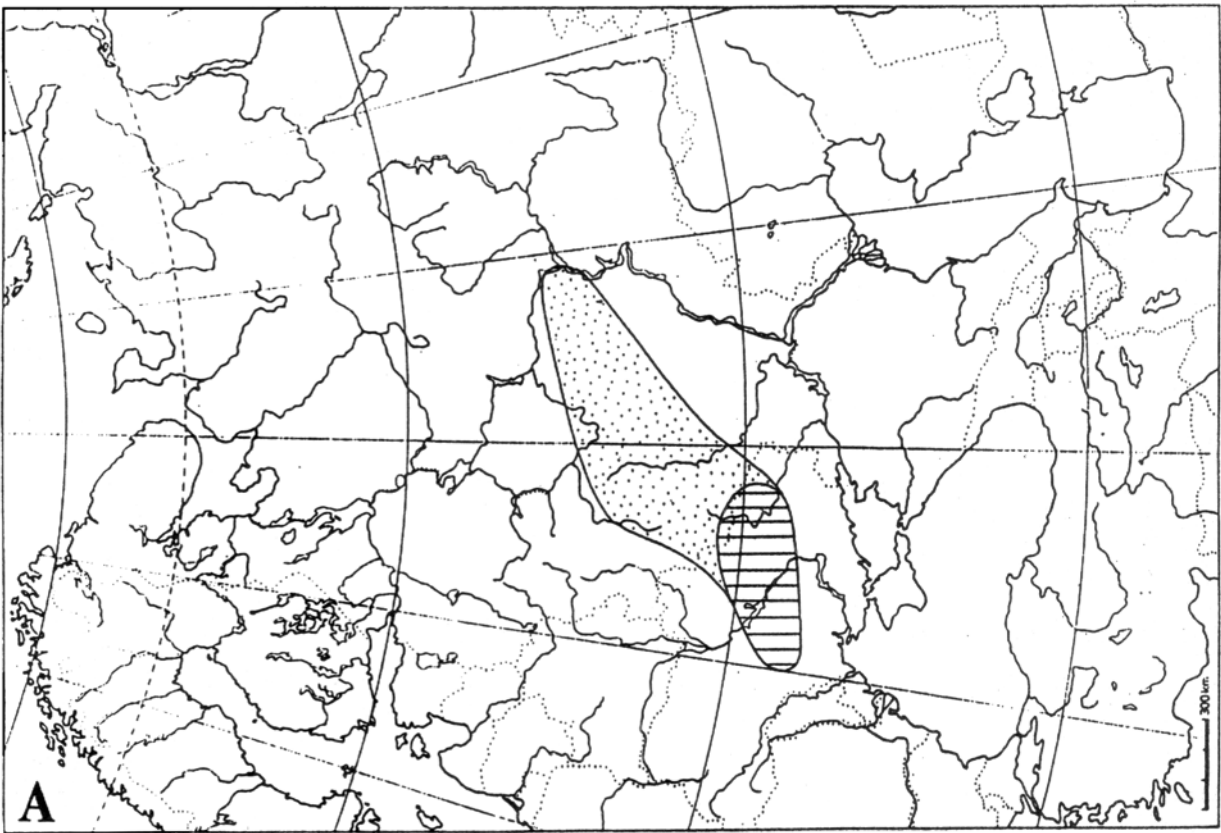


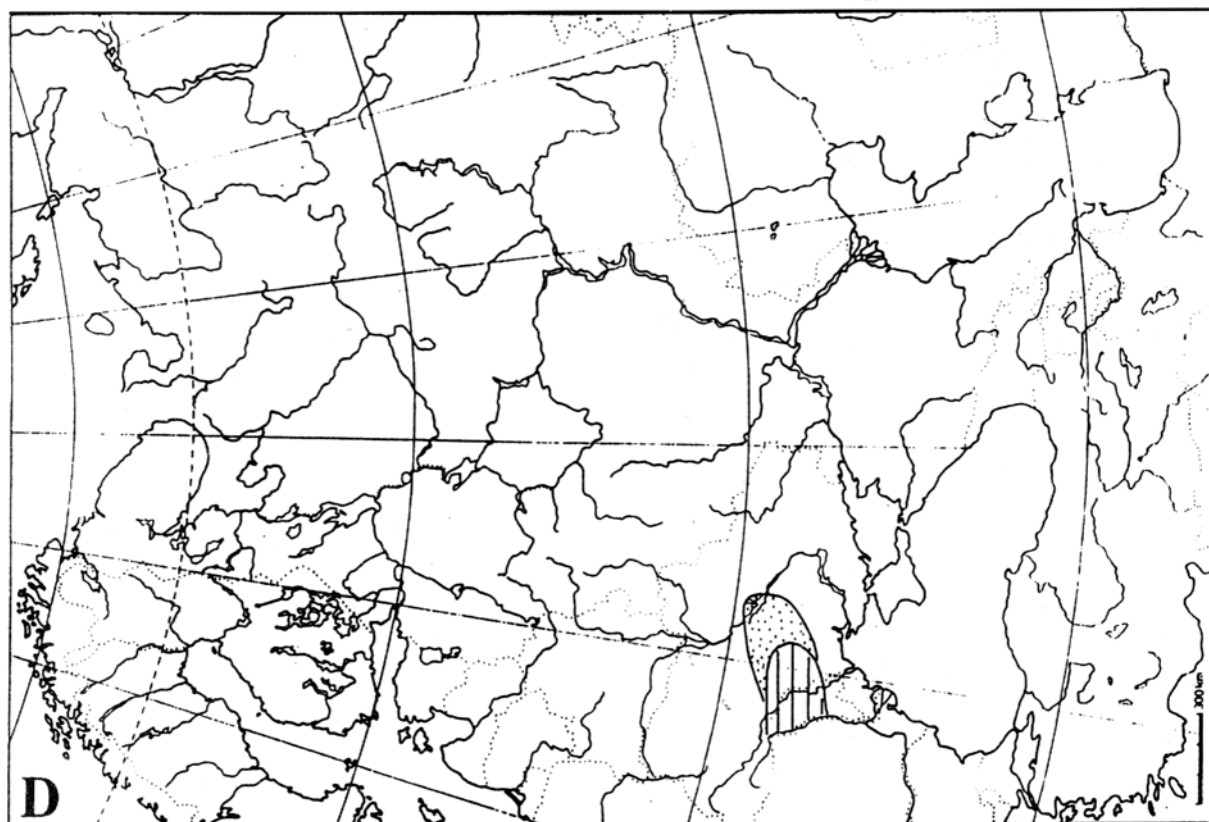
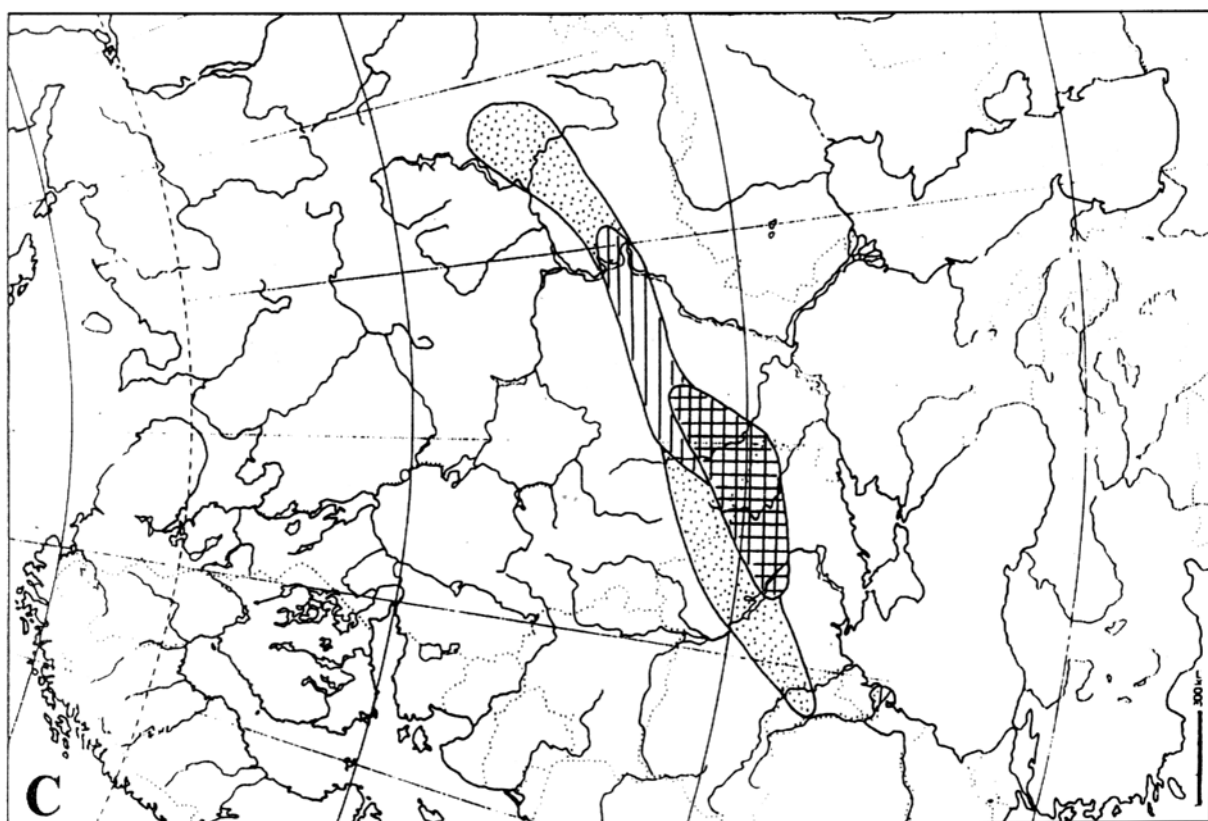
Map 2. Abundance isopleths of *Phrurolithus festivus* (A), *Abacoproeces saltuum* (B), *Panamomops menzei* (C), *Micragrus herbigradus* (D), *Lepthyphantes flavipes* (E), and *Diplocephalus picinus* (F) in East European oak forests.

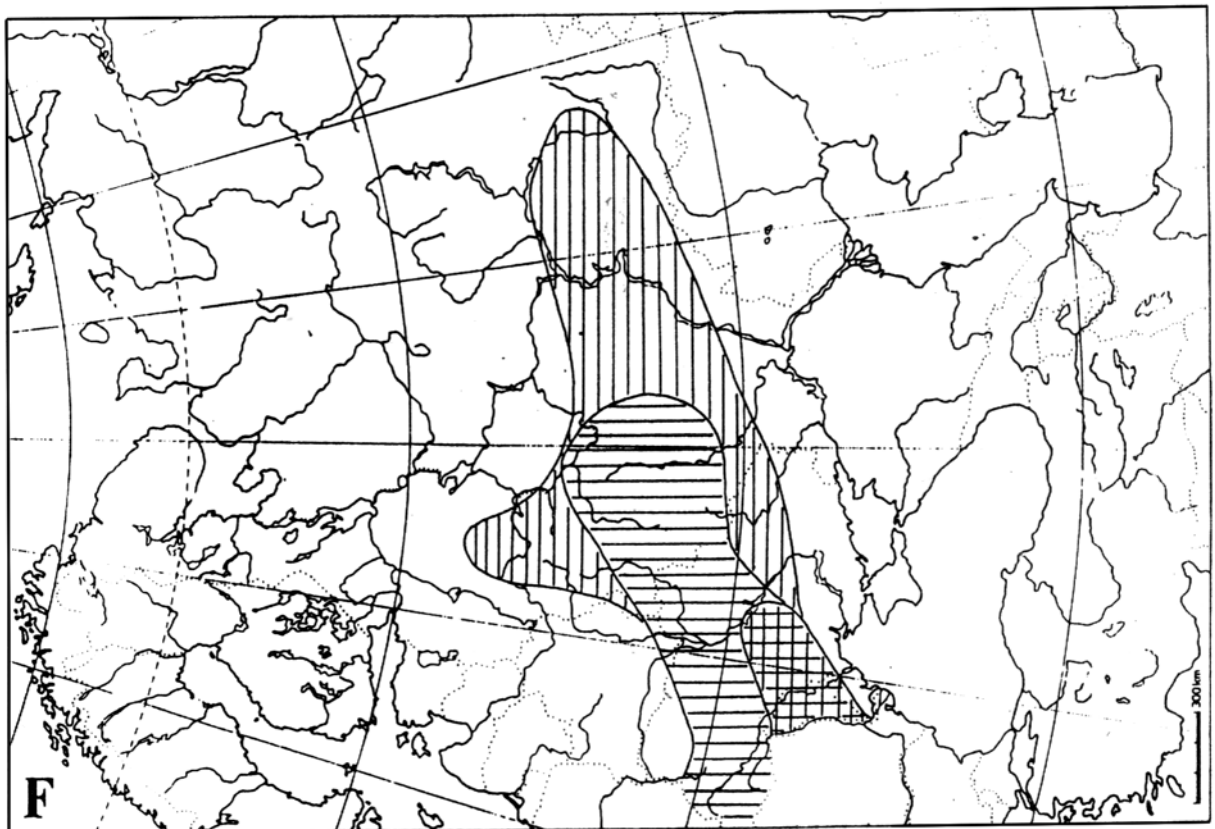
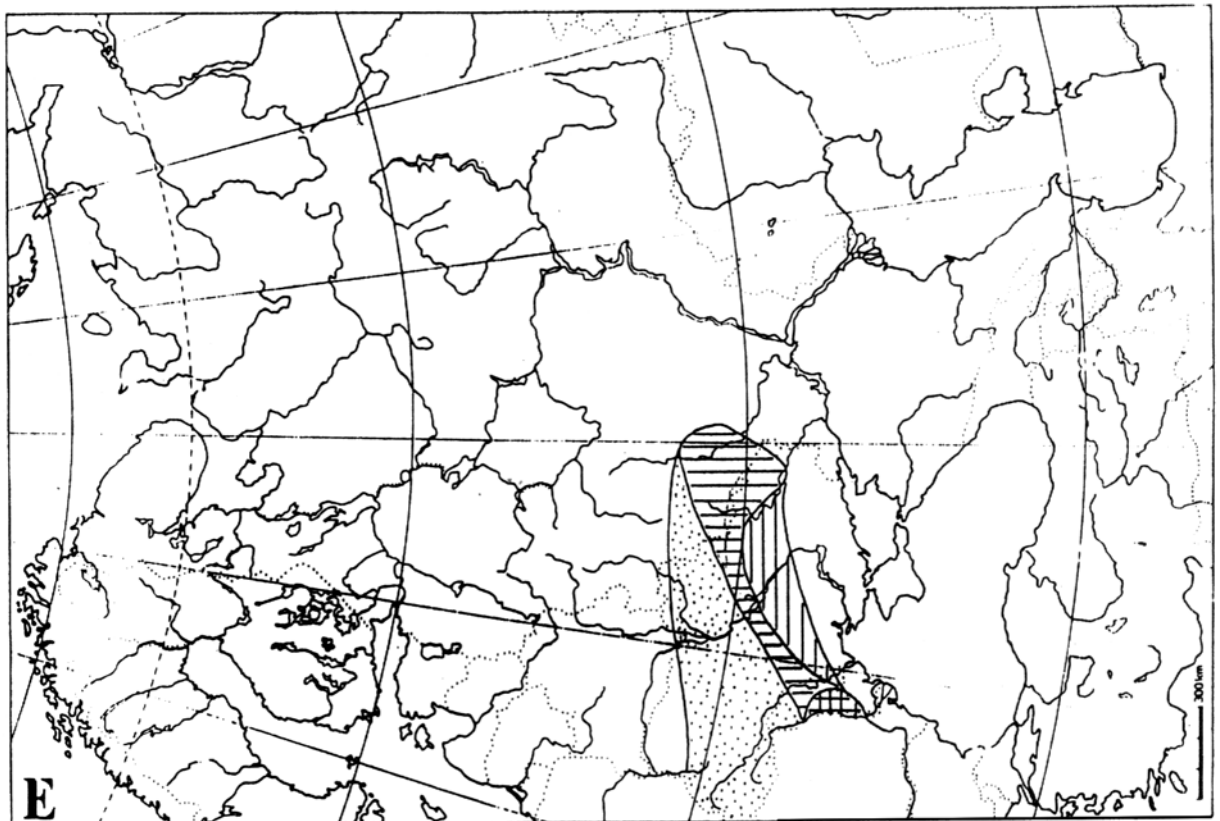
Symbols: 1 - 1 ind. per sq. m, 2 - 2-3 ind. per sq. m, 3 - 4-7 ind. per sq. m, 4 - 8-15 ind. per sq. m, 5 - 16-24 ind. per sq. m.

Карта 2. Изоплеты численности *Phrurolithus festivus* (A), *Abacoproeces saltuum* (B), *Panamomops menzei* (C), *Micragrus herbigradus* (D), *Lepthyphantes flavipes* (E) и *Diplocephalus picinus* (F) в дубравах Восточно-Европейской равнины.

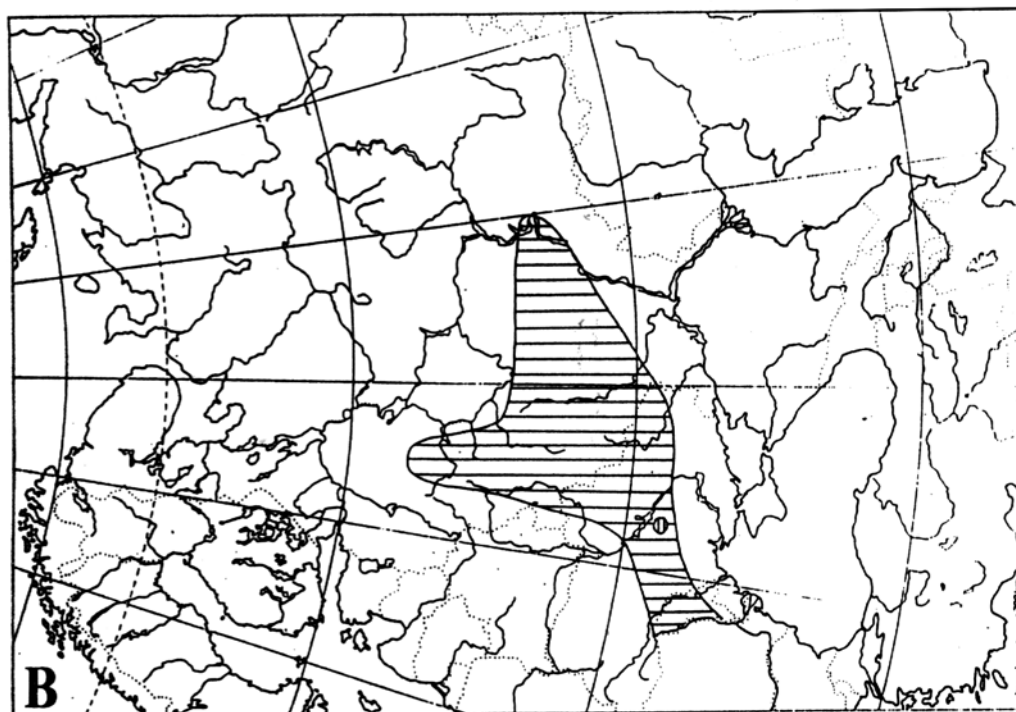
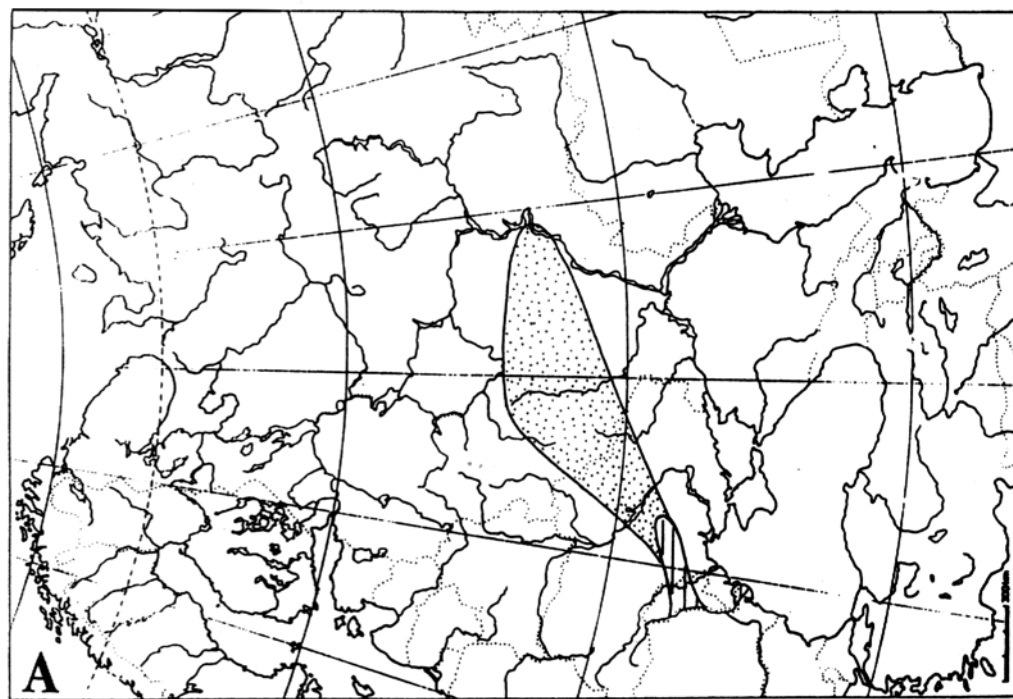
Обозначения: 1 - 1 экз/м<sup>2</sup>, 2 - 2-3 экз/м<sup>2</sup>, 3 - 4-7 экз/м<sup>2</sup>, 4 - 8-15 экз/м<sup>2</sup>, 5 - 16-24 экз/м<sup>2</sup>.









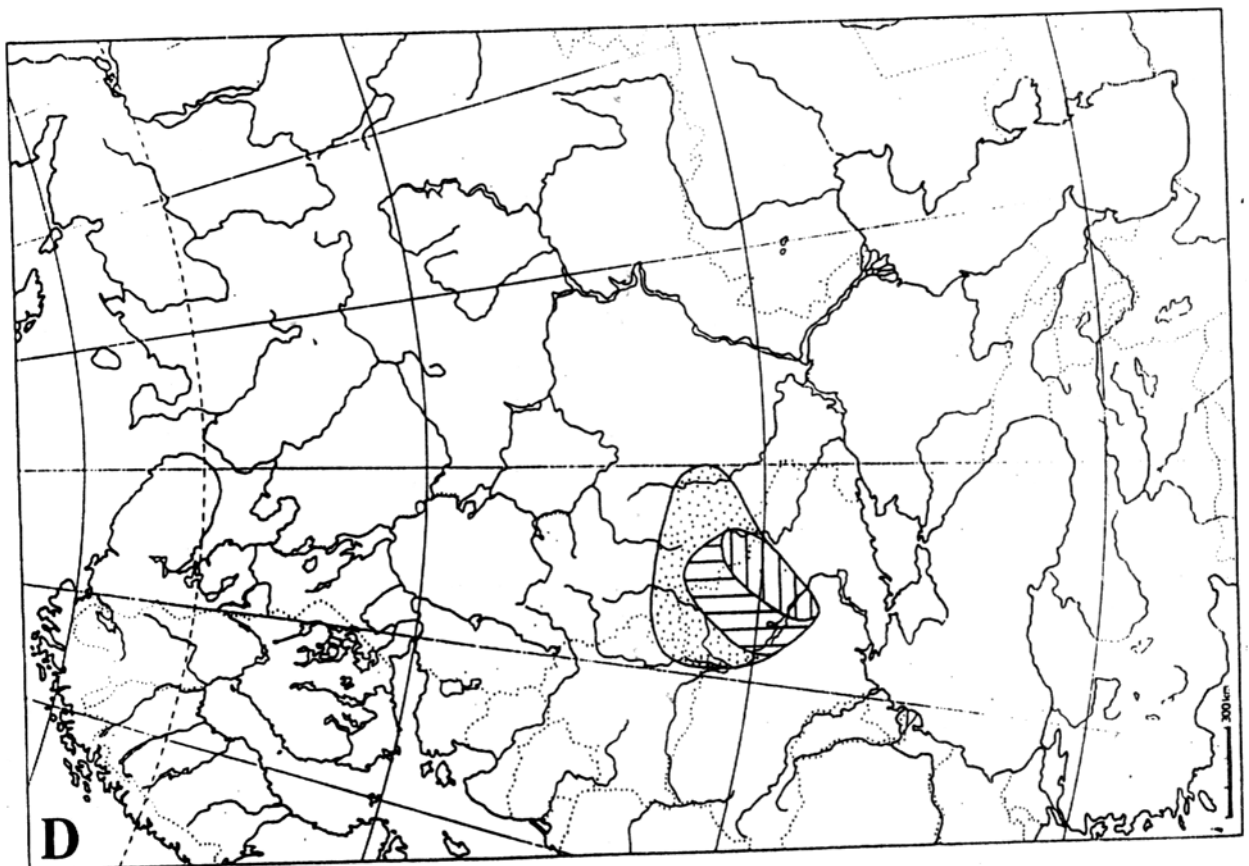
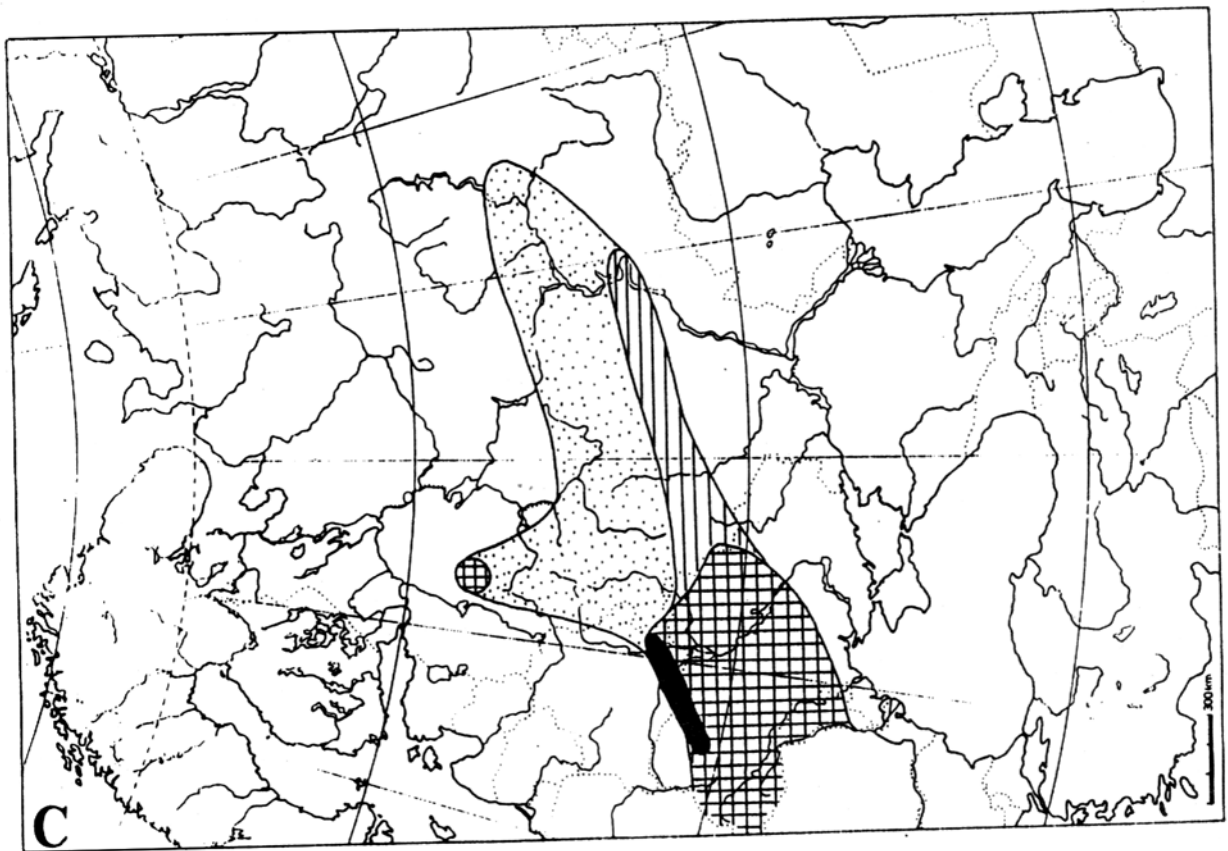


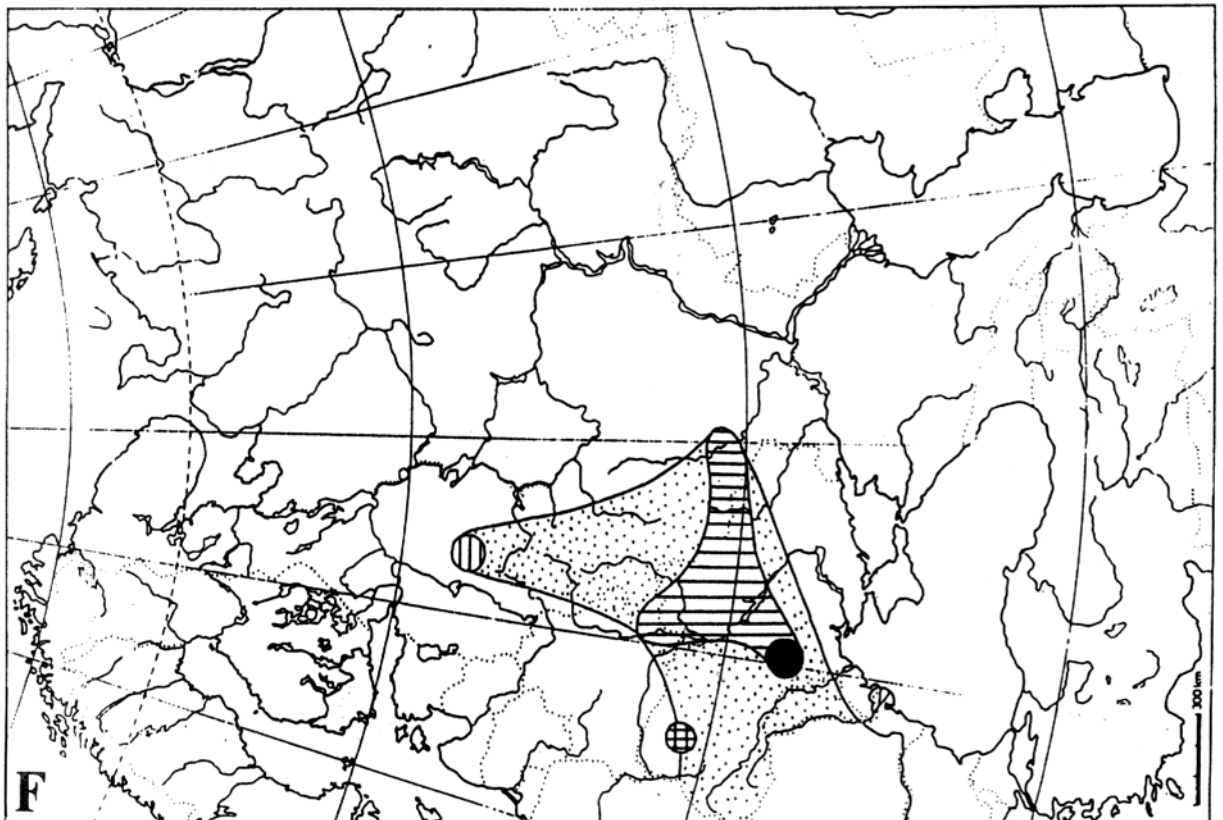
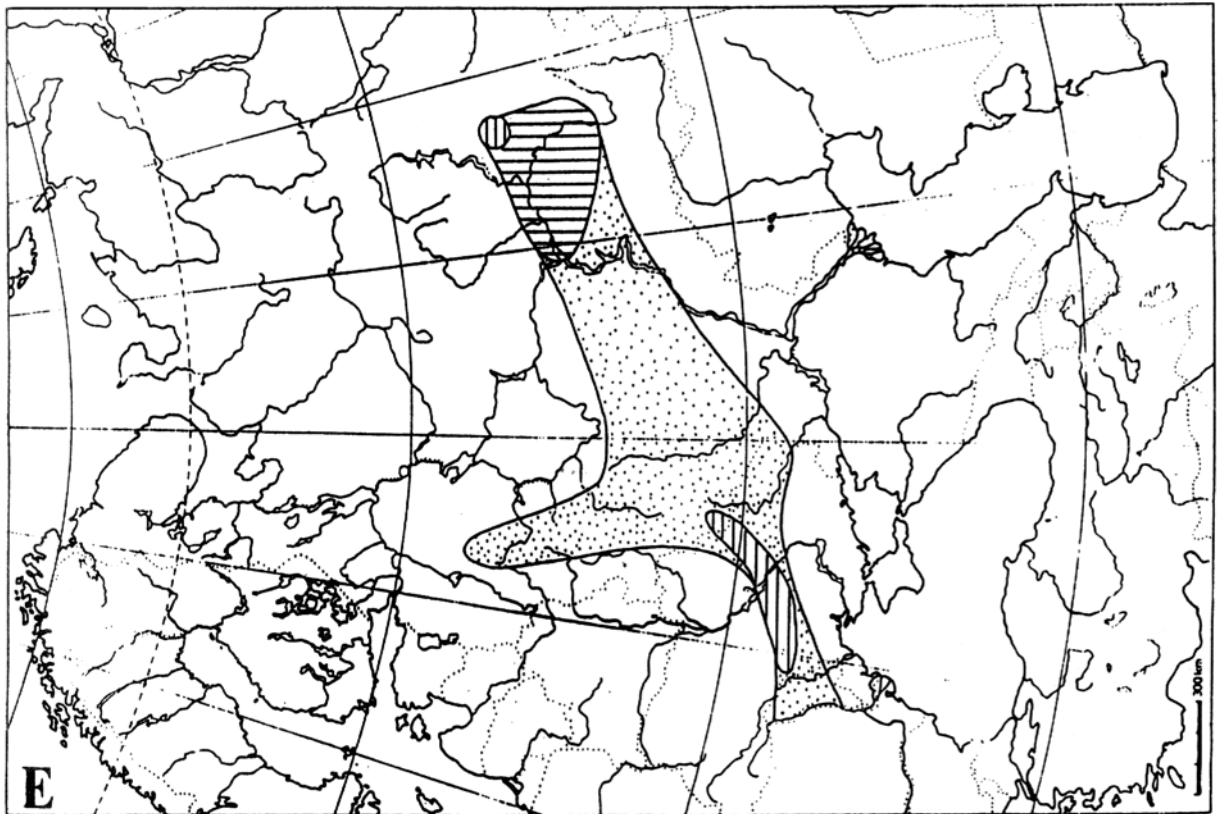
Map 3. Abundance isopleths of *Ozyptila praticola* (A), *Ballus depressus* (B), *Microneta viaria* (C), *Leptyphantes angulipalpis* (D), *Ceratinella brevis* (E), and *Tapinocyba insecta* (F) in East European oak forests.

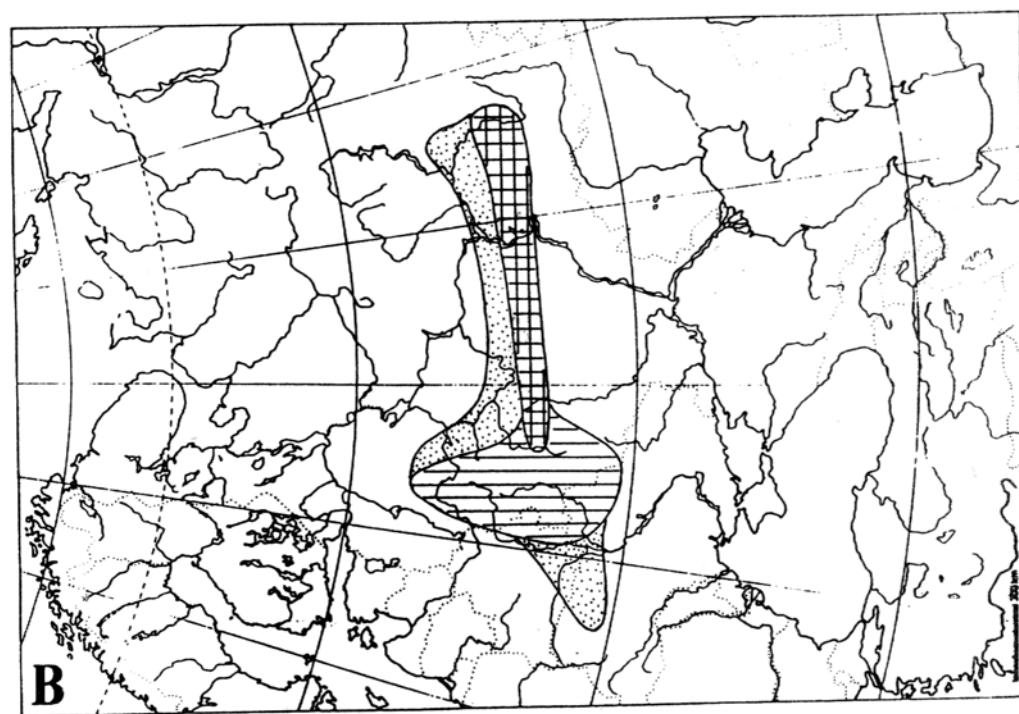
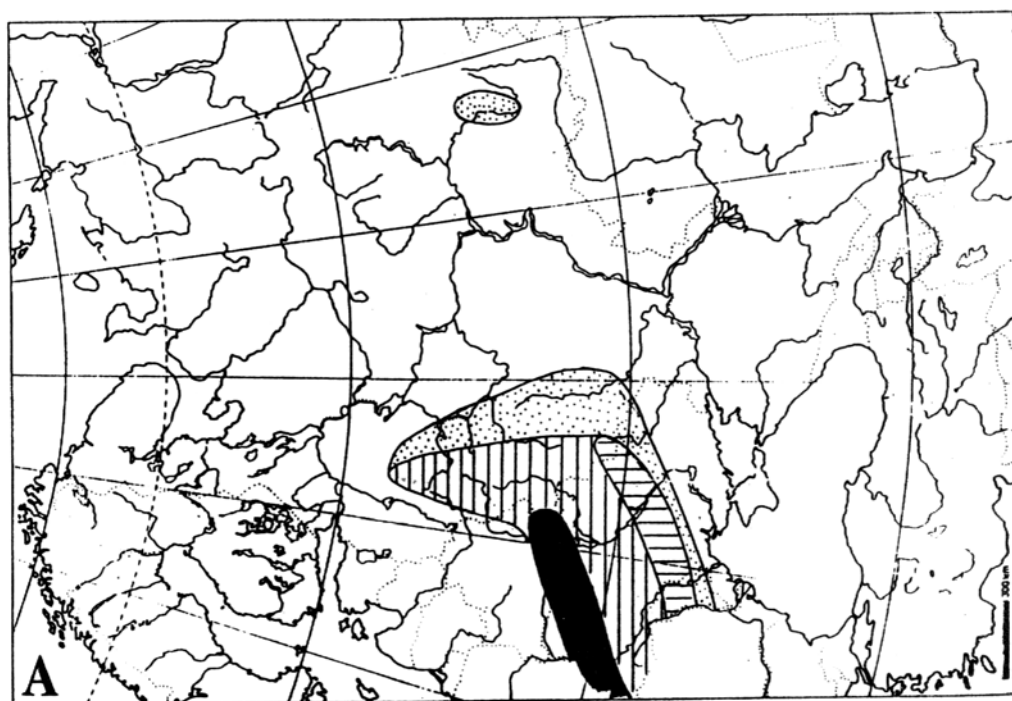
Symbols as in Map 2.

Карта 3. Изоплеты численности *Ozyptila praticola* (A), *Ballus depressus* (B), *Microneta viaria* (C), *Leptyphantes angulipalpis* (D), *Ceratinella brevis* (E) и *Tapinocyba insecta* (F) в дубравах Восточно-Европейской равнины.

Обозначения как на Карте 2.





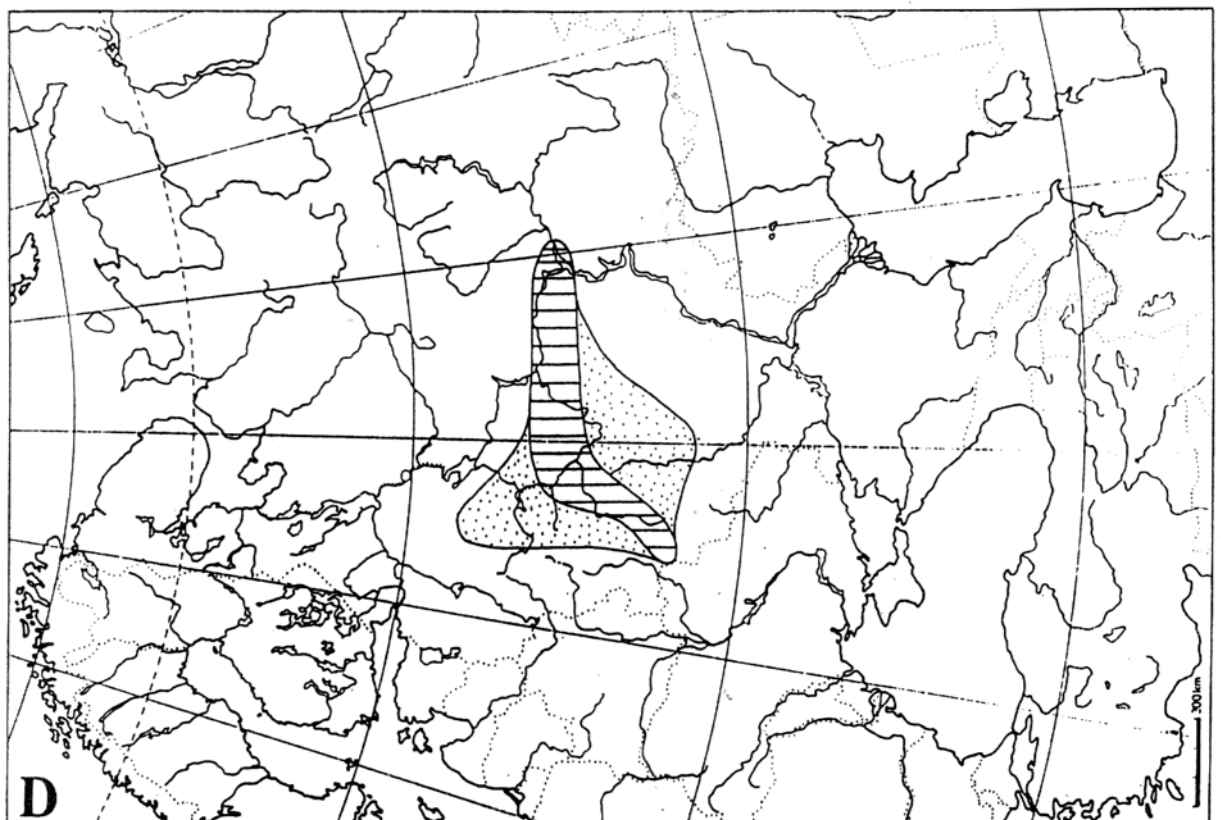
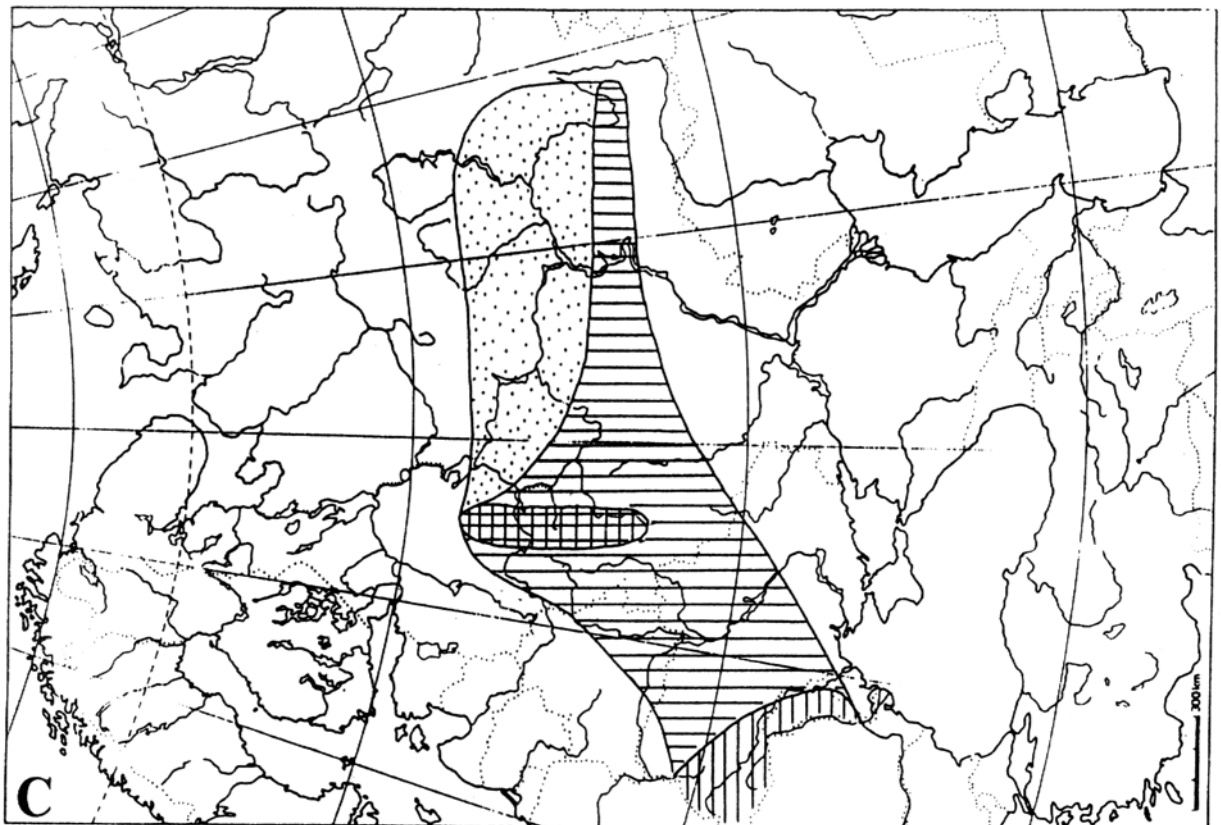


Map 4: Abundance isopleths of *Macrargus rufus* (A), *Helophora insignis* (B), *Robertus lividus* (C), *Gongylidium rufipes* (D), *Macrargus multesinus* (E), and *Centromerus sylvaticus* (F) in East European oak forests.

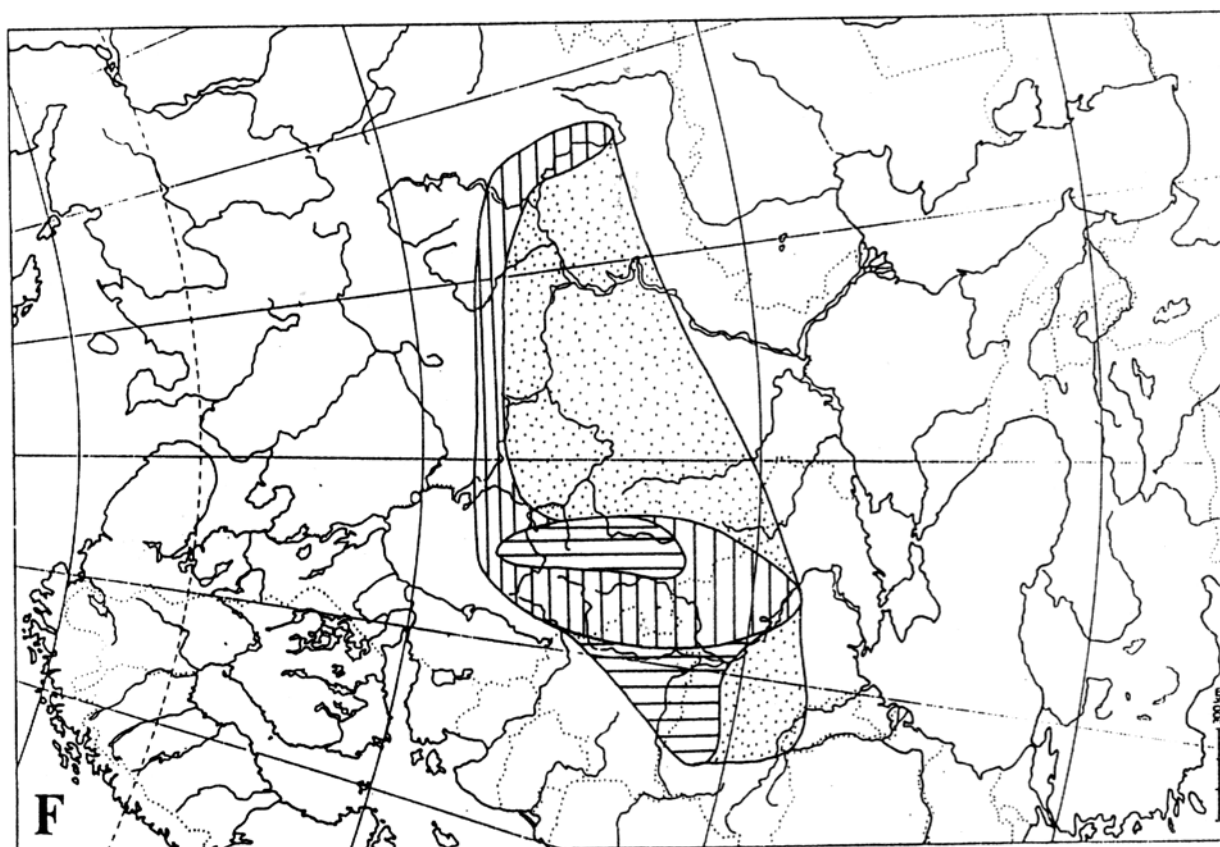
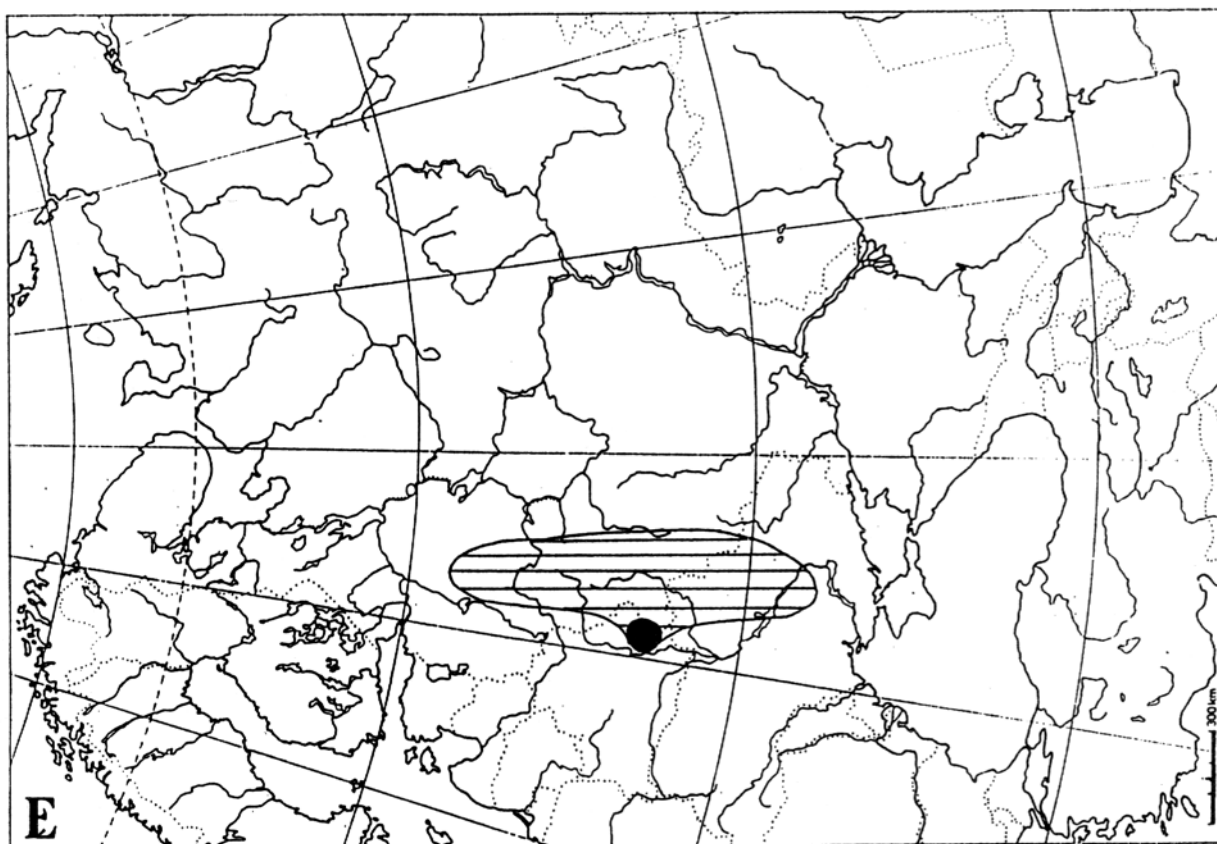
Symbols as in Map 2.

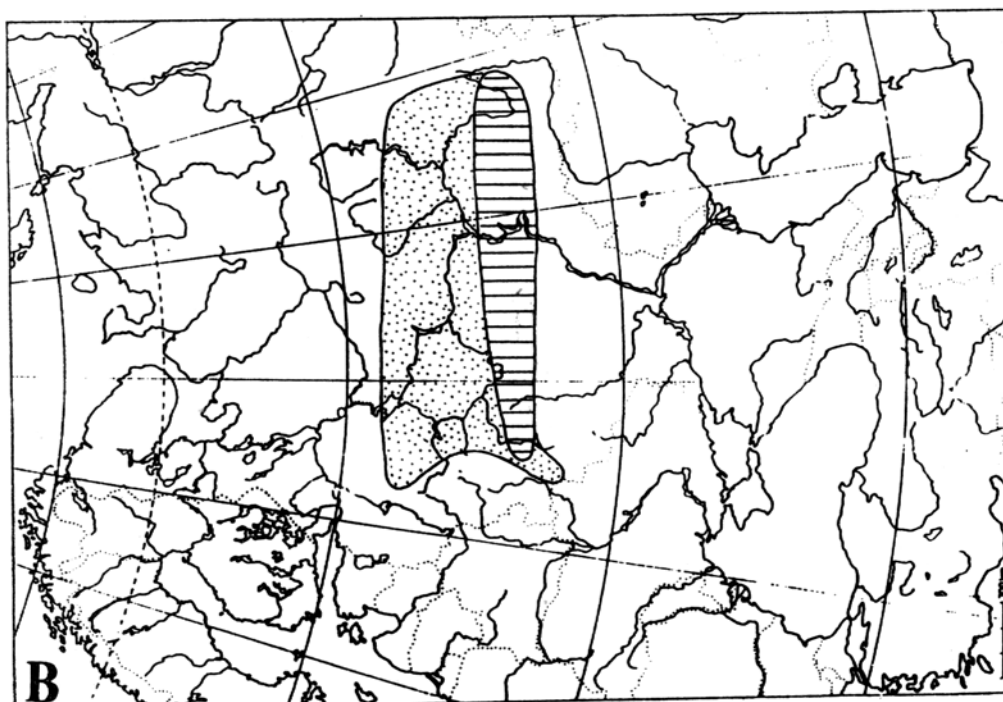
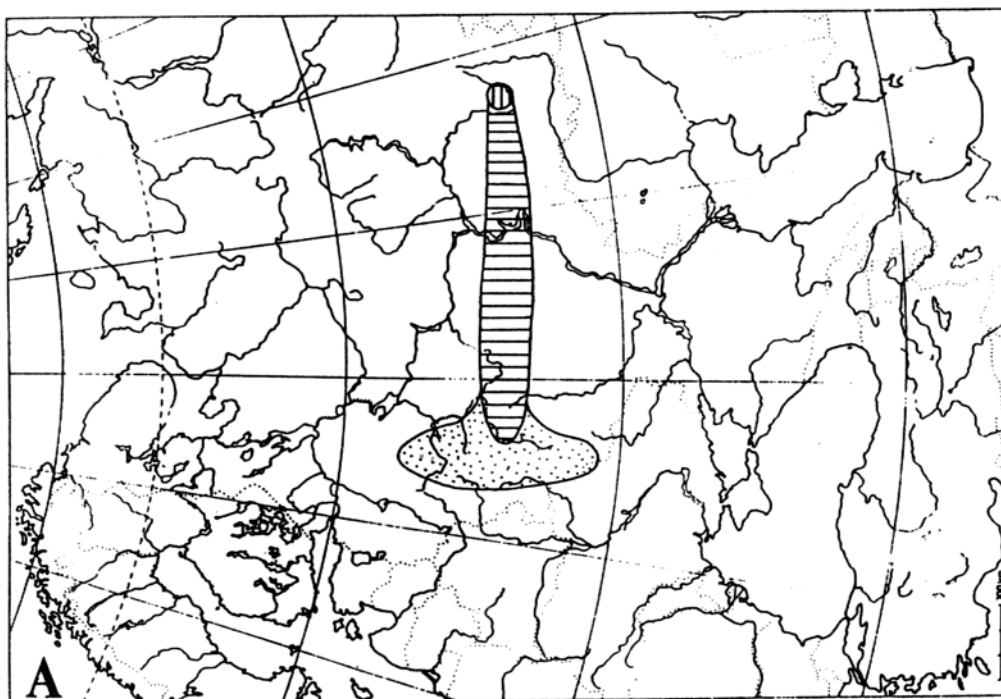
Карта 4. Изоплеты численности *Macrargus rufus* (A), *Helophora insignis* (B), *Robertus lividus* (C), *Gongylidium rufipes* (D), *Macrargus multesinus* (E) и *Centromerus sylvaticus* (F) в дубравах Восточно-Европейской равнины.

Обозначения как на Карте 2.







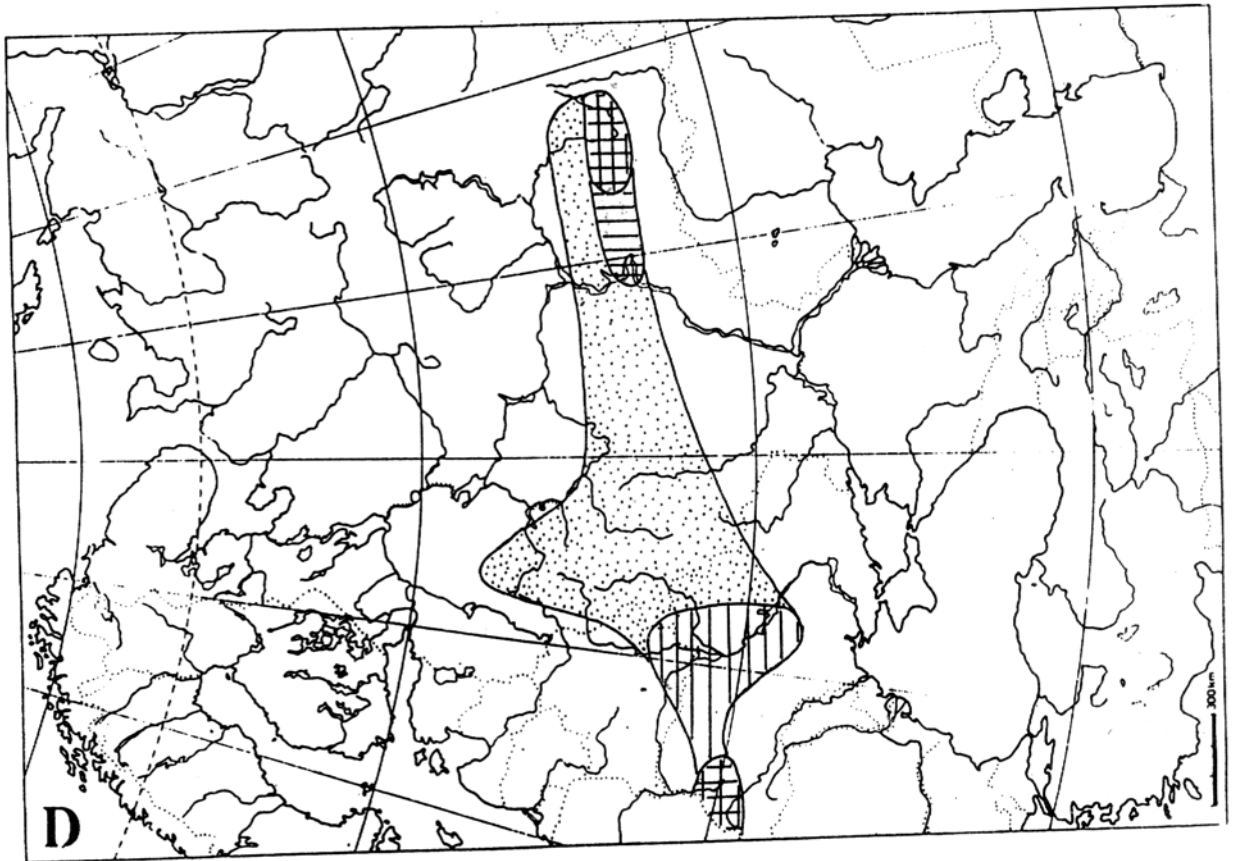
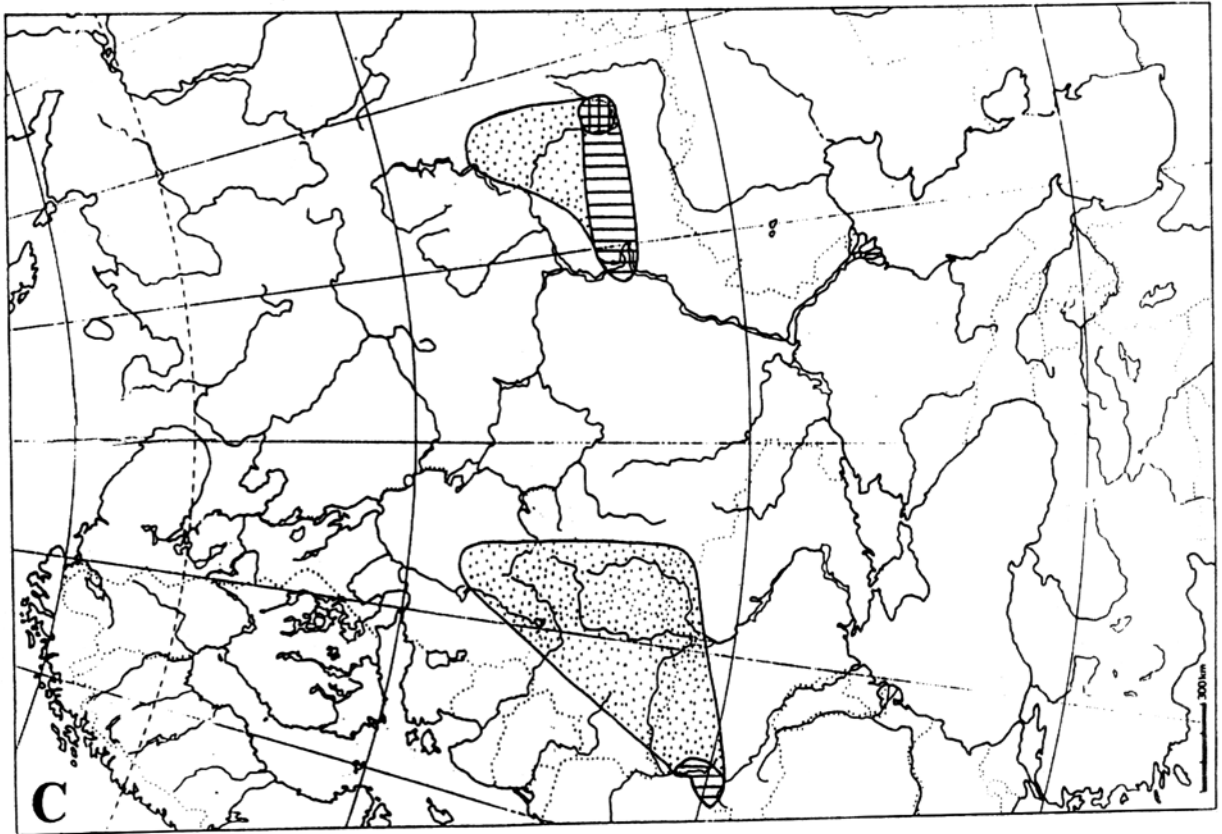


Map 5. Abundance isopleths of *Bolyphantes alticeps* (A), *Lepthyphantes nigriventris* (B), *L. mengei* (C), and *L. tenebricola* (D) in East European oak forests.

Symbols as in Map 2.

Карта 5. Изоплеты численности *Bolyphantes alticeps* (A), *Lepthyphantes nigriventris* (B), *L. mengei* (C), and *L. tenebricola* (D) в дубравах Восточно-Европейской равнины.

Обозначения как на Карте 2



position (Fig. 2b). The same can be observed as regards the spring dataset, this time concerning the highly peculiar Moldavian oak forests (sites 10, 11, 13, 14; cp. Figs 1A & 2A). Besides, all quantitative analyses are more preferable as being less dependent on the presence of rare species. Thus, a division of the spring assemblages of the forest-steppe zone into "western" and "central" can be revealed only using quantitative data (Fig. 2a), whereas the participation of rare species masks this border and produces a single conglomerate. Hence, the data obtained by means of quantitative divisive methods were basic for our classification of the East European Plain oak forests.

Virtually all methods of analysis applied reveal two distinct regions, Ural and Moldavian (Figs 1a & 2; Maps 6 & 7). The Ural oak forests are characterised by the predominance of *Helophora insignis* represented solely by spiderlings in the spring. The pronounced peculiarity of these oak forests is further reinforced in the autumn due to *Bolyphantes alticeps*, *Tapinopa longidens*, *Glyphesis* sp., etc. On the other hand, besides the species dominants characteristic of western forest-steppe as a whole (*Diplostyla concolor*, *Lepthyphantes flavipes*, *Microneta viaria*), the Moldavian oak stands possess their own dominants (*Harpactea saeva*, *Hahnina nava*). These forests are also peculiar in having a set of forms occurring nowhere else [cf. Esjunin et al., 1993], with *Walckenaeria furcillata* and *Atypus piceus* being particularly indicatory for the spring and autumn samples, respectively.

Most analyses of spider assemblages further divide the remaining oak forests, this time latitudinally, into forest belt ("northern") and both forest-steppe and northern steppe ("southern") (Figs 1 & 2; Maps 6 & 7). The oak forests located within northern steppe are only once clustered off the forest-steppe set, in particular when qualitatively analysed with agglomerative methods. Otherwise they are always clustered jointly and even subdivided equally. As a result, the border (Map 7c) between the "northern" and "southern" oak forests is sub-equal to the one drawn between the zones of mixed coniferous-broadleaved forests and forest-steppe [Gribova et al., 1980]. The presence/absence datasets

provide a northerly shift of this border, perhaps due to occasional northward penetrations of a few "southern" spider species, but again only when qualitatively analysed with agglomerative methods.

In addition to the above meridional borders isolating the Moldavian and Ural oak forests (Map 7a, b), there is still one more subdivision of the region's western and central sites (Map 7d). This border roughly coincides with the line connecting Tver, Kursk and Kharkov, being differently expressed in the northern and southern site complexes in the spring and autumn. In the spring dataset, it is clearly traceable within the forest-steppe zone (Figs 1a & 2a; Map 6A), whereas in the autumn only within the forest zones (Figs 1b & 2b; Map 6b). In general, differences between the western and central sectors are significant. Thus, in the spring the spider species dominating the oak forests west of the border **d** are *Enoplognatha ovata* and *Microneta viaria*, while *Panamomops menzei* and *Hahnina ononidum* predominate more to the east. The same pattern concerns species indicators (Fig. 2a: B<sub>2</sub> & B<sub>3</sub> groups). In the autumn, the differences in the composition of dominants become even more distinct. West of the border **d**, a whole set of dominating species is distinguishable, with *Microneta viaria* and *Macrargus rufus* being the most common among them. East of that border, there seem to be no dominant species, solely *Robertus lividus* being somewhat more abundant than the others at two sites only (16 & 23). The same pattern is likewise observed as regards species indicators (Fig. 2b). As noted above, distant southern penetrations by boreal species are observed along **d** (Map 3E & F). This is possibly due to historical processes of regional faunogenesis arising from the area's equidistant position between both major nemoral refuges in the Plain, i.e. Carpathian and southern Ural [Esjunin et al., 1993].

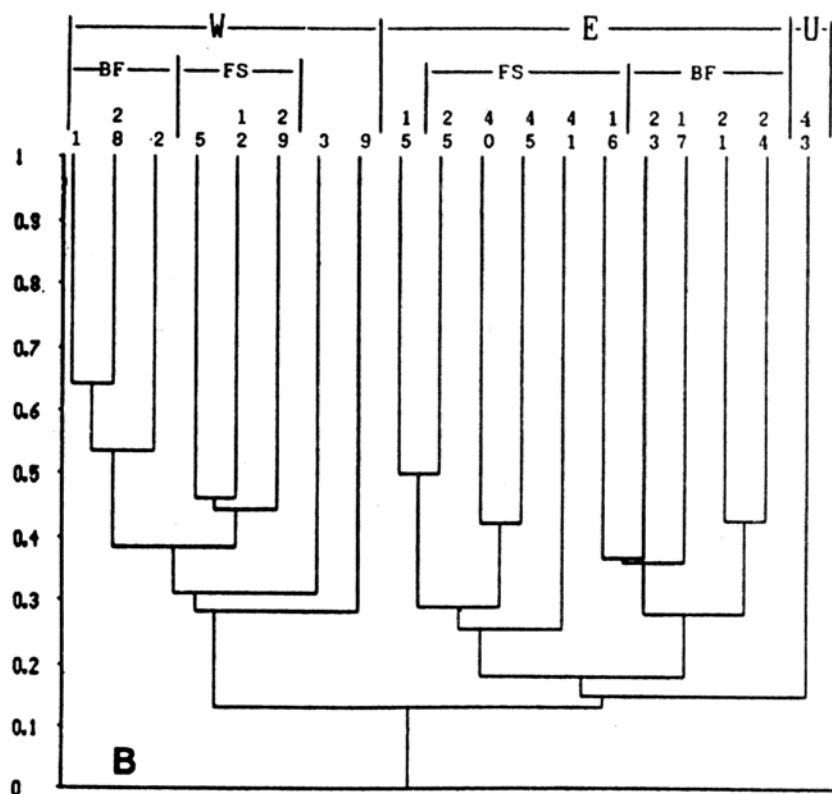
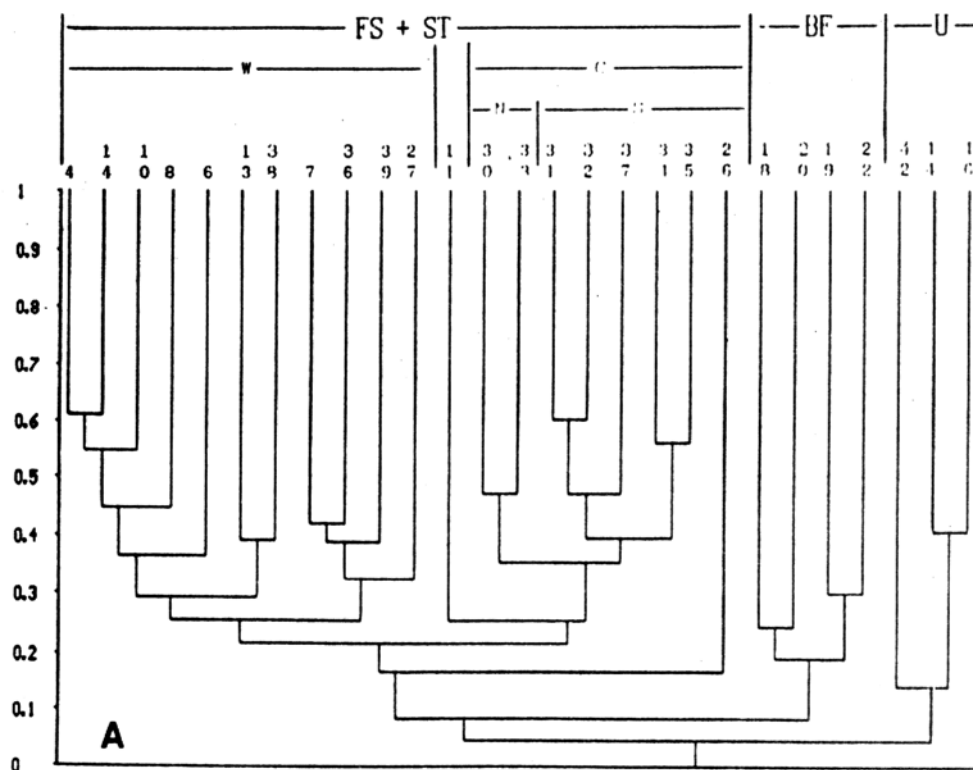
Hence, based on analysis of the litter-dwelling spider complex of East European Plain oak forests, one zonal (between the forest and forest-steppe belts) and three regional borders (Moldavian, central Russian, and Ural) are distinguishable (Map 7). When arranged according to their strength, the following sequence can be drawn. The strongest line seems to be the Ural one (Map 7a), followed by both

Figure 1. Group averaging clustering dendrogram of spider assemblages based on the Czekanowski-Soerensen similarity index for abundance spring (A) and autumn (B) data.

Symbols: Oak forests of FS — forest-steppe, ST — steppe, BF — broadleaved forests belt, U — Cisuralian forest-steppe, W — western, E — eastern, N — northern, S — southern, C — central.

Рисунок 1. Дендрограмма средневзвешенного разделения группировок пауков на основе коэффициента сходства Чекановского-Серенсена для весенних (А) и осенних (В) учетов численности.

Обозначения: Дубравы зон FS — лесостепи, ST — степи, BF — широколиственных лесов, U — предуральской лесостепи, W — западная, E — восточная, N — северная, S — южная, C — центральная части.





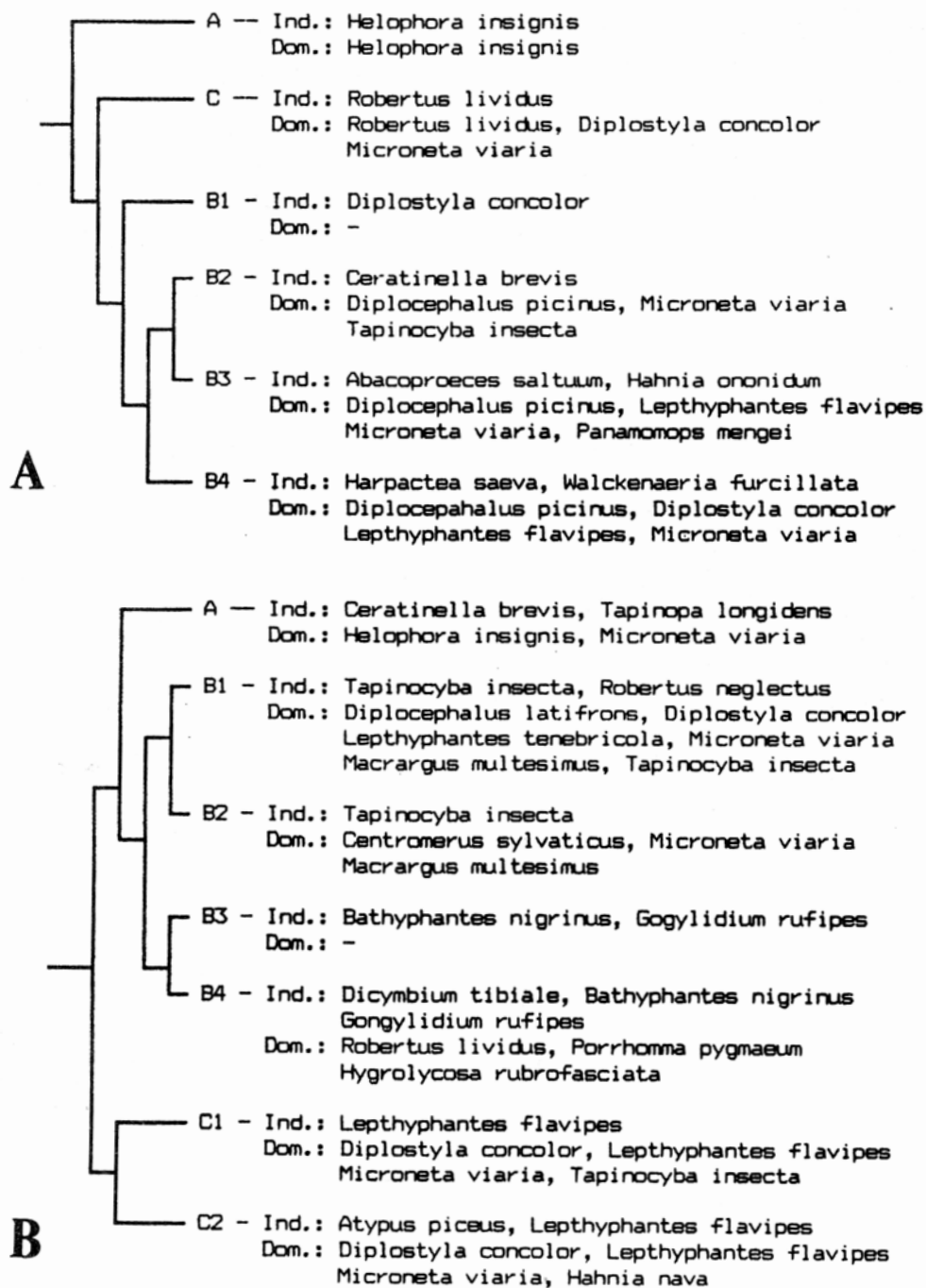
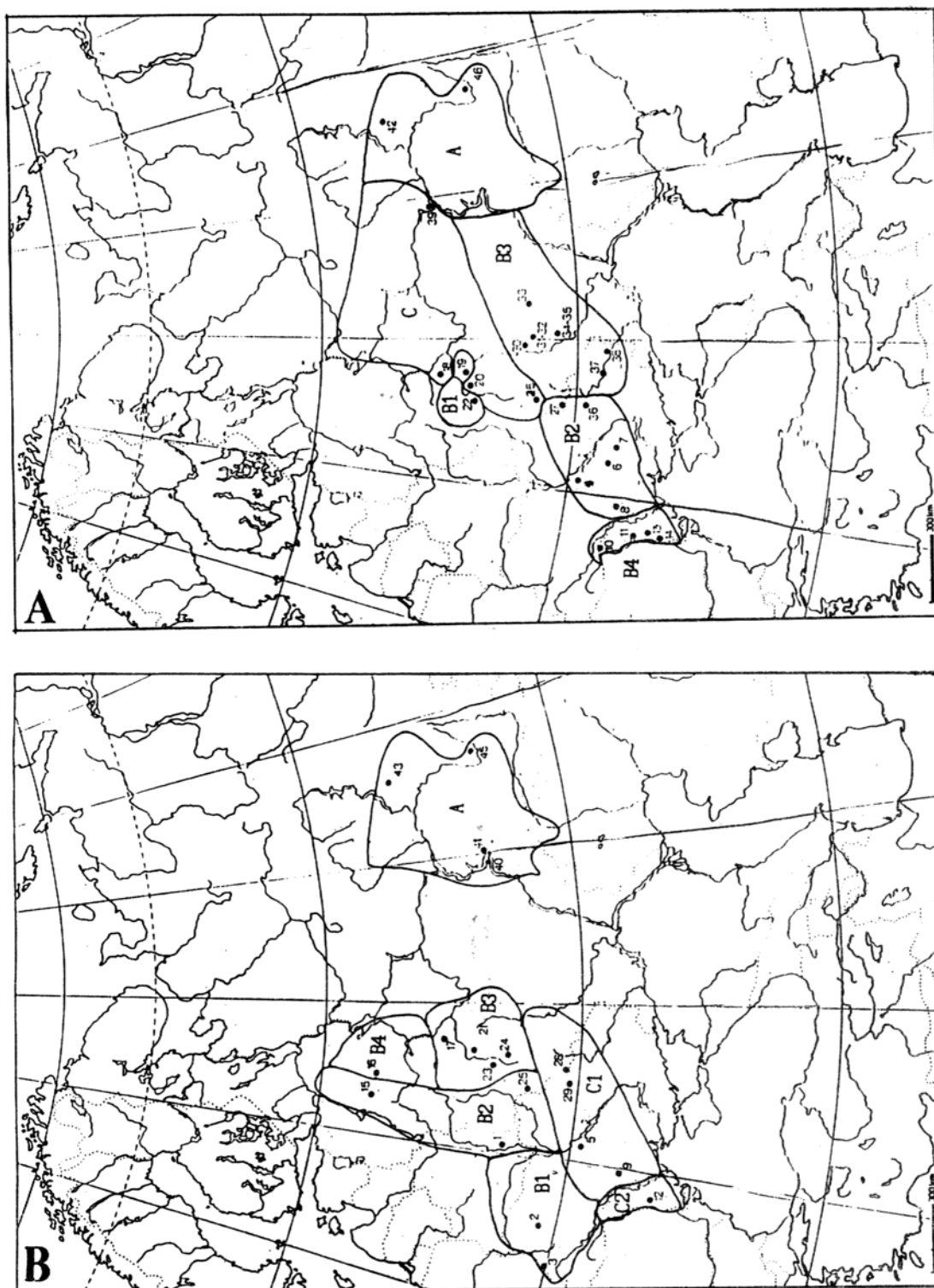


Figure 2. Dendrograms for a divisive classification using the TWINSpan algorithm for spring (A) and autumn (B) abundance data of spider assemblages.

Species indicators (Ind.) as well as dominants (Dom.) are listed for each assemblage group. Borders between assemblage groups (A-C) as well as site numbers as in Map 6.

Рисунок 2. Дендрограмма разделительной классификации с использованием алгоритма TWINSpan для весенних (A) и осенних (B) учетов численности пауков.

Виды-индикаторы (Ind.) и доминанты (Dom.) приведены для каждой группировки. Границы между группировками (A-C) и номера точек сборов как на Карте 6.



Map 6. Borders between oak forest groupings as revealed upon analysis of spring (A) and autumn (B) abundance data of spider assemblages using a divisive classification with the TWINSpan algorithm.

Site numbers as in Map 1, symbols as in Fig. 2.

Карта 6. Границы между группировками дубрав на основе анализа весенних (A) и осенних (B) учетов численности пауков с использованием алгоритма TWINSpan.

Номера точек сборов как на Карте 1, обозначения как на Рис. 2.

Moldavian (Map 7b) and zonal (Map 7c) lines. Finally, the central Russian line (Map 7d), differently expressed in different seasons, is perhaps the weakest among the araneographic borders of the East European Plain oak forests.

## 6. Discussion

### 6.1. The main patterns of spider species chorology in the East European Plain oak forests

Despite certain misrepresentations due to some taxa rare in our samples (e.g. the extremely widespread *Erigone atra* has joined the group of western forest-steppe spiders), a species classification according to their distributions over the East European Plain oak forests still reflects the main patterns of spider chorology of the nemoral biome.

Firstly, there are definitely zonal (**S**, **SC**, **NC**) and definitely (sub)regional (**M**, **U**) species. A regional aspect is likewise present in the distribution of numerous polyzonal spiders, with their centers of higher abundance restricted either to the western or to the central, or to the eastern parts of the forest-steppe zone.

Secondly, (sub)regionalism appears to be indistinct in "northern" species, whereas a good number of (sub)regional groupings are distinguishable amongst the "southern" taxa (**M**, **SC**, **U**). This is hardly explicable in terms of climatic changes [cf. Penev et al., 1994], rather historical reasons serving as the causal basis. Chernov [1975] already noted that, from south to north, the proportion of zonal species in animal communities in the Palearctic is increased at the expense of regionally restricted species.

Thirdly, the complex pattern of spider chorology in the East European Plain oak stands is further reinforced by the fact that oak woods are known to be extrazonal communities within both taiga and steppe zones. This determines the presence in the northernmost and southernmost oak forests of spiders uncharacteristic of oak stands lying in between. Such species within the range of *Quercus robur* mostly inhabit communities other than *Querceta*, but join the latter only peripherally, i.e. in the north

and in the south. In terms of the general law of ambient smoothing [Chernov, 1975], with the law of station change [Bei-Bienko, 1966] known to be its particular case, such mesophilous silvicoles as *Hahnian ononidum*, *Micrargus herbigradus*, the hygrophilous *Trochosa spinipalpis*, and the eurybitic *Pachygnatha degeeri* occur under the canopy of "southern" oak forests. Based on literature evidence [Mikitiuk, 1981, 1984], a southerly penetration of forest-dwelling spiders reaches as far as the insular oak (= bairak) stands or artificial spinneys within the subzone of southern steppes. At the same time, the northernmost oak stands being largely restricted to the southern, best insulated, slopes, their spider faunules contain thermo- and/or xerophilous taxa such as *Phrurolithus festivus*, *Diplostyla concolor*, *Agroeca brunnea*, *Euryopsis flavomaculata*, *Thanatus sabulosus*.

### 6.2. Classification of East European oak forests as based on the distribution of spider assemblages

Based on an analysis of the spider litter-dwelling assemblages, we classify the oak forests of the East European Plain as follows.

1. Moldavian forest-steppe.
2. The zone of mixed coniferous-broadleaved forests and southern taiga, with (a) western and (b) eastern subregions.
3. Forest-steppe and northern steppe belts, with (a) western and (b) central subregions.
4. Cisuralian forest-steppe.

It is of interest to compare the above pattern of the araneography of the East European Plain's nemoral biome with data of other authors. In terms of a historico-faunistic approach to zoogeography, the entire spider fauna of the central part of East European Plain has been considered by Eskov [1988] as referred to the European region, with only the Urals standing somewhat apart and belonging to the transitional West Siberio-Laplandian region. Out of other schemes of the Plain's regioning, Kuznetsov's [1950] zoogeographic one as well as the classification of forest-steppe oak forests first proposed by Milkov [1950] and later modified upon theriographic

Map 7. Araneographic regioning of the East European Plain as based on spider assemblage distributions in oak forests.

Symbols: Double line — eastern range margin of *Quercus robur* [after Milkov & Gvozdetzskii, 1976] Oak forests: **A** — Moldavian forest-steppe, **B1** — western and **B2** — eastern coniferous-broadleaved forest belt and southern taiga, **C1** — western and **C2** — central forest-steppe and northern steppe, **D** — Cisuralian forest-steppe.

Карта 7. Аранеографическое районирование Восточно-Европейской равнины на основе распределения группировок пауков в дубравах.

Обозначения: Двойная линия — восточная граница ареала *Quercus robur* (по: Мильков, Гвоздецкий, 1976). Дубравы: **A** — молдавская лесостепь, **B1** — западная и **B2** — восточная части зон хвойно-широколиственных лесов и южной тайги, **C1** — западная и **C2** — центральная лесостепь и северная степь, **D** — предуральская лесостепь.

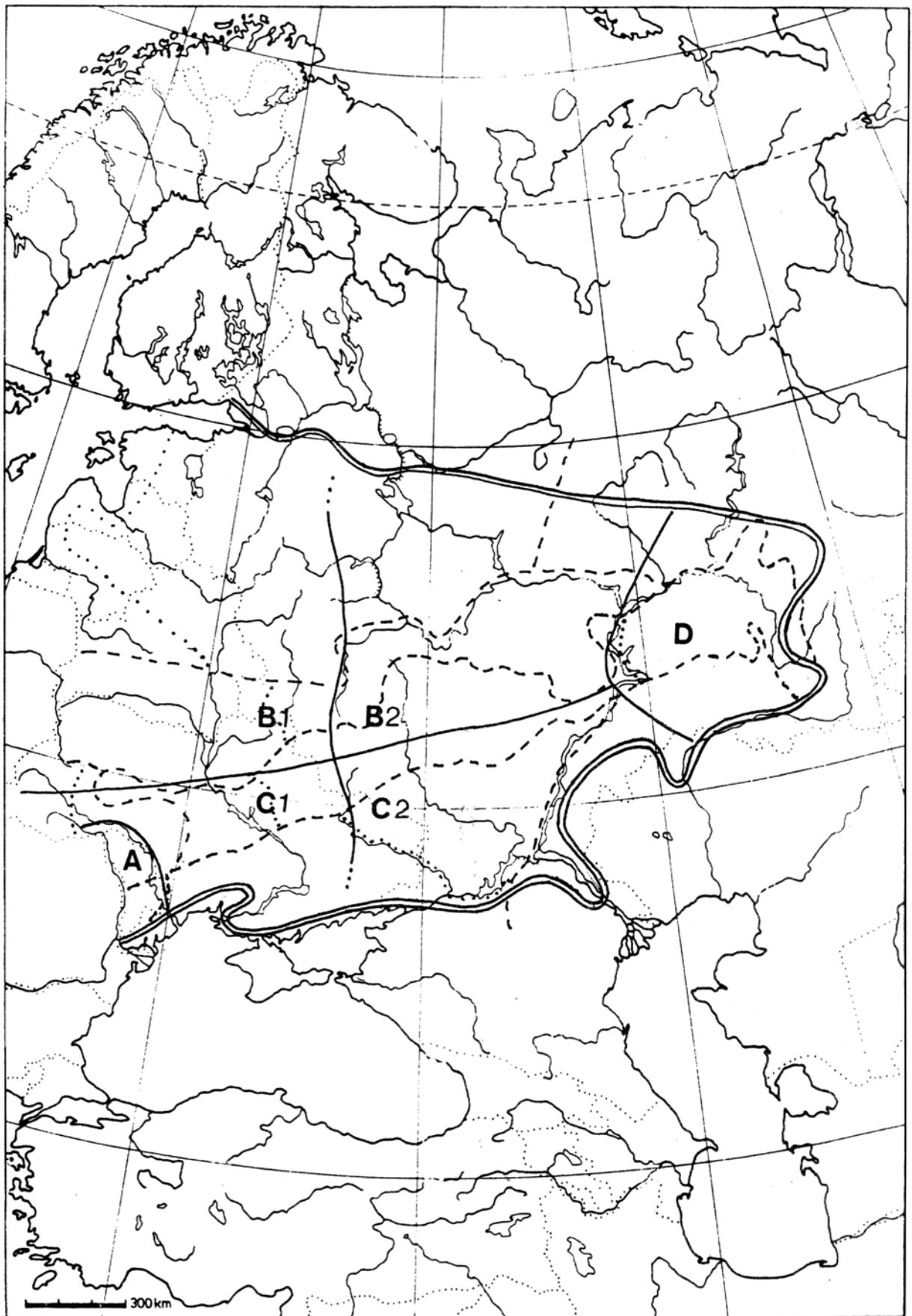


Table 3.  
Таблица 3.Comparison between zoochorological classifications of East European Plain oak forests  
Сопоставление зоохорологических классификаций дубрав Восточно-Европейской равнины.

after Kuznetsov, 1950	after Novikov, 1959	our data
IIIb. Province of broadleaved and mixed forests		
Subregions:		Eastern forest
1. Central Russian	—	
2. Polish	—	Western forest
IV. Forest-steppe	Forest-steppe	
Subregions:		
1. Central European	1. Transdnieper	Southwestern forest-steppe (Moldavian)
2. Bug-Dnieper		
3. Dnieper-Volga	2. East Ukrainian	Western forest-steppe
	3. Central	
	4. Cisvolga	Central forest-steppe
4. Transvolga	5. Transvolga	Cisuralian forest-steppe
	6. Cisuralian	

evidence by Novikov [1959] seem to be most appropriate.

When compared, all these three schemes are more or less similar, ours differing in a reduced number of regional borders and the presence of a central Russian line (Tab. 3). However, the latter line is not purely araneographic, as revealed by entomological and soil zoological evidence. Indeed, considerable differences in the insect faunas of the oak woods left of the Dnieper and those of the central forest-steppe regions have long been noted [Arnoldi, 1953, 1965]. Besides, significant variation has been reported in the abundance of soil faunistic complexes deriving from the Moscow and Kursk areas, on one hand, and the middle Volga flow and Voronezh Area, on the other [Ghilarov & Chernov, 1975]. All these areas lie on either side of the line, this being perhaps an additional argument to its existence. In many cases, the araneographic borders outlined here also coincide with those drawn by geobotanists [e.g. Gribova et al., 1980]. However, since no sites in our study are restricted to the subzone of southern steppes, it appears impossible to argue Astakhova's [1978] opinion that the spider faunas of the Plain's northern and southern steppe are markedly different.

Considering the reasons for such a variation pattern of the spider assemblages of the East European Plain oak forests, it is noteworthy that

only a single zonal border has been revealed, both Moldavian and Ural regional borders being the leading ones. This is perhaps evidence of a particular role of historical factors in the formation of the modern spider population of the Plain's oak forests. Thus, in explaining why the oak spider assemblages flanking the middle Volga flow (sites 39-41) are so markedly different, climatic variation is hardly significant enough to be seriously considered. The same seems to hold true for the oak forests divided by the Dniester (sites 8-14).

Nevertheless, climatic factors do affect the patterns of spatial variation in the spider assemblages of the Plain's oak forests. For example, it seems sufficient simply to refer here to the presence of both an araneographic zonal line and zonal distribution patterns. This problem deserves special attention and has already been dealt with elsewhere [Penev et al., 1994].

### 6.3. Determinism in spider phenological patterns

As noted above, the different seasonal representation in species of various distribution patterns (species groupings 1-9) in the East European Plain oak forests is important. Numerous "southern" taxa (22, **S**, **SC**) have been discovered solely in spring samples, and some "northern" ones (24, **NC**, **N**)



only in the autumn (Tab. 2). On the contrary, most polyzonal species tend to be "multiseasonal", being met with both in spring and autumn samples (Tab. 2: **PS, P, PN**).

The above suggests considerable differences in the phenology of the constituent taxa. Thus, the problem arises to outline the degree of stability, or determinism, of such phenological patterns in spiders deriving from distant parts of their ranges.

Before going further, a clear distinction ought to be drawn between the patterns of life history and their modifications. The latter are known to be very common, attracting special attention of specialists [e.g. Broen & Moritz, 1963; Palmgren, 1972; Olive, 1981], particularly if the species under observation display a shorter or longer breeding season in various parts of the range.

Unlike such modifications, the term "life history" focuses on the presence of active adults over periods of similar thermal regimes. Let us exemplify the above distinction by several phenologically relatively well-studied species commonly occurring in our samples.

In numerous spiders, e.g. *Erigonella hiemalis*, *Lepthyphantes tenebricola*, *Savignia frontata*, adults in western Europe, with its largely mild winters, are met with almost throughout the year [Palmgren, 1976; Thaler et al., 1987; Sechterova, 1990; Heimer & Nentwig, 1991], whereas in the mountainous regions of the Urals, where the vegetation season is restricted to three months only (June-August), they occur but in July-September [Esjunin, 1991]. Their maximal abundance is thereby observed usually within the first half of the warm season. Hence, we may regard such differences as modifications of a single spring-autumn life history pattern.

The species we tend to call "winter" are perhaps even more illustrative. For instance, in southeastern Europe, *Centromerus sylvaticus* has been recorded solely within the coldest months [Klimes & Spičáková, 1984; Weiss & Andrei, 1989], in central Europe already within autumn to spring [Miller & Obrtel, 1975; Thaler et al., 1987], in the Caucasus within August to April [Tanasevitch, 1990], in the Urals exclusively in autumn [Esjunin, 1991]. Hence, a prolonged, moderately cold season seems to extend the species' period of breeding activity, whereas a sharp fall in the mean winter temperatures (in the Urals) restricts the activity to autumn. We seem to face modifications of a single phenological pattern from the typically "winter" to both "autumn-spring" (extended) and "autumn" (shortened).

A similar pattern is observed in *Tapinocyba pallens* in Europe. It occurs from autumn to spring in central Europe [Thaler et al., 1987; Heimer &

Nentwig, 1991]. In the plain part of southern Finland, this species is multiseasonal, with its activity interrupted for only a very short time in the middle of summer, and its maximal abundances are recorded in October-November [Huhta, 1965, 1971]. In the mountainous part of southern Finland, *T. pallens* females are met with throughout the year, the males still retaining the midsummer break. In northern Finland, this species has been reported only within the second half of summer and in autumn [Palmgren, 1976]. Very similar phenologies are also known in *Asthenargus paganus*, *Bathypantes gracilis*, *Centromerus arcanus*, *Helophora insignis*, *Lepthyphantes cristatus*, *Walckenaeria cucullata*, *Hahnina pusilla*, all presumably attributable to a "winter" pattern.

However, in some cases, phenological determinism seems to be stronger, with no obvious modifications from the main pattern. Thus, *Diplocephalus latifrons* occurs from spring to autumn in southeastern [Sechterova, 1990] and central Europe [Thaler et al., 1987] as well as in the Caucasus [Tanasevitch, 1990]. Such seem also to be *Lepthyphantes menzei*, *Agroeca brunnea*, *Bromella falcigera*, which appear to be restricted solely to the warm season.

Hence, despite numerous lacunae in the knowledge of spider phenology, we may apparently state that (1) throughout the species' ranges, the main patterns of life history remain the same; (2) modifications of the life history are at best poorly expressed in the species breeding solely in summer; and (3) "winter" species seem to be purely "autumn" in the extremely cold conditions of the Urals, tend to become multiseasonal in northern Europe, finally breeding only in winter in western-central Europe.

#### 6.4. Historical background for spider phenological determinism.

In botany, the fact of close interrelations between a plant species' life cycle and the environmental conditions that determined its origin in the past has long been affirmed [Diels, 1918, cited after Kleopov, 1990]. Similar relationships can be presumed for animal species as well.

According to the famous Soviet botanist Y.D. Kleopov whose ideas were published before the World War II, but remained largely unknown until the recent memorial publication [Kleopov, 1990: 263], "the development of ecological relations in European forests amounts to both struggle and interpenetration of three main cenological groups: a shade, temperate, hygro- and thermophilous Fagetal; a photophilous and more cold-resistant Betuletal; and a photophilous and more thermophilous Quercetal". Based on the presumptions that (1) the Recent species

have largely retained the features of their life cycle that evolved under the impact of climatic factors in their origin center(s) and (2) representatives of the three historical biomes form the bulk of the Recent European nemoral communities, we attempt to explain certain particulars in the distribution of spider phenological patterns in terms of species origins. However, from the very start we emphasize that this attempt ought to be understood as highly preliminary and generalized.

In Europe, the humid thermophilous forests of the Fagetal cenotic element (Kleopov's term) are perceived to have derived in the Pliocene from the ancient Turgai flora supposed to have largely been evergreen and non-seasonal. Accordingly, the reproduction strategies in the animals associated with that type of biome are more likely to have been those extended throughout the year's warmer season, the species mainly being meso- or hygrophiles.

"In Polar lands and elevated regions of mountainous constructions, photophilous formations might have evolved in the Tertiary... This complex is termed here as Betuletal cenotic element, it represents the Arcto-Tertiary genetico-historical element sensu A. Engler (1879-1882) and J. Podpera (1925)" [Kleopov, 1990: 263]. A fauna restricted to a Betuletal biota could have originated in the conditions of constant cold. Animals deriving from such areas are likely to have become adapted to the year's coldest season. At the present, such seem to be typical winter-breeding species, in certain particular cases joined by autumn or autumn/spring taxa.

In the conditions of a Quercetal cenotic element presumed to have been formed in the Mediterranean (s.l.) in the end of the Pliocene [Kleopov, 1990], the leading factors determining species biology seem to have been both aridity and warmth. Such animals would typically breed over the warmest season, with a more or less well-expressed inclination to xerophily. Their phenological modifications are likely to have been spring-summer or summer-autumn species. Perhaps spring ephemers join this group as well.

It is quite natural to presume that each of the cenotic/phenological groups should be somehow restricted in range. Indeed, the species of a Quercetal biota would rather display preponderance to the Mediterranean. It seems next to impossible to there attribute a Holarctic and/or even a boreal trans-Palearctic species. On the contrary, species Betuletal in origin are more likely to be trans-Palearctic and even Holarctic in distribution. Among Fagetal elements, species can be supposed to be largely European, although some ancient subboreal trans-Palearctic ranges and amphi-Palearctic (= Euro-Far

Eastern) disjunctions can be possibly attributed to that complex as well.

Based on the above, we distinguish three main patterns of spider life cycle: (1) summer species associated with a Quercetal cenotic element, characterised by an inclination to the Mediterranean as well as to thermo- and xerophily; (2) multiseasonal species (spring-summer-autumn) representing a Fagetal biome, thermo- and hygrophilous, with a European or a subboreal trans-Palearctic distribution pattern; and (3) winter, Betuletal-biome, species resistant to warmth deficit, with preponderance to vast ranges (Tab. 4).

As one can notice (Tab. 4), multiseasonal spiders are numerous in both "northern" and "southern" species groups compared. So far as the ecological preferences of these forms are known, all are characterised by meso-, hygro- or thermophily. "The present-day climatic situation provides the victory for the first group [i.e. the Fagetal cenotic element], that is why its representatives are most widespread in the modern broadleaved forests despite their being genetically most ancient" [Kleopov, 1990: 263].

The active penetration of Betuletal species into the nemoral biome seems to have been possible due to their preadaptation to cold. They might have become ecologically diverged from there better adapted Fagetal forms due to heterochrony. Their southward penetration seems to be restricted by the increasingly shortened cold season, the latter growing too short to ensure a breeding period free from competition with the truly nemoral taxa.

Summer species characterised by thermo- and/or xerophily can be apparently regarded as representing a Quercetal biome in our samples. Their restricted number in this study might be due to the fact that our survey covered solely mesophilous oak stands. One can therefore expect their higher proportions in the southern, xerophytous (= bairak), oak forests.

## 7. Acknowledgements

We are most grateful to Prof. Y.I. Chernov (Moscow) for his support, valuable discussions, encouragement, as well as supervision of the entire project. Besides, Dr. R. Hengeveld provided both constructive criticism and linguistic help.

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Table 4.

Таблица 4.

Phenological and distribution patterns as well as ecological characteristics of spiders inhabiting oak forests within the forest and forest-steppe zones of the East European Plain.

Типы фенологии и ареалов и экологические характеристики пауков, населяющих дубравы в пределах зоны лесов и лесостепи Восточно-Европейской равнины.

Species groupings (s. Tab. 2)	Phenological patterns							
	"summer"			polyseasonal (spring-autumn)			"winter"	
"southern" (S+SC)	<i>Abacoproeces saltuum</i>	E		<i>Moebelia penicillata</i>	E		<i>Syedra gracilis</i>	E
	<i>Bromella falcigera</i>	E	t	<i>Panamomops menzei</i>	E			
	<i>Trichoncus affinis</i>	E		<i>Tapinocyba biscissa</i>	E			
	<i>Walckenaeria furcillata</i>	E	t	<i>Trichoncus vasconicus</i>	E			
	<i>Xysticus cambridgei</i>	E		<i>Trichopterna cito</i>	E	t		
	<i>Phrurolithus festivus</i>	WP	X,t	<i>Ceratinella scabrosa</i>	P			
				<i>Cicurina cicur</i> (?)	P			
				<i>Gonatium rubellum</i>	P	Hh		
				<i>Neon reticulatus</i>	P	Hh		
				<i>Centromerus sellarius</i>	E		<i>Asthenargus paganus</i>	E
"northern" (NC)				<i>Diplocephalus latifrons</i>	E	H	<i>Dicymbium tibiale</i>	E H
				<i>Lepthyphantes tenebricola</i>	E	Hh	<i>Habnia pusilla</i>	E H
				<i>L. minutus</i> (?)	EA		<i>Lepthyphantes cristatus</i>	E
				<i>Erigonella hiemalis</i>	ES	H	<i>Mioxena blanda</i>	E
				<i>Savignia frontata</i>	ES	H	<i>Tapinocyba pallidum</i>	E Hh
				<i>Agroeca brunnea</i>	P	Hh	<i>Walckenaeria cucullata</i>	E Hh
				<i>Lepthyphantes menzei</i>	P	Hh	<i>Centromerus arcanus</i>	ES H
							<i>Porrothomma pallidum</i>	ES H
							<i>Walckenaeria obtusa</i>	ES H
							<i>Dicymbium nigrum</i>	WC Hh
							<i>Bolyphantes alticeps</i>	P Eu
							<i>Bathyphantes gracilis</i> (?)	H H
							<i>Ero furcata</i>	H H
							<i>Helophora insignis</i>	H Hh
							<i>Centromerus sylvaticus</i>	H H

Abbreviations: Eu — Euryhygric, H — Hygrophilous, Hh — Hemihygrophilous, X — Xerophilous [after Huhta, 1971; Miller & Obrtel, 1975], t — Thermophilous [after Thaler, 1985]. Distribution patterns: E — European, EA — European-American, WP — western Palearctic, WCP — west-central Palearctic, ES — Euro-Siberian, H — Holarctic.

Обозначения: Eu — эвригигробионт, H — гидрофил, Hh — гемигидрофил, X — ксерофил [по: Huhta, 1971; Miller & Obrtel, 1975], t — термофил [по: Thaler, 1985]. Типы ареалов: E — европейский, EA — европейско-американский, WP — западнопаlearктический, WCP — западно-центральнопаlearктический, ES — европейско-сибирский, H — голарктический.

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## Appendix 1.

## Приложение 1.

TWINSPAN table of the spider assemblages based on species abundances using the default-cut levels (0 2 5 10 20) (see also text).

Таблица TWINSPAN для группировок пауков на основе численности видов с использованием уровней округления (0 2 5 10 20).

Vertical numbers above correspond to those in Map 1 and represent the sites. Numbers in the table are species abundance estimates according to the above five levels. Letters on the right are species groupings.

Вертикальные цифры над таблицей обозначают таковые на Карте 1 и соответствуют номерам точек сбора материала. Цифры в таблице означают оценку численности по вышеупомянутой пятибалльной шкале. Буквы справа - группировки видов.

	Numbers of subregions from west to east Номера субрегионов с запада на восток				
	1	2	3	4	
	Site numbers Номера точек сбора				
	1111 1234	_24_33333333_3_123 57171782345046690000	__2212222112112 2318955134780692	444444 045623	
<i>Atypus piceus</i>	-2--	-----	-----	-----	000000
<i>Harpactea rubicunda</i>	2-1-	-----	-----	-----	000000
<i>H. saeva</i>	2421	-----	-----	-----	000000
<i>Centromerus serratus</i>	1221	-----	-----	-----	000000
<i>Lepthyphantes mansuetus</i>	-11-	-----	-----	-----	000000 M
<i>Habnia nava</i>	2432	-----	-1-----	-----	000000
<i>Amaurobius pallidus</i>	12--	-----	-----	-----	000000
<i>Clubiona comta</i>	-1--	-----	-----	-----	000000
<i>Tapinocyba biscissa</i>	1---	-----1-	-----	-----	000001
<i>Neon reticulatus</i>	1---	-----1-----	-----	-----	000001
<i>Walckenaeria furcillata</i>	1--2	---1-----1-----	-----	-----	00001 S
<i>Trichoncus affinis</i>	1-22	----3--2-121-----	-----	-----	00001
<i>Brigittea vicina</i>	3---	-----1-22-----	-----	-----	00010
<i>Bromella falcigera</i>	-1--	-----21-----	-----	-----	00010
<i>Ceratinella scabrosa</i>	----	-----1-132----2	-----	---1--	00010
<i>Erigone atra</i>	----	-----1-----	-----	-----	00010
<i>Gonatium rubellum</i>	----	-----2----	-----	-----	00010
<i>Micrargus herbigradus</i>	----	-----1-233--	-----	-----	00010
<i>Syedra gracilis</i>	----	-----3-----1	-----	-----	00010 SC
<i>Thyreosthenius parasiticus</i>	----	-----11----	-----	-----	00010

	Numbers of subregions from west to east Номера субрегионов с запада на восток				
	1	2	3	4	
	Site numbers Номера точек сбора				
	1111 1234	_24_33333333_3_123 57171782345046690000	_2212222112112 2318955134780692	444444 045623	
<i>Troxochrus scabriculus</i>	----	-----1	-----	-----	00010
<i>Pachygnatha degeeri</i>	----	-----2---	-----	-----	00010
<i>Pardosa lugubris</i>	----	-----1	-----	-----	00010
<i>Cicurina cicurea</i>	----	-----11-----	-----	-----	00010
<i>Ceratinella wideri</i>	----	-1-----1-----	-----	-----	00011
<i>Gongyliidiellum latebricola</i>	----	-----1-----1--	-----	-----	00011
<i>Agyneta conigera</i>	----	-1-----	-----	-----	00011
<i>Bolyphantes crucifer</i>	----	1-----	-----	-----	00011
<i>Trichoncus vasconsinus</i>	----	--1-----	-----	-----	00011
<i>Clubiona pallidula</i>	----	-1-----1-----	-----	-----	00011
<i>Crustulina guttata</i>	----	1-1---3-----	-----	-----	0010
<i>Enoplognatha sp.</i>	----	-----1-----	-----	-----	0010
<i>Abacoproeces saltuum</i>	---2	1--22232-13-----11	-----	-----	0010
<i>Moebelia penicillata</i>	----	-----1-----	-----	-----	0010 S
<i>Trichopterna cito</i>	----	-----1-----	-----	-----	0010
<i>Trochosa spinipalpis</i>	----	-----1-----	-----	-----	0010
<i>Haplodrassus soerenseni</i>	----	-----1-----	-----	-----	0010
<i>Xysticus cambridgei</i>	----	-----1-----	-----	-----	0010
<i>Entelecara acuminata</i>	----	---2-11--1-1-11----	-----	-----	0010
<i>Hahnia ononidum</i>	----	2-2-2341212-23---1--	-----	--2---	0010
<i>Phrurolithus festinus</i>	----	-2--12-11-1--1-2---1	-----1---	-----	0010
<i>Panamomops menzei</i>	1---	113-234441-3-4-1----	----1-----	21--1-	0010
<i>Walckenaeria antica</i>	----	2-11-211-----221-11	---12-----	----1	0010
<i>Dictyna uncinata</i>	----	-----1---11-----2-	-----1---	-----	0011
<i>Nigma flavescens</i>	----	24-----3--1-2-	2-----	-----	0011
<i>Diplocephalus picinus</i>	2-24	--2242-33222442424-2	3--11----3212-2	---2--	0011
<i>Pirata hygrophilus</i>	----	-----111-----	-----1---	-----	0011 PS
<i>Haplodrassus silvestris</i>	-1-1	-----1--12-211-2----	--1-----1-----	-----	0011
<i>Zora spinimana</i>	----	-1-2-----1-----	-----1---	-----	0011
<i>Lepthyphantes flavipes</i>	3433	31-23232--2-311241--	---43-----	-----	0011
<i>Ozyptila praticola</i>	1--2	--2--22-----132-12--	---12-----22-	-----	01
<i>Ballus depressus</i>	2---	-----131-2---	---1-----1-----11	1----1	01
<i>Centromerus aequalis</i>	----	-----2---32-----	--3--2---1-----	-----	01
<i>Clubiona germanica</i>	----	-----1-----	-----1---	-----	01



	Numbers of subregions from west to east Номера субрегионов с запада на восток				
	1	2	3	4	
	Site numbers Номера точек сбора				
	1111 1234	_24_33333333_3_123 57171782345046690000	__2212222112112 2318955134780692	444444 045623	
<i>Clubiona lutescens</i>	----	-----1	-----1---	-----	01
<i>Trochosa terricola</i>	----	-----1-----2	-----	-----2	01
<i>Tapinocyba insecta</i>	---1	31-----1-22-222551--	4122131-----	-----	01
<i>Walckenaeria atrotibialis</i>	----	-----1-----1--	-----	----1-	01
<i>Maso sundevalli</i>	1---	-221-21-----	-1-1-2-----	---1--	01 P
<i>Microneta viaria</i>	2554	53342-42-22245343423	5455543-211-----	3--1-1	01
<i>Agyneta rurestris</i>	1---	-----1-----	-----	--2---	10
<i>Ceratinella brevis</i>	--1-	-11---1-----3123--2	--3-11-----2---	1-2133	10
<i>Thyreosthenius biovatus</i>	----	--1-----	-----	--11--	10
<i>Marpissa muscosa</i>	-1--	-----	-----	1-----	10
<i>Theridion pallens</i>	----	-----1-----	---1-----	-----	10
<i>Lepthyphantes angulipalpis</i>	----	221----1----2-----	--133-2-----	-----1	10
<i>Porrhomma pygmaeum</i>	----	-----2---	-----3--	-----	10
<i>Trematocephalus cristatus</i>	----	-1-----2-----2-----	--21----1112---	-----	10
<i>Diplostyla concolor</i>	143-	-----1-2144--	14-24--22-232122	1----1	110
<i>Clubiona caerulea</i>	-1--	-1-----	--11-----1---	2----2	110
<i>Zora nemoralis</i>	----	-----1-----	-----1-----	-----1	110
<i>Robertus lividus</i>	-3--	--2---1-----1-22-23	232222214-2133--	212--1	110
<i>Bathypantes nigrinus</i>	----	-----2-21----	2-----2-211-1--	-----	110 PN
<i>Macrargus rufus</i>	11--	-----1-1--2212212-	5544321---1-----	-11---	110
<i>Pachygnatha listeri</i>	----	--12-----1-	-1-212---11-1---	-----	110
<i>Anyphaena accentuata</i>	----	---1-----	-----2-	-----	110
<i>Gongylidium rufipes</i>	----	---1-----2	-----21-222-1--	-----	110
<i>Erigonella hiemalis</i>	----	-----	-----1---	-----	11100
<i>Lepthyphantes cristatus</i>	----	-----1-----	-1---1---1-21-	-----	11100
<i>Porrhomma montanum</i>	----	-----	-----1---	-----	11100
<i>Savignia frontata</i>	----	-----	-----1--	-----	11100
<i>Hygrolycosa rubrofasciata</i>	----	-----	-----3--	-----	11100
<i>Xysticus lanio</i>	----	-----	-----1---	-----	11100
<i>Dicymbium nigrum</i>	----	-----	31-----1	-----	11100
<i>Erigone dentipalpis</i>	----	-----	-----1-----1-	-----	11100
<i>Asthenargus paganus</i>	----	-----	-1-----	-----	11101
<i>Centromerus arcanus</i>	----	-----	-1---1-----	-----	11101
<i>C. sellarius</i>	----	-----	-2-----	-----	11101
<i>Diplocephalus latifrons</i>	2---	-----	51---2-----	-----	11101
<i>Floronia bucculenta</i>	----	-----	1-----	-----	11101

	Numbers of subregions from west to east Номера субрегионов с запада на восток				
	1	2	3	4	
	Site numbers Номера точек сбора				
	1111 1234	_24_33333333_3_123 57171782345046690000	_2212222112112 2318955134780692	444444 045623	
<i>Porrhomma pallidum</i>	----	-----	-1-----	-----	11101
<i>Walckenaeria cucullata</i>	----	-----	-1-----	-----	11101 NC
<i>Clubiona terrestris</i>	----	-----	12-----	-----	11101
<i>Ero furcata</i>	-1--	-----	--21---1-1---	-----	11101
<i>Robertus insignis</i>	----	-----	----1-----	-----	11101
<i>Allomengea vidua</i>	----	-----	----1-----	-----	11101
<i>Bathypantes gracilis</i>	----	-----	-----2-----	-----	11101
<i>Centromerus sylvaticus</i>	----	---1--1-----1--	2-33332212---2-1	1-3---	11101
<i>Dicymbium tibiale</i>	----	-----	----2-----1--	-----	11101
<i>Lepthyphantes minutus</i>	----	-----	---1-----	-----	11101
<i>Macrargus multesimus</i>	----	-----	--5222-----	-----1	11101
<i>Mioxena blanda</i>	----	-----	--1-----1-----	-----	11101
<i>Tapinocyba pallens</i>	----	-----	----23-----2--	-----	11101
<i>Walckenaeria obtusa</i>	----	-----	---1-----	-----	11101
<i>Pachygnatha clercki</i>	----	-----	----2-----1	-----	11101
<i>Zora armillata</i>	----	-----	----1-----	-----	11101
<i>Euophrys erratica</i>	----	-----	----1-----	-----	11101
<i>Robertus neglectus</i>	----	-----1-----	12----1-----	2-----	11110
<i>Lepthyphantes tenebricola</i>	----	-----1-----	242-----1----	213---	11110
<i>Habnia pusilla</i>	----	-----	-1-----2-13---	22----	11110
<i>Bolyphantes alticeps</i>	----	-----	---1--1211---1--	2-3---	11110
<i>Agroeca brunnea</i>	----	-----	---1-1--1-----	--1--1	11110 N
<i>Helophora insignis</i>	----	--1-----	--2232122-----	44351-	111110
<i>Lepthyphantes mengei</i>	----	-----	-2---11-----	2-4--1	111110
<i>L. nigriventris</i>	----	-----	-----11-2-1----	2-21-1	111110
<i>Euryopsis flavomaculata</i>	----	-----	-----	---1--	111111
<i>Agyneta subtilis</i>	----	-----	-----	----1-	111111
<i>Glyphesis sp.</i>	----	-----	-----	-1--12	111111
<i>Lepthyphantes pallidus</i>	----	-----	--1-----	--11-1	111111 U
<i>Tapinopa longidens</i>	----	--1-----	--1-----	2-1---	111111
<i>Zelotes subterraneus</i>	----	-----	-----	--1-1-	111111
<i>Thanatus sabulosus</i>	----	-----	-----	----1	111111
	0000	00000000000000000000	1111111111111111	111111	
	0000	11111111111111111111	0000000000000000	111111	