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ORIGINAL ARTICLE

The distribution of purse-web *Atypus* spiders (Araneae: Mygalomorphae) in central Europe is constrained by microclimatic continentality and soil compactness

Milan Řezáč[1,2]*, Veronika Řezáčová[3] and Stano Pekár[4]

[1]*Research Institute of Crop Production, Drnovská 507, 161 06 Prague 6-Ruzyně, Czech Republic,* [2]*Department of Zoology, Faculty of Sciences, Charles University, Viničná 7, 128 44 Prague 2, Czech Republic,* [3]*Microbiological Institute CAS, Vídeňská 1083, 142 20 Prague 4, Czech Republic and* [4]*Institute of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic*

*Correspondence: Milan Řezáč, Research Institute of Crop Production, Drnovská 507, 161 06 Prague 6-Ruzyně, Czech Republic.
E-mail: rezac@vurv.cz

ABSTRACT

Aim Three species of primitive spiders of the genus *Atypus* occur in European xerothermic habitats, where they live in burrows. The aim of this study is to explain their distribution by investigating environmental variables at sites where they occur in central Europe.

Location Over 50 sites in central Europe, Czech Republic.

Methods Data on climatic, edaphic and vegetational parameters were collected from more than 50 sites. Phytocenological data were processed using Ellenberg's indicator values.

Results *Atypus muralis* was found to occur almost exclusively in dry grassland (Festucion valesiacae), exposed to a continental microclimate. *Atypus affinis* usually occurred in dry sparse forests (Genisto germanicae–Quercion) that provide an Atlantic microclimate. *Atypus piceus* occurred in dry grassland (Bromion erecti) or forest fringes (Geranion sanguinei) characterized by an intermediate microclimate. *Atypus piceus* and *A. muralis* were restricted to agglutinate calcareous soils.

Main conclusions Our results show that *Atypus* species colonized sites with different continentality in central Europe. These differences correspond to differences among their probable glacial refugia. *Atypus muralis* and *A. piceus* occur in habitats with a markedly continental climate, and are restricted to calcareous agglutinate soils that more efficiently buffer temperature and humidity extremes. Habitats of *A. muralis* and *A. piceus* are threatened by overgrowth of vegetation after a recent decline in grazing and by the decalcification of the landscape. However, habitats of *A. affinis* are stable in the present central European climate.

Keywords
***Atypus*, burrowing spiders, central Europe, climatic conditions, distribution limitations, edaphic conditions, glacial refugia, habitat preferences, post-glacial colonization.**

INTRODUCTION

When Latreille used the name *Atypus* for purse-web spiders in the early 19th century, he emphasized their uniqueness. These spiders, with a body length of up to 2.5 cm, are the only central European members of the archaic infraorder Mygalomorphae. Except for *Atypus*, the family Atypidae contains two other genera – Asian and African *Calommata* and North American *Sphodros* (Platnick, 2006). *Sphodros* spiders, the closest relatives of *Atypus*, are inhabitants of dry forests on sandy soils. Some species can even be found in deep forests with damp soil (Gertsch, 1979).

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The majority of species in the genus *Atypus* occur in dense mountain forests of Southeast Asia (Schwendinger, 1990). A single species, *Atypus snetsingeri* Sarno, 1973, is found in the USA; three species, namely *Atypus piceus* (Sulzer, 1776), *Atypus muralis* Bertkau, 1890 and *Atypus affinis* Eichwald, 1830, are known from Europe (Schwendinger, 1990). European species are morphologically very uniform. They differ in the morphology of their posterior lateral spinnerets. In *A. muralis* the spinnerets are four-segmented, and in *A. affinis* three-segmented. In *A. piceus* there are hints of a fourth segment (Kraus & Baur, 1974). The species also differ in body size, *A. muralis* being the largest and *A. affinis* being the smallest (Kraus & Baur, 1974).

All three European species live inside simple vertical burrows. These spiders dig burrows using robust basal cheliceral segments (Miller, 1947). The depth of burrows depends on the age of a specimen and the type of soil; in adults it can be up to 90 cm deep (Meyer, 1928). Spiders line their burrows with a dense web, which protrudes above the surface as a purse-web about 10 cm long (Bristowe, 1958). The horizontal position of purse-webs, characteristic of European species, is considered to be an adaptation for capturing prey under snow cover (Schwendinger, 1989). It is difficult to find *Atypus* purse-webs as the spiders camouflage their outer surface with soil particles.

Atypus usually occur in clusters called colonies (Kraus & Baur, 1974). Their abundance in such spots can reach up to 90 individuals m^{-2} (Hiebsch & Krause, 1976). *Atypus* have the longest life cycle of all central European spiders. They do not mature before their third year and females can live for up to 10 years (Schwendinger, 1989). European species differ in the period of sexual activity. *Atypus muralis* and *A. piceus* are sexually active in summer while *A. affinis* is sexually active in autumn and spring (Kraus & Baur, 1974). Copulation takes place in the female's burrow and lasts for several hours (Wiehle, 1953). Females lay eggs in a cocoon during the following summer (Hiebsch & Krause, 1976). In spring of the following year juveniles of the second instar leave the maternal burrow and search for a place to establish their own burrows (Yoshikura, 1958; Žďárek, 1965). In contrast to the majority of other mygalomorph spiders, atypid juveniles still possess anterior lateral spinnerets that produce gossamer (Hajer, 1997). However, unlike araneomorph spiders, they can perform only primitive ballooning that allows them to disperse relatively short distances (Coyle *et al.*, 1985).

The centre of *A. affinis* distribution lies in western Europe, particularly in the Iberian Peninsula (Schwendinger, 1989). This species may also occur in North Africa as three taxa described from north Algeria and Morocco, *Atypus coriaceus* Simon, 1881, *Atypus cedrorum* Simon, 1881 and *Atypus affinis major* Simon, 1909, have been temporarily considered to be synonyms of this species (Schwendinger, 1989; Platnick, 2006). Of all *Atypus* species, the distribution of *A. affinis* is the northernmost, including Great Britain, Denmark and southern Sweden (Kraus & Baur, 1974). It reaches as far to the east as Belarus, western Ukraine and Moldova (Mikhailov, 1997). The distributional centre of *A. piceus* is in central Europe and the Balkan Peninsula (Schwendinger, 1989). A record from Iran probably refers to another, undescribed species (Schwendinger, 1989). The distribution centre of *A. muralis* is the area around the Black Sea (Kraus & Baur, 1974). This species reaches as far west as Germany, Switzerland and northern Italy (Schwendinger, 1989). Thus, the distributional areas of all three species overlap in central Europe, particularly in the Czech Republic, Slovakia, Germany, Austria, Hungary, Poland, northern Italy and Switzerland (Fig. 1; Kraus & Baur, 1974; Schwendinger, 1990; Gajdoš *et al.*, 1999).

As the distributional areas of these species contain different glacial refugia (in the sense of Lattin, 1949), it is suspected that they colonized central Europe from different refugia after the last glacial period. *Atypus muralis* arrived from a Caspian refugium, *A. affinis* from an Atlantic-Mediterranean refugium and *A. piceus* from a Ponto-Mediterranean refugium, presumably from the Balkans (Kraus & Baur, 1974; Malicky *et al.*, 1983; Schwendinger, 1989; names of refugia after Lattin, 1949). Thus, these spiders may represent three main colonization routes of thermophilic organisms to central Europe (see Hewitt, 2001). The refugia mentioned above differed in their environmental conditions. The Caspian refugium was characterized by a continental climate while the Atlantic–Mediterranean refugium was characterized by an Atlantic climate. The Ponto-Mediterranean refugium was climatically intermediate between these two (Lamb, 1972).

We hypothesized that if *Atypus* species dispersed to central Europe from refugia characterized by different conditions, they would have colonized similar habitats to those found in their respective glacial refugia. All three European species appear to occur on sunny xerothermic slopes (e.g. Miller & Valešová, 1964; Waitzbauer *et al.*, 1994; Šmaha & Chytrý, 1995; Hansen & Pedersen, 1997; Jonsson, 1998), but they have rarely been found together (Kraus & Baur, 1974; Řezáč & Kubcová, 2002), suggesting that they actually differ in some habitat requirements. As these spiders live permanently in burrows, we expected them to be especially sensitive to the microclimatic regime, the physical parameters of the soil and the stability of the habitat. Microclimate is significantly influenced by plants; they are also sensitive to soil parameters and habitat stability. Thus, we expected a strong association of atypids with particular plant species. We therefore focused on a detailed study of the climatic, edaphic and vegetational parameters of atypid habitats to find possible constraints on their current distribution in central Europe. Such a study has not been performed before due to the rarity of the spiders coupled with their cryptic lifestyle.

MATERIALS AND METHODS

The study sites were nearly all sites where *Atypus* species are known to occur in the western part of the Czech Republic (Bohemia) – the area of sympatric distribution of all the three species. Here the most common species is *A. affinis*, while the

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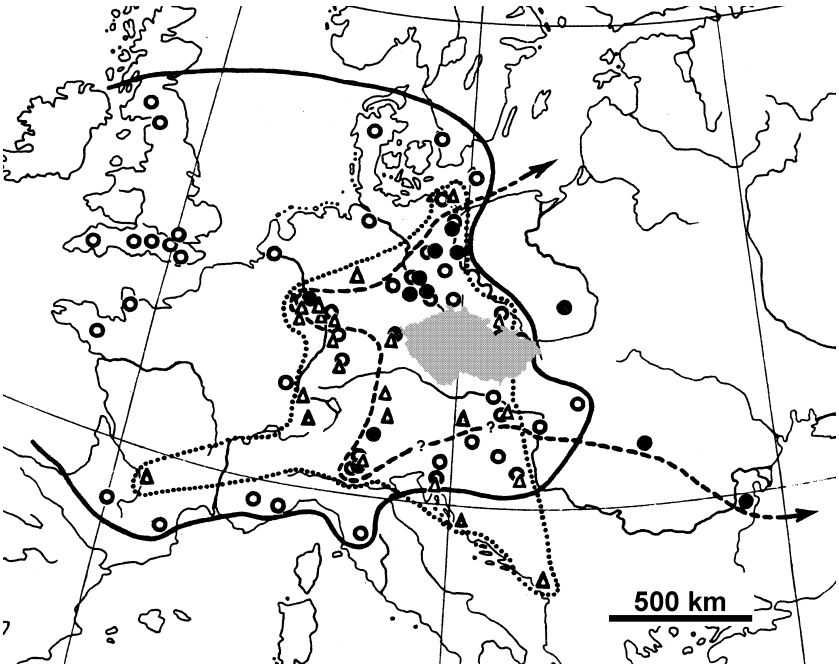

Figure 1 Distribution of *A. affinis* (solid line, circles), *A. muralis* (dashed line, full circles) and *A. piceus* (dotted line, triangles) in Europe (after Kraus & Baur, 1974). The Czech Republic, the region where the study was performed, is shaded.

rarest is *A. muralis* (Řezáč & Kubcová, 2002). Therefore, the number of studied sites was unequal. In total 28 sites with *A. affinis*, 13 sites with *A. muralis* and 14 sites with *A. piceus* were studied between 1996 and 2001 (Table 1).

At each site, a spot with an abundance of purse-webs was located by observation of the soil surface and by searching in the litter. Purse-webs of *A. muralis* and *A. piceus* usually lay exposed on the soil surface, whereas purse-webs of *A. affinis* were often completely covered by litter; in some spots the purse-webs were even deeply immersed in a thick layer of *Pinus sylvestris* needles. At each spot five adult specimens were dug out and released after identification. Apical

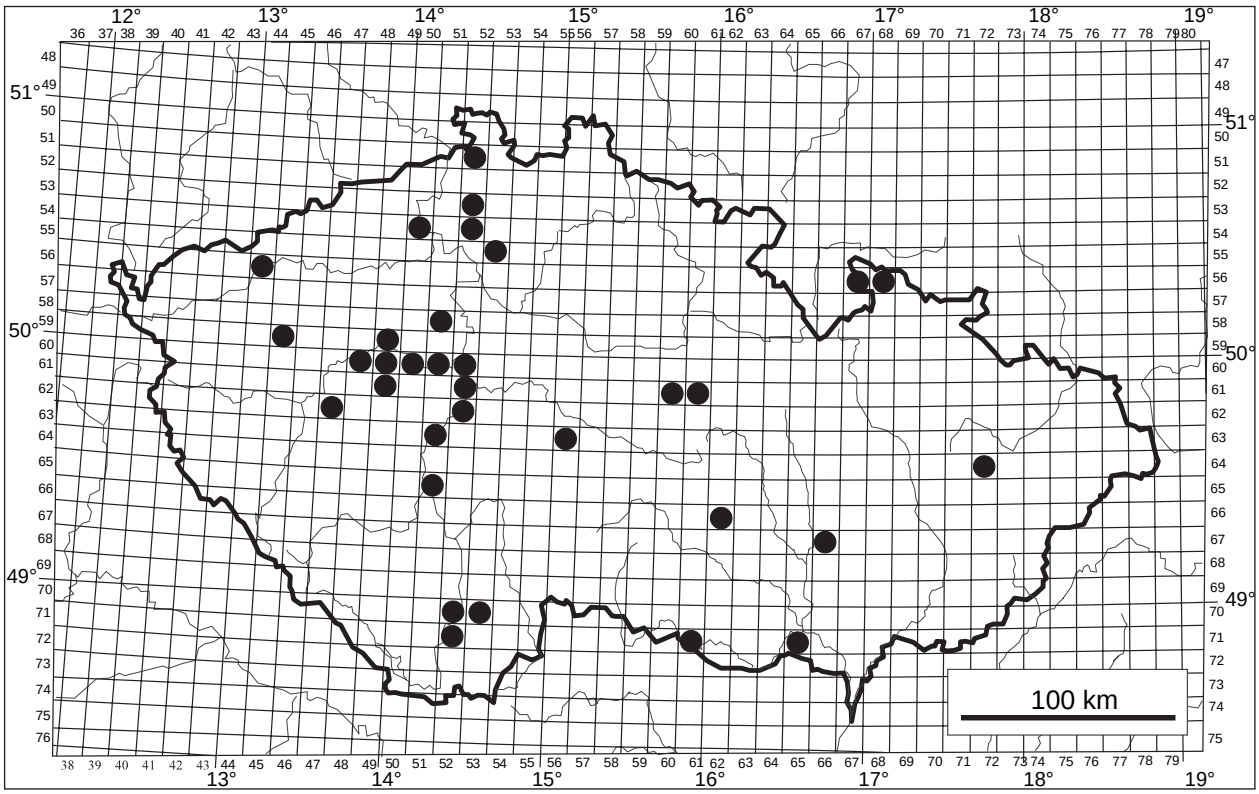

Figure 2 Distribution of *A. affinis* (circles) and the river network in the Czech Republic. M. Řezáč, unpublished data.

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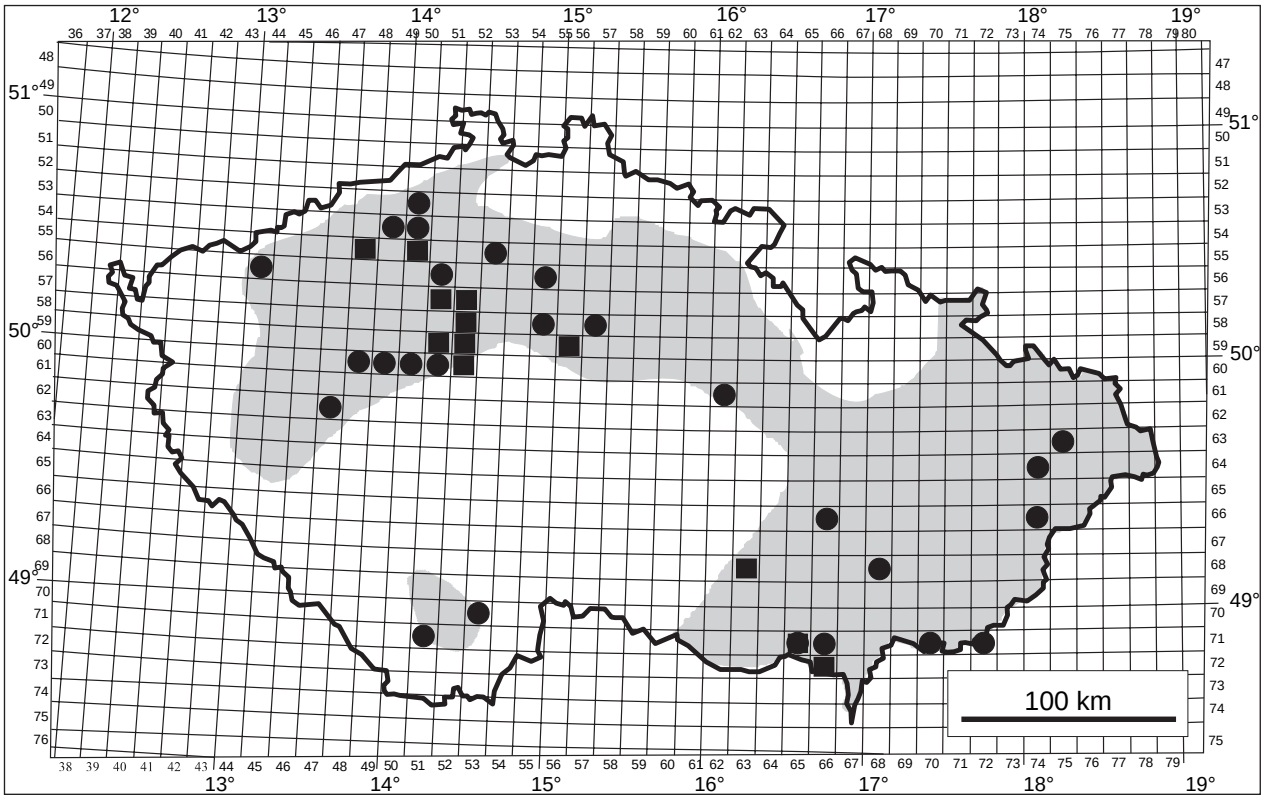

Figure 3 Distribution of *A. muralis* (squares), *A. piceus* (circles) and bedrocks rich in minerals (shaded, after Götz, 1966) in the Czech Republic. M. Řezáč, unpublished data.

segments of their posterior lateral spinnerets were examined using a magnifying glass to determine the species (Kraus & Baur, 1974). The following parameters were recorded at each spot:

1. soil depth: the depth (cm) of the soil was measured whilst digging out purse-webs,
2. compactness of soil: a two-point scale was used to characterize the soil around purse-webs: (1) soil falling into tiny particles, (2) soil falling into larger agglutinate particles,
3. litter layer (soil horizon A_{01}): a two-point scale was used: (1) soil surface visible through the sparse layer of dead organic matter, (2) soil surface completely covered with a coherent litter layer,
4. quantity of rubble: the number of stones on the surface or rocks protruding through the soil surface was assessed on a three-point scale: (1) stones covering less than 10% of the surface, (2) stones covering 10–50% of the surface, (3) stones covering more than 50% of the surface,
5. exposure: measured with a compass,
6. slope: measured with a goniometer as the angle between the horizontal plane and the slope of the surface,
7. phytocenological relevé: recorded in a 9 m^2 area. The cover was quantified using ranks according to Braun-Blanquet (1932) as follows: rare = 1, large and rare or small and numerous = 2, up to 5% = 3, 5–25% = 4, 25–50% = 5, 50–75% = 6 and 75–100% = 7.

Each site was further characterized by mean annual temperature (MAT) and mean annual rainfall (MAR), which were read from climatological maps at a scale of 1 : 2,000,000 (Götz, 1966), and by bedrock type that was read from geological maps at a scale of 1 : 1,000,000 (Götz, 1966) and 1 : 50,000 (Mašek, 1997).

Exposure and slope were used to calculate irradiation by means of the software POT_RAD (available from the Department of Botany, Charles University, Prague, Czech Republic). This gives a relative value of potential direct irradiation (sum of cosines of angles between sunbeams and a particular surface) for a selected day (arbitrarily chosen to be 21 January) according to Jeník & Rejmánek (1969). The slope was evaluated independently with reference to the stability of the soil surface.

On markedly heterogeneous and syntopic sites, several spots where purse-webs were concentrated were inspected. In such cases an average of recorded parameters, except for bedrock and vegetation type, was calculated for the whole site.

Processing of phytocenological relevés

The vegetation documented by the relevés was classified into phytocoenological associations according to Chytrý *et al.* (2001) and Moravec (1995) and evaluated as a habitat

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Table 1. Studied sites of *Atypus* spiders. All localities are situated in the western part of the Czech Republic (Bohemia). Sq.: square of the Central European grid map, the first two numbers indicate the row, the last two indicate the column (see Figs 2–3). r.: reserve.

Locality	Coordinates	Sq.
Atypus affinis (Fig. 2)		
Chřibská, Růžová zahrada rocks	N 50°53′21″ E 14°24′36″	5152
Hvězda, r. Vlhošt'	N 50°35′57″ E 14°27′24″	5352
Lovosice, r. Lovoš	N 50°31′36″ E 14°00′57″	5450
Hradsko, r. Kokořínský důl	N 50°25′40″ E 14°34′59″	5553
Černínov, r. Kokořínský důl	N 50°25′03″ E 14°34′47″	5553
Kokořín, r. Truskavenský důl	N 50°26′01″ E 14°32′28″	5553
Skryje, r. Týřov	N 49°59′05″ E 13°47′42″	6048
Týřovice, r. Velká Pleš	N 49°59′19″ E 13°48′17″	6048
Karlova Ves, r. Vysoký Tok	N 49°59′30″ E 13°51′04″	6049
Srbsko, r. Karlštejn	N 49°56′25″ E 14°09′30″	6050
Srbsko, r. Koda	N 49°56′00″ E 14°07′06″	6050
Suchomasty, r. Na Voskopě	N 49°54′09″ E 14°04′22″	6050
Prague 12, r. Šance	N 49°58′05″ E 14°24′53″	6052
Měchenice	N 49°54′43″ E 14°23′35″	6052
Třebsín, r. Kobylí draha	N 49°50′57″ E 14°26′40″	6152
Třebsín, Kletecko rock	N 49°50′52″ E 14°27′11″	6152
Petrov, Třeštibok hill	N 49°52′43″ E 14°27′03″	6152
Štěchovice	N 49°50′12″ E 14°24′40″	6152
Teletín, Mařenka rock	N 49°49′53″ E 14°27′20″	6152
Smrkový Týnec	N 49°53′14″ E 15°45′43″	6160
Žumberk	N 49°52′36″ E 15°51′18″	6161
Hůrky, r. Žd'ár	N 49°44′15″ E 13°39′29″	6247
Nebřich, former r. Na skalinách	N 49°46′33″ E 14°24′53″	6252
Nová Rabyně	N 49°48′00″ E 14°26′06″	6252
Sejcká Lhota, r. Vymyšlenská pěšina	N 49°44′38″ E 14°22′14″	6252
Borovsko	N 49°41′14″ E 15°05′49″	6356
Zvíkovské Podhradí	N 49°25′34″ E 14°11′50″	6551
Zlatá Koruna	N 48°51′05″ E 14°21′46″	7152
Atypus muralis (Fig. 3)		
Chraberce, r. Oblík	N 50°24′32″ E 13°48′28″	5548
Zeměchy, r. Sprašová rokle	N 50°13′30″ E 14°15′45″	5751
Libčice nad Vltavou	N 50°12′05″ E 14°21′36″	5752
Dolany	N 50°12′57″ E 14°21′00″	5752
Prague 7, r. Podhoří	N 50°07′45″ E 14°24′14″	5852
Prague 6, r. Podbabské skály	N 50°07′25″ E 14°23′38″	5852
Roztoky u Prahy, r. Roztocký háj-Tiché údolí	N 50°08′50″ E 14°23′01″	5852
Prague 8, r. Jabloňka	N 50°07′15″ E 14°26′10″	5852
Letky	N 50°10′59″ E 14°21′51″	5852
Prague 6, r. Divoká Šárka	N 50°05′42″ E 14°19′23″	5951
Prague 5, r. Prokopské údolí	N 50°02′32″ E 14°22′11″	5952
Vrbčany, r. Stráň u Chroustova	N 50°04′00″ E 14°59′40″	5956
Prague 5, r. Lochkovský profil	N 49°59′56″ E 14°20′14″	6052
Atypus piceus (Fig. 3)		
Brná nad Labem	N 50°37′25″ E 14°05′08″	5350
Štrbice, former r. Vršíček	N 50°33′14″ E 13°49′49″	5449
Kostomlaty pod Milešovkou, former r. Kajba	N 50°32′37″ E 13°51′28″	5449
Kokořín, r. Truskavenský důl	N 50°26′02″ E 14°32′16″	5553
Ctiněves, Říp hill	N 50°23′00″ E 14°17′23″	5651
Sýčina	N 50°22′24″ E 14°55′59″	5655
Hradčany, r. Báň	N 50°09′27″ E 15°17′08″	5857
Chot'ovice, r. Žehuňská obora	N 50°09′09″ E 15°18′51″	5857
Skryje, r. Týřov	N 49°59′04″ E 13°47′51″	6048
Karlova Ves, r. Vysoký Tok	N 49°59′29″ E 13°51′04″	6049
Srbsko, r. Koda	N 49°56′01″ E 14°07′21″	6050
Srbsko, r. Karlštejn	N 49°56′25″ E 14°09′29″	6050
Vidov u Nedabyle	N 48°55′51″ E 14°29′59″	7053
Český Krumlov, r. Vyšenské kopce	N 48°49′21″ E 14°17′57″	7151

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