

SHORT COMMUNICATION

Morphological adaptations of *Porrhomma* spiders (Araneae: Linyphiidae) inhabiting soil

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Abstract. We studied occurrence and morphological adaptations of two species of *Porrhomma* down to 135 cm soil depth. *Porrhomma microps* Simon 1884 inhabited soil layers at depths between 5 and 135 cm. *Porrhomma aff. myops* was found at depths of 35–95 cm. Specimens of both species were depigmented and had highly reduced eyes. Compared with the epigean *P. pygmaeum* (Blackwall 1834), *P. myops*, which inhabits scree and caves, exhibits significantly longer legs. We interpret it as an example of troglomorphism. Compared with the epigean *P. pygmaeum*, *P. aff. myops* is found deep in the soil and exhibits a significantly smaller cephalothorax. We interpret this as edaphomorphism. We assume the edaphomorphic population of *P. aff. myops* to be permanent soil dwellers.

Keywords: Araneae, soil profile, troglomorphisms, edaphomorphisms

Spiders inhabit a wide spectrum of underground habitats such as inner spaces in stony debris, scree layers in slope accumulations, fissure networks of the bedrock, karst and pseudokarst caves (Růžička 1999; Culver & Pipan 2009; Giachino & Vailati 2010). Numerous studies have been devoted to the cave arachnofauna (e.g., Deeleman-Reinhold 1978; Paquin & Dupérré 2009), and some studies have concerned spiders that inhabit the deep scree layers (Růžička et al. 1995; Růžička & Klimeš 2005). Other shallow underground habitats, known as superficial subterranean habitats, have also been investigated (Pipan et al. 2011; Deltshev et al. 2011). However, spiders occurring deep in soils have not yet been investigated. It has been assumed for a long time that spiders are not true soil inhabitants sensu Dunger (1983). But, very recently we (V. Laska unpublished) have found spiders deep in soil layers. How are these species adapted to life in the soil?

Zacharda (1979), studying the morphological adaptations of rhagidiid mites, distinguished two different classes of adaptations to life in the underground environment: edaphomorphism covers adaptations to life in the soil environment; and troglomorphism covers adaptations to life in the cave environment. Depigmentation, desclerotization, and the atrophy (even loss) of the eyes are characteristic for both types of adaptations. The shortening of appendages as well as shrinking of the body is typical for edaphomorphic species, whereas the elongation of appendages is typical for troglomorphic species. Christiansen (1992) surveyed the studies on troglomorphic species and concluded that the troglomorphic features are subject to selection and are therefore adaptive.

The tendency for colonization of shallow and deep subterranean space is characteristic of numerous species of the genus *Porrhomma*. Several species groups within this genus have been recognized. The *microphthalmum* group has been newly established, and the European species were revised by Růžička (2009). The *pygmaeum* group of the genus *Porrhomma* was studied by Bourne (1978). We studied occurrence of two *Porrhomma* species in the soil by means of subterranean traps. We then compared their morphology with other closely related species of the genus in order to identify adaptations for life in the soil.

We collected spiders at two sites: 1) A beech forest ($49^{\circ}50'N$, $16^{\circ}03'E$) near Skuteč, Eastern Bohemia, where the soil is composed of a thick layer of leaf litter covering an A-horizon (ca 15 cm), passing to

a thick clay soil layer above arenaceous marl bedrock; 2) A floodplain hardwood forest ($49^{\circ}39'N$, $17^{\circ}11'E$) dominated by *Fraxinus*, *Quercus* and *Tilia* on the bank of the Morava River near wet meadow, Litovelské Pomoraví Protected Landscape Area, Central Moravia. The soil there is a fluvisoil on gravels. The detritus fermentation layer is ca 3 cm thick. At both sites spiders were collected using subterranean traps (Schlick-Steiner & Steiner 2000) consisting of a set of removable plastic containers (volume of each = 250 ml) on a central metal axis. The containers were filled with a 4% formaldehyde solution and emptied at 6-wk intervals. Two traps with 14 containers were placed in the beech forest on 4 April 2008–20 April 2009; the deepest sampling depth was 135 cm. One trap with 10 containers was placed in the floodplain forest on 6 March–13 November 2008; the deepest sampling depth was 95 cm.

Material used for comparison came from various sites in the Czech Republic. *Porrhomma myops* Simon 1884 was collected in bare screes at Obří Zámek Mt., Ježerní Hora Mt., Týrov, Plešivec Mt., Kamenec Mt., Břidličná Mt., Suš Mt., Králický Sněžník Mt., Blansko; and in cave screes in Kateřinská cave, Horní v Chobotu cave and Ledové Sluje caves. *Porrhomma microps* (Roewer 1931) was collected in the soil in the same beech forest as above during our previous study and in forest litter in Lanžhot. *Porrhomma pygmaeum* (Blackwall 1834) was collected in wetlands in Míšov, Třeboň, Suchdol nad Lužnicí, Chlum u Třeboně-Lutová, Sedlec, and Milotice.

Specimens were measured using a BX-40 compound microscope. All measurements are in millimeters. Abbreviations: Cth = cephalothorax, Mt I = metatarsus of the first leg, PME – posterior median eye. Voucher specimens are deposited in the collection of V. Růžička at the Biology Centre, České Budějovice.

Porrhomma microps occurred at depths of 65–135 cm (mean = 80 cm) in the beech forest, and in the floodplain forest it was found at depths of 5–45 cm (mean = 20 cm). All specimens were pale with highly reduced eyes (Table 1). *Porrhomma microps* is known as an inhabitant of leaf litter (Buchar & Růžička 2002). Specimens from both microhabitats exhibited similar Mt I/Cth width ratio ($t = 1.2$, $df = 33$, $P = 0.229$, Fig. 1).

Porrhomma aff. myops was found at depths of 35–95 cm (mean = 80 cm) in the floodplain forest. It was pale and also had highly reduced eyes (Table 1). At this locality *P. aff. myops* was found significantly deeper in the soil profile than *P. microps* ($t = -4.9$, $df =$

Table 1.—Overview of characteristics for study *Porrhomma* species. See text for abbreviations. Mean (SD) is given for measurements.

Species	Microhabitat	No. of specimens	PME	PME–PME interdistance	Cth width	Mt I length
<i>P. microps</i>	litter	10	0.035	0.050	0.843 (0.052)	0.973 (0.058)
<i>P. microps</i>	soil	25	0.030	0.050	0.861 (0.034)	0.951 (0.043)
<i>P. aff. myops</i>	soil	8	0.015	0.040	0.574 (0.009)	0.499 (0.012)
<i>P. myops</i>	scree	26	0.025	0.045	0.686 (0.031)	0.862 (0.057)
<i>P. pygmaeum</i>	soil surface	31	0.050	0.050	0.670 (0.020)	0.562 (0.033)

10, $P < 0.001$). Additionally, the cephalothorax width of *P. aff. myops* was significantly smaller than that of *P. microps* ($t = -22.7$, $df = 10$, $P < 0.001$, Table 1).

In comparison with *Porrhomma myops*, an inhabitant of scree and caves (Buchar & Růžička 2002), the specimens of *P. aff. myops* from the deep soil layer exhibited a significantly different Mt I/Cth width ratio ($t = 20.8$, $df = 32$, $P < 0.001$, Fig. 2).

We compared *P. myops* from scree and *P. aff. myops* from the deeper soil layers with the closely related *Porrhomma pygmaeum*. This species is epigaeic and pigmented, with fully developed eyes. Both morphotypes of *P. myops* were distinguished from *P. pygmaeum* by reduction of the eyes (Table 1). Furthermore, there was a significant difference ($t = 31.6$, $df = 55$, $P < 0.001$) in the Mt I/Cth width ratio between *P. myops* and *P. pygmaeum* (Table 1). *Porrhomma myops* inhabiting scree exhibited relatively longer metatarsi of the first legs. We interpret this adaptation as a troglomorphism. There was a significant difference ($t = -9.3$, $df = 37$, $P < 0.001$) between the cephalothorax width of *P. aff. myops* and *P. pygmaeum* (Table 1). *Porrhomma aff. myops* inhabiting soil exhibited a smaller cephalothorax, which we interpret as an edaphomorphism.

Previously Růžička (1996) documented the occurrence of two other troglomorphic species in underground spaces (fissure caves, talus caves) in a decaying gneiss massif. Specifically, *Improphanes improbulus* (Simon 1929) inhabited the spaces at depths of about 0.5–5 m, and *Porrhomma egeria* Simon 1884 inhabited spaces at depths from 5 to 10 m. In this study, we documented the occurrence

of two microphthalmous species from the genus *Porrhomma* in the soil profile.

The leg elongation is characteristic for invertebrates inhabiting subterranean habitats fashioned by spaces larger than their body dimensions. It has been documented in a series of closely related cave spiders from the genus *Troglohyphantes* (Deeleman-Reinhold 1978), in a series of cave spiders from the genus *Nesticus* (Kratochvíl 1933, 1978), in two linyphiid subspecies *Bathyphantes eumenis buchari* (L. Koch 1879) and *Wubanoides uralensis lithodytes* Schikora 2004 (Růžička 1988, Schikora 2004), in subterranean populations of *Leptophantes improbulus* Simon 1929, and *Theonoe minutissima* (O. Pickard-Cambridge 1879) (V. Růžička 1998). Leg elongation has been also found in Sclerobuninae harvestmen from deep stony debris (Derkarabetian et al. 2010). J. Růžička (1998) documented a gradient of increasing length of body appendages from epigean – to rock debris dwelling – through cave-dwelling species of *Choleva* (Coleoptera).

The interstices in the deeper soil layers are of comparable dimensions to invertebrate body dimensions, and body diminution (compared with their epigean relatives) is characteristic for soil inhabitants. In addition to the troglomorphic *P. myops*, we found edaphomorphic *P. aff. myops*. Since the specimens of *P. aff. myops* were collected at similar depth throughout the season, we consider the population of *P. aff. myops* to be a permanent soil dweller sensu Dunger (1983).

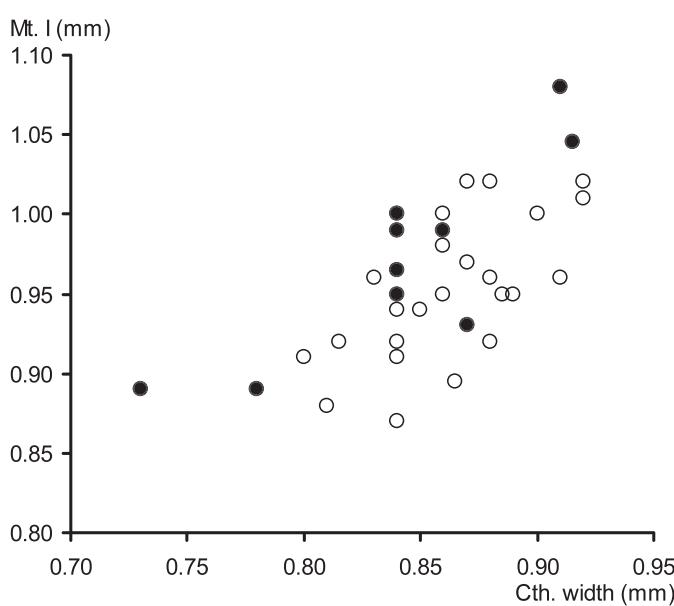


Figure 1.—Relationship between the cephalothorax width and the length of metatarsus I in *Porrhomma microps*. Specimens from leaf litter (full circles); specimens from soil (open circles).

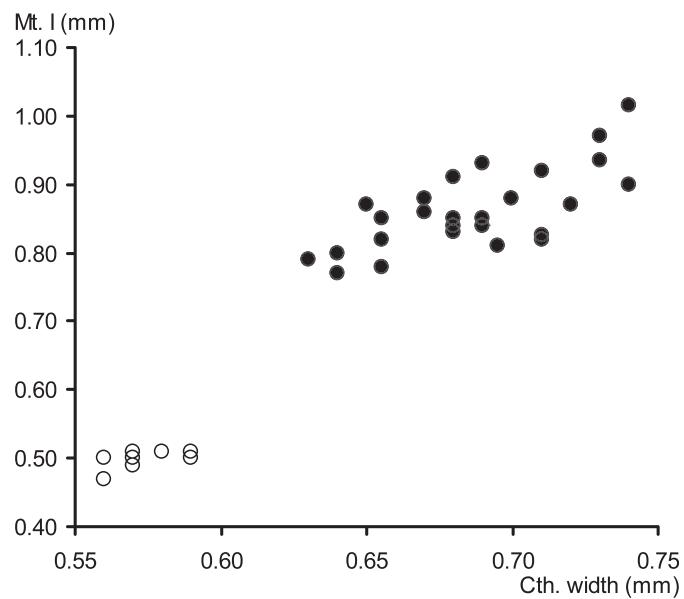


Figure 2.—Relationship between cephalothorax width and length of metatarsus I in *Porrhomma myops* (specimens from scree and caves, full circles) and *Porrhomma aff. myops* (specimens from soil, open circles).

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LITERATURE CITED

- Bourne, J.D. 1978. A contribution to the study of the genus *Porrhomma* (Araneae: Linyphiidae). Notes on a population of *P. egeria* (Simon) and other cavernicolous species. International Journal of Speleology 9:86–96.
- Buchar, J. & V. Růžička. 2002. Catalogue of Spiders of the Czech Republic. Peres, Praha.
- Christiansen, K. 1992. Biological processes in space and time. Cave life in the light of modern evolutionary theory. Pp. 453–478. In The Natural History of Biospeleology. (A.I. Camacho, ed.). Museo Nacional de Ciencias Naturales, Madrid.
- Culver, D.C. & T. Pipan. 2009. Superficial subterranean habitats – gateway to the subterranean realm? Cave and Karst Science 35[2008]:5–12.
- Deeleman-Reinhold, C.L. 1978. Revision of the cave-dwelling and related spiders of the genus *Troglohyphantes* Joseph (Linyphiidae), with special reference to the Yugoslav species. Slovenska akademija znanosti in umetnosti, Ljubljana.
- Deltshev, C., S. Lazarov, M. Naumova & P. Stoev. 2011. A survey of spiders (Araneae) inhabiting the euedaphic soil stratum and the superficial underground compartment in Bulgaria. Arachnologische Mitteilungen 40:33–46.
- Derkarabetian, S., D.B. Steinmann & M. Hedin. 2010. Repeated and time-correlated morphological convergence in cave-dwelling harvestmen (Opiliones, Laniatores) from montane western North America. PLoS One 5(5):e10388.
- Dunger, W. 1983. Tiere im Boden. A. Ziemsen, Wittenberg Lutherstadt.
- Giachino, P.M. & D. Vailati. 2010. The Subterranean Environment. Hypogean Life, Concepts and Collecting Techniques. WBA Handbooks, Verona.
- Kratochvíl, J. 1933. [European species of the family Nesticidae Dahl]. Práce Moravské přírodovědecké společnosti 8(10):1–69 (in Czech, French summary).
- Kratochvíl, J. 1978. Araignées cavernicoles des îles dalmates. Acta scientiarum naturalium Academiae scientiarum bohemoslovacae – Brno 12(4):1–59.
- 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.
- Pipan, T., H. López, P. Oromí, S. Polak & D.C. Culver. 2011. Temperature variation and the presence of troglobionts in terrestrial shallow subterranean habitats. Journal of Natural History 45:253–273.
- Růžička, J. 1998. Cave and rock debris dwelling species of the *Choleva agilis* species group from central Europe (Coleoptera, Leiodidae: Cholevinae). Pp. 261–286. In Phylogeny and Evolution of Subterranean and Endogeal Cholevidae (= Leiodidae Cholevinae). Proceedings of a Symposium. (P.M. Giachino & S.B. Peck, eds.). Museo Regionale di Scienze Naturali, Torino.
- Růžička, V. 1988. Problems of *Bathyphantes eumenis* and its occurrence in Czechoslovakia (Araneae, Linyphiidae). Věstník Československé společnosti zoologické 52:149–155.
- Růžička, V. 1996. Species composition and site distribution of spiders (Araneae) in a gneiss massif in the Dyje river valley. Revue Suisse de Zoologie, volume hors série, 561–569.
- Růžička, V. 1998. The subterranean forms of *Leptophantes improbus*, *Theonoe minutissima* and *Theridion bellicosum* (Araneae: Linyphiidae, Theridiidae). Pp. 101–105. In Proceedings of the 17th European Colloquium of Arachnology. (P.A. Selden, ed.). British Arachnological Society, Burnham Beeches, Buckinghamshire, UK.
- Růžička, V. 1999. The first steps in subterranean evolution of spiders (Araneae) in Central Europe. Journal of Natural History 33:255–265.
- 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 (Aranea, 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.
- Schikora, H.-B. 2004. *Wubanoides uralensis* (Pakhorkov 1981) – Geographic variation, mating behaviour, postembryonic development and description of a new subspecies (Araneae, Linyphiidae). Pp. 271–280. In Diversität und Biologie von Webspinnen, Skorpionen und Anderen Spinnentieren. (K. Thaler, ed.). Denisia 12. Biologiezentrum/Oberösterreichisches Landesmuseum, Linz, Austria.
- Schlück-Steiner, B.C. & F.M. Steiner. 2000. Eine neue Subterraneanfalle und Fänge aus Kärnten. Carinthia II 190:475–482.
- Zacharda, M. 1979. The evaluation of the morphological characters in Rhagidiidae. Pp. 509–514. In Recent Advances in Acarology I. (J.G. Rodriguez, ed.). Academic Press, New York.

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