Relict serpentine populations of *Knautia arvensis* s. l. (*Dipsacaceae*) in the Czech Republic and an adjacent area of Germany

Reliktní hadcové populace z okruhu *Knautia arvensis* s. l. (*Dipsacaceae*) v České republice a přilehlé části Německa

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Several distinct populations of *Knautia arvensis* (L.) Coulter s. l. restricted to serpentine outcrops have been found in the Czech Republic and an adjacent area of Germany. They have been determined as diploids or tetraploids despite the fact that only common, non-serpentine tetraploids occur in the area. These plants differ also in their morphology, florogenesis, and in their behaviour within a plant community from all other known taxa within the species. Their origin has been explained by the hypothesis of microevolution of a relict diploid ancestor. The isolated relict populations have not expanded their range, being confined to the place where they originated.

Keywords: *Knautia arvensis*, serpentine, microevolution, chromosome numbers, distribution, Czech Republic

Introduction

Two cytotypes of *Knautia arvensis* (L.) Coulter s. l. are known to occur in the Czech Republic: diploids with 20 chromosomes and tetraploids with 40 chromosomes (Štěpánek 1982; also present study, see Appendix). The tetraploid populations, here called *K. arvensis* (L.) Coulter subsp. *arvensis*, are the most widespread type within the group. It is widely distributed throughout the Czech Republic from the lowlands up to the submontane belt. It is absent only from the highest altitudes and rare in areas with poorly developed road networks and settlement. In contrast, the diploids, here called *K. arvensis* subsp. *pannonica* (Heuffel) O. Schwarz, are confined to a region of thermophilous Pannonian vegetation in southern and southeastern Moravia (Štěpánek 1997). Ehrendorfer (1962b: 142, Map 4) also indicates the occurrence of diploids in central Bohemia. However, this record was most likely based on an assumption rather than a fact. Karyological investigations of *Knautia* species in the Czech Republic (Štěpánek 1982) revealed that the diploid populations of *K. arvensis*, having their main area of distribution in the southern part of Central Europe, penetrate into southern Moravia but do not extend northwards in that area (see Fig. 1 herein, and Fig. 2 in den Nijs et al. 1990).

Besides the two named types with a more or less continuous distribution, several populations with different patterns of morphological variation and their own unique pattern of evolution occur scattered in small restricted relict areas within the range of the tetraploids (Štěpánek 1982). A mountain diploid population occurring in a single locality on outcrops of carbonate rocks in the Kotelné jámy glacial cirque, Krkonoše Mts, represents a distinct

stenoendemic taxon named *Knautia arvensis* subsp. *pseudolongifolia* (Szabó) O. Schwarz (Štěpánek 1989). Other distinct populations are confined to large beds of serpentines. On those sites, more or less stabilized, homogenous populations of *K. arvensis* s. l. (provisionally named *K. arvensis* subsp. *serpentinicola*) form a natural component of vegetation in relict serpentine pine woods or on serpentine rocks. They differ considerably from the tetraploid *K. arvensis* subsp. *arvensis*, which occurs abundantly in the surrounding areas. The recently established casual presence of a few tetraploid plants in serpentine areas connected with human activities is restricted to the immediate vicinity of forest roads (embankments and ditches). These last mentioned occurrences are omitted from further consideration.

Material and methods

Samples from natural populations of serpentine and non-serpentine types of *K. arvensis* s. l. were transferred for cultivation to the Experimental garden of the Institute of Botany, Průhonice. The plants were examined karyologically using root tips of mature plants. The rapid squash method was employed; root tips were subjected to two hours of p-dichlorbenzene pre-treatment, then fixed with a solution of ethanol + acetic acid, and lactic-propionic orcein stained after two minutes of ethanol + hydrochloric acid maceration. The origin of the material is listed, together with the results of the determination of chromosome counts, in the Appendix. Morphometric analysis has been performed on plant material collected in the original localities. No selection of plants for study has been made except for the exclusion of deformed and damaged individuals. Voucher specimens are deposited in the Institute of Botany, Průhonice.

Distribution of *Knautia arvensis* subsp. *serpentinicola*

The first localities of the relict serpentine diploids within the area of common continuous occurrence of the tetraploid *K. arvensis* subsp. *arvensis* were detected by Štěpánek (1982) near Borovsko and Staré Ransko. In addition to these stands of diploids, two other localities of tetraploid serpentine populations were reported in the above mentioned study (and by Štěpánek 1997) from the Mnichovské hadce serpentine outcrop system: Vlček and Mnichov (the latter is called Pluhův bor here, as more than one serpentine stand occurs in the vicinity of Mnichov village).

Altogether 16 large serpentine beds have recently been studied in the Czech Republic and Bavaria, Germany. True serpentine populations, as defined above, have been proved to occur at 9 of them (localities Woja, Borovsko, Staré Ransko, Dominova skalka, Křížky, Vlček, Pluhův bor, Planý vrch, Holubov; for their location see Appendix). The first three populations were found to be diploids, the rest represent tetraploids. The populations are isolated from each other by the size and distribution of serpentine outcrops in the region. Complete descriptions of the localities of the populations studied, with their chromosome numbers, is given in the Appendix, and the distribution of the serpentine populations is indicated on Fig. 1.

The populations of *K. arvensis* subsp. *serpentinicola* studied are accompanied by other serpentinophytes, many of which are also relict and/or endemic. Basic characteristics with notable plant taxa are given below.

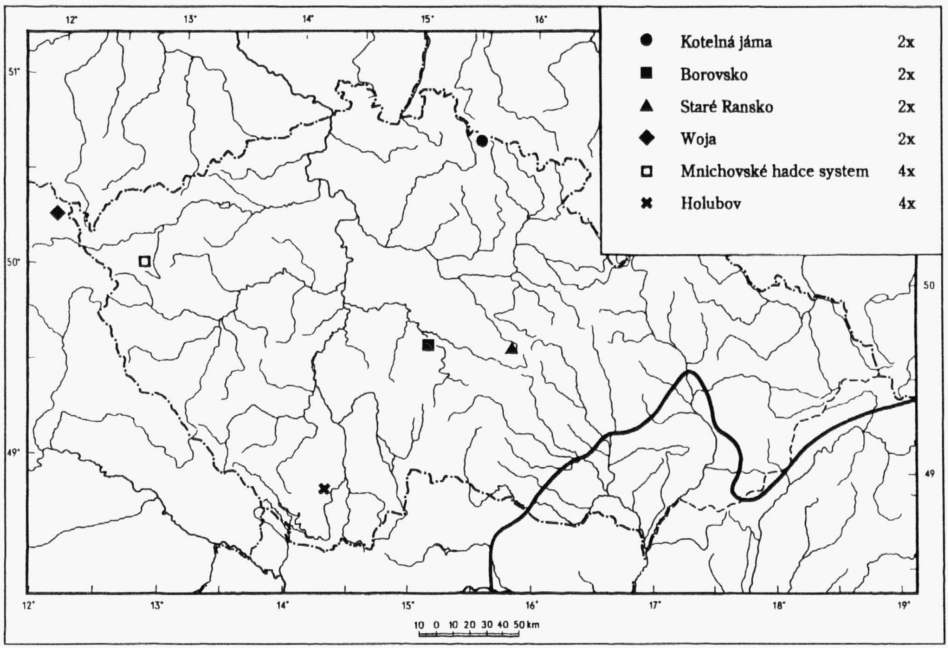

Fig. 1. – Distribution of relict populations of *Knautia arvensis* s. l. in the Czech Republic and an adjacent area of Germany. Solid circle represents the only locality of *K. arvensis* subsp. *pseudolongifolia*, other symbols illustrate the position of the localities of *K. arvensis* subsp. *serpentinicola*. Particular localities of the Mnichovské hadce serpentine outcrop system (Dominova skalka, Křížky, Vlček, Pluhův bor, and Planý vrch) are symbolized by a single open square. The ploidy levels of the populations are also given. The line corresponds to the northern limit of the continuous occurrence of the diploid *K. arvensis* subsp. *pannonica*.

The locality Woja is formed by serpentine rocky slopes with the occurrence of such plants as *Armeria vulgaris* Willd. subsp. *serpentini* (Gauckler) Holub, *Asplenium adulterinum* Milde, *A. cuneifolium* Viv., *Polygaloides chamaebuxus* (L.) O. Schwarz, etc. (see also Hartlieb 1992).

Several interesting plant taxa have been reported from the large outcrop of serpentines with rocky slopes and relict pine woods in the vicinity of the villages of Borovsko, Bernartice and Sedlice, close to Dolní Kralovice. It is the only locality of *Potentilla crantzii* (Crantz) Fritsch subsp. *serpentini* (Borbás) Hayek in the Czech Republic (Soják 1960), one of the few localities of *Minuartia smejkalii* Dvořáková (Dvořáková 1988), *Armeria vulgaris* Willd. subsp. *serpentini* (Gauckler) Holub (Holub 1960), *Dianthus carthusianorum* L. subsp. *capillifrons* (Borbás) Neumayer (Kovanda 1990), a serpentine form of *Myosotis* stenophylla Knaf s. l. (Štěpánková 1996, Štěpánková, in preparation), *Polygala amara* L. subsp. *brachyptera* (Chodat) Hayek (Kirschner 1997), *Asplenium cuneifolium* Viv., etc.

In contrast, the serpentine vegetation near Staré Ransko is rather poor, being limited, besides *K. arvensis* subsp. *serpentinicola*, to *Asplenium cuneifolium* Viv.

Several interesting plants are known to occur in the Mnichovské hadce serpentine outcrop system (with particular localities Dominova skalka, Křížky, Vlček, Pluhův bor, and Planý vrch): the endemic species *Cerastium alsinifolium* Tausch (Novák 1960, Smejkal 1990), with, in addition *Vicia oreophila* Žertová (Žertová 1962, Chrtková-Žertová 1973), *Galium sudeticum* Tausch (Krahulcová & Štěpánková, in preparation), *Asplenium adulterinum* Milde, *A. cuneifolium* Viv., *Polygaloides chamaebuxus* (L.) O. Schwarz, etc. (see also Jeník 1995).

In the area of Křemžské hadce serpentines system, which includes the locality Holubov, associated species include *Dianthus carthusianorum* L. subsp. *capillifrons* (Borbás) Neumayer (Kovanda 1984, 1990), *Vicia oreophila* Žertová (Žertová 1962), *Galium valdepilosum* H. Braun (Krahulcová & Štěpánková, in preparation, Štěpánková 1997), and *Asplenium cuneifolium* Viv.

Serpentine populations of *K. arvensis* s. l. were expected to be present also on a large serpentine outcrop between the villages of Mohelno and Dukovany, where many serpentinophytes occur: *Armeria vulgaris* Willd. subsp. *serpentini* (Gauckler) Holub (Holub 1960), a serpentine type of *Myosotis stenophylla* Knaf s. l. (Štěpánková, in preparation), *Asplenium adulterinum* Milde, *A. cuneifolium* Viv., *Notholaena marantae* (L.) Desv., *Tithymalus seguierianus* (Necker) Prochanov subsp. *minor* (Sadler) Chrtek et Křísa, etc. However, even though *K. arvensis* subsp. *arvensis*, *K. drymeia* Heuffel, and their hybrid swarms called *K.* ×*speciosa* Schur [= *K. arvensis* (subsp. *arvensis*) × *K. drymeia*] have been found in the area, no population displaying the characteristics of plants typical of serpentine populations has been proved to have established itself there so far. It cannot be excluded however, that a serpentine population formerly occurring there was later submerged by the *K.* ×*speciosa* hybrid swarms.

Sporadic occurrences of a few plants of *Knautia* taxa, recently introduced close to forest roads in serpentine areas of were located at 4 sites. *K. arvensis* subsp. *arvensis* occurs rarely at the localities of Loužnice, Chrastice and Malonty, and *K.* ×*posoniensis* Degen [= *K. arvensis* (subsp. *arvensis*) × *K. kitaibelii* (Schultes) Borbás] near Raškov.

Morphological pattern of serpentine populations

The serpentine populations studied exhibit an advanced stage of morphological differentiation both from the non-serpentine ones and from each other. The general appearance of plants of most populations of *K. arvensis* subsp. *serpentinicola* (except for that of Holubov) resembles somewhat that of *K. arvensis* subsp. *pannonica*. Both types (regardless of the cytotypes of the serpentine populations) also share for the most part characters best correlated with the ploidy level: mean capitula diameter, mean length of the exterior bracts, and mean length of the leaves. However, certain morphometric features (the total leaf shape, width and length of leaf segments, leaf length/width ratio and terminal lobe length/whole leaf length ratio) separate each of these populations to some extent. Five of these characters (mean capitula diameter, mean length of the exterior bracts, mean length of the leaves, leaf length/width ratio, terminal lobe length/whole leaf length ratio) have been used in a Principal Components Analysis based on 142 individuals of *K. arvensis* s. l. (41 plants of the tetraploid *K. arvensis* subsp. *arvensis*, 22 plants of the diploid *K. arvensis* subsp. *pannonica*, and 79 plants of *K. arvensis* subsp. *serpentinicola*, while

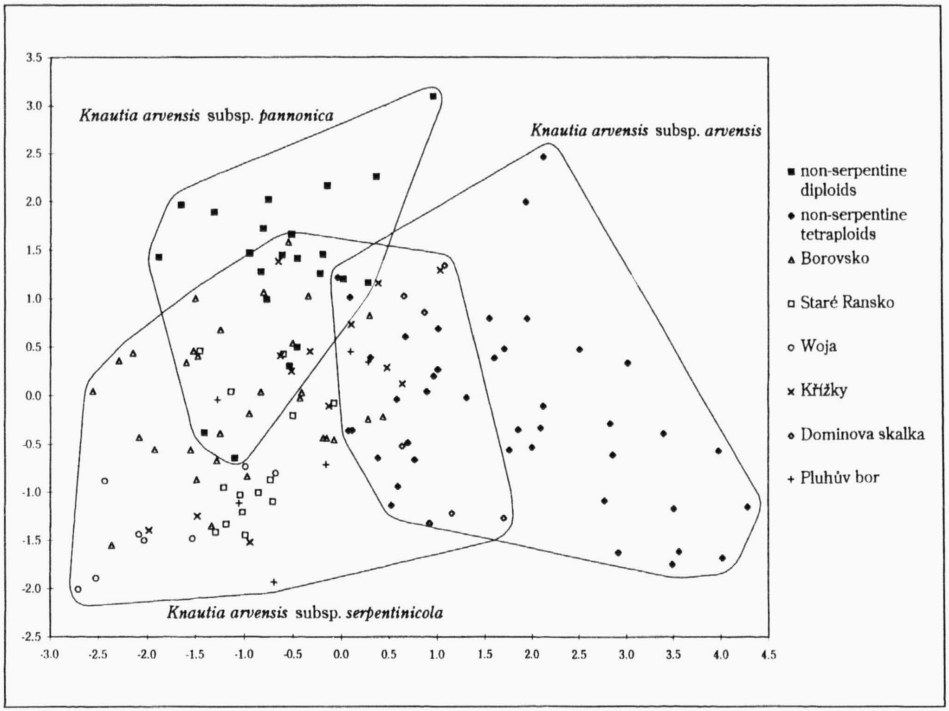

Fig. 2. – Plot of the first two axes of the Principal Component Analysis of 142 individuals of *Knautia arvensis* s. l. scored for five variables. Diamonds represent the 41 individuals of the tetraploid *K. arvensis* subsp. *arvensis*, solid squares 22 plants of the diploid *K. arvensis* subsp. *pannonica*, and other symbols 79 plants of *K. arvensis* subsp. *serpentinicola*.

both the serpentine diploids from the localities Woja, Borovsko, Staré Ransko, and the tetraploids from Křížky, Dominova skalka, Pluhův bor, were taken into account). In the resulting scatter diagram (Fig. 2), characters correlated with the ploidy level are separated horizontally, while differentiation due to morphological variation among particular populations is depicted vertically.

While most of the serpentine populations fall morphologically within the circumscription of *K. arvensis* s. l., plants from the Holubov serpentines display a different pattern. They approach morphotypes of *K. maxima* (Opiz) Ortmann, otherwise known from the southwestern parts of Bohemia and Moravia, in a set of features (shape of leaf lamina, character of leaf margins, flower colour). However, the local plants have been confirmed as being tetraploids, while the *K. maxima* populations known from the Czech Republic have been repeatedly found to be hexaploids (Štěpánek 1982). They may also represent shade morphotypes of *K. arvensis* s. l. or an extreme product of microevolution in the relict locality. In the first version of PCA, the Holubov population was separated from all other studied plants of *K. arvensis* s. l. The elucidation of relationships to other known *Knautia* taxon requires further study.

Evolution of serpentine populations

All the above named diploid populations from Bohemia and Bavaria constitute solitary "islands" in the distribution area of the tetraploids. The tetraploids could not have participated in the establishment of the diploids. The most likely origin of the type is by means of microevolution of relict populations of the ancestral diploid type. This occurred in the region of present-day Central Europe in the postglacial period with prevailing non-forest vegetation in a relatively mild climate, namely during the Preboreal and Boreal periods. The diploids, as the non-forest vegetation element, afterwards gradually became extinct from the major part of the area due to dense forest communities. The native *Knautia* has survived in only a few stands of relict character (Štěpánek 1989). The diploids forced out by the forest retreated to the southern part of Central Europe where *K. arvensis* subsp. *pannonica*, the diploid cytotype still occurs. When polyploidization took place, the subsequently evolved tetraploids spread along with human deforestation to most of the northern half of Europe. Meanwhile, the isolated relict serpentine populations have been subject to changes. The influence of the specific conditions of serpentines, together with the fact that new populations evolved from scanty relict populations isolated spatially and ecologically from their ancestor, played a crucial role in their microevolution.

This hypothesis explains the probable origin of the serpentine diploids. However, the precise chorological establishment of the tetraploid populations remains to be solved. Have the tetraploids evolved from ancient relict populations of diploids or have their localities been occupied by the more recently evolved common tetraploid type? It is suggested here that the former alternative is closer to reality, as supported by the following observations:

1. The behaviour of the tetraploids in the plant community is virtually identical with that of relict diploid populations. Individual plants are scattered throughout the herb layer of serpentine pine wood or heathland and they are morphologically homogeneous. In contrast, recent casual introductions of a few plants of various *Knautia* taxa into serpentine areas are confined solely to the immediate vicinity of thoroughfares, along which the plants have become commonly distributed. Recent penetration of the tetraploid *K. arvensis* subsp. *arvensis* has not been proved even onto the serpentine outcrop near Borovsko. Even though the area is densely transected by forest roads and even by a heavily used highway, all the samples examined from the forest margins along these thoroughfares proved to belong to the native diploid plants. If colonization had occurred very recently, Mohelno would has been occupied by a (serpentine) population of *K. arvensis* s. l., but it is not, even though the tetraploids recently introduced into the area along the roads have had many opportunities to do so. While relict populations have already evolved serpentine tolerance, non-serpentine plants in all likelihood cannot colonize the serpentine stands at present.
2. The corolla colour of the tetraploid *K. arvensis* subsp. *arvensis* is known to vary from rose or violet rose to bluish violet. However, the plants from most of the Czech Republic are often influenced by the introgression of *K. kitaibelii* (Schultes) Borbás resulting in rose-yellow to pale rose corollas with a lilac tinge. However, the tetraploid serpentine populations mostly have flowers of intense to deep red, whereby they differ from the common tetraploid *K. arvensis* subsp. *arvensis*, but conspicuously resemble the diploid relict populations.

3. The presence and density of glandular hairs on the peduncles below the inflorescence of both diploid and tetraploid non-serpentine populations varies, sometimes even within a single population. In contrast, all serpentine populations (except for that of Holubov) are characterized by densely glandular peduncles.
4. Certain quantitative morphological characters agree with the assumed origin of the plants. The result of Principal Components Analysis (Fig. 2) shows some distinctness of the serpentine populations (regardless of their ploidy level) from the other populations. Almost all the plant individuals from the serpentine populations occur on the left hand side of the graph where only the diploids had been expected. Their location indicates a morphological proximity with all the diploids, the direct descendants of the ancient diploid ancestor.
5. Even after two-years of cultivation of samples from the serpentine populations in normal garden substrate they have maintained their basic appearance. Observed morphological changes have remained restricted to alterations induced by the environment (plant size, width and length of leaf segments) known to occur also within other related taxa. Therefore, unique morphological characters of the serpentine populations cannot be considered pure ecomorphosis.

Conclusion

The serpentine populations of *K. arvensis* subsp. *serpentinicola* have gone through unique process of evolution, distinct from non-serpentine types of *K. arvensis* s. l. This study has shown that the effects of special chemical and physical properties of serpentine soils, repeatedly described in the literature (e. g. Walker 1954, Kruckeberg 1986, Kruckeberg & Kruckeberg 1990, Roberts & Proctor 1992, Štěpánková 1996, 1997), are reflected in a distinct combination of morphological features, acquired serpentine tolerance and incorporation into natural serpentine vegetation. A similar pattern of evolution and diversification has been reported for serpentine endemics within the *Streptanthus glandulosus* complex (*Cruciferae*) (Mayer & Soltis 1994).

Morphologically, the best-defined serpentine populations are those found by Štěpánek (1982) of Borovsko and Staré Ransko. In contrast, the tetraploids from the Mnichovské hadce system belong to a less distinct type. The reduced distinctness of the serpentine tetraploid plants from the non-serpentine ones can be explained by morphological changes connected with polyploidization or even by secondary amalgamation of differences by gene flow from *K. arvensis* subsp. *arvensis*. As crossing of even entirely distinct species of the same ploidy level is frequent within *Knautia* subgen. *Trichera* (Schrad. ex Roem. et Schult.) Rouy (Breton-Sintès 1975a, 1975b, Ehrendorfer 1962a, Štěpánek 1982, 1989), the possibility of hybridization has to be taken into account. Apparently transitional forms have been observed at the localities of Křížky and Dominova skalka.

While a relict character has been clearly proved for the diploid *K. arvensis* subsp. *serpentinicola* by karyological analysis, the relationship of the tetraploids of the Mnichovské hadce system requires confirmation by some more sensitive methods, e. g. by DNA analysis.

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Souhrn

Na území České republiky a těsně přilehlé části Německa se v oblastech hadcových výchozů nacházejí populace z okruhu *Knautia arvensis* (L.) Coulter s. l., které se však svými vlastnostmi odlišují od běžných chrastavců. Dosud známé lokality se nacházejí na bavorské lokalitě Woja a v České republice v hadcové oblasti ve Slavkovském lese, na křemžských hadcích u Holubova, na dolnokralovických hadcích mezi obcemi Borovsko, Bernartice a Sedlice a ve Žďárských vrších u Starého Ranska. Ačkoliv se v širokém okolí těchto lokalit nacházejí pouze rostliny *Knautia arvensis* s tetraploidním počtem chromozómů, u některých výše jmenovaných hadcových populací byla stanovena diploidní úroveň. Tyto hadcové populace jsou považovány za reliktní výskyty původního diploidního ancestora, které se mikroevolucí ve specifických podmínkách hadcového prostředí vyvinuly v typy s vlastní odlišnou morfologií a chováním ve společenstvu. Morfologickou diferenciaci je přitom možné pozorovat nejen mezi hadcovými a nehadcovými typy, ale i mezi jednotlivými hadcovými populacemi navzájem, což je důsledek jejich samostatné, unikátní evoluční historie.

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Appendix 1. – Synopsis of the chromosome numbers and the localities of the plants.

locality	location	2n	det. no.
1. *Knautia arvensis* (L.) Coulter s. l.			
1. A. Serpentine populations of *Knautia arvensis* (L.) Coulter subsp. *serpentinicola* nom. prov.			
Woja	Ge, N Bavaria: Rehau, serpentine rocky slopes "Wojaleite" above railway Oberkotzau - Rehau, 0.9 km S of Woja near Wurlitz. Z. Kaplan, herb. no. 96/301. 9 July 1996.	20	96/32, 96/34
Borovsko	Cz, C Bohemia: Dolní Kralovice, pine wood on the serpentine slopes above Želivská přehrada Reservoir on the left side of the Praha - Brno highway, 2.0 km SWS of Borovsko. 390 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun. 23 August 1995.	20	95/10
	Cz, C Bohemia: Dolní Kralovice, open pine wood on serpentine 0.6 km SWS of Borovsko. 410 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun. 23 August 1995.	20	95/2, 95/3
	Cz, C Bohemia: Dolní Kralovice, pine wood on serpentine on the left side of the forest road Borovsko - Bernartice, 1.2 km S of Borovsko. 410 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun., herb. no. 96/291. 5 July 1996.	20	96/31
	Cz, C Bohemia: Dolní Kralovice, pine wood 2.1 km NW of Bernartice. 390 m a.s.l. J. Štěpánková, Z. Skála, A. Krahulcová. 19 May 1994.	20	95/20

Staré Ransko	Cz, E Bohemia: Hlinsko, open pine wood on serpentine "U obrázku" 0.7 km ESE of the top of the hill Panský Babylón (673), 1.6 km S of Staré Ransko. 630 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun., herb. no. 96/290. 5 July 1996.	20	96/25, 96/26, 96/30
Dominova skalka	Cz, W Bohemia: Mariánské Lázně, serpentine crag "Dominova skalka" on the right side of the road Nová Ves near Bečov nad Teplou – Louka, 1.5 km SES of Nová Ves. B. Trávníček, herb. no. 96/347. 11 July 1996.	40	96/33
Křížky	Cz, W Bohemia: Mariánské Lázně, serpentine rocks "Křížky" on the right side of the road Prameny – Nová Ves village, 1.5 km NE of Prameny. B. Trávníček, herb. no. 96/348. 11 July 1996.	40	96/36
Vlček	Cz, W Bohemia: Mariánské Lázně, serpentine pine wood "Vlček" on the top of the hill Vlčí hřbet (883), 2 km S of Prameny. 880 m a.s.l. J. Štěpánková. 30 June 1995.	40	96/37
Pluhův bor	Cz, W Bohemia: Mariánské Lázně, serpentine pine wood "Pluhův bor" 1.5 km NWN of Mnichov. B. Trávníček, herb. no. 96/346. 11 July 1996.	40	96/35
	Cz, W Bohemia: Mariánské Lázně, serpentine rocks 1.5 km N of Mnichov. 660 m a.s.l. J. Štěpánková. 28 June 1995.	40	95/5
Planý vrch	Cz, W Bohemia: Mariánské Lázně, serpentine pine wood "Planý vrch" 1.5 km W of Mnichov. 770 m a.s.l. Z. Skála, A. Klaudisová. 8 June 1994.	ca. 40	95/21
Holubov	Cz, S Bohemia: Křemže, Holubov, open serpentine pine wood on the slopes above the left bank of the Křemžský potok stream, 1.3 km E of the Holubov railway station. 480 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun., herb. 95/525. 22 August 1995.	40 ca. 39	95/6 95/7
	Cz, S Bohemia: Křemže, Holubov, serpentine rock above the path leading to Holubovský mlýn mill. Z. Skála, A. Klaudisová. 18 August 1993.	40	95/16

1. B. Sporadic recent introductions of *Knautia arvensis* (L.) Coulter subsp. *arvensis* into serpentine areas

Loužnice	Cz, N Bohemia: Železný Brod, in quarry near the road 0.5 km S of Loužnice. Z. Skála, A. Klaudisová. 3 August 1993.	40	95/18
Malonty	Cz, S Bohemia: Kaplice, in small quarry on the left side of the road Malonty – Bukovsko. Z. Skála, A. Klaudisová. 19 August 1993.	40	95/17
Chrastice	Cz, N Moravia: Staré Město pod Kralickým Sněžníkem, Chrastice, on serpentines 1.25 km SWS of railway station. Z. Skála, A. Klaudisová. 3 August 1993.	40	95/19
Mohelno	Cz, S Moravia: Moravský Krumlov, serpentine rocks above the left bank of the Jihlava river, 1 km S of Mohelno. 320 m a.s.l. J. Štěpánková, J. Chrtek jun. 31 May 1994.	c. 40	96/39
	Cz, S Moravia: Moravský Krumlov, serpentine pine wood above the road Mohelno – Dukovany. 310 m a.s.l. J. Štěpánková, J. Chrtek jun. 1 June 1994.	40	95/12
	Cz, S Moravia: Moravský Krumlov, serpentine pine wood along the road Mohelno – Dukovany. 300 m a.s.l. J. Štěpánková. 22 June 1995.	40	95/13

1. C. Non-serpentine populations of *Knautia arvensis* subsp. *pannonica* (Heuffel) O. Schwarz

Děvín	Cz, S Moravia: Břeclav, short grasslands on limestone on the SW slopes of the Děvín hill (554), 1.1 km SE of Horní Věstonice. 460 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun., J. Danihelka. 4 July 1996.	20	96/22
Soutěska	Cz, S Moravia: Břeclav, small meadows in the defile between the hills Děvín and Obora, 1.3 km SE of Horní Věstonice. 360 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun., J. Danihelka, herb. no. 96/252. 4 July 1996.	20	96/23
Kočičí skála	Cz, S Moravia: Břeclav, grasslands around the Kočičí skála rock, 1.2 km N of Mikulov. 340 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun., J. Danihelka, herb. no. 96/257. 4 July 1996.	20	96/27

1. C. Non-serpentine populations of *Knautia arvensis* subsp. *arvensis*

Horní Poutnov	Cz, W Bohemia: Bečov nad Teplou, rocks 0.5 km SW of Horní Poutnov. 680 m a.s.l. J. Štěpánková. 28 June 1995.	40	95/4
Merklovice	Cz, E Bohemia: Rychnov nad Kněžnou, grassy balk between fields near the SES margin of Merklovice. 410 m a.s.l.. Z. Kaplan, herb. no. 96/298. 7 July 1996.	40	96/41
Horní Věžnice	Cz, E Bohemia: Polná, wood edge along the road under the dike of the Kukle fishpond, 0.6 km SE of Horní Věžnice. 460 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun., herb. no. 96/287. 5 July 1996.	40	96/40
Věžná	Cz, W Moravia: Bystřice nad Perštejnem, wood edge 1.5 km W of Věžná. 410 m a.s.l. J. Štěpánková, J. Chrtek jun.. 22 June 1995.	40	95/1
Lhánice	Cz, S Moravia: Moravský Krumlov, meadow in the bottom of the Jihlava river valley SW of Lhánice near Mohelno. J. Štěpánková, J. Chrtek jun. 22 June 1995.	40	95/15

2. *Knautia* ×*speciosa* Schur [= *K. arvensis* (subsp. *arvensis*) × *K. drymeia* Heuffel]

Dukovany	Cz, S Moravia: Moravský Krumlov, open serpentine pine wood on slopes in the forest Včelín, on the left above the road to Mohelno, 1.25 km N-NEN of Dukovany. 325 m a.s.l. Z. Kaplan, J. Štěpánková, J. Chrtek jun., herb. no. 96/276. 5 July 1996.	40	96/24, 96/28, 96/29

3. *Knautia* ×*posoniensis* Degen [= *K. arvensis* (subsp. *arvensis*) × *K. kitaibelii* (Schultes) Borbás]

Raškov	Cz, N Moravia: Raškov, forest road margin in the serpentine area 1.5 km NW of the village. 620 m a.s.l. Z. Kaplan, I. Krsková, herb. no. 96/412. 19 July 1996.	40	96/38