Fauna and populations of the petrophilous spiders (Arachnida: Araneae) of north-east Siberia and north-west Canada

Фауна и население петрофильных пауков (Arachnida: Araneae) северо-востока Сибири и северо-запада Канады

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ABSTRACT. Spiders associated with stony biotopes were studied in different parts of Magadan Area (Russia) and in Yukon Territory (Canada). Many of them are widespread in north-east Siberia and inhabit the tundra and taiga zones, as well as different altitudinal belts. Some species are restricted to the taiga zone, others to the tundra. The most common stony debris dwellers are Sibirocosa kolymensis, S. subsolana, Aculepeira carbonarioides and Lathys alberta. The most common dominants of the stony debris habitats in the forest belt of the taiga zone are Theridion sibiricum and L. alberta. Those of the mountain tundra belt are S. kolymensis and A. carbonarioides. Some species were found in one or two sites of very small size (Hybauchenidium holmi, Theridion thaleri, Chalcoscirtus carbonarius, 'Lepthyphantes' epigynatus). Brief reviews of the geographic and spatial distribution of the lithobiont and lithophilous (= petrophilous) spider species are given. The species composition of spiders living on rock debris in Yukon Territory is rather similar to that in north-east Siberia, while both faunas differ greatly from those of central European scree slope ecosystems. The European and Beringian faunas have only two species in common. Values for the narrow endemics among the petrophilous and the exclusively lithobiont species in north-east Siberia reach 24% and 46%, respectively. The value for endemic species in the whole fauna is nine percent.

РЕЗЮМЕ. Пауки связанные с каменными осыпями и россыпями изучались в разных частях Магаданской области и территории Юкон. Многие из них широко распространены на Северо-Востоке и населяют тундровую и таёжную зоны, а также разные высотные пояса. Часть видов приурочена к одной из зон и связана с одним из высотных поясов. Наиболее распространенные и массовые виды в каменных сообществах Sibirocosa kolymensis, S. subsolana, Aculepeira carbonarioides и Lathys alberta. В лесном поясе в зоне тайги на каменных осыпях доминируют Theridion sibiricum и L. alberta. Доминантами горнотундрового пояса являются S. kolymensis и A. carbonarioides. Некоторые из видов были найдены всего в одном—двух небольших биотопах (Hybauchenidium holmi, Theridion thaleri, Chalcoscirtus carbonarius, 'Lepthyphantes' epigynatus). Для всех облигатных литобионтов и наиболее массовых петрофильных видов приведены видовые очерки, включающие географическое распространение и биотопическую приуроченность. Видовые списки пауков каменных осы-

пей на северо-западе Канады и северо-востоке содержат около 50% общих видов, но сильно отличаются от пауков каменистых биотопов центральной Европы. Доля узких эндемиков среди петрофильных видов и облигатных литобионтов на северо-востоке Азии составляет 24% и 46%, в то время как общее число эндемиков в фауне — около девяти процентов.

KEY WORDS: Spiders, Araneae, north-east Siberia, Yukon Territory, scree, stony biotopes, petrophilous, lithobiont.

КЛЮЧЕВЫЕ СЛОВА: Пауки, Araneae, северо-восток Сибири, территория Юкон, осыпь, каменистые биотопы, петрофил, литобионт.

Introduction

Although stony ecosystems (i.e., screes, stony taluses, stone debris, pebble river banks, etc.) are very common and widespread throughout Siberia, there are no publications specifically dealing with their spider faunas. A number of papers, nevertheless, contain data on habitat preferences for certain Siberian and Nearctic species, including petrophilous spiders, particularly from north [Eskov, 1985; Tanasevitch, 1985] or middle [Eskov, 1988] Siberia and from the mountains of south Siberia [Logunov & Marusik, 1995, 1999, 2001; Logunov et al., 1998; Marusik et al., 2000; etc.]. Spiders associated with cliffs in Québec were briefly discussed by Koponen [1992]. In contrast to Siberia and North America, the spiders of stony debris (= scree slope) ecosystems in central Europe are well studied thanks to numerous publications by Růžička [1988, 1990a, 1993, 1996, 2002, etc.] and his co-authors.

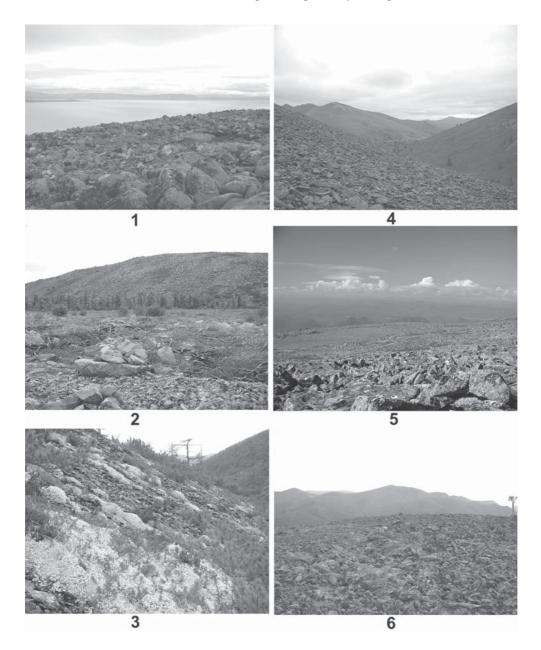
Stony ecosystems, morphologically and geologically belong to many types (see Figs 1–6) and are common both in north-east Asia and in north-west Canada. Both these territories make up parts of Beringia, a vast area between the Kolyma River in the Russian Far East to the Mackenzie River in the north-west Territories of Canada. The purpose of the present paper is to provide an account of the fauna and populations of the petrophilous spiders of Beringia.

Material and methods

Investigations of the spiders inhabiting stony ecosystems in north-east Siberia were started in 1983. The first and most detailed research was undertaken around the Aborigen Biological Station in the upper reaches of Kolyma River (62°N). It was only a small part of the spatial distribution research

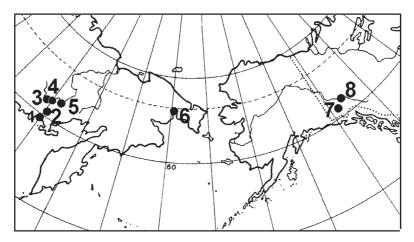
and no special preferences were given to the lithobiont spiders. After the first two years of research, the petrophilous spiders attracted more of my attention because they contained many interesting species. These studies were described in my Ph.D. thesis [Marusik, 1988]. In 1988 and 1989, the petrophilous spiders were investigated in Chukotka, viz., in Anadyr', Christ Bay, the Amguema and Bol'shaya Osinovaya River basins. In 1985–1993, some investigations were carried out in the northern Cisokhotia, Ola River basin (the upper and middle reaches) and the upper-middle Kolyma River (Map 1). In 1993 limited research was performed in Yukon Territory of Canada. A list of the stony habitats and the sites studied in north-east Siberia is given below:

- 1–6. The upper reaches of Kolyma River (62°N), Sibit-Tyellakh River basin (left tributary of Kolyma River), the environs of Aborigen Research Station (A):
- 1. Screes of a southern slope sometimes with mats of *Cetraria* lichens, 550–700 m.
- 2. The slatestone scree on an exposed north-facing slope, big stones covered with lichens, 550–600 m.
- 3. Granite screes and kurums¹ on an exposed south-facing slope near a flat plain in the mountain tundra, 1 100–1 250 m.
- 4. Granite-slatestone screes on an exposed east-facing slope, 1 300 m.
 - 5. Slatestone stone field on a flat crest, 800 m.
- 6. Small and elongate (0.5–1.5 m wide) rock debris on a south-facing slope within a semiclosed birch grove, margins fixed by Graminaceae and *Rosa* bushes, with a small brook underneath, 600 m.
- 7 K. The upper reaches of Kolyma River, Kontaktovy Creek basin, 61°51′N, 147°40′E, granite scree with lichen pillows on the south-facing slope, 900 m (Figs 5, 6).
- 8 MA. Different granite screes and rocks around Magadan (Figs 1, 2).
- 9 O. Ola Plateau, klippe scree, down moist edge, 1 200 m.
- ¹ Kurums in Siberia means the boulder screes, sometimes with huge blocks (0.5–2 m), common in the mountain tundra.



Figs 1–6. Different stony habitats of north-east Siberia: 1 — the stony desert near Magadan; 2 — the stony desert and talus near Magadan; 3 — a small scree on the north exposed slope near the Kontakt Field Station; 4 — the stony desert on the Kolyma-Okhotian watershed; 5 — the stony talus in the mountain tundra belt near the Kontakt Field Station; 6 — the stony polygons in the mountain tundra belt near the Kontakt Field Station.

Рис. 1—6. Различные каменные местообитания северо-восточной Сибири: 1 — каменная пустыня в окрестностях Магадана; 2 — каменная пустыня и россыпь вблизи Магадана; 3 — маленькие каменные осыпи на северном склоне в окрестностях стационара «Контакт»; 4 — каменная пустыня на Охотско-Колымском водоразделе; 5 — каменные осыпи в горных тундрах вблизи стационара «Контакт»; 6 — каменные полигоны в горных тундрах вблизи стационара «Контакт».



 $\label{eq:map-1} {\it Map 1. Main study areas. 1-Magadan, 2-Ola Plateau, 3-Kontakt, 4-Aborigen, 5-Seimchan, 6-Christ Bay, 7-Kluane Lake, 8-Carmacks.}$

Карта 1. Основные районы исследований. 1 — Магадан, 2 — Ольское Плато, 3 — Контакт, 4 — Абориген, 5 — Сеймчан, 6 — залив Креста, 7 — оз. Клуэйн, 8 — Кармакс.

10 S. Environs of Seimchan, slatestone scree in a canyon, 600 m.

11 E. Christ Bay, Egvekinot Town, south-facing slope in canyon along a small creek.

12 E. same locality, kurums, and big stony debris on the east-facing slope.

13 CH. Cumulative data of Amguema River basin, Christ Bay and the upper reaches of Bol'shaya Osinovaya River.

All specimens were collected either by hand or by using an aspirator. In population studies, species were attributed to different dominant categories after the criteria suggested by Palmgren [1930, 1972] for birds and spiders: viz., dominants or D, > 10% of specimens collected in a certain habitat; subdominants or S, 5–10%; common (or influents) or C, 2–5%; and others rare or R. Spiders of different predation guilds such as wandering (Lycosidae, Gnaphosidae, Philodromidae Liocranidae, Salticidae), ambush spiders (Thomisidae) and web builders were attributed to dominant categories independently, because they required different collecting methods.

Stone debris ecosystems in northeast Siberia

While there are some similarities between morphological types of the stony ecosystems in middle Europe (particularly in the Czech Republic, see Růžička [1990a, 1993]) and Siberia, the differences are more discernable, especially as far as north-east Siberia is concerned.

Stony biotopes are very diverse and cover huge areas. North-east Siberia, like other Arctic and Subarctic territories, has landscapes known as cold goltsy deserts (fell-fields, alpine stony deserts and rock deserts are their American equivalents) [see Kuvayev, 1985]. In some areas of the taiga belt, the cold stony deserts occupy more than 90% of the surface (e.g., in the Kolyma upland), and they are very common in the mountainous regions of Chukotka.

Other quite common stony habitats are the stony slopes (scree slopes, screes or talus) within the taiga belt composed of small (less than 0.5 m blocks) or large stones. In many cases, the screes have independent origins, but quite often they are formed by stony desert tongues. In continental highlands, as well as in coastal parts, the tongues of the stony deserts can reach the valley bottoms or the sea coast.

Besides the two most widespread kinds of stony ecosystems mentioned above, the following habitats are also present in the upper Kolyma: kurums, stone polygons and belts in mountain tundra, cliff screes (mountain tundras), forest debris, small stone taluses on low and flat mountain ridges and trains, and different kinds of morains.

The kurums in Siberia mean the boulder screes, sometimes with huge blocks of 0.5–2 m in diameter, mostly occurring in the mountain tundra. Stone polygons (circles) and belts are

characteristic for the tundra and in some places for the mountain tundra, where they were formed because of the permafrost.

The characteristic aspects of the goltsy deserts, which separate them from the tundra and nival zones, are (1) extremely strong winter winds (hurricanes) and (2) snow storms. While precipitation in the mountains where the goltsy are situated is higher than in lowlands, winds and hurricanes blow out all the snow. This loss of snow causes winter drying and wind erosion of the vegetation and stones. Together with extremely low winter temperatures (down to minus 60°C), rapid temperature and moisture changes within one day, the lack of snow and a short growing season creates an extremely severe climate [Kuvayev, 1985]. The stony deserts, in general, occupy flat and semi-flat surfaces of the mountains and uplands and mountain slopes (1 200-2 000 m).

The other difference of European and Siberian stony biotopes is connected with the presence of permafrost in Asia, causing the scree bottom to be permanently cold with temperatures below 0°C. Therefore, lower depths of the Siberian screes are uninhabited. Because of the permafrost, caves cannot exist in most parts of Siberia, and consequently there are no cavernicolous faunas in eastern Siberia (unlike Europe), which could enrich the species diversity of spiders in screes.

Another important difference between Siberian and central European stony ecosystems is related to the surroundings of these habitats. The mountain and taiga belt ecosystems in eastern Siberia are open and usually include gravel, pebbles, rocks, etc. Therefore, many species are pre-adapted for living in stony debris, even though they seem not to be true lithobionts or petrophilous species. In Europe, stony ecosystems are always surrounded with shadowed forests or meadows with thick litter and therefore with no open gravel habitats.

To conclude with the dissimilarities, it should be mentioned that unlike in Europe, the stony ecosystems of north-east Siberia are not relics, and such ecosystems are not discontinuous because of the mountain ranges stretching from the south to the extreme north. Therefore, species can easily spread (in a historical sense) from one area to another, and recent ecosystems which are closely separated can have gradual species interchanging.

Spiders of the stony biotopes of the upper Kolyma river

The majority of stony slopes, except for the goltsy, in the upper reaches of Kolyma are restricted to the southerly exposed slopes, and the adjacent ecosystems consist of dry meadow or northern steppe (tundra-steppe) discontinuous vegetation. Therefore, wandering spiders (Gnaphosidae, Lycosidae, Liocranidae) can migrate to or from the scree habitats, and microcave dwellers such as the Micronetini and Theridiidae can inhabit the neighbouring biotopes, which have separate, flat stones.

In the environs of Aborigen Field Station, stony slopes are formed from two different rocks, viz., slatestones (slatestone sheet) at 500–1000 m, and granite intrusions (800–2500 m). The presence of slatestones in the taiga belt, makes conditions very favourable for spiders (and for arachnologists to study them). Small sites with slatestones on the border between slatestones and granite belts, and within granite belts are inhabited by exotic species such as *Hybauchenidium holmi*, *Chalcoscirtus carbonarius*, 'Lepthyphantes' epigynatus and Theridion thaleri.

Spiders inhabiting the stony ecosystems can be considered in the following four groups:

- 1) Obligate scree dwellers (moist and dry), not active hunters: Aculepeira carbonarioides, Chalcoscirtus grishkanae, C. carbonarius, Flagelliphantes flagellifer, 'Lepthyphantes' punctulatus, 'L.' epigynatus, Poeciloneta pallida, P. petrophila, Theridion thaleri.
- 2) Dwellers predominantly of scree ecosystems (belonging to dominants): Acantholycosa aborigenica, A. norvegica, Agroeca maculata, Clubiona propinqua, Enoplognatha serratosignata, Incestophantes incestoides, Lathys alberta, Procerocymbium sibiricum, Sibirocosa kolymensis, Scotinotylus protervus, Tanasevitchia uralensis, Thanatus kolymensis, Theridion sibiricum, Xysticus rugosus.
- 3) Spiders found both under stones and on the screes: Agyneta birulai, Chalcoscirtus gla-

cialis, Drassodes cupreus, D. neglectus, Erigonoplus minaretifer, Hahnia glacialis, Parasyrisca holmi, Poeciloneta variegata.

4) Eury- or polytopic (= eurybionts) dwellers: Euophrys proszynskii, Gnaphosa similis, Maso sundevalli, Microneta viaria, Pardosa eiseni, Philodromus alascensis, Scotinotylus kolymensis, Thanatus bungei, Titanoeca sibirica, T. nivalis, Wubanoides fissus, Xysticus albidus.

Species in the first group were not found outside the screes. Some of them are known from a few specimens and only one or two localities in north-east Siberia ('L'. punctulatus (two localities) in Kolyma and Chukotka; *C. carbonarius* (one locality in Siberia); *T. thaleri* (two localities in the world, both of which are in the upper Kolyma), *H. holmi* (a single locality in the world).

Survey of the most common scree dwellers

Araneidae

Aculepeira carbonarioides (Keyserling, 1892)
A widespread Siberio-American species distributed as far as the Arctic Ocean coast and everywhere strictly restricted to stony ecosystems, viz., kurums, cliffs, stone circles, screes, where it builds its orb web between the stones. In Kolyma area it inhabits only mountains, whereas in coastal and tundra parts it can be found at low elevations. It is the only orbweaver in the stony habitats of north-east Siberia, i.e., a single representative of the ecological group 'weavers' and therefore, here it is always considered dominant in spite of its actual low densities at some

Clubionidae

Clubiona propingua L. Koch, 1879

Siberian range; the species reaches the south tundra and is associated everywhere with screes. In the taiga zone, it inhabits the mountains at 800–1 400 m a.s.l. In both Chukotka and the upper Kolyma, the species belongs to the common, dominant and subdominant species groups.

Clubiona praematura Emerton, 1909

Chukotka–Nearctic range [Mikhailov & Marusik, 1996]; in Asia it is restricted exclusively to the tundra zone, occurring in several habitats but most common in the small screes or stony debris below cliffs.

Dictynidae

Dictyna tyshchenkoi Marusik, 1988

Siberian range; known from the Polar Urals, the upper Kolyma and Chukotka, including Wrangel Island. In the upper Kolyma, it is restricted to the dry mountain tundra and low mountain ridges (800–1400 m). Common under separate stones, but very rarely occurs on the margins of screes.

Lathys alberta Gertsch, 1946

East Siberio—north-west American range, reaching the south tundra in Chukotka. Associated mostly with screes, but also common under separate stones in dry habitats. In the taiga zone it is restricted to the forest belt and absent from the mountain tundra. In the tundra zone, it occurs in lowlands on the southfacing exposed slopes. In many places it is a dominant species and occurs at high densities.

Gnaphosidae

Drassodes cupreus (Blackwall, 1834)

Trans-Palaearctic polyzonal (?) range. In northwest Siberia, it is restricted to the taiga zone and taiga belt, occurring on dry stony south-facing slopes and screes, rarer than *D. neglectus*, and inhabiting only lowland slopes up to 600–700 m. In some habitats it reaches high densities. This species inhabits screes in Tuva, south Siberia and the Kurile Islands [Logunov *et al.*, 1998: sub (?) *D. lapidosus*; Marusik *et al.*, 2000; etc.].

Drassodes neglectus (Keyserling, 1887)

Siberio-Nearctic polyzonal range; it is associated with dry habitats. In the upper Kolyma it is often associated with separate stones at the edges of screes at elevations up to 1100 m. In the tundra zone it was found in a taiga oasis of Bol'shaya Osinovaya River only.

Gnaphosa similis Kulczyński, 1926

East Siberian range, from east Mongolia to Chukotka. Associated with open gravely, south-facing exposed slopes. Common both under separate stones and in shallow screes.

Gnaphosa orites Chamberlin, 1922

Circum-Holarctic range. In Asia, it occurs from the highlands of Tuva [Marusik et al., 2000: sub Gnaphosa sp.1 (cf. orites)] to Wrangel Island. In the upper Kolyma it occurs at elevations over 700 m. In the mountain tundra the species inhabits various biotopes including screes and gravelly places; in screes it never attains a high density.

Parasyrisca holmi Ovtsharenko, Platnick et Marusik, 1995

East Siberian range, from Amur to the upper Kolyma. Associated with separate stones in stony habitats occurring in the mountain tundras (continental parts) and the dwarf pine belt at the sea coast. Very seldom occurs in screes.

Hahniidae

Hahnia glacialis Sørensen, 1898

North-east Siberian—Nearctic range; in Asia it is known from the continental parts of Magadan Area and from Chukotka [Marusik *et al.*, 1996]. Most specimens of this species were collected from the mountain tundra among gravel and under stones, but it is also present in the forest belt. In some screes it is a dominant species.

Linyphiidae

Agyneta birulai (Kulczyński, 1908)

Siberio—north-west Nearctic range, from the Polar Urals via Putorana Plateau and Arctic Yakutia to Wrangle Island and southward to south Transbaikalia [Eskov, 1994]. A dweller of the southfacing exposed slopes, occasionally can be collected among scree or under separate stones.

Bathyphantes eumenis (L. Koch, 1879) Siberian (?) range: from Yenisei to Chukotka, south to south Transbaikalia and Manchuria [Eskov, 1994]. Eurybiontic species.

Centromerus pacificus Eskov et Marusik, 1992

East Siberian range, from south-east Cisbaikalia south-eastward to Maritime Province and north-eastward to the upper Kolyma [Eskov, 1994]. A dweller of several habitats, rarely occurring under stones or in scree.

Eborilaira alpina Eskov, 1989

North-east Siberian range, from the upper Kolyma westward to the upper Indigirka and north-east to Chukotka [Marusik *et al.*, 1992]. In the upper Kolyma it dwells in the stony deserts, screes and stony taluses in the mountain tundra (1000 m and higher).

Entelecara sombra (Chamberlin et Ivie, 1947) Siberio-trans-Nearctic range, from Yenisei to the upper Kolyma, southward to Tuva and south Sakhalin [Eskov, 1994]. It inhabits two different biotopes: stony (the kurums near Magadan, pebbles or stones in moist ground) and birch trees (under bark).

Erigone arcticola Chamberlin et Ivie, 1947 Siberio–Alaskan hypoarctic range, from Novaya Zemlya to Chukotka Peninsula, southward to north Cisokhotia [Eskov, 1994]. In the upper Kolyma and

northern Cisokhotia, the species occurs on pebbly banks, whereas in Chukotka it inhabits scree and some other biotopes.

Erigonoplus minaretifer Eskov, 1986

Endemic to the continental parts of north-east Siberia. Most common in the goltsy and subgoltsy (an intermediate belt between the goltsy and taiga) belts under separate stones or in small stone fields, which are free of snow during the winter. Unknown from north of the taiga zone and never reaching a high density.

Flagelliphantes flagellifer (Tanasevitch, 1987)

Endemic of north-east Asia, was found in the upper Kolyma, northern Cisokhotia and the north Kuriles (Shumshu Isl.) only. Occurs in moist habitats with embedded stone fields (slatestones or moraine pebbles). Very rare.

Hybauchenidium holmi Marusik, 1988 Known from a single locality and habitat (see Table legend) in the upper Kolyma.

Incestophantes incestoides (Tanasevitch et Eskov, 1987)

North-east Siberian widespread endemic species, occurring up to the southern tundra. Can be found under separate stones, but most common in elongate thin scree. In some places may reach high densities.

Incestophantes kochiellus (Strand, 1900)

Trans-Palaearctic boreo-hypoarctic range, from northern Scandinavia to Chukotka [Eskov, 1994]. Inhabits scree in Chukotka only.

Islandiana falsifica (Keyserling, 1886)

Trans-Palaearctic—north-west Nearctic range, from north Scandinavia to Chukotka Peninsula and Wrangel Island, southward to Kamchatka [Eskov, 1994]. In the upper Kolyma, and northern Cisokhotia it lives on pebbly beaches. It also inhabits scree in Chukotka.

Kolymocyba petrophila Eskov, 1989

North-east Siberian hypoarctic range, known from the upper Kolyma and Amguema River basin in Chukotka Peninsula [Marusik *et al.*, 1992]. Inhabits stony places on north-facing exposed slopes in the forest belt and south-facing slopes in the mountain tundra up to 1 400 m; rare.

'Lepthyphantes' epigynatus Tanasevitch, 1988

Endemic to the upper Kolyma and known from a single habitat (see Table legend).

'Lepthyphantes' punctulatus Holm, 1939

Trans-Palaearctic subarctic range. Besides the upper Kolyma, it was found in two localities in Chukotka, in all cases on open scree. A high density was observed only in Chukotka.

Maso sundevalli (Westring, 1851)

Circum-Holarctic range. Eurybiont. Rarely occurs in scree.

Microneta viaria (Blackwall, 1841)

Circum-Holarctic polyzonal range [Eskov, 1994]. Rare species in the upper Kolyma and northern Cisokhotia. A leaf litter dweller, however it rarely occurs in shaded screes.

Oreoneta leviceps (L. Koch, 1879)

Siberio-Nearctic range [Eskov, 1994], restricted to the tundra zone and occurs in different habitats including stony polygons and stony debris.

Oreonetides kolymensis Eskov, 1991

North-east Siberian endemic, inhabiting different biotopes. A high density was found only in the embedded and moist moraine pebble debris on Lankovaya River.

Poeciloneta petrophila Tanasevitch, 1989

Beringian range; in addition to the upper Kolyma, it was found in the northern Cisokhotia and in two localities in Chukotka (together with 'L'. punctulatus). For habitats in Kolyma area, see the table legend. Other habitats: open screes with a moist base.

Poeciloneta pallida (Kulczyński, 1908)

Endemic to north-east Siberia, reaches south tundra, everywhere quite rare. Associated with dry stony habitats. Never reaches high density.

Poeciloneta tanasevitchi Marusik, 1988

North-east Siberian endemic, know from three localities only: one in eastern Yakutia and two around Magadan. In the environs of Magadan it was found in the shaded, small and somewhat moist screes. Very rare but can occur at a high density.

Poeciloneta variegata (Blackwall, 1841)

Trans-Palaearctic-west Nearctic range. In the upper Kolyma this species lives at elevations of

400–1400 m in various open habitats with stones. A high density was observed on pebbly beaches. In Chukotka, it inhabits scree only.

Perro tshuktshorum (Eskov et Marusik, 1991)

Endemic to Chukotka. Inhabits stony deserts.

Porrhomma boreale Banks, 1892

Siberio–Alaskan range, from Yenisei southward to the Commander Islands and eastward to Alaska [Eskov, 1994]. Very rare. Approximately ten specimens have been found in screes within the forest belt (600–900 m).

Porrhomma cf. kulczynskii Staręga, 1974 Known in the upper Kolyma and Chukotka only. Rare. All specimens were collected in stony deserts.

Procerocymbium sibiricum Eskov, 1989

East Siberian hypoarcto-montane range, occurring from Transbaikalia to Chukotka. In the taiga zone of the upper Kolyma it exclusively inhabits scree in mountain tundra. In some sites it may attain high densities.

Scotinotylus alpinus (Banks, 1896)

Siberio-trans-Nearctic range [Eskov, 1994]. Eurybiont. As a scree dweller it was found only in Ola Plateau.

Scotinotylus kolymensis Eskov et Marusik, 1994

North-east Siberian range, known from northern Cisokhotia and the upper Kolyma only. A litter dweller, but was found once in a stony habitat.

Scotinotylus protervus (L. Koch, 1879)

Siberio-Alaskan range. A dweller of the forest belt stone moraines. In mountains and in the tundra zone it is associated with the moraines and moist lower edges of the stone trains. In several habitats it attains high densities.

Tanasevitchia uralensis (Tanasevitch, 1983)

Siberian range; in north-east Siberia it was found only in the taiga zone, and only in scree (with a few exceptions). It occurs either in the scree with flat stones, or in those with lichen carpets (most common), in the latter case it dwells both on the lichen cover and underneath the stones. In some scree it is very abundant. In Tuva, southern Siberia, the species was found among scree with lichen cover [Marusik *et al.*, 2000].

Wubanoides fissus (Kulczyński, 1926)

East Siberian endemic, the most eurybiontic linyphiid species in Siberia. At a high density it was found only in a single alder grove. A relatively high density was observed in the north-exposed (and correspondingly cold) screes. In the tundra zone, it is restricted to warm screes only.

Liocranidae

Agroeca maculata (L. Koch, 1879)

Siberian boreal range, from east Kazakhstan and Perm Area north-east to the upper Kolyma and southward to central Mongolia [Mikhailov & Marusik, 1996]. It occurs in xeromorphic gravelly habitats, but is most abundant in scree, also in the ground layer of thin larch forest with sparse vegetation and in aspen stands.

Lycosidae

Acantholycosa aborigenica Zyuzin et Marusik, 1988

Endemic to eastern Siberia, occurring from eastern Mongolia to Sikhote-Alin' Mt Ridge and northward to the upper Kolyma. Associated with dry stony slopes, where it can be found in scree and other gravelly habitats. In many cases it is a coinhabitant with *Acantholycosa norvegica*, but never in the same proportion. Elevation: 600–800 m. It should be noted that all species of the genus *Acantholycosa*, except for *A. lignaria* (Clerck, 1757) are associated with scree or stony slopes.

Acantholycosa norvegica (Thorell, 1872)

Trans-Palaearctic range, present in the taiga belt only, on dry southern exposed slopes. Common in continental and coastal parts of north-east Siberia.

Pardosa eiseni (Thorell, 1875)

Trans-Palaearctic range [Marusik *et al.*, 2000], occurs in a wide range of habitats. In several scree slopes it reaches relatively high densities.

Sibirocosa kolymensis Marusik, Azarkina et Koponen, 2004

Endemic to the upper Kolyma and northern Cisokhotia, widespread and common everywhere in the goltsy zone. Among the lycosids, this species is most strongly afilliated with stone debris habitats and because of this it is very uncommon in pitfall traps in adjacent biotopes. In Kolyma area it inhabits the mountain tundra belt only (1000 m and higher), whereas in the coastal tundras near Magadan it can occur in lowland stony debris. Previously, this species was confused with *S. subsolana* [cf. Marusik *et al.*, 2004].

Sibirocosa subsolana (Kulczyński, 1907)

Endemic to Chukotka, occurring from the Kolyma river mouth to eastern Chukotka and northward to Wrangel Island. Exclusively restricted to scree and stony deserts.

Philodromidae

Philodromus alascensis Keyserling, 1884 Siberio-American range, from China to the southern tundra zone. The species has no special preference for stones, but rather to flat surfaces in general: tree trunks, big stones, ice fields.

Philodromus cespitum (Walckenaer, 1902) Circum-Holarctic range. A dweller of herbaceous and shrub strata, occasionally found in scree.

Thanatus bungei (Kulczyński, 1908)

Range is almost the same as in *P. alascensis*, but restricted to the taiga and tundra zones, common on tree trunks, *Veratrum* leaves, but most common in kurums and scree.

Thanatus kolymensis Marusik, 1991

This species is known from two localities in the upper Kolyma, occurring in the subgoltsy and goltsy belts among stony deserts. Logunov [1996] treats this species as a junior synonym of *T. arcticus* Thorell, 1872, although in north-east Siberia and Tuva [cf. Logunov *et al.*, 1998] the latter species never occurs in stony biotopes. In the upper Kolyma *T. arcticus* inhabits the forest belt and occurs in various herbaceous or boggy biotopes.

Salticidae

Chalcoscirtus carbonarius Emerton, 1917 North-east Siberio–north-west Nearctic range, within the Palaearctics it is known from the upper Kolyma only. Rare. It was found in a relatively high number in only one biotope: the slatestone scree (c. 1000 m) in the subgoltsy zone.

Chalcoscirtus glacialis Caporiacco, 1935

Siberio—north-west Nearctic range northward to the southern tundra, restricted to dry and xeric stony habitats. In the taiga zone, it occurs in the taiga belt and subgoltsy zone. In south Siberia (Tuva), this species is recorded as a typical dweller of the mountain steppes [cf. Logunov *et al.*, 1998], but it seems a separate (sub)species lives there.

Chalcoscirtus grishkanae Marusik, 1991

East Siberian range, from Chita Area to the upper reaches of Kolyma River. In the upper Kolyma and in northern Cisokhotia, it is restricted to scree only within the taiga belt.

Euophrys proszynskii Logunov, Cutler et Marusik, 1993

Siberian range, does not exceed the taiga zone. Restricted to dry stony habitats in the taiga and subgoltsy belts. Most numerous in the small, stone fields or small sites within scree, where females build their retreats and lay egg-sacs.

Theridiidae

Enoplognatha serratosignata (L. Koch, 1879)

Trans-Palaearctic boreo-montane range [Marusik et al., 2000], from Switzerland and Finland eastward to the Kolyma River mouth, southward to Tuva, Mongolia and Gansu. In the upper Kolyma, all specimens were collected in open biotopes on slopes and plain places at elevations of 500–900 m. The highest density of this species was observed in small stony taluses along mountain ridges with sparse Carex and lichen vegetation.

Theridion sibiricum Marusik, 1988

Siberian boreo-nemoral range, known from Tuva to Kolyma and Kamchatka Peninsula, southward to Maritime Province, where it is restricted to dry stony habitats. In some open scree sites the species attains high densities.

'Theridion' thaleri Marusik, 1988

Was found in two localities in the upper Kolyma, for localities see the table legend.

Thymoites bellissimus (L. Koch, 1879)

Trans-Palaearctic boreal range. One or more species with similar epigynes occur in north-east Siberia. There are at least two morphs, one specific for the stone hills and fields in northern Cisokhotia and Kolyma, as well as in Amur River and Karelia, and the other is known only from Kolyma area. The species lives in the *Chosenia* belt forests along small rivers.

Thymoites oleatus (L. Koch, 1879)

Siberio-Nearctic range [Marusik *et al.*, 2000]. In the upper Kolyma the only female was collected in leaf litter of an alder stand on a north exposed slope (650 m), whereas in Chukotka it is common among scree and stony debris.

Thomisidae

Xysticus albidus Grese, 1908

Trans-Palaearctic species, restricted to mountain tundra scree on southern slopes and the pebbly river banks in the taiga zone. Eurytopic in the tundra zone. In the mountain tundra it is primarily restricted to dry and warm meadows and separate stones.

Xysticus rugosus Buckle et Redner, 1964

Siberio-west Nearctic range. In the upper Kolyma it occurs in the subgoltsy belt, where it is found in xeric snowless habitats, under separate stones or in small-stone fields. In Yukon Territory, the habitats of this species are almost identical.

Titanoecidae

Titanoeca nivalis Simon, 1874

Trans-Palaearctic-west Nearctic range [Marusik *et al.*, 2000]. In the upper Kolyma and northern Cisokhotia it inhabits southern exposed slopes with gravel or semi-shaded but warm aspen and birch stands.

Titanoeca sibirica L. Koch, 1879

Trans-Siberian range Marusik et al., 2000], from the South Urals north-eastward to the Kolyma River mouth and southward to north Mongolia. In the upper Kolyma it occurs on steppe slopes, however in some places it inhabits pebbly river banks. In northern Cisokhotia this species forms high density populations on the seashore scree.

Tetragnathidae

Zygiella dispar (Kulczyński, 1885)

Far East–Nearctic range. In north-east Siberia it occurs on seashore cliffs and rock debris around them.

Spider communities of the major stone debris habitat types of north-east Siberia

The stony deserts

In addition to the petrophilous taxa, the edges of stony deserts are inhabited by mountain tundra and xerophilous species. Usually only a single true wandering spider commonly occupies such habitats, either Sibirocosa kolymensis or S. subsolana (in Chukotka). Another species, Parasyrisca holmi, is restricted to the goltsy but is rare. Occasionally Drassodes neglectus (in the south) and Gnaphosa orites can also be found. Thanatus bungei is quite common. Thanatus kolymensis occasionally occurs at low altitudes (about 1 000 m). Aculepeira carbonarioides, the largest orb-weaver in northeast Siberia, builds its web between stones, usually in small hollows. In the tundra zone this species is primarily restricted to scree. Other inhabitants of the goltsy are Eborilaira alpina, Porrhomma cf. kulczynskii and Procerocymbium sibiricum. In two small sites of the upper Kolyma very different and exotic populations were found: in the first, Chalcoscirtus carbonarius and 'Lepthyphantes' epigynatus predominated, while other species were occasional; in the second site, Hybauchenidium holmi and 'Theridion' thaleri predominated. In Chukotka, in huge stony deserts, Perro tchuktchorum, Clubiona propinqua and Mughiphantes sobrius were found in addition to Sibirocosa subsolana.

The kurums

Surface dwellers were Sibirocosa kolymensis or S. subsolana (in Chukotka), Thanatus bungei, sometimes Philodromus alascensis, Parasyrisca holmi, in addition to Aculepeira carbonarioides.

The south-exposed scree of the taiga zone

Surface dwellers are as follows: (1) wandering species dominants and influents (= common): Acantholycosa aborigenica, A. norvegica, Drassodes neglectus, D. cupreus, Thana-

tus bungei; (2) the jumping spiders, Chalcoscirtus glacialis, C. grishkanae (both rare); (3) the weavers are Lathys alberta and Theridion sibiricum (dominants in the majority of biotopes); the influents: Incestophantes incestoides.

The south-exposed scree of the tundra zone

The most common species are Sibirocosa kolymensis or S. subsolana, Clubiona propinqua, Incestophantes incestoides, Lathys alberta, Pardosa eiseni, Scotinotylus protervus.

An interesting fact regarding stone-affiliated spiders was revealed in the upper Kolyma. Some of the lithobionts and petrophilous spiders have closely related siblings, which live allopatrically in a very different habitat. They can be considered ecological vicariants. They are: *Hybauchenidium holmi – H. aquilonare* (L. Koch, 1879) (the litter of a closed flood plain forest); *Theridion thaleri – T. ohlerti* Thorell, 1870 (dwarf birches, willows and *Vaccinium* in lowlands); *Parasyrisca holmi – P. tyshchenkoi* Ovtsharenko, Platnick et

Table 1.

Spider populations in several stone debris ecosystems in north-east Siberia.

Explanation of the numbers is given in 'Material and methods'.

Dominant categories: D and d = dominant, S = subdominant, C or i = common or influent (abundant), o occasional, R or r = rare. Capital letters are used for calculated abundances and small ones for generalized and subjective estimations.

Occurrence: T = true (obligatory), N = most numerous in stony areas, S = stony debris and separate stones, E = eurybionts, O = occasional.

Таблица 1.

Население пауков некоторых каменистых биотопов на северо-востоке Сибири. Расшифровка точек приведена в 'Material and methods'.

Массовость: D и d = доминанты, S = субдоминанты, C или i = обычные или инфлюэнты, R или r = редкие. Заглавные буквы использованы для расчетных данных, прописные для оценочных данных. Встречаемость: T = исключительно каменистые биотопы (облигатные петробионты), N = наиболее массовы в в каменистых биотопах, S = осыпи или отдельные камни, E = эврибионт, O = случайный.

Таха	Occurrence	-	2 bori	3 igen	4 Fie	5 6 Id Sta	tion	7 K	8 MA (9 10 O S	11 E		13 CH
ARANEIDAE													
Aculepeira carbonarioide	es T	D		D					d			R	d
CLUBIONIDAE Clubiona propingua	Т			С	С			D				D	d
C. praematura	Ė							_				_	i
DICTYNIDAE	_												
Dictyna tyshchenkoi	S												
Lathys alberta	NT	D			С	D		D	İ	S		S	d
GNAPHOSIDAE	N	R						S	:				
Drassodes cupreus D. neglectus	N N	R	S					3	1				2
Gnaphosa similis	N	R	3					C	i				í i
G. orites	N	11		С		R		0	'			R	i
Parasyrisca holmi	TN			Č				R	r				•

Table 1 (continued). Таблица 1 (продолжение).

Таха	Occurrence		2 bori	3 gen	4 Fie	5 Id S	6 Station	7 K	8 MA	9 O	10 S	11 E		13 CH
HAHNIIDAE														
Hahnia glacialis	N		D			С			i					i
LINYPHĬIDAE														
Agyneta birulai	S			С				S	r					
Bathyphantes eumenis	E											S		i
Centromerus pacificus	E	R							r					
Eborilaira alpina	T									S				i
Entelecara sombra	S				С				i					
Erigone arcticola	S											С		i
Erigonoplus minaretifer	S			R		С								
Flagelliphantes flagellife							С							
Lepthyphantes' epigyna														
'L.' nenilini	Ν													i
L.' punctulatus	Т							R				D	R	i
Hybauchenidium holmi	Т				С									
Incestophantes incestoid		R						С	i					i
I. kochiellus	N													i
Islandiana falsifica	?											D		i
Kolymocyba petrophila	T	R												r?
Maso sundevalli	E	R												
Microneta viaria	E	R							i					
Mughiphantes flexilis	N	R												
M. sobrius	Ţ											_		į
Oreoneta leviceps	?											S		i
Oreonetides kolymensis									i					
Perro tchuktchorum	T	_			_	_								į
Poeciloneta pallida	T	С			С	С	_					_		į.
P. petrophila	T						D		i,			D		d
P. tanasevitchi	T								d				П	ا.
P. variegata	N												R	d
Porrhomma borealis	T?									П		П		
P. cf. kulczynskii Dragorogymbiym, cibirio	T?									R		R		:
Procerocymbium sibiricu Saatinatulus alninus	ım T E									_				İ
Scotinotylus alpinus	Ē						S			С				
S. kolymensis	N			D			3		r	D		D	S	٨
S. protervus Tanasevitchia uralensis	T	D		D					ı	ט	П	ט	3	d
Walckenaeria fraudatrix	Ó	D									D		С	i
W. holmi	0		С										C	
Wubanoides fissus	N	С	D				D	R	r		S	С	D	i
LIOCRANIDAE	14	U	D				D	/\	,		0	C	D	,
Agroeca maculata	Т	С												
LYCOSIDAE	•	•												
Acantholycosa aborigen	ica T	С												
A. norvegica	Ť	Č						R						
Sibirocosa kolymensis	Ť	Ŭ		D					i					
S. subsolana	Ť			_					•				R	d
Pardosa eiseni	Ė			С					r					i
PHILODROMIDAE	_			-					•					•
Philodromus alascensis	E		С						i					
P. cespitum	Ō		-				R		•					
Thanatus bungei	EN	R	D					S	i					i
T. kolymensis	T	•	_		С			_	•					•
SALTICIDAE	•				_									
Chalcoscirtus carbonarii	us T													
C. glacialis	S	R				С								
						_								
C. grishkanae	Т	С							i					

Table 1 (continued). Таблица 1 (продолжение).

Taxa	Occurrenc		2	-	•	5	6	7	8	9	10	11	12	13
-		Α	bori	gen l	Field	d S	tation	K	MA	0	S	Е	Е	СН
THERIDIIDAE														
Enoplognatha serratosig	nata S								i					
Theridion sibiricum	TS	D						D	d		D			
'T.' thaleri	Т				D			R						
Thymoites bellissimus	Т	R						R	d		С			
T. oleatus	0?													i
THOMISIDAE														
Xysticus albidus	E					D								i
X. rugosus	T													
TITANOECIDAE														
Titanoeca nivalis	S													
T. sibirica	S	С							d					
TETRAGNATHIDAE														
Zygiella dispar	Cliffs								d					

Marusik, 1995 (larch and birch tree trunks, under bark), *Xysticus rugosus – X. sibiricus* Kulczyński, 1908 (under larch bark), *Thanatus kolymensis – T. arcticus* Thorell, 1872 (habitats with thick vegetation, mostly in lowlands); *Chalcoscirtus glacialis – C. hyperboreus* (bogs in the mountain tundras, lichen pillows); *Euophrys proszynskii – E. flavoatra* (Grube, 1861) (the taiga belt, bogs). *Sibirocosa kolymensis* and *S. subsolana* are geographical vicariants.

As is evident from Table 1 and the comments in the species distributions above, stony debris spiders in the taiga zone can be assigned to two groups: mountain dwellers (mountain tundra belt) and those which inhabit the taiga. Species of both groups that reach the tundra zone inhabit the same stony biotopes (or same belt). For example, in Chukotka the dwellers of the mountain tundra belt of the upper Kolyma, viz., Clubiona propinqua, Aculepeira carbonarioides, Procerocymbium sibiricum, 'Lepthyphantes' punctulatus, Eborilaira alpina and Dictyna tyshchenkoi are sympatric with dwellers of the taiga belt: Lathys alberta, Incestophantes incestoides, Poeciloneta petrophila, P. pallida, Wubanoides fissus, etc. Correspondingly, there is no subdivision among stone debris dwellers according to altitude in the tundra zone of Chukotka.

Not all the species, which inhabit the mountain stony debris in Kolyma Area, occur (i.e., were found) in Chukotka, namely: Sibirocosa kolymensis, Parasyrisca holmi, Hybauchenidium holmi, 'Lepthyphantes' epigynatus, Theri-

dion thaleri, Chalcoscirtus carbonarius, Thanatus kolymensis. However, many species from the taiga belt are known in Chukotka. Among the characteristic (common and widespread) species of the taiga zone, only *Theridion sibiri*cum does not inhabit scree of the tundra zone.

Harvestman and spiders associated with the stony debris near Kluane Lake, Yukon Territory. Explanation of site numbers is given below.

Таблица 2. Сенокосец и пауки, связанные с каменистыми сообществами в окрестностях оз. Клюэйн, территория Юкон. Номера биотопов расшифрованы ниже

Species/site	1	2	3	4	5
Liopilio yukon	5				50
Lathys alberta	120	18	2	27	10
Enoplognatha intrepida	10	2		7	40
Theridion petraeum	2	6	8		
Thymoites oleatus	1				
Steatoda borealis	17	3			1
'Lepthyphantes' sp.	9	11			2
Scotinella pugnata	3	16			
Pardosa mackenziana	20				
P. albomaculata		2			
Aculepeira carbonarioide	es	3			
Steatoda albomaculata		4			
Drassodes neglectus		3			
Chalcoscirtus glacialis			3		
Terralonus mylothrus			24		
Xysticus deichmanni			1		
Scotinotylus alpinus				1	2
S. protervus					3
Poeciloneta variegata					2
Porrhomma sp.					2
Bathyphantes eumenis					2 3 2 2 2
Gnaphosa muscorum					6 2 5
G. orites					2
Erigoninae gen. sp. 1					5

Spiders of the rock debris of Yukon Territory

Spiders associated with stony debris around Kluane Lake were examined (Table 2). Additionally, a small collection was made near Carmacks Town. Unlike north-east Siberia but similar to European stony debris, the Yukon stony debris ecosystems studied were formed in regions lacking permafrost. In all cases, the spider species studied inhabited both surface and bottom layers. Most of the spiders were studied in the following five stony habitats around the south-east corner of Kluane Lake:

- 1) rock debris in a poplar grove (without continuous soil cover) on the bank (900 m);
- 2) open (unshaded) rock debris above site 1 and under cliff (950 m);
 - 3) cliff and cliff scree (1000-1300 m);
 - 4) slatestone scree (1900 m);
- 5) klippe, klippe debris and moist scree in the mountain tundra (1 850 m)

In other stony debris sites around Kluane Lake, which are not shown in Table 2, *Xysticus rugosus*, '*Lepthyphantes*' alpinus (Emerton, 1882) and *Scotinotylus majesticus* (Chamberlin et Ivie, 1947) were also collected. The most exciting observation in Kluane Lake happened to be the similarity between the lake-shore and the high mountain scree fauna, and the absence of many species in the intermediate zone. Such a situation can apparently be explained by the similarity of the moisture in low and upland stone debris; at least the ground beneath the stones was wet both in low and upland sites. Rock debris of the steep south slope with steppe vegetation was dry and shallow.

As can be seen from Tables 1 and 2, the similarity of species composition between northeast Asian and north-west American stony debris faunas is quite high (c. 50%), viz., of the 23 Canadian species, 12 are also recorded in Magadan Area. It should be noted that the habitat preferences of *Bathyphantes eumenis* are different in different parts of Beringia. In northeast Siberia it lives in herbaceous vegetation or the moraine pebbles in tundra, while in Yukon Territory it occurs in the deep and moist layers of rock debris.

In the moist pebble moraine scree near Carmacks, a new species of *Poeciloneta* was found together with *Lepthyphantes* sp. The former species is closely related to the north-east Siberian *P. tanasevitchi* and occupies the same habitats.

Discussion

The similarity between the spider faunas of central European and north-east Siberian stony debris habitats is very weak at species level. There are only two species in common: Acantholycosa norvegica (a true lithobiont) and Maso sundevalli (a litter dweller, occasionally occurring in stony habitats). However, there are more common species in the two faunas (central Europe and the upper Kolyma) like *Bathyphantes* simillimus (L. Koch, 1879), Drassodes cupreus, Diplocentria bidentata (Emerton, 1882), Microneta viaria, Philodromus cespitum and Poeciloneta variegata. B. simillimus and D. bidentata are scree dwellers in central Europe only [Růžička, pers. comm.]. D. bidentata inhabits only the lower (bottom) margins of scree, whereas in Siberia it is never associated with stones

There are at least two cases of vicariance among stone dwellers between European and east Siberian screes: *Wubanoides fissus* and *W. uralensis* (Pakhorukov, 1981) (central and west Siberia, south Germany and Czech Republic) and *Xysticus rugosus* (Siberia and north-west America) and *X. bonneti* Denis, 1935 (south-west Siberia, the Urals and south European Mts).

The family composition of the two faunas is also different. On the one hand, the Czechian scree fauna includes more families (Amaurobiidae, Pholcidae, Agelenidae, Nesticidae, Tetragnathidae), whereas the diversity of the erigonine species is much lower. On the other hand, three families such as Titanoecidae, Philodromidae and Hahniidae, which were found in the Siberian screes, have not been recorded as scree dwellers in the Czech Republic [Růžička, 1988, 1990b; Růžička *et al.*, 1989].

A comparison of the beetle fauna of Czechian stony debris [Růžička *et al.*, 1989] and that of north-east Siberia shows at least five common species [A.S. Ryabukhin, pers. comm.].

Taxonomic positions of some Siberian Aleocharinae (Staphylinidae) are unclear. All the common rove and carrion beetle species: *Omalium caesum*, *Scyodrepoides watsoni*, *Quedius limbatus*, *Tachinus rufipennis* and *Nicrophorus vespilloides* are litter and carcass dwellers in Siberia and are not connected to the stony debris habitats.

The stony debris fauna of north-east Siberia, as it is seen from Table 1 and in V.Růžička's papers, is more diverse (69 species in Table 1 [33 without occasional] and 55 [28 without occasional] inRůžička[1986]). It is worth mentioning that the similarity between the lithobiont spider faunas of north-east Siberia (particularly the upper Kolyma) and the Czech Republic (3%) is distinctly lower than that of the total araneofaunas: 21% (18% upper Kolyma—Czech Republic).

The faunas of Scandinavia and north-east Siberia are more similar [cf. Marusik, 1986]. In addition to D. cupreus and A. norvegica, there are some more common species: Thymoites bellissimus, 'Lepthyphantes' punctulatus, Gnaphosa orites and some other common or rare species. A further interesting conclusion can be drawn from reviewing the north-east Siberian stony debris fauna. Of the 72 petrophilous species, 27 were described recently (from 1985-2003). This reflects the rather poor state of our former knowledge on spiders from stony debris ecosystems. It is worth noting that the percentage of narrow (i.e., confined to a very small particular area) endemics among the petrophilous species (24%) in north-east Siberia is twice that of the whole arachnofauna (about 9% [see Marusik, 1988]). Having only counted the true (exclusive) lithobionts (37 species), the percentage of endemic species restricted to northeast Siberia is as high as 46%.

The two lithobiont faunas of the relatively close geographical regions of north-east Asia and north-west America have more than 50% of their species in common, especially if one merges sibling species. The similarity of the entire araneofaunas of these two areas is approximately 52%.

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