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A SURVEY OF SPIDERS (ARANEAE) WITH HOLARCTIC DISTRIBUTION

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ABSTRACT. Of the 13,800 species distributed in the Holarctic Region only 395 are known both from Eurasia and North America. Of these only 105 species are distributed throughout the whole Holarctic (circum-Holarctic species). In addition, 28 species have an almost complete Holarctic distribution, occurring from Europe to northwestern North America (subcircum-Holarctic species). Species with a circum-Holarctic distribution were found in 13 families. The highest numbers of circum-Holarctic species were in the families Linyphiidae (37), Theridiidae (14), Araneidae (13) and Gnaphosidae (11). The percentage of the circum-Holarctic species among the Holarctic spiders is highest in Philodromidae (2.4%), Araneidae (2.2%), Theridiidae (2.0%) and Tetragnathidae (1.9%). These families encompass mainly herb-bush-tree dwellers. Somewhat unexpectedly it was found that most circum-Holarctic species occupy the boreo-nemoral zone (41%), or may even have a polyzonal range (23%). Twenty-nine species (28%) of the circum-Holarctic spiders have a northern distribution; most of them occurring both in arctic and boreal zones.

Keywords: Holarctic region, circum-Holarctic species, distribution types, zonal distribution, spiders

The Holarctic region, an area covering the Northern Hemisphere approximately north of 25° N, is the largest zoogeographical realm of the Earth. Around 13,800 species of spiders are listed in Platnick's (2004) catalogue as inhabitants of this realm. Without a doubt, the Holarctic is the best studied region in all groups of living organisms.

Most biogeographers divide the Holarctic region into two subunits, Palaearctic and Nearctic, lying in the Old and New World respectively. Among the species of spiders known in the Holarctic, only 395 species (or around 3%) are known from both Palaearctic and Nearctic regions. Most of them are listed in Platnick's (2004) and other catalogues as Holarctic or Cosmopolitan species.

Considering different meanings of the word Holarctic, we wish to stress that in this paper under the term Holarctic species (or distribution, range) or circum-Holarctic species (or distribution, range) we mean species occurring (distributed) throughout the whole or at least most of Eurasia and North America. Many authors consider distribution of species as Holarctic if they are known from two continents, although a species may be known only from one locality in one continent (e.g., Platnick 2004). Holarctic species possibly introduced by man, long ago or more recently, have been treated here like the others, "naturally Holarctic" species.

The longitudinal width of the range of the circum-Holarctic species restricted to boreal or hypoarctic zones is slightly wider than that of species occurring in the nemoral zone (Figs. 1–2), although the real length (in kilometers) is longer in the nemoral zone. The nemoral zone starts in the Palaearctic at the Canary Islands (15°W) and continues to Kamchatka (160°E) (total length of the zone is about 180°); in the Nearctic this zone stretches from about 150°W (Alaska) to about 60°W (Nova Scotia) (length = 90°). Altogether the nemoral zone covers about 270°. The boreal and hypoarctic zones start at about 10°E (Fennoscandia) and continue almost without break to about 40°W (Greenland), and altogether comprise 310°. Species having polyzonal ranges or those that are synantropic have the widest ranges and can occur almost throughout the whole Holarctic.

The goal of this paper is to list all species of spiders which have a wide Holarctic range (either circum- or subcircum-Holarctic). Such a list can be a useful source for many fields

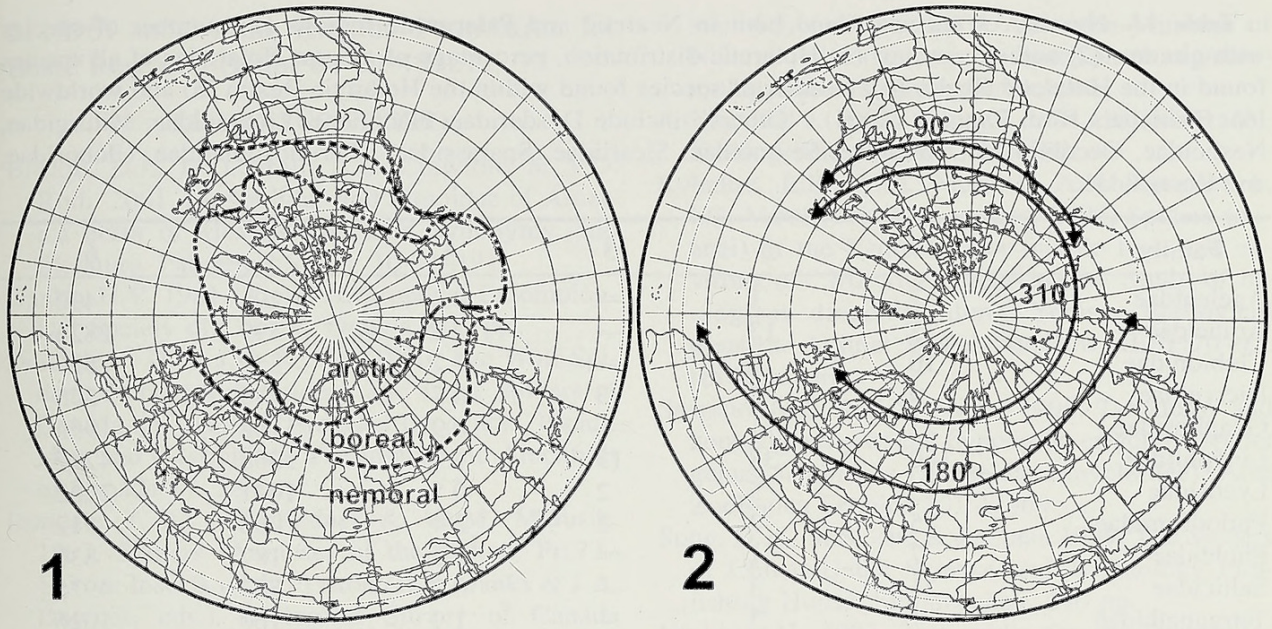

Figure 1–2.—1. Distributional zones in the Holarctic region. 2. The width of nemoral and boreal-hypoarctic zones in the Holarctic region.

of arachnology, like population genetics (variability across the wide range), ecology (comparative ecology and ethology of widespread species), taxonomy (morphological variation across the range), and physiology (study of cold resistance or thermal preferences in different parts of the wide range). Often comparative study, either ecological or morphological, on distant populations of widespread species reveals important differences which can lead to separation of new taxa.

METHODS

The major source of potential Holarctic species is the catalogue of Platnick (2004), from which the species mentioned as Holarctic were chosen. These species were studied using personal knowledge and recent species lists (e.g., Dondale et al. 1997; Marusik et al. 2000; Buckle et al. 2001). Many other publications have also been used, the most important are, in alphabetic order: Dondale & Redner (1990), Levi & Randolph (1975), Logunov (1996), Logunov & Marusik (2001), Marusik (1994), Marusik et al. (1992, 2002a, 2002b), Mikhailov (1997), Rybalov et al. (2002), Saaristo & Eskov (1996), Song et al. (1999) and Yoshida (2003).

The following main distribution types (abbreviations in brackets) have been distinguished (cf. Appendix 1): Arctic = tundra zone (ar); Boreal = taiga or coniferous forest belt (bo); Hypoarctic = arctic + northern taiga + mountain tundra in boreal zone (hy); Nemoral = zone south of boreal: mixed or deciduous forest, steppe, desert (ne); Polyzonal = wide range within above types (po); Montane = mountains in nemoral zone (mo); Cosmopolitan (cos), see also Fig. 1.

RESULTS AND DISCUSSION

Of the more than 13,800 species recorded in the Holarctic Realm only 395 are known in both Eurasia and North America, and only 105 of them are distributed throughout the entire Holarctic, i.e. they are circum-Holarctic. In addition, 28 species have an almost Holarctic distribution, occurring from Europe to northwestern North America, i.e. they are subcircum-Holarctic. This means that less than 1% of all species in the Holarctic region are circum- or subcircum-Holarctic (Table 1). Thus, the number of truly Holarctic species of spiders is much lower than usually estimated (cf. Platnick 2004).

Of the 65 species listed as Holarctic in Prószyński & Staręga (1971) at least 16 are not really Holarctic. On the other hand, the number of species within the Holarctic has subsequently increased considerably due to active research in Siberia and the Nearctic (cf. Marusik et al. 2000). Marusik listed most of the present Holarctic species ten years ago (Ma-

Table 1.—Number of species found both in Nearctic and Palaearctic regions (1), number of species with circum- (2) and subcircum- (3) Holarctic distribution, percentage of circum-Holarctics of all species found in the Holarctic Realm (4), number of species found within the Holarctic Realm (5) and worldwide (6). Basic data from Platnick (2004). "Others" include Dysderidae, Hahniidae, Liocranidae, Miturgidae, Nesticidae, Oecobiidae, Oonopidae, Scytodidae, Sicariidae, Sparassidae, Theridiosomatidae, Uloboridae, and Zorapsidae.

Family	1	2	3	4	5	6
Agelenidae	7	1	—	0.3	295	490
Araneidae	23	13	—	2.2	599	2824
Clubionidae	10	3	—	1.2	259	529
Dictynidae	9	3	3	0.7	446	555
Gnaphosidae	27	11	—	0.9	1162	1955
Linyphiidae	160	38	13	1.3	3003	4247
Lycosidae	25	5	2	0.5	1041	2262
Philodromidae	15	7	2	2.4	286	512
Pholcidae	7	1	—	0.5	187	836
Salticidae	21	3	—	0.2	1382	4975
Tetragnathidae	7	3	—	1.9	160	1026
Theridiidae	45	14	5	2.0	690	2209
Thomisidae	15	3	1	0.5	609	2028
Amaurobiidae	3	—	1	—	444	626
Titanoecidae	1	—	1	—	34	46
Others	21	—	—	—	3189	13302
Total	395	105	28	0.8	13786	38432

rusik 1994); however, nine species have now been added and eleven omitted.

Species occurring both in the New and Old World parts of the Holarctic belong to 28 spider families (Table 1); however, species with circum-Holarctic distribution are known in 13 families only. Two additional families each have one subcircum-Holarctic species.

The following families have most Holarctic species: Linyphiidae (38), Theridiidae (14), Araneidae (13), Gnaphosidae (11), Philodromidae (7) and Lycosidae (5). The percentage of circum-Holarctic species among all the species found in the Holarctic Region, is highest in Philodromidae (2.4%), Araneidae (2.2%), Theridiidae (2.0%) and Tetragnathidae (1.9%) (Table 1). These families encompass mainly herb-bush-tree dwellers. Among genera, the most rich in circum-Holarctic species are *Micaria* (5), *Thanatus* (5) and *Theridion* (6). The last-mentioned genus seems to be paraphyletic, and its six species with circum-Holarctic range belong to three different groups.

We expected that, like in many other groups of living organisms (see Danks 1981), most of the species with a circum-Holarctic distribution would be restricted to the northern (boreal and/or arctic) zones. The main reasons for this expectation were the smaller area and post-glacial history of the boreal, and especially the arctic zones, compared to the nemoral zone. However, it was found that most of circum-Holarctic species occur in the boreo-nemoral zone (41% or 43 species), and many even have a polyzonal range (23% or 24 species).

Among circum-Holarctic species, only 28% (or 29 species) have a northern distribution (arctic, hypoarctic and/or boreal range). Most of them occur both in tundra and boreal zones, and three species are known from the boreal zone only. Among the 28 subcircum-Holarctic species, as many as 16 (57%) have this kind of northern (arctic, hypoarctic and/or boreal) distribution pattern.

The proportion of cosmopolitans among circum-Holarctic species was highest in Theridiidae (4 species). Many species with a cosmopolitan range are absent from Siberia, like *Ostearius melanopygius* (O.P.-Cambridge 1879), *Tenuiphantes tenuis* (Blackwall 1852), *Diplocephalus cristatus* (Blackwall 1833), and two *Oecobius* species.

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Appendix 1.—Species with a circum- and subcircum-Holarctic range.

The distribution types used are: arctic (ar), boreal (bo), hypoarctic (hy), nemoral (ne), polyzonal (po), montane (mo) and cosmopolitan (cos), see also Methods. Species with a subcircum-Holarctic distribution have been marked with an asterisk (*).

Agelenidae 1/0 (circum-Holarctic/subcircum-Holarctic)

Tegenaria domestica (Clerck 1757)–Cos.

Amaurobiidae 0/1

* *Arctobius agelenoides* (Emerton 1919)—ar-bo, unknown in eastern half of the Nearctic.

Araneidae 13/0

Aculepeira carbonarioides (Keyserling 1892)—hy; *A. packardi* (Thorell 1875)—hy-ne; *Araneus diadematus* Clerck 1757—bo-ne; *A. marmoreus* Clerck 1757—bo-ne; *A. nordmanni* (Thorell 1870)—bo-ne; *A. saevus* (L. Koch 1872)–bo-ne; *Araniella displicata* (Hentz 1847)—bo-ne; *A. proxima* (Kulczyński 1885)—bo; *Cercidia prominens* (Westring 1851)—po; *Cyclosa conica* (Pallas 1771)—bo-ne, although absent in NE Siberia (east of Lena river); *Hypsosinga pygmaea* (Sundevall 1831)—po; *Larinioides cornutus* (Clerck 1757)—po; *L. patagiatus* (Clerck 1757)—po.

Clubionidae 3/0

Clubiona kulczynskii Lessert 1905—bo-ne; *C. pal-*

lidula (Clerck 1757)—bo-ne; *C. trivialis* C.L. Koch 1874—bo-ne.

Dictynidae 3/3

* *Arctella lapponica* (Holm 1945)—ar-bo, in Nearctic known only from the North-West; * *Dictyna alaskae* Chamberlin & Ivie 1947—bo, in Nearctic is known from Alaska only; *D. arundinacea* (Linnaeus 1758)—po; *D. major* Menge 1869—po; *Emblyna annulipes* (Blackwall 1846)—bo-ne; * *Hackmania prominula* (Tullgren 1948)—ar-bo, in Nearctic known only from the North-West.

Gnaphosidae 11/0

Gnaphosa microps Holm 1939—hy-bo; *G. muscorum* (L. Koch 1866)—po, absent in NE Siberia and Far East; *G. orites* Chamberlin 1922—hy; *Haplodrassus signifer* (C.L. Koch 1839)—po; *Micaria aenea* Thorell 1871—bo-ne; *M. alpina* L. Koch 1872—hy-bo; *M. pulicaria* (Sundevall 1831)—bo-ne; *M. rossica* Thorell 1875–po; *M. tripunctata* Holm 1978—hy-bo; *Trachyzelotes jaxartensis* (Kroneberg 1875)—steppe-semidesert; *Zelotes puritanus* Chamberlin 1922—disjunctive polyzonal range, restricted to warm and xeric habitats from tundra zone to steppes and mountains.

Linyphiidae 38/13

Agyneta olivacea (Emerton 1882)—hy-ne; * *Allomengea scopigera* (Grube 1861)—bo-ne, in Nearctic restricted to the western half; *Aphileta misera* (O.P.-Cambridge 1882)—bo-ne; *Bathyphantes gracilis* (Blackwall 1841)—bo-ne; *Carorita limnaea* (Crosby & Bishop 1927)—bo; *Centromerus sylvaticus* (Blackwall 1841)—bo-ne; *Cnephalocotes obscurus* (Blackwall 1834)—bo-ne; *Collinsia holmgreni* (Thorell 1872)—hy-bo; *Diplocentria bidentata* (Emerton 1882)—bo-ne; *Diplocentria rectangulata* (Emerton 1915)—bo; *Dismodicus bifrons* (Blackwall 1841)—bo-ne; *Erigone arctica* (White 1852)—ar-bo-mo, represented by series of subspecies, none of which has Holarctic range; *E. atra* Blackwall 1833—po; *E. psychrophila* Thorell 1872—hy; *E. tirolensis* L. Koch 1872—hy (ar-mo); *Estrandia grandeva* (Keyserling 1886)—hy-ne; *Helophora insignis* (Blackwall 1841)—bo-ne; *Hilaira herniosa* (Thorell 1875)—hy-bo-mo; * *H. nubigena* Hull 1911—bo, in Nearctic known from Alaska only; * *Horcotes strandi* (Sytchevskaya 1935)—hy-bo, in Nearctic known from Yukon Territory only; * *Hybauchenidium ferrumequinum* (Grube 1861)—hy, in Nearctic known from Yukon Territory only; * *Hypselistes jacksoni* (O.P.-Cambridge 1902)—hy-ne, in Nearctic known only from Alaska to Utah; *Improphantes complicatus* (Emerton 1882)—bo-mo; * *Islandiana falsifica* (Keyserling 1886)—hy, in Nearctic known from NW part (Alaska to Northwestern Territories, south to British Columbia); *Kaestneria pullata* (O.P.-Cambridge 1863)—bo-ne; "*Lepthyphantes*" *leprosus* (Ohlert 1867)—po, north of 55°N exclusively synantropic; *Macrargus multesimus* (O.P.-Cambridge 1875)—hy-ne; * *Maso sundevalli* (Westring 1851)—bo-ne, in Nearctic known in Alaska only; * *Mecynargus monticola* (Holm 1943)—hy-bo, in Nearctic known only from Western Canada only; *M. paetulus* (O.P.-Cambridge 1875)—bo-ne; *M. sphagnicola* (Holm 1939)—hy-bo, in Nearctic it occurs in Yukon and NW Territories; *Megalepthyphantes nebulosus* (Sundevall 1830)—po, north of 55°N exclusively synantropic; * *Metopobactrus prominulus* (O. P.-Cambridge 1872)—bo-ne, in Nearctic known east of Saskatchewan; *Microlinyphia impigra* (O.P.-Cambridge 1871)—bo-ne; *M. pusilla* (Sundevall 1830)—po; *Microneta viaria* (Blackwall 1841)—po; *Neriene clathrata* (Sundevall 1830)—bo-ne; *N. radiata* (Walckenaer 1841)—bo-ne; *Oreonetides vaginatus* (Thorell 1872)—hy-bo-mo; *Pelecopsis mengei* (Simon 1884)—bo-ne; *Pocadicnemis pumila* (Blackwall 1841)—bo-ne; * *Poeciloneta variegata* (Blackwall 1841)—hy-bo-mo, in Nearctic restricted to the West; * *Semljicola lapponicus* (Holm 1939)—hy, in Nearctic known from Alaska only; *Sisicus apertus* (Holm 1939)—bo-ne; *Thyreostenius parasiticus* (Westring 1851)—bo-ne; * *Tibioplus diversus* (C.L. Koch 1879)—bo, in Nearctic known from Alaska and Yukon Territory; *Tiso aestivus* (L. Koch 1872)—hy-bo, in Nearctic known from Yukon Territory and Greenland; * *Walckenaeria capito* (Westring 1861)—bo-ne, in Nearctic known from Ontario only; *W. cuspidata* Blackwall 1833—bo-ne; *W. karpinskii* (O.P.-Cambridge 1837)—ar-bo-mo; *W. lepida* (Kulczyński 1885)—bo-ne.

Lycosidae 5/2

Alopecosa aculeata (Clerck 1757)—po; *Pardosa hyperborea* (Thorell 1872)—hy-bo, absent between Lena River and Alaska; * *P. lapponica* (Thorell 1872)—hy-bo-mo, in Nearctic unknown west of the Hudson Bay; * *P. palustris* (Linnaeus 1758)—bo-ne, in Nearctic known from Alaska, Yukon Territory and northern British Columbia; *Pirata piraticus* (Clerck 1757)—po; "*Tricca*" *alpigena* (Dolleschall 1852)—hy-bo-mo; *Trochosa terricola* Thorell 1856—bo-ne, in Siberia found only in areas free of permafrost, and rather rare in South Siberia.

Philodromidae 7/2

Philodromus cespitum (Walckenaer 1802)—po; *P. rufus* Walckenaer 1826—bo-ne; *Thanatus arcti-*

cus Thorell 1872—ar-bo-mo (=?hy), in Siberia it has polyzonal range, in Scandinavia and Nearctic it is restricted to northern taiga and tundra; * *T. coloradensis* Keyserling 1880—bo-mo, this species has disjunctions between Alps and Siberia (Marusik et al. 2000); *T. formicinus* (Clerck 1757)—bo-ne; *T. striatus* C.L. Koch 1845—po; * *T. vulgaris* Simon 1870—ne (?), in Siberia it has disjunction between Xinjiang and Far East; *Tibellus maritimus* (Menge 1875)—bo-ne; *T. oblongus* (Walckenaer 1802)—bo-ne.

Pholcidae 1/0

Pholcus phalangioides (Fuesslin 1775)—Cos. In northern Palaearctic it is exclusively synantropic species, and most probably absent in South Siberia.

Salticidae 3/0

Chalcoscirtus alpicola (L.Koch 1876)—disjunctive hy-bo-mo range, in Eurasia known from Alps and Siberia east of Ural; *Salticus scenicus* (Clerck 1757)—bo-ne; *Sitticus ranieri* Peckham & Peckham 1909—hy-bo.

Tetragnathidae 3/0

Pachygnatha clercki Sundevall 1823—po; *Tetragnatha dearmata* Thorell 1873—bo-ne; *T. extensa* (Linnaeus 1758)—po.

Theridiidae 14/5

Achaearanea tepidariorum (C.L. Koch 1841)—Cos, in northern Holarctic it is a synantropic species; *Crustulina sticta* (O.P.-Cambridge 1861)—bo-ne; *Enoplognatha caricis* (Fickert 1876)—bo-ne; *Euryopis saukea* Levi 1951—po (?), until 1972 it was known from the Nearctic and Poland only. Later it was found in many places in Nearctic, Europe and Asia; * *Neottiura bimaculata* (Linnaeus 1757)—bo-ne, in Nearctic known from British Columbia and Washington State; * *Robertus lividus* (Blackwall 1836)—bo-ne, in Nearctic known from Alaska only; * *R. lyrifer* Holm 1939—hy-mo, in Nearctic know from Alaska only; *Rugathodes aurantius* (Emerton 1915)—bo; *Steatoda albomaculata* (De Geer 1778)—po; * *S. bipunctata* (Linnaeus 1758)—bo-ne, in Nearctic known from Ontario to Newfoundland; *S. grossa* (C.L. Koch 1838)—Cos, in northern Eurasia it is an exclusively synantropic species; *S. triangulosa* (Walckenaer 1802)—Cos; * *Theridion impressum* L. Koch 1881—po, in Nearctic known from Alaska to western Northwest Territories and southward to northern Alberta; *T. montanum* Emerton 1882—bo-ne; *T. ohlerti* (Thorell 1870)—hy-bo-mo; *T. petraeum* L. Koch 1872—bo-ne; *T. pictum* (Walckenaer 1802)—bo-ne; *T. varians* (Hahn 1833)—bo-ne; *Theridula gonygaster* (Simon 1873)—Cos, in Palaearctic disjunctive distribution: in Asia known from Caucasus, Guangxi and Sichuan and Japan; in Nearctic known from Arizona and Florida.

Thomisidae 3/1

Misumena vatia (Clerck 1757)—po; * *Ozyptila arctica* Kulczyński 1908—hy-mo, in Nearctic known from Alaska to western Northwest Territories, south to northern British Columbia; *Xysticus luctuosus* (Blackwall 1836)—bo-ne; *X. obscurus* Collet 1877—bo-mo.

Titanoecidae 0/1

* *Titanoeca nivalis* Simon 1874—bo-mo, in Nearctic restricted to the western half.