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KARYO-TAXONOMIC STUDY OF THE GENUS *PSEUDOLYSIMACHION* (*SCROPHULARIACEAE*) IN THE CZECH REPUBLIC AND SLOVAKIA

Bohumil Trávníček[1], Martin A. Lysák[2,3], Jarmila Číhalíková[2] & Jaroslav Doležel[2]

1) Department of Botany, Faculty of Sciences, Palacký University in Olomouc, Svobody 26, CZ-771 46, Olomouc, Czech Republic; travnicek@prfholnt.upol.cz
2) Laboratory of Molecular Cytogenetics and Cytometry, Institute of Experimental Botany, Sokolovská 6, CZ-772 00, Olomouc, Czech Republic; dolezel@risc.upol.cz, cihal@risc.upol.cz
3) Present address: Department of Cytogenetics, Institute of Plant Genetics and Crop Plant Research (IPK), Corrensstrasse 3, Gatersleben, D-06466, Germany; lysak@ipk-gatersleben.de

Abstract: Flow cytometry was used to determine ploidy levels in the Czech and Slovak taxa of the genus *Pseudolysimachion* (W.D.J. KOCH) OPIZ (= *Veronica* auct. p.p., *Scrophulariaceae*). In total, 123 populations from the Czech Republic, Slovakia, Ukraine (one locality), Austria (one locality) and Hungary (one locality) were analyzed. In *P. maritimum* (L.) Á. LÖVE et D. LÖVE and *P. spicatum* (L.) OPIZ, two cytotypes were found: diploid (2n=2x=34) and tetraploid (2n=4x=68). In both species the tetraploid cytotype predominated (*P. maritimum*: 41 tetraploid populations out of 45; *P. spicatum*: 57 tetraploid populations out of 58). The two cytotypes of *P. maritimum* have no taxonomic significance because ploidy level is not obviously correlated with morphology, distribution pattern or ecology. Tetraploid populations of *P. spicatum* belong to two morphologically different subspecies, subsp. *spicatum* and subsp. *fischeri* TRÁVNÍČEK. The diploid cytotype (one population only) should be provisionally classified as a third subspecies of *P. spicatum*, which is morphologically similar to the Asian subsp. *porphyrianum* (PAVLOV) TRÁVNÍČEK. Only diploid plants (2n=2x=34) of *P. orchideum* (CRANTZ) WRABER were found; all 13 populations that were analyzed belong to *P. orchideum* s.str. One diploid population sample of *P. spurium* subsp. *foliosum* (WALDST. et KIT.) HOLUB (2n=2x=34) and one tetraploid sample of *P. incanum* subsp. *pallens* (HOST) TRÁVNÍČEK (2n=4x=68) were also analyzed. In addition, three tetraploid populations of hybrid origin were investigated: *P. maritimum* × *P. spicatum* subsp. *spicatum* (one population) and *P. maritimum* × *P. spurium* subsp. *foliosum* (two populations). While hybrid plants of *P. maritimum* × *P. spicatum arose* from tetraploid parental species, plants of *P. maritimum* × *P. spurium* probably resulted from a cross between tetraploid *P. maritimum* and diploid *P. spurium*. The putative origin and evolutionary importance of polyploids in the *Pseudolysimachion* are discussed.

Keywords: Chromosome numbers, Cytogeography, Flow cytometry, Karyology, Origin of polyploids, Polyploidy, Taxonomy

INTRODUCTION

The genus *Pseudolysimachion* (W.D.J. KOCH) OPIZ, separated from the genus *Veronica* L. (*Scrophulariaceae*), includes approx. 25–30 species distributed mainly in the temperate zone of Eurasia. Five species that occur in Central Europe belong to two sections (cf. TRÁVNÍČEK 1998a: 195): sect. *Pseudolysimachion* (i.e., *P. orchideum* (CRANTZ) WRABER, *P. spicatum* (L.) OPIZ, and *P. incanum* (L.) HOLUB) and sect. *Longifolia* (T. YAMAZ.) TRÁVNÍČEK (*P. maritimum* (L.) Á. LÖVE et D. LÖVE (= European species from the *P. longifolium* group, see TRÁVNÍČEK 2000a) and *P. spurium* (L.) RAUSCHERT). All species have been found in Slovakia (TRÁVNÍČEK 1998b) although *P. spurium* is considered to be extinct (cf. TRÁVNÍČEK 1998b: 276), and four of them (i.e., excl. *P. incanum*) are also present in the Czech Republic (TRÁVNÍČEK 2000b). The most common species of the area of the former Czechoslovakia, *P. spicatum* and *P. maritimum*, show great individual and population variability (SKALICKÝ 1956, TRÁVNÍČEK 1998b, 2000b) and comprise diploid (2n=2x=34) and tetraploid (2n=4x=68) cytotypes in Europe (cf. GRAZE 1933, LEHMANN 1940, BRANDT 1953, RAITANEN 1967, etc.). The distribution of these cytotypes in the Czech Republic and Slovakia has not yet been determined.

In this paper, we present a karyo-taxonomical study focused mainly on *P. spicatum* and *P. maritimum* in the Czech Republic and Slovakia. Our aims were: (1) to analyze karyo-geographical variation in these two species, and (2) to look for any relationship between ploidy level and/or morphological and ecological characteristics, which might be taxonomically relevant.

Apart from these two species, we examined the remaining *Pseudolysimachion* taxa occurring in the Czech Republic and Slovakia and also a few populations of the studied taxa from the neighbouring countries.

The preliminary results of this study were published in the Flora of Slovakia (TRÁVNÍČEK 1998b) and the Flora of the Czech Republic (TRÁVNÍČEK 2000b).

MATERIAL AND METHODS

Plant material, sampling and cultivation

Herbarium specimens from the Czech and Slovak herbaria (BRA, BRNM, BRNU, LIM, LTM, MMI, OL, OLM, OP, PR, PRC, ROZ, SAV, SLO; abbreviations by HOLMGREN et al. 1990) were used to define the geographic distribution and to estimate the phenotypic variability of the investigated taxa, and subsequently to select collection sites.

Selected populations were studied in the field from 1991 to 1999. From these populations, herbarium specimens for further study of morphological variation were collected and deposited in OL (Herbarium of Faculty of Sciences, Palacký University, Olomouc). Living plants were sampled for subsequent chromosome counting and flow-cytometric ploidy estimations and were grown either in an experimental garden or a greenhouse. When more individuals were analyzed from a population, an attempt was made to cover as a wide morphological variation as possible. Voucher specimens are deposited at OL. A list of localities, together with numbers of analyzed plants is given in Appendix 1.

Chromosome counting

Root tips were excised from mature plants cultivated in pots. The tips were pre-treated in 8-hydroxyquinoline (0.002 M) for 4 hrs, fixed in cold ethanol : acetic acid fixative (3 : 1) overnight and stored in 70% ethanol. The Feulgen method was used for chromosome staining, by hydrolyzing in 5N HCl at room temperature for 25 min, and staining in Schiff's reagent for 60 min at room temperature. At least five metaphase plates were examined in each analyzed plant. Approximately 1–3 plants per population were counted.

Flow-cytometric ploidy analysis

All ploidy measurements were performed with a PAS flow cytometer (Partec GmbH, Münster, Germany). DNA-specific fluorochrome 4', 6-diamino-2-phenylindole (DAPI) was used to stain nuclei samples for flow-cytometric analyses. An amplification of the instrument was set so that the peak representing G_1 nuclei of a diploid plant was placed on channel 50. At least 5000 nuclei were analyzed in each sample, and ploidy level of a sample was determined based on the relative position of its G_1 peak on a histogram. Plants of known chromosome numbers (see Appendix 1) of the same taxon were used as internal and/or external standards for ploidy estimations.

Samples for flow-cytometric analyses were prepared according to DOLEŽEL et al. (1989): approx. 20 mg of a young-leaf tissue was chopped with a razor blade in 1 ml of ice-cold LB01 buffer containing DAPI (4 μg/ml). The sample was subsequently filtered through a 50-μm nylon filter and subjected to flow-cytometric analysis.

Further methodological notes

Literature records on *Pseudolysimachion* chromosome numbers from the whole distribution area have been thoroughly checked and the taxonomic identification was compared with the geographic origin. Only reliable records were taken into consideration. Most of the literature records were annotated (see column 5 of Appendix 2). Phytogeographical division of the Czech Republic in Appendix 1 follows SKALICKÝ (1988), that of Slovakia FUTÁK (1966).

RESULTS AND DISCUSSION

1. *Pseudolysimachion maritimum* (L.) Á. LÖVE et D. LÖVE (syn.: *Veronica maritima* L.)

Pseudolysimachion maritimum was found in many phytogeographical districts of the Czech Republic and Slovakia (cf. TRÁVNÍČEK 1998b, 2000b) and we analyzed samples from 45 populations (altogether 148 plants, see Appendix 1, no. 1–45; Fig. 3) which were diploid (2n=2x=34, Fig. 1a; four populations) or tetraploid (2n=4x=68, Fig. 1b; 41 populations). No population consisted of both tetraploid and diploid plants although most samples were rather limited in respect to the number of plants studied. The two populations that were studied in detail, i.e., diploid (Appendix 1, no. 1, Želnava, 25 plants) and tetraploid (Appendix 1, no. 24, Kojetín, Včelín, 20 plants), were homogeneous regarding their ploidy level.

We found large intra-population variation in morphological characters of *P. maritimum*; particularly prominent differences were found in leaf positions on stems: opposite-leaved plants vs. plants with 3 (– 4) leaves in whorls. We also examined characters such as leaf shape, petiole length, length and shape of bracts and calyx teeth, and hair density. However, there was no obvious correlation between these morphological characters and ploidy level as was ascertained for the present karyologically analyzed material (TRÁVNÍČEK, unpubl.). Indeed, opposite-leaved plants and plants with leaves in whorls grew together within a single tetraploid or diploid population.

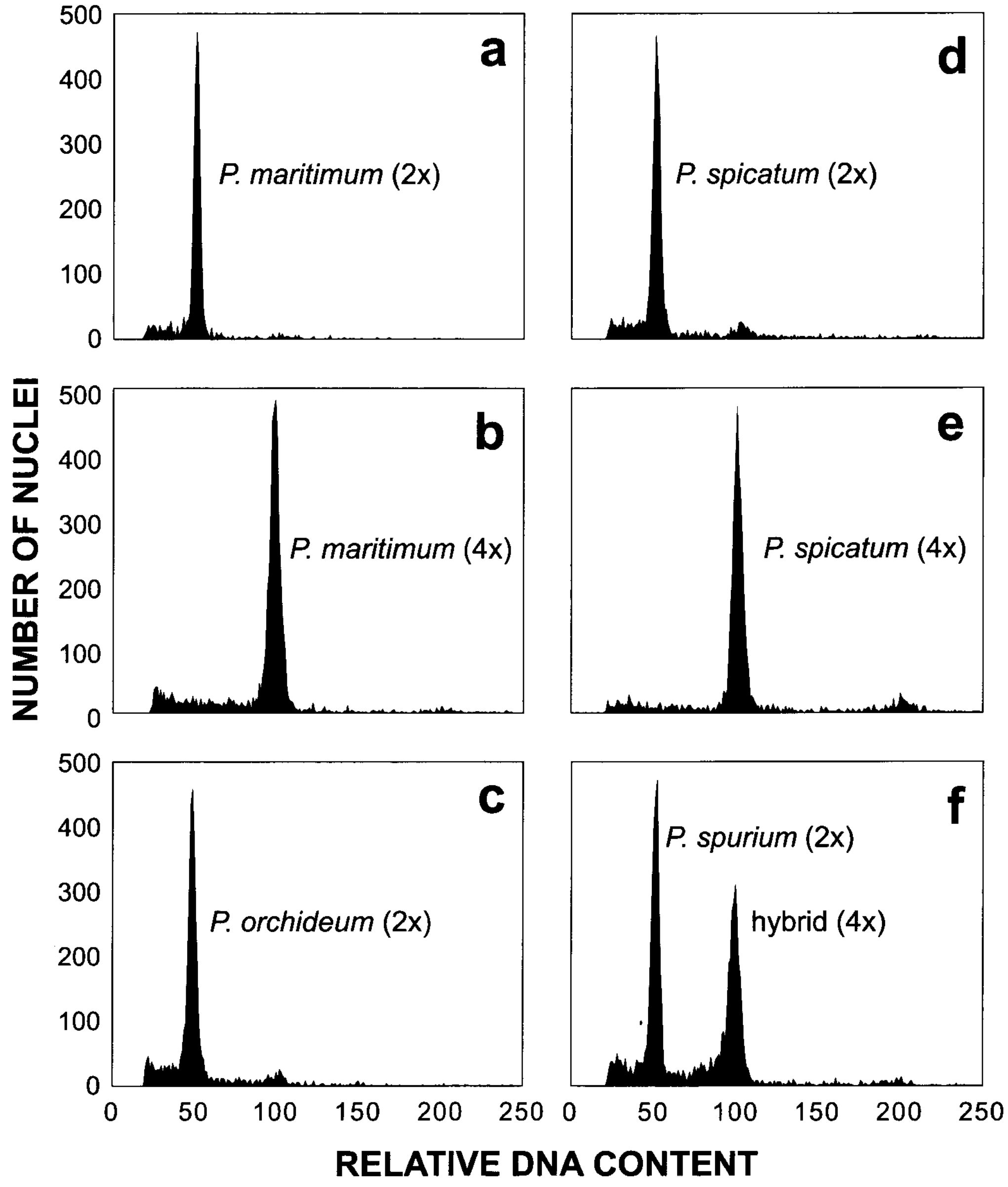

Fig. 1. Histograms of relative DNA content obtained after flow-cytometric analysis of DAPI-stained nuclei isolated from leaves of *Pseudolysimachion* taxa. The instrument was adjusted so that the peaks representing G_1 nuclei of diploid plants were placed on channel 50. a – *P. maritimum*, diploid cytotype (2n=2x=34), b – *P. maritimum*, tetraploid cytotype (2n=4x=68), c – *P. orchideum* (2n=2x=34), d – *P. spicatum*, diploid cytotype (2n=2x=34), e – *P. spicatum*, tetraploid cytotype (2n=4x=68), f: simultaneous analysis of *P. spurium* (2n=2x=34) and a tetraploid hybrid plant *P. maritimum* × *P. spurium* (2n=4x=68).

Diploid populations have been found in two geographically and ecologically different areas (Appendix 1, no. 1–4; Fig. 3). One region (S Bohemia, Šumava Mts.: phytogeographical region 88g. Hornovltavská kotlina) is relatively cold and has an oceanic climate. The species reaches here its maximum altitude within the region of interest (ca. 750 m a.s.l.). The second area (S Slovakia: phytogeographical region 2. Ipeľsko-rimavská brázda) is warmer and has a continental type of climate. *Pseudolysimachion maritimum* grows here at 170 m a.s.l. on sites that are humid in the spring and dry during the summer. Tetraploid populations have been found in 21 phytogeographical districts and in ecologically diverse habitats (Appendix 1, no. 5–45; Fig. 3). As there is no striking relationship between ploidy level and geographical distribution and/or ecological requirements and morphology of *P. maritimum* cytotypes, they should be considered as units without any taxonomic significance.

The *Pseudolysimachion longifolium* group occupies an extensive Eurasian geographical range. TRÁVNÍČEK (2000a) distinguished here two species: European *P. maritimum* and Asian *P. longifolium* (L.) OPIZ. Chromosome counts for this group were reported from different regions of its distribution area, including Siberia and the Far East (cf. KROGULEVICH & ROSTOVTSEVA 1984: 227, PROBATOVA & SOKOLOVSKAYA 1989: 123, etc.). Appendix 2 summarizes those chromosome numbers based on literature records that probably refer to *P. maritimum*, whereas data that possibly refer to the Asian *P. longifolium* s.str., and data based on plants of unknown geographical origin were excluded from the Appendix.

Since the 18th century, the taxonomic status of two Linnean species (LINNAEUS 1753: 10), *Veronica maritima* L. and *V. longifolia* L. has been vigorously debated. According to Linnaeus' brief descriptions, he distinguished the two species mainly on the basis of the number of leaves per node and the character of leaf margin indentation:

V. maritima: "spicis terminalibus, foliis ternis inaequaliter serratis",

V. longifolia: "spicis terminalibus, foliis oppositis lanceolatis serratis acuminatis".

Both names have recently been typified by FISCHER (1997: 113–114). According to the lectotypes, the name *Veronica maritima* (i. e., *Pseudolysimachion maritimum*) refers to European and W Asian populations, while the other name (*Veronica longifolia* or *Pseudolysimachion longifolium*) refers to the Asian (i.e., eastern) populations (TRÁVNÍČEK 2000a). The Asian populations, treated as a separate species (*P. longifolium* s.str.) by TRÁVNÍČEK (2000a), differ from the European ones (*P. maritimum*) primarily by differences in calyx indumentum, shape of calyx teeth and length of leaf petioles. The Asian species has only opposite-leaved stems, whereas the European taxon includes both opposite-leaved plants and plants with leaves in whorls. Linnaeus himself (LINNAEUS 1753: 10) did not delimit his two species correctly. The original material and distribution data show that he united opposite-leaved individuals of the European species (*P. maritimum*) with the Asian taxon (i.e., *P. longifolium* s.str.) and the same treatment was later adopted by most authors (for details see TRÁVNÍČEK 2000a).

Indeed, the most remarkable morphological variability of the European *Pseudolysimachion maritimum* is the leaf arrangement along the stem and leaf shape (in the following text we assign the opposite-leaved type of *P. maritimum* as "*longifolia*" morphotype and the type with 3-leaved whorls as "*maritima*" morphotype). The main difficulty in the taxonomic application of these characters is that the two morphotypes do not obviously differ in their ecological requirements, nor do they form distinct populations. Moreover, they are linked by a series of intermediate morphotypes (HÄRLE 1932: 15, SKALICKÝ 1956: 125, 130, BORSOS 1967: 7, RAITANEN 1967: 483, 484). There have been, however, two major arguments stressed in the past against treating the two types as taxonomically identical. First, it seemed that the morphotype "*maritima*" is prevalent in northern Europe (particularly on coastal habitats in Scandinavia) and it may therefore have a certain geographical and perhaps ecological preference (LEHMANN 1940: 485, 486). However, such a preference is rather weak because the "*maritima*" morphotype is found less frequently growing albeit in mixed populations with the "*longifolia*" morphotype elsewhere in Europe (HÄRLE 1932: 14, 15, LEHMANN 1940: 485, SKALICKÝ 1956: 125). In addition, even in regions where the prevailing morphotype is "*maritima*" the second morphotype is not rare (RAITANEN 1967, KUKKONEN 1986; the authors' herbarium findings). Thus, the difference is merely the relative frequency of the two morphotypes in different regions. Another argument supporting an independent status of the two morphotypes is the alleged absolute dominance of diploid populations over regions where the "*maritima*" morphotype predominates (RAITANEN 1967: 471, KUKKONEN 1986: 41). Furthermore, the first chromosome counts made on morphologically characterized plants indicated a certain correlation between ploidy level and morphological characters (HÄRLE 1932, GRAZE 1933: 519–521, 1935). As a consequence, the "*maritima*" morphotype has been repeatedly reported as being diploid, and the "*longifolia*" morphotype as tetraploid (GRAZE 1935, LEHMANN 1940: 481–482, HARTL 1966: 152 –153, FISCHER 1969: 438, ROTHMALER et al. 1982: 465). However, results of detailed studies of RAITANEN (1967) and KUKKONEN (1986) in Finland cast serious doubts on such a generalization. Apart from one exception, the Finnish plants were found to be diploid and this ploidy level was also recorded in the "*longifolia*" morphotype occurring in Finland.

In our study we focused on a possible relationship between the morphological characters mentioned above and ploidy level. As no such relationship has been established (TRÁVNÍČEK, upubl.), classification of the "*maritima*" morphotype as diploid and the "*longifolia*" morphotype as tetraploid is clearly incorrect. In both cytotypes a similar range of morphological variation, especially regarding leaf position on the stem and leaf shape was found. Most of the populations were characterized by the predominance of plants with 3-leaved whorls, but opposite-leaved plants also occurred in these populations (see also SKALICKÝ 1956). When other characters such as shape of leaf basis, leaf width, petiole length, etc. were considered, no correlation was found among these characters and the above-mentioned two morphotypes (cf. also BORSOS 1967: 7–9). The obvious conclusion from these data is that the two morphotypes have no taxonomical relevance.

Because a distinction between the two *P. maritimum* cytotypes based on these morphological characters cannot be made, an examination of pollen and stomatal characters was carried out (TRÁVNÍČEK & VINTER 1999). However, only a weak tendency of tetraploid plants to possess increased stomata and pollen grain size was found. Similar results were obtained in our preliminary investigation into a relationship between selected quantitative morphological characters (plant height, leaf size, corolla and calyx size) and ploidy level (TRÁVNÍČEK, unpubl.). These data show that quantitative characters are unreliable for distinguishing both cytotypes, and differences were only found between average values from a large set of diploid or tetraploid individuals. Similarly, discrimination of tetraploids according to pollen grain quality was not possible: malformed and poorly developed pollen were found in both diploid and tetraploid plants (cf. GRAZE 1933, RAITANEN 1967, KUKKONEN 1986). Thus, it is not possible unambiguously to estimate ploidy level of *P. maritimum* plants according to morphological characters only, but it remains to be seen whether both cytotypes differ in their geographical distribution and ecological requirements.

Although the coexistence of two *P. maritimum* cytotypes within a single population has not been recorded from the Czech Republic and Slovakia, it cannot be excluded. As shown by HÄRLE (1932) and GRAZE (1933, 1935), gene flow between different ploidy levels in the genus *Pseudolysimachion* is possible (for a general review of this topic see PETIT et al. 1999). Crossing between diploid, especially as female, and tetraploid plants may give rise to sterile triploids as well as fertile tetraploid hybrids (GRAZE 1933: 556, 1935: 658, 659). This breeding behaviour has already been found in the two cytotypes of *P. maritimum* (GRAZE 1935: 636, 654), and it is likely that a tetraploid hybrid may more easily backcross with a tetraploid parent than a diploid one. In mixed populations, this process may lead to a gradual elimination of diploids resulting in a purely tetraploid population. Taking into account the frequent wider range of habitats and higher competitive ability of established polyploids (perennials in particular) over their diploid ancestors (LEVIN 1983, BROCHMANN & ELVEN 1992), this scenario may explain the prevalence of tetraploid populations in the study area. Diploid populations might then be considered as relic groups of individuals not yet replaced by gradually expanding tetraploid populations.

It is noteworthy that in the Czech Republic and Slovakia, diploid *Pseudolysimachion maritimum* populations have been found outside the regions where the species normally occur, i.e., outside alluvia of large rivers (Labe basin, Morava basin, Podunajská nížina lowland, Východoslovenská nížina lowland), in isolated areas where the tetraploid type is absent.

Taking into account the above-mentioned arguments we conclude that both diploid and tetraploid populations of *Pseudolysimachion maritimum* belong to a single, karyologically variable species. As there are no reliable morphological characters distinguishing both cytotypes, they cannot be classified as independent microspecies or subspecies.

The *P. longifolium* group (and the entire section *Longifolia*) has its centre of origin in Eastern Asia (see TRÁVNÍČEK 1998a: 195) and only a few taxa extend into Europe. Considering the negligible morphological differences between diploid and tetraploid *P. maritimum* cytotypes, the autopolyploid (probably polytopic) origin of the tetraploid type might be assumed (Fig. 2). Since it seems that an ancestral diploid type of *P. maritimum* did not originate in Southern Europe, it is possible that it was a more psychrophilous taxon occurring in habitats that were humid thorough the growing season. Expansion of the ancestral diploid type towards "dry summer" habitats in continental European regions (e.g. Pannonian lowland) was probably a result of its secondary adaptation. This adaptation could have evolved at the diploid level by the selection of individuals with useful traits and/or by the formation of more vigorous polyploid populations. As newly established *P. maritimum*

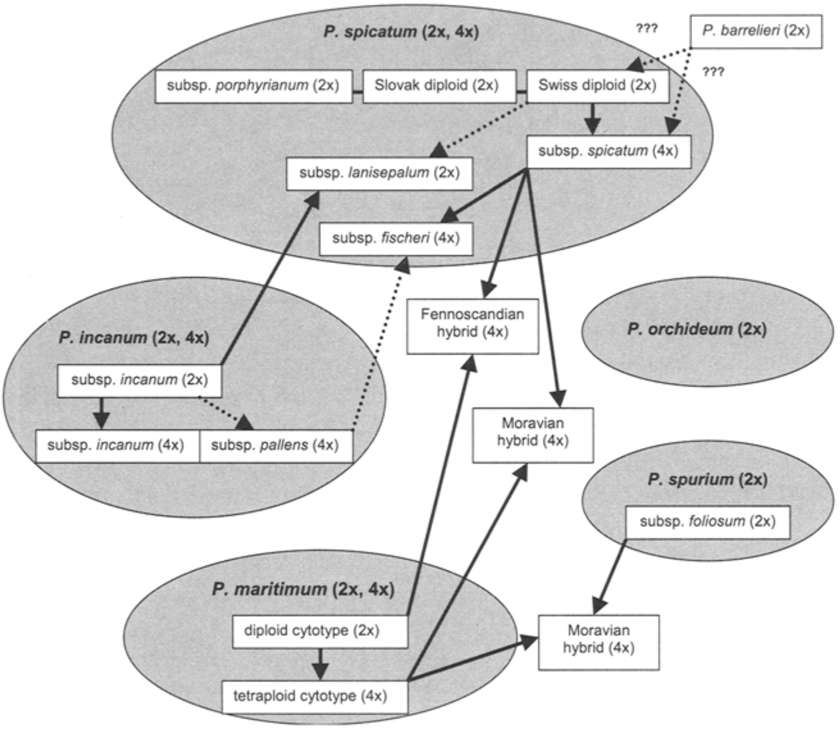

Fig. 2. Supposed relationships of the investigated *Pseudolysimachion* taxa (solid lines – very probable relationships; dotted lines – less probable relationships).

polyploids expanded to more continental areas of Europe, e.g. Central Europe, the diploid populations in Europe might be regarded as relics of the primary migration.

2. *Pseudolysimachion spurium* (L.) RAUSCHERT (syn.: *Veronica paniculata* L.; *Veronica spuria* L.)

Only a single population of *Pseudolysimachion spurium* from south-eastern Moravia was analyzed (altogether 11 plants, Appendix 1, no. 46, Čertoryje; Fig. 4). Past records indicate that the species has occurred in Bohemia (one locality) and in Western Slovakia (two localities) (TRÁVNÍČEK 1998b: 276, 2000b). The plants collected from Moravia were diploid (2n=2x=34, Fig. 1f) and corresponded morphologically to *P. spurium* subsp. *foliosum* (WALDST. et KIT.) HOLUB (see SKALICKÝ 1956, HARTL 1966: 149, HOLUB in HOLUB & POUZAR 1967: 426, TRÁVNÍČEK 1998b: 273–274).

Appendix 2 summarizes the published reports on chromosome numbers of *Pseudolysimachion spurium* from Poland, Hungary and Bulgaria. Tetraploid plants (2n=68) have been reported only from Bulgaria by PEEV (1972: 500) and were classified as *Veronica spuria* subsp. *spuria*. Diploid plants (2n=34) have been reported from Poland (IZMAILOW 1991: 34–35) as *V. paniculata* subsp. *paniculata* (= *Pseudolysimachion spurium* subsp. *spurium*), Hungary (GRAZE 1933: 522) as *V. foliosa* WALDST. et KIT., and Bulgaria (PEEV sec. VAN LOON 1987: 200) as *V. paniculata*. Plants of unknown geographic origin were also exclusively diploid (GRAZE 1933: 522, SIMONET 1934: 1153, MESHKOVA 1965 sec. AGAPOVA 1993: 360) and these data therefore agree with our findings. Plants analyzed in our study belong to *P. spurium* subsp. *foliosum* (≡ *Veronica foliosa*).

From the above-mentioned data it seems that both subspecies, *Pseudolysimachion spurium* subsp. *spurium* and *P. spurium* subsp. *foliosum*, are characterized by the same (diploid) chromosome number (together with the tetraploid one in subsp. *spurium*).

3. *Pseudolysimachion orchideum* (CRANTZ) WRABER (syn.: *Veronica orchidea* CRANTZ)

Samples of 13 populations of *Pseudolysimachion orchideum* were analyzed (altogether 21 plants, Appendix 1, no. 47–59; Fig. 4). In the Czech Republic, this species occurs only in Moravia (especially SE part; see TRÁVNÍČEK 2000b), while it is relatively common in the warmer regions of Slovakia (TRÁVNÍČEK 1998b: 280–283). The analyzed plants originated from six phytogeographical regions in the study area and all were diploid (2n=2x=34, Fig. 1c) and classified as *P. orchideum* var. *orchideum*. No other infraspecific taxa occur in the area studied (TRÁVNÍČEK 1998b, 2000b).

Only diploid chromosome counts (2n=34, 36) were reported for *Pseudolysimachion orchideum* (see Appendix 2) in Austria (FISCHER 1969: 438), Slovakia (VÁCHOVÁ 1974: 22, VÁCHOVÁ & FERÁKOVÁ 1986: 59), Ukraine (ANDROSHCHUK 1988: 454) and Bulgaria (GRAZE 1933: 523, PEEV 1972: 499, 500). Data from Austria, Slovakia and Ukraine refer undoubtedly to *P. orchideum* var. *orchideum* (see TRÁVNÍČEK 1998b: 277–278, 2000b). At least one of the records from Bulgaria (PEEV 1972: 500) refers to *P. orchideum* var. *bulgaricum* (PEEV) PEEV et M.A. FISCH. (≡ *Veronica spicata* var. *bulgarica* PEEV – see FISCHER & PEEV 1995: 195–196). Plants of unknown origin were also all diploids (cf. GRAZE 1933: 523) or tetraploids (GRAZE 1935: 631). Thus, the published reports along with our findings confirm that *P. orchideum* is largely a diploid taxon.

4. *Pseudolysimachion spicatum* (L.) OPIZ (syn.: *Veronica spicata* L.)

Fifty-eight population samples of *Pseudolysimachion spicatum* from the Czech Republic and Slovakia, and one sample from the border of Ukraine and Slovakia, one sample from Austria and one from Hungary were analyzed (altogether 133 plants, Appendix 1, no. 60–119; Figs. 5, 6). Two cytotypes were found: diploid (2n=2x=34, Fig. 1d) and tetraploid (2n=4x=68, Fig. 1e). One population sample was a diploid cytotype, while the remaining ones were tetraploid. Tetraploid plants were found in 27 different phytogeographical regions of the Czech Republic and Slovakia (Appendix 1, no. 61–119; Figs. 5, 6). These tetraploid populations are classified as two subspecies of *P. spicatum* (cf. TRÁVNÍČEK 1998a,b). The type subspecies (subsp. *spicatum*) occurs throughout the whole study area (TRÁVNÍČEK 1998b, 2000b), whereas *P. spicatum* subsp. *fischeri* TRÁVNÍČEK is restricted to the middle part of southern Slovakia (TRÁVNÍČEK 1998b).

Diploid *P. spicatum* plants were found only on the eastern periphery of the studied area along the border between Slovakia and Ukraine (Appendix 1, no. 60, Stinská; Fig. 5). The population occurs in a relict community covering mountain summit rocks at 1070 m a.s.l.We consider the population from Mt. Stinská as a separate subspecies of *P. spicatum*. The

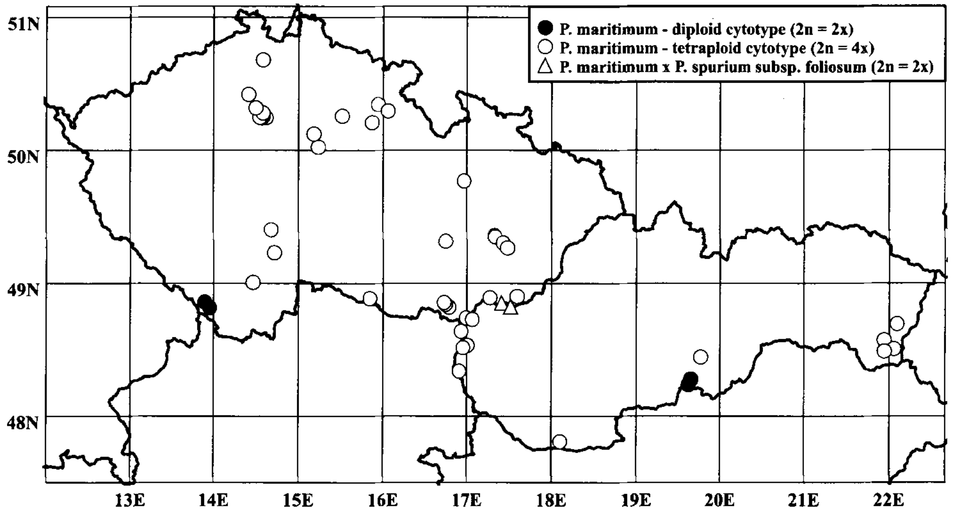

Fig. 3. Distribution of populations of *P. maritimum* and *P. maritimum* × *P. spurium* subsp. *foliosum* analyzed for ploidy level.

population differs from others in a set of minor characters (cf. TRÁVNÍČEK 1998a: 210, 1998b: 286–287) characteristic for "the eastern group" of *P. spicatum* subspecies, i.e., subsp. *porphyrianum* (PAVLOV) TRÁVNÍČEK, subsp. *viscosulum* (KLOKOV) TRÁVNÍČEK, and subsp. *bashkiriense* (TSVELEV) SOJÁK. However, a detailed taxonomic evaluation of the population is needed.

A tentative conclusion is that there is a certain relationship between ploidy level and morphology, ecology and distribution pattern within the species *P. spicatum* in the study area.

Taxonomic classification of *Pseudolysimachion spicatum* is quite complicated due to probable introgressive hybridization with other species of the sect. *Pseudolysimachion*, namely *P. incanum* and *P. barrelieri* (SCHOTT ex ROEM. et SCHULT.) HOLUB (cf. TSVELEV 1981, TRÁVNÍČEK 1998a). We have adopted the taxonomic classification by TRÁVNÍČEK (1998a) that defines a large distribution area of *P. spicatum*. It spreads throughout most of Europe, including France and Great Britain in the west, and S Scandinavia, the Baltic states, the Onega Lake region and the basin of Petschora River in the north and north-east. To the south, it reaches NE Spain, N Italy, countries of the former Yugoslavia, Bulgaria, and in the south-east, the lower Volga and the Urals. In Asia, the species occurs in the northern region of the Aral Sea, in the southern part of W Siberia, the basin of upper Yenisei and Angara, and the Tien-Shan Mts., the Balkhash Lake region, the Altai and the Sayany Mts. (BORISOVA 1955: 382, ELENEVSKIĬ 1971: 216–218, TSVELEV 1981, etc).

Pseudolysimachion spicatum consists of nine subspecies (for their geographic distribution see TSVELEV 1981: 85–86, TRÁVNÍČEK 1998a), some of which are of assumed hybrid origin (e.g. subsp. *fischeri*). Caution should be exercised when comparing our findings with published reports (see Appendix 2). For example, under the name *P. spicatum* (or *Veronica spicata*) other species have also been included (particularly *Pseudolysimachion orchideum*

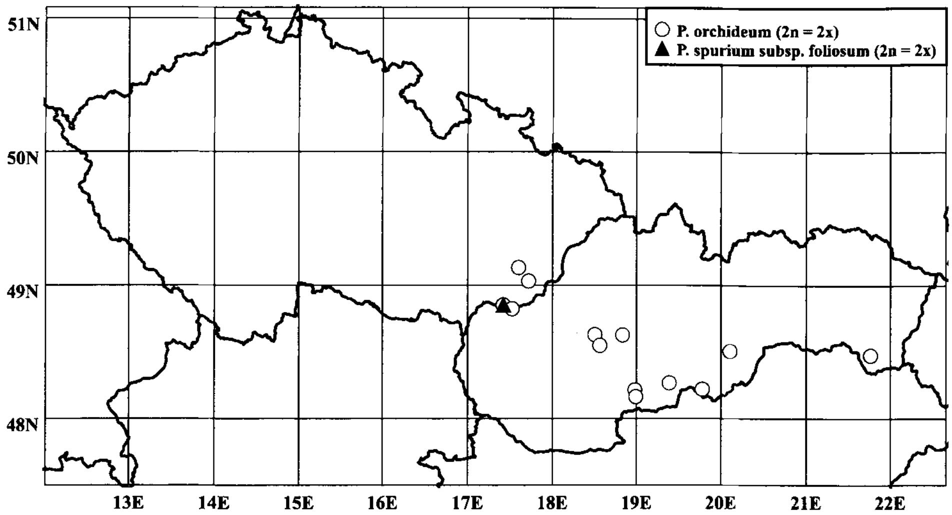

Fig. 4. Distribution of populations of *P. orchideum and P. spurium* subsp. *foliosum* analyzed for ploidy level.

and *P. barrelieri*). In addition, the subspecific classification of karyologically analyzed plants was not given in a number of records. Therefore, most literature records are annotated in the Appendix. For records of known geographic origin, a probable subspecific classification is given.

Considering our findings and the available records, the following conclusions on karyology of *Pseudolysimachion spicatum* can be drawn:

(1) The type subspecies of *P. spicatum* is probably solely a tetraploid taxon. All populations analyzed in this study were tetraploid. In Switzerland (cf. GRAZE 1933: 523, BRANDT 1953: 114), diploid populations exist that are morphologically similar to tetraploid populations of subsp. *spicatum* (GRAZE 1935: 531–532, LEHMANN 1940: 487–488). These diploid populations are either direct ancestors of tetraploid subsp. *spicatum* if the latter is an autopolyploid, or one of the parents of the tetraploids if they evolved via allopolyploidy (see Fig. 2). The taxonomic status of diploid plants from Switzerland is currently uncertain; they may represent a new subspecies.

(2) *P. spicatum* subsp. *fischeri* is a tetraploid taxon likely derived from hybridization between tetraploid populations of *P. spicatum* subsp. *spicatum* and populations of *P. incanum*, probably in southeastern Europe (cf. TRÁVNÍČEK 1998a: 216; see Fig. 2).

(3) *P. spicatum* subsp. *lanisepalum* TRÁVNÍČEK is a diploid subspecies morphologically similar to subsp. *fischeri*. It is a relict taxon that perhaps evolved as a result of hybridization between a diploid cytotype of *P. spicatum* (? above-mentioned Swiss one) and diploid populations of *P. incanum* (TRÁVNÍČEK 1998a: 216; see Fig. 2). Both *P. spicatum* subsp. *lanisepalum* and *P. spicatum* subsp. *fischeri*, probably had similar origins but they differ in their ploidy level.

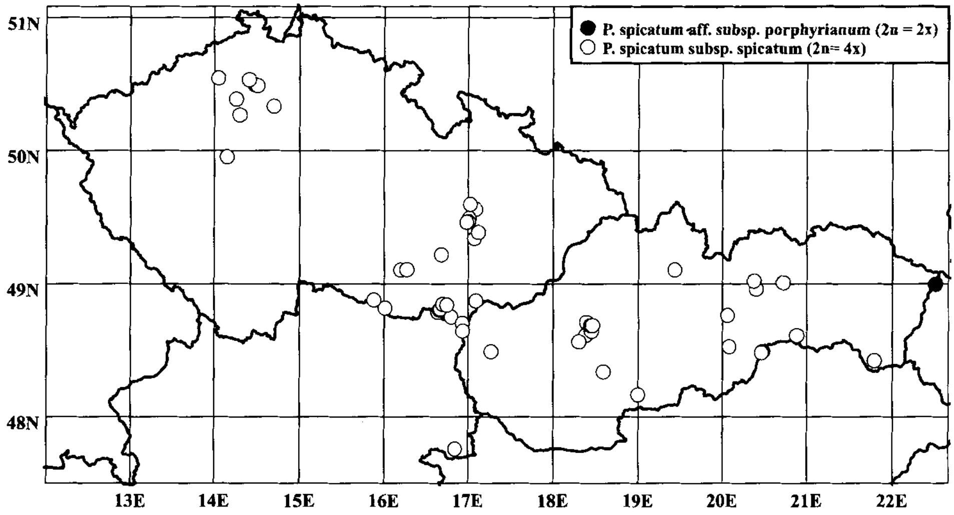

Fig. 5. Distribution of populations of *P. spicatum* subsp. *spicatum* and *P. spicatum* aff. subsp. *porphyrianum* analyzed for ploidy level.

(4) *P. spicatum* subsp. *porphyrianum* is probably a diploid taxon (see AFANASIEVA & MESHKOVA 1961: 255, TSVELEV 1981: 87 and also Appendix 2 – records from the Altai Mts.). The analyzed diploid population of *P. spicatum* (Appendix 1, no. 60, Stinská) morphologically bears a close resemblance to *P. spicatum* subsp. *porphyrianum*. However, the classification of the population as *P. spicatum* subsp. *porphyrianum* is questionable because it is geographically very isolated from the area where true *P. spicatum* subsp. *porphyrianum* is found (Altai, Tien-Shan and adjacent regions).

(5) The remaining subspecies of *P. spicatum* have not yet been karyologically characterized. Further karyological analyses are needed to elucidate the evolutionary relationships within *P. spicatum*.

The conclusions summarized above have led us to formulate a hypothesis concerning the relationship between *P. spicatum* subsp. *spicatum* and *P. spicatum* subsp. *porphyrianum*. A diploid ancestor of *P. spicatum*, which probably arose somewhere in south-eastern Europe (evolutionary centre of sect. *Pseudolysimachion* – cf. TRÁVNÍČEK 1998a: 195), might have occupied a large area in the south – probably from Western Europe to Western Asia. Certain taxonomic differentiation could have taken place in this area due to the geographic isolation of some populations. Diploid relict populations of *P. spicatum* in Europe (Switzerland, Eastern Slovakia-Ukraine) and *P. spicatum* subsp. *porphyrianum* in Western Asia seem to be remnants of the ancestral taxon. The diploid populations likely gave rise to the tetraploid *P. spicatum* subsp. *spicatum* that predominates in Europe today. A further study is needed to determine whether the tetraploids originated from diploids via autopolyploidy or whether other species (e.g. *P. barrelieri*) have participated in the polyploidization process (Fig. 2; see also TSVELEV 1981: 87). It is possible that the ancestral diploid type was replaced by

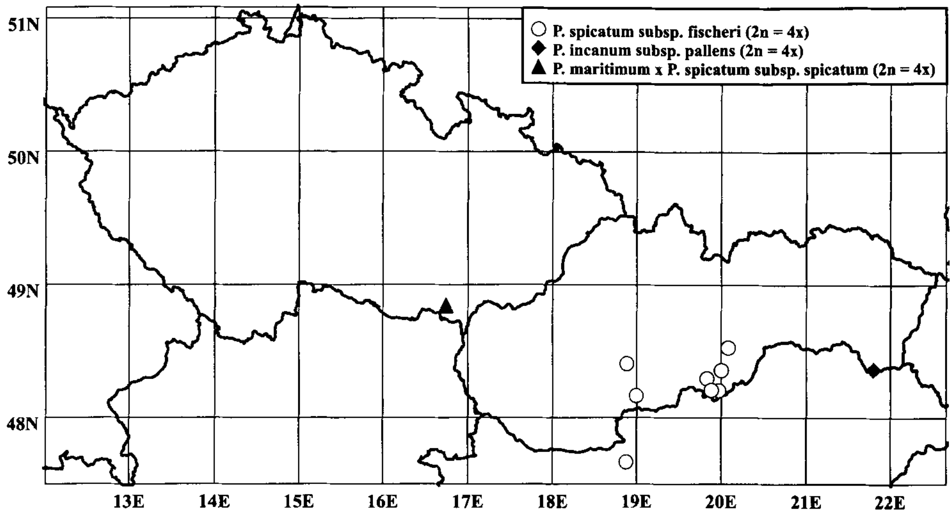

Fig. 6. Distribution of populations of *P. spicatum* subsp. *fischeri* (and intermediates between subsp. *fischeri* and subsp. *spicatum*), *P. incanum* subsp. *pallens* and *P. maritimum* × *P. spicatum* subsp. *spicatum* analyzed for ploidy level.

polyploid populations of *P. spicatum* subsp. *spicatum*, or even genetically "swallowed" by an analogous mechanism similar to that which is hypothesized in *P. maritimum* (see above), and survives as a relict in isolated regions (e.g. closed Alpine valleys in Switzerland or relict plant community on Mt. Stinská on the Slovak-Ukrainian border). The higher competitive ability of polyploids might have allowed the wide expansion of tetraploid *P. spicatum* subsp. *spicatum* to northern regions of Europe since only tetraploids have been reported from Great Britain and Fennoscandia (WALTERS 1954, RAITANEN 1967, KUKKONEN 1986).

Diploid *P. spicatum* subsp. *porphyrianum* is morphologically rather different from tetraploid subsp. *spicatum*. Thus, its classification as independent species would be justified. However, there are also other intermediate types that have only been superficially examined (subsp. *viscosulum*, subsp. *bashkiriense*, Swiss diploids). Therefore, we prefer not to adopt a species rank for this taxon for the time being (see also TRÁVNÍČEK 1998a: 210).

5. *Pseudolysimachion incanum* (L.) HOLUB (syn.: *Veronica incana* L.)

In the study area, *Pseudolysimachion incanum* is restricted to south-eastern Slovakia. Only *P. incanum* subsp. *pallens* (HOST) TRÁVNÍČEK occurs in the region (cf. TRÁVNÍČEK 1998a: 207–208,1998b: 275, 293–295). One population sample was analyzed (altogether 5 plants) in the present study and all plants were tetraploid (2n=4x=68, Appendix 1, no. 120, Tarbucka; Fig. 6).

A tetraploid status of *P. incanum* subsp. *pallens* agrees with the record of MÁJOVSKÝ & VÁCHOVÁ (1986: 64) who analyzed plants from the same region. Diploid plants (2n=2x=32, 34), probably belonging to the *P. incanum* subsp. *incanum* (cf. TRÁVNÍČEK 1998a: 208), have been reported from the geographically remote region of NE Siberia (Yakutia) (cf. ZHUKOVA et al. 1973: 1341, 1977: 232, YURTSEV & ZHUKOVA 1982: 782). Other literature records refer to tetraploid *P. incanum* (GRAZE 1933: 529, AFANASIEVA 1960 sec. AGAPOVA 1993: 357, AFANASIEVA & MESHKOVA 1961: 249, MESHKOVA 1965 sec. AGAPOVA 1993: 358, ZHUKOVA 1967 sec. AGAPOVA 1993: 357, DZHUS & DMITRIEVA 2001: 145). However, these records are based mainly on plant material of unknown geographic origin (often from botanical gardens). As plants of *P. incanum* subsp. *incanum* are usually grown in gardens, the tetraploids of garden origin should probably be included in this subspecies (cf. TRÁVNÍČEK 1998a: 208, 1998b: 294).

Pseudolysimachion incanum subsp. *pallens* shows a restricted distribution limited only to the eastern periphery of the Pannonian lowland. The subsp. *incanum* is widely distributed from Ukraine and Belorussia eastwards, reaching Anadyr and Kamchatka (see TRÁVNÍČEK, 1998a, for details). It is highly likely that besides diploid populations of *P. incanum* subsp. *incanum*, (auto)tetraploid populations also exist within this taxon (see Fig. 2 and above). However, this possibility should be subjected to further analysis.

6. Hybrids

Two interspecific hybrids have been found and analyzed in the present study. One hybrid *P. maritimum* × *P. spicatum* (= *P.* ×*medium* (SCHRAD.) TRÁVNÍČEK) was found in the Dyje basin and hybrids between *P. maritimum* and *P. spurium* were discovered at two locations in the Bílé Karpaty Mts.

Pseudolysimachion maritimum x *P. spicatum*

Hybrids and both parental species (*P. maritimum* and *P. spicatum* subsp. *spicatum*) were found at the same site (Appendix 1, no. 21, 73, 121, Bulhary, Fig. 6) and the hybrids appear to form a hybrid swarm. Both hybrid and parental plants are tetraploids and hybrid plants were fertile and set seeds. The hybrids are only observed in a few localities where both species are sympatric and able to cross because *P. maritimum* is a hygrophilous and *P. spicatum* a xerophilous taxon. The location of the hybrid population that we analyzed fulfils the condition for an appropriate location: *P. spicatum* grows on an elevated steppe-covered hill in alluvium of the Dyje river, while *P. maritimum* occurs in wet depressions nearby.

Apart from these naturally occurring hybrid plants, four plants from an experimental cross between tetraploid *P. maritimum* and tetraploid *P. spicatum* were analyzed. All progeny from this cross were tetraploid and highly fertile.

Other reports of this hybrid from Central Europe are those from Germany and Hungary (cf. BORSOS 1967: 10). In Central Europe both parental species occur as tetraploid cytotypes. HÄRLE (1932) and GRAZE (1933) reported that hybridization between *Pseudolysimachion* taxa of the same ploidy level readily occurs. Hybrid plants were fertile and could be backcrossed to their parents. The hybrid plants from the field that we analyzed were highly fertile and some might be backcross products.

Hybrid plants between these taxa are particularly frequent in the southern Fennoscandia (cf. DU RIETZ 1930: 377, HÄRLE 1932: 21, 81, 82, LEHMANN 1940: 491, RAITANEN 1967: 479–483, etc.), where *P. maritimum* occurs mainly as a diploid cytotype, while *P. spicatum* (subsp. *spicatum*) occurs as a tetraploid (RAITANEN 1967, KUKKONEN 1986). KUKKONEN (1986: 45) speculated that the hybrid populations in southern Finland, close to *P. spicatum*, have originated in Central Europe and later expanded northwards. This hypothesis is supported by the fact that hybrid populations without their parents occur at some localities in Fennoscandia (cf. DU RIETZ 1930: 377, LEHMANN 1940: 491). We, however, agree with the opinion of RAITANEN (1967) and others that the Scandinavian hybrids arose *in situ*. GRAZE (1935) has shown that crossing between the *Pseudolysimachion* taxa of different ploidy is possible and fertile tetraploid hybrids can develop especially when the maternal plant is diploid (HÄRLE 1932, GRAZE 1933, 1935). In such cases the backcrossing of F_1 hybrids to the tetraploid parental species (i.e., *P. spicatum*) is highly probable. This view is confirmed by the fact that most hybrid plants in Fennoscandia are morphologically more similar to *P. spicatum* (cf. RAITANEN 1967: 483). Moreover, hybrids occur very rarely in Central Europe and the migration of whole hybrid populations to the north is unlikely.

While different ploidy levels do not impede hybridization between *P. maritimum* and *P. spicatum* (see also Fig. 2), different ecological requirements of both taxa probably prevent more frequent hybridization and they can therefore be classified as independent species (cf. DU RIETZ 1930: 377).

Pseudolysimachion maritimum x *P. spurium*

The hybrid that was found in two Moravian localities (Bílé Karpaty Mts., see Fig. 3) was tetraploid (Fig. 1f). At the first locality (Appendix 1, no. 122, Čertoryje) the hybrid plants grew alongside the diploid parental species *P. spurium* (subsp. *foliosum*). We did not observe the second parental species, *P. maritimum*, at this locality, but it has been recorded and herbarium specimens are available (WEBER 1925 PR). As only tetraploid populations of *P. maritimum* have been found in south-eastern Moravia (Fig. 3), the extinct *P. maritimum* plants are assumed to be tetraploid. Only hybrid plants were recorded at the second locality (Appendix 1, no. 123, Machová), but herbarium specimens indicate that both parental species have existed at these sites (herbarium specimens: WEBER 1926, 1927 PR).

Hybrid plants from the first locality (no. 122, Čertoryje) differ morphologically from both parental species and they may indeed be F_1 generation. The hybrid plants from the second locality (no. 123, Machová) are morphologically more similar to *P. maritimum* than to *P. spurium*. Therefore, they probably resulted from a backcross of F_1 plants to *P. maritimum*. Hybrid plants of both populations reproduce by subterranean rhizomes, but they set seeds as well.

To our knowledge, no natural hybrids between *P. maritimum* and *P. spurium* have yet been found, although hybrid plants can be obtained artificially by crossing (cf. HÄRLE 1932: 65). The tetraploid hybrid populations referred to here probably arose from a cross between diploid *P. spurium* (subsp. *foliosum*) and a tetraploid cytotype of *P. maritimum* (Fig. 2). This conclusion agrees with the findings of HÄRLE (1932) and GRAZE (1933, 1935), who suggested that tetraploid plants originate more frequently than triploid ones when diploid and tetraploid taxa cross.

Parental species of *P. maritimum* × *P. spurium* differ in their ecological requirements: *P. maritimum* prefers wet and swampy localities whereas *P. spurium* occurs in mesophilous types of drought-tolerant vegetation. Both types of habitats occur adjacent to each other in the flysch rocks territory of the Bílé Karpaty Mts. and hybridization between the two species is therefore not prevented by ecological isolation. As with crosses between *P. maritimum* and *P. spicatum* (see above), crossability between *P. maritimum* and *P. spurium* is not hampered by the different parental ploidy levels and probably results in unidirectional introgression.

An important population is that of Suchov in Bílé Karpaty Mts. (Appendix 1, no. 35), which was originally classified as *P. maritimum*. Nevertheless, there are differences between this population and *P. maritimum* plants from other localities: indumentum of calyx teeth with admixed glandular hairs (absent in typical *P. maritimum*), the lower part of stems are sometimes hairy (lower parts glabrous in *P. maritimum* s.str.). The occurrence of such traits in the population is probably a result of introgression of *P. spurium* (subsp. *foliosum*) into *P. maritimum*.

Comparing our results with hybridization records between diploid *P. maritimum* and tetraploid *P. spicatum* in Fennoscandia (see above), we found some interesting links. Similarly to *P. maritimum* × *P. spicatum*, the hybridogenous populations of *P. maritimum* and *P. spurium* from the Bílé Karpaty Mts. are more close to the tetraploid parent (i.e., *P. maritimum*). This observation supports the hypothesis of an introgressive origin of the investigated populations, i.e., backcrosses of tetraploid hybrids (F_1) to a tetraploid parental species.

The populations Machová (Appendix 1, no. 123) and Suchov (no. 35) most likely arose as a result of unevenly strong unidirectional gene introgression of *P. spurium* (subsp. *foliosum*) into *P. maritimum*. The morphotype found at Machová was first documented in 1924 (herbarium specimen: STANĚK 1924 BRNM) and still has the same phenotype.

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APPENDIX 1

List of *Pseudolysimachion* populations analyzed for ploidy level. [1] – see also TRÁVNÍČEK 1998b, [2] – see also TRÁVNÍČEK 1998a. (1 – consecutive number of a sample; 2 – working designation of a sample (corresponding with designation in TRÁVNÍČEK & WINTER 1999); 3 – phytogeographical district (with number), locality, altitude, collector and year of sample collection (in parenthesis a quadrant number of the Central European grid mapping program, cf. NIKLFELD 1971); 4 – number of analyzed plants/number of voucher specimens; 5 – chromosome number determined by chromosome counting).

1	2	3	4	5
		***P. maritimum*– diploid cytotype (2n=2x)**		
		Czech Republic		
1a.	Želnava (P-091)	S Bohemia, 88g. Hornovltavská kotlina: wet meadows ca. 1 km NW of the village of Želnava, ca. 730 m, leg. M. ŠTECH 1995 (7149d)	2/0	-
1b.	Želnava (P-110)	S Bohemia, 88g. Hornovltavská kotlina: wet meadows ca. 1 km NW of the village of Želnava, ca. 730 m, leg. B. TRÁVNÍČEK, M. ŠTECH, V. ŽÍLA and V. CHÁN 1996 (7149d)	23/5	-
2.	Chlum (P-109)	S Bohemia, 88g. Hornovltavská kotlina: banks of the river Studená Vltava near the confluence with Teplá Vltava River, SW of the village of Chlum near Volary, ca. 730 m, leg. B. TRÁVNÍČEK, M. ŠTECH, V. ŽÍLA and V. CHÁN 1996 (7149a)	6/3	-
		Slovakia		
3.	Trenč (P-015)	S Slovakia, 2. Ipeľsko-rimavská brázda: wet meadows along the road Trenč – Veľká nad Ipľom, ca. 1 km NE of the village of Trenč, ca. 170 m, leg. B. TRÁVNÍČEK 1993 (7783d)	1/0	-
4.	Veľká nad Ipľom (P-041)	S Slovakia, 2. Ipeľsko-rimavská brázda: small wet meadow ca. 1.5 km NE of the village of Veľká nad Ipľom, ca. 170 m, leg. B. TRÁVNÍČEK 1993 (7783b)	4/4	2n=34[1]
		***P. maritimum* – tetraploid cytotype (2n=4x)**		
		Czech Republic		
5.	Horní Počaply (P-039)	C Bohemia, 7b. Podřipská tabule: bush between power-station and the Labe River SE of the village of Horní Počaply, ca. 160 m, leg. J. RYDLO 1993 (5552c)	2/1	-
6.	Ovčáry (P-038)	C Bohemia, 11a. Všetatské Polabí: shore of water reservoir SE of the village of Ovčáry, ca. 170 m, leg. J. ŠTĚPÁNKOVÁ 1993 (5753d)	1/2	-
7.	Chrást (P-037)	C Bohemia, 11a. Všetatské Polabí: wet meadow (the locality "Boroví") SE of the village of Chrást, ca. 170 m, leg. J. RYDLO 1993 (5753a)	1/1	-
8.	Kozly (P-035)	C Bohemia, 11a. Všetatské Polabí: wet meadow (the locality "Pod ploty") SSE of the village of Kozly, ca. 170 m, leg. J. RYDLO 1993 (5753c)	1/1	-
9.	Lobkovice (P-028)	C Bohemia, 11a. Všetatské Polabí: town Neratovice, wet meadows SE of the suburb Lobkovice, ca. 170 m, leg. B. TRÁVNÍČEK 1993 (5753c)	3/3	2n=68
10.	Všetaty (P-026)	C Bohemia, 11a. Všetatské Polabí: wet ruderal place near the railway station of the village of Všetaty, ca. 170 m, leg. J. RYDLO 1993 (5753a)	1/1	-
11.	Kly (P-033)	C Bohemia, 11a. Všetatské Polabí: wet meadows "Kelštice" NNW of the village of Kly, ca. 160 m, leg. J. RYDLO 1993 (5652d)	2/0	-
12.	Kolín (P-023)	C Bohemia, 11b. Poděbradské Polabí: town Kolín, small wet meadow on the right bank of the Labe River E of the railway station, ca. 200 m, leg. B. TRÁVNÍČEK 1993 (5957c)	1/0	-
13.	Libice nad Cidlinou (P-064)	C Bohemia, 11b. Poděbradské Polabí: banks of the Cidlina River in the S peripheria of the village of Libice nad Cidlinou, ca. 190 m, leg. B. TRÁVNÍČEK 1994 (5857c)	3/1	-

14.	Sloupno (P-046)	E Bohemia, 14a. Bydžovská pánev: town Nový Bydžov, banks of the Cidlina River in the E periphery of the village of Sloupno, ca. 230 m, leg. B. TRÁVNÍČEK and Z. KAPLAN 1993 (5759a)	2/4	-
15.	Josefov (P-045)	E Bohemia, 15a. Jaroměřské Polabí: town Jaroměř, wet meadow on the left bank of the Metuje River NE of the suburb Josefov, ca. 250 m, leg. B. TRÁVNÍČEK and Z. KAPLAN 1993 (5661d)	1/0	-
16.	České Meziříčí (P-044)	E Bohemia, 15b. Hradecké Polabí: wet meadows (the locality "Zbytky") NE of the village of České Meziříčí, ca. 270 m, leg. B. TRÁVNÍČEK and Z. KAPLAN 1993 (5762a)	1/0	-
17.	Malšova Lhota (P-047)	E Bohemia, 15b. Hradecké Polabí: town Hradec Králové, wet meadows on the left bank of the Orlice River in the N peripheria of the suburb Malšova Lhota, ca. 250 m, leg. B. TRÁVNÍČEK and Z. KAPLAN 1993 (5761c)	1/2	-
18.	Lanžhot (P-010)	S Moravia, 18a. Dyjsko-svratecký úval: wet meadows NNW of the confluence of the rivers Morava and Dyje S of the village of Lanžhot, ca. 150 m, leg. B. TRÁVNÍČEK 1993 (7367d)	5/4	-
19.	Kostice (P-087)	S Moravia, 18a. Dyjsko-svratecký úval: meadow stripe along blind arm of the Morava River 1.3 km SE of the village of Kostice, leg. B. TRÁVNÍČEK 1995 (7267d)	4/1	-
20.	Nejdek (P-077)	S Moravia, 18a. Dyjsko-svratecký úval: small wet meadow NNE of the village of Nejdek near Lednice, ca. 170 m, leg. B. TRÁVNÍČEK and J. DANIHELKA 1994 (7166d)	5/4	-
21.	Bulhary (NP-09)	S Moravia, 18a. Dyjsko-svratecký úval: wet meadows on the left bank of the Dyje River NNW of the village of Bulhary, ca. 170 m, leg. B. TRÁVNÍČEK 1999 (7166c)	6/1	-
22.	Nové Mlýny (P-079)	S Moravia, 18a. Dyjsko-svratecký úval: margin of a wet wood along the road Nové Mlýny – Milovice WSW of the village of Nové Mlýny, ca. 170 m, leg. B. TRÁVNÍČEK and J. DANIHELKA 1994 (7166a)	1/2	-
23.	Petrov (P-050)	S Moravia, 18b. Dolnomoravský úval: wet meadows (the locality "Petrovské louky") N of the village of Petrov, ca. 170 m, leg. B. TRÁVNÍČEK 1994 (7169b)	3/3	-
24.	Kojetín, Včelín (P-030)	C Moravia, 21b. Hornomoravský úval: wet meadow near the gamekeeper's lodge Včelín ENE of the town of Kojetín, ca.190 m, leg. B. TRÁVNÍČEK 1995 (6670a)	20/0	-
25.	Kojetín, Dolní les (P-065)	C Moravia, 21b. Hornomoravský úval: margin of a wet wood (the locality "Dolní les") near the road Kojetín – Chropyně E of the town of Kojetín, ca. 190 m, leg. B. TRÁVNÍČEK 1995 (6670c)	7/0	-
26.	Bílany (P-048)	C Moravia, 21b. Hornomoravský úval: small wet meadow along the railway Kroměříž-Hulín SSE of the village of Bílany, ca. 190 m, leg. B. TRÁVNÍČEK 1993 (6670d)	4/2	2n=68
27.	Záhlinice (P-106)	C Moravia, 21b. Hornomoravský úval: wet meadows ca. 2 km S of the village of Záhlinice, ca. 190 m, leg. B. TRÁVNÍČEK 1995 (6770b)	1/1	-
28.	České Budějovice (P-029)	S Bohemia, 38. Budějovická pánev: town České Budějovice, right bank of the Vltava River ca. 2 km N of the N town margin, ca. 370 m, leg. M. ŠTECH 1994 (6952d)	2/3	2n=68
29.	Dráchov (P-021)	S Bohemia, 39. Třeboňská pánev: banks of the Lužnice River in NE peripheria of the village of Dráchov, ca. 410 m, leg. B. TRÁVNÍČEK 1993 (6754c)	3/1	-
30.	Tábor (P-018)	S Bohemia, 42b. Táborsko-vlašimská pahorkatina: town Tábor, right bank of the Lužnice River ca. 2 km S of the railway station, ca. 390 m, leg. B. TRÁVNÍČEK 1993 (6554c)	1/0	-
31.	Česká Lípa (P-063)	N Bohemia, 53a. Českolipská kotlina: town Česká Lípa, wet meadows on the banks of the Ploučnice River NE of the settlement Žizníkov, ca. 250 m, leg. B. TRÁVNÍČEK 1994 (5353a)	1/3	-

32.	Ledové sluje (P-108)	S Moravia, 68. Moravské podhůří Vysočiny: wet meadow on the right bank of the Dyje River near the locality "Ledové sluje" WNW of the village of Čížov, ca. 300 m, leg. B. TRÁVNÍČEK 1995 (7161a)	4/5	-
33.	Křtiny (P-020)	C Moravia, 71b. Drahanská plošina: wet meadow near arboretum N of the village of Křtiny, ca. 470 m, leg. B. TRÁVNÍČEK and J. KOBLÍŽEK 1993 (6666c)	2/4	2n=68
34a.	Moravičany (P-006)	N Moravia, 72. Zábřežsko-uničovský úval: wet meadow between a water reservoir and Morava River NNE of the village of Moravičany, ca. 250 m, leg. P. KUSÁK (6267b)	1/0	-
34b.	Moravičany (P-016)	N Moravia, 72. Zábřežsko-uničovský úval: wet meadow between a water reservoir and Morava River NNE of the village of Moravičany, ca. 250 m, leg. B. TRÁVNÍČEK 1993 (6267b)	2/1	-
35.	Suchov (P-111)	S Moravia, 78. Bílé Karpaty lesní: slope meadows (the locality "Přední louky") S of the Lipinka Hill (504 m) ESE of the village of Suchov, ca. 460 m, leg. B. TRÁVNÍČEK 1996 (7071d)	1/0	-

Slovakia

36.	Gbely (P-090)	SW Slovakia, 4. Záhorská nížina: town Gbely, ditch along the road ca. 2 km W of the railway station, ca. 150 m, leg. B. TRÁVNÍČEK 1995 (7268c)	1/0	-
37a.	Abrod (P-049)	SW Slovakia, 4. Záhorská nížina: wet meadows (the locality "Abrod") WSW of the village of Závod, ca. 150 m, (leg. M. KRÁL 7468c)	1/0	-
37b.	Abrod (P-085)	SW Slovakia, 4. Záhorská nížina: wet meadows (the locality "Abrod") WSW of the village of Závod, ca. 150 m, leg. B. TRÁVNÍČEK 1995 (7468c)	2/1	-
38.	Malé Leváre (P-088)	SW Slovakia, 4. Záhorská nížina: inundate meadows on the left bank of the Morava River ca. 3 km WNW of the village of Malé Leváre, ca. 150 m, leg. B. TRÁVNÍČEK 1995 (7467d)	2/1	-
39.	Vysoká pri Morave (P-083)	SW Slovakia, 4. Záhorská nížina: wet bush in the NW peripheria of the village of Vysoká pri Morave, ca. 150 m, leg. B. TRÁVNÍČEK 1995 (7667c)	1/1	-
40.	Kava (P-102)	S Slovakia, 6. Podunajská nížina: town Komárno, margin of the wet bush ca. 2 km SE of the village of Kava, ca. 110 m, leg. B. TRÁVNÍČEK 1995 (8174d)	1/1	-
41.	Blatná Polianka (P-098)	SE Slovakia, 8. Východoslovenská nížina: wet meadows ca. 1 km W of the village of Blatná Polianka, ca. 110 m, leg. B. TRÁVNÍČEK 1995 (7398b)	1/1	-
42.	Veľké Raškovce (P-072)	SE Slovakia, 8. Východoslovenská nížina: wet meadows on the right bank of the Laborec River ca. 3 km ENE of the village of Veľké Raškovce, ca. 100 m, leg. B. TRÁVNÍČEK 1994 (7497b)	2/0	-
43.	Veľké Kapušany (P-002)	SE Slovakia, 8. Východoslovenská nížina: town Veľké Kapušany, wet bush on the banks of the Latorica River near the road Veľké Kapušany – Kráľovský Chlmec, ca. 100 m, leg. B. TRÁVNÍČEK 1991 (7498c)	3/6	-
44.	Boľ (P-074)	SE Slovakia, 8. Východoslovenská nížina: wet meadows and bush ca. 3 km N of the village of Boľ, ca. 100 m, leg. B. TRÁVNÍČEK 1994 (7597b)	1/0	-
45.	Zelené (P-103)	C Slovakia, 15. Slovenské rudohorie: shore of the pond NW of the village of Zelené near Poltár, ca. 230 m, leg. B. TRÁVNÍČEK 1995 (7584d)	4/3	-

***P. spurium* subsp. *foliosum* (2n=2x)**

Czech Republic

46a.	Čertoryje (P-107)	S Moravia, 19. Bílé Karpaty stepní: slope meadows (the locality "Vojšické louky") SSE of the Čertoryje Hill (443 m) SSE of the water reservoir Lučina near the village of Radějov, ca. 410 m, leg. B. TRÁVNÍČEK and M. HÁJEK 1995 (7170d)	2/0	-
46b.	Čertoryje (P-112)	S Moravia, 19. Bílé Karpaty stepní: slope meadows (the locality "Vojšické louky") SSE of the Čertoryje Hill (443 m) SSE of the water reservoir Lučina near the village of Radějov, ca. 410 m, leg. B. TRÁVNÍČEK 1996 (7170d)	1/0	2n=34

46c.	Čertoryje (NP-14, NP-15, NP-16)	S Moravia, 19. Bílé Karpaty stepní: slope meadows (the locality "Vojšické louky") SSE of the Čertoryje Hill (443 m) SSE of the water reservoir Lučina near the village of Radějov, ca. 410 m, leg. B. TRÁVNÍČEK 1999 (7170d)	8/3	-

P. orchideum (2n=2x)

Czech Republic

47.	Šumice (P-024)	S Moravia, 19. Bílé Karpaty stepní: dry slope meadow in NW peripheria of the village of Šumice, ca. 240 m, leg. B. TRÁVNÍČEK 1993 (6972c)	1/1	-
48.	Čertoryje (NP-07, NP-12)	S Moravia, 19. Bílé Karpaty stepní: dry meadows (the locality "Vojšické louky") on the SW slope of the Čertoryje Hill (443 m) SSE of the water reservoir Lučina near the village of Radějov, ca. 380 m, leg. B. TRÁVNÍČEK 1999 (7170a)	3/0	-
49.	Machová (NP-17)	S Moravia, 78. Bílé Karpaty lesní: steppe slope at the W foot of the Machová Hill (579m) (near the railway station Vrbovce) S of the village of Javorník, ca. 370 m, leg. B. TRÁVNÍČEK 1999 (7171c)	3/0	-
50.	Březolupy (P-051)	C Moravia, 79. Zlínské vrchy: dry wood margin (the locality "Boří") along the road Březolupy – Šarovy NE of the village of Březolupy, ca. 230 m, leg. B. TRÁVNÍČEK 1993 (6871d)	2/3	2n=34

Slovakia

51.	Horné Rykynčice (P-070)	S Slovakia, 2. Ipeľsko-rimavská brázda: dry bush slopes in NE peripheria of the village of Horné Rykynčice, ca. 200 m, leg. B. TRÁVNÍČEK 1994 (7779d)	1/1	-
52.	Plášťovce (P-012)	S Slovakia, 2. Ipeľsko-rimavská brázda: dry oak-wood on the slopes in NE peripheria of the village of Plášťovce, ca. 240 m, leg. B. TRÁVNÍČEK 1993 (7879b)	1/0	-
53.	Chaláska (P-014)	S Slovakia, 2. Ipeľsko-rimavská brázda: dry meadows SE of the Chaláska Hill (358 m) N of the village of Dolné Strháre, ca. 320 m, leg. B. TRÁVNÍČEK 1993 (7782a)	2/3	2n=34[1]
54.	Mravec (P-040)	S Slovakia, 2. Ipeľsko-rimavská brázda: SW bush slopes on the Mravec Hill (310 m) WNW of the village of Čakanovce, ca. 280 m, leg. B. TRÁVNÍČEK 1993 (7784d)	1/1	-
55.	Hostišovce (P-067)	S Slovakia, 2. Ipeľsko-rimavská brázda: dry pastures along the road WNW of the village of Hostišovce, ca. 310 m, leg. B. TRÁVNÍČEK 1994 (7486d)	1/2	-
56.	Cejkov (P-008)	SE Slovakia, 8. Východoslovenská nížina: Zemplínske vrchy Hills, dry bush slope in NW peripheria of the village of Cejkov, ca. 190 m, leg. B. TRÁVNÍČEK 1992 (7596b)	1/3	-
57.	Fančová (P-053)	W Slovakia, 14b. Vtáčnik: dry meadow in WNW peripheria of the settlement Fančová SE of the village of Čereňany, ca. 290 m, leg. P. LUSTYK 1994 (7377c)	3/2	2n=34[1]
58.	Stráž (P-057)	W Slovakia, 14b. Vtáčnik: dry meadow on the S slope of the Stráž Hill (857 m) NW of the village of Veľké Pole, ca. 660 m, leg. B. TRÁVNÍČEK 1994 (7477c)	1/3	-
59.	Lutila (P-099)	C Slovakia, 14b. Vtáčnik: town Žiar nad Hronom, mesophilous pastures on the SW slopes SE of the suburb Lutila, ca. 300 m, leg. B. TRÁVNÍČEK 1995 (7379c)	1/2	-

***P. spicatum* aff. subsp. *porphyrianum* (2n=2x)**

Slovakia/Ukraine

60.	Stinská (P-097)	NE Slovakia – W Ukraine, 31. Bukovské vrchy: small rocky ridge at the Slovak-Ukrainian border (Stinská Mt., 1092 m) ESE of the village of Zboj, ca. 1070 m, leg. B. TRÁVNÍČEK 1995 (6901c)	2/2	2n=34

P. spicatum subsp. spicatum (2n=4x)

Czech Republic

61.	Kalvárie (NP-04)	N Bohemia, 4b. Labské středohoří: SW rocky slopes on the right bank of the Labe River (the locality "Kalvárie") WSW of the Strážiště Hill (362 m) NW of the village of Velké Žernoseky, ca. 260 m, leg. B. TRÁVNÍČEK 1997 (5450c)	1/0	-
62.	Kleneč (NP-05)	N Bohemia, 7b. Podřipská tabule: town Roudnice nad Labem, sandy wood margin SE of the village of Kleneč, ca. 210 m, leg. B. TRÁVNÍČEK 1997 (5651b)	1/0	-
63.	Nelahozeves (P-032)	C Bohemia, 7c. Slánská tabule: town Kralupy nad Vltavou, steppe slope ca. 1 km N of the village of Nelahozeves, ca. 200 m, leg. B. TRÁVNÍČEK 1993 (5751b)	1/0	-
64.	Doutnáč (P-022)	C Bohemia, 8. Český kras: S dry bush slope of the Doutnáč Hill (433 m) NNE of the village of Srbsko, ca. 350 m, leg. B. TRÁVNÍČEK 1994 (6050b)	3/3	2n=68
65.	Krpy (P-036)	C Bohemia, 12. Dolní Pojizeří: steppe slopes ca. 1 km NE of the village of Krpy, ca. 230 m, leg. B. TRÁVNÍČEK 1993 (5654c)	1/0	-
66.	Mohelno (P-061)	S Moravia, 16. Znojemsko-brněnská pahorkatina: serpentine steppe slopes along the road Mohelno – Dukovany (the locality "Mohelenská hadcová step") S of the village of Mohelno, ca. 340 m, leg. B. TRÁVNÍČEK 1994 (6863c)	3/0	-
67.	Popice (P-043)	S Moravia, 16. Znojemsko-brněnská pahorkatina: town Znojmo, heathered dry meadows SW of the village of Popice, ca. 310 m, leg. B. TRÁVNÍČEK 1993 (7162c)	2/3	2n=68
68.	Šibeničník (P-095)	S Moravia, 17b. Pavlovské kopce: steppe top of the Šibeničník Hill (238 m) S of the town of Mikulov, ca. 230 m, leg. B. TRÁVNÍČEK 1995 (7265b)	1/0	-
69.	Svatý Kopeček (P-093)	S Moravia, 17b. Pavlovské kopce: rocky steppe slopes of the Svatý Kopeček Hill (363 m) in ESE peripheria of the town of Mikulov, ca. 350 m, leg. B. TRÁVNÍČEK 1995 (7165d)	1/1	-
70.	Mikulov (P-080)	S Moravia, 17b. Pavlovské kopce: steppe margins of the quarry near the road Mikulov – Milovice in E peripheria of the town of Mikulov, ca. 300 m, leg. B. TRÁVNÍČEK and J. DANIHELKA 1994 (7165d)	2/0	-
71.	Milovice (P-081)	S Moravia, 17c. Milovicko-valtická pahorkatina: steppe slopes (the locality "Milovická stráň") near the S margin of the village of Milovice, ca. 210 m, leg. B. TRÁVNÍČEK and J. DANIHELKA 1994 (7166c)	2/0	-
72.	Valtice (P-082)	S Moravia, 18a. Dyjsko-svratecký úval: dry place near the romantic construction Rendezvous, ENE of the town of Valtice, ca. 200 m, leg. B. TRÁVNÍČEK 1994 (7266b)	4/3	2n=68
73.	Bulhary (NP-11)	S Moravia, 18a. Dyjsko-svratecký úval: dry part of meadows on the left bank of the Dyje River NNW of the village of Bulhary, ca. 170 m, leg. B. TRÁVNÍČEK 1999 (7166c)	6/0	-
74.	Doubravka (P-092)	S Moravia, 18a. Dyjsko-svratecký úval: dry parts of meadows (the locality "Doubravka") SSE of the settlement Lány SW of the village of Lanžhot, ca. 150 m, leg. V. PLUHAŘ 1995 (7367b)	1/1	-
75.	Košarské lúky (P-094)	S Moravia, 18a. Dyjsko-svratecký úval: dry part of the meadows (the locality "Košarské louky") ca. 3 km N of the confluence of the rivers Morava and Dyje, ca. 150 m, leg. V. PLUHAŘ 1995 (7367d)	1/1	-
76.	Dúbrava (P-086)	S Moravia, 18b. Dolnomoravský úval: town Hodonín, dry wood margin along a road in Doubrava woodland ca. 3 km NW of the railway station, ca. 180 m, leg. B. TRÁVNÍČEK 1995 (7168b)	2/1	-
77.	Hády (P-019)	S Moravia, 20b. Hustopečská pahorkatina: town Brno, steppe wood margins on the Hády Hill (424 m) NW of the suburb Líšeň, ca. 390 m, leg. B. TRÁVNÍČEK 1993 (6766c)	2/0	-

78.	Drysice (NP-03)	C Moravia, 21a. Hanácká pahorkatina: steppe margins of a quarry near the road Drysice-Želeč (the locality "Bílá skála") NE of the village of Drysice, ca. 280 m, leg. B. TRÁVNÍČEK 1998 (6668c)	2/0	-
79.	Dobrochov (P-060)	C Moravia, 21a. Hanácká pahorkatina: E dry slope of the Předina Hill E of the village of Dobrochov, ca. 290 m, leg. B. TRÁVNÍČEK 1994 (6668b)	1/1	-
80.	Malý Kosíř (P-011)	C Moravia, 21a. Hanácká pahorkatina: heathered dry meadow on the top of the Malý Kosíř Hill (316 m) SW of the village of Slatinice, ca. 310 m, leg. B. TRÁVNÍČEK 1993 (6468b)	2/3	2n=68
81.	Medonosy (P-034)	C Bohemia, 51. Polomené hory: dry slope near the village of Medonosy, ca. 250 m, leg. L. HROUDA 1993 (5552b)	1/0	-
82.	Osinalice (P-027)	C Bohemia, 51. Polomené hory: dry meadow ca. 1 km SW of the village of Osinalice, ca. 300 m, leg. J. ŠTĚPÁNKOVÁ 1993 (5553a)	1/1	-
83.	Velký Hubenov (P-031)	N Bohemia, 51. Polomené hory: dry slope ENE of the village of Velký Hubenov, ca. 270 m, leg. J. SÁDLO 1993 (5452c)	1/0	-
84.	Biskoupky (P-062)	S Moravia, 68. Moravské podhůří Vysočiny: dry meadows on the Biskoupský kopec Hill (397 m) NW of the village Biskoupky, ca. 370 m, leg. B. TRÁVNÍČEK 1994 (6863d)	2/1	-
85.	Čížov (P-005)	S Moravia, 68. Moravské podhůří Vysočiny: small dry meadow in SE peripheria of the village of Čížov, ca. 400 m, leg. B. TRÁVNÍČEK 1992 (7161a)	1/0	-
86.	Ohrozim (P-007)	C Moravia, 71c. Drahanské podhůří: dry margins of a small quarry (the locality "Horka") ca. 1 km NW of the village of Ohrozim, ca. 350 m, leg. B. TRÁVNÍČEK 1993 (6568a)	3/3	2n=68
87.	Plumlov (P-003)	C Moravia, 71c. Drahanské podhůří: dry meadows on a hill in W peripheria of the village of Plumlov, ca. 310 m, leg. B. TRÁVNÍČEK 1993 (6568a)	2/1	-
88.	Žárovice (P-004)	C Moravia, 71c. Drahanské podhůří: dry meadow on the hill (the locality "Pavlečkova skalka") in NW peripheria of the village of Žárovice, ca. 350 m, leg. B. TRÁVNÍČEK 1993 (6567b)	1/0	-
89.	Náměšť' na Hané (P-009)	C Moravia, 71c. Drahanské podhůří: dry oak-wood on the S slopes in the Terezské údolí Valley ca. 3 km SW of the village of Námešt' na Hané, ca. 320 m, leg. B. TRÁVNÍČEK 1993 (6468a)	2/1	-
		Slovakia		
90.	Plášt'ovce (P-013)	S Slovakia, 2. Ipeľsko-rimavská brázda: dry meadow with bush ca. 1 km NE of the village of Plášt'ovce, ca. 270 m, leg. B. TRÁVNÍČEK 1993 (7879b)	1/2	-
91.	Slizké (P-066)	S Slovakia, 2. Ipeľsko-rimavská brázda: dry meadows (the locality "Podbanište") ca. 1 km NNW of the village of Slizké, ca. 380 m, leg. B. TRÁVNÍČEK 1994 (7486d)	4/2	2n=68[1]
92.	Kečovo (P-025)	S Slovakia, 3. Slovenský kras: steppe meadows with bush in SSW peripheria of the village of Kečovo, ca. 360 m, leg. B. TRÁVNÍČEK 1991 (7588b)	1/1	-
93.	Domica (P-073)	S Slovakia, 3. Slovenský kras: bush steppe slope above the cave Domica, ca. 370 m, leg. B. TRÁVNÍČEK 1994 (7588b)	4/2	2n=68[1]
94.	Turniansky hrad (P-075)	S Slovakia, 3. Slovenský kras: E slopes of the locality "Turniansky hradný vrch" (castled hill) N of the village of Turnianske Podhradie, ca. 270 m, leg. B. TRÁVNÍČEK 1994 (7391c)	3/0	-
95.	Ladmovce (P-115)	SE Slovakia, 8. Východoslovenská nížina: steppe slopes in NE peripheria of the village of Ladmovce, ca. 150 m, leg. P. KUSÁK (7596d)	1/0	-
96.	Plavecké Podhradie (P-084)	W Slovakia, 10. Malé Karpaty: W bush slopes of the Pohanská Hill (495 m) NNE of the village of Plavecké Podhradie, ca. 330 m, leg. B. TRÁVNÍČEK 1995 (7569b)	3/1	-
97.	Malé Uherce (P-056)	W Slovakia, 12. Tríbeč: town Partyzánske, oak-woods ca. 2 km SW of the suburb Malé Uherce, ca. 400 m, leg. B. TRÁVNÍČEK 1994 (7376c)	2/1	-
98.	Kostrín (P-054)	W Slovakia, 12. Tríbeč: slopes of the Kostrín Hill (390 m) SSW of the village of Klátova Nová Ves, ca. 380 m, leg. L. TICHÝ 1994 (7475b)	1/1	-

99. Osľany (P-052)	C Slovakia: 13. Strážovské a Súľovské vrchy: rocky slope at S foot of the Veľký vrch Hill (456 m) NW of the village of Osľany, ca. 230 m, leg. B. TRÁVNÍČEK 1994 (7376d)	4/2	$2n=68^{1}$
100. Dolné Vestenice (P-055)	W Slovakia, 13. Strážovské a Súľovské vrchy: bush steppe slope above a road ca. 1 km W of the village of Dolné Vestenice, ca. 250 m, leg. B. TRÁVNÍČEK 1994 (7276c) (var. *spicatum* and var. *pseudoorchideum* (PACZ.) TRÁVNÍČEK)	5/3	$2n=68^{1}$
101. Stráže (P-059)	W Slovakia, 13. Strážovské a Súľovské vrchy: slopes of the Stráže Hill (496 m) SW of the village of Nitrica, ca. 450 m, leg. J. HADINEC 1994 (7376b)	1/1	-
102. Nitrica (P-058)	W Slovakia, 13. Strážovské a Súľovské vrchy: steppe meadows ca. 2 km S of the village of Nitrica, ca. 500 m, leg. B. TRÁVNÍČEK 1994 (7376b)	1/1	-
103. Hronský Beňadik (P-078)	C Slovakia, 14e. Štiavnické vrchy: the valley ca. 2 km E of the village of Hronský Beňadik, ca. 300 m, leg. P. KUSÁK (7677d)	1/0	-
104. Muráň (P-101)	C Slovakia, 16. Muránska planina: rocky top of Mt. Cigánka (935 m) (in area of the castle ruin) NNE of the village of Muráň, ca. 930 m, leg. B. TRÁVNÍČEK 1995 (7286a)	1/1	-
105. Hrabušice (P-105)	C Slovakia, 17. Slovenský raj: rocky slopes on the left bank of the Hornád River at SW foot of Mt. Zelená hora (654 m) S of the village of Hrabušice, ca. 560 m, leg. B. TRÁVNÍČEK 1995 (7088a)	1/1	-
106. Bešeňová (P-104)	C Slovakia, 26a. Liptovská kotlina: rocky travertine slope (the locality "Bešeňovské travertiny") ca. 1 km NNW of the village of Bešeňová, ca. 580 m, leg. B. TRÁVNÍČEK 1995 (6882d)	2/1	-
107. Sivá Brada (P-100)	C Slovakia, 26b. Spišské kotliny: travertine hill Sivá Brada NW of the village of Spišské Podhradie, ca. 520 m, leg. B. TRÁVNÍČEK 1995 (6990c)	2/1	-
108. Primovce (P-096)	C Slovakia, 26b. Spišské kotliny: S slope above the road Primovce – Hôrka NE of the village of Primovce, ca. 610 m, leg. B. TRÁVNÍČEK 1995 (6988c)	2/1	-

Austria

109. Lange Lacke (P-089)	Lower Austria: region of the lake Neusiedler See, dry meadows on the shore of the salt lake Lange Lacke NE of the village of Apetlon, ca. 120 m, leg. B. TRÁVNÍČEK 1995 (8267a)	1/0	-

P. spicatum subsp. _fischeri_ (2n=4x)

Slovakia

110. Plášťovce (P-013)	S Slovakia, 2. Ipeľsko-rimavská brázda: dry meadow with bush ca. 1 km NE of the village of Plášťovce, ca. 270 m, leg. B. TRÁVNÍČEK 1993 (7879b)	6/4	-
111. Šávoľ (P-042)	S Slovakia, 2. Ipeľsko-rimavská brázda: steppe slope above the road Fiľakovo – Šávoľ (Kerčík Hill, 302 m) N of the town of Fiľakovo, ca. 260 m, leg. B. TRÁVNÍČEK 1993 (7784b)	1/2	-
112. Matrač (P-068)	S Slovakia, 2. Ipeľsko-rimavská brázda: S slope of the Javorník, Matrač Hill (410 m) SSE of the village of Hajnáčka, ca. 350 m, leg. B. TRÁVNÍČEK 1994 (7785d)	4/2	$2n=68^{1,2}$
113. Radzovce (P-069)	S Slovakia, 2. Ipeľsko-rimavská brázda: oak-woods on the S slopes of the Monica Hill (584 m) ESE of the village of Radzovce, ca. 530 m, leg. B. TRÁVNÍČEK 1994 (7785c)	5/1	-
114. Dúžava (P-017)	S Slovakia, 2. Ipeľsko-rimavská brázda: town Rimavská Sobota, bush slope ca. 1 km NE of the suburb Dúžava, ca. 240 m, leg. B. TRÁVNÍČEK 1991 (7685b)	1/1	-
115a. Slizké (P-001)	S Slovakia, 2. Ipeľsko-rimavská brázda: dry meadows (the locality "Podbanište") ca. 1 km NNW of the village of Slizké, ca. 380 m, leg. B. TRÁVNÍČEK 1991 (7486d)	4/4	$2n=68^{1,2}$
115b. Slizké (P-066)	S Slovakia, 2. Ipeľsko-rimavská brázda: dry meadows (the locality "Podbanište") ca. 1 km NNW of the village of Slizké, ca. 380 m, leg. B. TRÁVNÍČEK 1994 (7486d)	5/0	-

116. Sitno (P-071)	C Slovakia, 14e. Štiavnické vrchy: dry meadow on the top of Mt. Sitno (1009 m), SSW of the town of Banská Štiavnica, ca. 1000 m, leg. B. TRÁVNÍČEK 1994 (7579c)	2/1	-
	P. spicatum **– intermediates between subsp.** ***spicatum*** **and subsp.** ***fischeri*** **(2n=4x)**		
	Slovakia		
117. Šávol (P-042)	S Slovakia, 2. Ipeľsko-rimavská brázda: steppe slope above the road Fiľakovo – Šávoľ (Kerčík Hill, 302 m) N of the town of Fiľakovo, ca. 260 m, leg. B. TRÁVNÍČEK 1993 (7784b)	4/1	2n=68
118. Sitno (P-071)	C Slovakia, 14e. Štiavnické vrchy: dry meadow on the top of Mt. Sitno (1009 m), SSW of the town of Banská Štiavnica, ca. 1000 m, leg. B. TRÁVNÍČEK 1994 (7579c)	4/3	2n=68
	Hungary		
119. Pilis (NP-19)	N Hungary, Pilis Mts., S rocky slope of Mt. Pilis (756 m) NNW of the village of Pilisszántó, ca. 650 m, leg. B. TRÁVNÍČEK 1999 (8379a)	1/0	-
	P. incanum **subsp.** ***pallens*** **(2n=4x)**		
	Slovakia		
120. Tarbucka (P-076)	SE Slovakia, 8. Východoslovenská nížina: dry grassy place in vineyards at the E foot of the Tarbucka Hill (277 m) W of Veľký Kamenec, ca. 180 m, leg. B. TRÁVNÍČEK 1994 (7696b)	5/5	2n=68[1,2]
	P. maritimum **×** ***spicatum*** **(2n=4x)**		
	Czech Republic		
121. Bulhary (NP-06)	S Moravia, 18a. Dyjsko-svratecký úval: meadows on the left bank of the Dyje River NNW of the village of Bulhary, ca. 170 m, leg. J. DANIHELKA 1997 (7166c)	3/0	-
	P. maritimum **×** ***spurium*** **(2n=4x)**		
	Czech Republic		
122a. Čertoryje (P-107)	S Moravia, 19. Bílé Karpaty stepní: slope meadows (the locality "Vojšické louky") SSE of the Čertoryje Hill (443 m) SSE of the water reservoir Lučina near the village of Radějov, ca. 410 m, leg. B. TRÁVNÍČEK 1995 (7170d)	1/0	-
122b. Čertoryje (P-113)	S Moravia, 19. Bílé Karpaty stepní: slope meadows (the locality "Vojšické louky") SSE of the Čertoryje Hill (443 m) SSE of the water reservoir Lučina near the village of Radějov, ca. 410 m, leg. B. TRÁVNÍČEK 1996 (7170d)	2/1	-
122c. Čertoryje (NP-13)	S Moravia, 19. Bílé Karpaty stepní: slope meadows (the locality "Vojšické louky") SSE of the Čertoryje Hill (443 m) SSE of the water reservoir Lučina near the village of Radějov, ca. 410 m, leg. B. TRÁVNÍČEK 1999 (7170d)	7/5	-
123a. Machová (P-114)	S Moravia, 78. Bílé Karpaty lesní: mesophilous meadows on the W slope of the Machová Hill (579 m) S of the village of Javorník, ca. 440 m, leg. B. TRÁVNÍČEK 1996 (7171c)	8/0	-
123b. Machová (NP-18)	S Moravia, 78. Bílé Karpaty lesní: mesophilous meadows on the W slope of the Machová Hill (579 m) S of the village of Javorník, ca. 440 m, leg. B. TRÁVNÍČEK 1999 (7171c)	10/8	-

APPENDIX 2

List of literature records on chromosome numbers in the *Pseudolysimachion* (1 – geographic origin of analyzed plant; 2 – chromosome number; 3 – number of localities (in parenthesis number of records); 4 – reference; 5 – remarks). [1] – abbreviatons of phytogeographical regions by UOTILA & PELLINEN 1985: 2.

1	2	3	4	5
P. maritimum				
The Netherlands (distr. Overijssel)	2n=68 (4x)	1	GADELLA & KLIPHUIS 1973: 307	ut *Veronica longifolia* L.
Norway (N Norway, Masi)	n=17 (2x)	1	LAANE 1965: 171, 187	ut *Veronica longifolia* L. (s. lat.)
Sweden (E Sweden, Ornö)	n=17 (2x)	1	GRAZE in LEHMANN 1940: 482	ut *Veronica maritima* L.
Finland (St)[1]	n=ca. 15 (ca. 2x)	1	RAITANEN 1967: 471	ut *Veronica longifolia* L.
Finland (Ab, Ka, N, Oa)[1]	n=17 (2x)	5	RAITANEN 1967: 471	ut *Veronica longifolia* L.
Finland (Oa)[1]	2n=ca. 33 (ca. 2x)	1	RAITANEN 1967: 471	ut *Veronica longifolia* L.
Finland (Kb, Li, N)[1]	2n=34 (2x)	3	RAITANEN 1967: 471	ut *Veronica longifolia* L.
Finland (Ab)[1]	2n=34 (2x)	1	AROHONKA 1982	ut *Veronica longifolia* L.
Finland (Ab, Al, N)[1]	2n=34 (2x)	4	KUKKONEN 1986: 41	ut *Veronica longifolia* var. *maritima*
Finland (Lks, Ks)[1]	n=17 (2x)	2	KUKKONEN 1986: 41	ut *Veronica longifolia* L.
Finland (Ks)[1]	2n=68 (4x)	1	RAITANEN 1967: 471	ut *Veronica longifolia* L.
Italy (N Italy, Pavia)	n=17 (2x)	1	GRAZE 1933: 520, 521	ut *Veronica ticinensis* POLLINI
Germany (Schleswig-Holstein)	n=34 (4x)	1	TISCHLER 1934: 15	ut *Veronica longifolia* L.
Austria (Lower Austria)	n=17 (2x)	2	FISCHER 1969: 438	ut *Pseudolysimachion longifolium* subsp. *maritimum* (L.) HARTL
Austria (Lower Austria)	n=ca. 34 (ca. 4x)	1	FISCHER 1969: 438	ut *Pseudolysimachion longifolium* (L.) OPIZ subsp. *longifolium*
Slovakia (Záhorská nížina Lowland)	2n=68 (4x)	1	VÁCHOVÁ & ZÁBORSKÝ 1980: 724	ut *Pseudolysimachion longifolium* (L.) OPIZ
Slovakia (Východoslovenská nížina Lowland)	2n=68 (4x)	1	MÁJOVSKÝ & MURÍN 1987: 7	ut *Pseudolysimachion longifolium* (L.) OPIZ
Hungary (S of Budapest)	n=17 (2x)	1	GRAZE 1933: 520, 521	ut *Veronica maritima* L.
Hungary (E of Debrecen)	n=34 (4x)	1	GRAZE 1933: 519, 520	ut *Veronica longifolia* L.
Bulgaria (distr. Razgrad)	2n=68 (4x)	1	PEEV 1972: 499	ut *Veronica longifolia* L. subsp. *longifolia*
Ukraine (distr. Rovno)	2n=36 (ca. 2x)	1	ANDROSHCHUK 1988: 454	ut *Veronica longifolia* L.
Byelorussia	2n=34 (2x)	2	DZHUS & DMITRIEVA 2001: 145	ut *Veronica longifolia* L.
Byelorussia	2n=68 (4x)	6	DZHUS & DMITRIEVA 2001: 145	ut *Veronica longifolia* L.
Byelorussia	2n= ca. 70 (ca. 4x)	1	DZHUS & DMITRIEVA 2001: 145	ut *Veronica longifolia* L.

Byelorussia (Berezina R. basin)	2n=68 (4x)	1	PARFENOV & DMITRIEVA 1987: 67	ut *Veronica longifolia* L.
Russian Federation (Komi ASSR)	2n=34 (2x)	1	LAVRENKO et al. 1991 sec. GOLDBLATT & JOHNSON 1994: 207	ut *Veronica longifolia* L.
Russian Federation (Sankt-Peterburg)	n=34 (4x)	1	GRAZE 1935: 627	ut *Veronica longifolia* L.
Russian Federation (Tatarian ASSR)	2n=68 (4x)	2	MESHKOVA 1965 sec. AGAPOVA 1993: 358	ut *Veronica longifolia* L.
Russian Federation (Kolguev Island)	2n=ca. 68–70 (ca. 4x)	1	SOKOLOVSKAYA & STRELKOVA 1960: 372	ut *Veronica longifolia* var. *glabra* KOCH; this record might refer to *Pseudolysimachion longifolium* (L.) OPIZ s.str. (cf. TRÁVNÍČEK 2000a)
P. spurium				
Poland (Lublin Upland)	2n=34 (2x)	1	IZMAILOW 1991: 34–35	ut *Veronica paniculata* L. subsp. *paniculata*
Hungary (N of Debrecen, Hajduhadház)	n=17 (2x)	1	GRAZE 1933: 520, 522	ut *Veronica foliosa* WALDST. et KIT.
Bulgaria	2n=34 (2x)	1	PEEV sec. VAN LOON 1987: 200	ut *Veronica paniculata* L.
Bulgaria (distr. Silistra)	2n=68 (4x)	1	PEEV 1972: 500	ut *Veronica spuria* L. subsp. *spuria*
sine loco	n=17 (2x)	(1)	GRAZE 1933: 522	ut *Veronica spuria* L.
sine loco	n=17 (2x)	(1)	GRAZE 1933: 522	ut *Veronica foliosa* WALDST. et KIT.
sine loco	2n=34 (2x)	(1)	SIMONET 1934: 1153	ut *Veronica spuria* L.
sine loco	2n=34 (2x)	(1)	MESHKOVA 1965 sec. AGAPOVA 1993: 360	ut *Veronica spuria* L.
P. orchideum				
Austria (Lower Austria)	n=17 (2x)	1	FISCHER 1969: 438	ut *Pseudolysimachion spicatum* subsp. *orchideum* (CRANTZ) HARTL
Austria (Lower Austria)	2n=ca. 34 (ca. 2x)	2	FISCHER 1969: 438	ut *Pseudolysimachion spicatum* subsp. *orchideum* (CRANTZ) HARTL
Slovakia (Tríbeč Mts.)	2n=34 (2x)	1	VÁCHOVÁ 1974: 22	ut *Veronica spicata* subsp. *orchidea* (CRANTZ) HAYEK
Slovakia (Malé Karpaty Mts.)	2n=34 (2x)	1	VÁCHOVÁ & FERÁKOVÁ 1986: 59	ut *Pseudolysimachion orchideum* (CRANTZ) WRABER
Bulgaria	n=17 (2x)	1	GRAZE 1933: 524	ut *Veronica orchidea* CRANTZ
Bulgaria (distr. Varna)	2n=34 (2x)	1	PEEV 1972: 499	ut *Veronica orchidea* CRANTZ
Bulgaria (distr. Tolbuhin)	2n=34 (2x)	1	PEEV 1972: 500	ut *Veronica spicata* subsp. *bulgarica* D. PEEV; this record refers to *Pseudolysimachion orchideum* var. *bulgaricum* (PEEV) PEEV et M.A. FISCHER
Ukraine (distr. Beregovo)	2n=36 (ca. 2x)	1	ANDROSHCHUK 1988: 454	ut *Veronica orchidea* CRANTZ
sine loco	n=17 (2x)	(1)	GRAZE 1933: 523, 524	ut *Veronica orchidea* CRANTZ
sine loco	n=34 (4x)	(1)	GRAZE 1933: 631	ut *Veronica orchidea* CRANTZ
P. spicatum				
Great Britain	2n=ca. 68 (ca. 4x)	?	WALTERS 1954: 89	ut *Veronica spicata* L. and *V. hybrida* L.; the record refers probably to subsp. *spicatum*
Norway (S Norway, Baerum)	2n=68 (4x)	1	ENGELSKJON 1979: 29	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Finland (Ab)[1]	2n=ca. 62 (ca. 4x)	1	RAITANEN 1967: 471	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*

Finland (Ab)[1]	n=34 and 2n=68 (4x)	1	RAITANEN 1967: 471	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Finland (Ab, N)[1]	2n=68 (4x)	4	PELLINEN in UOTILA & PELLINEN 1985: 30; KUKKONEN 1986: 41	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Finland (Al)[1]	2n=ca. 68 (ca. 4x)	1	KUKKONEN 1986: 41	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Finland (Al)[1]	2n=68 (4x)	1	KUKKONEN 1986: 41	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Switzerland (Wallis, Visp)	n=17 (2x)	1	GRAZE 1933: 523, 524	ut *Veronica spicata* L.; ? the record refers to subsp. *spicatum*
Switzerland (Neuchâtel)	2n=34 (2x)	1	BRANDT 1953: 115	ut *Veronica spicata* L.; ? the record refers to subsp. *spicatum*
Germany (Würtenberk)	n=32–35 (ca. 4x)	1	HUBER 1927: 366	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Germany (Schleswig-Holstein)	n=34 (4x)	1	TISCHLER 1934: 15	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Austria (Lower Austria, Wien)	2n=68 (4x)	1	GRAZE 1933: 523, 524	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Austria (Burgenland)	n=ca. 34 (ca. 4x)	1	FISCHER 1969: 439	ut *Pseudolysimachion spicatum* (L.) OPIZ subsp. *spicatum*; the record refers probably to subsp. *spicatum*
Italy (Alpi Apuane)	2n=34 (2x)	1	GIORDANI et al. 1980: 328	ut *Veronica spicata* L.; the record refers probably to *Pseudolysimachion barrelieri* (ROEM. et SCHULT.) HOLUB – see also FISCHER 1982: 556.
Poland (distr. Krakow)	2n=34 (2x)	3	PRZYWARA 1982: 173	ut *Veronica spicata* L.; the record can refer to *Pseudolysimachion orchideum* – see TACIK & TRZCINSKA-TACIKOVA 1963: 297.
Poland (distr. Krakow)	2n=68 (4x)	2	PRZYWARA 1982: 173	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Slovakia (Podunajská nížina Lowland)	2n=68 (4x)	1	PALKOVÁ 1970: 24	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum*
Hungary (SE of Budapest, Ökeny)	2n=34 (2x)	1	KLIPHUIS 1977: 268	ut *Veronica spicata* L. subsp. *spicata*; the record requires revision
Hungary (N of Debrecen, Hajduhadház)	n=34 (4x)	1	GRAZE 1933: 523, 524	ut *Veronica spicata* L.; the record refers probably to subsp. *spicatum* or (?) to subsp. *fischeri*
Croatia (Adriatic coast, Novi Vinodolski)	2n=68 (4x)	1	NILSSON & LASSEN 1971: 275	ut *Veronica spicata* L.; the record requires revision
Bosnia (Hrasnica near Sarajevo)	2n=ca. 34 (ca. 2x)	1	FISCHER 1974: 38	ut *Pseudolysimachion pallens* (HOST) M.A. FISCH.; the record refers to subsp. *lanisepalum*
Ukraine (distr. Kyiv)	2n=36 (ca. 2x)	1	ANDROSHCHUK 1988: 455	ut *Veronica spicata* f. *pineticola*; the record requires revision
Ukraine (Crimea)	2n=18	1	ANDROSHCHUK 1988: 455	ut *Veronica viscosula* KLOKOV; very doubtful record
Ukraine (distr. Kyiv)	2n=17–21	1	ANDROSHCHUK 1988: 454	ut Veronica ×*psedoorchidea* (PACZ.) KLOKOV; very doubtful record
Ukraine (distr. Donetsk)	2n=18	1	ANDROSHCHUK 1988: 454	ut *Veronica maeotica* KLOKOV; very doubtful record
Ukraine (distr. Kyiv)	2n=18	1	ANDROSHCHUK 1988: 454	ut *Veronica paczoskiana* KLOKOV; very doubtful record
Ukraine (distr. Kiyv)	2n=18	1	ANDROSHCHUK 1988: 454	ut *Veronica* ×*pseudoorchidea* (PACZ.) KLOKOV; very doubtful record
Byelorussia (Berezina R. basin)	2n=68 (4x)	1	DMITRIEVA 1986: 27	ut *Veronica spicata* L.; the record might refer to subsp. *spicatum*

Byelorussia	2n=68 (4x)	5	DZHUS & DMITRIEVA 2001: 146	ut *Veronica incana* L.; the record refers probably to subsp. *spicatum*
Byelorussia	2n=68 (4x)	1	DZHUS & DMITRIEVA 2001: 146	ut *Veronica pseudoorchidea* (PACZ.) KLOKOV; the record refers to var. *pseudoorchideum* (PACZ.) TRÁVNÍČEK
Russian Federation (N Caucasus)	2n=56	1	MAGULAEV 1984: 516	ut *Veronica spicata* L.; doubtful record
Russian Federation (Tatarian ASSR)	2n=68 (4x)	1	MESHKOVA 1965 sec. AGAPOVA 1993: 360	ut *Veronica spicata* L.; the record requires revision
Russian Federation (Altai)	2n=34 (2x)	1	SOKOLOVSKAYA & STRELKOVA 1948: 193	ut *Veronica spicata* L.; the record refers probably to subsp. *porphyrianum*
Russian Federation (Altai)	2n=34 (2x)	1	ROSTOVTSEVA 1977: 1039	ut *Veronica spicata* L.; the record refers probably to subsp. *porphyrianum*
Russian Federation (Altai)	2n=34 (2x)	1	ROSTOVTSEVA et al. 1981: 219	ut *Veronica spicata* L.; the record refers probably to subsp. *porphyrianum*
sine loco	2n=34 (2x)	(?)	AFANASIEVA & MESHKOVA 1961: 255	ut *Veronica porphyriana* PAVLOV; probably adopted record (no reference given)
sine loco	2n=34 (2x)	(?)	TSVELEV 1981: 87	ut *Veronica porphyriana* PAVLOV; probably adopted record (no reference given)
sine loco	n=34 (4x)	(1)	GRAZE 1933: 522	ut *Veronica spicata* L.
sine loco	2n=64-68 (ca. 4x)	(1)	SIMONET 1934: 1153	ut *Veronica spicata* L.
sine loco	2n=68 (4x)	(1)	AFANASIEVA 1960 sec. AGAPOVA 1993: 360	ut *Veronica spicata* L.
sine loco	2n=68 (4x)	(1)	AFANASIEVA & MESHKOVA 1961: 249	ut *Veronica spicata* L.
P. incanum				
Slovakia (Východoslovenská nížina Lowland)	2n=68 (4x)	1	MÁJOVSKÝ & VÁCHOVÁ 1986: 64	ut *Pseudolysimachion incanum* (L.) HOLUB; the record refers to subsp. *pallens*
Byelorussia	2n=68 (4x)	1	DZHUS & DMITRIEVA 2001: 145	ut *Veronica incana* L.
Russian Federation (Yakutia)	2n=32 (ca. 2x)	1	ZHUKOVA et al. 1973: 1341	ut *Veronica incana* L.; the record refers probably to subsp. *incanum*
Russian Federation (Yakutia)	2n=34 (2x)	1	ZHUKOVA et al. 1977: 232	ut *Veronica incana* L.; the record refers probably to subsp. *incanum*
Russian Federation (Yakutia)	2n=34 (2x)	1	YURTSEV & ZHUKOVA 1982: 782	ut *Veronica incana* L.; the record refers probably to subsp. *incanum*
sine loco	n=34 (4x)	(1)	GRAZE 1933: 517, 529	ut *Veronica incana* L.
sine loco	2n=68 (4x)	(1)	AFANASIEVA 1960 sec. AGAPOVA 1993: 357	ut *Veronica incana* L.
sine loco	2n=68 (4x)	(1)	AFANASIEVA & MESHKOVA 1961: 249	ut *Veronica incana* L.
sine loco	2n=68 (4x)	(1)	MESHKOVA 1965 sec. AGAPOVA 1993: 358	ut *Veronica incana* L.
sine loco	2n > 60	(1)	ZHUKOVA 1967 sec. AGAPOVA 1993: 357	ut *Veronica incana* L.