Distribution patterns of wolf spiders (Araneae: Lycosidae) along a transect from Greece to the Czech Republic

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ABSTRACT Contrib. Nat. Hist. 12: 315–340.

Recent national lists of lycosid spiders were analysed along a transect leading from the Mediterranean to Central Europe (GR – CZ). This transect follows the probable direction of postglacial dispersal of lowland species. In total, 99 lycosid species were listed in the territory of the transect, 67 of which are lowland species whose ranges, contrary to those of the montane, boreo-montane, and euryzonal species, expanded into Central Europe during the climatic optimum of the Holocene (except for the species of the Pannonian refuge). Particular attention was paid to 34 lowland species, which, dispersing from the Bulgarian Submediterranean Refuge, colonised the Central European Temperate zone lying north of the limit of the Submediterranean. In addition, the northern limit of the above-mentioned refuge was crossed by 9 Submediterranean species which did not expand as far as the northern limit of the Submediterranean. The natural division into five territories according to the distribution patterns of the lowland species is described and illustrated.

SUMMARY

Information on 99 lycosid species ascertained in the territory of the transect under study (GR, BG, RO, H, SK, CZ) was gleaned from an analysis of recent national lists of these countries. Of these, 67 were lowland species whose ranges may show, during advanced Holocene climate, tendencies towards expanding from temporary refuges. 32 species were montane and boreo-montane species whose ranges were most extensive at the beginning of the postglacial period but show various restriction in the recent climate. Three species are euryzonal, occurring permanently in all basic climatic zones of Europe. In agreement with the generally valid climatic division, the transect under study was found to consist of five characteristic territories, distinguishable from one another by the presence of certain lowland species (Map 1):

The Greek Mediterranean Refuge (GMR) is characterised by the occurrence of 16 Mediterranean species; the extra-Mediterranean species show only marginal occurrence.

The Bulgarian Submediterranean Refuge (BSR) is inhabited by all lowland species found in the Greek Mediterranean Refuge and, moreover, by species from other parts of Mediterranean or the neighbouring Caspian refuges. Considering the territory of the transect, 14 stationary species did not expand over the northern limit of the BSR. The remaining species emigrated in a northward direction. Of these, the 9 Submediterranean ones did not go over the northern limit of the Submediterranean, whereas 34 Temperate species did so.

The Romanian Intermediate Territory (RIT) between the BSR and the Pannonian Submediterranean Refuge is characterised by the occurrence of 4 species additional to the group of 34 Temperate ones.

The Pannonian Submediterranean Refuge (PSR) is characterized, first of all, by two species immediately tied to this refuge. Moreover, its northwestern part is inhabited by three Atlantic species.

The Central European Temperate Zone (CTZ) lacks Submediterranean species. Besides species tolerating the Temperate climate (34+4), there is the important presence of two Atlantic species, particularly in the west of CZ.

The 34 Temperate species that crossed the northern limit of the Submediterranean from the Bulgarian Submediterranean Refuge are of great importance for the transect under study. A document is available of the expansion of *L. singoriensis* from the Bulgarian Submediterranean Refuge up to the northern limit of the Submediterranean in 1888–1950. The environmental requirements of the Temperate and Submediterranean spider species expanding from BSR are in full agreement with data on the expansion of molluscs, obtained by using paleontological methods. In either case the expanding species were tied to non-woodland habitats. In the second part of the Holocene, their expansion was apparently facilitated, besides optimum climatic conditions, mainly by anthropogenic landscape transformation.

Introduction

In memory of Professor Dr. Konrad Thaler (Innsbruck), outstanding arachnologist and my close friend and colleague.

As early as in the beginning of the 20th century, the high abundance of lycosids in the epigeic fauna of most Central European habitats stimulated the implementation of an important ecological and zoogeographic project in the territory of Germany (Dahl 1908). It was confirmed in earliest papers based

Map 1. Transect divided into natural territories according to the distribution patterns of wolf spiders (abbreviations in main text). Inset: Countries lying on the selected transect.

on mater-ial readily collected in pitfall traps (e.g. Tretzel 1952). In 1970–1982, 41.8% of all spider species collected in Bohemia by applying this collecting method were species of the family Lycosidae (Buchar 1995). The easy way of collecting lycosid spiders, however, did not invariably result in unequivocal development of knowledge. Often there arose numerous synonyms as well as homonyms. As late as in the second half of the 20th century, there appeared modern manuals permitting an integral species identification. They pertained, e.g., to the genera *Arctosa* (Lugetti & Tongiorgi 1965, 1966), *Alopecosa* (Lugetti & Tongiorgi 1969), *Pardosa* (Tongiorgi 1966a,b, Holm & Kronestedt 1970), and *Trochosa* (Engelhardt 1964). Subsequent papers differentiated hitherto

neglected cryptic species (Cordes & von Helversen 1990, Kronestedt 1990, Töpfer-Hofmann & al. 2000) or, on the contrary, pointed out widely used yet invalid names, e.g. *Pirata moravicus* (Michelucci & Tongiorgi 1975), *Pardosa strigillata* (Buchar & Thaler 2002). The problem of homonyms and mutual mistaking of related species are the topics of papers by e.g. Buchar & Thaler (2004) and Buchar & al. (2006).

Moreover, it is interesting to note that in the Mediterranean fauna the lycosid spiders do not constitute a similarly important component of the epigeic fauna as they do in Central Europe (Thaler & al. 2000), and that they may be almost absent from certain types of xerothermic habitats (Chatzaki & al. 1998). In contrast, actual and comprehensive national lists of species of the family Lycosidae are available at present in all countries lying on the characteristic transect from the Greek Mediterranean up to the Central European Czech Republic (GR, BG, RO, H, SK, CZ, cf. Map 1). The transect corresponds with the traditional idea of the directions along which the thermophilous fauna dispersed from southern refuges to Central Europe during the Holocene (Mařan 1965, Ložek 1982). The fact that the transect under analysis does not comprise the territories of Serbia and Macedonia is due to the much lower degree of knowledge of their lycosid faunae (Deltshev & al. 2003).

The author himself participated in field investigations in the territories of five of the above countries: besides CZ (Buchar 1995), above all SK (Buchar 1999), BG (Buchar 1968), and GR (Thaler & al. 2000) and, to a smaller extent, also H.

The present paper contains an analysis of the recent distribution of lycosid species along the transect, particularly regarding the known division of the concerned part of Europe into the Mediterranean, Submediterranean, and Temperate zones. Main attention was paid to lowland species whose ranges expand in a south-north direction, whereas the montane and boreo-montane faunae were only studied marginally, as their history is quite diverging in the territory of Europe. Their expanding Central European ranges followed the retreating glaciation and at present the Central European parts of their ranges are distinctly disjunctive. In detail, these relationships have been documented by molecular phylogenetic methods on the example of populations of the *Pardosa saltuaria* group (Muster & Berendonk 2006).

This paper is based on the concept of faunal centres (de Lattin 1967: 322), which, at the same time, represent a refuge system of the thermophilous Palaearctic fauna from which, in each interglacial period as well as in the Holocene, many species dispersed to regions being not under influence of glaciation. With its southern end, the transect reaches the secondary Ponto-Mediterranean and Cretan faunal centres of the primary Mediterranean one.

The nearest Caspian primary centre lies south of the Caucasus, between the Black Sea and the Caspian Sea. Further centres, continuing up to the east of the Asian continent, show no more immediate effects on the fauna of the present transect, save for species showing a polycentric character, such as *Pardosa lugubris* with its extensive trans-Palearctic range. Species that did not expand beyond the limits of the refuges are termed stationary. Besides the basic de Lattin system of refuges, the fauna of the transect is affected by Atlantic species (whose centres lie at the Atlantic coast) and Pannonian species (most of whose centres lie directly in the territory of the transect).

Methods

It was necessary to adapt the national lists so that they are mutually comparable and fit for final statistical processing.

In the first stage, the adaptation consisted in replacing all subspecific names by specific ones, in eliminating all species names marked with a question mark (?) or otherwise considered doubtful by the authors of the lists. Besides, the names of those species which, in subsequent taxonomic revisions, appeared to be synonyms, or their presence in a given territory was found to be highly improbable, were left out. On the other hand, the national lists were completed by names of species recorded in a given territory after the publication of the respective list. See review of adaptation done in national lists.

In the next stage of adaptation of the national lists, lowland species were differentiated from montane and/or euryzonal ones.

The relationships between the lowland species faunae inhabiting different natural parts of the transect were expressed by means of Jaccard's similarity index (S), where a = number of species in the larger fauna, b = number in the smaller fauna, c = number of commonly occurring species:
$S\ (\%) = 100\ c / (a + b + c)$.

Abbreviations used to denote the natural parts of the transect (Map 1):

GMR	Greek Mediterranean Refuge (central and southern Greece and its islands including Crete)
BSR	Bulgarian Submediterranean Refuge (northern GR + BG + Dobruja)
RIT	Romanian Intermediate territory between BSR and PSR (RO without Dobruja)
PSR	Pannonian Submediterranean Refuge (H + southern parts of SK and CZ)
CTZ	Central European Temperate Zone (northern parts of CZ + SK).

Abbreviations of the generic names of Lycosidae:

Ac. *Acantholycosa*
A. *Alopecosa*
Ar. *Arctosa*
Au. *Aulonia*
G. *Geolycosa*
Ho. *Hogna*
H. *Hygrolycosa*
L. *Lycosa*
P. *Pardosa*
Pi. *Pirata*
Tr. *Tricca* (this original generic name for *Tricca lutetiana* has been retained after Buchar & Thaler 1995)
T. *Trochosa*
X. *Xerolycosa*

All species are listed alphabetically. For this reason the abbreviations of generic names may only be used for the first representative of any genus. In the text that follows a list, the specific names may be given without the generic abbreviations.

(Mat) unpublished data given in Index 2.

Material

Review of national lists

Greece (GR): 55 species. Most of them from Bosmans & Chatzaki (2005), who list 65 specific and 2 subspecific names.

For the purpose of the present paper, two subspecific names (*P. proxima poetica* Simon, 1876 and *P. tatarica saturatior* Caporiacco, 1948) cannot be used, as they lack exact taxonomic definition. The same holds true for the names of 6 species (*L. narbonensis, T. robusta, T. ruricola, Ho. graeca, Megarctosa naccai, H. strandi*) whose actual occurrence was doubted by the authors themselves, and for the synonyms of 4 species that appear in the paper cited together with their valid names: *A. fuscipes* = *A. pentheri* and *P. invenusta* = *Ar. leopardus* (see Thaler & al. 2000), *P. tatarica* = *P. atomaria* (see Buchar & Thaler 2002), *Ar. latithorax* = *Ar. variana* (see Buchar & Thaler

2004). Finally, it is difficult to use the quite isolated find of *Wadicosa fidelis* in the island of Rhodes. The nearest European localities lie in the Iberian Peninsula and southern France. The species is absent also from the recent collections made from Sardinia down to the southern coast of Turkey. Similarly, it is necessary to exclude the isolated old record of *P. nigriceps,* the species being unknown so far in Bulgaria and Serbia (Deltshev & al. 2003), as this is one of the species characteristic of western Europe and inhabiting a considerably limited area. The only historic record comes from the north of Greece, from where numerous recent data are available (Wolf 2003), yet do not include this species.

In all, Bosmans & Chatzaki (2005) yield 53 useful specific names to which it is necessary to add two more names not given in this monograph, viz. *A. kalavrita* (Buchar 2000) and *P. cribrata* (Mat).

Bulgaria (BG): 70 species, all from the paper by Deltshev & Blagoev (1995). This paper contains 75 names, the following of which are provided with a question mark and have not been used for the purpose of the present analysis: *A. fabrilis, Ar. figurata, Ar. variana* (sensu Lugetti & Tongiorgi 1965), *P. pontica. P. roscai = P. cribrata* (see Fuhn & Niculescu-Burlacu 1971). The following names have been corrected: *P. atomaria* for *P. tatarica* (after Buchar & Thaler 2002), *A. mariae* for *A. striatipes* (after Buchar & Thaler 2004), and *Ar. variana* for *Ar. latithorax* (after Buchar & al. 2006).

Romania (RO): 77 species. The main source is the revised list by Weiss & Petrisor (1999) which contains 81 names. Three of these (*Ac. norvegica, Ar. strandi, P. schenkeli*) are provided with a question mark and therefore have not been used in the present study, the same goes for *A. striatipes,* a species vicarious with *A. mariae* (see Buchar & Thaler 2004). Furthermore, it is highly improbable that *A. similis* does occur in the north of Romania, as the nearest localities of its revised occurrence are found in the area of the town Split on the Adriatic coast (Buchar & al. 2006). The subspecific name *P. cribrata roscai* has been replaced by *P. cribrata*. The remaining 76 species were supplemented by *P. italica,* a species included in the fauna of Romania (Fuhn & Niculescu-Burlacu 1971) after having been found in the SE part of Romania (Mat).

Hungary (H): 55 species. The main source is the paper by Samu & Szinetar (1999), containing 54 specific names, of which only *A. striatipes* may be problematic (see Buchar & Thaler 2004). Besides, another two species have recently been published from Hungary, viz., *A. psammophila* (Szinetar & al. 2005) and *P. maisa* (Szinetar & Guitprecht 2001).

Note: Dr. C. Szinetar (Szombathely) showed me some new species of the genus *Trebacosa* collected in H.

Slovakia (SK): 66 species. The list of Slovakian species (Gajdoš & al., 1999) comprises 69 names, from which *A. striatipes* has been removed on the basis of a discussion with Mgr. J. Svatoň (Buchar & Thaler 2004), the same applies to four names listed with a question mark: *A. cronebergi*, *A. reimoseri*, *P. kratochvili*, *P. poecila*. On the other hand, two more species, *P. fulvipes* and *A. psammophila* have been added (Kronestedt 1999a, Buchar 2000).

Czech Republic (CZ): 62 species. The Czech list comprises 62 specific and one subspecific names (Buchar & Růžička 2002), two of which have to be removed: *A. mariae* (misidentification, see Buchar & Thaler 2004) and *Al. singoriensis* (not found after 1950). The subspecific name *Ar. alpigena lamperti* has been replaced by *Ar. lamperti* (after Almquist 2005). After the list had been published, the occurrence of *P. agricola* was documented (Majkus 2003).

In total, 99 lycosid species have been considered to occur in the territory of the transect (Index 1).

Altitudinal and latitudinal zonation

From these given species, the euryzonal ones differ in occurring in all three basic climatic zones of Europe, and it is assumed that they dispersed in this way in all Pleistocene periods. While two of the three euryzonal species (*Ar. cinerea, Pi. piraticus*) show continuous ranges and occur in all parts of Europe, the third one (*A. fabrilis*) has been found to occur only sporadically. The montane and boreo-montane species alike prefer higher altitudes and latitudes. They dispersed mainly during the colder periods of the glacial cycle. Most European montane species can be considered to be endemic to the Alpine mountain system (in the sense of Ozenda 1988). The lowland species on the the other hand prefer low altitudes and disperse during the contemporary warm part of the glacial cycle. Their recent distribution expresses the present development of faunal genesis.

Greece (GR): After montane and boreo-montane species (*A. aculeata, dryada, kalavrita, P. albatula, blanda, drenskii, olympica, pertinax, riparia, tasevi, Pi. knorri*) and two euryzonal ones have been removed, there remain 42 lowland species. Sixteen of those have recently been confirmed to occur south of the

Corinthian Canal: *A. albofasciata, pentheri, Ar. leopardus, variana, tbilisiensis, G. vultuosa, Ho. radiata, L. praegrandis, P. atomaria, alacris, cribrata* (Mat), *hortensis* (Mat), *luctinosa* (Mat), *proxima* (which in this case it is probably a complex of several cryptic species), *Pi. latitans, T. hispanica.*
The remaining species penetrate from the north down to central GR: *A. accentuata, cuneata, cursor, inquilina, pulverulenta, solitaria, sulzeri, trabalis, Ar. maculata, perita, Au. albimana, kratochvili, P. agrestis, agricola, amentata, bifasciata, lugubris, morosa, nebulosa, prativaga, pullata, vittata, Pi. hygrophilus, piscatorius, T. terricola, X. nemoralis.* Mostly these species are reported to occur in the northern frontier regions.

Bulgaria (BG): Removing from the list two euryzonal and 12 montane and boreo-montane species (*A. aculeata, pinetorum, P. albatula, blanda, drenskii, ferruginea, incerta, mixta, nigra, riparia, tasevi, Pi. knorri*), there remain 56 lowland species for the present analysis. Most of them (41 spp.) are shared with Greece (only *Au. kratochvili* is not included in the Bulgarian list). Moreover, there occur the following 15 lowland species: *A. etrusca, mariae, taeniopus, Ar. stigmosa, L. sigoriensis, P. italica, monticola, paludicola, palustris, pseudostrigillata, Pi. tenuitarsis, Tr. lutetiana, T. robusta, ruricola, X. miniata.*

Romania (RO): Three euryzonal and 20 montane and boreo-montane species (*Ac. lignaria, A. aculeata, pinetorum, taeniata, Ar. lamperti, P. albatula, blanda, cincta, ferruginea, mixta, nigra, riparia, saltuaria, sordidata, sphagnicola, tasevi, wagleri, Pi. insularis, knorri, uliginosus*) and five species living only off the Bulgarian frontier (*A. albofasciata, taeniopus, P. cribrata, italica, vittata*) have been removed from the list, the remaining 49 lowland species occurring in most of the territory of Romania. They include, on the one hand, 43 species shared with Bulgaria and, on the other, six species discovered in RO for the first time during the present transect analysis (*A. schmidti, Ar. figurata, H. rubrofasciata, P. baehrorum, nigriceps, T. spinipalpis*).

The species shared with Bulgaria can be divided into three groups:

Eight of the 16 species enumerated as typical representatives of Mediterranean species occurring all over the Greek territory: *Ar. leopardus, G. vultuosa, Ho. radiata, P. alacris, hortensis, luctinosa, proxima, Pi. latitans.*

25 species penetrating to the north of Greece from Bulgaria. Only *P. vittata* does not occur among these species.

Eleven of the 15 lowland species, reported as newly discovered during the present transect analysis in the territory of Bulgaria. Only four of these species are absent from the RO list: *A. etrusca, taeniopus, P. italica, pseudostrigillata.*

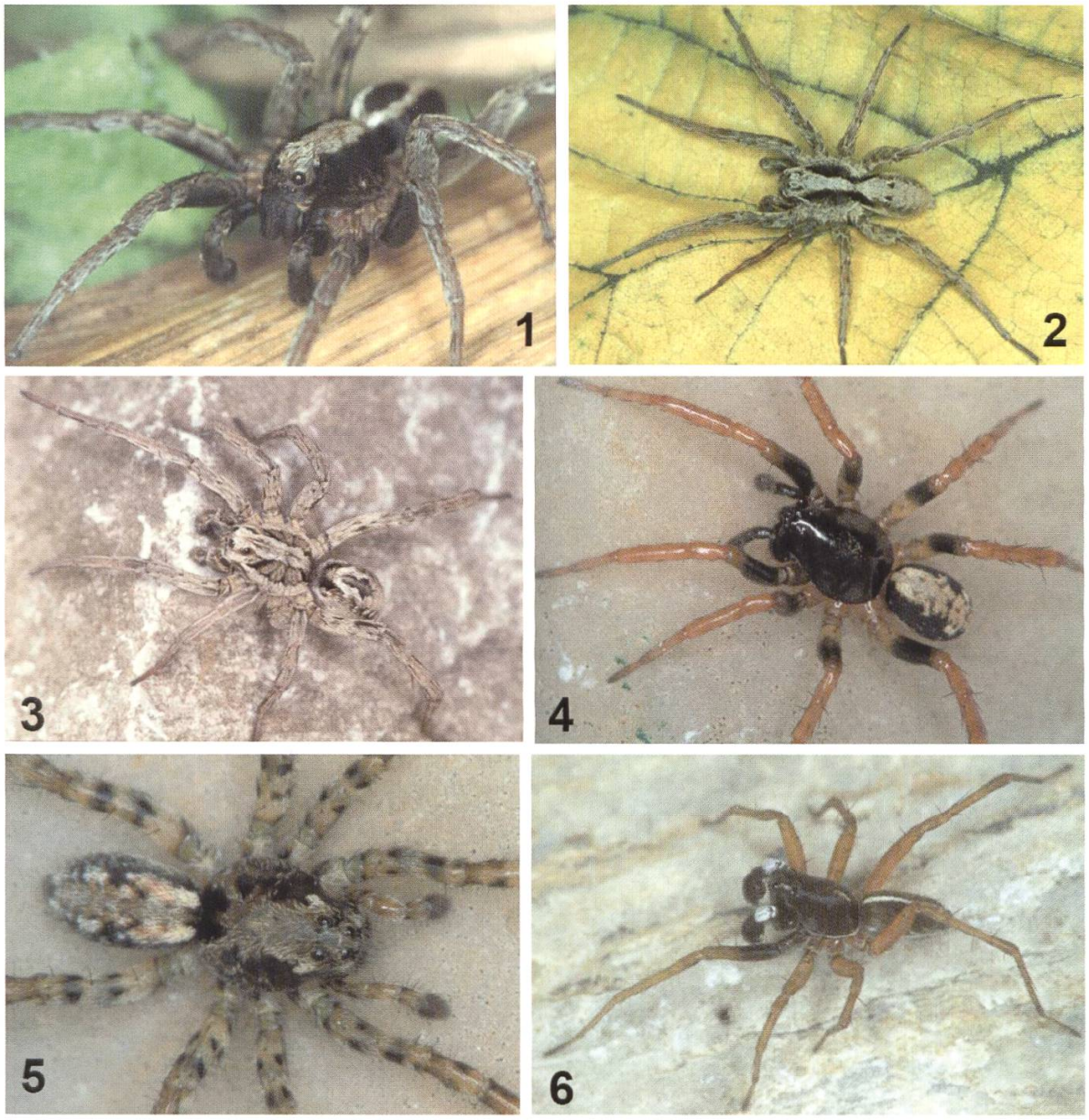
It is interesting to note that none of the species of the Pannonian refuge have been discovered so far in the west of RO, adjacent to Pannonia.

Hungary (H): Three euryzonal and four montane and boreo-montane species (*A. aculeata, P. riparia, Pi. knorri, uliginosus*) have been removed from the national list. Their low number is due to the absence of high mountains in H. There remain 48 lowland species. Of the 49 Romanian lowland species mentioned above, four are missing in H (*Ar. stigmosa, P. baehrorum, luctinosa, nigriceps*), but another three have been added (*A. psammophila, P. cribrata* and *maisa*).

The territories of CZ and SK represent the northern boundary of the Submediterranean zone, dividing the two countries into the southern Pannonian zone and the northern Central European zone. Thus, the account of lowland species will be based on these two zones rather than the territories of the two countries.

The territory of CZ houses 62, that of SK 66 species; 56 species are shared, the number of species occurring in the two countries totalling 72. Of them, three are euryzonal and 18 are montane and boreo-montane species (*Ac. lignaria, norvegica, A. aculeata, pinetorum, taeniata, Ar. lamperti, P. albatula, ferruginea, fulvipes, hyperborea, nigra, riparia, saltuaria, sordidata, sphagnicola, wagleri, Pi. knorri, uliginosus*). There remain 51 lowland species for the present analysis. Contrary to the fauna of H, *P. cribrata* is absent but there are four additional species, viz., *A. striatipes, Ar. stigmosa, P. nigriceps* and *saltans*.

As regards the division of the two countries into two zones, 11 species occur only in the southern Pannonian zone (*A. mariae, psammophila, solitaria, striatipes, Ar. stigmosa, G. vultuosa, Ho. radiata, L. singoriensis, P. maisa, nebulosa* and *proxima*), three species occur only in the Central European zone (*P. agricola, morosa* and *saltans*); and 37 species occur in both zones. Like in H and the Pannonian lowland, almost all montane species are missing.



Figs. 1–6. – 1: *Alopecosa albofasciata* male, Corsica, Galeria, 1. 5. 2001; – 2: *Alopecosa kalavrita* male, Peloponnesos, Helmos 2300 m, 18. 9. 1993; – 3: *Alopecosa inquilina* male, Austria, Northern Tyrol, Innsbruck, 9. 11. 1996; – 4: *Arctosa tbilisiensis* male, Chalkidiki, Nikiti, 27. 4. – 4. 5. 2000; – 5: *Arctosa variana* male, Chalkidiki, Nikiti, 27. 4. – 4. 5. 2000; – 6: *Aulonia kratochvili* male, Chalkidiki-E, Gomati, 2. 5. 2000. All leg. Knoflach & Thaler, photos B. Knoflach.

Results

Using lowland species in national lists to divide the transect into natural territorial units

The southernmost part of the transect is a natural part of the Pontic-Mediterranean refuge in the sense of de Lattin (1967). The territory of GR contains only a minute part of this refuge, reaching westward along the sea coast to

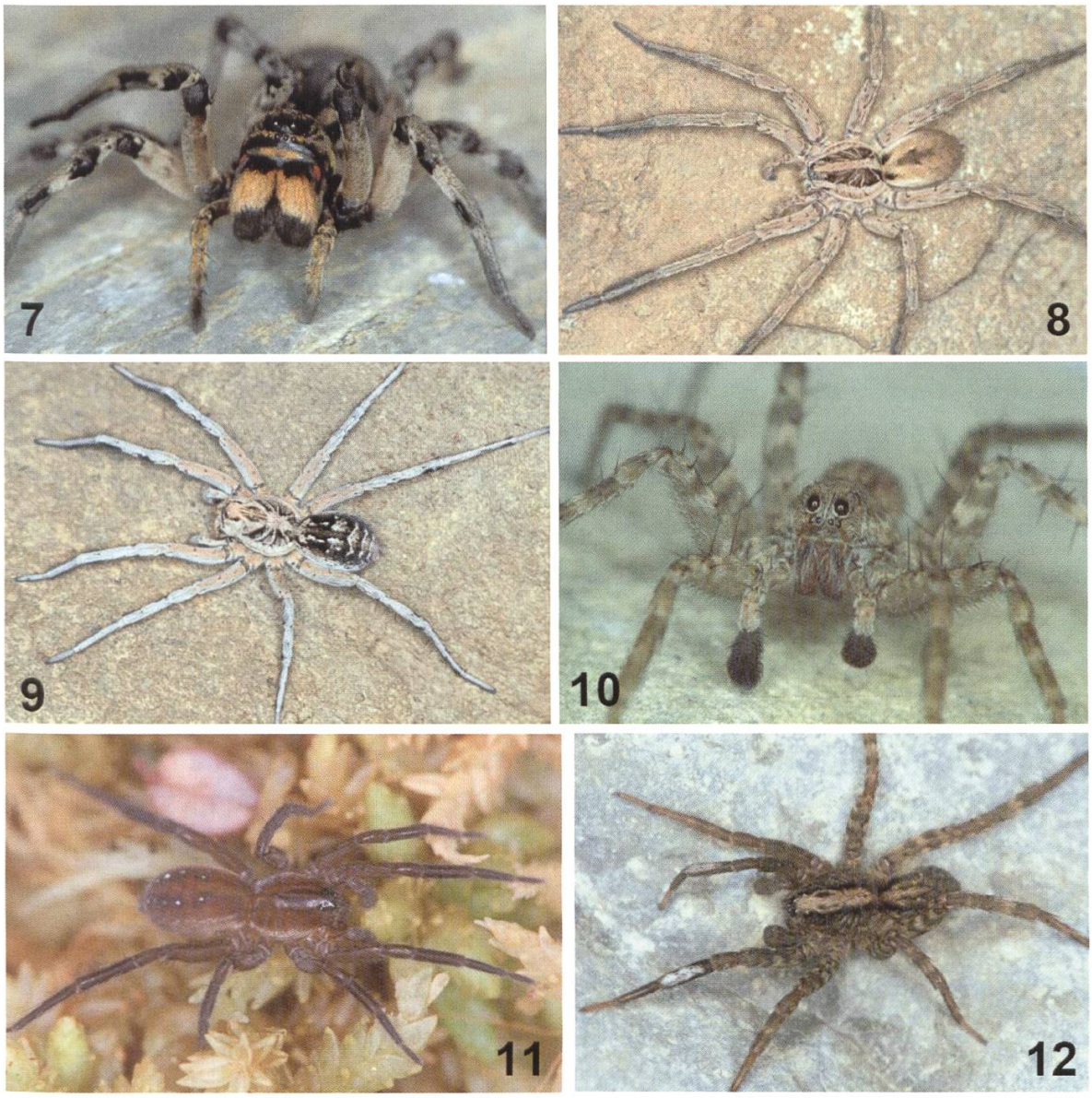
Dalmatia, and eastward to the sea coast of Israel. The part lying on the transect can be called Greek Mediterranean Refuge (GMR). No endemic species are known for the GMR.

Determining the northern limit of the Greek Mediterranean Refuge and the southern limit of the Submediterranean

At present, sixteen typically Mediterranean species have been shown to occur south of the Corinthian Canal: *A. albofasciata, pentheri, Ar. leopardus, variana, tbilisiensis, G. vultuosa, Ho. radiata, L. praegrandis, P. proxima, atomaria, alacris, cribrata, hortensis, luctinosa, Pi. latitans, T. hispanica.* Most of these species occupy extensive ranges reaching to the Iberian or Apennine peninsulae, four of them (*pentheri, tbilisiensis, praegrandis, luctinosa*), show a relationship to the Caspian centre, and only two (*vultuosa, alacris*) are probably limited to the Balkan part of the Mediterranean. Save for *Ar. tbilisiensis,* the remaining species clearly reach the territory of BG. In this respect, the Caspian species, *Au. kratochvili,* occupies a special position, as it is the seventeenth typical Mediterranean species that reaches only the north of GR via the territory of Turkey (Mat.)

The remaining species can be termed extra-Mediterranean. They occupy extensive ranges within the Temperate Zone, reaching from the north only as far as the border mountain provinces: Ionian islands, Ipeiros, Macedonia, Thraki (*A. accentuata, cuneata, cursor, inquilina, pulverulenta, sulzeri, trabalis, Ar. maculata, perita, P. agrestis, agricola, amentata, bifasciata, lugubris, morosa, prativaga, Pi. hygrophilus, piscatorius, T. terricola*) or quite singly some of the Greek Mediterranean Refuge regions (*A. solitaria, Au. albimana, P. nebulosa, pullata, vittata*). The last three species were reported by earlier authors only.

It is very difficult to include, in the present analysis, seven additional species inhabiting the Temperate Zone, which were found and identified by earlier authors in the southernmost regions of GR incl. Crete. As to *A. cuneata* and *pulverulenta*, they may have been confused with the very abundant Mediterranean species, *A. albofasciata*, since they have not been recently found in that region. As to *P. agricola*, Tongiorgi (1966) points out the absence of this species from the Mediterranean. Moreover, all specimens of the tentatively endemic species, *P. olympica,* were described from Roewer's material, collected by Roewer partly in the same localities as *P. agricola* (see Bosmans & Chatzaki 2005). Similar preliminary doubts may pertain to *P. agrestis*, reported from Rhodes as *P. amnicola.* Furthermore, one may point out that in



Figs. 7–12. – 7: *Geolycosa vultuosa* female, GR, Chalkidiki, Sithonia, Parthenon, 30. 4. 2000; – 8: *Hogna radiata* male, Chalkidiki, Nikiti, 28. 4. 2000; – 9: *Lycosa praegrandis* male, Crete, Lassithiou, Tzermiado, Ag. Timios, ca. 1100 m, 10. 4. 1998; – 10: *Pardosa atomaria* male, Crete, Ierapetra, Sarakinas gorge, 28. 9. 1998; – 11: *Pirata piscatorius* male, Austria, Northern Tyrol, Walchsee, Schwemm, 9. 6. 2006; – 12: *Trochosa hispanica* male, GR, Kephallinia, lake Avithos near Ag. Nikolaos, 22. 9. 1999. All leg. Knoflach & Thaler, photos B. Knoflach.

Rhodes the species *Ar. perita* may have been mistaken for a very similar species, *Ar. variana,* abundant in the south of GR (locus typicus: Peloponnesos) and also ascertained in Rhodes. Similarly, *P. lugubris* may have been mistaken for *P. alacris,* and *A. cursor* for *A. pentheri.*

In conclusion, it can be stated that the occurrence of lycosid spiders tends to confirm the presence of a boundary between the Mediterranean and the Submediterranean zones in the north of GR. This boundary, however, is not determined by the occurrence of typical Mediterranean species, most of which continue to occur in BG, but by the commonly ending occurrence of extra-Medi-

terranean species that reach the north of GR from the north. However, one cannot exclude the possibility of recording, in the Greek Mediterranean Refuge, the isolated occurrence of additional lowland species that may reach the local mountain altitudes or the islands off the Turkish coast. For instance, one male of *A. cuneata* is known so far from Roewer's material from Crete (T. Kronestedt in litt.).

The Bulgarian Submediterranean Faunal Refuge (BSR)

A more detailed analysis of the ranges of Bulgarian lycosid species shows that there is, in the territory of the transect, a kind of separate faunal refuge lying near the southern limit of the Submediterranean. Besides that part of BG, this refuge includes northern GR on the one hand and the adjacent lowlands of RO on the other, in particular the maritime part of Dobruja, and rarely also isolated localities on the left bank of the Danube (see maps showing the occurrence of Bulgarian species *A. albofasciata, taeniopus, P. cribrata, italica* and *vittata* in the territory of RO in Fuhn & Niculescu-Burlacu 1971). This situation appears to provide a basis for defining the Bulgarian Submediterranean Refuge (BSR). Compared to the Bulgarian national list of species, this refuge contains a single additional species, *Au. kratochvili*. The territory of the BSR has been found to comprise 58 lowland species.

The fauna of the BSR shows the following characteristics:

First of all, it comprises all Mediterranean species occurring in the territory of the Greek Mediterranean Refuge. Moreover, compared with that of the Greek Mediterranean Refuge, the fauna of the BSR comprises, on the one hand, species from quite different parts of the Mediterranean (*A. etrusca, P. italica, pseudostrigillata*) and, on the other, from the neighbouring, more eastern, Caspian centre (*A. taeniopus, Au. kratochvili, P. nebulosa* and *vittata*). It should be pointed out that the data on the latter two species (Bosmans & Chatzaki 2005) might indicate that they probably expanded up to the marginal regions of the Greek Mediterranean Refuge. Nevertheless, the main part of the fauna of the Bulgarian Submediterranean Refuge consists of species inhabiting vast ranges in the Temperate Zone, or at least the whole of the Submediterranean (71%). So far only two of them (*A. solitaria, Au. albimana*) have recently been registered in central GR, yet it is assumed that more such data will be published in the near future without reducing the importance of the BSR in the territory of the transect.

The main importance of the Bulgarian Submediterranean Refuge lies in the fact that it was only from this area that the thermophilous species could

expand in a northward direction. In this respect, one can distinguish between three species groups.

The first group (stationary species) occupied only the territory of the BSR and did not go over the northern limit of this refuge: *A. albofasciata, etrusca, pentheri, taeniopus, Ar. tbilisiensis, variana, Au. kratochvili, L. praegrandis, P. atomaria, cribrata, italica, pseudostrigillata, vittata, T. hispanica* (14). Here, the species behave as stationary in the sense of de Lattin (1967). A special position here is occupied by *P. cribrata,* a species which, lacking data on its occurrence in RO outside Dobruja for the time being, nevertheless occurs in the transect again near the northern limit of the Submediterranean (western H) to which area it probably dispersed. For that reason, the species can even be included in the next group of Submediterranean species. A large part of the Greek Mediterranean Refuge is inhabited by eight species only (*Al. albofasciata, pentheri, Ar. tbilisiensis, variana, L. praegrandis, P. atomaria, cribrata, T. hispanica*). Two of these species (*tbilisiensis, kratochvili*), however, appeared rather to be stationary towards the more southern ancient refuges (Caspian and Mediterranean) of Tertiary character and occupied only the marginal part of the BSR. Therefore, the Bulgarian Submediterranean Refuge appears to be a distinctly younger refuge.

The second group (Submediterranean species) did cross the northern limit of the BSR but ceased expansion of their range still in the territory of the Submediterranean: *A. mariae, solitaria, Ar. stigmosa, G. vultuosa, Ho. radiata, L. singoriensis, P. luctinosa, nebulosa, proxima* (9). But for *P. luctinosa,* all these species reached the northern limit of the Submediterranean in the territory of SK. At the same time *P. luctinosa* did not occur beyond the western limit of RO. Only five species (*vultuosa, radiata, cribrata, luctinosa, proxima*) inhabit most of the Greek Mediterranean Refuge, *A. solitaria* and *P. nebulosa* only a small part of it, whereas the southern limits of *A. mariae, Ar. stigmosa* and *L. singoriensis,* lie entirely in the territory of the Bulgarian Submediterranean Refuge.

The third group (Temperate species) crossed the northern limit of the Submediterranean: *A. accentuata, cuneata, cursor, inquilina, pulverulenta, sulzeri, trabalis, Ar. leopardus, maculata, perita, Au. albimana, P. agrestis, agricola, alacris, amentata, bifasciata, hortensis, lugubris, monticola, morosa, paludicola, palustris, prativaga, pullata, Pi. hygrophilus, latitans, piscatorius, tenuitarsis, Tr. lutetiana, T. robusta, ruricola, terricola, X. miniata, nemoralis.* (34). Only four of these species occur all over (*leopardus, alacris, latitans*) or in a large part (*hortensis*) of the Greek Mediterranean Refuge. However, two of them (*leopardus, latitans*) do not appear as typical Mediterranean species, as they do not prefer thermophilous habitats. One cannot exclude their more probable

connection to the Temperate fauna that populated the litoral habitats of the Mediterranean from the southern parts of the Submediterranean. In general, a large majority of species in this group inhabit extensive ranges that reach to the Siberian faunal centres, and they probably expanded to the Bulgarian Submediterranean Refuge from the east during earlier interglacial periods.

The Romanian Intermediate Territory (RIT) between the BSR and the PSR

The fauna of this intermediate territory is characterised as follows: Most of its 49 lowland species are among the Temperate ones. It comprises all 34 species ascertained in the Bulgarian Submediterranean Refuge. Besides, there are all 9 Submediterranean species. Moreover, another six species occur in the RIT quite independent of the 34 species ascertained in the Bulgarian Submediterranean Refuge, four of which (*A. schmidti, Ar. figurata, H. rubrofasciata, T. spinipalpis*) show similar distribution in central Europe as the Temperate species mentioned. The remaining two species (*P. baehrorum, nigriceps*) occupy dot-like areas lying far from their continuous ranges.

Species richness of the Pannonian Submediterranean Refuge (PSR) in the transect territory

H is the central part of Pannonia. The northern limit of Pannonia lies in the southern parts of CZ and SK, its eastern limit in the territory of RO. The core of the Pannonian fauna consists of Temperate species from the Bulgarian Submediterranean Refuge, enriched by 4 widely distributed species (*A. schmidti, Ar. figurata, H. rubrofasciata, T. spinipalpis*) recently discovered in RO (38). It should be pointed out that while *Ar. stigmosa* is missing in the territory of H, it does occur in the periphery of Pannonia in SK.

The second important component consists of nine Submediterranean species enumerated in the characteristics of the Bulgarian Submediterranean Refuge. Here one may add a tenth species, *P. cribrata*, which apparently immigrated to the west of H from another direction than through RO. Besides, *P. luctinosa* can be included in the Pannonian fauna, notwithstanding the fact that it was found in the west of RO, since that part can be understood to be the eastern periphery of Pannonia.

The third group comprises two characteristic Pannonian species, *A. psammophila* and *P. maisa*. While the former occupies a stationary range here, the latter expanded northward to Finland although not a single locality of this species is known in CZ or SK beyond the territory of the Submediterranean.

The fourth group corresponds to the Atlantic faunal element, here represented by *A. striatipes, P. nigriceps* and *saltans*. The latter two species are missing from the Hungarian national list. However, all these three species occur at the western periphery of Pannonia, in CZ.

In all, 53 lowland species have been ascertained in the territory of Pannonia.

Species richness of the Central European Temperate Zone (CTZ) in CZ and SK

Compared with the structure of the Pannonian Submediterranean Refuge, that of the Central European Temperate Zone depends on only two of the four components represented in the PSR: the first (totalling 38 species) and the fourth (minus *A. striatipes*) represented by two Atlantic species (*P. nigriceps* and *saltans*) and showing a marked eastward decrease in the occurrence of these two species.

Relationships between the lowland species faunae, as shown by the natural division of the transect (Map 1), expressed by Jaccard's similarity index (S)

As regards the lowland species, the greatest similarity is found between RIT and PSR (S = 47.1%). This can be explained by the fact that both lie on the same geographic latitude. Lower similarity degrees are found between faunulae mutually separated by the northern limit of the Submediterranean: CTZ vs. RIT (S = 43.8%) and CTZ vs. PSR (S = 43.0%). The least similarity was found between BSR and RIT (S = 40.6%), corresponding with the accumulation of stationary ranges in the BSR and its major function in the transect. The limit between the Mediterranean and Submediterranean, GMR vs. BSR, appears somewhat less marked (S = 41.2%) than that between BSR and RIT (S = 40.6%). The latter probably expresses a shift of the northern limit of species of the Mediterranean refuge towards the boundary between BSR and RIT.

As regards similarity on the level of montane and boreo-montane species, the faunula of PSR cannot be considered, as it distinctly lacks mountain habitats. The much lower values of S found between the different faunulae tend to demonstrate the absence of recent dispersal between the montane faunulae. All of that took place during, or shortly after, glaciation periods. The greatest

similarity is found between CTZ and RIT (S = 39%), much smaller between RIT and BSR (S = 29.4%), in which case the influence of glaciation may not have been as significant, and the very low similarity in GMR vs. BSR (S = 15.8%) obviously demonstrates the slight influence of the montane fauna of the Alpine Massif (sensu Ozenda 1988) on the fauna of Mediterranean mountain ranges.

Discussion

Connection between the faunae on the transect and those in the neighbouring territories

The study discussing the spider fauna of oak woods in the eastern European lowland (Esjunin & al. 1993) is an important paper, immediately linking with the two species groups described in the analysis of the Bulgarian Submediterranean Refuge, whose ranges suggest the expansion of those species in a northward direction. Whereas within the transect study 100% of temperate species reach the territory of the Central European Temperate Zone, seven of these species are missing from the list of lycosid spiders inhabiting oak woods in the eastern European lowland, viz., *Ar. perita, P. alacris, bifasciata, monticola, Pi. latitans, piscatorius* and *tenuitarsis*. According to the data gathered by Mikhailov (1997), this should be objectively valid only for *P. alacris* and *monticola*. Most of the 34 Temperate species occupy extensive polycentric ranges reaching, in the eastward direction, at least the western part of Siberia (Mikhailov 1997), and ten of the species as far as the eastern end of the Asian continent. On the other hand, besides the two species mentioned above, also *Ar. maculata, Tr. lutetiana* and *T. robusta* inhabit exclusively European ranges. Instead of Siberia, some European ranges are directed to the Caucasus and Azerbaijan: *Ar. perita, Au. albimana, P. morosa, P. latitans*.

At the same time, it is interesting to note that in contrast to the end part of the transect (CTZ), four of the ten so-called Submediterranean (*A. mariae, solitaria, L. singoriensis, P. proxima*) have been registered in the faunulae tied to oak woods in the eastern European lowland (Esjunin & al. 1993). In particular, the occurrence of *L. singoriensis* attains, in the easternmost part of its European range, incomparably higher geographic altitudes than what has been observed within the present transect study.

It is very interesting to note that the paper (Esjunin & al. 1993) documents the way of populating the woodland and forest-steppes in the eastern European lowland from the Carpathian arboreal refuge, lying in immediate contact

with the post-glacial migration realised from the Bulgarian Submediterranean Refuge. At the same time, one cannot exclude the possibility that some of the Central European species remained in the territory of the Caspian refuge on the level of stationary ranges, as exemplified by *Au. albimana* and *Pi. latitans,* which are probably missing from the Ural Mts. (Mikhailov 1997).

Six species known only from the Romanian Intermediate territory as regards the present transect study (*A. schmidti, Ar. figurata, H. rubrofasciata P. baehrorum, nigriceps* and *T. spinipalpis*) occupy a special position. No evidence has been found of their being tied to the Bulgarian Submediterranean Refuge. Two of them occupy spot-like ranges lying in RO beyond their continuous ranges lying far in the west. *P. nigriceps* is an Atlantic species whose record in RO has even been found to be erroneous (Fuhn & Niculescu-Burlacu 1971: 114), *P. baehrorum* has rarely been found so far, exclusively in the upper part of the Danube drainage area: Germany and Austria (Kronestedt 1999b), Switzerland (Hänggi 1999), so that it is very difficult to evaluate the new Romanian data without any further investigations.

The remaining four species are rather abundantly represented not only in the Central European Temperate Zone but they have been mentioned by Esjunin & al. (1993) as living in the eastern European oak woods. Immediate links with the Siberian fauna can be assumed in *A. schmidti, H. rubrofasciata* and *T. spinipalpis*. It is difficult to find the origin of the Eastern European species, *Ar. figurata,* which shows no apparent immediate relationship to any of the Tertiary refuges. One of the hypotheses may point to the Pannonian Submediterranean Refuge.

Comparing the structure of the lycosid fauna of Serbia (Deltshev & al. 2003) with that of the Bulgarian Submediterranean Refuge shows unequivocally the dissatisfactory results of the hitherto undertaken investigations in Serbia: while 44 lowland species are shared by the two territories, of the so-called stationary species typical of the Bulgarian Submediterranean Refuge, the most important ones are missing in Serbia. Of the 14 stationary ones, only three are shared (*A. albofasciata, Ar. variana* and *P. vittata*) and, of the other groups, two rather important species (*P. luctinosa* and *Pi. tenuitarsis*) are missing in Serbia. Only three Serbian species have not been ascertained in the territory of the Bulgarian Submediterranean Refuge: *Ar. figurata, L. narbonensis* and *P. profuga*. The first of these suggests an immediate linkage between the Serbian fauna and the Pannonian Submediterranean Refuge, the remaining two, apparently lacking data required for inevitable revision, do not offer enough information for further discussion. In conclusion, it should be stated that the results of arachnological studies in Serbia cannot replace the Bulgarian one in the present transect study.

Besides pollen analyses, important contributions to knowledge of development of natural conditions in central Europe are found in malacological studies (e.g. Ložek 1982) based on the occurrence of snail conchs found in successively deposited Holocene as well as earlier Pleistocene sediments. The layers deposited during the first half of the Holocene and during earlier interglacial periods are characterised by the occurrence of woodland snails. In the second part of the Holocene, however, the development of nature was diverted by man's agricultural activities disturbing the dominant occurrence of woodland and hence also its fauna, and the dispersal of woodland species was replaced by mass expansion of species typical of open habitats. Contrary to molluscs, however, the lycosid family under the present study lacks typical woodland species. Even the species rather firmly tied to the woodland habitat do not prefer, as a rule, the typical shaded woodland environment but invariably seek clearings and especially ecotonal habitats. Representatives of the ancient central European woodland fauna can be seen, above all, in such boreo-montane types as *Ac. lignaria, A. aculeata, A. pinetorum* and *A. taeniata*. In the present paper, these species have been set apart for the transect as montane. On contrary, the expansion of lowland species was facilitated by the anthropogenic transformation of Europe, providing conditions for their existence on woodland edges, along streams, as well as within agrocoenoses. This can be seen in the description of "habitat requirements" in the catalogue by Buchar & Růžička (2002). All 36 species assumed to have migrated to CZ from the Bulgarian Submediterranean Refuge, are said to prefer open habitats. Except for *Al. singoriensis* and *A. solitaria,* they constitute a group of species denoted within the Bulgarian Submediterranean Refuge as Temperate species (34). The habitat type of 11 of these species is denoted in the catalogue as "rock steppe", or "forest steppe". The habitat of 8 species is denoted as "meadow" or "fields", that of 7 species as "wetland". Only five species (*A. inquilina, P. alacris, P. lugubris, T. terricola* and *X. nemoralis*) show a rather distinct connection with the woodland environment, invariably with its edges, however. The habitats of the remaining 5 species (incl. *L. singoriensis*) are sands or littoral gravelly habitat types.

The concrete range expansion of the biggest central European lycosid, *L. singoriensis,* from the northern limit of the Bulgarian Submediterranean Refuge up to the territory of Moravia in the eastern part of CZ in 1888 – 1950, described by Kratochvíl (1951), is a singular example documenting the importance of the Bulgarian Submediterranean Refuge.

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Index 1

List of species ascertained in the transect. Lowland species are in bold and marked by an asterisk.

Acantholycosa lignaria (Clerck, 1757), *Ac. norvegica* (Thorell, 1872).

***Alopecosa accentuata* (Latreille, 1817)**, *A. aculeata* (Clerck, 1757), ***A. albofasciata* (Brullé, 1832)**, ***A. cuneata* (Clerck, 1757)**, ***A. cursor* (Hahn, 1831)**, *A. dryada* Cordes, 1996, ***A. etrusca* Lugetti & Tongiorgi, 1969**, *A. fabrilis* (Clerck, 1757), ***A. inquilina* (Clerck, 1757)**, *A. kalavrita* Buchar, 2001, ***A. mariae* (Dahl, 1908)**, ***A. pentheri* (Nosek, 1905)**, *A. pinetorum* (Thorell, 1856), ***A. psammophila* (Buchar, 2001)**, ***A. pulverulenta* (Clerck, 1757)**, ***A. schmidti* (Hahn, 1835)**, ***A. solitaria* (Herman, 1879)**, **A. striatipes (C. L. Koch, 1837)**, ***A. sulzeri* (Pavesi, 1873)**, *A. taeniata* (C. L. Koch, 1835), ***A. taeniopus* (Kulczyński, 1895)**, ***A. trabalis* (Clerck, 1757)**.

Arctosa cinerea (Fabricius, 1777), ***Ar. figurata* (Simon, 1876)**, *Ar. lamperti* (Dahl, 1908), ***Ar. leopardus* (Sundevall, 1833)**, ***Ar. maculata* (Hahn, 1822)**, ***Ar. perita* (Latreille, 1799)**, ***Ar. stigmosa* (Thorell, 1875)**, ***Ar. tbilisiensis* Mcheidze, 1947**, ***Ar. variana* (C. L. Koch, 1872)**.

***Aulonia albimana* (Walckenaer, 1805)**, ***Au. kratochvili* Dunin, Buchar & Absolon, 1986.**

***Geolycosa vultuosa* (C. L. Koch, 1839).**

***Hogna radiata* (Latreille, 1817).**

***Hygrolycosa rubrofasciata* (Ohlert, 1865).**

***Lycosa praegrandis* C. L. Koch, 1836**, ***L. singoriensis* (Laxmann, 1770).**

***Pardosa agrestis* (Westring, 1861)**, ***P. agricola* (Thorell, 1856)**, ***P. alacris* (C. L. Koch, 1833)**, *P. albatula* (Roewer, 1951), ***P. amentata* (Clerck, 1757)**, ***P. atomaria* (C. L. Koch, 1848)**, ***P. baehrorum* Kronestedt, 1999**, ***P. bifasciata* (C. L. Koch, 1834)**, *P. blanda* (C. L. Koch, 1833), *P. cincta* (Kulczyński, 1887), ***P. cribrata* Simon, 1881**, *P. drenskii* Buchar, 1968, *P. ferruginea* (L. Koch, 1870), *P. fulvipes* (Collett, 1875), ***P. hortensis* (Thorell, 1872)**, *P. hyperborea* (Thorell, 1872), *P. incerta* Nosek, 1905, ***P. italica* Tongiorgi, 1966**, ***P. luctinosa* Simon, 1876**, ***P. lugubris* (Walckenaer, 1802)**, ***P. maisa* Hippa & Mannila, 1982**, *P. mixta* (Kulczyński, 1887), ***P. monticola* (Clerck, 1757)**, ***P. morosa* (L. Koch, 1870)**, ***P. nebulosa* (Thorell, 1872)**, *P. nigra* (C. L. Koch, 1834), ***P. nigriceps* (Thorell, 1856)**, *P. olympica* Tongiorgi, 1966, ***P. paludicola* (Clerck, 1757)**, ***P. palustris* (Linné, 1758)**, *P. pertinax* von Helversen, 2000, ***P. prativaga* (L. Koch, 1870)**, ***P. proxima* (C. L. Koch, 1848)**, ***P. pseudostrigillata* Ton-**

GIORGI, 1966, *P. pullata* (CLERCK, 1757), *P. riparia* (C. L. KOCH, 1833), ***P. saltans* TÖPFER-HOFMANN, 2000**, *P. saltuaria* (L. KOCH, 1870), *P. sordidata* (THORELL, 1875), *P. sphagnicola* (DAHL, 1908), *P. tasevi* BUCHAR, 1968, *P. wagleri* (HAHN, 1822), ***P. vittata* (KEYSERLING, 1863)**.

***Pirata hygrophilus* THORELL, 1872**, *Pi. insularis* EMERTON, 1885, *Pi. knorri* (SCOPOLI, 1763), ***Pi. latitans* (BLACKWALL, 1841)**, *Pi. piraticus* (CLERCK, 1757), ***Pi. piscatorius* (CLERCK, 1757)**, ***Pi. tenuitarsis* SIMON, 1876**, *Pi. uliginosus* (THORELL, 1856).

***Tricca lutetiana* (SIMON, 1876).**

***Trochosa hispanica* SIMON, 1870, *T. robusta* (SIMON, 1876), *T. ruricola* (DEGEER, 1778), *T. spinipalpis* (F.O.P.-CAMBRIDGE, 1895), *T. terricola* THORELL, 1856.**

***Xerolycosa miniata* (C. L. KOCH, 1834), *X. nemoralis* (WESTRING, 1861).**

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Information on unpublished material (Collection J. Buchar)

Aulonia kratochvili Southern Turkey: Manavgat, partly shaded river bank, 10 m, 2 June 2002, 1 ♀, leg. JB

Pardosa albatula GR: Boiotia, Mt. Parnassos, 1800 m, 22 June 1974, 3 ♂, 2 ♀, leg. J. Švihla

Pardosa cribrata GR: Peloponnesos, Nafplion, richly overgrown bank of a small brook emptying into the sea, 3 m, 17 June 2000, 2 ♂, leg. JB

Pardosa hortensis GR: Peloponnesos, Tolo, temporary pool in a ditch along a road, 15 m, 20 June 2000, 1 ♀, leg. V. Smola

Pardosa italica RO: Dobruja (FNB 71: 97): Eforia, near sea shore, 10 m, 4 July 1969, 1 ♂, leg. K. Hůrka

Pardosa luctinosa GR: Peloponnesos, Nafplion, richly grown bank of a small brook empting into the sea, 3 m, 17 June 2000, 1 ♀ with cocoon, leg. JB