2011. The Journal of Arachnology 39:393–398

Vertical distribution of spiders in soil

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Abstract. Research studies of the shallow subterranean habitats as environments for arthropods have been sparse up to this point. Using subterranean traps, we studied the distribution of spiders in soil profile over a depth span of 5–95 cm at six sites. Although almost 40% of individual specimens (1088 in total) were obtained from the epigeon (5 cm depth), spiders colonized all parts of the soil profiles examined. Beside ground-dwelling species with significant preferences for the upper layers, some species (*Porrhomma microphthalmum* (O. Pickard-Cambridge 1871), *Centromerus cavernarum* (L. Koch 1872), *Cicurina cicur* (Fabricius 1793), *Dysdera lantosquensis* Simon 1882, and *Nesticus cellulanus* (Clerck 1757)) commonly inhabited the whole range of the profiles studied, without any depth preference. In contrast, depigmented and microphthalmous *Porrhomma microps* (Roewer 1931) and *Maro* sp. exclusively inhabited deep soil layers adjoining void systems in bedrock.

Keywords: Mesovoid shallow substratum, superficial underground compartment, subterranean environment, Araneae

The soil is an aphotic environment inhabited by casual transmigrants as well as fauna adapted for subterranean life (e.g., microphthalmy, depigmentation etc.). Soil porosity limits the size of its inhabitants; nevertheless, soil spaces vary in dimension from sand fissures to cave systems (Christian 1999). Three distinct types of habitats in relation to the soil can be formally distinguished: 1) epigean, inhabited by surface dwelling animals; 2) endogean, with mainly edaphic animals; and 3) hypogean, with subterranean species inhabiting void systems, including caves (Giachino & Vailati 2010).

Our knowledge of endo- and hypogeic animals is limited, due to difficulties in collecting samples. Invertebrates inhabiting a subterranean environment can be studied with the use of only a few methods. One such method is the use of pitfall traps, modified in various ways (e.g., a collar around the nose, perforation of walls), dug to different depths and exposed for an extended period of time (Růžička 1982, 1988; Yamaguchi & Hasegawa 1996). Another type is Barber's Shingle Trap (Barber 1997), with bait inside and a long hose exposed at the depth studied. A frequently used method involves traps installed in drills (Illie 2003; Illie et al. 2003; Negrea 2004). One clever modification of drill trapping is the subterranean trap designed by Schlick-Steiner and Steiner (2000) that collects animals in one drill at various depths.

Beside an extensive knowledge of cave spiders (e.g., Paquin & Dupérré 2009), we have some information on spiders in scree slopes (Růžička et al. 1995; Růžička 1999a, 1999b, 2002; Růžička & Klimeš 2005). In stony alpine debris, spiders are generally most abundant in the upper layers, but differ significantly depending on locality (Schlick-Steiner & Steiner 2000). A similar pattern of abundance was found in the vertical distribution of spiders in peat bogs (Biteniekytė & Rėlys 2006). However, we have limited knowledge about spiders inhabiting soil, as endogeic and hypogeic spiders have only been studied recently in Bulgaria (Deltshev et al. 2011). The present study aims to reveal whether spiders inhabit deep soil layers and to characterize the vertical distribution of spider communities at several sites with different soil types in Central Europe.

METHODS

Site description.—The research was carried out at six sites in the Czech Republic; three of them (*Above cave, Rock, Debris*) were situated in Central Moravia near the town of Hranice na Moravě (320 m a.s.l.). The other three sites (*Beech wood, Quarry, Valley*) were situated 10 km east of the town of Skuteč, on the border of Žďárské vrchy Protected Landscape Area (Eastern Bohemia, approx. 450 m a.s.l.).

Above cave (49°31′N, 17°44′E)*:* This site is situated above Zbrašov Aragonite Caves. The cave system is linked with stony debris above through shafts, ending approximately one meter below the surface. The upper soil layer was covered by leaf litter from deciduous forest. The debris was partially filled by soil particles created by interskeletal erosion forming lithosol soil type.

Rock (49°32′N, 17°44′E)*:* This site is one kilometer from *Above cave* under a limestone rock face in deciduous forest. In this renzic leptosol soil type, the upper organic layer is about 5 cm thick, the A-horizon with a mixture of organic and inorganic particles (about 15 cm thick) passing to the C-horizon with broken-down lime bedrock (stones several centimeters in diameter) and clay.

Debris (49°32′N, 17°44′E)*:* This site is only about 50 m from the *Rock* site on a slope in deciduous forest. The soil is similar to the previous one, but with larger stones (20–30 cm).

Beech wood (49°50′N, 16°3′E)*:* This site with cambisol soil type has a thick layer of leaf litter covering an A-horizon (ca 15 cm) passing to a 50 cm-thick cambic horizon above arenaceous marl bedrock.

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Table 1.—List of spider species in subterranean traps, with the number of trapped specimens and their depth range (uppermost to undermost record). Nomenclature of spiders according to Platnick (2010) with two exceptions: *Dysdera lantosquensis* sensu Řezáč et al. (2008) and *Porrhomma microps* (= *lativelum*) sensu Růžička (2009).

Family / Species	# Specimens	Depth distribution
Dysderidae		
Dysdera lantosquensis Simon 1882	25	5–95 cm
Harpactea lepida (C.L. Koch 1838)	101	5–95 cm
Harpactea rubicunda (C.L. Koch 1838)	3	5–15 cm
Nesticidae		
Nesticus cellulanus (Clerck 1757)	28	5–85 cm
Theridiidae		
Pholcomma gibbum (Westring 1851)	14	5–95 cm
Robertus lividus (Blackwall 1836)	13	5–35 cm
Robertus truncorum (L. Koch 1872)	2	15 cm
Linyphiidae		
Asthenargus perforatus Schenkel 1929	1	15 cm
Bathyphantes gracilis (Blackwall 1841)	1	5 cm
Centromerus cavernarum (L. Koch 1872)	28	5–75 cm
Centromerus silvicola (Kulczyński 1887)	37	5–55 cm
Ceratinella brevis (Wider 1834)	16	5–15 cm
Diplocephalus picinus (Blackwall 1841)	5	5–25 cm
Diplostyla concolor (Wider 1834)	7	5–15 cm
Entelecara acuminata (Wider 1834)	1	55 cm
Maro sp.	2	45–65 cm
Micrargus herbigradus (Blackwall 1854)	5	5–15 cm
Microneta viaria (Blackwall 1841)	6	5 cm
Neriene emphana (Walckenaer 1841)	1	25 cm
Oedothorax apicatus (Blackwall 1850)	223	5–55 cm
Palliduphantes alutacius (Simon 1884)	83	5–95 cm
Porrhomma microphthalmum (O. Pickard-Cambridge 1871)	185	5–85 cm
Porrhomma microps (Roewer 1931)	21	25–85 cm
Porrhomma oblitum (O. Pickard-Cambridge 1871)	1	15 cm
Saaristoa firma (O. Pickard-Cambridge 1905)	1	25 cm
Saloca diceros (O. Pickard-Cambridge 1871)	15	5–95 cm
Tenuiphantes flavipes (Blackwall 1854)	21	5–35 cm
Tenuiphantes tenebricola (Wider 1834)	1	5 cm
Walckenaeria atrotibialis (O. Pickard-Cambridge 1878)	2	5 cm
Walckenaeria dysderoides (Wider 1834)	1	15 cm
Walckenaeria furcillata (Menge 1869)	3	5–15 cm
Walckenaeria obtusa Blackwall 1836	2	5 cm

Table 1.—Continued.

Family / Species	# Specimens	Depth distribution
Walckenaeria vigilax (Blackwall 1853)	5	15 cm
Araneidae		
Araneus diadematus Clerck 1757	1	5 cm
Lycosidae		
Trochosa terricola Thorell 1856	2	25–35 cm
Agelenidae		
Histopona torpida (C.L. Koch 1834)	7	5–85 cm
Malthonica silvestris (L. Koch 1872)	6	5–65 cm
Cybaeidae		
Cybaeus angustiarum L. Koch 1868	8	5–75 cm
Hahniidae		
Hahnia nava (Blackwall 1841)	1	25 cm
Dictynidae		
Cicurina cicur (Fabricius 1793)	123	5–95 cm
Amaurobiidae		
Amaurobius fenestralis (Ström 1768)	2	5 cm
Callobius claustrarius (Hahn 1833)	2	5–15 cm
Coelotes terrestris (Wider 1834)	9	5–25 cm
Eurocoelotes inermis (L. Koch 1855)	12	5 cm
Liocranidae		
Apostenus fuscus Westring 1851	5	5–15 cm
Clubionidae		
Clubiona brevipes Blackwall 1841	3	5 cm
Salticidae		
Ballus chalybeius (Walckenaer 1802)	3	5 cm
Neon reticulatus (Blackwall 1853)	9	15–25 cm

Quarry (49°50′N, 16°2′E)*:* This site was situated in an abandoned basalt quarry. The soil profile consisted entirely of pieces of basalt about 10 cm in size. The upper soil layers, including vegetation, were removed during excavation.

Valley (49°50′N, 16°2′E)*:* This site is ca 1 km from the preceding one, situated in the Krounka stream basin. This debris slope is covered by deciduous forest and large stones overgrown with mosses. The homogenous soil profile comprised of basalt stones is about 20–25 cm in size with space partially filled by organic material from trees and inorganic particles created by erosion to a depth of one meter.

Sampling.—Spiders were collected using subterranean traps (Schlick-Steiner & Steiner 2000). The trap, made of rigid plastic, consists of a tube (10 cm in diameter) with three fissures (ca 4 mm wide, 6–7 cm long) at 10 cm intervals. The traps are over one meter long, and the last sampling fissure was 95 cm deep. A hole, about 1.5 × 0.7 m and 1.3 m deep was dug at each site, and soils of different layers were separated carefully using plastic sheets. Three tubes were put in the hole in line with each other, 50 cm apart, and the hole was then filled with soil in the proper order. A set of ten removable plastic containers (250 ml) situated on a central metal axis was placed in each tube; the position of the containers corresponded to the fissures in the tube. Through this arrangement, the containers collected animals entering the tube through fissures at particular depths. The traps were filled with a 4%

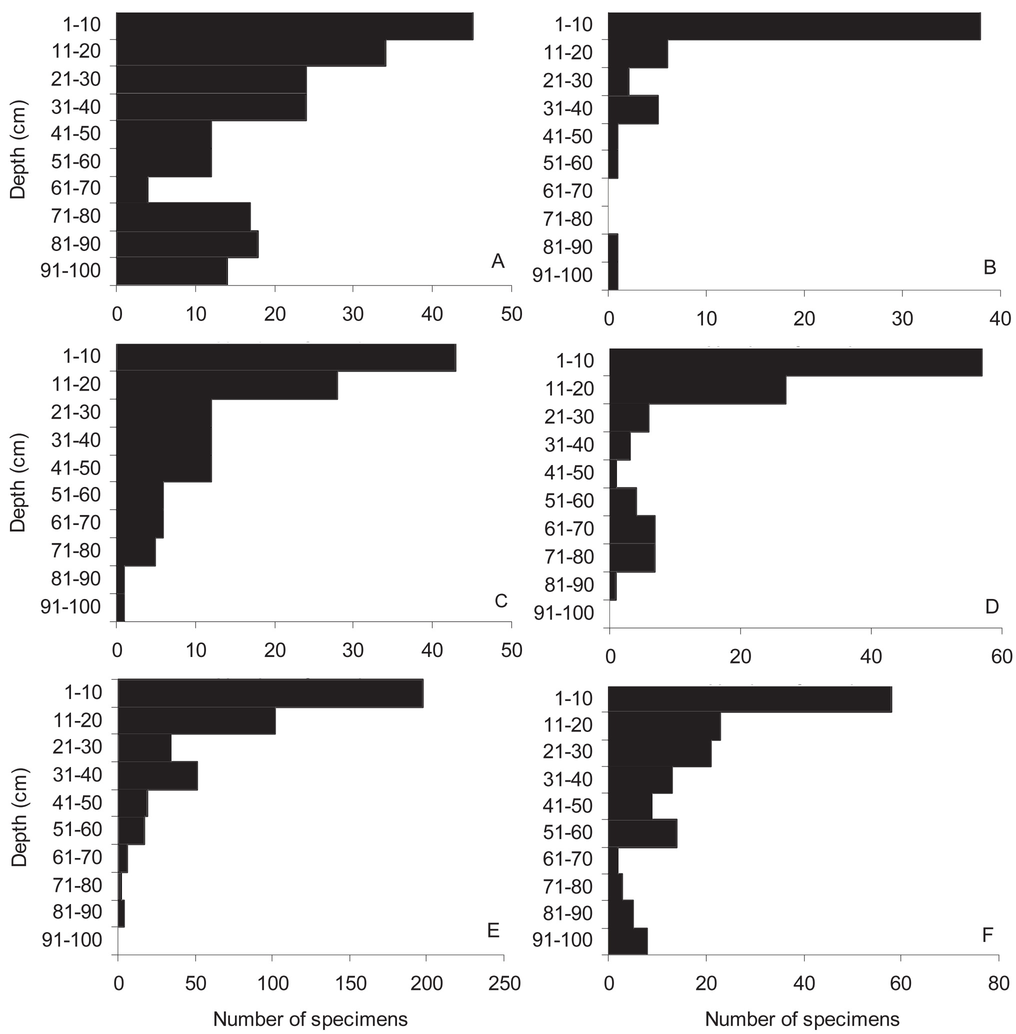

Figure 1.—Depth distribution of spider individuals at sites studied (number of all collected specimens). A – *Above cave* (altogether 205 individuals, 17 spp.), B – *Rock* (55 individuals, 12 spp.), C – *Debris* (126 individuals, 20 spp.), D – *Beech wood* (113 individuals, 17 spp.), E – *Quarry* (433 individuals, 9 spp.), F – *Valley* (156 individuals, 18 spp.).

formaldehyde solution and emptied at six-week intervals between 7 March 2005 and 17 March 2007. Voucher specimens are deposited in the collection of V. Růžička at the Institute of Entomology, Biology Centre, AS CR in České Budějovice.

Data analysis.—In the analysis, we used only species with more than 10 individuals and/or species found in more than four sites. RDA (Canonical redundancy analysis) was used to study the effect of depth and individual site. The significance of the first axis was determined by a Monte Carlo permutation test (499 permutations). Data standardized by error variance were used for RDA. Generalized linear models (GLM) with Poisson errors were used to study the relationship of each species and environmental variables (site, depth). CANOCO software was used for these analyses (Ter Braak, Šmilauer 1998).

RESULTS

The most numerous taxa collected were Collembola (44.7%), followed by Diptera (13.0%), Oniscidea (12.5%), Coleoptera (10.8%), Araneae (10.0%), and other rare taxa (Diplopoda 2.7%, Acarina 2.0%, Chilopoda 1.3%, Pseudoscorpiones 1.1%, Formicidae 0.8%, Dermaptera 0.6%, and Opiliones 0.4% respectively). Altogether, 1088 spider specimens of 48 species were trapped (Table 1). Among 14 spider families, the Linyphiidae was the richest in species (26 species), followed by the Amaurobiidae (4 species), Theridiidae and Dysderidae (3 species each) and Agelenidae and Salticidae (2 species each). We only evaluated the distribution of the 17 most numerous species statistically.

Quarry was the site with the greatest number of trapped spiders (433 individuals, 9 species); the highest number of species was recorded at *Debris* (20 species). The most numerous catches were in the upper level, at a depth of 5 cm (almost 40% of the individuals), and the lowest were at a depth of 95 cm (2.5%). Beside the most abundant spiders at the uppermost level, no common pattern was typical for all sites (Fig. 1). The number of spider species below 55 cm was highest in the *Above cave* site (over 30%), followed by *Debris*, *Beech wood*, and *Valley* sites (about 20%), followed by *Rock* and *Quarry* sites (only approximately 6%).

The RDA model revealed significant differences among the distribution of species ($F = 9.07$, $P < 0.01$). The sum of all

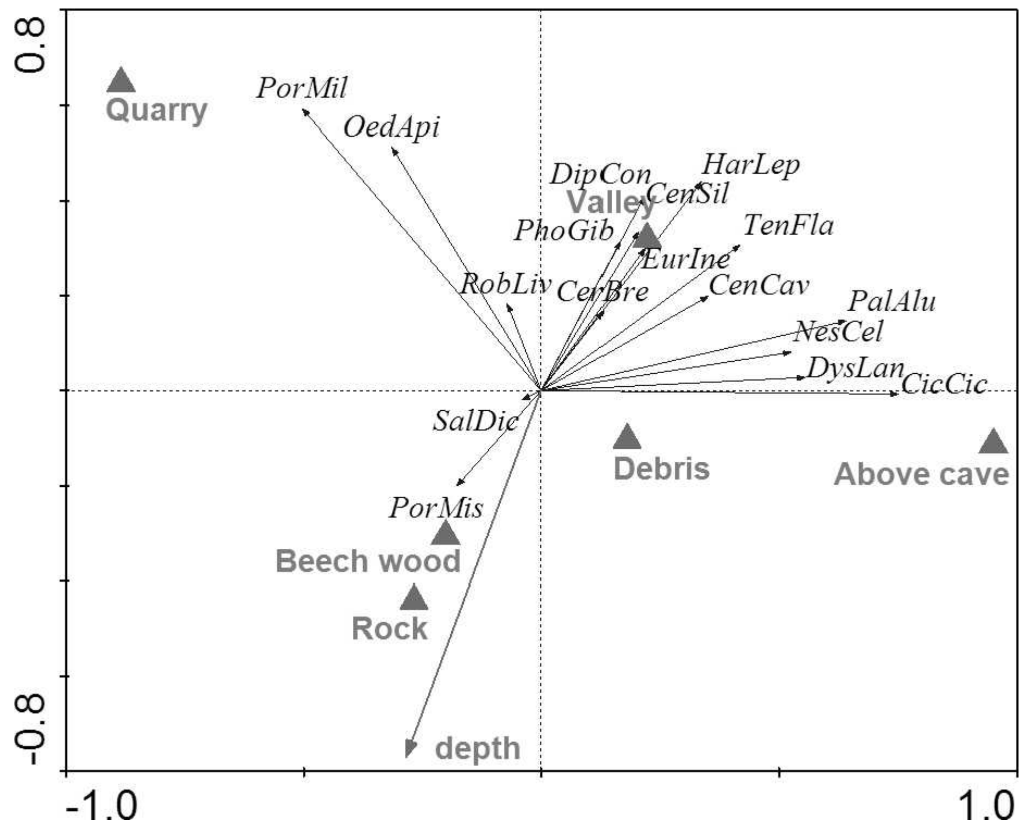

Figure 2.—RDA ordination biplot illustrating distribution of spiders in relation to sites and depth. Abbreviations: CenCav – *Centromerus cavernarum*, CenSil – *Centromerus silvicola*, CerBre – *Ceratinella brevis*, CicCic – *Cicurina cicur*, DipCon – *Diplostyla concolor*, DysLan – *Dysdera lantosquensis*, EurIne – *Eurocoelotes inermis*, HarLep – *Harpactea lepida*, NesCel – *Nesticus cellulanus*, OedApi – *Oedothorax apicatus*, PalAlu – *Palliduphantes alutacius*, PhoGib – *Pholcomma gibbum*, PorMil – *Porrhomma microphthalmum*, PorMis – *Porrhomma microps*, RobLiv – *Robertus lividus*, SalDic – *Saloca diceros*, TenFla – *Tenuiphantes flavipes*.

canonical eigenvalues explains 50.7% of variability. Although there is no common pattern of depth distribution of spiders, depth is a significant general predictor ($F = 7.74$, $P < 0.01$), and distribution patterns and community compositions differ among sites ($F = 3.18$, $P = 0.04$). The ordination diagram shows that *Porrhoma microps* (Roewer 1931) is positively correlated with soil depth (Fig. 2).

GLM modeling of the response of the 17 dominant spider species to depth showed significant pattern for ground-dwelling species mainly; the spiders inhabiting the entire profile do not significantly prefer any depth (Table 2). These 17 species can be separated into four categories according to their depth distribution and preferences (distributions of 11 species with more than 20 trapped specimens are displayed in Fig. 3):

1. Exclusively surface dwelling species: *Eurocoelotes inermis* (L. Koch 1855), *Diplostyla concolor* (Wider 1834), *Ceratinella brevis* (Wider 1834)
2. Surface-dwelling species (significant preference for upper layers) penetrating into deeper layers: *Centromerus silvicola* (Kulczyński 1887), *Oedothorax apicatus* (Blackwall 1850), *Tenuiphantes flavipes* (Blackwall 1854), *Harpactea lepida* (C.L. Koch 1838), *Robertus lividus* (Blackwall 1836), *Palliduphantes alutacius* (Simon 1884), *Saloca diceros* (O. Pickard-Cambridge 1871)
3. Species inhabiting whole soil profile (without preference for any depth): *Pholcomma gibbum* (Westring 1851), *Porrhomma microphthalmum* (O. Pickard-Cambridge 1871), *Centromerus cavernarum* (L. Koch 1872), *Cicurina cicur* (Farricius 1793), *Dysdera lantosquensis* Simon 1882, *Nesticus cellulanus* (Clerck 1757)
4. Species inhabiting exclusively (any) of the deeper layers: *Porrhomma microps*. Two other species, too rare for statistical evaluation, were found in the deeper layers: *Entelecara acuminata* (Wider 1834) at 55 cm and *Maro* sp. at 45 cm and 65 cm (identification is complicated by expanded palps; these two specimens have slightly reduced eyes, unlike species of *Maro*, posterior median eyes 1.2 diameters apart).

DISCUSSION

Studies of the deep soil layer environment have been scarce due to the difficulty of sampling these arthropod communities. We present evidence for the occurrence of spiders (invertebrates larger than typical soil invertebrates such as mites and collembolans) in soil layers down to one meter in depth.

Vertical distribution of spiders in the soil profile differed according to the habitat type. Although we were not able to evaluate the soil porosity due to the presence of large stones (making it impossible to take intact soil samples), we assume that there were relatively large spaces at some study sites (e.g., in fractured, arenaceous marl bedrock). This seems to be an important factor for the vertical distribution of spiders.

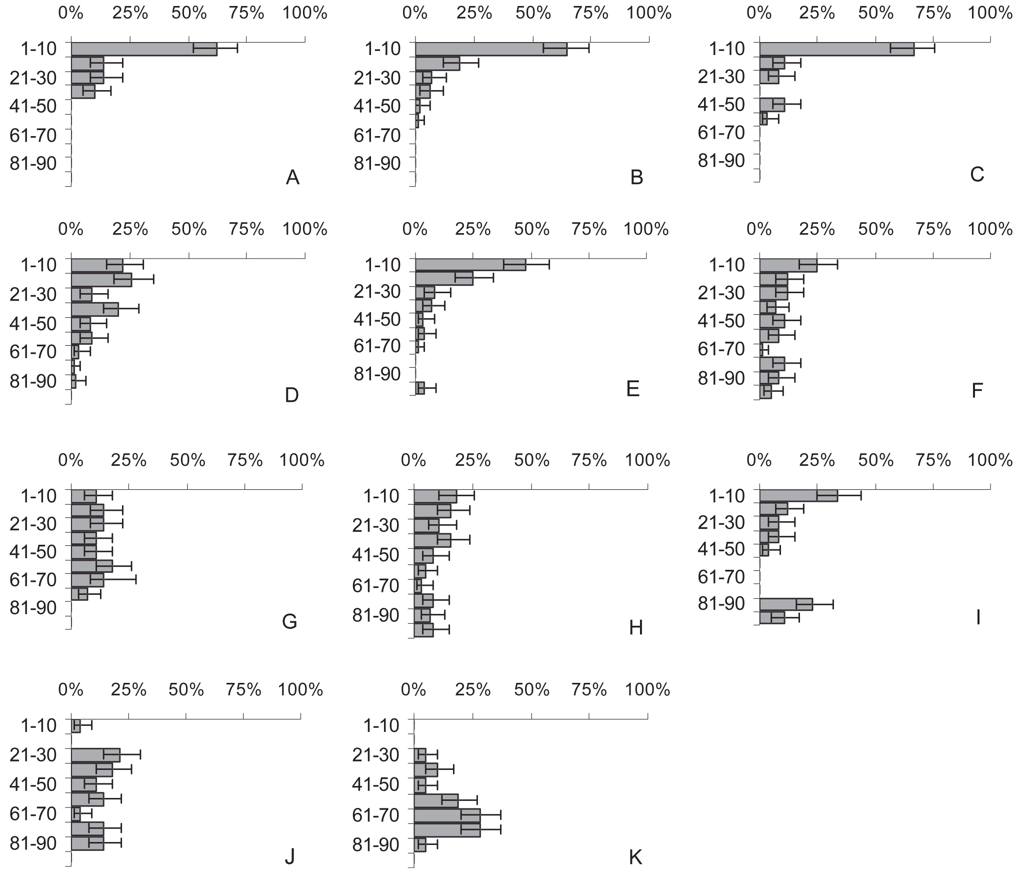

Figure 3.—Depth distribution of 11 species (more than 20 trapped specimens apiece). Bars represent mean proportions, whiskers are 95% confidence intervals. A – *Tenuiphantes flavipes* (mean record at 12 cm), B – *Oedothorax apicatus* (mean record at 11 cm), C – *Centromerus silvicola* (mean record at 10 cm), D – *Porrhomma microphthalmum* (mean record at 27 cm), E – *Harpactea lepida* (mean record at 19 cm), F – *Palliduphantes alutacius* (mean record at 38 cm), G – *Centromerus cavernarum* (mean record at 39 cm), H – *Cicurina cicur* (mean record at 40 cm), I – *Dysdera lantosquensis* (mean record at 40 cm), J – *Nesticus cellulanus* (mean record at 48 cm), K – *Porrhomma microps* (mean record at 61 cm).

Spiders were found to inhabit deeper soil layers in scree slopes with large soil spaces (*Above cave*, *Debris*, *Valley*, *Beech wood*, Fig. 1). Spiders were less common in the deeper soil layers in sites with small spaces and small stones. The *Beech wood* site was a different case, hosting spiders in the deep soil layer, which likely did not penetrate it from the surface. Spiders found here were microphthalmous species that can inhabit the subterranean environment created by systems of voids (MSS) in arenaceous marl bedrock exclusively. Presence of MSS is evident at sites *Above Cave* (corresponding with cave environment) and also *Valley* (Fig. 1).

Several species exhibit a clear tendency to live in deep soil layers. These belong to the families Linyphiidae, Dictynidae, and Nesticidae. Small body size results in a large ratio of surface area to volume, and vulnerability of desiccation. The deeper layers of soil can protect these individuals against desiccation. Such a pattern was described by Wagner et al. (2003) in the litter at a microscale level.

An affinity to a broad spectrum of subterranean habitats is found in species of the genus *Porrhomma*. A species recorded in this study, *P. microps*, has been repeatedly found in caves in Italy and in leaf litter in Germany (Růžička 2009). Although it also inhabits leaf litter in floodplain forests of the Czech Republic (Buchar & Růžička 2002), it was also recently found

Table 2.—Categorization of species by their affinity to depth and results of GLM model (Note: only values related to depth are presented).

Species	Category	*F*	*P*
Ceratinella brevis	1	3.78	0.03
Diplostyla concolor	1	24.91	< 1.0e-6
Eurocoelotes inermis	1	20.18	< 1.0e-6
Centromerus silvicola	2	5.12	0.01
Harpactea lepida	2	12.56	0.00
Oedothorax apicatus	2	3.51	0.04
Palliduphantes alutacius	2	3.62	0.03
Robertus lividus	2	4.71	0.01
Saloca diceros	2	3.17	0.05
Tenuiphantes flavipes	2	13.93	0.00
Centromerus cavernarum	3	1.75	0.18
Cicurina cicur	3	1.45	0.24
Dysdera lantosquensis	3	2.21	0.12
Pholcomma gibbum	3	2.97	0.06
Porrhomma microphthalmum	3	2.06	0.14
Nesticus cellulanus	3	0.96	0.39
Porrhomma microps	4	1.67	0.20

in karst and pseudokarst caves. *Porrhomma egeria* Simon 1884 was recorded in basalt scree slopes at a depth of about 1 m (Růžička et al. 1995) and in the block accumulations and crevice caves in a decaying gneiss massif at depths greater than 5 m (Růžička 1996). A troglomorphic population of *Porrhomma myops* Simon 1884 was recorded in caves and in andesite scree slopes at a depth of 40–100 cm (Růžička 2002), whereas an edaphomorphic population of this species was described from a deep soil layer (35–95 cm) in floodplain forest (Růžička et al. 2011). *Porrhomma microcavense* Wunderlich 1990 was recorded in an arenaceous marl layer (Kůrka et al. 2006). This rock is known to form extensive underground void systems, and we consider these void systems to be ideal locations for the future research of invertebrates in shallow subterranean habitats. This assumption is supported by a record of microphthalmous *Maro* sp. in a beech forest on arenaceous marl bedrock during our research.

Another species, *Zangherella relicta* (Kratochvíl 1935) (Anapidae) was described from caves in Montenegro, and recently it was found at several localities in Bulgaria, where it occurs exclusively in mountain scree slopes at depths of 40–50 cm (Deltshev et al. 2011). All these findings document individual phases of the evolutionary process leading to colonization of subterranean environment over the entire depth profile of the terrain (Růžička 1999a; Culver & Pipan 2009; Giachino & Vailati 2010).

ACKNOWLEDGMENTS

We hereby wish to thank G. Hormiga (George Washington University, Washington, D.C.) for his help with the identification of *Maro* species. The project was partially supported by the Ministry of Education, Youth, and Sport of the Czech Republic (IRP MSM 6046070901 and G4-2350/2008), by the National Research Program II (2B 06101), and by the Ministry of Agriculture of the Czech Republic (0002070203). We also wish to thank two anonymous reviewers and in particular the editor for valuable comments.

LITERATURE CITED

Barber, A.D. 1997. A simple shingle trap for myriapods. Bulletin of the British Myriapod Group 13:27–28.

Biteniekytė, M. & V. Rėlys. 2006. Investigation of activity and vertical distribution of spiders in *Sphagnum* tussocks of peat bogs. Biologija 1:77–82.

Buchar, J. & V. Růžička. 2002. Catalogue of Spiders of the Czech Republic. Peres, Praha.

Christian, E. 1999. From sand fissures to cave systems – subterranean biology in Austria. Pp. 121–126. *In* Lebensraum Blockhalde – Zur Ökologie periglazialer Blockhalden im außeralpinen Mitteleuropa. (B.M. Möseler & R. Molenda, eds.). Decheniana – Beihefte (Bonn).

Culver, D.C. & T. Pipan. 2009. Superficial subterranean habitats – gateway to the subterranean realm? Cave and Karst Science 35:5–12.

Deltshev, C., S. Lazarov, M. Naumova & P. Stoev. 2011. A survey of spiders (Araneae) inhabiting the eudaphic soil stratum and the superficial underground compartment in Bulgaria. Arachnologische Mitteilungen 40:33–46.

Giachino, P.M. & D. Vailati. 2010. The Subterranean Environment. Hypogean Life, Concepts and Collecting Techniques. WBA Handbooks, Verona.

Ilie, V. 2003. Chilopoda species from the edaphic and subterranean environments of the Cloşani karstic area (Romania). Travaux du Muséum National d′ histoire Naturelle "Grigore Antipa" 45:129–137.

Ilie, V., Ş. Negrea & B. Mitić. 2003. The diversity of the Chilopoda species from the karstic area of the Anina mountains (Banat, Romania). Archives of Biological Sciences, Belgrade 55:93–99.

Kůrka, A., J. Buchar, L. Kubcová & V. Bryja. 2006. Spiders (Araneae) of Kokořínsko Protected Landscape Area. Bohemia Centralis 27:91–135.

Negrea, Ş. 2004. On the Chilopoda from south-eastern Dobrogean karstic area (Romania). 3. The material collected using deep traps placed in drillings and artificial microcaves. Travaux du Muséum National d′ histoire Naturelle "Grigore Antipa" 47:111–128.

Paquin, P. & N. Dupérré. 2009. A first step towards the revision of *Cicurina*: redescription of type specimens of 60 troglobitic species of the subgenus *Cicurella* (Araneae: Dictynidae), and a first visual assessment of their distribution. Zootaxa 2002:1–67.

Platnick, N.I. 2010. The World Spider Catalog, version 10.5. American Museum of Natural History, New York. Online at http://research.amnh.org/entomology/spiders/catalog/index.html.

Řezáč, M., J. Král & S. Pekár. 2008. The spider genus *Dysdera* (Araneae, Dysderidae) in central Europe: revision and natural history. Journal of Arachnology 35:432–462.

Růžička, V. 1982. Modifications to improve the efficiency of pitfall traps. Newsletter of the British Arachnological Society 34:2–4.

Růžička, V. 1988. The longtimely exposed rock debris pitfalls. Acta Societatis Zoologicae Bohemicae 52:238–240.

Růžička, V. 1996. Species composition and site distribution of spiders (Araneae) in a gneiss massif in the Dyje river valley. Revue Suisse de Zoologie, vol. hors serie, 561–569.

Růžička, V. 1999a. The first steps in subterranean evolution of spiders (Araneae) in Central Europe. Journal of Natural History 33:255–265.

Růžička, V. 1999b. The freezing scree slopes and their arachnofauna. Pp. 141–148. *In* Lebensraum Blockhalde – Zur Ökologie periglazialer Blockhalden im ausseralpinen Mitteleuropa. (B.M. Möseler & R. Molenda, eds.). Decheniana – Beihefte (Bonn).

Růžička, V. 2002. Spatial distribution of spiders (Araneae) on scree slopes in Křivoklátsko and Moravský Kras Protected Landscape Areas. Acta Societatis Zoologicae Bohemicae 66:321–328.

Růžička, V. 2009. The European species of the *microphthalmum*-group in the genus *Porrhomma* (Araneae: Linyphiidae). Contributions to Natural History 12:1081–1094.

Růžička, V., J. Hajer & M. Zacharda. 1995. Arachnid population patterns in underground cavities of a stony debris field (Araneae, Opiliones, Pseudoscorpionidea, Acari: Prostigmata: Rhagidiidae). Pedobiologia 39:42–51.

Růžička, V. & L. Klimeš. 2005. Spider (Araneae) communities of scree slopes in the Czech Republic. Journal of Arachnology 33:280–289.

Růžička, V., V. Laška, J. Mikula & I.H. Tuf. 2011. Morphological adaptations of *Porrhomma* spiders (Araneae: Linyphiidae) inhabiting soil. Journal of Arachnology 39:355–357.

Schlick-Steiner, B.C. & F.M. Steiner. 2000. Eine neue Subterranfalle und Fänge aus Kärnten. Carinthia II 190:475–482.

Ter Braak, C.J.F. & P. Šmilauer. 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, New York.

Wagner, J.D., S. Toft & D.H. Wise. 2003. Spatial stratification in litter depth by forest-floor spiders. Journal of Arachnology 31:28–39.

Yamaguchi, T. & M. Hasegawa. 1996. An experiment on ant predation in soil using a new bait trap method. Ecological Research 11:11–16.

Manuscript received 15 August 2009, revised 9 May 2011.