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Unexpected diversity of wandering spiders (Aranei: Gnaphosidae, Philodromidae, Salticidae) in the tundra zone of Northeastern Siberia

Удивительное разнообразие бродячих пауков (Aranei: Gnaphosidae, Philodromidae, Salticidae) в тундровой зоне Северо-Восточной Сибири

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KEY WORDS: Araneae, Western Chukotka, heat supply, microclimate, local fauna.

КЛЮЧЕВЫЕ СЛОВА: Araneae, Западная Чукотка, теплообеспеченность, микроклимат, локальная фауна.

ABSTRACT. It was found that diversity of spiders in Kolyma River delta (68.66º–69.25ºN), located in the southern tundra, is about the same as in four other well studied local spider faunas located above the Polar Circle in boreal and tundra zones. But three families, Gnaphosidae, Philodromidae and Salticidae, have higher species diversity in the Kolyma River delta than in other local faunas of the boreal and tundra zones. To understand reasons for this phenomenon, we compared zoogeographical aspects of spiders from Northeastern Siberia and Finland and analyzed climate and microclimates indicators in five localities. Most likely the highest species diversity of named families in the tundra zone and even highest diversity among all local faunas lying north of Polar Circle can be explained by a combination of two major factors: history and microclimate. The Kolyma River delta was never covered by the ice shield like other compared areas; and its high climate continentality led to a higher heat supply of the soil surface in the warmest habitats.

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РЕЗЮМЕ: Установлено, что видовое разнообразие пауков низовий Колымы (68.66°–69.25° с.ш.), региона, относящегося к южным тундрам, в целом сходно с таковым в локальных фаунах, расположенных к северу от Полярного круга и относимых к южным тундрам и Субарктике (север бореальной зоны). Однако, три семейства бродячих пауков, а именно Gnaphosidae, Philodromidae и Salticidae представлены бóльшим числом видов, чем во всех других хорошо изученных локальных фаунах. Чтобы установить причины этого феномена мы сравнили, с одной стороны региональное богатство фаун Финляндии и Северо-Востока Азии, а с другой стороны — климатические и микроклиматические характеристики в пяти локальных фаунах. Судя по всему, аномальное высокое видовое разнообразие трёх названных семейств связано с сочетанием исторического фактора и микроклимата. Низовья Колымы, в отличии от других сравниваемых регионов не подвергались оледенению, а благодаря высокой степени континентальности климата поверхность грунта наиболее теплых биотопов имеет высокую теплообеспеченность.

Introduction

A decade ago, we published a paper on spider diversity in the lower reaches of the Kolyma River [Marusik, Alfimov, 2012]. Sixty-five species of spiders have been found there (Appendix). The lower Kolyma or Kolyma River delta was found to be the northernmost locality in their range for 32 species, and for nine species, the northernmost in Asia. Several species have been found 4–7° north of their previously known northernmost localities. Among these species, surprisingly many occupied rather warm habitats in the Aborigen Field Station located in the upper reaches of the Kolyma (62°N). It was found that all species in common between the upper and lower Kolyma, except two, due to strong microclimate differentiation occupied the same range of heat supply conditions (sums of

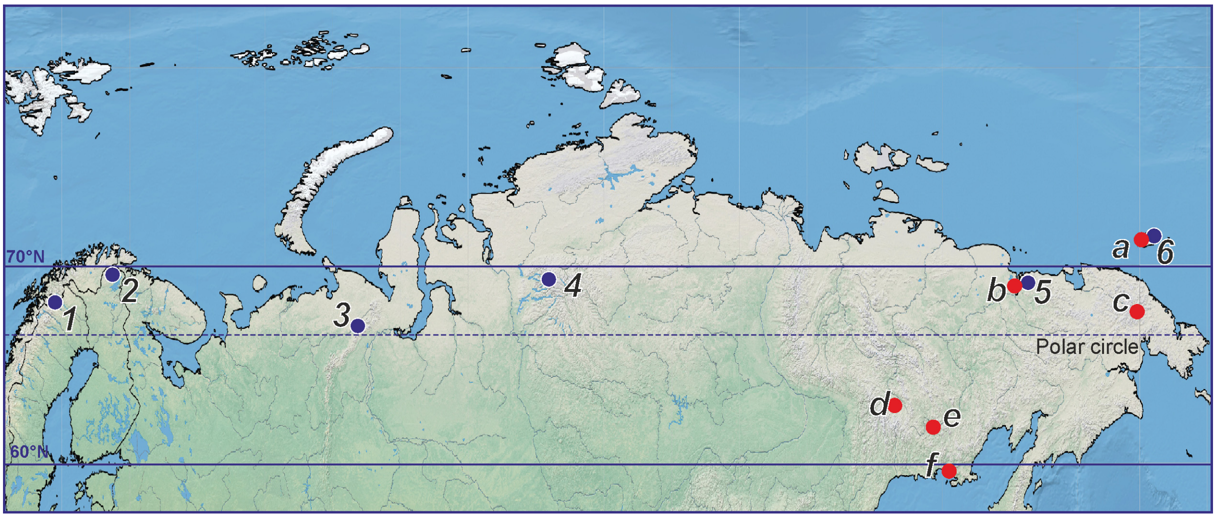

Fig. 1. Local faunas compared: 1 — Abisko, 2 — Kevo, 3 — Polar Ural, 4 — Putorana Plateau, 5 — the lower Kolyma, 6 — Wrangel Isl. and localities where temperature of the soil in the warmest habitats were studied: a — Wrangel Isl., b — the lower Kolyma, c — middle flow of Amguema River, d — Indigirka River upper reaches, e — Kolyma River upper reaches, f — Sea of Okhotsk coast.

Рис. 1. Локальные фауны (синие точки): 1 — Абиско, 2 — Кево, 3 — Полярный Урал, 4 — плато Путорана, 5 — устье Колымы, 6 — о. Врангеля) и локалитеты, где измерялась температура почв в наиболее тёплых биотопах: a — о. Врангеля, b — устье Колымы, c — среднее течение Амгуэмы, d — верховья Индигирки, e — верховья Колымы, f — побережье Охотского моря.

the positive temperatures of the soil surface). In addition, we found that species diversity of three families (Gnaphosidae, Philodromidae and Salticidae) is higher than in well studied localities in Fennoscandia and Polar Ural, located in boreal zone. This fact contradicts the well-known pattern of animal diversity where species number declines with decline of temperatures in the Subarctic and Arctic [Chernov, 2008].

Goals of this paper are: to provide a detailed comparison of ground dwelling spiders of the lower Kolyma in the southern tundra with well-studied local faunas or three islands in the Subarctic (northern part of boreal zone) and the High Arctic; and to analyze the impact of microclimate and zoogeography of the regions on high diversity of three spider families.

Material and methods

Detailed information on material and methods is given in Marusik & Alfimov [2012]. Invertebrates, including spiders, were collected in July–August 1998 and in June–July 1999 in the Kolyma River delta (below, "lower Kolyma"). The study was focused on the warmest habitats. All studied localities lie in tundra close to southern boundary of this zone as defined by Walker *et al*. [2005]. Climate indicators are after Handbook on the Climate of the USSR [1965–1969], Handbook on the Climate of the Western Europe [1979], microclimate data are from Marusik & Alfimov [2012] and Alfimov [2007].

Spiders were collected by pitfall traps (20–35 traps per habitat) and sweeping. Temperatures of the soil and in air in the lower Kolyma were measured by mean of loggers. Continuous period of study in one locality varied from 30 to 60 days [Marusik, Alfimov, 2012]. Three islands are included here just for comparison of species diversity, but not for heat supply. All three islands are well studied during a period of time.

Comparison with other Arctic and Subarctic faunas

We include for comparison three well-studied islandic faunas: Iceland [Agnarsson, 1996], Greenland [Marusik *et al.*, 2006], Wrangel Island [Khrulyova *et al.*, 2022] and four local faunas lying at similar latitudes in Eurasia: Abisko, Sweden [Holm, 1950], Kevo, Finland [Koponen, 1984], Polar Ural [Esyunin, 2015], Putorana Plateau [Eskov, 1988], and the lower Kolyma [Marusik *et al.*, 1992; Marusik, Alfimov, 2012; Alfimov, Marusik, 2022] (Fig. 1). Of these faunas, the lower Kolyma, Putorana Plateau, Polar Ural, Greenland and Wrangel Island lie in tundra zone (Arctic), while three other localities lie in boreal zone (Subarctic) according to zonation given by Walker *et al*. [2005].

According to this zonation, the southern boundary of the Arctic is represented by the isotherm of mean July temperature of 12 °C. Although the lower Kolyma, Putorana and Polar Ural lie in the southern tundra and two other mainland localities from Fennoscandia lie in boreal zone, their mean July temperature and index of summer warmth in all these localities are rather similar.

It is worth noting that spiders in Iceland, Abisko, Kevo, Polar Ural, Greenland and Wrangel Island were collected during long period and by professional arachnologists and list of species found there can be considered as exhaustive. In our case, due to short

Table 1. Comparison of species diversity of wandering spiders in well-studied island and mainland faunas located in the Subarctic and Arctic.
Таблица 1. Сравнение видового разнообразия бродячих пауков в хорошо изученных островных и локальных фаунах Северной Евразии расположенных в Арктике и Субарктике.

	Iceland	Abisko	Kevo	Polar Ural	Putorana	Lower Kolyma	Wrangel Island	Green-land
Latitude °N	64.7° center	68.42°	69°	66.7°–67°	68–69.3°	68.66°–69.25°	70.9–71.6°	60–83°
Gnaphosidae	3	8	10	9	4	**12**	1	2
Lycosidae	5	15	14	16	14	14	5	8
Philodromidae	0	3	4	6	3	**7**	0	1
Salticidae	1*	2	3	4	1	**5**	1	1*
Thomisidae	1	5	5	8	4	5	1	2
Total	84	173	164	179	No data	75+	57	76

Table 2. Diversity of wandering spiders in local and regional faunas in the Northeastern Siberia (east of Lena River and north of 60ºN) and Finland.
Таблица 2. Видовое разнообразие бродячих пауков в двух локальных и двух региональных фаунах Северо-востока Азии и Финляндии.

	Aborigen[1]	Tvärminne[2]	NE Siberia[3]	Finland[4]
Gnaphosidae	27	28	33	47
Lycosidae	27	37	42	51
Philodromidae	11	14	**21**	**15**
Salticidae	24	32	29	43
Thomisidae	11	17	19	28
total	365	424	550	658

[1] Marusik [1988]; [2] Palmgren [1972]; [3] Marusik *et al*. [1992] & Mikhailov [2022]; [4] Nentwig *et al.* [2022].

period of collecting by trapping and sweeping, the most species-rich family, Linyphiidae, was not properly sampled. This family requires special methods of collecting like sifting litter, mosses and lichens, searching in stony debris, under logs, etc. In Table 1 we list only five families that can be properly collected by pitfall traps.

In the lower Kolyma three spider families, Gnaphosidae, Philodromidae and Salticidae demonstrate the highest species diversity among eight local faunas (five mainland and three island ones). Number of philodromid and salticid species found in the lower Kolyma is 1.7 times higher than in Kevo Station. Number of thomisid species is as high as in faunas located in the Subarctic. Almost the same pattern can be observed in Lycosidae. Only Abisko and Polar Ural have more species of wolf spiders. Earlier [Marusik *et al.*, 2002] it was shown than percentage of lycosids (in comparison to other families) in various local faunas within boreal and tundra zones remains almost the same, ranging from 7 to 10%. The same pattern is true for faunas treated in this work: Lycosidae represent 6% in Iceland to 10.5% in Greenland. Therefore, the entire spider fauna in the lower Kolyma could be as rich as in Kevo, i.e. ca. 160 species. It is also worth mentioning that all species of Lycosidae occurring in Western and Central Chukotka were found in the lower Kolyma.

In order to found whether the differences in species richness in five faunas are not caused by regional affinities, we compared two well-studied local faunas located at similar latitudes, Aborigen Field Station (ca. 62°N) located in the upper reaches of the Kolyma River and at the Tvärminne Zoological Station in the southern Finland (ca. 60°N). Species diversity at the Tvärminne Station is higher in all families compared and excessing 1.04 in Gnaphosidae to 1.54 in Thomisidae. Comparison of entire spider fauna of Finland and the Northeastern Siberia reveals similar pattern, Finnish fauna is more species rich, with exception for Philodromidae. Species diversity of this family in the Northeastern Siberia is higher also in comparison to Sweden (19 species: Nentwig *et al*. [2022]).

Same diversity of Lycosidae and Thomisidae in the lower Kolyma and in northern Sweden and Finland may indicate that either the lower Kolyma or norther Fennoscandia are not correctly attributed to the tundra (Arctic) or boreal zone (Subarctic). However, the higher diversity of Gnaphosidae, Philodromidae and Salticidae indicates that there is another reason for this pattern. Chernov [2008: 311, 457] noted a certain anomaly of species richness of spiders and Rhopalocera in Northeastern Siberia and West-Central Siberia occurring in the regions with equal mean July temperature.

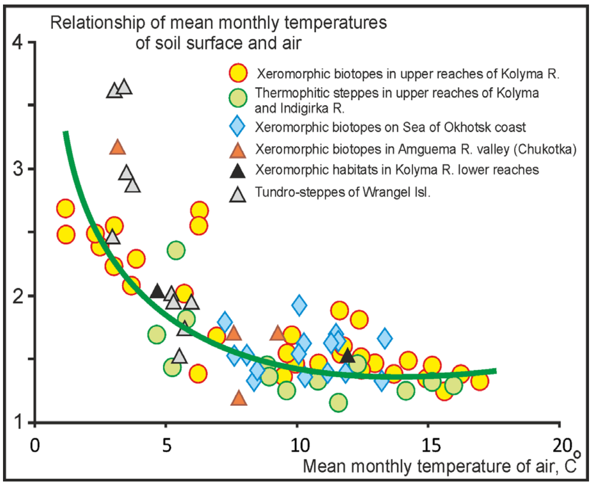

Fig. 2. Relationship between mean monthly temperatures of air (x axis) and ground surface (y axis) in the warmest habitats in different parts of the Northeastern Siberia [Alfimov, 2007].

Рис. 2. Соотношение среднемесячных температур воздуха и поверхности почвы в наиболее тёплых биотопах Северо-Восточной Сибири [Алфимов, 2007].

from the data of a weather station. The difference in ground and air temperatures depends (among other factors) from the level of continentality during the summer period, also called an index (or coefficient) of summer continentality. The higher value of this index indicates the greater temperature differences. Among compared mainland local faunas, the highest index of summer continentality is found in the lower Kolyma (Table 3). Actual heat supply (the sum of mean daily temperatures above 0 °C) on the ground in the warmest habitat in the lower Kolyma reaching 1700–1800 ºC, almost twice of that in a weather booth, 947 ºC [Marusik, Alfimov, 2012; Handbook ..., 1966].

The most important indicators of heat supply: mean July temperatures and summer warmth index, are very similar in all localities (except Wrangel Island) and cannot explain the extraordinary diversity of three spider families in the lower Kolyma. We have no measurement data permitting us to estimate the sums of temperatures on the surface of the warmest habitats in other localities. The only climatic indicator that allows to assess these values is the index of continentality that

Table 3. Comparison of some climatic parameters in six local faunas in northern Eurasia.
Таблица 3. Сравнение некоторых климатических показателей в шести локальных фаунах, расположенных в Северной Евразии.

	Abisko	Kevo	Polar Ural	Putorana	Lower Kolyma	Wrangel Island
Latitude, °N	68.42º	69º	66.7–67.03º	68–69.3º	68.66–69.25º	70.9-71.6º
Mean July temperature (°C)	11.5	13.5	12.1	12.6	9–12	6.7
Summer warmth index*	33	44	32	32	24–32	14
Index of summer continentality**	2.2	2.0	1.6	2.0	3.5–3.9	5.6

* Sum of mean monthly temperature greater than 0 °C [Walker *et al*., 2005].
** Index of summer continentality after Sokolov & Kuznetsova [2020].

Mean July temperature is a highly important parameter to analyze pattern of distribution of large animals in the Arctic, but not sufficient for study of ground dwelling invertebrates who depend not on the general climatic but rather on microclimatic conditions. In the upper reaches of the Kolyma River, which lie in the Subarctic zone (62°N), mean daily temperature of the bare ground surface on steep south-facing slopes in sunny day in spring could be positive (0.2–0.5 °C) even when mean daily temperature in a weather booth is below zero (about –8.5…–9.0 °C, Alfimov, pers. data).

In spring, or in the regions where low temperature holds during all summer (e.g. Wrangel Island), the mean monthly temperature of bare ground surface on south-facing slope can be 3–4 times higher than temperature in the weather booth located in the same place (Fig. 2).

Therefore, the heat supply used by the ground dwelling spiders in fact can be much higher than estimated in the lower Kolyma is significantly higher than in other localities (3.5–3.9 vs. 1.6–2.2). With other indicators of heat availability being equal, this allows us to assume that in the lower Kolyma the sums of temperatures on the soil surface of the warmest habitats are higher than in other localities.

Conclusions

We cannot conclude for sure what single factor led to high diversity of three spider families in the lower Kolyma River. Several factors are likely involved, such as higher continentality and therefore, higher ground temperatures, history, and landscape diversity. For example, the Chukotka Peninsula was not glaciated like other compared regions, and its fauna includes spider species ranging from tundra zone to Tibet and the Himalayas, *Chalcoscirtus galcialis*, *Enoplognatha serratosignata*, *Micaria lenzi*, *Psammitis baltistana*.

Chernov [2008] noted that, in the tundra zone, diversity of spider and butterfly species strongly depends on the July temperature. However, in different parts of this zone (Northeastern, West, and Middle Siberia), the same diversity (number of species) is achieved at different July temperatures. Chernov suggested that diversity depends not only on temperature, but also on other factors, including microclimate. It appears that these conditions can be evaluated by the index of summer continentality, which in the Northeastern Siberia is very high indicating high thermal differentiation and, as a result, the high diversity of spiders.

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Appendix. List of species found in the lower Kolyma (1) and number of specimens collected (2).
Приложение. Список видов, собранных в низовьях Колымы (1) и количество экземпляров (2).

1	2	1	2
Araneidae		*Pardosa algens* (Kulczyński, 1908)	2
Araniella displicata (Hentz, 1847)	1	*Pardosa atrata* (Thorell, 1873)	15
Larinioides cornutus (Clerck, 1757)	2	*Pardosa eiseni* (Thorell, 1875)	9
Larinioides patagiatus(Clerck, 1757)	1	*Pardosa lapponica* (Thorell, 1872)	143
Dictynidae		*Pardosa lyrata* (Odenwall, 1901)	7
Dictyna alaskae Chamberlin et Ivie, 1947	1	*Pardosa podhorskii* (Kulczyński, 1907)	1
Dictyna major Menge, 1869	33	*Pardosa sodalis* Holm, 1970	3
Dictyna t. tyshchenkoi Marusik, 1988	5	*Pardosa tesquorum* (Odenwall, 1901)	46
Gnaphosidae		*Sibiricosa subsolana* (Kulczyński, 1907)	18
Drassodes neglectus (Keyserling, 1887)	1	**Philodromidae**	
Gnaphosa borea Kulczyński, 1908	11	*Rhysodromus alaskensis* (Keyserling, 1884)	4
Gnaphosa gracilior Kulczyński, 1901	2	*Rhysodromus histrio* (Latreille, 1819)	3
Gnaphosa microps Holm, 1939	4	*Thanatus albomaculatus* Kulczyński, 1908*	10
Gnaphosa orites Chamberlin, 1922	2	*Thanatus arcticus* Thorell, 1872	9
Gnaphosa similis Kulczyński, 1926	10	*Thanatus bungei* (Kulczyński, 1908)	3
Haplodrassus hiemalis (Emerton, 1909)	1	*Tibellus asiaticus* Kulczyński, 1908	1
Haplodrassus pugnans (Simon, 1880)	3	*Tibellus maritimus* (Menge, 1875)	2
Haplodrassus signifer (C.L. Koch, 1839)	4	**Salticidae**	
Micaria alpina L. Koch, 1872	8	*Chalcoscirtus glacialis* (Caporiacco, 1935)	8
Micaria lenzi Bösenberg, 1899	108	*Dendryphantes czekanowskii* Prószyński, 1979	4
Micaria rossica Thorell, 1875	31	*Euophrys proszynskii* Logunov *et al*., 1993	10
Linyphiidae		*Pellenes ignifrons* (Grube, 1861)	2
Agyneta affinisoides (Tanasevitch, 1984)	1	*Sittisax ranieri* (Peckham et Peckham, 1909)	8
Agyneta pseudosaxatilis (Tanasevitch, 1984)	1	**Tetragnathidae**	
Cnephalocotes obscurus (Blackwall, 1834)	1	*Tetragnatha extensa* (Linnaeus, 1758)	8
Incestophantes incestoides (Tanasevitch et Eskov, 1987)	2	**Theridiidae**	
Kaestneria pullata (O. Pickard-Cambridge, 1885)	1	*Enoplognatha serratosignata* (L. Koch, 1879)	1
Microlinyphia pusilla (Sundevall, 1829)	26	*Euryopis saukea* Levi, 1951	5
Minyrioloides trifrons (O. Pickard-Cambridge, 1863)	1	*Ohlertidion ohlerti* (Thorell, 1870)	3
Procerocymbium sibiricum Eskov, 1989	21	*Phylloneta impressa* (L. Koch, 1881)	1
Tmeticus tolli Kulczyński, 1908	27	**Thomisidae**	
Walckenaeria tystchenkoi Eskov et Marusik, 1994	2	*Ozyptila arctica* Kulczyński, 1908	5
Lycosidae		*Psammitis albidus* (Grese, 1909)	42
Arctosa alpigena (Doleschall, 1858)	40	*Spiracme baltistana* (Caporiacco, 1935)	10
Alopecosa aculeata (Clerck, 1757)	12	*Xysticus britcheri* Gertsch, 1934	25
Alopecosa borea (Kulczyński, 1908)	182	*Xysticus emertoni* Keyserling, 1880	11
Alopecosa sibirica (Kulczyński, 1908)	242	**Titanoecidae**	
Pardosa adustella (Roewer, 1951)	36	*Titanoeca sibirica* L. Koch, 1879	63

* Considered by YM as a separate species, but junior synonym of *T. coloradensis* Keyserling in WSC [2022].