1998. P. A. Selden (ed.). *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997.*

The subterranean forms of *Lepthyphantes improbulus*, *Theonoe minutissima* and *Theridion bellicosum* (Araneae: Linyphiidae, Theridiidae)

Vlastimil Růžička

Institute of Entomology, Czech Academy of Sciences, Branišovská 31, 370 05 České Budějovice, Czech Republic

Summary

Three new spider forms are described. The subterranean forms of *Lepthyphantes improbulus* Simon, 1929, and of *Theonoe minutissima* (O. P.-Cambridge, 1879) are characterized by leg elongation (troglomorphism); the subterranean form of *Theridion bellicosum* Simon, 1873, is characterized by leg shortening (edaphomorphism). All three forms occur within scree accumulations or in shallow cave spaces. They represent indicators of the first steps of underground evolution of spiders which take place on microclimatic gradients in shallow underground spaces.

Introduction

Steep microclimatic gradients exist between the surface and the inner spaces in scree accumulations. The temperature at the scree surface fluctuates appreciably during the day and during the year, whilst the sheltered inner spaces at depths below 1 m exhibit no daily fluctuations, and yearly fluctuations are about half those at the surface (Růžička *et al.*, 1995; Molenda, 1996). The temperature range narrows in deeper scree layers and in subsurface rock fissures (shallow underground spaces). The temperature stabilizes to an average temperature for the respective region in deep underground spaces (caves which are accessible to man). Humidity exhibits a similar stabilizing trend. The adaptation of invertebrates to underground conditions takes place on this microclimatic gradient. Depigmentation, desclerotization, eye reduction, elongation of extremities and hypertrophy of sensory organs represent characteristic expressions of this process (Christiansen, 1992). Subterranean forms can be connected with surface ones by a continuous series of transition forms; specimens of *Porrhomma egeria* have fully pigmented eyes in the surroundings of mountain snow fields, reduced eyes in boulder accumulations, and exhibit various degrees of eye loss in caves (Miller & Kratochvíl, 1940; Sanocka, 1982). Two forms have been recognized morphologically, related to ecological differentiation: *Bathyphantes simillimus buchari* Růžička, 1988, living within scree accumulations, has significantly longer legs in comparison with *B. s. simillimus* (L. Koch, 1879), living among sandstone rocks (Růžička, 1988b).

Here, I compare the length of leg segments and other morphological features of surface and subterranean populations of three species.

Lepthyphantes improbulus Simon, 1929

Material

Subterranean form: 17♂, south Moravia, Podyjí (Thayatal) National Park, Vranov nad Dyjí, Ledové Sluje (Ice Caves) locality, pseudokarst caves and block debris, desk pitfall traps, collected 1992–1994 (Růžička, 1996b). Other ♂♂ and ♀♀ from boulder debris in Podyjí National Park and from other localities in the Czech Republic and Austria (Růžička, 1996a).

Diagnosis and comments

The specimens from shallow underground spaces in Central Europe differ from type specimen from the Pyrenees in their smaller bodies and relatively longer legs (Fig. 1); they represent the subterranean form. The males and females of this form are identical in their genitalia with those described by Moritz (1972). The subterranean form occurs in Central and Southern Europe in shallow undergound spaces—inner spaces of stony debris (Thaler, 1986b; Růžička, 1996a), pseudokarst caves (Růžička, 1996b), cave entrances (Kratochvíl & Miller, 1939), shallow caves in sulphate karst (Moritz, 1972), under rocks and in rock fissures (Miller & Svatoň, 1978). However, in the case of other material from the Pyrenees it is not known whether the subterranean forms are connected with the surface ones, with transitional forms, or if these two forms are morphologically and ecologically separated.

Theonoe minutissima (O. P.-Cambridge, 1879)

Material

Subterranean form: 13♂, 9♀, from scree slopes in the Czech Republic (see Růžička, 1988a; Růžička *et al.*, 1989; Růžička & Hajer, 1996).

Typical form for comparison: 10♂, 10♀, North Moravia, Jeseníky Mts, Rejvíz peat bog, leg. P. Kasal; 1♂, North Bohemia, peat bog at the Břehyně pond, 7 October 1993, leg. A. Kůrka; 1♀, Finland, Koli, peat bog, 21 September 1961; 1♀, Finland, Tvärminne, swamp spruce forest, 22 August 1964, leg. P. Palmgren; 4♂, Norway, Hovdane and Sœlelid, pine forest, 23 April–21 May 1992, leg. G. A. Helversen.

Diagnosis and comments

The subterranean form differs from the typical form in having relatively longer legs; Ta I is not shorter than 0.29 mm at the same cephalothorax width (0.40–0.44 mm) (Fig. 1). Růžička & Hajer (1996) pointed to the diplostenoecy in this species. The subterranean form occurs within scree accumulations, whilst the typical form occurs in peat bogs in Central Europe and in peat bogs and in the moss of swamp forests in Northern Europe .

Theridion bellicosum Simon, 1873

Material

Subterranean form: 2♀, North Bohemia, Lovosice, Lovoš Mt, basalt scree slope, desk pitfall trap, May–August 1980 (Růžička, 1989); 2♂, 6♀, Montenegro, Durmitor, individual sampling, 7–9 July 1985 (Růžička, 1992).

Typical form for comparison: 54♀ and an adequate number of ♂♂ from throughout the Czech Republic (Růžička, 1989).

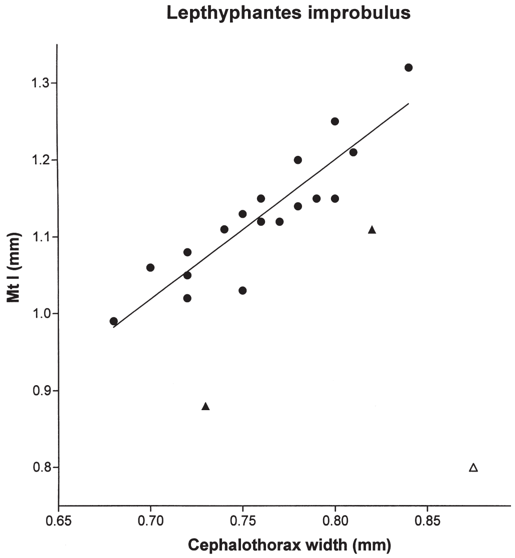
Diagnosis and comments

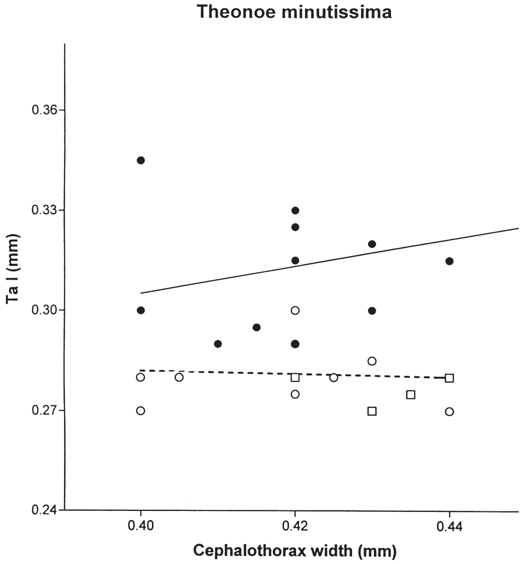
The depigmentation and smaller body size of specimens from the inner spaces of scree slopes was described by Růžička (1989). In comparison with the typical form, the subterranean form exhibits relatively shorter legs and the absence of dark pigment. Mt I of the subterranean form in not longer than 1 mm (Fig. 1). The typical pigmented form occurs in Central Europe in scree slopes and in other stony habitats at higher altitudes. The subterranean form was found within scree accumulations in North Bohemia, in the warmest territory of the Czech Republic, and in mountain scree slopes on Durmitor. All specimens from Durmitor are quite depigmented. They are identical with Czech specimens in body dimensions and leg length, but they differ from them in showing dark eye pigmentation.

Discussion

The subterranean forms of *L. improbulus* and *T. minutissima* differ from typical forms by their relatively long legs, which is taken as an adaptation to underground life: troglomorphism. In contrast, the subterranean form of *T. bellicosum* exhibits relatively shorter legs in comparison with the typical form. This can be explained as edaphomorphism (Zacharda, 1979): adaptation to life in narrow soil spaces. Maybe the subterranean form of *T. bellicosum* inhabits somewhat deeper, narrower spaces in scree accumulations or the cracks in massive rock into which we are not able to penetrate.

The evolutionary history of the subterranean forms of *T. minutissima* and *Bathyphantes simillimus buchari* (see Růžička, 1988b, 1994) is connected with faunal migrations during the





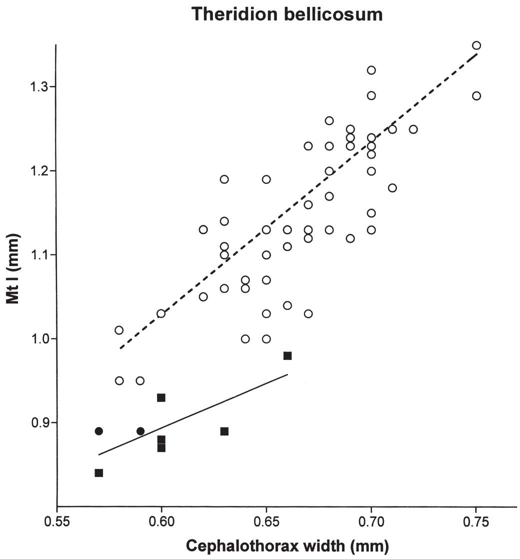


Fig. 1: Correlation of podomere length and cephalothorax width in the three species studied. Filled symbols = underground forms, empty symbols = surface forms. Circles = material examined from the Czech Republic, squares = material examined from other countries, triangles = literature data.

Lepthyphantes improbulus. ♂♂, cephalothorax width and length of Mt I. Underground form: filled circles = material from scree fields and shallow caves in Podyjí National Park, $y = 1.82x - 0.25$; filled triangles = literature data, material from shallow caves in sulphate karst in Kyffhäusergebirge Mts (Moritz, 1972), and cave entrance in Moravian karst (Kratochvíl & Miller, 1939). Typical form: open triangle = type material from the Pyrenees (Moritz, 1972).

Theonoe minutissima. ♂♂, cephalothorax width and length of Ta I. Subterranean form: filled circles = material from the scree fields in the Czech Republic, $y = 0.40x + 0.14$. Typical form: open circles = material from peat bogs in the Czech Republic, open squares = material from peat bogs and forests in Norway and Finland.

Theridion bellicosum. ♀♀, cephalothorax width and length of Mt I. Subterranean form: filled circles = material from scree fields in North Bohemia, filled squares = material from scree fields in Montenegro, $y = 1.07x + 0.25$. Typical form: open circles = material from scree slopes in the Czech Republic, $y = 2.07x - 0.23$.

Quaternary glaciations. Both species are of northern provenance: the surface form of *T. minutissima* inhabits northern forests and peat bogs; *B. simillimus simillimus* is known from stony habitats in higher latitudes. These surface forms migrated under pressure of the glaciation in Central Europe. They were probably widespread in the cold climate tundra in the periglacial zone, and moved back into cold territories during climate warming in interglacials and during the Holocene, and/or searched for suitable habitats in the territory colonized. In both cases, they found two cold and humid habitats: sandstone rocks and stony debris by *B. simillimus*; peat bogs and stony debris by *T. minutissima*. These two habitats started to differentiate and become isolated during climate warming and thus the ecological barrier between the two populations was formed. Surface populations persisted in island ecosystems; the populations inhabiting the stony debris started to search for more cold and humid environments in the deeper layers and therefore became adapted to the underground environment.

An analogous separation between a surface dweller and an underground form living within stony debris has also been demonstrated in the genus *Troglohyphantes* (Deeleman-Reinhold, 1978; Thaler, 1986b). Deeleman-Reinhold (1981) studied blind cave spiders in Yugoslavia; in all cases studied, the blind species were found to be closely associated taxonomically with normal-eyed species, but they were never from the same area. In the Czech Republic, I found that where ancestral surface populations still persist in island habitats in the same area as the descendent troglomorphic populations, the surface and subterranean forms were separated by ecological factors.

All three forms described occur within scree accumulations or in shallow cave spaces and void systems, and represent indicators of the first steps of underground evolution of spiders, which take place on microclimatic gradients in shallow underground spaces.

Acknowledgements

I dedicate this study to my mother Vlasta Růžičková, and to master watchmakers, my father František Růžička sen. and my brother František Růžička jun. I thank the Museum of Zoology, University of Bergen (Drs E. Hauge and L. Greve Jensen), the Zoological Museum, University of Helsinki (Dr J. Terhivuo), MUDr P. Kasal and RNDr A. Kůrka for the kind loan of material. I thank Ing. J. Havelka for his help with graph preparation. This study was supported by the Grant Agency of the Czech Republic (Project No. 206/96/0326).

References

CHRISTIANSEN, K. 1992: Biological processes in space and time. Cave life in the light of modern evolutionary theory. *In* A. I. Camacho (ed.). *The natural history of biospeleology*. Monografias del Museo nacional de Ciencias Naturales. Madrid: C.S.I.C.: 453–478.

DEELEMAN-REINHOLD, C. 1978: Revision of the cave-dwelling and related spiders of the genus *Troglohyphantes* Joseph (Linyphiidae), with special reference to the Yugoslav species. *Razpr. Slov. Akad. Znan. Umet*. **23**: 3–220.

DEELEMAN-REINHOLD, C. 1981: Remarks on origin and distribution of troglobitic spiders. *In* B. F. Beck (ed.). *Proceedings of the 8th International Congress of Speleology, Bowling Green, USA*. USA: International Union of Speleology: 305–308.

KRATOCHVÍL, J. & MILLER, F. 1939: *Lepthyphantes spelaeomoravicus* n. sp. (Aran.) de la grotte »Býčí skála« en Moravie. *Sb. Klubu přír. Brně* **22**: 1–7. [In Czech, French abstract].

MILLER, F. & KRATOCHVÍL, J. 1940: Ein Beitrag zur Revision der mitteleuropäischen Spinnenarten aus der Gattung *Porrhomma* E. Sim. *Zool. Anz.* **130**: 161–190.

MILLER, F. & SVATOŇ, J. 1978: Einige seltene und bisher unbekannte Spinnenarten aus der Slowakei. *Annotnes Zool. Bot. Bratislava* **126**: 1–19.

MOLENDA, R. 1996: Zoogeographische Bedeutung Kaltluft erzeugender Blockhalden im außeralpinen Mitteleuropa: Untersuchungen an Arthropoden, insbesondere Coleoptera. *Verh. naturw. Ver. Hamburg N.F.* **35**: 5–93.

MORITZ, M. 1972: *Lepthyphantes improbulus* Simon, 1929, eine troglobionte Spinne des Kyffhäusergebirges (Araneae, Linyphiidae). *Dt. ent. Z. N.F.* **19**: 307–314.

RŮŽIČKA, V. 1988a: Pavouci šumavských sutí a balvanových moří. Spinnen (Araneae) aus Blockfeldern in Šumava (Böhmerwald, Südböhmen). *Sb. Jihočesk. Muz. Českých Budějovicích* **28**: 73–82. [In Czech, German abstract].

RŮŽIČKA, V. 1988b: Problems of *Bathyphantes eumenis* and its occurrence in Czechoslovakia (Araneae, Linyphiidae). *Věst. čsl. Spol. zool.* **52**: 149–155.

RŮŽIČKA, V. 1989: On the lithobionts *Lepthyphantes notabilis*, *Rugathodes bellicosus* and on *Rugathodes instabilis* (Araneae: Linyphiidae, Theridiidae). *Acta ent. bohemoslovaca* **86**: 432–441.

RŮŽIČKA, V. 1992: Some spider species from the rock debris of the Rumanian and Yugoslav mountain ranges. *Fragm. balcan.* **15**: 1–6.

RŮŽIČKA, V. 1994: Spiders of the Průčelská Rokle defile, Klíč Mt. and Zlatník Mt. in North Bohemia. *Fauna Bohem. Septentr.* **19**: 129–138.

RŮŽIČKA, V. 1996a: Pavouci kamenitých sutí a pseudokrasových slují Národního parku Podyjí. Spiders of stony debris and pseudokarst caves in Podyjí National Park. *In* B. Gruna & A. Reiter (eds.). *Výzkum lokality Ledové sluje u Vranova nad Dyjí (NP Podyjí). Přír. Sb. Prací Ochr. přír. Praha* **3**: 123–132. [In Czech, English abstract].

RŮŽIČKA, V. 1996b: Species composition and site distribution of spiders (Araneae) in a gneiss massif in the Dyje river valley. *Revue suisse Zool.* **Vol. hors série 2**: 561–569.

RŮŽIČKA, V., BOHÁČ, J., SYROVÁTKA, O. & KLIMEŠ, L. 1989: Bezobratlí kamenitých sutí v severních Čechách (Araneae, Opiliones, Coleoptera, Diptera). Invertebrates from rock debris in north Bohemia (Araneae, Opiliones, Coleoptera, Diptera). *Sb. severočesk. Mus.* **17**: 25–36. [in Czech, English abstract].

RŮŽIČKA, V. & HAJER, J. 1996: Spiders (Araneae) of stony debris in North Bohemia. *Arachnol. Mitt.* **12**: 46–56.

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

SANOCKA, E. 1982: Eye regression in *Porrhomma moravicum* Mill. et Krat. (Aranei). *Zoologica Pol.* **29**: 13–21.

THALER, K. 1986a: Über einige Funde von *Troglohyphantes*-Arten in Kärnten (Österreich) (Arachnida, Aranei: Linyphiidae). *Carinthia II* **176/96**: 287–302.

THALER, K. 1986b: Vier bemerkenswerte *Lepthyphantes*-Arten aus dem Mittelmeergebiet und aus Vorderasien (Arachnida: Aranei, Linyphiidae). *Sber. öst. Akad. Wiss., Abt. I* **194** [1985]: 311–325.

ZACHARDA, M. 1979: The evaluation of the morphological characters in rhagidiidae. *In* J. G. Rodriguez (ed.). *Recent advances in acarology,* **I**. New York: Academic Press: 509–514.