

Studies in *Phyteuma*

Studie rodu *Phyteuma*

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Czechoslovak species of *Phyteuma* L. have been surveyed for chromosome numbers, variation patterns, reproductive biology and capability of hybridization. All material proved diploid, with $n = 11$. In addition to this number, $n = 12$ was also found in one sample of *P. nigrum* F. W. SCHMIDT. No evidence was obtained as to the possibility of spontaneous autogamy, often referred to in the literature. Artificial autogamy is possible on a limited scale, resulting in poorly viable seed. Hybridization was successful between any two of the three species in either direction and a triple hybrid, *P. nigrum* F. W. SCHMIDT $\times$ *P. spicatum* L. $\times$ *P. orbiculare* L., was also obtained. A taxonomic revision of the material studied confirmed the presence in Czechoslovakia of the three species previously recognized, *P. spicatum* L., *P. nigrum* F. W. SCHMIDT and *P. orbiculare* L. The latter is subdivided into three subspecies differing in their morphology, ecological preferences and geographical distribution. The distinguishing characters of all these taxa have been re-evaluated and a determination key is provided.

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INTRODUCTION

The genus *Phyteuma* L. is distinguished from the other genera in the *Campanulaceae* by its densely spicate or capitate inflorescence, curved flower buds, sessile or subsessile flowers with linear corolla lobes which are connate in the upper part but become free during florescence, and capsule opening by lateral pores. It is entirely European in its geographical distribution, the area of the greatest diversity being the Alps where the vast majority of the species are concentrated (see SCHULZ 1904, SCHARFETTER 1953).

The concept of the genus was established by LINNAEUS (1753) who recognized six species: *P. pauciflora* L., *P. hemisphaerica* L., *P. orbicularis* L., *P. spicata* L., *P. comosa* L. and *P. pin-nata* L., of which the latter two are now placed in separate genera, respectively *Physoplexis* (ENDL.) SCHUR and *Petromarula* VENT. ex HEDWIG fil. The monographer of the genus, SCHULZ (1904), lists 29 species of *Phyteuma*, almost all of them subdivided into an elaborate system of subordinate units from subspecies to formae. Many of them were proposed on the basis of a few simple characters, which do not correlate well with others, and without understanding of living material or of habitat and distribution. Apart from KUNZ (1940), little attempt has been made to reconsider these taxa critically, so that additional confusion to the taxonomy of the genus has been caused, resulting in controversial treatments in various floras. For instance, one should note the wide divergence of opinion regarding the subdivision of *P. spicatum* L. or *P. orbiculare* L. or the circumscription of some variable species, such as *P. globulariifolium* STERNB. et HOPPE. In *Flora Europaea* (DAMBOLDT 1976), the number of species was reduced to 24 and very few infraspecific taxa were admitted. The genus as a whole deserves a careful population and experimental taxonomic study.

Early treatments of the genus in this country have been very confused. From Bohemia alone, SCHMIDT (1794) reported no less than nine species: *P. orbiculare* L., *P. Charnelii* VILL., *P. Michellii* ALL., *P. Scheuchzeri* ALL., *P. nigrum* F. W. SCHMIDT (described as new), *P. ovatum* SCHRANK, *P. spicatum* L., *P. betonicifolium* VILL. and *P. scorzonrifolium* VILL. Of this impressive list of

names, however, six are obvious misapplications, *P. Charmelii*, *P. Michelii* and *P. Scheuchzeri* belonging to *P. orbiculare*, *P. betonicifolium* and *P. scorzonerifolium* to *P. spicatum* and *P. ovatum* to *P. nigrum*. (For a criticism of Schmidt's approach, see e.g. TAUSCH 1828). POHL (1809) recognized four species in Bohemia (*P. Scheuchzeri* ALL., *P. orbiculare* L., *P. spicatum* L. and *P. Halleri* ALL.), reducing Schmidt's *P. nigrum* to a variety of *P. spicatum*. The treatment of the genus in the first complete Czech flora by PRESL et PRESL (1819) is a relatively critical one, including only *P. orbiculare* L., *P. nigrum* F. W. SCHMIDT, *P. ovatum* F. W. SCHMIDT and *P. spicatum* L. OPIZ (1852) followed the brothers Presl but listed *P. ovatum* under the name of *P. Halleri* ALL. Only ČELAKOVSKÝ (1871) excluded this close ally of *P. spicatum* from the flora of Bohemia, recognizing merely *P. spicatum* L., *P. nigrum* F. W. SCHMIDT and *P. orbiculare* L. Czechoslovak species of *Phyteuma* were first listed by DOMIN et PODPĚRA (1928). No comprehensive taxonomic revision of the genus in Czechoslovakia has ever appeared but distribution maps for Bohemia and Moravia have been prepared by Vondrová (VONDROVÁ 1971, VONDROVÁ in HENDRYCH 1973; *P. nigrum* and *P. orbiculare*) and Mladý (MLADÝ in KUBÁT 1978; *P. nigrum* only).

The present work was undertaken to clarify the variation patterns, cytology, reproductive biology and taxonomy of the genus *Phyteuma* in Czechoslovakia. A large-scale experimental study combined with hybridization experiments was planned but could not be carried out, partly because of the involvement of the present author in other research projects and partly because of the continued decrease of *P. orbiculare* in this country. This species, which was to be the chief object of the study, is now on the verge of extinction in the western half of Czechoslovakia, its habitats being steadily converted into arable land. In most localities known from the literature and/or herbarium specimens, only few plants, if any, were found, and a number of the sites have ceased to exist. It is hoped, however, that even these incomplete results will contribute to a better understanding of the genus.

The three species discussed below fall into two major subdivisions of the genus as delimited by SCHULZ (1904), the section *Spicata* including *P. spicatum* L. and *P. nigrum* F. W. SCHMIDT, and section *Capitata* containing *P. orbiculare* L. This subdivision of the genus is quite natural but, being based on one single morphological character, does not necessarily correspond to separate phylogenetic lines.

MATERIAL AND METHODS

The morphological variation has been studied in terms of population samples rather than single herbarium specimens, because of the importance of assessing the amount of variation within populations and comparing this with the variation between populations. A large number of *Phyteuma* populations have been studied in the field and considerable quantities of material were cultivated at the experimental plot of the Botanical Institute of the ČSAV at Průhonice. Plants easily adapt to cultivation and the majority of the material was in the form of transplants from natural populations. Field studies of *P. orbiculare* were conducted in C., W., N. and E. Bohemia, N. Moravia and W. and N. Slovakia. Populations of *P. spicatum* were sampled mainly in C. Bohemia, Šumava Mts., Krušné hory Mts., Jizerské hory Mts. and Hrubý Jeseník Mts., those of *P. nigrum* in S. Bohemia, Šumava Mts., Krušné hory Mts. and N. Bohemia. Care was taken to see that the samples came from as different edatopes as possible.

Chromosome counts were determined from squashes of pollen mother cells. For these studies, young floral buds of the various species were fixed in the standard 3 : 1 absolute ethanol-glacial acetic acid solution. After a period of 24 hours, the fixative was replaced with 70 % ethanol and the vials were stored in a refrigerator until the material could be examined. Voucher specimens will be deposited in PR.

Tab. 1 gives the localities of the population samples used in the present study. Each sample was assigned a number by which it is referred to in the text. Hyphenated numbers designate particular individuals; for instance, P140-2 is the individual No. 2 from the sample P140. The meiotic chromosome number is given if determined from the sample in question.

Tab. 1. — List of topodemes examined

Taxon	Number	Locality	n
<i>P. spicatum</i>	P8	Západne Beskydy Mts.: <i>Pinetum mughi</i> in the summit area of Mt. Babia hora, 1600 m	11
	P102	Srbsko near Beroun, mixed woodland in the valley of the Bubovický potok brook, S. of Doutnáč hill, 320 m	11
	P113	Šumava Mts.: Wet meadow N. of Modrava, 980 m	11
	P115	Šumava Mts.: Swampy meadow at Velký Bor, E. of Prášily, 880 m	11
	P134	Krušné hory Mts.: meadow S. of Krásný Les, 650 m	11
	P137	Šumava Mts.: Meadows along the Řezná brook, 2.5 km NE. of Železná Ruda, 850 m	11
	P139	Šumava Mts.: Meadow at Nový Brunst, NNE. of Železná Ruda, 970 m	11
	P143	Šumava Mts.: Holetín, near Kašperské hory, meadows on the Opolenecký potok brook, 580 m	11
	P160	Hrubý Jeseník Mts.: Dry mountain grassland on S. slope of Mt. Praděd, 1300 m	11
	P161	Hrubý Jeseník Mts.: Mountain grassland in the Velká kotlina glacial cirque, 1200 to 1300 m	11
	P203	Leskovec nad Moravicí, near Bruntál, meadow by the Moravice river at Frankův mlýn, 450 m	11
	P207	Nizký Jeseník Mts.: Meadows along the Opava river SE. of Kunov, near Bruntál, 390 m	11
	P240	Eastern margin of the Kersko wood, near Sadská, 187 m	11
	P254	Strážovská hornatina Mts., beech wood below the summit of Mt. Rokoš, 1010 m	11
	P258	Bílé Karpaty Mts.: grassy hillside S. of V krátkých, near Starý Hrozenkov, 430 m	11
	P260	Bílé Karpaty Mts.: Mikulčín vrch hill, grassy slope (N.-facing) above Uhliska, 700 m	11
	P272	Krušné hory Mts.: Spring terrain SSW. of Loučná, 980 m	11
	P281	Krušné hory Mts.: meadows at Vykmanov, near Klášterec nad Ohří, 680 m	11
	P287	Krušné hory Mts.: Meadows along Křimovský potok brook, NW. of Křimov, 750 m	11
	P312	Jizerské hory Mts.: Meadow S. of Mt. Bukovec, near Jizerka, 910 m	11
	P314	Štěchovice, near Prague, spruce forest in the valley of the Vltava river, 1 km E. of the dam, 230 m	11
	P320	Krušné hory Mts.: grassy roadside in a wood at the "Pod Meluzinou" road junction, near Stráž nad Ohří, 970 m	11
	P321	Krušné hory Mts., Roadside ditch 1 km E. of Rýžovna, near Horní Blatná, 970 m	11
	P323	Krušné hory Mts.: grassy slope in the valley of the Rolava brook, 0.5 km of the railway bridge at Nové Hamry, 700 m	11

Tab. 1. (Contd.)

<i>P. nigrum</i> F, W, SCHMIDT	P325	Krušné hory Mts.: Meadows at Jelení, near Nejdek, 870 m	
	P326	České středohoří Mts.: mixed woodland in the Opárenské údolí valley, 1 km E of Císařský mlýn mill, 190 m	11
	P328	N. Moravia: eastern part of the Hněvošický háj wood, near Opava, 280 m	11
	P330	Slavkovský les Mts.: Grassy roadside S. of Pluhův bor wood, near Mnichov, 680 m	
	P112	Šumava Mts.: Wet meadow N. of Modrava, 980 m	
	P124	S. Bohemia: Týn nad Vltavou, dry grassland in the valley of the Bilinský potok brook, near U Bártů, NNW. of Vesce, 360 m	11
	P126	S. Bohemia: Grassland SW. of Chotýčany railway station, near České Budějovice, 520 m	11
	P136	Šumava Mts.: Meadows along the Řezná brook, 2,5 km NE. of Železná Ruda, 850 m	
	P140	Šumava Mts.: Holetín, near Kašperské Hory, meadows on the Opolenecký potok brook, 580 m	
	P142	Šumava Mts.: Zdíkov, meadow on road to Vimperk, 780 m	11
	P145	Šumava Mts.: Kubova Huť, meadow on road to Horní Vltavice, 980 m	11
	P148	Šumava Mts.: Volary, meadows NE. of the town, 790 m	11
	P150	S. Bohemia: Lhenice, near Netolice, meadow on road to Vadkov, 570 m	11
	P152	S. Bohemia: Novohradské hory Mts., grassy roadside in a wood NE. of Huťský rybník pond, near Pohorská Ves, 780 m	11
	P154	S. Bohemia: Obora wood near Protivín, E. margin, 400 m	11
	P156	S. Bohemia: Vráž near Písek, grassland near Novovrážský rybník pond, 420 m	11
	P274	Krušné hory Mts.: Dolina near Přísečnice, meadow on road to Měděnec, 780 m	11
	P280	Krušné hory Mts.: meadows at Vykmánov, near Klášterec nad Ohří, 680 m	
	P286	Krušné hory Mts.: Meadows along the Křimovský potok brook, NW. of Křimov, 750 m	
	P298	Krušné hory Mts.: Meadows NE. of Rusová, 810 m	11
	P299	Krušné hory Mts.: Meadows E. of Přísečnice, 720 m	11
	P306	N. Bohemia: Dolní Žleb, near Děčín, dry grassy slope (E.-facing) above the Elbe river, 130 m	11, 12
	P315	C. Bohemia: Mixed woodland in the valley of the Vltava river N. of Hrazany (distr. Příbram), 270 m	11
	P324	Krušné hory Mts.: Meadows at Jelení, near Nejdek, 870 m	
	P329	Slavkovský les Mts.: Lobežský potok valley, near Sokolov, small meadow SW. of Lobežský vrch hill, 620 m	

<i>P. orbiculare</i> L. subsp. <i>orbiculare</i>	P331	W. Bohemia: Skalka, near Cheb, grassy roadside on road to Cheb, 450 m	
	P104	C. Bohemia: Bílichovské údolí valley, near Bílichov (distr. Kladno), in moist alder wood, 390 m	11
	P105	C. Bohemia: Small meadow in a wood on road from Kozí Hory to Hranice gamekeeper's house, S. of Nový Knín, 440 m	11
	P110	C. Bohemia: Dry grassland between Lysá nad Labem and the Mlýnařice irrigation canal, 180 m	11
	PI18	E. Bohemia: Kukle near Svitavy, small meadow on road to Sněžník hill, 560 m	11
	P120	W. Bohemia: Moist alder wood (spring terrain) just south of a road junction (point 497 m) between Těškov and Volduchy, near Rokycany	11
	P129	W. Bohemia: Mýto, near Rokycany, dry grassland between Štěpánský rybník pond and Loulín mill, 450 m	11
	P130	C. Bohemia: Olešná, near Hořovice, meadow on road to Jivina, 500 m	
	P133	Krušné hory Mts.: Krásný Les, near Ústí nad Labem, meadows S. of the village, 650 m	11
	P135	W. Bohemia: Dolní Bělá, near Kaznějov, thickets at Spálený mlýn mill, on the Bělá Bělá brook, 450 m	11
	P204	N. Moravia: Leskovec nad Moravicí, near Bruntál, meadow by the Moravice river at Frankův mlýn mill, 450 m	11
	P256	Bílé Karpaty Mts.: Grassy hillside S. of V krátkých, near Starý Hrozenkov, 430 m	
	P259	Bílé Karpaty Mts.: Mikulčín vrch hill, grassy slope (N.-facing) above Uhliska, 700 m	
<i>P. orbiculare</i> L. subsp. <i>montanum</i> R. SCHULZ	P270	Prague: Písnice, Vrtilka meadow SW. of the village, 310 m	
	P271	C. Bohemia: Alder grove just E. of Nový rybník pond, near Loučeň (distr. Nymburk), 230 m	11
	P315	C. Bohemia: Třtice, near Nové Strašecí, swampy meadow S. of the village, 420 m	11
<i>P. orbiculare</i> L. subsp. <i>flexuosum</i> R. SCHULZ	P164	N. Moravia: Hrubý Jeseník Mts., rocky slope in the Velká kotlina glacial cirque, graphitic phyllite, 1200—1300 m	11
	P12	E. Slovakia: Slovenský raj, limestone rocks at Železné vráta, on the Hornád river, near Spišská Nová Ves, 620 m	
	P16	E. Slovakia: Slovenský raj, limestone rocks in the Hnilec river valley, W. of Stratená, 850 m	
	P80	N. Slovakia: Chočské pohorie Mts., rocks in the summit area of Mt. Ostrá, limestone, 1765 m	

	P81	N. Slovakia: Nízke Tatry Mts., rocks in the summit area of Mt. Kraková hora, limestone, 1753 m	
	P83	N. Slovakia: Malá Fatra Mts., SE. slope of Mt. Veľký Rozsutec, limestone, 1450 m	
	P218	N. Slovakia: Baba hill, near Svit, limestone rocks in a pine wood, 800 m	
	P250	W. Slovakia: Strážovská hornatina Mts., limestone cliffs on Čihoc hill, near Horné Vestenice, 820 m	
	P251	W. Slovakia: Strážovská hornatina Mts., meadow in the summit area of Mt. Rokoš, 1010 m	11
	P256	E. Moravia: Bílé Karpaty Mts., grassy hillside S. of V krátkých, near Starý Hrozenkov, 430 m	11
	P259	E. Moravia: Bílé Karpaty Mts., Mikulčín vrch hill, grassy slope (N.-facing) above Uhliska, 700 m	
	P262	W. Slovakia: Biele Karpaty Mts., limestone rocks in a saddle S. of Chmelová hill, near Vršatské Podhradie, 850 m	11
	P264	W. Slovakia: Biele Karpaty Mts., limestone rocks at Vršatec ruin, 750 m	
	P268	W. Slovakia: Strážovská hornatina Mts., meadow in the summit area of Baske hill, limestone, 955 m	
<i>P. × adulterinum</i> WALLR.	P138	Šumava Mts.: Meadows along the Řezná brook, 2.5 km NE. of Železná Ruda, 850 m	11
	P114	Šumava Mts.: Wet meadow N. of Modrava, 980 m	
	P141	Šumava Mts.: Holetín, near Kašperské Hory, meadows on the Opolenecký potok brook, 580 m	11
	P282	Krušné hory Mts.: Meadows at Vykmánov, near Klášterec nad Ohří, 680 m	
	P288	Krušné hory Mts.: Meadows along the Křímovský potok brook, NW. of Křímov, 750 m	

CYTOLOGY

The results of the chromosome number studies (see Tab. 1) may be summarized as follows:

1. In all the species examined, the meiotic chromosome number $n = 11$.
2. The material under study is nearly uniform in its chromosome numbers. The only exception is P306 (*P. nigrum* F. W. SCHMIDT) in which, besides $n = 11$, also the gametic number of $n = 12$ was found. It should be noted, however, that both the numbers occurred in the same anther — a case of mixoploidy. It might be interesting to investigate the behaviour of the

$n = 12$ pollen grains and their role in pollination. The possibility cannot be excluded that whole mixoploid individuals exist in natural populations of *Phyteuma nigrum*. On the other hand, no variation in the chromosome number was observed in the polymorphic *P. orbiculare* L. and *P. spicatum* L.

3. There is no evidence of polyploidy, not even in geographically separated and morphologically clear-cut populations, such as P164. This is remarkable,



Fig. 1. — Pollen mother cells of *Phyteuma* species: a, *P. spicatum* (metaphase I), $n = 11$; b, *P. nigrum* (metaphase II), $n = 12$; c, *P. orbiculare* subsp. *orbiculare* (metaphase II), $n = 11$. Scale: 10 μ m.

for in the related genus *Campanula* nearly all variable species contain polyploid series (see e.g. GADELLA 1964, KOVANDA 1970a, 1970b, 1977).

4. Meiotic behaviour was quite normal in all cases studied, leading to high pollen fertility.

5. The chromosomes of all three species are small and appear to be of fairly uniform size, although no attempt has been made to analyze their structure in detail.

These findings are, for the most part, in accordance with the results of previous chromosome number studies, including those by the present author.¹⁾ Both meiotic and mitotic chromosome numbers are available. OCHLEWSKA (1965) and POLATSCHEK (1966) examined plentiful material of *P. spicatum* L. and *P. orbiculare* L. from Poland and Austria, respectively, and reported $2n = 22$ as the somatic chromosome number. Both these authors have observed B chromosomes fairly often, the first in *P. spicatum*, the latter in *P. orbiculare*. For *P. spicatum*, the number of $2n = 22$ (or $n = 11$) has also been ascertained by GADELLA et KLIPHUIS (1968; B chromosomes reported) and MÁJOVSKÝ et al. (1974), for *P. nigrum* by GADELLA (1966; cultivated material of unknown origin), for *P. orbiculare* by RITTER (1974). Discordant chromosome number reports include: for *P. spicatum*, $n = 12$ and $2n = 24$ (CONTANDRIOPOULOS 1962), for *P. nigrum*, $2n = 26$ (SUGIURA 1941, 1942b; cit. sec. FEDOROV et al. 1969), for *P. orbiculare*, $n = 12$ (TISCHLER 1950), $2n = 24$ (BAKSAY 1956, CONTANDRIOPOULOS 1962, GADELLA 1966, NILSSON et LARSEN 1974), $2n = 26$ [SUGIURA 1942a (cit. sec. FEDOROV et al. 1969)], BAKSAY 1956). The report of $n = 18$ for *P. spicatum* (ARMAND 1912; cit. sec. OCHLEWSKA 1965) is obviously in error.

Occasional doubling of the chromosome number has been observed by OCHLEWSKA (1965) in root meristems of *P. spicatum*. So far, this is the only

¹⁾ In Flora der Schweiz (HESS, LANDOLT et HIRZEL 1972), the first chromosome count of $n = 11$ for *P. nigrum* F. W. SCHMIDT of known wild origin (KOVANDA in LÖVE 1970) is ascribed to JACKSON (JACKSON in LÖVE 1970) who does not appear to have ever worked with *Phyteuma*.

indication of polyploidy in the genus *Phyteuma* (see FAVARGER 1953, CONTANDRIOPOULOS 1962, OCHLEWSKA 1965, POLATSCHKE 1966). *P. campanuloides* BIEB., for which the polyploid number of $2n = 102$ has been published (SUGIURA 1940, 1942b; cit. sec. FEDOROV et al. 1969) is actually *Asyneuma campanuloides* (BIEB.) BORNM. With chromosome numbers now available for nearly all species of *Phyteuma*, it may be concluded therefore that polyploidy has not played any role in the differentiation of the genus. Apparently, this operated solely on the basis of dysploid changes in the chromosome number (see also POLATSCHKE 1966) — a situation not paralleled in any other genus of the *Campanulaceae* which has been subjected to detailed cytological investigation.

LIFE FORM AND DURATION OF PLANTS

All three species are hemicryptophytes, with the roots alone surviving the winter. In cultivation, they proved short-lived perennials. None of the plants transferred from natural habitats, which were understandably of different age, lived more than five years. In the absence of a rhizome, this is not surprising.

BREEDING BEHAVIOUR

The three species examined are sexual, as is the whole genus and the vast majority of the *Campanulaceae*. There is no indication of apomictic behaviour or cleistogamy. Effective reproduction is by seed which is produced regularly in quantities every year. Vegetative propagation is impossible, except by the establishment of root cuttings in cultivation.

FLORAL BIOLOGY

The floral biology of *Phyteuma* has been a much debated topic. In *P. spicatum* it was studied by SPRENGEL as early as 1793. His accurate observations have been supported by a number of authors (see e.g. KERNER 1891, KIRCHNER 1897, SCHULZ 1904) and are also confirmed on *P. nigrum* and *P. orbiculare* in the present study. The flower mechanism may briefly be described as follows: In the bud, the five thin corolla lobes are coherent to form a narrow, curved (very conspicuously in *P. orbiculare*, less so in *P. spicatum* and *P. nigrum*) tube closed at the apex. The upper part of the tube is occupied by the closely packed introrse anthers, surrounding the top of the style. Pollen (light yellow in *P. spicatum*, violet in *P. nigrum* and *P. orbiculare*) is shed before the flower opens. The corolla lobes then begin to separate in their lower parts and bend outwards together with the filaments, thus forming a dome above the ovary. In this way the lobes get contracted, allowing the elongating style to push through the tube and to drive the pollen out. After a period of time, when the pollen has been collected by the insects, the threadlike, papillose stigmas begin to spread out. The separation of the corolla lobes continues up to the top of the tube, until finally they get free and fall back. By that time the stamens are withered and stigmas fully unfolded.

Flowering is in May and June in all three species, extending into July in mountain habitats. The flowers of *Phyteuma* are nectar flowers, with nectar produced by an epigynous disc. Whereas the pollen is freely exposed

Tab. 2. — Seed set following isolation

Taxon	Individual	Seed set
<i>P. spicatum</i>	P240-6	—
<i>P. nigrum</i>	P154-10	—
<i>P. orbiculare</i>		
subsp. <i>orbiculare</i>	P120-2	—
subsp. <i>montanum</i>	P164-3	—
subsp. <i>flexuosum</i>	P251-6	—

Scoring code: — none
 + poor
 ++ moderately good
 +++ good

and available to virtually any insect, the nectar is well protected by the dilated and ciliate bases of the filaments. Yet it seems that it is primarily the nectar that the flowers of *Phyteuma* are visited for, bees, humble-bees, butterflies and flies being the most frequent clients. It might be interesting to investigate the nutritional value of the pollen and its part in insect diet.

AUTOGAMY

The mechanism described above has clearly developed to facilitate cross-pollination and to prevent self-pollination. As in *Campanula*, there has been much speculation about “emergency self-pollination” (where the stigmas should roll down so far as to touch the surface of the style where the remains of the pollen might be deposited), and reports to that effect are perennially copied from one textbook to another. In the absence of any experimental evidence, it was decided to test this hypothesis on the material in cultivation. Whole inflorescences were isolated in paper bags and left thus until free-pollinated plants grown in the same conditions produced ripe seed. No seed-setting was observed in the isolated plants (see Tab. 2). Nor did any seed-setting take place in plants of *P. orbiculare* (P120 and P315) transferred to the laboratory and left to their own devices. On the other hand,

Tab. 3. — Seed set following artificial autogamy

Taxon	Individual	Seed set
<i>P. spicatum</i>	P240-6	—
	P160-10	+
<i>P. nigrum</i>	P124-3	—
	P150-4	—
	P154-6	++
	P306-2	+
<i>P. orbiculare</i>		
subsp. <i>orbiculare</i>	P120-4	+
	P129-8	+
subsp. <i>montanum</i>	P164-12	—
	P164-14	—
subsp. <i>flexuosum</i>	P250-4	—
	P262-9	+

Scoring code as in Tab. 2.

Tab. 4. — Interspecific crosses of *P. spicatum* (♀)

Taxon	Individual		Taxon	Individual	Seed set
<i>P. spicatum</i>	P160-5	×	<i>P. nigrum</i>	P152-1	+++
	P102-9	×	<i>P. orbiculare</i> subsp. <i>montanum</i>	P160-3	+++
	P160-5	×	<i>P. orbiculare</i> subsp. <i>montanum</i>	P164-14	+
	P161-3	×	<i>P. orbiculare</i> subsp. <i>montanum</i>	P264-4	+++
	P207-5	×	<i>P. orbiculare</i> subsp. <i>montanum</i>	P264-3	+++
	P102-9	×	<i>P. orbiculare</i> subsp. <i>flexuosum</i>	P250-4	+++
	P161-2	×	<i>P. orbiculare</i> subsp. <i>flexuosum</i>	P250-4	+++
	P240-6	×	<i>P. orbiculare</i> subsp. <i>flexuosum</i>	P250-4	+++
	P240-7	×	<i>P. orbiculare</i> subsp. <i>flexuosum</i>	P250-4	+++

Scoring code as in Tab. 2.

self-pollination experiments effected with another lot of individuals demonstrated that autogamy is possible, albeit on a limited scale (see Tab. 3). The number of morphologically good seed varied from 0 to 3 per capsule. Because of the limited number of plants, the results of the isolating and selfing experiments are admittedly of a rather tentative nature.

A certain amount of autogamy (and of geitonogamy as well) probably takes place in natural populations. An insect visiting a fully developed inflorescence can well transfer the remains of the pollen sticking among the hairs on the surface of the style to the stigmas of the same flower, or carry fresh pollen from one flower to another in the same inflorescence. It remains to be ascertained whether the selfed progenies survive in the outbreeding populations or whether they are eliminated by natural selection.

HYBRIDIZATION

Although many spontaneous interspecific hybrids (many based on single herbarium specimens; see e.g. SCHULZ 1904) have been reported in *Phyteuma*, no attempt has previously been made to study these in more detail or to produce them artificially. In the present research programme, special attention was paid to natural hybrids, and a series of artificial crosses was carried out to determine the degree of genetic relationships among the species studied. All potential hybrid combinations were realized and reciprocal crosses were also made. As the hybrid between *P. nigrum* and *P. spicatum* (both belonging to the same section) is of common occurrence in nature, the hybridization experiments were focused on crosses among members of different sections. The possibility of spontaneous self-pollination not having

Tab. 5. — Interspecific crosses of *P. nigrum* (♀)

Taxon	Individual		Taxon	Individual	Seed set
<i>P. nigrum</i>	P152-1	×	<i>P. orbiculare</i> subsp. <i>orbiculare</i>	P120-2	+++
	P156-9	×	<i>P. orbiculare</i> subsp. <i>orbiculare</i>	P271-7	+++
	P156-9	×	<i>P. orbiculare</i> subsp. <i>orbiculare</i>	P135-2	+++
	P150-4	×	<i>P. orbiculare</i> subsp. <i>montanum</i>	P164-3	+++
	P152-1	×	<i>P. orbiculare</i> subsp. <i>flexuosum</i>	P251-5	+++
	P154-6	×	<i>P. orbiculare</i> subsp. <i>flexuosum</i>	P251-5	—
	P306-2	×	<i>P. orbiculare</i> subsp. <i>flexuosum</i>	P262-2	+++
	P154-6	×	<i>P. spicatum</i>	P160-5	+++

Scoring code as in Tab. 2.

Tab. 6. — Interspecific crosses of *P. orbiculare* (♀)

Taxon	Individual		Taxon	Individual	Seed set
<i>P. orbiculare</i> subsp. <i>orbiculare</i>	P120-1	×	<i>P. nigrum</i>	P124-3	+++
	P120-1	×	<i>P. nigrum</i>	P152-1	+++
	P133-6	×	<i>P. spicatum</i>	P207-4	+++
	P133-6	×	<i>P. spicatum</i>	P160-5	+++
	P120-7	×	<i>P. spicatum</i>	P160-5	+++
	P120-4	×	<i>P. spicatum</i>	P207-4	+++
	P129-8	×	<i>P. spicatum</i>	P160-5	+++
	P271-7	×	<i>P. spicatum</i>	P160-5	+++
	P164-14	×	<i>P. nigrum</i>	P150-7	+++
	P164-10	×	<i>P. spicatum</i>	P160-5	+++
subsp. <i>montanum</i>	P164-10	×	<i>P. spicatum</i>	P102-9	+++
	P164-12	×	<i>P. spicatum</i>	P102-9	+++
	P164-15	×	<i>P. spicatum</i>	P240-8	+++
	P164-15	×	<i>P. × adulterinum</i>	P141-1	++
	P250-4	×	<i>P. nigrum</i>	P154-3	+++
subsp. <i>flexuosum</i>	P259-3	×	<i>P. nigrum</i>	P154-3	+++
	P262-2	×	<i>P. spicatum</i>	P207-5	+++
	P262-2	×	<i>P. spicatum</i>	P160-5	+++
	P262-9	×	<i>P. spicatum</i>	P102-9	+++
	P268-3	×	<i>P. spicatum</i>	P207-4	+++
	P251-6	×	<i>P. spicatum</i>	P207-5	—

Scoring code as in Tab. 2.

been proven (see above), the flowers were not emasculated but care was taken to see that the pollen of the donor was not contaminated with that of the mother plant. The method of isolation was the same as in the selfing experiments referred to above. The results are summarized in Tab. 4—6. It will be seen that of the three species involved, each produced hybrids with all of the remaining two in either direction. Out of 38 interspecific crossings, 36 were successful, resulting in a fair amount of viable seed. The two failures may be due to unsuitable time chosen for the crossing (stigmas not yet or no longer receptive) rather than to intrinsic incompatibility.

The hybrid *P. nigrum* × *P. spicatum* (*P. × adulterinum* WALLR.) arises spontaneously wherever the two species occur together in one habitat and was also produced in the present study (see Tab. 4, 5). No disturbances in the meiotic chromosome pairing were observed, suggesting that the two genomes are largely homologous. Back crossing with either parent was successful and a triple hybrid, *P. orbiculare* × *P. × adulterinum*, was also obtained (see Tab. 6).

Except for the doubtful report of the hybrid *P. nigrum* × *P. orbiculare* from S. Bohemia, which will be further discussed below, no hybrids between the two sections of *Phyteuma* have been reported (see e.g. SCHULZ 1904). The results of the crosses involving *P. orbiculare* (including all three sub-species; see Tab. 6) are therefore surprising but, in the light of the cytological information now at hand, not entirely unexpected. Interestingly, even taxa widely separated geographically, with no possibility of gene exchange in nature, such as *P. orbiculare* subsp. *flexuosum* R. SCHULZ and *P. nigrum* F. W. SCHMIDT, proved crossable. The ease with which the two major subdivisions of *Phyteuma* hybridize would suggest that their taxo-

onomic value as sections is perhaps overestimated, but, pending a critical revision of the whole genus, any re-arrangement of their species contents would be useless.

The putative intergeneric hybrid *Campanula Hausmannii* REICHENB. fil. [*Campanula barbata* L. $\times$ *Phyteuma hemisphaericum* L.; syn. *Fockeanthus Hausmannii* (REICHENB. fil.) WEHRHAHN; see REICHENBACH fil. 1877, WEHRHAHN 1931] probably belongs to the realm of fantasy. It seems to be clear from the diagnosis (REICHENBACH fil. l.c.) that the individual was a monstrosity of *P. hemisphaericum* L. with a proliferating inflorescence.

It is hoped that a more detailed study of *Phyteuma* hybrids will be published later. Additional observations on the spontaneous hybrids will be found in the taxonomic part of this paper.

SOME USEFUL MORPHOLOGICAL CHARACTERS

When flowering in the field, the three species are easily distinguished by their morphology but in certain stages of development or in herbarium material the species limits may sometimes be blurred, making certain identification difficult. Even so distinct a species as *P. orbiculare* is sometimes mistaken for *P. nigrum*, as are also certain forms of *P. spicatum*.

The following survey is intended to define some distinguishing characters with more precision and to draw attention to those which have been neglected.

Root

All *Phyteumas* are perennials with stout, fleshy roots emitting innovation shoots from the axils of cataphyllary leaves. The roots of *P. orbiculare* are basically fusiform and not conspicuously thickened, those of *P. spicatum* and *P. nigrum* are swollen and are usually described as napiform (see e.g. HAYEK 1915, DAMBOLDT 1976) but their shape varies considerably, often assuming a bizarre appearance. In Central Europe, roots of *P. spicatum* were at one time used a vegetable.

Leaf

The diagnostic description of the leaves — both basal and cauline — presents serious difficulties because no two successive leaves on an individual are equivalent in terms of morphology, resulting in confused and sometimes contradictory descriptions. Only leaves of the same order may be compared, and this is virtually impossible in natural populations. All *Phyteumas* are heterophyllous and the rate at which the basal leaves become transformed into cauline ones is different in different species. Of the three Czechoslovak species, heterophylly is most pronounced in *P. orbiculare* but is somewhat less conspicuous in *P. spicatum*.

Basal leaves are always petiolate and do not normally wither before the onset of flowering. The length of the petiole, if combined with other features, is a valuable taxonomic character separating the three subspecies of *P. orbiculare*, the longest petioles being diagnostic of the type subspecies. In *P. orbiculare*, the basal leaves are numerous (up to 10–12), usually forming a distinct rosette; in the other two species they are fewer (usually 2–6, rarely more). The form of the blade in *P. orbiculare* varies from lanceolate

to elliptic (rarely almost orbicular), the margin is crenate or serrate, the basis cordate to cuneate. Both *P. spicatum* and *P. nigrum* have cordate basal leaves but the sinus is less distinct and the ratio blade-length : blade-width is higher in the latter. The leaves are coarsely (often doubly) serrate in *P. spicatum* but irregularly crenate to subentire in *P. nigrum*.

The shape of the cauline leaves is also diagnostic in all three species. In *P. orbiculare*, the lower leaves are narrowly ovate or lanceolate to linear-lanceolate, crenate or finely serrate, petiolate to sessile; the others are successively smaller and narrower, remotely serrate to entire and sessile. They are diagnostic for each of the three subspecies. *P. spicatum* differs in having lower cauline leaves more or less similar to the basal ones; the others gradually become smaller, with blades obtuse or cuneate at base, the ratio blade-length : blade-width increasing and the length of the petiole decreasing. The uppermost leaves are lanceolate and sessile. *P. nigrum* is somewhat intermediate between these two species, having lower cauline leaves lanceolate to oblong-ovate, finely crenate to subentire, with blade cuneate at base, the other leaves decreasing rapidly in size and in length of the petiole; the uppermost leaves are strongly reduced.

Basal leaves of *P. spicatum* and *P. nigrum* often have black or brown markings along the main veins, mainly at the base of the blade. The presence of these markings is apparently accidental and does not seem to be a useful character to distinguish infraspecific taxa. The markings have never been observed in *P. orbiculare*.

Inflorescence

The inflorescence of *Phyteuma* is essentially racemose. Its morphology is characteristic of most species of *Phyteuma* and was made the basis of the subdivision of the genus into two sections, *Spicata* (with flowers in spikes) and *Capitata* (with flowers in capitula; see SCHULZ 1904). In *P. spicatum* (sect. *Spicata*) the spike is ovoid or cylindrical, its rhachis elongating considerably between the onset of flowering and the maturity of the seed. *P. nigrum*, the other Czechoslovak member of sect. *Spicata*, has the spike ovoid, beginning to elongate only towards the end of anthesis. In fruit, both *P. spicatum* and *P. nigrum* may be described as having cylindrical infrutescences. In both species single flowers are sometimes found in the axils of the uppermost one or two cauline leaves and both occasionally produce variants with short, subglobose spikes. *P. orbiculare* (sect. *Capitata*) has a distinct capitulum. Its rhachis does not show any propensity to elongate during flowering but it does elongate in fruit, resulting in an ovoid to shortly cylindrical infrutescence, not unlike those of certain forms of *P. nigrum*. It follows therefore that no clear dividing line can be drawn between these two sections.

In all species, the opening of the flowers proceeds acropetally. No deviations have been observed.

Involucre

The inflorescence of *Phyteuma* is subtended by what is conventionally called the involucre (see e.g. SCHULZ 1904, DAMBOLDT 1976). In *P. spicatum* and *P. nigrum* it is indistinct, consisting of non-imbricating, narrowly lanceolate to linear bracts which do not differ much from the uppermost cauline leaves.

Rarely only one bract develops, sometimes placed at a distance from the inflorescence. Size, shape and position of the bracts vary greatly in these species and are useless as taxonomic characters. In *P. orbiculare* the involueral bracts are arranged into imbricating rows, thus forming a structure not unlike the genuine involucre of the *Asteraceae*. They are foliar as in *P. spicatum* and *P. nigrum* but tend to differ from the upper cauline leaves, being ovate-lanceolate and usually distinctly acuminate. Their shape, size and position (in relation to the flowers) have been used to separate infra-specific taxa in *P. orbiculare* (see SCHULZ 1904). On examination, however, these characters prove to be rather unsatisfactory. Schulz's key and original diagnoses require the involueral bracts to be subacute, as long as or longer than the flowers for all three Czechoslovak subspecies; in subsp. *pratense* they are described as patent to reclinate, often conduplicate at the apex, in subsp. *montanum* as appressed or rarely patent, and in subsp. *flexuosum* as appressed to patent, rarely reclinate. In the present material, these features were found to vary over a wide range even within individuals. In all populations studied, plants with involueral bracts shorter than the flowers were recorded: those referred to subsp. *montanum* had bracts generally shorter than those belonging to the other two subspecies. Conduplicate bracts are by no means confined to subsp. *pratense*. The position of the bracts also varies from appressed to reclinate in all three subspecies. It follows then that the morphology of the involucre is generally too phenotypically plastic to be used for diagnostic purposes. If used in a key, the characters of the involucre should not be applied too rigidly or without reference to other characters.

Colour of corolla

This character has attracted the attention of botanists perhaps more than any other because, though distinctive for each of the three species discussed in the present study, it varies strikingly.

P. spicatum is unusual in the genus in having white to yellowish coloured corollas with green tips. In the genus *Phyteuma*, only *P. pyrenaicum* R. SCHULZ and *P. cordatum* BALBIS are predominantly (though not entirely) whitish-flowered. Colour variants do occur in *P. spicatum* also, ranging from pale blue to bluish-violet. They have been repeatedly described under various names mainly from the more western parts of the range and some of them, such as subsp. *occidentale* R. SCHULZ and subsp. *jurassicum* R. SCHULZ, seem to represent relatively distinct regional facies of the species. Elsewhere in the distribution area they are more or less accidental, occurring in normal white-flowered populations, and are obviously thrown up repeatedly by the gene pools of the respective gamodemes.

The corollas of *P. nigrum* are blackish-violet (almost black in bud), sometimes light-violet to bluish. White-flowered variants have been reported in the literature but have not been observed in the material under study.

The corollas of *P. orbiculare* display various shades of blue. The two monicolous taxa, subsp. *montanum* R. SCHULZ and subsp. *flexuosum* R. SCHULZ, tend to have darker corollas (sometimes with a tint of violet) than the predominantly lowland subsp. *orbiculare*. White-flowered individuals have been observed in subsp. *orbiculare* (P129) and subsp. *flexuosum* (P262) but not in subsp. *montanum*.

In both *P. nigrum* and *P. orbiculare* the colour of the corolla fades as the flowering period draws to a close and is mostly completely lost in herbarium material.

TAXONOMIC TREATMENT

Phyteuma L. Sp. Pl. 170, 1753

Perennials. Stem simple, often furcate, hollow. Leaves simple, alternate, serrate, crenate or entire. Flowers sessile or subsessile, in dense spikes or heads. Calyx 5-merous. Corolla 5-merous, with linear lobes coalesced in bud, becoming separated almost to the base during anthesis. Stamens 5, with filaments dilated at base; anthers linear, introrse. Ovary inferior, 2–3-celled; style elongate, with 2–3 filiform stigmas. Capsule 2–3-locular, obconic to sphaerical, opening laterally.

Type species: *P. spicatum* L.

Key to species and subspecies of *Phyteuma* L. in Czechoslovakia

- 1a Root swollen; inflorescence ovoid to cylindrical; involucre bracts not imbricating; corolla blackish-violet or white to yellowish, rarely blue
- 2a Blade of basal leaves $\pm$ as long as wide, coarsely serrate; blade of lower cauline leaves cordate at base; corolla white to yellowish: *P. spicatum*
- 2b Blade of basal leaves longer than wide, irregularly crenate to subentire; blade of lower cauline leaves obtuse to cuneate at base; corolla blackish-violet, rarely blue: *P. nigrum*
- 1b Root thin; inflorescence globose; involucre bracts imbricating; corolla blue
- 3a Remnants of previous year's leaves present at base of stem during anthesis; basal leaves regularly crenate; middle and upper cauline leaves tapering to the base: *P. orbiculare* subsp. *flexuosum*
- 3b Remnants of previous year's leaves absent during anthesis; basal leaves $\pm$ irregularly serrate; middle and upper cauline leaves semiamplexicaul
- 4a Petiole of basal leaves longer or at most as long as blade; middle and upper cauline leaves entire or nearly so: *P. orbiculare* subsp. *orbiculare*
- 4b Petiole of basal leaves shorter than blade; middle and upper cauline leaves serrate: *P. orbiculare* subsp. *montanum*

Phyteuma spicatum L. Sp. Pl. 171, 1753 [“*spicata*”]

Root swollen, $\pm$ napiform. Stem 20–80 cm tall. Basal leaves petiolate, blade cordate, about as long as wide, coarsely or doubly serrate, acute to acuminate at apex. Lower and middle cauline leaves petiolate, blade cordate, serrate; uppermost shortly petiolate to sessile, lanceolate, obtuse at the base. Inflorescence spicate, cylindrical or ovoid (rarely globose), elongating in fruit. Involucre bracts not imbricating, narrowly lanceolate to linear, patent to reclinate. Corolla white to yellowish, with green tips, rarely bluish, slightly curved in bud. Pollen light yellow. Ovary 2-celled, rarely 3-celled.

P. spicatum is a highly variable species occurring usually in populations of many hundreds of individuals. This focuses attention upon its variability, especially in obvious morphological characters. The characters that vary most are the type of leafiness, shape of the leaves, shape and size of involucre bracts, shape of inflorescence and colour of corolla. Marginal members of the various variation ranges might well be given taxonomic recognition, perhaps even at specific level, as was often done in the past. The variation is continuous, however, and apparent discontinuities are liable to disappear as more material is examined. It is most unfortunate therefore

that the infraspecific classification was based on these characters. Over the years, the species has been subjected to excessive splitting into infraspecific taxa which culminated in Schulz's monograph (SCHULZ 1904). Of the four subspecies recognized there, three (subsp. *jurassicum* R. SCHULZ, subsp. *occidentale* R. SCHULZ and subsp. *coeruleum* R. SCHULZ) accommodate colour variants, while the fourth, subsp. *ochroleucum* DÖLL, represents the type of the species. All subspecies are subdivided into varieties, subvarieties and forms, based primarily on individual variation in the shape of the leaves and involucre bracts.

In Czechoslovakia, this subdivision of the species does not apply. There does not seem to be any marked geographical pattern conformable to Schulz's varieties and forms. (It is of some interest that none of the taxa was explicitly reported from our area.) Few, if any, topodemes are morphologically distinct. Perhaps the only exception is plants from the Hrubý Jeseník Mts. in which the subglobose inflorescence is fairly frequent. They have been described as var. *sphaerocephalum* FORMÁNEK (see FORMÁNEK 1887a, 1887b) but because this character occurs throughout the distribution range of the species, they hardly warrant taxonomic recognition. Similar plants have been recorded in nearly all the topodemes examined.

In the material studied, the shape of the leaves and of the involucre bracts also proved useless as a basis for infraspecific classification, as did the type of leafiness. The two different kinds of leafiness (whether the cauline leaves are crowded in the lower part of stem or spaced more or less evenly) grade imperceptibly into one another, the latter kind being more frequent than the first.

Blue-flowered individuals of *P. spicatum* are extremely rare in this country. They are found scattered in populations of normal white-flowered plants and the deviating colour of the corolla does not correlate well with other morphological features. They have been noted on several occasions (see e.g. ČELAKOVSKÝ 1871) and are also documented by herbarium material but did not occur in the population samples examined by the present author. It now seems certain that at least some of the reports of the blue-flowered *P. spicatum* actually refer to the hybrid *P. nigrum* × *P. spicatum*.

It is proposed therefore, on the basis of the above discussion, that no infraspecific units be recognized in *P. spicatum* in Czechoslovakia. Further study is required to ascertain whether Schulz's subdivision is applicable elsewhere and whether the character-combinations given for the three "coloured" subspecies are correlated with ecology and geographical distribution.

Of all the members of the genus, this species has by far the largest area of distribution, reaching from Brittany to the Upper and Middle Dnepr Regions in the Ukraine and from S. Norway to C. Italy and the Crna Gora, Yugoslavia.

In Czechoslovakia, *P. spicatum* extends from the lowlands to the alpine belt. It is only locally frequent at lower altitudes (with considerable disjunctions in the distribution, as for instance in the Bohemian-Moravian Highlands) and is largely confined to the mixed deciduous woodlands (mainly of the order *Fagetalia*). In the mountains it is common both in woodlands (order *Athyrio-Piceetalia*) and in mountain grasslands, being particularly abundant in leeward situations (alliance *Calamagrostion villosae*)

and in tall herb communities (alliance *Adenostylien*). It favours deep, rich soils and is indifferent to the geological substratum.

Phyteuma nigrum F. W. SCHMIDT Fl. Boëm. Cent. 2 : 87, 1794

Syn.: *P. spicatum* γ *P. nigrum* (F. W. SCHMIDT) POHL Tent. Fl. Boh. 1 : 210, 1809. — *P. spicatum* b) *nigrum* (F. W. SCHMIDT) DÖLL Rhein. Fl. 462, 1843.

Root swollen, ± napiform. Stem 20–40 cm tall. Basal leaves petiolate, blade cordate, up to twice as long as wide, obtusely crenate to subentire, ± obtuse at apex. Lower cauline leaves petiolate, blade lanceolate to oblong-ovate, finely crenate to entire, obtuse to cuneate at base; upper and middle leaves ± sessile, lanceolate, entire, cuneate at base (uppermost often bracteal). Inflorescence spicate, ovoid to cylindrical, considerably elongating in fruit. Involucral bracts not imbricating, narrowly lanceolate to linear, patent to reclinate. Corolla blackish-violet, sometimes greyish-blue, slightly curved in bud. Pollen violet. Ovary 2-celled, rarely 3-celled.

A species often included as a variety into *P. spicatum* by the early authors (see e.g. POHL 1809), but readily distinguished by its basal leaves distinctly longer than wide, irregularly crenate to subentire, cauline leaves (except 1–2 lowermost) tapering to the base and corolla blackish-violet (see also SCHOTT 1891). The variation patterns are similar to those of *P. spicatum*, the characters showing most variation within the species limits being the shape of the leaves, type of leafiness, shape and size of the involucral bracts, form of the inflorescence and colour of the corolla. Again, these features vary more or less continuously over the range of the species and quite independently of one another. As in *P. spicatum*, the characters which have been used for subdivision of *P. nigrum* are taxonomically unreliable because of the phenotypic plasticity and genetically controlled variation within populations.

Colour variants (with corolla bluish or greyish-blue) are more frequent than in *P. spicatum* but are not at all common. They have been recorded in P124 and P154. Pending further studies, they are not accorded any taxonomic rank. SCHULZ (1904) reports that var. *coeruleum* R. SCHULZ is the only representative of the species in the SW. part of its range.

P. nigrum is endemic to Central Europe, occurring from the Netherlands and Lüneburger Heide in the north to the Schwarzwald, Bayerische Hochebene and Waldviertel in the south (for a distribution map, see SCHULZ 1904). The eastern boundary of its range winds through the western part of Czechoslovakia. In this country it is particularly abundant in the Šumava (including foothills) and Krušné hory Mts. Outlying localities are found in the Labské pískovce district, Šluknovská pahorkatina hilly country, Lužické hory Mts., Frýdlantská pahorkatina hilly country, Lužická kotlina basin, Jizerské hory Mts. and western Krkonoše Mts. Along the Vltava river, *P. nigrum* extends from the south far into Central Bohemia. The report of this species from between Bruntál and Nové Heřminovy in Northern Moravia (OTRUBA 1925) is unexplained; a search of the locality by the present author revealed only the presence of *P. spicatum*. Perhaps the plant occurred there only temporarily as a garden escape. Nor could the reported occurrence below the hill Bezděz in Northern Bohemia (ZOUPLNA 1859) be confirmed. Adventive occurrences of *P. nigrum* have been noted in Eastern Bohemia (Hradec Králové; VLČEK et PROŠEK 1909), Southern Bohemia

(vicinity of Kamenice nad Lipou; KOVANDA unpublished) and Eastern Moravia (Rožnov pod Radhoštěm; SVOBODA 1930 BRNU, vicinity of Vsetín; ŘÍČAN 1926 BRNU, SVOBODA 1930 BRNU).²⁾

Two distribution maps of *P. nigrum* in the Czech Socialist Republic have been published: a dot map by Vondrová (VONDROVÁ in HENDRYCH 1973) and a grid map by Mladý (MLADÝ in KUBÁT 1978). Neither map is complete, both disregarding much of the published evidence from Northern Bohemia (see e.g. MILITZER 1954), the latter ignoring even herbarium records from Central and Western Bohemia.

Vertically, *P. nigrum* extends from 120 m alt. on the banks of the Elbe river at Dolní Žleb near Děčín to about 1200 m alt. in the Šumava Mts. It is ecologically plastic and occurs in a variety of habitats. In the mountains it is locally characteristic of the meadows (alliances *Arrhenatherion*, *Molinion* and *Trisetum-Polygonum bistortae*). At lower altitudes it favours mixed deciduous woodlands (alliances *Carpinion betuli* and *Fagion sylvaticae*, rarely also *Alno-Ulmion*); examples of silvicolous topodemes include P154 and P315. In the sandstone canyon of the Elbe river in Northern Bohemia it is frequent in dry, open habitats harbouring thermophilous vegetation. Unlike *P. spicatum*, this species is strictly calcifuge throughout its distribution range.

SCHMIDT (1794), establishing *P. nigrum* as a new species, provided a succinct diagnosis and a detailed description. The plant is reported from one single locality, the vicinity of Karlovy Vary in Western Bohemia. Interestingly, Schmidt recognized, in addition to *P. nigrum*, one more dark-flowered *Phyteuma* in Bohemia: *P. ovatum* F. W. SCHMIDT. It is said to occur in the Šumava Mts. and on the middle Vltava. This is one of the many mystifications perpetrated by Schmidt in his Flora. It is evident from the diagnosis ("*Phyteuma* foliis petiolatis; radicalibus cum infimis caulinis cordatis duplicato serratis, superioribus lanceolatis simpliciter serratis; spica ovata obaesa; stylis hirsutis; bracteis linearibus"), synonymy and illustration (Tab. 229) that the plant is in reality *P. ovatum* HONCKENY, a native of the Alps, Pyrenees and Balkan Peninsula. It has never been found in Bohemia and plants from the localities reported by Schmidt agree in every respect with his description of *P. nigrum*.

Phyteuma orbiculare L. Sp. Pl. 170, 1753 ["orbicularis"]

Syn.: *P. orbiculatum* POHL Tent. Fl. Boh. 1 : 209, 1809.

Root not conspicuously swollen, fusiform. Stem 10–30 cm tall. Basal leaves petiolate, blade lanceolate, ovate-lanceolate to elliptic (rarely almost orbicular), crenate or serrate, acute to obtuse at apex, cordate, obtuse to cuneate at base. Lower cauline leaves petiolate to subsessile, blade narrowly ovate to lanceolate, the others progressively smaller and narrower, sessile, crenate or serrate to entire, glabrous or sparsely hairy, uppermost sometimes diminishing into bracts. Inflorescence capitate, globose, somewhat elongating in fruit. Involucral bracts imbricating, ovate-lanceolate, acuminate, ap-

²⁾ Cases of naturalization, even far beyond the autochthonous distribution area, are not at all rare in *P. nigrum*. There are reports from Berlin (SCHULZ 1904), Babelsberg near Potsdam (JACOBASCH 1885), a number of localities in Poland (UECHTRITZ 1876, 1882, 1883) and in the vicinity of Moscow (FEDOROV 1957).

pressed to flowers to patent or reclinate. Corolla blue, rarely white, strongly curved in bud. Pollen violet. Ovary 3-celled, rarely 2-celled.

This is an interesting polymorphic complex in Central Europe, varying chiefly with regard to the length of petioles of basal leaves, shape of leaves and shape and position of involucre bracts. A useful comparison can be made with the variation patterns of *P. spicatum* and *P. nigrum*: the variation of *P. orbiculare* is quite different, showing, in some features at least, a clear correlation with geographical distribution and ecological preferences. Obviously, the process of infraspecific differentiation began only in the post-glacial period, when the species started to spread from its original distribution area in the Alps (see HENDRYCH 1980), and it still continues; hence the many intermediate situations and resulting taxonomic difficulties. The various infraspecific units tend to replace one another geographically but in many cases the geographical discontinuities are not marked by clear differences in morphology. Although significant differences can often be demonstrated between populations, these may prove insufficient to assign a single plant to a particular taxon.

Opinions as to the correct taxonomic treatment differ widely. One may contrast the divergent proposals of SCHULZ (1904) and DAMBOLDT (1976). On the basis of the present studies, neither of these two approaches is thought to be very satisfactory and an intermediate position is adopted. In the material examined, three distinct taxa could be distinguished. They may be considered ecological races of approximately equal rank and conveniently treated as subspecies, corresponding to three of the six subspecies delimited by SCHULZ (1904): subsp. *orbiculare*³⁾ (= subsp. *pratense* R. SCHULZ), subsp. *montanum* R. SCHULZ and subsp. *flexuosum* R. SCHULZ. In contradistinction to Schulz, no taxa are recognized below subspecific level, for the reasons explained under *P. spicatum*. It should also be pointed out that the position of the involucre bracts, which was used as one of the distinguishing characters by Schulz, proved the least useful character, since in the material studied it showed a complete range of variation. The other characters proved reasonably reliable as markers of subspecific limits. In addition, the presence of a tuft of remnants of the previous year's leaves at the base of the stem during anthesis was found to be a good character safely separating subsp. *flexuosum* from the other two subspecies.

Phyteuma orbiculare L. subsp. *orbiculare*

Syn.: *P. orbiculare* L. subsp. *pratense* R. SCHULZ Monogr. Gatt. *Phyteuma* 116, 1904.

Tuft of leaf remnants absent at the base of the stem. Basal leaves irregularly obtusely serrate, blade cuneate, obtuse or cordate at base. Petioles of the basal leaves usually much longer than blades. Stem often $\pm$ leafless in the upper part. Middle and upper cauline leaves entire (one or two uppermost strongly reduced, often bracteal), straight, spreading at an angle of 30–45°, semiamplexicaul at base. Involucre bracts mostly shorter than or as long as flowers.

This is a plant of meadows and grasslands (alliances *Bromion* and *Molinion*) on mineral-rich, moderately moist soils at lower altitudes. In the Elbe

³⁾ This typification follows ROTHMALER (1963). Further study is required to decide whether some other subspecies name is eligible.

lowland (Central Bohemia) it used to be characteristic of fens (alliance *Caricion davallianae*) but is now almost completely extinct there. In the Alps it extends up to the montane belt but in this country it is only exceptionally found above the 700 m contour. Geographically it is distributed from Switzerland to the central part of European Russia. In Czechoslovakia it is found scattered in Bohemia (mainly West Central; see SLAVÍK 1980) and parts of Moravia (except much of the south and northeast). Contrary to Schulz's statement, it shows no preference to calcareous habitats, though it occurs preferentially on basic to neutral soils. It is probably absent from the whole of the Carpathians, except for two localities (P256, P259) where it intermingles with subsp. *flexuosum*. The distribution map for *P. orbiculare* in Bohemia and Moravia compiled by Vondrová (VONDROVÁ 1971, VONDROVÁ in HENDRYCH 1973) refers largely to *P. orbiculare* subsp. *orbiculare*; only the record from the Hrubý Jeseník Mts. belongs clearly to subsp. *montanum*. It should also be pointed out that the records from Southern Bohemia (České Budějovice, Lhenice and Vyšší Brod) are based on incorrectly determined herbarium material and refer, in reality, to *P. nigrum*, as do also some from the Krušné hory Mts. *P. orbiculare* as a whole is absent from Southern Bohemia. As indicated in the introduction, *P. orbiculare* s. str. is an endangered taxon (see also HOLUB et al. 1979) and many of its localities, reported in literature and documented by herbarium material, no longer exist. Of the topodemes examined, four (P110, P118, P130 and P270) had been destroyed before this manuscript was finished.

Representative herbarium specimens

District of Džbán

Bílichov, anon. 1931 PRC; Bílichovské údolí, KOŠTÁL 1894 PR; "na rašelinné louce v Bílichovských lesích", KABÁT 1885 BRNU; Smradovna, KOLÁŘ 1930 PR; "rašeliníště u Třtice", NE-TUŠIL 1941 PRC; Smečno, DOMIN 1924 PRC; "rašelinná louka u Hradečna", VANDAS 1883 PR; "Obora u Smečna", VANDAS 1882 PR; Libušín, anon. 1930 PRC; "lesní louka u dolu Max u Libušína", ŠINDELÁŘ 1934 PRC; "nad libušínským koupalištěm", ŠVEJDA et ŠINDELÁŘ 1941 PRC; "v lese u Velké skály u Hnidous", ŠINDELÁŘ 1935 PRC; "na opukovém svahu u Hnidous", ŠOUREK 1940 PR.

District of Český kras

"in pratis ad vic. Horní Roblín", DOSTÁL 1931 PRC.

District of Střední Polabí

Hrabanov, DIVIŠ 1921 PR, KLÁŠTERSKÝ 1921 PR, SCHUSTLER 1922 PR, KRAJINA 1926 PRC, PUCHMAJEROVÁ 1926 PRC; "Rand eines Wiesengrabens zwischen d. Elbe und dem alten Übungsplatz bei Lissa", POHL 1843 PRC.

District of Dolní Pojizeří

"louky nad Josefodolem", PODPĚRA 1895 BRNU.

District of Rožďalovická tabule

"na vlhké louce nedaleko Dětenic", DIVIŠ 1922 PR; "na mokré louce u Loučenské myslivny", MEJDR 1944 PRC; "in silva Vlkovský revír prope oppid. Chlumec", DEYL 1944 PR; "in silva Domanovický les prope vicum Radovesnice", DEYL 1944 PR; "Pod borem prope vicum Hlavečnick", DEYL 1944 PR.

District of Východní Polabí

"u Komárova u Dašic", MATOUŠKOVÁ 1927 PRC; Zbytky, ŠOUREK 1940 PR, KLIKA 1942 PR, KLÁŠTERSKÝ 1958 PR.

District of Haná

Hlусovice, PICBAUER 1908 BRNM; "louka u Hlусovic", PICBAUER 1908 BRNU; "louky za Klásterem Hradiskem", SPITZNER 1888 BRNU; "křoviny mezi Hradiskem a Černovírem", SPITZNER 1888 BRNU; "Moorwiesen bei Černovír", LAUS 1930 BRNU; "Czernowirer Torfwiesen", LAUS 1907 BRNM; Lazce ("Laska"), LAUS 1934 PRC; "slatinné louky u Olomouce",

PODPĚRA s.d. BRNM; "Olomouc: louky u vodovodu", OTRUBA 1931 BRNU, 1941 PRC; "Olomouc: vojenská střelnice", OTRUBA 1912 BRNU; "in den Auen der March oberhalb Olmütz", anon. s.d. PRC.

District of Doupovské vrchy

Tunkov ("Tunkau"), STELZHAMMER 1910 PR; "ad pedes montis Pustý zámek supra oppidum Doupov", KLÁŠTERSKÝ 1949 PR; "sub summo montis Hradiště (Burgstadl)", DOMIN 1914 PRC.

District of Plzeňská pahorkatina

"palouk nad Spáleným mlýnem u Dolní Bělé", MALOCH 1906 PR.

District of Křivoklátsko

Lány, JIRUŠ 1862 PR; "in valle rivi Klíčava haud procul ab oppido Zbečno", KLÁŠTERSKÝ 1948 PR.

District of Podbrdsko

Mýto, PODHAJSKÁ 1931 PRC; "palouk mezi Svatoštěpánským rybníkem a Loudovic mlýnem", MALOCH 1912 BRNU, PRC; "louky u Hluboše", DOMIN 1912 PRC; "krátkotravná louka před Květnou", TOCL 1909 PR.

District of Ralsko-bezdězská tabule

Staré Splavy, ZELINKA 1930 PRC; "louka u Paterova", PODPĚRA 1896 BRNU; "na loukách u Rečkova", BAYER 1902 PR.

District of Orlické opuky

"louky u rybníka Močidlo", KREJCAR 1962 PR.

District of Litomyšlská pánev

"louka mezi Litrbasškými háji a Novou Vsí", ZÖRNIG 1898 BRNU, PR; "za Litrbachy v údolí táhnoucím se k Sebranicům", ZÖRNIG 1891 PR; "in pratis ad Litrbachy", FLEISCHER 1927 PRC; Čistá ("Litrbachy"), VODÁK 1897 PRC.

District of Českomoravské mezihoří

"palouk v lesním údolí nad Kuklé", MALOCH 1892 BRNU; "lesní louka v údolí u Kukle", MALOCH 1892 PR; "lesní louka u Kukle", MALOCH 1892 PRC; Hřebeč ("Schönhengst"), FRÖHLICH 1919 BRNU.

District of Hornosázavská pahorkatina

"Uhlířské Janovice: suchá louka pod Hladíkovou cihelnou", HRADEC 1942 PRC.

District of Českomoravská vrchovina

"Kamenné Sedliště, louky u rybníka Zimky", KOPECKÝ s.d. PR; "na louce v lese u rybníka Zimky", KROULÍK 1941 PRC.

District of Moravské podhůří Vysočiny

"seč doubravy na Zlobici", STANĚK 1919 BRNU.

District of Moravský kras

"mokré louky východně od Ochoze", VESELÝ 1927 BRNU; Křtiny ("Kiriten"), ROTHE 1892 BRNU; TEUBER 1897 BRNM, TEUBER 1917 BRNM; "Křtiny, u silnice k Adamovu", POSPÍŠIL 1946 BRNM; Josefské údolí ("Josefsthal"), anon. 1903 BRNM; Josefské údolí, MÜLLER 1940 BRNU.

District of Dražanská vrchovina

"Waldwiese Hatě bei Brodek u Prostějova ("Prödlitz")", SPITZNER 1888 BRNU; "na louce pod Kozákovem u Myslejovic", KLÁPA 1914 BRNM; Ferdinandsko, PODPĚRA 1914 BRNU, SUZA 1914 BRNU; "in pratis prope pagum Hostěnice", DOLEŽAL 1928 BRNU; "na lukách u Hostěnice", DOLEŽAL 1934 BRNU; "náhorní louky u Hostěnice", SKŘIVÁNEK 1943 PRC; "svažité louky v údolí Rakovec u Račic", SKŘIVÁNEK 1925 PRC; "feuchte Wiesen, Rakowetzthal", anon. 1926 BRNM; "v Rakoveci na lukách mezi Jedovnicemi a Račicemi", BÍLÝ 1932 BRNU; "na lukách u Račic", DOLEŽAL 1933 BRNU; Račice, HANÁČEK s.d. BRNM.

District of Zábřežsko-uničovský úval

"louky u Moravičan", OTRUBA 1927 BRNU; "Moravičany, in pratis siccis", E. HEJNÝ 1922 PRC.

District of Slezská pahorkatina

Kylešovice ("Gilschwitz"), anon. s.d. BRNM.

District of Jesenícké podhůří

Bruntál ("Freudenthal"), anon. s.d. BRNM, Václavov ("Wenzelsdorf"), SCHENK 1910 BRNM; Luboměř, POSPÍŠIL 1949 BRNM; "in pratis sub monte Raudenberg (Roudno)", UHRVÁ 1928.

Phyteuma orbiculare L. subsp. *montanum* R. SCHULZ Monogr. Gatt. Phyteuma 116, 1904

Tuft of leaf remnants absent at the base of the stem. Basal leaves irregularly obtusely serrate, blade cuneate or obtuse at base. Petiole of basal

leaves $\pm$ as long as or shorter than blade.⁴⁾ Stem often $\pm$ leafless above. Middle and upper cauline leaves serrate (with at least one or two pairs of teeth), straight, spreading at an angle of $30-45^\circ$, semi-amplexicaul at base; one or two uppermost leaves often strongly reduced, bracteal. Involucral bracts mostly shorter or as long as flowers.

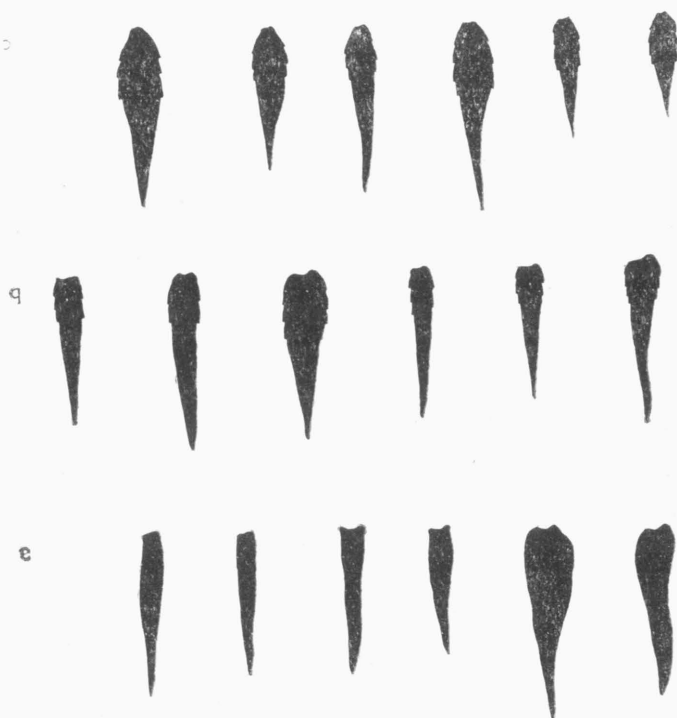


Fig. 2. — Upper cauline leaves of *P. orbiculare* subsp. *orbiculare* (a), subsp. *montanum* (b) and subsp. *flexuosum* (c).

A submontane to montane variant, occurring in Central European mountain systems and hilly country, including foothills (Jura, Alps, Bayerische Hochebene, Thüringer Wald, Harz, Eastern Sudeten). In Czechoslovakia it is restricted to the Velká kotlina glacial cirque in the Hrubý Jeseník Mts. (Eastern Sudeten) where it grows in the open plant communities of the alliance *Agrostion alpinae* (see JENÍK, BUREŠ et BUREŠOVÁ 1980) on steep, rocky slopes. There are also records from the adjacent Mt. Vysoká hole and Mt. Máj but the occurrence of the taxon there has never been confirmed. Nor was any *P. orbiculare* found in the summit area of Mt. Králický Sněžník, whence it was reported by HRUBY (1914). Reports of *P. orbiculare* from Mt. Sněžka (HAENKE 1791) and the Kotelné jámy glacial cirque (DOMIN, Ms.)

⁴⁾ In Rothmaler's Exkursionsflora (ROTHMALER 1963), the petioles of the basal leaves of subsp. *montanum* R. SCHULZ are described as "1 1/2mal länger als die Spreite" — a clear misinterpretation of Schulz's (SCHULZ 1904) concept.

in the Krkonoše Mts. (Western Sudeten) may perhaps be referable to subsp. *montanum* also. Unfortunately, no herbarium material is available and the plant has never been collected there since.

Some plants from the Krušné hory Mts. and Western Bohemia come, judging from the length of petioles, very close to subsp. *montanum* and have been included in it by SCHULZ (1904) but the respective populations, taken as a whole, are best classified as belonging to subsp. *orbiculare*. Herbarium material from Eastern Bohemia and the vicinity of Prague was also referred to subsp. *montanum* by Schulz but is not mentioned in his monograph.

Representative herbarium specimens

District of Hrubý Jeseník

Velká kotlina ("Grosser Kessel"), OBORNÝ 1867 PRC, 1879 PRC, BUBELA 1884 PRC, BAENITZ 1893 PRC, SCHIERL 1893 BRNU, 1899 BRNM, OBORNÝ 1903 BRNM, SUZA 1909 BRNU, STANĚK 1920 BRNU, ŠMARD 1920 PR, LENEČEK 1929 PRC, SCHUSTLER 1929 PR, MATAUCH 1934 PRC, OTRUBA 1934 BRNM, 1934 PRC, anon. 1934 PRC, JEDLIČKA 1946 BRNU, DEYL 1947 PR, 1949 PR, 1951 PR, 1952 PR, KLÁŠTERSKÝ 1958 PR, VICHEREK 1958 BRNU, MÉŠÍČEK 1961 PR, DEYL 1966 PR, 1967 PR; Vysoká hole ("Hohe Haide"), FRÖHLICH 1900 BRNU; Máj ("Maiberg"), KOLENATÍ s.d. PRC.

Phyteuma orbiculare L. subsp. *flexuosum* R. SCHULZ Monogr. Gatt. Phyteuma 121, 1904

Tuft of remnants of last year's leaves present at the base of the stem during anthesis. Basal leaves $\pm$ regularly crenate, blade mostly obtuse to cuneate at base, rarely cordate. Petiole of basal leaves mostly longer than blade. Stem $\pm$ evenly leafy up to the inflorescence. Middle and upper cauline leaves serrate, mostly arcuate, tapering to the base. Involucral bracts mostly as long as or exceeding flowers.

A taxon morphologically clear-cut throughout most of its range (Carpathians and mountains of Balkan Peninsula, extending as far south as Albania), except the Eastern Alps where it intergrades on a large scale with subsp. *montanum* R. SCHULZ and subsp. *delphinense* R. SCHULZ. In Czechoslovakia, the only intermediates are those to subsp. *orbiculare* (probably of hybrid origin) which can be traced in the Bílé Karpaty Mts. where both the subspecies co-occur. Aside the Bílé Karpaty Mts., subsp. *flexuosum* is the only representative of the species complex in the whole of the Western Carpathians. Reports of subsp. *orbiculare* from the Polish part of the Pieniny Mts. (OCHLEWSKA 1965) appear referable to subsp. *flexuosum*.

Ecologically, subsp. *flexuosum* clearly prefers rocky habitats. In the western Carpathians it is a constant element of the species-rich plant communities of the order *Seslerietalia calcariae* on weathered calcareous and dolomitic rocks in the montane and subalpine belt, being particularly abundant in the Strážovská hornatina Mts., Velká and Malá Fatra Mts., Chočské pohorie Mts., Nízke Tatry Mts. and Belianske Tatry Mts. Occasionally it is found also in mountain grasslands and is tolerant even of acid substrata. It is on these that it attains the upper limit of its vertical range in Czechoslovakia: 2400 m on the granitic Zadný Ladový štít in the Vysoké Tatry Mts. (see PACLOVÁ 1979).

Concerning the distinguishing characters, it should be pointed out that the stems of subsp. *flexuosum* — in the Carpathians at least — are only rarely, and then only slightly flexuous, as the name would imply.

Representative herbarium specimens

District of Juhoslovenský kras

Zadielská dolina, DOSTÁL 1927 PRC.

District of Biele Karpaty

"Vápenica ad v. Starý Hrozenkov", PODPĚRA et al. 1931 BRNU; Vršatec, SILLINGER 1927 PR, SUZA 1930 BRNU, 1930 PR, 1930 PRC, WEBER 1934 PR, 1934 PRC.

District of Malé Karpaty

Ostrý kameň, SUZA 1924 BRNU.

District of Strážovská hornatina

Súľovské skály, SILLINGER 1930 PRC; Manínska tiesňava, ŠOUREK 1947 PR, VICHEREK 1969 BRNU; Vápeč, NEVOLE 1938 BRNU, VICHEREK 1969 BRNU; Žihlaviník, KLÁŠTERSKÝ 1922 PR; Tematínske kopce, SILLINGER 1929 PR, 1929 PRC, VLACH 1930 PRC, SMEJKAL 1969 BRNU.

District of Slovenské rudohorie

"ad declive australe montis Radzim", SOJÁK 1958 PR.

District of Muránska vysočina

Veľká Stozka, SUZA 1937 PRC; "nad Smutnou dolinou u Muráně", KLIKA 1946 PR; "supra pag. Muráň", KRIST 1929 BRNU; "Suchá dolina prope oppidum Muráň", KLÁŠTERSKÝ et DEYL 1933 PR.

District of Slovenský raj

"in angustis rivi Veľký Sokol sub monte Glac", KLÁŠTERSKÝ 1947 PR; „kolem Letanovského mlýna a na ceste ke Kláštorisku“, BRYM 1930 PRC; "in valle Kysel", SUZA 1930 BRNU; "in declivibus vallis Hnilec ad vicum Stratená", KLÁŠTERSKÝ 1947 PR; "in pratis ad Havrania skala", KLÁŠTERSKÝ 1935 PR.

District of Branisko

"Branisko, in jugo inter cotas 1043 et 1131", DEYL 1938 PR; "in rupibus trachyticis montis Rudník", DOSTÁL 1928 PRC.

District of Fatra

Malá Fatra: Suchý, ŠVESTKA 1924 BRNU, KRIST 1933 BRNU; Rozsutec, WEBER 1935 PR; "in valle rivuli Šútovka", KRIST 1934 BRNU; Stoh, ŠMARDOVÁ 1951 BRNU; "ad cacumen montis Chleb", SOJÁK 1967 PR; Fatranský Kriváň, KLÁŠTERSKÝ 1946 PR, SVRČEK 1947 PR. Veľká Fatra: Čierny kameň, KLÁŠTERSKÝ 1946 PR; "in jugo Križná", DEYL 1951 PR; Ostrý, DEYL 1951 PR; Drienok, KLIKA 1924 PRC, Gaderská dolina, MALOCH 1920 PRC.

District of Nízke Tatry

"in valle Demänovská dolina", SUZA 1925 BRNU; Siná, DEYL 1938 PR; Smrekovica, FOTT 1928 PRC; Ohnište, DVOŘÁK 1969 BRNU; Kráľička, VICHEREK 1964 BRNU; Ďumbier, KUPČOK 1896 PR, DEYL et SOJÁK 1967 PR; "in valle fontis Chmelince", FILIPÍ 1933 BRNU.

District of Vysoké Tatry

Západné Tatry: Sivý vrch, DOSTÁL 1926 PRC, SILLINGER 1929 PR, DOSTÁL 1926 PRC; Osobitá, DEYL 1938 PR; Bobrovec, DOSTÁL 1928 PRC; Predný Úplaz, DOSTÁL 1928 PRC; "nad dolným plesom Roháčským", DOSTÁL 1928 PRC.

Vysoké Tatry: Bielovodská dolina, DOSTÁL 1954 PR; Zámky, KLÁŠTERSKÝ 1925 PR, DOSTÁL 1954 PR; "in alpinis prope Zelené pleso", DEYL 1938 PR.

Belianske Tatry: "in jugo inter montibus Muráň et Kôň", KLÁŠTERSKÝ 1962 PR; Havran, VAŠÁK 1967 PR; Ždiarska vidla, KRAJINA 1925 PRC, VAŠÁK 1967 PR; Bujačí, ŠIRJAJEV 1929 BRNU; "in jugo inter cacumina Bujačí et Jatky", VAŠÁK 1967 PR, Holý vrch, DOMIN 1935 PRC; "in valle Holubyho dŕľ", VYTOUŠ 1959 PR; "supra casam Hviezdoň-Protěž", SOJÁK 1969 PR.

District of Pieniny

"in declivibus silvaticis loco dicto Červený Kláštor", SMEJKAL 1958 BRNU; "in declivibus montis Golica", DOMIN 1932 PRC; "in valle fluminis Dunajec", DEYL 1953 PR.

District of Nízke Poloniny

"při vreholu skal na hřebenu Stinky mezi kotami 1073 a 1078", SOJÁK 1957 PR; "skalky na hřebenu Stinky na stát. hranici na kótě 1073", SOJÁK 1957 PR.

HYBRIDS

Phyteuma × *adulterinum* WALLR. Linnaea 14 : 558, 1840

(*P. nigrum* × *P. spicatum* WALLR. Linnaea 14 : 558, 1840)

As suggested above, hybridization between *P. nigrum* F. W. SCHMIDT and *P. spicatum* L. takes place wherever the two come into contact, which they do quite often in the mountains in the western half of Bohemia. F₁ hybrids

are fertile and can back-cross with either parent species, resulting in bizarre assemblages of individuals recombining in various degrees the differentiating characters of the parents. Complex hybrid swarms flourish in a number of localities in the Krušné hory and Šumava Mts. and would be worth a detailed genetical study. It is important to note that nowhere does the large-scale hybridization lead to the breakdown of the individual gene patterns of the parents and to the disappearance of specific identities, "pure" parental forms surviving in all the topodemes examined. Nor is there any evidence for the spread of genes away from the area of hybridization.

Phyteuma $\times$ *orbiculariforme* DOMIN in DOMIN et PODPĚRA Klíč Úplné Květ. Rep. Českosl. 542, 1928

(*P. nigrum* $\times$ *P. orbiculare* R. SCHULZ Monogr. Gatt. *Phyteuma* 173, 1904)

This hybrid was described by SCHULZ (1904) on the basis of one single herbarium specimen from near Výtoň (formerly Heuraffl) in the Šumava Mts., Southern Bohemia, which the collector (Willkomm) himself had identified as *P. nigrum* F. W. SCHMIDT. No other records from this country or abroad are available and considering the fact that *P. orbiculare* is not known to occur in the locality, the nature of the putative hybrid remains doubtful. Schulz's description would seem to indicate that the plant falls within the variation range of *P. nigrum* F. W. SCHMIDT. This is not to query the possibility of the hybrid *P. orbiculare* $\times$ *P. nigrum* arising elsewhere. It must be remembered, however, that the parent species only rarely have an opportunity to hybridize in nature because they tend to occur in dissimilar habitats. In this country they have never been observed to occur in one and the same habitat. In the hybridization trials (see Tabs. 5–6), *P. nigrum* and *P. orbiculare*, though belonging to different sections, proved crossable.

P. orbiculare $\times$ *P. spicatum*

This is another intersectional hybrid. It has not been reported previously but was obtained easily with a number of plants (see Tab. 4, 6). Spontaneous hybridization of *P. orbiculare* and *P. spicatum* is probably rare, if indeed it ever occurs, because, again, the parental forms are separated by an ecological barrier. For instance, of the *P. orbiculare* subsp. *orbiculare* topodemes studied, only P133 and P204 partially intermingle with sizeable populations of *P. spicatum* (P134, P203). No hybrids have been found, however, even though the flowering times of both species coincide. In view of the cytological information now available, this is quite surprising. In the Velká kotlina glacial cirque, *P. orbiculare* subsp. *montanum* (P164) is confined to the rocky habitat which is clearly avoided by *P. spicatum* (P161) which occurs copiously in adjacent mountain grassland and tall herb communities. Nor can any of the *P. orbiculare* subsp. *flexuosum* topodemes investigated be expected to hybridize with *P. spicatum*, because their habitats are, at the very best, juxtaposed but not identical. Perhaps the only exceptions are P256 and P259 which share the same habitat with *P. spicatum* (P258, P260).

SOUHRN

U československých zvonečníků (*Phyteuma* L.) byl studován počet chromosomů, variabilita, způsob rozmnožování a schopnost mezidruhové hybridizace. Studovaný materiál se ukázal být diploidní, s $n = 11$. Odehlyný počet, $n = 12$, byl zjištěn (kromě $n = 11$) pouze v jednom pří-

padě u druhu *P. nigrum* F. W. SCHMIDT. Polyploidie nebyla pozorována a protože se nevyskytuje ani u ostatních druhů, je vyslovena hypotéza, že evoluce rodu spočívala primárně na dysploidních změnách základního počtu chromosomů. Tím se rod *Phyteuma* liší od ostatních rodů čeledi *Campanulaceae* (např. *Campanula*, *Jasione*, *Asyneuma*), v jejichž vývoji hrála polyploidie důležitou roli. Průběh meiose byl u všech sledovaných taxonů pravidelný.

Naše druhy zvonečníků jsou téměř dokonale autosterilní. Autogamie je sice zásadně možná, ale jen ve velmi omezeném měřítku a v přirozených populacích se pravděpodobně výrazněji neuplatňuje. Možnost spontánní autogamie ("samoopylení z nouze") předpokládaná hlavně ve starší literatuře, nebyla u studovaného materiálu prokázána.

Všechny tři druhy jsou mezi sebou křížitelné; každý z nich se podařilo zkřížit s kterýmkoliv ze zbývajících dvou v obou směrech. Byl získán i trojnásobný hybrid *P. nigrum* × *P. spicatum* × *P. orbiculare*. Hybrid *P. nigrum* × *P. spicatum* (= *P. × adulterinum* WALLR.) vzniká spontánně všude, kde se společně vyskytují oba rodičovské druhy; častým jevem jsou hybridní roje. Křížence *P. nigrum* × *P. orbiculare* (= *P. × orbiculariforme* DOMIN) byl sice z našeho území popsán, jeho existence v přírodě je však pochybná, protože rodičovské druhy jsou od sebe odděleny ekologickou bariérou. Spontánní vznik nebyl pozorován ani u křížence *P. orbiculare* × *P. spicatum*.

Druhy *P. spicatum* L. a *P. nigrum* F. W. SCHMIDT jsou značně variabilní, nejví však významnější taxonomickou diferenciací. Nejsou proto u nich rozlišovány žádné vnitrodruhové taxony. U druhu *P. orbiculare* L. je v Československu možno vymezit tři subspecie, dobře charakterizované morfologickými znaky, ekologii a geografickým rozšířením. *P. orbiculare* subsp. *orbiculare* (bez zbytků loňských listů při basi lodyhy v době květu; přizemní listy ± nepravidelně pilovité, s řádkem delším než čepel; střední a horní lodyžní listy poloobjímavé, ± celokrajné) se vyskytuje roztroušeně až vzácně v českých zemích, převážně ve stupni pahorkatiny. Revise rozšíření ukázala, že velká část nalezišť, známá z literatury a doložená herbářovým materiálem, už zanikla. Údaje z jižních Čech jsou založeny na záměně s druhem *P. nigrum*. *P. orbiculare* subsp. *montanum* R. SCHULZ (bez zbytků loňských listů při basi lodyhy v době květu; přizemní listy ± nepravidelně pilovité, s řádkem kratším než čepel; střední a horní lodyžní listy poloobjímavé, pilovité) roste v současnosti v typické podobě pouze ve Velké kotlině v Hrubém Jeseníku; dříve se snad vyskytovala i v Krkonoších a na Králickém Sněžníku. *P. orbiculare* subsp. *flexuosum* R. SCHULZ (se zbytky loňských listů při basi lodyhy v době květu; přizemní listy ± pravidelně vroubkované; střední a horní lodyžní listy k basi zúžené, pilovité) je hojná v celé karpatské oblasti, zvláště na vápencích a dolomitech. Přechodné formy jsou dosti časté mezi subsp. *orbiculare* a subsp. *montanum*; mezi subsp. *orbiculare* a subsp. *flexuosum* se vyskytují jen ojediněle. Všechny tři subspecie mají rozšíření i mimo Československo. K jejich identifikaci slouží určovací klíč.

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