Squills (*Scilla* s.lat., Hyacinthaceae) in the flora of the Czech Republic, with taxonomical notes on Central-European squill populations

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TRÁVNÍČEK B., DUCHOSLAV M., ŠARHANOVÁ P. & ŠAFÁŘOVÁ L. 2009: Squills (*Scilla* s.lat., Hyacinthaceae) in the flora of the Czech Republic, with taxonomical notes on Central-European squill populations. *Acta Musei Moraviae, Scientiae biologicae* (Brno) **94:** 157–205. – The division of the genus *Scilla* L. (*sensu latissimo*) into several narrowly defined genera is discussed. These narrow genera are, with exceptions, accepted; with reference to this, a few new nomenclatural combinations are proposed: *Nectaroscilla littardierei* (Breistr.) Trávníček, *Othocallis amoena* (L.) Trávníček, *O. siberica* subsp. *armena* (Grossh.) Trávníček, subsp. *caucasica* (Miscz.) Trávníček and subsp. *otschiauriae* (Mordak) Trávníček. The division of the genus *Scilla* s.str. into two sections is proposed: (1) sect. *Scilla*, comprising all species of the *S. bifolia* group in the broader sense, and (2) sect. *Chionodoxa* (Boiss.) Trávníček, which contains taxa formerly included in the genus *Chionodoxa* Boiss. The first section consists of taxa native to the Czech Republic, the second of solely alien and cultivated taxa. A spontaneous hybrid between *S. bifolia* subsp. *bifolia* from sect. *Scilla* and a species from the group of *S. luciliae* from sect. *Chionodoxa* was found in a park in the Czech Republic. A new taxonomic concept of the *S. bifolia* group in the Czech Republic, central Europe, and adjacent parts of the Carpathians and the Pannonian Plain, is proposed. Three species are recognized: the diploid (2n = 18, 2x), Carpathian *S. kladnii* Schur (= *S. subtriphylla* Schur), the diploid (2n = 18, 2x), predominantly Pannonian *S. vindobonensis* Speta and the widely distributed *S. bifolia* L. The microspecies *S. buekkensis* Speta, *S. drunensis* (Speta) Speta, *S. laxa* Schur and *S. spetana* Kereszty are co-opted as well as *S. bifolia* s.str. into the latter species. Three relatively widely distributed and vicariant subspecies are recognized within *S. bifolia*: (1) subsp. *bifolia* from the Alps and adjacent parts of Europe, comprising *S. bifolia* s.str. and (peri-)Alpine populations of *S. drunensis*; (2) subsp. *buekkensis* (Speta) Soó from the Carpathians and the Matricum, comprising *S. buekkensis*, *S. laxa*, and Carpathian populations formerly classified as *S. drunensis*; and (3) subsp. *spetana* (Kereszty) Trávníček from the Pannonian Plain, comprising *S. spetana* and also some Pannonian populations formerly classified as *S. laxa* and *S. drunensis*. A fourth subspecies is described herein: subsp. *rara* Trávníček, endemic to a single locality in south-western Moravia in the Czech Republic. Subsp. *bifolia* comprises diploid populations (2n = 18, 2x) treated as var. *bifolia* and tetraploid ones (2n = 36, 4x) treated as var. *drunensis* (Speta) Trávníček and the stenoendemic var. *bohemica* Trávníček, newly described from Bohemia. Populations of subsp. *buekkensis* and subsp. *rara* are tetraploid (2n = 36, 4x). Populations of subsp. *spetana* are hexaploid (2n = 54, 6x), and may be divided morphologically into two varieties: var. *spetana* and var. *magnomoravica* Trávníček, which is known from only a single locality in South Moravia. In subpopulations of the subspecies mentioned, there is a significant proportion of individuals morphologically strongly converging towards other subspecies of *S. bifolia*, and plants with an aberrant ploidy level sometimes occur (except in subsp. *rara*). Therefore, all four subspecies can be identified only at the population level and not at the level of individual plants.

Keywords. *Scilla* s.lat., *Scilla bifolia* group, taxonomy, nomenclature, variability, distribution, the Czech Republic, Central Europe

Introduction

Populations of native squills, as well as cultivated alien species that run wild in favourable circumstances, can be found in the Czech Republic. In older floras (Čelakovský 1887, Dostál 1948–1950), only a single native species is mentioned: *Scilla bifolia* L. An additional few escaped species are reported in literature: *S. amoena* L., *S. siberica* Haw. and *S. puschkinioides* Regel (Dostál 1948–1950, 1989). Among the close relatives, the literature (Dostál l.c.) also mentions the rarer escaped species *Chionodoxa luciliae* Boiss.

Since the 1970's, considerable attention to the research of squills in Europe and W Asia has been paid by F. Speta, J. Greilhuber, Z. Kereszty and certain others (Mordak 1970, 1971; Speta 1971, 1972, 1974, 1976a,b,c, 1977a,b, 1979, 1981a,b, 1982, 1987, 1998a,b; Greilhuber & Speta 1977, 1978, 1985; Greilhuber 1978, 1979, 1982; Greilhuber *et al.* 1981; Svoma 1981; Deumling & Greilhuber 1982; Meikle 1984, Kereszty & Podani 1984; Kereszty & Szilágyi 1984, 1986; Greilhuber & Strehl 1985; Kereszty 1987, 1988a,b, 1993, 1995; Kereszty *et al.* 1987; Svoma & Greilhuber 1988, 1989; Szilágyi & Kereszty 1988; Kereszty & Gondár 1990; Berger & Greilhuber 1993; Kricsfalusy *et al.* 1993; Trávníček 1993, 1996, 2002; Adler & Speta 1994; Kricsfalusy & Vajnagi 1994; Ebert *et al.* 1996; Pfosser & Speta 1999; Kochjarová *et al.* 2004, 2005; Kochjarová 2005). During this period, thanks to the effort of these researchers, a vast number of new findings have accumulated that needed to be considered in the taxonomic-chorological approach to the genus *Scilla* s.lat. for the eighth volume of "Flora of the Czech Republic", a task for the primary author of this study. Some taxonomic and nomenclatural problems were, of course, encountered.

The first author of this study has been addressing native populations of the genus *Scilla* for some time. His pilot study of squills in the wild and in public herbaria in the Czech Republic and Slovakia extended upon findings published by F. Speta and Z. Kereszty (see above). The study was based on a karyological analysis of selected Czech and Slovak populations (cf. Kulová 1991) and finally led to some preliminary papers (Trávníček 1993, 1996, 2002). It is evident from these studies that native populations of *Scilla* in the Czech Republic can be divided into three separate stabilized taxa worthy of species rank, under the names *S. kladnii* Schur, *S. vindobonensis* Speta and *S. drunensis* (Speta) Speta. From the beginning, the taxonomic-chorological approach to the former two species in the Czech Republic appeared quite straightforward. However, the populations temporarily grouped within the name *S. drunensis* exhibited some variation, conspicuous in morphological and partially in karyological characteristics. It was evident that further focused research, dealing with a wider geographical area than that of the Czech Republic, would have to be conducted (cf. Trávníček 1996). This research is now under way and is primarily focused on the morphometric, karyological and geographical characteristics of populations grouped under the names *S. bifolia* L., *S. buekkensis* Speta, *S. drunensis*, *S. laxa* Schur and *S. spetana* Kereszty (see Šarhanová 2008). These taxa make up what is known as the "narrow group" of *Scilla bifolia*, that is, excluding *S. kladnii* and *S. vindobonensis*. Although this research is not yet complete, it

has yielded some results of taxonomic significance that must be considered in the approach to this group for "Flora of the Czech Republic" (B. Trávníček in prep.). In addition, it transpires that the Czech Republic is a region with great variation within the narrow group of *S. bifolia* in Central European terms.

Alien species of the genus *Scilla* (*sensu latissimo*) are, albeit not to the extent of the native taxa, a notable part of the Czech flora, and should also, therefore, be mentioned in "Flora of the Czech Republic". These species originate in various regions, especially southern Europe and south-western Asia and are not closely related to the native species. A detailed analysis of the taxonomic relationships within genus *Scilla* s.lat., originally understood as wide, has been assembled over time in a number of works by F. Speta (SPETA 1971, 1976a, 1998a, 1998b; PFOSSER & SPETA 1999), leading to a proposed classification based on an understanding of all the fundamental groups of squills as separate narrow genera. According to this classification, species native to the Czech Republic remain in the narrowly defined genus *Scilla* (*sensu strictissimo*). Of the species alien to the Czech Republic, the *Chionodoxa luciliae* group has been co-opted into the genus thus defined. In contrast, all other introduced and occasional escaped species in the Czech Republic belong, according to this new generic taxonomic concept, to separate genera (see below).

The present study is primarily dedicated to species native to the Czech Republic but, from the standpoint of taxonomy, also addresses species and populations of the genus *Scilla* s.lat. outside its borders, chiefly in adjacent Central European countries. The main objective of the present paper is to convey the results of research into squills with reference to the approach to this group for "Flora of the Czech Republic" and, in particular, to publish those results that cannot be placed within the framework of "Flora".

Material and methods

The study of squills concentrated largely on populations in the Czech Republic. Between 1985 and 2006, more than 50% of all known Czech localities recorded in public herbaria and in literature were visited. Approximately 95% of extant local populations of the narrow group of *S. bifolia* (i.e. excl. *S. kladnii* and *S. vindobonensis*) were studied. Live material was collected from selected populations for cultivation in a garden and for archiving in a herbarium; vouchers are deposited in OL (for abbreviations of collections see HOLMGREN *et al.* 1990).

Morphometric investigation was conducted on only live material, partially in the wild and partially under cultivation. In the vast majority of populations, at least 25 individual plants were measured. Absolutely minute specimens, usually those with 1–3 blossoms, were excluded from the morphometric analysis; some of them were juvenile specimens, others growing in extremely unfavourable microhabitats. Only a preliminary morphometric study involving a limited number of populations was carried out for *S. kladnii* and *S. vindobonensis*. For the narrow group of *S. bifolia*, plants from 90% of the localities visited in the Czech Republic (13 altogether) were measured, together with selected populations from other parts of Central Europe (Bavaria, Austria, Slovakia,

Hungary, NE Croatia and Romania; a total of 42). Plants included in the morphometric study were also analysed for ploidy using flow cytometry. The morphometric and karyological study of the narrow group of *S. bifolia* is only partly complete (Šarhanová 2008), and a more detailed assessment of its results will be published elsewhere (B. Trávníček *et al.*, in prep.).

The values of quantitative characters given in the descriptions in the present paper come from measurements performed on plants from the Czech Republic. The length of the inflorescence is included in the length of the above-ground part of the scape. Morphometric characteristics of blossoms do not apply to the uppermost blossoms of many-flowered individuals, which often show lower values for all quantitative characters. The elaiosome is not included in the dimensions of seeds. The values of morphometric characters apply to living plants; these values are usually 10–20 % lower in herbarium specimens.

The distribution in the Czech Republic is given only for taxa native to the country and is usually described only in general terms by a list of phytogeographical regions (*sensu* Skalický 1988) from which they were recorded. This summary of distribution is essentially based on the study of squills in the main Czech public herbaria (primarily BRNM, BRNU, GM, LIT, MMI, MP, OL, OLM, OP, PR, PRC, ROZ, VM and ZMT; see Holmgren *et al.* 1990). A more detailed summary of the localities of these taxa as well as localities of naturalized species will be published elsewhere (B. Trávníček, in prep.) along with more detailed notes on the ecological and coenological ties of these taxa.

Results and discussion

Notes on the generic treatment of squills

During work on the approach to squills for "Flora of the Czech Republic" (B. Trávníček, in prep.), the taxonomic concept of narrow genera was generally adopted. It is based upon all the many findings gathered in the studies of F. Speta and his co-workers (Speta 1972, 1976a, 1981a, 1982, 1987, 1998a,b; Greilhuber & Speta 1978, Greilhuber 1979, 1982; Greilhuber *et al.* 1981, Svoma 1981, Svoma & Greilhuber 1988, 1989; Pfosser & Speta 1999). The keystone of this concept is the exclusion of numerous species from the widely understood genus *Scilla* s.lat. and their placement into several separate genera while co-opting the genus *Chionodoxa*, whose separate position was broadly accepted in the past, into *Scilla* s.str. (see Pfosser & Speta 1999, Speta 1998a,b). This new taxonomic approach is based upon long-term, detailed study of morphological and anatomical (Speta 1972, 1976a, 1981a, 1982, 1987), karyological (Greilhuber 1979, 1982; Greilhuber *et al.* 1981, Greilhuber & Speta 1978), embryological (Svoma 1981, Svoma & Greilhuber 1988, 1989) and molecular (Pfosser & Speta 1999) characters of many species of squill, partially including other groups of the *Hyacinthaceae*.

The inclusion of the genus *Chionodoxa* in the genus *Scilla* s.str. appears entirely justified. Not only is it supported by unity in many of their important taxonomic characters (e.g. number and shape of the scapes, perhaps even the number of leaves;

character of the inflorescence, including bracts; shape and colouring of pistils; persistence of the perianth on young fruit; structure of the testa; and type of elaiosome formation), but also by correspondence in karyological properties and, finally, the fact that members of *Chionodoxa* can easily hybridize with some species traditionally placed in the genus *Scilla* s.str. (cf. SPETA 1971, 1972, 1976a, 1981a; GREILHUBER 1979, 1982; GREILHUBER *et al.* 1981). In contrast, its exclusion from the genus *Scilla* was based only on differences in the structure of the perianth and stamens coalescent with it (see also below).

It is still necessary to discuss the transfer of the many species formerly classified in the genus *Scilla* s.lat. into several separate genera and subject it to further investigation. STEDJE (2001) criticizes Speta's concept of narrow genera in the family *Hyacinthaceae*, largely with reference to South African (Sub-Saharan) taxa but acknowledges its usefulness in Mediterranean and European contexts. This author generally criticizes Speta's extremely narrow concept of some genera, especially those that are monotypic or oligotypic. Although Speta's concept (PFOSSER & SPETA 1999, SPETA 1998a, b) is based on an analysis of many different kinds of characters (see above), molecular characters (in plastid DNA) evaluated by strictly cladistic methods apparently provide the decisive criteria (cf. PFOSSER & SPETA 1999), requiring the establishment of new, very narrowly defined genera. That is to say, the molecular cladistic approach taken (PFOSSER & SPETA 1999) often leaves no another option if some genera traditionally defined on the basis of important structural morphological characters are to be retained (e.g. *Muscari* versus *Scilla* or *Hyacinthus* versus *Scilla*). It must also be noted that the segregation of the species traditionally placed in the genus *Scilla* s.lat. into three distinct clades (i.e. the "*Scilla* clade", the "*Fessia* clade" and the "*Hyacinthoides* clade"), based on molecular characters (PFOSSER & SPETA l.c.) is, to a certain extent, in agreement with the division outlined earlier, which is based upon morphology, embryology and karyology. In particular, the distant relationship between the species newly placed into the genera *Othocallis* Salisb., *Fessia* Speta, and *Prospero* Salisb. that belong to the "*Fessia* clade", *Hyacinthoides* Med. and *Oncostema* Raf. (incl. *Tractema* Raf.) that are members of the "*Hyacinthoides* clade" and species of the genus *Scilla* L. s.str., falling into the "*Scilla* clade" is confirmed once again. The exclusion of these groups from the genus *Scilla* s.str. thus seems already well-founded and therefore acceptable. Still, the relationships between some genera within the three main clades remain problematic. They are still unclear in some cases, and it is possible that further molecular analyses will provide somewhat different insight. In such cases, the approach to classification based largely on strict cladistic reliance on molecular characters (moreover, using a single method; PFOSSER & SPETA 1999) does not seem entirely appropriate (see also STACE 2005). Other characters, especially the morphological, anatomical and karyological, should be considered at least equally important for the delimitation of these groups (genera). It is also imperative to take account of the geographical distribution of species. This applies to relationships among some very narrowly defined (oligotypic) genera and the "main" genera within a single clade, for example, *Pfosseria* Speta 1998 (with a single species in south-eastern Europe) and *Othocallis* Salisb. 1866 (with more species in eastern and

south-eastern Europe and south-western Asia) within the *Fessia* clade. The close relationship of the species *Pfosseria bithynica* (Boiss.) Speta with species of the genus *Othocallis* is suggested by some earlier studies based on morphological and karyological characters (Greilhuber 1982, Greilhuber & Speta 1978, Speta 1971, 1972, 1981a; Svoma & Greilhuber 1989). The situation is partly similar in the case of the relationship between the genera *Schnarfia* Speta 1998 (with two species in Albania and Greece) and *Scilla* L. 1753 s.str. (with about 30 species growing from France, northern Spain and Central Europe to Asia Minor and the Caucasus; see also Greilhuber 1979, 1982; Greilhuber *et al.* 1981: 258, Svoma 1981: 114). This second case is complicated by the insufficiently explained relationship between the species of these two genera and the species of the traditionally-distinguished genus *Muscari* Mill. 1754, with which they share a clade, i.e. the "*Scilla* clade" (Pfosser & Speta 1999).

Species of oligotypic genera such as *Chouardia* Speta 1998 (containing two species from south-eastern Europe) and *Nectaroscilla* Parl. 1854 (1–2 species from the eastern Mediterranean) also belong to the "*Scilla* clade", and are prominently close to each other in their important morphological characters, but also notably different to species of the genus *Scilla* s.str.: bulb scales perennial, not coalescent; scape usually single, ± round, developing later than leaves, erect even during the fruiting period; leaves (2–)3–10(–12); racemes dense, with 20–150 flowers; bud peduncles erect; flower peduncles slightly erecto-patent to patent; bracts and bracteoles minute, about 1 mm long, tepals free, stellate, only 4–7 mm long, after anthesis drying on maturing fruit; anthers purple; ovaries purple-blue, with style only 1–2(–4) mm long; only two side-by-side ovules per locule; capsule pergamentaceous; seeds dark, without elaiosome. The morphological differences between the genera *Chouardia* and *Nectaroscilla* mainly concern the length and shape of the flower peduncles (i.e. 30–80 cm long and smooth in *Nectaroscilla*, whereas 20–30 mm long and sulcate in *Chouardia*), the length of inflorescence (longer in *Nectaroscilla*), number of flowers, bulb size (larger in *Nectaroscilla*), leaf indument (shortly ciliate at the edge in *Nectaroscilla*, absent in *Chouardia*) and the type of germination (cotyledon epigeal in *Nectaroscilla*, short and hypogeal in *Chouardia*; cf. Speta 1981a: 27, 1998a: 270). These differences are not too significant taxonomically. Not even the dissimilar germination constitutes sufficient support for the separation of the two genera, as both types of germination are present within the narrowly defined genus *Fessia*: cotyledon short and hypogeal in *F. greilhuberi* (Speta) Speta and epigeal in the remaining species. Considering these facts, it appears more suitable to merge the two genera into one: *Nectaroscilla* Parl. (Nuovi Gen. Sp. Monocot. 26, 1854). The southern European species *Chouardia littardierei* (Breistr.) Speta (syn.: *Scilla pratensis* Kit. in W. et K. Pl. Rar. Hung. 2: 207, t. 189, 1804, nom. illeg., non J. P. Bergeret 1803), occasionally planted in Central Europe (see also Adler & Speta 1994) therefore has to bear the name *Nectaroscilla littardierei* (Breistr.) Trávníček (see Appendix).

From the perspective of important morphological characters and the geographical distribution of the species concerned, the position of the genus *Tractema* Raf. 1837 (about six species from western Europe to north-western Africa) as separate from the genus *Oncostema* Raf. 1837 (about ten species, from the south-western Mediterranean to

southern Italy, northern Africa and the Near East) also seems superfluous. Both belong to the "*Hyacinthoides* clade" and correspond in several important taxonomic characters (Speta 1998a, b). In this case the division into two genera is not necessarily required even by cladograms based on molecular characters (Pfosser & Speta 1999: 858, 861). Therefore, Speta's earlier concept (Speta 1987), which merges the two genera into one (i.e. *Oncostema* Raf. with two subgenera: subg. *Oncostema* and subg. *Petranthe* (Salisb.) Speta), seems more appropriate. An analogy may be found in the genus *Hyacinthoides* Med. 1791 in which two morphologically relatively distinct groups are also considered as subgenera (i.e. subg. *Hyacinthoides* and subg. *Somera* (Salisb.) Speta) of a single genus (see Speta 1987, Pfosser & Speta 1999).

The relationship between the genera *Fessia* Speta 1998 and *Othocallis* Salisb. 1866, both belonging to a single clade ("*Fessia*"), can also be regarded as very close (Pfosser & Speta 1999). This requires further research in order to shed light on the relationship between the two genera and their ties to species of the genus *Hyacinthus* L. 1753 belonging to the same clade and bearing the nomenclaturally oldest generic name.

Notes on the treatment of the genus *Othocallis*

The position of the genus *Othocallis* as separate from the genus *Scilla* s.str. is highly acceptable (see above) and is also, therefore, adopted in the approach to squills for "Flora of the Czech Republic" (B. Trávníček, in prep.). Speta (1998b) transferred most of the relevant species from the genus *Scilla* into the genus *Othocallis*. Through mere oversight, the nomenclatural transfer of the species *Scilla amoena* L., once cultivated in the Czech Republic and an occasional escaped, has not yet been performed. Even the author of the name *Othocallis* Salisbury (1866: 28) failed to transfer it, as he did not explicitly associate the epithet "*amoena*" with the generic name "*Othocallis*" (see Art 33.1 of ICBN). Not even Speta (1998b: 111), who omitted to cite the basionym (see Art 33.4 of ICBN), managed to transfer the species. Formally, this transfer is therefore proposed in this study (see Appendix).

Sometimes naturalized in the Czech Republic, the most commonly planted species of the genus *Othocallis* is *O. siberica* (Haw.) Speta. This species is addressed in two different ways in the literature. The narrow concept is advocated by Speta (1998b), whereas Mordak (1971, 1984) leans towards a wider concept in her reviews, according to which the species also comprises (but within the genus *Scilla*) the closely related microspecies *S. armena* Grossh., *S. caucasica* Miscz. and *S. otschiauriae* Mordak which she considers subspecies of the species *S. siberica* Haw. Because these microspecies differ from *Othocallis siberica* only in taxonomically less important characters and their areas lie in mutual proximity (Mordak 1971: 1447), and based on the study of a number of vouchers of these taxa, the wider concept of the species *O. siberica* is adopted in the manuscript of "Flora of the Czech Republic" (B. Trávníček, in prep.). As well as the type subspecies, the species thus contains subsp. *armena* (Grossh.) Trávníček, subsp. *caucasica* (Miscz.) Trávníček and subsp. *otschiauriae* (Mordak) Trávníček (see Appendix).

Infrageneric classification of the genus *Scilla* L. s.str.

The genus *Scilla* s.str. is represented in the flora of the Czech Republic both by native species of the wider group of *S. bifolia* and by taxa from the group of *S. luciliae* (= *Chionodoxa luciliae* group) that are cultivated and occasionally run wild. The mutual taxonomic relationships of these two morphologically easily distinguishable groups have been addressed in rather inconsistent fashion. In older literature, the *S. luciliae* group was constantly placed in the separate genus *Chionodoxa* Boiss., which is characterized by tepals fused at base, coalescent with flattened, usually white stamens that completely cover the ovary and bear vertical anthers with yellow pollen. This approach persists to this day, especially in gardening literature. Lately, determination manuals increasingly prefer to place this group in the genus *Scilla* (e.g. ADLER & SPETA 1994, TRÁVNÍČEK 2002, ROTHMALER *et al.* 2005). Further, in the approach to squills for "Flora of the Czech Republic" (B. Trávníček, in prep.), the placement of this group into the genus *Scilla*, already proposed by SPETA (1971), is adopted (see also above). SPETA (1976a) further proposed that the species of the original genus *Chionodoxa* should be included in the genus *Scilla* as a separate series, ser. *Chionodoxa* (Boiss.) Speta. The relationships between the species within the genus *Scilla* s.str. were later studied, largely employing karyological methods (especially nuclear DNA content and chromosome structure; *vide* GREILHUBER & SPETA 1977, GREILHUBER 1978, 1979; GREILHUBER *et al.* 1981). These studies arrived at the conclusion that species of ser. *Chionodoxa* are closest in nuclear DNA content to species of the *Scilla nivalis* group, despite notable differences in flower structure (tepals free to base; stamens narrow, blue, not covering the ovary; anthers ± horizontal, usually with blue-grey pollen). By contrast, species of the *S. nivalis* group correspond in flower structure with the rest of the species of the genus *Scilla* s.str., to which they are also profoundly similar in most other morphological characters. However, it has been found that, at well as exhibiting a similar nuclear DNA content, species of ser. *Chionodoxa* also correspond with species of the *S. nivalis* group in the colour of mature seeds, which are black, unlike the remaining species of the genus *Scilla* with seeds coloured from yellowish to dark brown. All this apparently led SPETA (1981a) to propose his intrageneric division of the genus *Scilla* s.str., primarily based on the seed colour of individual species. He placed the species with mainly paler seeds, which usually have a higher nuclear DNA content, into sect. *Luteoscilla* Speta, assigned the species with dark brown seeds, with intermediate nuclear DNA content, to sect. *Scilla* (which contains the type species of the genus, i.e. *S. bifolia* L.) and finally classified species with black seeds and a predominantly low nuclear DNA content as sect. *Nigriscilla* Speta. Only within the last group, on the basis of differences in flower structure, are species of ser. *Nivales* Speta (= *S. nivalis* group) and ser. *Chionodoxa* distinguished. Species with a high nuclear DNA content are thought to be ancestral in evolutionary terms; species with a low content are considered derived (GREILHUBER 1979, 1982; GREILHUBER *et al.* 1981).

Seed colour, as well as nuclear DNA content, in the genus *Scilla* s.str. is relatively variable, which poses a considerable problem; moreover, these traits do not always completely comply with the principles outlined above. For example, *S. kladnii* has darker

seeds (even brown when dry) than *S. vindobonensis* (with dry seeds ± yellowish, straw-coloured), even though both species have a high nuclear DNA content (see Table 1) and are placed together in sect. *Luteoscilla*. The Turkish *S. decidua* Speta with grey straw-coloured seeds (Speta 1977a: 66) and a nuclear DNA content nearing that of species of sect. *Scilla* (Table 1), which usually have dark-brown seeds, is placed in this section. The nuclear DNA content of *S. bulgarica* (see Table 1), classified as a member of sect. *Luteoscilla* because of its seed colour (see Speta 1981a), falls within the range of sect. *Scilla*. Because of the black colour of their seeds – and other morphological characters typical of the *S. nivalis* group – the species *S. longistylosa* Speta, *S. pneumonanthe* Speta, *S. reuteri* Speta and *S. subnivalis* (Halácsy) Speta are placed into sect. *Nigriscilla* (ser. *Nivales*) although they rank among taxa of sect. *Scilla* (Table 1) in terms of nuclear DNA content. There is a small difference between the nuclear DNA content of taxa from sect. *Scilla* and the "standard" taxa of sect. *Nigriscilla*. This difference is smaller than the difference between some species within sect. *Luteoscilla* (Table 1). The notable homogeneity of nuclear DNA content within sect. *Scilla* loses its information value for taxonomy when the whole group is considered as single variable species (i.e. *S. bifolia*), as is proposed in the present study (see below). Differences in seed colour can be found even among populations within narrowly defined taxa: for example, in the tetraploid cytotype of the narrow group of *S. bifolia* treated, according to the narrow species concept, as the separate species *S. drunensis*, one Bohemian population (classified in the present paper as *S. bifolia* subsp. *bifolia* var. *bohemica*; see below) differed in having paler seeds than other tetraploid populations studied in the Czech Republic. In colour, they rather approach *S. kladnii* from sect. *Luteoscilla* (see Figs 2c and 6b). A similarly appreciable difference in nuclear DNA content has also been found within the narrowly defined species *S. bifolia* s.str.: from 5.5 pg (see Greilhuber 1979: 267) to 6.41 pg (see Greilhuber & Speta 1985: 436). An even larger range of values of nuclear DNA content has been revealed in the single species *P. autumnale* (L.) Speta (within a single, diploid, ploidy level) of the related genus *Prospero*: from 4.26 pg to 7.50 pg (Ebert *et al.* 1996). In contrast, the nuclear DNA content in *Othocallis*, another related genus, is barely in agreement with the grouping based on morphological and other karyological characters. *Othocallis mordakiae* (Speta) Speta, placed according to these characters in the *O. siberica* group, is closer to *O. amoena* and *O. ingridae* (Speta) Speta in its nuclear DNA content (25.3 pg) from the *O. amoena* group (with nuclear DNA content between 23.3 and 24.5 pg) than to the "fundamental" species of the group, that is, *O. siberica* (with nuclear DNA between 31.9 and 32.0 pg). *O. mischtschenkoana* (Grossh.) Speta from the *O. mischtschenkoana* group, which is – from a morphological standpoint as well as from that of chromosome structure – isolated from the species of the other groups under study, is fairly close in nuclear DNA (21.6 pg) to species of the *O. amoena* group (cf. Greilhuber & Speta 1978, Greilhuber *et al.* 1981, Deumling & Greilhuber 1982). The values of nuclear DNA within the genus *Scilla* s.str. are not related to heterochromatin content in any simple way (Greilhuber 1979, 1982, Greilhuber *et al.* 1981), type of embryo sac (Greilhuber *et al.* 1981, Svoma 1981, Greilhuber 1982) or plastid DNA characters (Pfosser & Speta 1999: 858, 861).

Sections (series) Species	Chromosome number – 2n (ploidy level)	DNA content 1 C value (pg) (x-level)	References
Sect. *Luteoscilla*			
S. *vindobonensis* Speta	18 (2x)	9.4	Greilhuber 1979: 271
S. *vindobonensis* Speta	18 (2x)	9.32	Greilhuber & Speta 1985: 436
S. *voethorum* Speta	18 (2x)	9.1	Greilhuber 1979: 271
S. *kladnii* Schur	18 (2x)	8.6	Greilhuber 1979: 271
S. *kladnii* Schur	18 (2x)	8.51	Greilhuber & Speta 1985: 436
S. *resslii* Speta	18 (2x)	7.6	Greilhuber 1979: 271
S. *taurica* (Regel) Fuss	18 (2x)	7.3	Greilhuber et al. 1981: 254
S. *decidua* Speta	18 (2x)	7.1	Greilhuber 1979: 271
S. *bulgarica* Speta	18 (2x)	5.14	Greilhuber & Speta 1985: 436
Sect. *Scilla*			
S. *bifolia* L. (s.str.)[1]	18 (2x)	6.28	Greilhuber & Speta 1985: 436
S. *bifolia* L. (s.str.)[2]	18 (2x)	5.75	Greilhuber & Speta 1985: 436
S. *bifolia* L. (s.str.)	18 (2x)	5.7	Greilhuber 1979: 271
S. *buekkensis* Speta	36 (4x)	6.0	Greilhuber 1979: 271
S. *drunensis* (Speta) Speta (excl. S. *buekkensis*)	36 (4x)	5.9	Greilhuber 1979: 271
S. *drunensis* (Speta) Speta (incl. S. *buekkensis*)	36 (4x)	5.69	Greilhuber & Speta 1985: 436
S. *laxa* Schur	36 (4x)	5.50	Greilhuber & Speta 1985: 436
S. *laxa* Schur[3]	54 (6x)	5.40	Greilhuber & Speta 1985: 436
S. *laxa* Schur	36 (4x)	5.2	Greilhuber 1979: 271
S. *spetana* Kereszty[4]	54 (6x)	5.02	Greilhuber & Speta 1985: 436
Sect. *Nigriscilla* – ser. *Nivales*			
S. *reuteri* Speta	36 (4x)	5.4	Greilhuber et al. 1981: 254
S. *longistylosa* Speta	18 (2x)	5.3	Greilhuber et al. 1981: 254
S. *pneumonanthe* Speta	54 (6x)	5.3	Greilhuber 1979: 271
S. *subnivalis* (Halacsy) Speta	18 (2x)	5.3	Greilhuber et al. 1981: 254
S. *nivalis* Boiss.	18 (2x)	4.4	Greilhuber et al. 1981: 254
S. *nivalis* Boiss.	18 (2x)	4.1	Greilhuber 1979: 271
S. *xanthandra* C. Koch	18 (2x)	4.3	Greilhuber 1979: 271
Sect. *Nigriscilla* – ser. *Chionodoxa*			
S. *tmoli* (Whittall) Speta	18 (2x)	4.7	Greilhuber 1979: 271
S. *siehei* (Stapf) Speta	18 (2x)	4.5	Greilhuber 1979: 271
S. *luciliae* (Boiss.) Speta	18 (2x)	4.3	Greilhuber 1979: 271
S. *nana* (J.A. et J.H.Schultes) Speta	18 (2x)	4.3	Greilhuber 1979: 271
S. *sardensis* (Barr et Sugden) Speta	18 (2x)	4.2	Greilhuber 1979: 271
S. *albescens* Speta	18 (2x)	3.8	Greilhuber 1979: 271

Table 1. Values of nuclear DNA content (average values, calculated for the basic chromosome set – x) in species of the genus *Scilla* s.str. and their assignment to sections *sensu* Speta (1981a); taken from works cited in the table.

[1] Plants from the northern boundary of the distribution area of *S. bifolia*, i.e. eastern Germany (cf. Greilhuber & Speta 1985).

[2] Plants from Lower Austria and southern Italy (cf. Greilhuber & Speta 1985).

[3] Mentioned under the name `*Scilla* sp.' in the work cited (Greilhuber & Speta 1985: 436), but plants from the given locality are classified as *S. laxa* in studies between 1981 and 1982 (Speta 1981a: 44, 1982: 8).

[4] Mentioned under the name `*Scilla* sp.' in the work cited (Greilhuber & Speta 1985: 436), but plants from both localities cited in the study were later treated as the species *S. spetana* (Kereszty 1987, Kereszty *et al.* 1987, Adler & Speta 1994: 896).

It stems from the facts above that characters involving seed colour or nuclear DNA content can hardly be considered main criteria for classification, although they undoubtedly have their information value for the taxonomic approach to squills. Therefore, the intrageneric classification of the genus *Scilla* of the three sections discussed above (Speta 1981a) appears problematic, insufficiently stable and also somewhat impractical. However, it is possible to classify the species of the genus *Scilla* s.str., using distinctive morphological characters in flowers, into two well-defined groups that do not vary substantially in terms of morphology, facilitating the classification of all known species of the genus into one of these two groups in a sufficiently obvious way. The characters concerned are those on the basis of which the genus *Chionodoxa* (see also above) is defined as against the genus *Scilla*. These characters are concisely arranged in the following key, which at the same time provides indications for the assignation of species of the genus *Scilla* s.str. to one of the two groups proposed, which herein bear the taxonomic rank of section.

1a Tepals free almost to base; filaments standing apart, blue-purple (white in albinos), free almost to base, narrow, linear, subuliform to narrowly lanceolate (rarely broadly lanceolate), acute; anthers usually blue-purple, ± horizontal during anthesis, markedly apart from filaments, with anther lobes rounded on both sides; pollen usually pale blue-grey; pistil easily visible between stamens ....… **sect. *Scilla***

1b Tepals coalescent at base, coalescent section comprising 15%–40% of their total length; filaments erect to mutually inclined, white (rarely blue in upper section), coalescent with perianth in bottom half, broad, broadly taeniform (rarely lanceolate), rounded at end (rarely ± acute); anthers yellow, rarely blue, vertical even during anthesis, partly appressed to filament, with anther lobes pointed on both sides; pollen pale yellow; pistil hidden behind stamens ....
.... **sect. *Chionodoxa* (Boiss.) Trávníček** (see Appendix)

Although it cannot be proved that both the above sections are monophyletic (especially in the narrow, cladistic sense), the same may be said of extant findings about the sections proposed by Speta (1981a). However, from the standpoint of practicality, the intrageneric classification of the genus *Scilla* s.str. into two morphologically easily distinguishable groups proposed above is notably more lucid and usable – and from a non-cladistic standpoint undoubtedly more natural. This approach is also therefore preferred in the approach to the genus *Scilla* for "Flora of the Czech Republic" (B. Trávníček, in prep.). As far as Central European species of the genus are concerned, this classification also resolves the somewhat paradoxical position in which two morphologically really close species, *S. vindobonensis* and *S. bifolia*, belong to different sections of the genus (i.e. sect. *Luteoscilla* and sect. *Scilla*, respectively).

Notes on interspecific hybridization in the genus *Scilla* L. s.str. in the Czech Republic

Only species of the section *Scilla* are indigenous to the Czech Republic: *S. bifolia* (in the wider sense used in this paper; see below), *S. kladnii* and *S. vindobonensis*. No more than one of these species occurred at any locality visited, and no plant was found that could be reliably marked as an interspecific hybrid. The species mentioned were cultivated together and spread spontaneously for at least fifteen years in the park section of the botanical garden at the Faculty of Science at Palacký University in Olomouc (BGUP). No hybrid plant between these species was detected there either. Such hybrids are not even mentioned in credible literature. It is therefore highly probable that hybridization between the three central European species mentioned does not take place at all, or is extremely rare. This may be related to the fact that the species are rather different in chromosome structure (Greilhuber & Speta 1977, Greilhuber 1979, 1982; Speta 1982, Kereszty 1987).

Almost no reliable information is available regarding hybridization between species of sect. *Chionodoxa* (cf. Speta 1976a: 51). Any possible hybridization should be studied both at localities where these species occur together naturally, as well as experimentally. In culture, plants from the group of *S. luciliae* that stand morphologically between the species of this group (*S. forbesii* (Baker) Speta, *S. luciliae* (Boiss.) Speta and *S. sardensis* (Barr et Sugden) Speta) may be found in the Czech Republic, but it is not clear whether these are only extreme (convergent) forms within the scope of the microspecies or whether they are products of interspecific hybridization.

Spontaneous hybridization between species of sect. *Scilla* (in the sense adopted herein; see above) and sect. *Chionodoxa* has repeatedly been recorded in literature, both in culture and in natural mixed populations (Speta 1971, 1976a). These hybrids may be distinguished relatively easily on the basis of floral morphological characters because the parental species differ notably from one another in these characters (see above). Speta (1976a) found hybrids in Austrian botanical gardens resulting from spontaneous hybridization between the diploid species *Scilla nivalis* Boiss. from sect. *Scilla* and the diploid species *S. sardensis* and *S. siehei* (Stapf) Speta (= *S. forbesii*) from sect. *Chionodoxa*. He explains the easy generation of these hybrids by stating that species of the group of *S. luciliae* are closely related to species of the *S. nivalis* group. In the BGUP park, the few plants that are obviously a result of hybridization between a member of sect. *Scilla* and a species of sect. *Chionodoxa* (see Figs 13d, e) occur spontaneously. These were discovered where specimens of *S. bifolia*, *S. forbesii* and *S. sardensis* occur together. *S. bifolia* is obviously one of the parental species; in morphological terms, the plants belong to subsp. *bifolia* in the sense adopted in this paper (see below). The second parent is either *S. forbesii* or *S. sardensis*. The hybrid plants are closer in habit to *S. bifolia*, from which they may easily be distinguished by their conspicuously widened filaments, paler (yellowish) anthers and a perianth coalescent in a short section at the base (see Figs 13d, e). The plants are archived in the OL herbarium (leg. Trávníček). Flow cytometric analyses have shown that plants of one of the presumed parents (i.e. *S. bifolia* subsp. *bifolia*) probably correspond in their nuclear DNA content with the tetraploid

level, whereas plants of the second parent (i.e. the *S. luciliae* group) are diploid. The nuclear DNA content of hybrid plants stands between the values of the presumed parents, but closer to the latter taxon (i.e. the *S. luciliae* group).

Taxonomic classification of native taxa of the genus *Scilla* (sect. *Scilla*) in the Czech Republic and adjacent parts of Europe

Older floras report only a single native species, *S. bifolia*, from the Czech Republic. DOSTÁL (1948–1950) distinguishes between three subspecies of this species, of which he reports from the Czech Republic subsp. *eubifolia* Domin nom. inval. (= subsp. *bifolia*) and, with a question mark, subsp. *subtriphylla* (Schur) Domin (= *S. kladnii* Schur). TRÁVNÍČEK (1993, 1996, 2002), who follows Speta's taxonomic concept of the group of *S. bifolia* (SPETA 1974, 1977b, 1981a, 1982; ADLER & SPETA 1994), complemented by the studies of Kereszty and his Hungarian colleagues (KERESZTY *et al.* 1987, KERESZTY 1987, 1988a, b, 1993), distinguishes between three separate species in the Czech Republic: the diploid *S. kladnii* and *S. vindobonensis*, both belonging to the wide group of *S. bifolia*, and the tetraploid to hexaploid *S. drunensis*, which belongs to the narrow group of *S. bifolia* (= sect. *Scilla sensu* SPETA 1981a). TRÁVNÍČEK (l.c.) preliminarily assigns the Czech populations of the last-mentioned species to subsp. *drunensis* and reports a second subspecies recognized (subsp. *buekkensis* (Speta) Kereszty, nom. inval.) from Slovakia. SPETA (l.c.), KERESZTY (l.c.) and their co-workers also report from Central Europe the diploid *S. bifolia* s.str. (in southern and south-western Europe and the western to south-western parts of Central Europe; being closest to the Czech Republic in Austria and Bavaria) and the hexaploid *S. spetana* Kereszty (at one locality in the north-western part of Hungary and another in Lower Austria); both taxa belong to the narrow group of *S. bifolia*. Within this group, SPETA (1977b, 1981a) additionally recognizes as separate the tetraploid to hexaploid species *S. laxa* Schur, which he reports from Romania, Serbia and north-eastern Croatia.

In recent years, a detailed study of native populations of the genus *Scilla* has been carried out in the Czech Republic. It was complemented by research in other Central European countries and in adjacent parts of the Pannonian Plain and the Carpathians (Bavaria, Austria, Slovakia, Hungary, north-eastern Croatia and Romania). Ploidy screening of 55 populations of the narrow *S. bifolia* group coupled with morphometric analysis was performed as part of this research (see ŠARHANOVÁ 2008). Detailed results of this will be published separately (B. Trávníček *et al.*, in prep.). Some new contexts have been discovered that have led to the creation of a new taxonomic concept of the *S. bifolia* group, employed in the approach in "Flora of the Czech Republic" (B. Trávníček, in prep.). The recognition of only three separate species, *S. kladnii*, *S. vindobonensis* and *S. bifolia* (as against the 6–7 considered by Speta and Kereszty; see above), is the essence of this new approach to the classification of the *S. bifolia* group in the Czech Republic, the whole of Central Europe and adjacent parts of the Carpathians and the Pannonian Plain. All species of the narrow group of *S. bifolia* (= sect. *Scilla sensu* SPETA 1981a) are included in the latter species; these are, besides *S. bifolia* s. *strictissimo*, *S. buekkensis*, *S. drunensis*, *S. laxa* and *S. spetana*. These taxa, with the exception of

S. drunensis and *S. laxa*, are understood as subspecies of *S. bifolia*, i.e. subsp. *bifolia* (comprising *S. drunensis* as a variety), subsp. *buekkensis* (considered taxonomically identical to *S. laxa*) and subsp. *spetana*. This taxonomic approach is based on the following findings and contexts.

(1) A morphometric analysis of more than 1800 individuals from 55 subpopulations of the narrow group of *S. bifolia* (Šarhanová 2008, B. Trávníček *et al.*, in prep.) has revealed the existence of three main groups, in particular on the basis of quantitative floral characters. The lowest values of dimensions for the respective floral parts were found in populations from the Alps and adjacent regions of Central Europe; differences between diploid ("*S. bifolia* s.str.") and tetraploid ("*S. drunensis*") (peri-)Alpine populations were only inconspicuous. These populations are therefore assigned together into a single subspecies, subsp. *bifolia*. Somewhat higher values for the dimensions of the floral parts were found in populations in the Carpathians and in adjacent northern Hungary and southern Slovakia (Matricum), but populations from the western Carpathians and the Matricum did not differ from populations from the southern Carpathians; one of them (near the village of Talmaciu in central Romania) had been previously assigned to the separate species *S. laxa* (Speta 1977b, 1981a; Greilhuber & Speta 1985). In all these populations, only tetraploid individuals occur, or at least dominate. These Carpathian-Matricum populations are treated as subsp. *buekkensis*. Distinctly the highest values for floral part dimensions were found in one group of populations inhabiting a wide strip along the rivers Danube (in north-eastern Croatia, Hungary, south-western Slovakia and Lower Austria) and Moravia (in the Czech Republic). Some of these populations had previously been assigned to *S. laxa*, *S. drunensis* s.str. or to subsp. *buekkensis* (see below for details). In all of these populations, hexaploid individuals occur solely or predominantly. These populations are treated as subsp. *spetana*.

(2) It has therefore emerged (see 1, above) that the floral morphology of the narrow *S. bifolia* group is most notably associated with the populations' geographical distribution (the Alps, the Pannonian Plain and the Carpathians). This accords well with the presumption that myrmecochorous populations of the genus *Scilla* can spread only with difficulty (extremely slowly) over larger distances (Speta 1974); their occurrence is often of a relict nature. Therefore, exchange of genes among populations from more remote geographical areas must be extremely limited, if not impossible. This may contribute to the taxonomic differentiation of populations in the Alps, the Pannonian Plain and in the Carpathians. It is also noteworthy that the distribution of two additional Central European species of the genus, *S. kladnii* and *S. vindobonensis*, is obviously attached to these geographical units: *S. kladnii* is a Carpathian subendemic, while *S. vindobonensis* has its centre of distribution in the Pannonian Plain. The distribution of the three

main types from the narrow group of *S. bifolia* (i.e. subsp. *bifolia*, subsp. *buekkensis* and subsp. *spetana*) also correlates, to a large extent, with the distribution of three prominent Central European types of hornbeam oakwoods (the *Carpinion* Issler 1931 alliance), in the moister variants of which these squills often occur: (a) Hercynian hornbeam oakwoods (as. *Melampyro nemorosi-Carpinetum* Passarge 1962), which also grow in Germany and Austria, for example, as well as the Hercynian part of the Czech Republic; (b) Carpathian hornbeam oakwoods (as. *Carici pilosae-Carpinetum* Neuhäusl et Neuhäuslová-Novotná); and (c) Pannonian hornbeam oakwoods (as. *Primulo veris-Carpinetum* Neuhäusl et Neuhäuslová-Novotná ex Neuhäuslová-Novotná 1964), see KNOLLOVÁ & CHYTRÝ (2004).

(3) Although the correlation between floral morphology and ploidy level is also apparent (larger flowers correspond to a higher ploidy level) but less pronounced, it transpires that (peri-)Alpine tetraploids are closer in floral morphology to (peri-)Alpine diploids than to Carpathian-Matricum tetraploids. The number of chromosomes, regarded in earlier studies as one of the most important characters for the separation of distinct species within the *S. bifolia* group (GREILHUBER & SPETA 1977, SPETA 1977b, 1981a), remains a relevant taxonomic character, but its importance for the classification of the group under discussion is definitely lower than previously thought. This is also suggested by the results of screening for ploidy, which revealed that in some populations, alongside individuals of the predominant ploidy level, plants of a different ploidy occur; for example, tri- and tetraploid individuals in the predominantly diploid populations of subsp. *bifolia* in Austria and Bavaria, hexaploid individuals in mostly tetraploid populations of subsp. *bifolia* in western Hungary, and tetraploid and rarely even octoploid individuals in predominantly hexaploid populations of subsp. *spetana* in south-western Slovakia and Moravia. This phenomenon was discovered some time ago by Speta and Greilhuber, who found tetra-, penta- and hexaploid plants at the *locus classicus* of *S. buekkensis* (SPETA 1977b, 1981a, GREILHUBER & SPETA 1985), tetra- and hexaploid plants at an *S. laxa* locality in Romania (SPETA 1977b, 1981a; GREILHUBER 1979, GREILHUBER & SPETA 1985) and di-, tri- and tetraploid plants at a locality of *S. bifolia* (*sensu strictissimo*) in southern Italy (GREILHUBER & SPETA 1985). KOCHJAROVÁ (2005) also found co-occurrence of tetraploid and hexaploid plants in one population in south-western Slovakia. Due to the relatively rare frequency of squills in the wild, it is truly improbable that the respective cytotypes of the narrow group of *S. bifolia* in local populations represent separate natural taxa. In contrast, it is highly probable that at least a partial exchange of genes can take place between individuals of different ploidies within such a population. Non-reduced gametes, for example, may play a certain role in this. A difference

in ploidy is probably not a sufficiently effective mechanism for isolation in the group discussed, as has been presumed in the past (Greilhuber & Speta 1977), geographical isolation of populations proving apparently more efficient. In this context, it is possible to view ploidy in subpopulations (or individuals within them) from a similar perspective as that for other characters, for example the morphological. For the taxa recognized, a certain ploidy level is "typical", but deviations within populations of these taxa can exist. Morphological characters in the group discussed function similarly, that is, only "statistically", so the taxonomic assignment of a subpopulation to one of the taxa recognized often requires a morphometric or a karyological analysis of a larger number of individuals from the population (see also below).

(4) Chromosome structure, and probably nuclear DNA content are, without doubt, karyological characters that are more important than ploidy in the wider group of *S. bifolia* (i.e. that including *S. kladnii* and *S. vindobonensis*). Both were subjects of special attention on the part of Greilhuber (Greilhuber & Speta 1977, 1985, Greilhuber 1978, 1979, 1982; Greilhuber *et al.* 1981), and marked differences in these characters were found among *S. kladnii*, *S. vindobonensis* and *S. bifolia*. This appears to be why hybridization has not been found between *S. kladnii*, *S. vindobonensis* and *S. bifolia sensu strictissimo*, although all these taxa are diploid (see above). Differences in these taxonomically important karyological characters correlate very well with other differences: in morphology (see the identification key below) and in embryology (in *S. vindobonensis* a tetrasporic embryo sac has been found, whereas a monosporic one is present in *S. kladnii* and in taxa from the narrow group of *S. bifolia* (Greilhuber *et al.* 1981, Svoma 1981)). The morphological and karyological characters under discussion are largely constant in populations of *S. kladnii*, *S. vindobonensis* and *S. bifolia* (in the wider sense, adopted in this study), so the assignment of a subpopulation of squill to one of these three taxa (species) is unequivocal and can be done on the basis of a single, or at most a few, specimens. In contrast, less significant differences, or none of them, in these karyological characters were found among taxa of the narrow group of *S. bifolia* (cf. Greilhuber & Speta 1977, 1985; Greilhuber 1978, 1979, 1982; Kereszty 1987). For example, in tetraploid populations regarded as the distinct species *S. drunensis*, an almost identical karyotype structure was found to that in diploid *S. bifolia* s.str. (Greilhuber & Speta 1977), as well as an almost identical double nuclear DNA content corresponding to the double number of chromosomes (Greilhuber 1978, 1979; Greilhuber & Speta 1985, Kereszty 1987; see also Table 1). It is therefore highly probable that tetraploid individuals (populations) of *S. bifolia* have arisen via simple autopolyploidization from diploid individuals (populations). It is possible that, in the area of the Alps, this process took place in a polytopic and polychronic manner, so it cannot

even be ruled out that diploid populations, for example, from the eastern to the north-eastern margins of the Alps, are genetically (evolutionarily) closer to tetraploid populations occurring there than to diploid populations from areas west of the Alps (e.g. from France), from which they are probably geographically isolated. The separation of tetraploid populations in the Alps from Alpine diploid populations at the species level (*S. drunensis*) is hardly justified.

(5) The assignment of subpopulations of the narrow group of *S. bifolia* to one of the taxa recognized, on the basis of morphological or karyological characters (chromosome count), is usually possible only after a morphometric or a karyological analysis of a larger number of individuals from the population (see also above), and a single individual or a small group may often prove unidentifiable. Moreover, the taxonomy of a small percentage of populations cannot be unequivocally decided even after such analyses. All taxa from the narrow group of *S. bifolia* recognized are therefore classified at ranks below species, that is, subspecies or variety. The taxon most different from the rest is subsp. *spetana*, population samples of which were either completely hexaploid or with admixed individuals of other ploidy levels (the hexaploid level being typical only of populations of this taxon) and at the same time can be identified best using morphological characters (especially style length). The difference between the (peri-)Alpine subsp. *bifolia* and the Carpathian-Matricum subsp. *buekkensis* is less pronounced, whether in floral morphology, ploidy (subpopulations of subsp. *buekkensis* are predominantly or solely tetraploid, subsp. *bifolia* is either tetraploid or diploid) or nuclear DNA content (see Table 1). Therefore, the variety category was considered for their classification as well as the rank of subspecies. The subspecies category was finally chosen because of presumed long-term vicariance between populations and their continued mutual isolation. The least pronounced morphological differences were detected between populations of (peri-)Alpine tetraploids and diploids which are, in addition, sympatric so, despite a different ploidy level, they are classified only as varieties (i.e. var. *bifolia*: 2x and var. *drunensis*: 4x) within subsp. *bifolia*. This classification in its entirety also stems from the presumption that type specimens of *S. bifolia* are diploid because they come from the Danube region of Bavaria or an adjacent part of Switzerland ("Basilea et Ingolstadii sponte" – typus of *S. bifolia*; see below). Ploidy screening of three populations in the Danube region of Bavaria (ŠARHANOVÁ 2008) detected solely or overwhelmingly (>93%) diploid individuals.

(6) As well as these previously recognized taxa, three additional morphologically identifiable types from the narrow group of *S. bifolia*, which were not considered in earlier classifications, were discovered in the Czech Republic. At a single locality in south-western Moravia,

a morphotype that taxonomically differs in fairly important characters from all other knowns morphotypes of the group has been found (see below). It is regarded as a separate stenoendemic subsp. *rara*. Two somewhat isolated tetraploid populations found in the eastern Elbe river basin in Bohemia (near the town of Kolín) differ from other tetraploid populations of subsp. *bifolia* by a paler perianth – and seeds, apparently – and are considered a separate variety within this subspecies: var. *bohemica* (see also below). Finally, one Moravian population of subsp. *spetana* differs from other populations of this subspecies in having somewhat higher values of quantitative floral characters; it is classified as a separate variety within the same subspecies: var. *magnomoravica* (see also below).

(7) Populations of the narrow group of *S. bifolia* (hereinafter termed *S. bifolia*) grow only in the eastern half of the Czech Republic. It is therefore rather surprising that this group shows such high variability in such a small area – in contrast to many larger areas south of the country. Apparently, this can be explained by two factors: (a) The flora of the eastern Czech Republic is simultaneously influenced by all three important Central European florogenetic migration streams, the Alpine, the Pannonian and the Carpathian; and (b) This area is located at the fringe of the distribution area of *S. bifolia* where subpopulations are considerably isolated from one another and probably lack genetic contact over a prolonged period of time.

(8) In contrast to *S. bifolia*, which is extensively variable both morphologically and karyologically in the Czech Republic, as well as in the whole of Central Europe (see above), no taxonomically significant variability was found in *S. kladnii* and *S. vindobonensis* in these areas (see below for details).

(9) In all recognized taxa of the genus *Scilla* that occur in the Czech Republic, intrapopulation morphological variability (differences in habit between individuals) is rather conspicuous. This variability applies to most characters and very probably arises from two different causes. Minute genetic differences between individuals in the population have originated by sexual reproduction which, to a certain extent, manifests in some taxonomically significant characters (e.g. perianth and scape colour, and size of floral parts). It would therefore be productive to carry out morphometric analysis of a larger number of individuals from the populations examined. This mainly applies to the identification of intraspecific taxa of *S. bifolia*. The other cause apparently relates to the overall robustness of the individual, which depends on its ontogenetic age and on the microhabitat conditions under which it occurs. This chiefly concerns the overall size of a plant but also, for example, the number of flowers in the inflorescence and the number of leaves. The second cause does not represent true variability but a plasticity that is completely irrelevant to taxonomic classification. For taxonomic purposes individuals of approximately the same size (e.g. with bulbs of approximately the same

size) should be compared. It is particularly desirable to exclude individuals that are too small (often with only 1–3 flowers) from taxonomic analysis. The morphological differences among the taxa recognized are best manifested in adult individuals (or populations) that grow under favourable habitat conditions.

A summary of taxa of the genus *Scilla* L. s.str. native to the Czech Republic

Key to species

1a Inflorescence multilateral, ± pyramid-shaped during anthesis, usually comprising only 1/5–1/3 of the length of the above-ground scape, peduncles of bottom-most flowers relatively short, frequently slightly arched upwards; leaves 2–3(–4), widest leaves during anthesis only shallowly sulcate to almost flat in upper part, with only a 0.5–1.5 mm long cucullate tip, margins of leaf sheaths usually yellow-green; seeds in each locule most often only 1–3; maturing capsules ± pale green, not inflated. – Tepals (7.0–)7.5–9.5(–10.5) mm long, pale violet-blue, ± both sides unicolorous (buds pale violet-blue to lilac), lacking a pale to white spot at base; scape (except inflorescence axis) usually green; fresh mature seeds brownish-white to pale brown, greyish-brown after dessication. .... ***Scilla kladnii***

1b Inflorescence unilateral during anthesis, in multiflowered specimens comprising 1/3–2/3 of the length of above-ground scape, peduncles of bottom-most flowers sometimes conspicuously long, frequently slightly arched backwards; leaves in pairs (exceptionally triplets), entirely markedly sulcate during anthesis, with a (1.5–)2–3 mm long cucullate tip, margins of leaf sheaths reddish to markedly reddish-tinted, more rarely yellow-green; seeds most often 2–8 in each locule; maturing capsules green to dark green, often purple-tinted, slightly to markedly inflated. ... **2.**

2a Tepals (7.0–)7.5–10.0(–11.0) mm long, bicolorous: inner side deep dark violet-blue, outer side greenish- or whitish-blue, at base of inner side with a *c*. 1 mm-long, sharply outlined white spot, buds greenish or whitish; mature seeds yellowish-white to pale ochraceous when fresh, strawy yellow to yellow-brown when dried, caruncule ± compact, spiral in shape, resembling a black pudding. – Entire scape and leaf sheaths usually conspicuously tinted brownish-red. .... ***Scilla vindobonensis***

2b Tepals (7.8–)8.0–13.0(–14.5) mm long, ± identically coloured on both sides, usually violet-blue, lacking sharply outlined white spot at base, buds (pale) violet-blue; mature seeds greyish pale to dark brown when fresh, brown to black-brown when dry, caruncle composed of spherical, pearl-like structures. – Scape under the inflorescence usually less remarkably brownish-red tinted or green, leaf sheaths reddish or yellow-green. .... ***Scilla bifolia***

1. *Scilla kladnii* Schur (Figs 1, 2)

Scilla kladnii Schur, Verh. Mitth. Siebenbürg. Vereins Naturwiss. Hermannstadt 1/2: 39, 1850.

Synonyms:
= *Scilla alpina* Schur Sert. Fl. Transs. 75, 1853.
= *S. subtriphylla* Schur Enum. Pl. Transs. 668, 1866.
  ≡ *S. bifolia* subsp. *subtriphylla* (Schur) Domin, Preslia 13–15: 19, 1936.
  ≡ *S. bifolia* var. *subtriphylla* (Schur) T. Simon, Ann. Biol. Univ. Debrecen 1: 154, 1950.
– *S. bifolia* auct., non L. Sp. Pl. 309, 1753.
– *S. praecox* auct., non Willd. Sp. Pl. 2/1: 128, 1799: Dostál 1989: 1203.

Typus: ”Zirnathal, VIII. 1837. [leg.] Kladni” in SIB (lectotypus Speta 1977b: 19).

Note. The type material of the name *S. kladnii* Schur 1850 consists of two herbarium vouchers: an isotype (isolectotype) exists in addition to the lectotype (see above; cf. Speta 1977b). The voucher specimens (three altogether) of the type material are minute, single- to sparsely-flowered individuals (see Speta l.c.) that only slightly resemble typical (i.e. well-developed) plants of the species concerned. Unfortunately, this also applies to the type material of the second-oldest name *S. alpina* Schur 1853 (see Speta l.c.). In both cases the *loci classici* are located at rather high elevations in the Romanian Făgăraş mountains. In contrast, the type of the name *S. subtriphylla* Schur 1866 (see Speta l.c.) consists of two very well developed (many-flowered) specimens that leave no doubt that they belong to the species. These plants were collected at a lower elevation, probably with more favourable conditions for the growth of squills, in the vicinity of the town of Sibiu. Speta's nomenclatural interpretation of the names *S. kladnii* and *S. alpina*, which is commonly accepted in recent literature, is also adopted in this study (see Speta l.c.). Apparently, this interpretation is based primarily on the geographical location of the type material of both names concerned (i.e. *S. kladnii* and *S. alpina*) and also on the presumption that only the diploid species discussed here grows in the higher parts of the Făgăraş range (cf. Speta 1977b: 47), which has also been confirmed karyologically although at a different locality. But around the town of Sibiu, which is situated not far from the Făgăraş, *S. bifolia* (subsp. *buekkensis*) occurs alongside the species discussed here, and the species *S. bifolia* is also reported from the vicinity of the town of Braşov (under the name *S. drunensis*; cf. Speta 1977b), which also lies at the foot of the Făgăraş range. It therefore cannot be completely ruled out that both of these species ascend to the high parts of the range, and, consequently, that the type material of the names *S. kladnii* and/or *S. alpina* belongs to the species *S. bifolia*. In the western Carpathians (i.e. in the Slovak range of Veľká Fatra), both species grow at altitudes around 1500 m at localities not too far apart.

Description. Bulbs ovoid to globose, 1.3–3.0(–3.5) cm long, 0.7–2.5 cm wide, greyish-brown. Leaves 2–3(4), subterranean sheaths of the leaves 7–12(–17) cm long, whitish below, in the upper part usually yellowish-green, rarely with reddish-violet tint, above-ground part of the leaves linear to taeniform-oblanceolate, in the major leaf (6–)8–13(–15) cm long at anthesis, after anthesis lengthened by half, (0.8–)1.0–1.8(–2.2) cm wide (smaller leaves only 0.4–1.1 cm wide), shallowly sulcate, in the upper part

almost flat, particularly after anthesis, erecto-patent to erect, light green to mid-green, rarely reddish in the margins and tip, cucullate tip only 0.5–1.5(–2.0) mm long. Scape erect at anthesis, above-ground part 5–17(–20) cm long, as long as the leaves or longer, in the lower part green, sometimes with brownish-red tint, in the inflorescence usually deeper coloured, sometimes up to brownish-red. Raceme (1–)3–10(–15)-flowered, pyramidal in many-flowered plants (never markedly unilateral), usually as long as 1/5–1/3(–1/2) of the above-ground length of the scape, peduncles erect or erecto-patent, lower peduncles often slightly curved upwards, relatively short, lowermost peduncle only (0.7–)1.0–3.0(–4.0) cm long, often with red-brownish tint; bracts usually absent, rarely present small lanceolate whitish bracts up to 4 mm long. Flower-buds erect, light violet (lilac), rarely deeper; tepals soon radially arranged (stellate), oblong to oblong-elliptic, (7.0–)7.5–9.5(–10.5) mm long, (2.0–)2.5–3.5 mm wide, equally coloured on both sides, lacking pale to white spot at the base, usually pale violet-blue, rarely deeper; filaments erecto-patent, standing apart, linear to subulate, sometimes slightly tapered at base, (4.0–)4.5–5.5(–6.0) mm long, (0.5–)0.7–1.0 mm wide, whitish at base, pale violet above; anthers 2.0–3.5 mm long, deep greyish-blue, usually darker than tepals; pollen grains greyish violet-blue; ovary ± globose, with 6 longitudinal shallow furrows, 2.5–3.5 mm in diameter, (light) blue-violet, with 2–4(–6) spherical whitish ovules in each loculus; style 1.8–2.5(–2.7) mm long, violet-blue, narrowly cylindrical, broadened to the base and gradually merging into the ovary. Capsule irregularly globose or obtuse triangular, not inflated, 7–10(–12) mm in diameter, usually pale green, seeds (0–)1–3(–5) in each loculus; seeds ± spherical, mature fresh seeds brownish-white to pale brown, shiny, 2.3–2.8 mm in diameter, dried smaller, greyish-brown, matt; caruncle irregularly hemispherical, whitish, pellucid, consisting of globose, pearl-like units. Flowerage: III–IV.

Remarks. Within *S. kladnii* no intraspecific taxa are distinguished in any part of its area of distribution (Speta 1977b, 1981a, 1982; Kereszty 1987, 1993, Kereszty *et al.* 1987, Kochjarová *et al.* 2005). In the Czech Republic as well, this species shows extraordinarily little variability that is only individual. The visually most striking differences exist in the overall robustness of individuals, depending on ontogenetic age and microhabitat conditions. The number of flowers in an inflorescence and the overall shape of the inflorescence, as well as the numbers of leaves, all depend on the robustness of the plant. Smaller specimens have a lower number of flowers in an irregular sparse raceme and usually only two leaves. More vigorous individuals have a richer inflorescence, typically pyramidal during anthesis, and usually bear three or four leaves. A certain amount of individual variability shows in the presence, or even the intensity, of reddish-brown colouring of the scape and leaves; the above-ground part of leaf sheaths is usually yellow-green, but can sometimes be slightly reddish. The shade of flower colour, as well as practically all the quantitative characters, can also vary a little.

Only a single chromosome number has been obtained to date for *S. kladnii*: 2n = 18 (2x); it is therefore a diploid species (see Speta 1977b, 1981a; Greilhuber 1979, Greilhuber & Speta 1985, Kereszty 1987, Kochjarová 2005). This count has been confirmed from two localities in the Czech Republic (Kulová 1991).

According to all extant findings, *S. kladnii* is a Carpathian (sub-)endemic. Its occurrence has been recorded in an area spanning southern Poland, eastern Moravia and Slovakia through western Ukraine and north-eastern Hungary to Romania (Speta 1977b, 1981a, 1982; Kereszty *et al.* 1987, Kereszty 1993, Kricsfalusy *et al.* 1993, Kricsfalusy & Vajnagi 1994, Trávníček 1996, Piekos-Mirkowa & Mirek 2003, Kochjarová *et al.* 2004, 2005).

In the Czech Republic, *S. kladnii* has been found only in Moravia, where it occurs only in the part that is influenced by the Carpathian flora. It grows scattered alongside the river Bečva between the towns of Vsetín and Přerov, and also at a few localities in the woods between the confluence of the rivers Morava and Bečva and the town of Kroměříž. The localities are situated in the following phytogeographical regions: 21a. Hanácká pahorkatina (only a fringe occurrence); 21b. Hornomoravský úval; 76a. Moravská brána vlastní; 80a. Vsetínská kotlina; 81. Hostýnské vrchy (?). Its habitats extend from the lowlands to upper hill country at altitudes ranging from 190 m to *c*. 340 m. The western boundary of its distribution runs through the Czech Republic.

2. *Scilla vindobonensis* Speta   (Figs 3, 4)

Scilla vindobonensis Speta, Naturk. Jb. Stadt Linz 19(1973): 17, 1974.

Synonyms:
= *Scilla montenegrina* Speta, Naturk. Jb. Stadt Linz 22(1976): 66, 1977.
  ≡ *S. vindobonensis* var. *montenegrina* (Speta) Speta, Naturk. Jb. Stadt Linz 25(1979): 52, 1981.
– *S. bifolia* auct., non L. Sp. Pl. 309, 1753.

Typus: "In silva ad flumen Ivesem (Ybbs) inter Adiuvensem (Ybbs) et Ad pontem Ises (Neumarkt/Ybbs), altitudo circa 220 m. s. m., in Austria inferiore. Leg. F. Speta, 28. 3. 1973" in herbarium F. Speta, Linz, Austria (holotypus Speta 1974: 17).

Description. Bulbs ovoid to globose, 1.3–3.0 cm long, 0.7–2.3 cm wide, greyish-brown. Leaves 2(3), subterranean sheaths of the leaves 7–13(–18) cm long, whitish below, in the upper part usually yellowish-green with brownish-red tint, above-ground part of the leaves linear to taeniform-lanceolate, in the major leaf (6–)8–15(–18) cm long at anthesis, after anthesis lengthened by half or almost doubled, (0.6–)0.8–1.7(–2.0) cm wide (smaller leaves 0.5–1.2 cm wide), straight or slightly arcuate backwards, usually markedly sulcate, rarely (after anthesis) shallowly sulcate or almost flat, erecto-patent or ascending from decumbent base, usually deep to dark green, often red-brownish on the margins (sometimes whole leaves red-brownish), cucullate tip narrow, (1.5–)2.0–3.0(–5.0) mm long. Scape erect at anthesis or sometimes tilted sideways and than slightly curved, above-ground part 5–15(–20) cm long, as long as leaves or longer, usually wholly (sometimes deeply) red-brownish. Raceme (1–)3–12(–20)-flowered, unilateral (predominantly those when young and in many-flowered plants), usually as long as 1/3–2/3 of the above-ground length of scape, peduncles erect or erecto-patent, lower peduncles sometimes slightly curved backwards, usually conspicuously longer that the upper; lowermost peduncle (1.0–)1.5–4.0(–6.0) cm long, with distinct red-brownish

tint; bracts usually absent, diminutive and whitish if present. Flower-buds erect, pale, greenish- or whitish-blue (greenish or whitish strips are more distinct on midribs of tepals); tepals soon radially arranged (stellate), oblong to oblong-elliptic, (7.0–)7.5–10.0(–11.0) mm long, (2.0–)2.5–3.5 mm wide, conspicuously bicolorous: inner side deep, dark violet-blue, outer side whitish- or greenish-blue, markedly lighter, at base of inner side with a *c*. 1 mm-long, sharply-outlined white spot; filaments erecto-patent, standing apart, linear to subulate, sometimes slightly broadened at base, (4.0–)4.5–5.5(–6.0) mm long, (0.6–)0.8–1.1 mm wide, violet-blue, at base with 1 mm-long whitish section; anthers (2.0–)2.3–3.6(–4.0) mm long, deep violet-blue, usually darker than tepals; pollen grains greyish violet-blue; ovary ± globose, with 6 shallow longitudinal furrows, 2.5–3.5 mm in diameter, usually deep blue-violet, with 5–8 spherical whitish ovules in each loculus; style (2.0–)2.3–2.9(–3.5) mm long, violet-blue, narrowly cylindrical, broadened to the base and gradually merging into the ovary. Capsule irregularly globose, inflated, 8–15 mm in diameter, dark green, often with dark brownish-purple tint, seeds (2–)4–8 in each loculus; seeds ± spherical to ovate-spherical, mature fresh seeds yellowish-white to pale ochraceous, shiny, 2.3–2.8 mm in diameter, dried smaller, strawy yellow to yellow-brown, matt; caruncle ± compact, irregularly formed, spiral in shape (resembling a black pudding), whitish, pellucid. Flowerage: III–IV.

Remarks. Reports of var. *montenegrina* come from the southernmost part of the distribution area of *S. vindobonensis* (Albania, Serbia and Montenegro). It is alleged to differ from the type variety in its minute stature and darkly reddish-brown tinted leaves (SPETA 1977a, 1981a). It has not been reported from Central Europe. Populations of reportedly more vigorous plants (with tepals up to 12 mm long) were described from north-western Hungary as var. *transdanubialis* Kereszty (Symb. Bot. Upsal. 27: 111, 1987); populations of reportedly very small plants (with only 1–5 flowers) were described from south-western Hungary as subsp. *borhidiana* Kereszty (Symb. Bot. Upsal. 27: 111, 1987). The results of comparisons between plants from the type localities of both these taxa with plants from numerous localities ascribable to *S. vindobonensis* s.str. (i.e. var. *vindobonensis*), all cultivated together under standard conditions, did not reveal any of the morphological differences reported in literature (KERESZTY *et al.* 1987, KERESZTY 1988b). The same ploidy level (2x) had previously been established in all of these types, as well as an identical nuclear DNA content (KERESZTY 1987). Their separate taxonomic status, therefore, can hardly be justified. Similarly, material from the Czech Republic seems taxonomically uniform and ascribable to *S. vindobonensis* s.str. Occasionally, a larger proportion of minute individuals with a small number of flowers may be found at some localities (e.g. around the village of Drahlov near the town of Kroměříž in central Moravia), but the minute stature apparently results, above all, from sub-optimal habitat conditions, and this "aberration" is therefore merely a manifestation of the species' plasticity. This is also confirmed by cultivation experiments. Individual variability manifests itself most conspicuously in the colour of flowers: the whitish or greenish of the outer side of the perianth (or buds) may sometimes be less pronounced,

and a whitish to white ovary, or even a whole whitish (albinotic) flower, may occur sporadically. Similar variability can also be observed in the intensity of reddish-brown colouring of leaves, scapes and, to a certain extent, all quantitative characters.

To date, only the diploid chromosome number has been established in *S. vindobonensis*: 2n = 18 (2x; see SPETA 1974, 1977b, 1981a; GREILHUBER & SPETA 1977, GREILHUBER 1978, 1979; GREILHUBER & SPETA 1985, KERESZTY 1987, KOCHJAROVÁ 1995). At the *locus classicus* of var. *montenegrina*, B chromosomes were also found in its cells, but they were not detected at the second locality studied (SPETA 1981a). The diploid chromosome count was has also been verified twice in the Czech Republic, at one Bohemian locality and one in Moravia (KULOVÁ 1991).

The centre of distribution of this species lies in the Pannonian region, from whence it extends to certain adjacent regions of Central and south-eastern Europe. To date, it has been recorded from the following countries: Germany (the Elbe river basin in Saxony), the Czech Republic, eastern Austria, south-western Slovakia, Hungary, Croatia (Dubrovnik), Montenegro, Serbia and Albania (SPETA 1974, 1977b, 1981a, 1982; KERESZTY *et al.* 1987, KERESZTY 1993, TRÁVNÍČEK 1996, KOCHJAROVÁ *et al.* 2004, 2005; ROTHMALER *et al.* 2005).

In the Czech Republic this species has been recorded in the warmer regions of both Bohemia and Moravia. In Bohemia it occurs most frequently in the lower reaches of the River Ohře and is scattered in the České středohoří Hills, from whence it has occasionally spread to the gorge of the River Elbe (see also KUBÁT 2006); isolated localities are documented from the vicinity of the town of Nymburk and from the region of Český ráj (native occurrence?). In Moravia, this species is scattered in the lower reaches of the River Dyje (between the villages of Ivaň and the town of Břeclav) and in the southern part of the Bílé Karpaty Mountains; isolated localities are also known from the surroundings of the towns of Šternberk and Kroměříž, from the Moravská brána region (village of Blazice) and from the Znojmo region (village of Višňové). In the literature (SPETA 1981a: 52), this species is additionally reported from the south-western fringes of the town of Brno. The localities lie in the following phytogeographical regions: 2a. Žatecké Poohří (probably planted); 4b. Labské středohoří; 4c. Úštěcká kotlina; 5a. Dolní Poohří; 7a. Libochovická tabule; 11b. Poděbradské Polabí; 16. Znojemsko-brněnská pahorkatina; 17c. Milovicko-valtická pahorkatina; 18a. Dyjsko-svratecký úval; 19. Bílé Karpaty stepní; 20a. Bučovická pahorkatina; 21a. Hanácká pahorkatina; 45a. Lovečkovické středohoří; 46b. Kaňon Labe; 53a. Českolipská kotlina (?); 55d. Trosecká pahorkatina (native occurrence?); 75. Jesenické podhůří (native occurrence?); 76a. Moravská brána vlastní; 78. Bílé Karpaty lesní. Its localities range from the lowlands to the upper hill country belt, at altitudes of *c.* 120 to *c.* 590 m.

3. *Scilla bifolia* L.

Scilla bifolia L. Sp. Pl. 309, 1753.

Synonyms:
= ? *Scilla praecox* Willd. Sp. Pl. 2/1: 128, 1799.
= *S. laxa* Schur Enum. Pl. Transs. 669, 1866.
= *S. buekkensis* Speta, Naturk. Jb. Stadt Linz 22(1976): 42, 1977.
= *S. drunensis* (Speta) Speta, Naturk. Jb. Stadt Linz 22(1976): 34, 1977.
= ? *S. bulgarica* Speta, Naturk. Jb. Stadt Linz 25(1979): 46, 1981.
= *S. spetana* Kereszty, Symb. Bot. Upsal. 27: 111, 1987.

Typus: "Basilea et Ingolstadii sponte, [leg. J. Burser]", Herb. Burser vol. III: fol. 23 in UPS (lectotypus VAN RAAMSDONK in WISSKIRCHEN 1997: 106).

Description. Bulbs ovoid to globose, 1.3–3.0 cm long, 0.7–2.5 cm wide, greyish-brown. Leaves 2(3), subterranean sheaths of the leaves 7–15(–20) cm long, whitish below, in the upper part usually yellowish-green, sometimes with brownish-red tint, above-ground part of the leaves linear to taeniform-lanceolate, in the major leaf (5–)8–15(–17) cm long at anthesis, after anthesis lengthened by half or more, (0.7–)0.9–1.8(–2.0) cm wide (smaller leaves 0.4–1.3 cm wide), straight or slightly arcuate backwards, usually markedly sulcate, rarely (after anthesis) shallowly sulcate or almost flat, erecto-patent or ascending from decumbent base, most often mid-green, sometimes red-brownish on the margins (rarely whole leaves with red-brownish tint), cucullate tip narrow, (1.5–)2.0–3.5(–5.0) mm long. Scape erect at anthesis or sometimes tilted sideways and then slightly curved, above-ground part 5–17(–20) cm long, as long as leaves or longer, green (particularly at base) or with red-brownish tint, rarely whole red-brownish. Raceme (1–)3–18(–22)-flowered, unilateral (predominantly when young and in many-flowered plants), most often as long as 1/3–2/3(–1/1) of the above-ground length of scape, peduncles erect or erecto-patent, lower peduncles sometimes slightly back-curved, usually conspicuously longer than the upper; lowermost peduncle (1–)2–5(–10) cm long, with red-brownish tint to a greater or lesser extent; bracts usually absent, diminutive and whitish if present. Flower-buds erect, light (greyish) blue to violet-blue, sometimes with pale violet midribs on tepals; tepals soon radially arranged (stellate), oblong to oblong-elliptic, (7.8–)8.0–13.0(–14.2) mm long, (2.2–)2.5–4.5(–5.0) mm wide, on inner side pale to deep violet blue, sometimes with paler (to whitish), not clearly delineated, 2–4 mm long section at the base, on outer side of the same colour or rarely lighter; filaments erecto-patent, standing apart, linear to subulate, often slightly broadened at base, (4.5–)4.7–7.6(–8.2) mm long, (0.7–)0.9–1.5(–1.8) mm wide, pale to deep violet-blue, at base usually whitish; anthers 3.0–4.9(–5.2) mm long, deep (greyish) violet-blue, usually darker than tepals; pollen grains greyish violet-blue; ovary globose, with 6 longitudinal shallow furrows, 2.5–4.0 mm in diameter, pale to deep violet blue, with 5–10 spherical whitish ovules in each loculus; style (2.0–)2.5–4.7(–5.3) mm long, violet-blue, thin cylindrical to filiform, broadened to the base and usually gradually merging into the ovary. Capsule irregularly globose, inflated, 8–15(–17) mm in diameter, usually green,

rarely with dark brownish-purple tint, seeds (0–)1–6(–8) in each loculus; seeds spherical to ovate-spherical, mature fresh seeds greyish pale to deep dark brown, shiny, (2.2–)2.4–3.0 mm in diameter, dried smaller, brown to black-brown, matt; caruncle irregularly hemispherical, whitish, pellucid, consisting of globose (sometimes irregular), pearl-like units. Flowerage: III–IV.

Key to subspecies

1a A number of flowers on more robust specimens at nearly identical height, or higher than, the length of the above-ground part of scape in centimetres, their inflorescence usually comprising approximately 2/3 of this length; tepals only (2.2–)2.4–3.2(–3.5) mm wide, usually vividly violet-blue on inner side, rather dark, often with a markedly paler (to whitish), 2(–3) mm-long section at the base, not sharply delineated, usually with an overall markedly paler outer side than inner side; filaments most frequently only 0.8–1.0 mm wide. – Tepals only (7.8–)8.3–10.2(–10.7) mm long; styles only (1.9–)2.2–3.2(–3.4) mm long; scape and leaf margins often markedly tinted brownish-red .... **subsp. *rara***

1b A number of flowers on more robust specimens at a usually markedly lower height than the length of the above-ground stem in centimetres, their inflorescence usually comprising approximately 1/2 of this length; tepals (2.4–)2.8–4.6(–5.1) mm wide, (greyish) pale violet-blue on inner side, less often to vividly violet-blue and darker, without a paler bottom section, or the colour of this section is less pronounced, identically coloured on both sides or only slightly paler on the outer side; filaments most frequently 0.9–1.3 mm wide .... **2.**

2a Style (3.2–)3.6–4.7(–5.3) mm long; tepals (9.0–)10.0–13.5(–14.2) mm long; filaments (6.0–)6.4–7.6(–8.2) mm long .... **subsp. *spetana***

2b Style (2.2–)2.4–3.8(–4.4) mm long; tepals (7.2–)8.2–12.2(–13.1) mm long; filaments (4.5–)4.8–7.0(–7.5) mm long .... **3.**

3a Tepals usually 8.3–11.3 mm long and 2.7–3.8 mm wide; style most often 2.4–3.2 mm long; filaments usually 4.8–6.5 mm long .... **subsp. *bifolia***

3b Tepals usually 9.0–12.2 mm long and 3.2–4.3 mm wide; style most often 2.9–3.7 mm long; filaments usually 5.3–7.0 mm long .... **subsp. *buekkensis***

3a. *Scilla bifolia* L. subsp. *bifolia*   (Figs 5, 6, 7a)

Synonyms:
= *Scilla bifolia* subsp. *danubialis* Speta, Naturk. Jb. Stadt Linz 19(1973): 16, 1974.
= *S. bifolia* subsp. *drunensis* Speta, Naturk. Jb. Stadt Linz 19(1973): 17, 1974.
  ≡ *S. drunensis* (Speta) Speta, Naturk. Jb. Stadt Linz 22(1976): 34, 1977.

Description. Above-ground part of the major leaf at anthesis (6–)8–12(–16) cm long, (0.9–)1.0–1.6(–2.0) cm wide, all leaves shallowly to markedly sulcate, green, sometimes red-brownish on the margins, overground parts of sheaths of the leaves more or less distinctly reddish, rarely yellowish-green. Scape at anthesis almost green or light to distinctly reddish-brown (including inflorescence axis), above-ground part (6–)8–13(–15) cm long. Raceme (2–)4–8(–14)-flowered, 3–7(–11) cm long, usually as long as 1/2 (rarely up to 2/3) of the above-ground length of scape, tepals (8.0–)8.3–11.3(–12.0) mm long, (2.5–)2.7–3.8(–4.3) mm wide, on both sides equally coloured or rarely below a little lighter, usually pale (greyish) violet-blue, sometimes darker, rarely at base with indistinctly lighter, 2–3 mm-long spot with diffuse margin; filaments (4.5–)4.8–6.5(–6.8) mm long, (0.8–)1.0–1.4(–1.7) mm wide; anthers (3.0–)3.3–4.7(–5.0) mm long; style (2.3–)2.4–3.2(–3.6) mm long. Mature capsule 8–14 mm in diameter; mature fresh seeds 2.3–2.9 mm in diameter, pale to dark brown, rarely ochre.

Remarks. The description given above does not involve diploid populations of var. *bifolia*, which does not occur in the Czech Republic. These populations differ in somewhat lower average values for some flower parts (particularly the lengths of anthers and styles).

In the taxonomic concept adopted in this paper, subsp. *bifolia* encompasses populations that were recently ascribed to two separate species, the diploid *S. bifolia* s.str. and the tetraploid *S. drunensis* (Greilhuber & Speta 1977, 1985; Speta 1977b, 1981a, 1982, 1998b; Greilhuber 1978, 1979; Svoma 1981, Kereszty 1987, 1988a, b, 1993, 1995; Kereszty *et al.* 1987, Trávníček 1993, 1996, 2002; Adler & Speta 1994, Kochjarová 2005). These species were assumed to differ, apart from in chromosome numbers, in quantitative morphological characters, especially tepal length, and also in seed size (*vide* Speta 1974, 1981a: 39). Morphometric and karyological analyses of 24 populations from the (peri-)Alpine regions (Bavaria, Austria, the Czech Republic and western Hungary; Šarhanová 2008, B. Trávníček *et al.*, in prep.) did not demonstrate a sufficiently strong correspondence between the ploidy of these populations and their morphological characters. Morphological differences between diploid and tetraploid populations originated by autopolyploidy are not distinctive; moreover, it is very difficult indeed to distinguish between these two cytotypes because of the immensely overlapping values of their quantitative characters. Apparently, tetraploid and diploid populations of *S. bifolia* from the region of the Alps are remarkably close to each other in a genetic and evolutionary sense (see above for details), and are therefore treated here merely as two varieties within subsp. *bifolia*: the diploid var. *bifolia* and the tetraploid var. *drunensis* (Speta) Trávníček (see Appendix).

Diploid plants (var. *bifolia*) have not been found in the Czech Republic. The subspecies is probably represented in this country by only tetraploid populations; rarely, plants of a higher ploidy level have been found in one of them. The mutual isolation of the three separate subareas (see below) has probably led to a certain degree of genetic differentiation in these populations. Plants from Bohemia (east of the town of Kolín) have markedly paler flowers than plants from other regions of Central Europe; their scapes are paler and they also have paler seeds. They may therefore be treated as the third variety within the type subspecies: var. *bohemica* Trávníček (see Appendix). Plants from the other two subareas in the Czech Republic (see below) may be ascribed to var. *drunensis*, although they are slightly different: populations from the northern Moravian subarea on average have somewhat darker flowers and more markedly red-brown coloured scapes than populations from the southern subarea. Similarly, minute differences have also been found between subpopulations of var. *bifolia* and var. *drunensis* in Austria and Bavaria. Individual morphological variability within populations of both varieties in the Czech Republic is primarily confined to quantitative characters on most parts of a plant, but it also manifests, to a certain extent, in the shade of the colour of the perianth or in the intensity of the reddish-brown colouring of the scape and leaf sheaths.

Individual variability within subpopulations has also been detected in the number of chromosomes, which applies to all three varieties recognized (see also above). However, samples of the populations under investigation (B. Trávníček *et al.*, in prep., see also Šarhanová 2008) of all three varieties recognized always contained only, or in a vast majority of cases (>85%), individuals of the ploidy level typical of the given variety (i.e. diploid in var. *bifolia* and tetraploid in var. *drunensis* and var. *bohemica*).

Following the taxonomic concept adopted in this paper (see above), subsp. *bifolia* grows in the Alps and in adjacent regions: France, Switzerland, central and southern Germany, Italy (possibly including Sicily), the Czech Republic, Austria, Slovenia, western Croatia and western Hungary. It is not certain whether reports from northern Spain, Sardinia and Holland relate to this taxon. Earlier authors reported localities of this taxon under the names *S. bifolia* s.str., *S. bifolia* subsp. *danubialis*, *S. bifolia* subsp. *drunensis*, *S. drunensis* (s.str.) or *S. drunensis* subsp. *drunensis* (Speta 1974, 1977b, 1981a, 1982; Kereszty 1987, 1988b, 1993; Kereszty *et al.* 1987, Trávníček 1996, 2002). Many localities of subsp. *bifolia* are concentrated in the valleys of rivers and their tributaries running down from the Alps. These rivers and streams have probably played an influential role in the spread of populations over larger distances.

In the Czech Republic this subspecies occurs only in the Hercynian region. In Bohemia its rare occurrence has been recorded in the eastern part of the River Elbe basin (east of the town of Kolín), where var. *bohemica* grows. In Moravia it occurs (exclusively as var. *drunensis*) mainly at the eastern fringe of the Bohemian massif, where it can be found in two distinct subareas. The southern subarea lies the valleys of the rivers Jihlava and Rokytná between the towns of Třebíč, Moravský Krumlov and the village of Moravské Bránice. The northern subarea is located at the eastern fringe of the Drahanská vrchovina Hills between the villages of Náměšť na Hané, Laškov and Kostelec na Hané, north of the town of Prostějov. The localities fall into the following phytogeographical

regions: 11b. Poděbradské Polabí (var. *bohemica*); 16. Znojemsko-brněnská pahorkatina (var. *drunensis*); 21a. Hanácká pahorkatina (var. *drunensis*); 68. Moravské podhůří Vysočiny (var. *drunensis*); 71c. Drahanské podhůří (var. *drunensis*). This subspecies occurs in the lowlands (in Bohemia), in the hill country and in the upper hill country belts (in Moravia) at elevations between 200 m and *c*. 480 m. The north-eastern border of this subspecies' area of distribution runs through the Czech Republic; the closest known localities lie in Lower and Upper Austria.

3b. *Scilla bifolia* subsp. *buekkensis* (Speta) Soó   (Figs 7b–d, 8)

Scilla bifolia subsp. *buekkensis* (Speta) Soó, Acta Bot. Acad. Sci. Hung. 23: 388, 1978.

Synonyms:
≡ *Scilla buekkensis* Speta, Naturk. Jb. Stadt Linz 22(1976): 42, 1977.
= *S. laxa* Schur Enum. Pl. Transs. 669, 1866.
  ≡ *S. bifolia* subsp. *laxa* (Schur) Soó, Acta Bot. Acad. Sci. Hung. 23: 388, 1978.
– *S. drunensis* subsp. *buekkensis* (Speta) Kereszty, Bot. Közlem. 74–75(1987–1988): 69, 1988, nom. inval. (Art. 33.4 of ICBN).

Typus: "In der Nähe eines Erholungsheimes, 1,5 km nordwestlich von Répáshuta, Bükk-Gebirge, 13. 3. 1974, [leg.] F. Speta" in herbarium F. Speta, Linz, Austria (holotypus Speta 1977b: 42).

Note: The type material for the name *S. laxa* comes from a locality not far from the town of Sibiu in central Romania ("in monte Götzenberg bei Heltau" [= Mount Magura above the village of Cisnadie]) and is composed of five well-developed specimens that, it appears, belong to *S. bifolia* (see Speta 1977b). No plants of the genus *Scilla* were found during a visit to the *locus classicus* in spring 2007. The area of the Magura mountain is relatively large, and the weather there was unfavourable, so it is still possible that the locality will be confirmed at some other time. However, populations of *S. bifolia* were found at two localities around the town of Sibiu, 12–17 km away from the *locus classicus* of *S. laxa*. These are, on the basis of morphometric and karyological analysis (Šarhanová 2008, B. Trávníček *et al.*, in prep.), taxonomically identical with populations from the *locus classicus* of subsp. *buekkensis*. One of these Romanian populations (near the village of Talmaciu) was also studied by Speta and identified as *S. laxa* (Speta 1977b, 1981a). Speta's presumption that plants from this locality are taxonomically identical to plants from the not-too-distant *locus classicus* of *S. laxa* seems appropriate. Thus two names of the same age at the rank of subspecies exist for the Carpathian-Matricum taxon (see above), from which the name subsp. *buekkensis* has been chosen, as it is used much more often in recent literature. If the Carpathian-Matricum taxon is to be considered a separate species, the name *S. laxa* Schur 1866 should have priority before the name *S. buekkensis* Speta 1977.

Description. Above-ground part of the major leaf at anthesis (6–)8–13(–15) cm long, (0.9–)1.0–1.6(–2.0) cm wide, all leaves shallowly to markedly sulcate, green or red-brownish on the margins, overground parts of sheaths of leaves more or less distinctly reddish, rarely yellowish-green. Scape at anthesis indistinctly to distinctly reddish-brown (including inflorescence axis), rarely almost green, above-ground part (6–)8–13(–15) cm

long. Raceme (2–)4–8(–12)-flowered, 3–7(–9) cm long, usually as long as 1/2 of the above-ground length of scape; tepals (8.5–)9.0–12.2(–13.0) mm long, (3.0–)3.2–4.3(–4.8) mm wide, on both sides equally coloured or rarely a little lighter below, pale to deeply violet-blue, sometimes at base with indistinctly lighter 2–3(–4) mm-long spot with diffuse margin; filaments (5.0–)5.3–7.0(–7.5) mm long, (0.9–)1.0–1.4(–1.8) mm wide; anthers (3.0–)3.3–4.7(–5.0) mm long; style (2.6–)2.9–3.7(–4.2) mm long; mature capsule 9–15 mm in diameter. Mature fresh seeds 2.4–3.0 mm in diameter, pale to dark brown.

Remarks. The literature provides almost no information of taxonomic significance regarding the morphological variability of subsp. *buekkensis*. This is partly because this taxon was perceived in different ways by earlier authors: as a separate species (SPETA 1977b, 1981a, 1982; GREILHUBER 1979, KERESZTY *et al.* 1987), as a subspecies of *S. drunensis* (KERESZTY 1988b, 1993; TRÁVNÍČEK 1996, KOCHJAROVÁ 2005) or even as completely taxonomically identical to *S. drunensis* (GREILHUBER & SPETA 1985, see also SPETA 1998b). During a morphometric analysis of about 20 populations from the Czech Republic, Slovakia, Hungary and Romania (ŠARHANOVÁ 2008), certain intra-population differences were discovered within subsp. *buekkensis*. However, no other notable geographical or other pattern emerged, rendering further taxonomic evaluation unlikely, at best. A more detailed discussion of this will be published elsewhere (B. Trávníček *et al.*, in prep.). The occurrence of subsp. *buekkensis* in the Czech Republic is confined to a relatively small area (see below). Despite this, in one of three populations analysed morphometrically (near the village of Veletiny), individuals approaching, in their somewhat shorter tepals and styles, plants of subsp. *bifolia* predominated, although they were a good match for the description of subsp. *buekkensis* in the width of their tepals. The individual variability of subsp. *buekkensis* in Czech populations manifests primarily in the colour shade of the perianth (albinos occurred sporadically), the intensity of reddish-brown colouring of the scape and leaf sheaths, and also in most quantitative characters.

A certain variability within subsp. *buekkensis* was found in the number of chromosomes, even in plants from the *locus classicus* of the taxon; as well as tetraploid individuals (2n = 34, 4x), penta- and hexaploid and aneuploid individuals were found (cf. SPETA 1977b, 1981a, GREILHUBER & SPETA 1985). However, flow cytometric screening for ploidy in 20 populations of subsp. *buekkensis* (including population from the *locus classicus*; ŠARHANOVÁ 2008) has shown that these populations are composed solely or predominately (>83%) of tetraploid individuals. This accords well with data from Kereszty and Kochjarová (KERESZTY 1987, KERESZTY *et al.* 1987, KOCHJAROVÁ 2005) who report only tetraploid counts from a larger number of localities in Slovakia and northern Hungary. Tetraploid counts were also obtained from three populations in the Czech Republic (KULOVÁ 1991, KOCHJAROVÁ 2005; under the name *S. drunensis* subsp. *drunensis*).

SPETA (1977b, 1981a), KERESZTY *et al.* (1987), KERESZTY (1993), TRÁVNÍČEK (1996) and KOCHJAROVÁ (2005) report this subspecies only from Slovakia and northern Hungary, that is, from the western Carpathians and from the Matricum region. According

to morphometric analysis (ŠARHANOVÁ 2008, B. Trávníček *et al.*, in prep.), a group of populations from the easternmost (the Carpathian) part of the Czech Republic is also ascribable to this taxon (TRÁVNÍČEK (1996) preliminarily ascribed these populations to *S. drunensis* s.str.). But all three populations from the Romanian Carpathians, in which the morphometric and karyological analyses were carried out (two localities near the town of Sibiu, one in the Banat), also belong to subsp. *buekkensis*. It may therefore be presumed with a great deal of certainty that *S. bifolia* is represented in the entire Carpathians only by this subspecies. SPETA (1977b, 1981a, 1982) ascribed Romanian populations to *S. laxa* and *S. drunensis* s.str. (see also above). He also reports the latter taxon from Bulgaria, Serbia and Macedonia. It is possible that these records, too, relate to subsp. *buekkensis*, but this requires verification. In contrast those of subsp. *bifolia*, localities of the present subspecies are concentrated on hill slopes and even plateaus (such as in the Slovak Karst in Slovakia or in the Banat region in Romania) and not in river or stream valleys, although they are not completely absent from such places.

In the Czech Republic, the subspecies has been recorded solely in south-eastern Moravia between the towns of Uherské Hradiště and Uherský Brod. Four to five localities were found altogether, situated in the following phytogeographical regions: 18b. Dolnomoravský úval; 19. Bílé Karpaty stepní (at one locality, morphologically less typical plants converging towards subsp. *bifolia* in some characters); 78. Bílé Karpaty lesní (?). The localities are usually situated in the hill country belt, rarely in the lowland belt, at altitudes between 177 m and 340 m. The western to north-western border of the subspecies' area of distribution runs through the Czech Republic. The nearest localities abroad are located in the Tríbeč range in western Slovakia.

3c. *Scilla bifolia* subsp. *spetana* (Kereszty) Trávníček
(Figs 9, 10, 11a, b, see Appendix)

Typus: "Hungary, central part, Fejér, Velencei mountains, Mount Templomhegy above Nadap, c. 250 m a. s. l., 10. IV. 1980, [leg.] Z. Kereszty" in VBI (holotypus KERESZTY *et al.* 1987: 112).

Description. Above-ground part of the major leaf at anthesis (5–)7–15(–17) cm long, (0.8–)0.9–1.6(–1.8) cm wide, all leaves shallowly to deeply sulcate, green or red-brownish on the margins, overground parts of sheaths of the leaves yellowish-green or light to distinctly red-brownish. Scape at anthesis almost green, indistinctly to distinctly reddish-brown (including inflorescence axis), above-ground part (5–)7–14(–17) cm long. Raceme (1–)2–6(–8)-flowered, usually rather lax, 3–7(–9) cm long, usually as long as 1/2 of the above-ground length of scape, tepals (9.0–)10.0–13.5(–14.2) mm long, (3.0–)3.3–4.4(–5.0) mm wide, on both sides equally coloured or rarely a little lighter below, usually pale, rarely deep violet-blue, sometimes with indistinctly lighter, 2–4 mm long spot with diffuse margin at base; filaments (6.0–)6.4–7.6(–8.2) mm long, (0.8–)1.0–1.3(–1.5) mm wide; anthers (3.3–)3.6–4.9(–5.2) mm long; style (3.2–)3.6–4.7(–5.3) mm long; mature capsule 10–16 mm in diameter. Mature fresh seeds 2.5–3.0 mm in diameter, pale to dark brown.

Remarks. Within its geographical area, subsp. *spetana* is represented by local populations, probably isolated geographically for a long period of time, which has apparently led to certain, albeit indistinctive, differentiation among such populations. This is supported by a morphometric analysis of samples from 10 populations from north-eastern Croatia, Hungary, south-western Slovakia, Lower Austria and the Czech Republic (Šarhanová 2008, B. Trávníček *et al.*, in prep.). This between-population morphological variability is most pronounced in the size of floral parts: the population near the village of Mikulčice near the town of Hodonín in South Moravia has on average somewhat larger flower parts than all other known populations of subsp. *spetana*; this population comprises individuals with the largest floral parts within the entire area of *Scilla bifolia*. This population may be classified as a separate variety: var. *magnomoravica* Trávníček (see Appendix).

Between-population differences in subsp. *spetana* involve, to a certain extent, the colouring of the plants as well: those from the vicinity of the town of Břeclav (in the area of the confluence of the rivers Morava and Dyje) usually have more conspicuously reddish-brown tinted stems and leaf sheaths than those from other Moravian localities. Between-population individual variability is similar to that in other subspecies and shows especially in the quantitative characters of most parts of the plant.

Kereszty (1987) and Kereszty *et al.* (1987) report a hexaploid chromosome count (2n = 54, 4x) from the *locus classicus* of subsp. *spetana* in Hungary. Greilhuber & Speta 1985 (see also Greilhuber & Strehl 1985 and Table 1) also obtained exactly the same count from this taxon's single known Austrian locality. Both reports have been confirmed by Kochjarová (2005). The hexaploid count from the population of var. *magnomoravica* near the village of Mikulčice (see above) is also recorded in the literature (under the name *S. bifolia* agg.; Kulová 1991, Kochjarová 2005). Ploidy level screening was performed using flow cytometry in all population samples of subsp. *spetana* analysed morphologically (see above), in which all or at least 85% of the individuals were hexaploid (Šarhanová 2008). In samples of two populations from the Czech Republic, only hexaploid individuals were found; in the third population ascribed to var. *magnomoravica* tetra- and octoploid plants were also disclosed as well as the predominating (90%) tetraploid cytotype. It is remarkable that the co-occurrence of tetraploid (2n = ca 36) and octoploid (2n = ca 72) cells within a single individual was detected via classical chromosome counting (V. Jarolímová, pers. comm.). Kochjarová also found tetraploid plants besides hexaploid ones at a locality in the Malé Karpaty Mts. in Slovakia (under the name *S. bifolia* agg.; Kochjarová 2005).

Nuclear DNA content has been ascertained in plants from both localities of subsp. *spetana* mentioned in the literature (Nadap in Hungary and Kreuttal in Austria) (Greilhuber & Speta 1985, Greilhuber & Strehl 1985, Kereszty 1987). It was established that its value is almost identical at both localities and at the same time significantly lower than in all populations of other taxa within *S. bifolia* (see Table 1). The preliminary estimate of nuclear DNA content in the population of var. *magnomoravica* in Czech territory (B. Trávníček *et al.*, in prep.) also yielded a rather similar result. Some priority should be given to estimating the values of nuclear DNA

content for the remaining populations of subsp. *spetana* as well, and to find out whether this relatively low nuclear DNA content occurs throughout the entire distribution area of this taxon and whether it may thus be regarded as one of its characteristic traits.

KERESZTY (1987, 1993), KERESZTY *et al.* (1987) and ADLER & SPETA (1994) report subsp. *spetana* (as a species) only from the *locus classicus* (near the village of Nadap) and its surroundings in the northwestern part of Hungary and from one locality in Lower Austria (the Kreuttal valley, north of Vienna). But on the basis of a morphological and karyological analysis (ŠARHANOVÁ 2008), at least nine additional populations belong to this taxon. They are situated in a wide strip along the rivers Danube (one locality in north-eastern Croatia, three in Hungary, two in south-western Slovakia and one in Lower Austria) and Moravia (four localities in the south-eastern part of the Czech Republic). Some of these localities were ascribed by previous authors to *S. laxa* (Vučedol near the town of Vukovar in north-eastern Croatia; SPETA 1981a, see also 1982: 8), *S. drunensis* s.str. (near the villages of Pálfa and Kisbajom in south-western Hungary; SPETA 1977b: 38, KERESZTY 1993) or subsp. *buekkensis* (the Malé Karpaty Mts. in south-western Slovakia; TRÁVNÍČEK 1996). It is highly probable that the distribution area of subsp. *spetana* extends even farther south-east and that it also encompasses the hexaploid populations near the village of Bagrdan in the basin of the river Morava in Serbia, which SPETA (1981a: 44, see also SPETA 1982: 8) reports under the name *S. laxa*. Everything suggests that subsp. *spetana* is a Pannonian subspecies of *S. bifolia* that, like the primarily Pannonian species *S. vindobonensis* (in contrast to the Carpathian taxa *S. kladnii* and *S. bifolia* subsp. *buekkensis* and the Alpine *S. bifolia* subsp. *bifolia*), never in its entire area of distribution ascends to higher altitudes, i.e. submountainous and mountainous positions.

In the Czech Republic subsp. *spetana* grows in South Moravia in the lower reaches of the River Morava, in the surroundings of the villages Mikulčice close to the town of Hodonín (var. *magnomoravica*) and Lanžhot near the town of Břeclav. It can also be found in central Moravia at two localities close to one another at the north-western margin of the Chřiby range (near the village of Roštín) and at the adjacent eastern margin of the Litenčické vrchy Hills (near the village of Troubky). The localities lie in the following phytogeographical regions: 18a. Dyjsko-svratecký úval (var. *spetana*), 18b. Dolnomoravský úval (var. *magnomoravica*); 77b. Litenčické vrchy (var. *spetana*); 77c. Chřiby (var. *spetana*). The elevation range of the subspecies extends from the lowlands to the hill country belt, between altitudes of *c*. 150 and 320 m. The northern to north-western border of the subspecies' area of distribution runs through the Czech Republic.

3d. *Scilla bifolia* subsp. *rara* Trávníček (Figs 11c, 12, 13a–c, see Appendix)

Description. Above-ground part of the major leaf at anthesis 5–9(–11) cm long, (0.8–)0.9–1.3(–1.5) cm wide, both leaves markedly sulcate, mostly red-brownish on the margins, overground part of sheaths of the leaves usually with reddish tint. Scape at anthesis usually distinctly reddish-brown (including inflorescence axis), above-ground

part 5–9(–11) cm long. Raceme (2–)4–16(–22)-flowered, usually dense, (2–)3–8(–10) cm long, usually as long as 2/3 of the above-ground length of scape, tepals (7.8–)8.3–10.2(–10.7) mm long, (2.2–)2.4–3.2(–3.5) mm wide, usually vividly violet-blue on inner side, rather dark, often with a markedly paler (to whitish), 2(–3) mm-long section at the base not sharply delineated, usually with an overall markedly paler outer side than inner side (often with pale violet strip on outer side); filaments (4.5–)4.8–6.0(–6.4) mm long, narrow, (0.7–)0.8–1.0(–1.2) mm wide, not prominently dilated towards the base; anthers (2.8–)3.0–4.2(–4.5) mm long; style (1.9–)2.2–3.2(–3.4) mm long; mature capsule 9–13 mm in diameter. Mature fresh seeds 2.4–2.8 mm in diamater, pale to dark brown.

Remarks. Although all three subspecies of *S. bifolia* mentioned above have wide distribution ranges and differ mainly in quantitative characters of individual floral parts, subsp. *rara* is known from only the single locality of the type, and differs from the other three subspecies chiefly in a different set of characters (see above). When samples of populations of subsp. *rara* and of other subspecies were cultivated for several years in similar and favourable conditions, most individuals grew conspicuously robust and an especial difference emerged between subsp. *rara* and the other subspecies in that the ratio between the number of flowers and the length of the entire scape became more pronounced. In subsp. *rara* individuals with a bulb of around the same size as individuals of other subspecies produced a noticeably higher number of relatively small flowers on a relatively short scape, and their inflorescence took up a larger portion of the above-ground part of the scape than in the other subspecies. It is striking that plants of subsp. *rara* have rather small flowers, even considering their ploidy level. The population is tetraploid, but it corresponds to typical populations of the diploid var. *bifolia* (from subsp. *bifolia*) in the sizes of floral parts and not to the tetraploid var. *drunensis*, to which subsp. *rara* is geographically nearest (20–30 km away). At the same time, it was subsp. *rara* in which individuals with the largest number of flowers (20–24) within *S. bifolia* were found during a morphometric analysis (Šarhanová 2008, B. Trávníček *et al.*, in prep.). The comparatively conspicuous darkness and colour of the inside of the tepals of most individuals in the population of subsp. *rara* contrasts with the often-present pale spot with a diffuse margin at the base of the tepals and, in part, the less vividly coloured outside of the perianth as well. In this character as well, the tetraploid population of subsp. *rara* differs markedly from tetraploid populations of var. *drunensis*, which have an overall paler, homochromatic perianth and grow in the adjacent part of south-western Moravia and Lower Austria. The more saturated colouring of the inside of the perianth also appears to correlate with the more distinctly reddish-brown tinted scapes in most individuals of the subsp. *rara* population, in contrast to populations of subsp. *bifolia*, in which most individuals usually have paler scapes, sometimes even almost green below the inflorescence (cf. Speta 1974). It is in the coloration of the perianth and scapes (and the small flowers) that subsp. *rara* somewhat resembles *S. vindobonensis*, so the thought comes to mind that the subspecies may be a

hybridogeneous taxon originated by a cross between *S. bifolia* and *S. vindobonensis*. However, in the colouring of the seeds (dark brown) and the appearance of the elaiosome (composed of spherical structures), the population of subsp. *rara* clearly differs from populations of *S. vindobonensis* and fits perfectly among typical populations of *S. bifolia* (Fig. 13b). A preliminary estimate of the nuclear DNA content of subsp. *rara* (B. Trávníček *et al.*, in prep.) does not indicate a hybrid origin for this taxon because it appears that its value is even lower than would be typical for populations of subsp. *bifolia*, or even the other two subspecies (compare with the markedly contrasting higher nuclear DNA content in *S. vindobonensis*, Table 1). The relatively important morphological differences between populations of subsp. *rara* and populations of all other intraspecific taxa of *S. bifolia* suggest that this taxon may even possibly be treated as a separate species. Nonetheless, the fact that less typical specimens approaching certain individuals, especially of subsp. *bifolia*, are also found in the population of subsp. *rara*, together with the complete correspondence in the colouring and morphology of seeds among subsp. *rara* and other subspecies of *S. bifolia*, support the classification of this population at the rank of subspecies.

The variability of subsp. *rara* is particularly evident in flower colour: as well as plants with perianth typically dark blue on the inside, individuals with notably paler flowers occur at times. A conspicuous difference in habit is evident between individuals with a low number of flowers in the inflorescence and those with far more, but these differences are apparently not conditioned genetically and depend on the age of a plant and the ecological conditions under which it grows. The number of flowers on a plant corresponds roughly to the size of its bulb.

Subsp. *rara* is a tetraploid taxon. Its chromosome count of $2n = 36$ ($4x$) has been obtained from several individuals by the classical method (V. Jarolímová). The tetraploid level has been established exclusively (ŠARHANOVÁ 2008) in all 32 specimens of subsp. *rara* analysed employing flow cytometry. Kulová's report (KULOVÁ 1991) of a hexaploid chromosome count from the population discussed, which has also been adopted by TRÁVNÍČEK (1996, 2002), is almost certainly incorrect.

The subspecies has been found at only a single locality, which is strictly limited in size, in south-western Moravia in the Czech Republic. It grows in the central part of Purkrábka Wood between the villages of Suchohrdly and Těšetice, not far from the town of Znojmo, in the following phytochorion: 16. Znojemsko-brněnská pahorkatina, at an altitude of *c.* 310 m. Subsp. *rara* grows in a moist woodland habitat below a canopy of deciduous trees, especially *Fraxinus excelsior* L., to a lesser extent *Carpinus betulus* L. and *Quercus* sp. In the wider neighbourhood of the locality, mixed and relatively dry (largely secondary) woods prevail. The population is threatened by the planting of coniferous trees (*Pinus sylvestris* L., *Larix decidua* Mill., *Picea abies* (L.) Karsten) in its immediate proximity, and its size is steadily diminishing. It is most probably a rare and critically endangered taxon of the flora of the Czech Republic that deserves the greatest attention possible from the standpoint of nature conservation.

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Souhrn

V článku je diskutováno členění rodu *Scilla* L. (*sensu latissimo*) ve větší počet samostatných úzkých rodů, tyto užší rody jsou – až na výjimky – akceptovány. V souvislosti s tím je navrženo několik nových nomenklatorických kombinací: *Nectaroscilla littardierei* (Breistr.) Trávníček, *Othocallis amoena* (L.) Trávníček, *O. siberica* subsp. *armena* (Grossh.) Trávníček, subsp. *caucasica* (Miscz.) Trávníček a subsp. *otschiauriae* (Mordak) Trávníček. Dále je navrženo členění rodu *Scilla* s.str. na 2 sekce: sect. *Scilla* (zahrnující všechny druhy z širšího okruhu *S. bifolia* agg.) a sect. *Chionodoxa* (Boiss.) Trávníček, která obsahuje taxony řazené dříve do rodu *Chionodoxa* Boiss.; první sekce obsahuje taxony v ČR původní, druhá jen taxony pěstované a zplaňující. Na území ČR (v parku) byl nalezen spontánně vzniklý hybrid mezi druhem *S. bifolia* (subsp. *bifolia*) ze sect. *Scilla* a druhem z okruhu *S. luciliae* agg ze sect. *Chionodoxa*.

V práci je také navržena nová taxonomická koncepce zpracování okruhu *S. bifolia* agg. v ČR, resp. ve střední Evropě a přilehlé části Panonie a Karpat. Jsou rozlišovány 3 druhy: diploidní ($2n = 18$, $2x$), karpatská *S. kladnii* Schur (= *S. subtriphylla* Schur), diploidní ($2n = 18$, $2x$), převážně panonská *S. vindobonensis* Speta a široce rozšířená *S. bifolia* L. Do posledně zmíněného druhu jsou vedle *S. bifolia* s.str. kooptovány i mikrospecie *S. buekkensis* Speta, *S. drunensis* (Speta) Speta, *S. laxa* Schur a *S. spetana* Kereszty. U druhu *S. bifolia* jsou rozlišovány 3 poměrně široce rozšířené, geograficky vikarizující poddruhy: subsp. *bifolia* (Alpy a přilehlá území Evropy; zahrnuje *S. bifolia* s.str. a perialpské populace *S. drunensis*), subsp. *buekkensis* (Speta) Soó (Karpaty a Matricum; zahrnuje *S. buekkensis* a *S. laxa*, resp. karpatské populace dříve řazené k *S. drunensis*) a subsp. *spetana* (Kereszty) Trávníček (Panonie; zahrnuje *S. spetana* a také některé panonské populace dříve řazené k *S. laxa* a *S. drunensis*). Je popsán ještě čtvrtý podruh, subsp. *rara* Trávníček, endemit jediné lokality na jz. Moravě v ČR. Subsp. *bifolia* zahrnuje populace diploidní ($2n = 18$, $2x$), hodnocené jako var. *bifolia*, a tetraploidní ($2n = 36$, $4x$), řazené k var. *drunensis* (Speta) Trávníček a nově z Čech popsané stenoendemické var. *bohemica* Trávníček. Populace subsp. *buekkensis* a subsp. *rara* jsou tetraploidní ($2n = 36$, $4x$). Populace subsp. *spetana* jsou hexaploidní ($2n = 54$,

6x), morfologicky je lze rozlišit ve 2 variety: var. *spetana* a var. *magnomoravica* Trávníček, známou z jediné lokality na j. Moravě. V ČR se vyskytují všechny rozlišované vnitrodruhové taxony druhu *S. bifolia*, vyjma var. *bifolia*. V dílčích populacích jednotlivých poddruhů se občas vyskytují také jedinci s odchylnou ploidií (vyjma subsp. *rara*) a také nezanedbatelný podíl jedinců silně konvergujících svými morfologickými znaky k ostatním poddruhům *S. bifolia*; tudíž všechny 4 poddruhy lze identifikovat jen na úrovni populací, nikoliv na úrovni jedinců.

V ČR se druh *Scilla kladnii* vyskytuje pouze na Moravě v oblasti ovlivněné karpatskou květenou: roste roztroušeně podél řeky Bečvy mezi Vsetínem a Přerovem a na několika lokalitách mezi soutokem Moravy s Bečvou a městem Kroměříž. Druh *Scilla vindobonensis* je nejčastějším zástupcem rodu v ČR, roste v teplejších částech Moravy a Čech: v Čechách především v oblasti Dolního Poohří a Českého Středohoří, izolovaně ještě u Nymburka a v Českém ráji; na Moravě se vyskytuje na dolním toku Dyje (mezi Břeclaví a obcí Ivaň), v jižní části Bílých Karpat, izolovaně na Znojemsku (Višňové), Kroměřížsku (Blazice a Kroměříž) a u Šternberka; v literatuře je zmíněn ještě výskyt u Brna. Druh *S. bifolia* je v ČR velmi variabilní, zastoupený 4 poddruhy. Subsp. *bifolia* je známá pouze z hercynské oblasti. V Čechách roste vzácně v okolí Kolína (pouze var. *bohemica*), na Moravě (pouze var. *drunensis*) na východním okraji Českého masívu ve 2 samostatných arelách: první se nachází mezi Třebíčí a obcemi Moravský Krumlov a Moravské Bránice, druhá mezi obcemi Náměšť na Hané, Laškov a Kostelec na Hané na Prostějovsku. Druhý poddruh, subsp. *buekkensis*, se v ČR vyskytuje pouze na jihovýchodní Moravě mezi Uherským Hradištěm a Uherským Brodem. Subsp. *spetana* roste v ČR pouze na dolním toku řeky Moravy a vzácně v oblasti Středomoravských Karpat na Kroměřížsku (u obcí Roštín a Troubky). Poslední poddruh, subsp. *rara*, je kriticky ohrožený endemický taxon známý pouze z jediné lokality na Znojemsku (les Purkrábka).

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A P P E N D I X

Descriptions of new taxa

Scilla bifolia subsp. *bifolia* var. *bohemica* Trávníček, var.nov. (Figs 5, 6a, b)

Diagnosis. *Scilla bifolia* var. *bohemica* differt a var. *bifolia* et var. *drunensis* perianthi phyllis pallidioribus, dilute violaceis atque seminibus pallidioribus (in vivo fusco-luteis, in sicco fuscis).

Holotypus: C Bohemia, distr. phytogeogr. ”11b. Poděbradské Polabí”: Kobylnice village near Kolín town, bushes along water leading 0.2 km SSE from the settlement of Lanžov, *c*. 205 m.a.s.l., 50°00’33” N, 15°21’46” E, leg. B. Trávníček, 16. IV. 2006, OL (no. 20668). Isotypes: OL (nos. 20669, 20670, 20671).

Derivatio nominis. The name of the variety is derived from its area of occurrence.

Scilla bifolia subsp. *spetana* var. *magnomoravica* Trávníček, var.nov. (Figs 10, 11a, b)

Diagnosis. *S. bifolia* subsp. *spetana* var. *magnomoravica* differt a var. *spetana* perianthi phyllis longioribus (phylla 11.0–13.5 mm longa, non 10.0–12.5 mm ut in var. *spetana*), filamentis longioribus (6.7–7.6 mm, non 6.4–7.3 mm), antheris longioribus (4.2–4.9 mm, non 3.6–4.7 mm) item stylis longioribus (4.0–4.7 mm, non 3.6–4.3 mm).

Holotypus: S Moravia, distr. phytogeogr. ”18b. Dolnomoravský úval”: Mikulčice village near Hodonín town, Skařiny Wood near the archaeological site of ”Mikulčice-Valy”, *c*. 3 km SE of the Lužice railway station, *c*. 160 m.a.s.l., 48°48’30” N, 17°05’27” E, leg. B. Trávníček, 12. IV. 2003, OL (no. 20667).

Derivatio nominis. The name of the variety is derived from the name of the historical empire of ”Moravia Magna”*,* archaeological remnants of which have found near the locality of this taxon.

Scilla bifolia subsp. *rara* Trávníček, subsp.nov. (Figs 11c, 12, 13a–c)

Diagnosis. *Scilla bifolia* subsp. *rara* alliis subspeciebus differt floribus magis numerosis (in plantis robustis florum numerus quasi idem vel superior quam longitudine scapi supraterranei data in numero centimetrorum), perianthi phyllis supra expresse caeruleis, basi (2–3 mm) saepe dilute violaceis usque albidis, subtus plerumque pallidioribus, filamentis plerumque tantum 0.8–1.0 mm latis.

Holotypus: S Moravia, distr. phytogeogr. ”16. Znojemsko-brněnská pahorkatina”: Suchohrdly village near Znojmo town, central part of Purkrábka Wood, *c*. 1.8 km NE of the Purkrábka settlement (along green marked tourist path), stand of *Fraxinus excelsior*, ca. 48°33’ N, 16°07’ E, leg. B. Trávníček, 12. IV. 2003, OL (no. 20666).

Derivatio nominis. The name of the subspecies is derived from the presumed scarcity of the taxon.

New combinations

Nectaroscilla littardierei (Breistr.) Trávníček, comb.nov.

bas.: *Scilla littardierei* Breistr. Bull. Mens. Soc. Linn. Soc. Bot. Lyon 23: 129, 1954.

Othocallis amoena (L.) Trávníček, comb.nov.

bas.: *Scilla amoena* L. Sp. Pl. 309, 1753.

Othocallis siberica subsp. *armena* (Grossh.) Trávníček, comb.nov.

bas.: *Scilla armena* Grossh. Vestn. Tbilis. Bot. Sada, ser. 2, 3: 198, 1927.

Othocallis siberica subsp. *caucasica* (Miscz.) Trávníček, comb.nov.

bas.: *Scilla caucasica* Miscz. Tr. Bjuro Prikl. Bot. 5: 48, 1912.

Othocallis siberica subsp. *otschiauriae* (Mordak) Trávníček, comb.nov.

bas.: *Scilla otschiauriae* Mordak Nov. Sist. Vysš. Rast. 1968: 60, 1968.

Scilla sect. *Chionodoxa* (Boiss.) Trávníček, comb.nov.

bas.: *Chionodoxa* Boiss. Diagn. Pl. Or. Nov. 1/5: 61, 1844.

Scilla bifolia subsp. *bifolia* var. *drunensis* (Speta) Trávníček, comb.nov.

bas.: *S. bifolia* subsp. *drunensis* Speta, Naturk. Jb. Stadt Linz 19(1973): 17, 1974.

### *Scilla bifolia* subsp. *spetana* (Kereszty) Trávníček, comb.nov.

bas.: *Scilla spetana* Kereszty, Symb. Bot. Upsal. 27: 111, 1987.
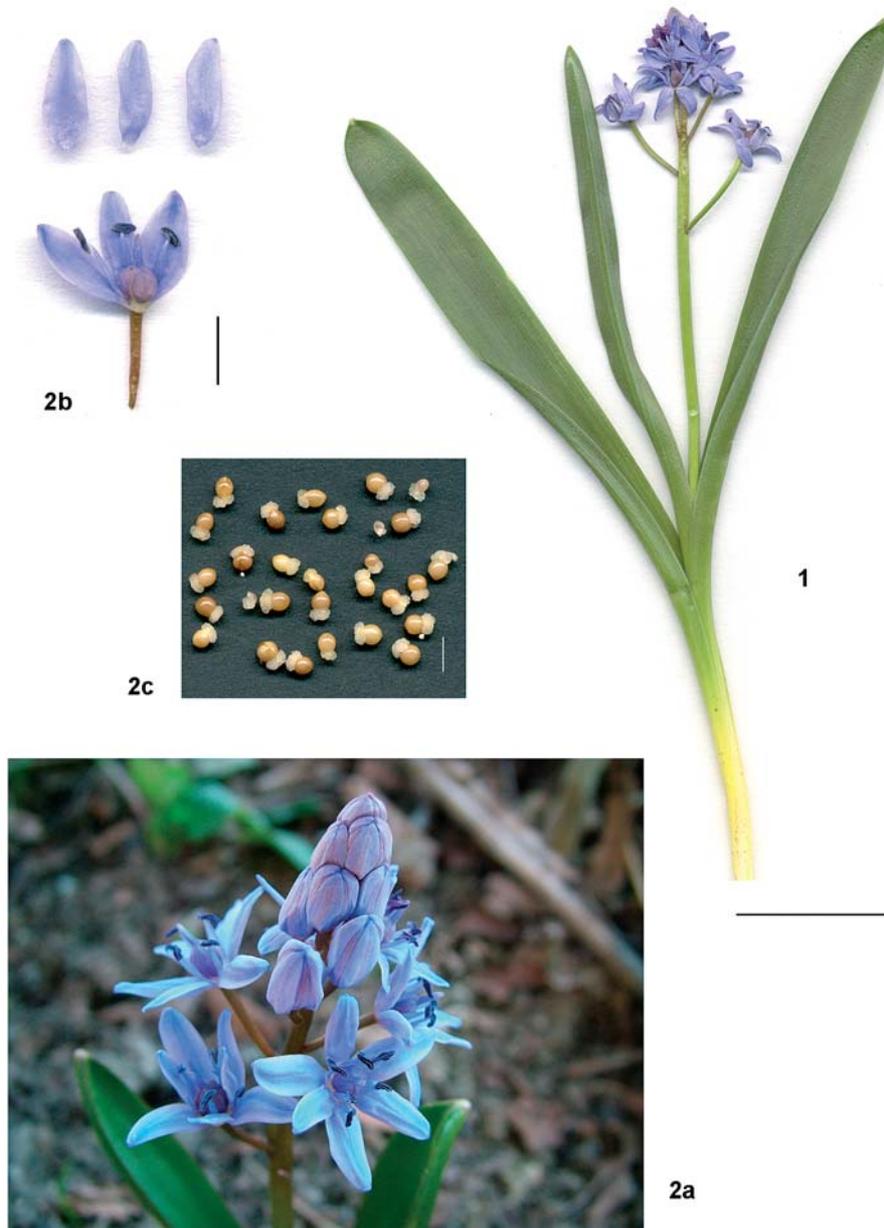
Figs 1–2. 1 – *Scilla kladnii*: general habit, live plant (locality: central Moravia, Troubky nad Bečvou village near Přerov, Chrbovský les Wood), scale bar = 3 cm. 2 – *Ščilla kladnii*: a – photo of inflorescence (locality: central Moravia, Troubky nad Bečvou village near Přerov, Chrbovský les Wood), b – flower (above left – inside of tepals, above right – outside of tepal, locality: Troubky nad Bečvou, Chrbovský les), scale bar = 5 mm, c – seeds (locality: Slovakia, Veľká Fatra range, Mt. Ploská – 1532 m), scale bar = 5 mm.
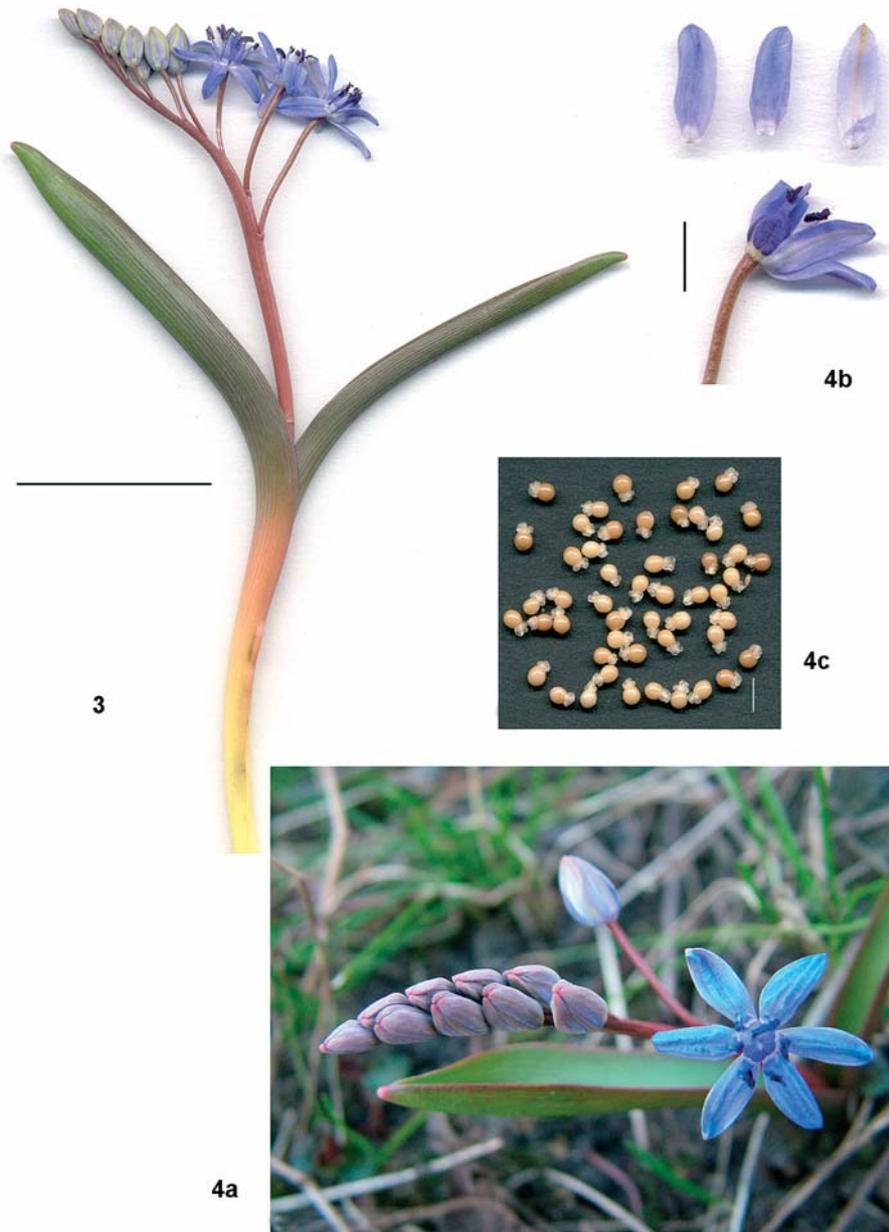
Figs 3–4. 3 – *Scilla vindobonensis*: general habit, live plant (locality: northern Bohemia, Hrdly village near Litoměřice), scale bar = 3 cm. 4 – *Scilla vindobonensis*: a – photo of inflorescence (locality: northern Bohemia, Hrdly village near Litoměřice), b – flower (above left – inside of tepals, above right – outside of tepal, locality: Hrdly), scale bar = 5 mm, c – seeds (locality: northern Bohemia, Zahořany village near Litoměřice), scale bar = 5 mm.
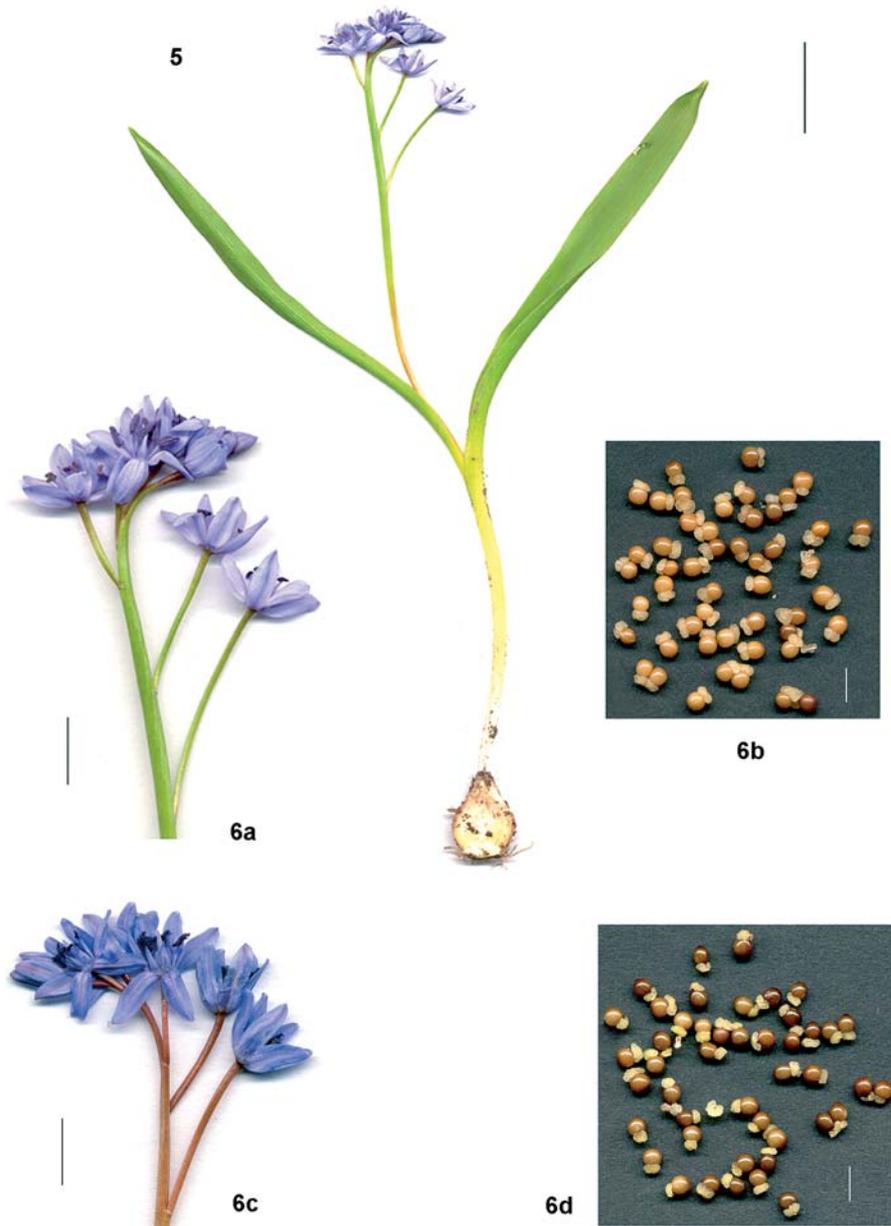
Figs 5–6. 5 – *Scilla bifolia* subsp. *bifolia* var. *bohemica*: general habit, live plant of the holotype specimen (locality: central Bohemia, Kobylnice village near Kolín), scale bar = 3 cm. 6 – a, b: *Scilla bifolia* subsp. *bifolia* var. *bohemica* (locality: central Bohemia, Kobylnice village near Kolín): a – inflorescence, live plant of the holotype specimen, scale bar = 1 cm, b – seeds, scale bar = 5 mm; c, d – *S. bifolia* subsp. *bifolia* var. *drunensis*: c – inflorescence, live plant (locality: central Moravia, Náměšť na Hané village near Olomouc), scale bar = 1 cm, d – seeds (locality: South Moravia, Moravské Bránice village near Ivančice), scale bar = 5 mm.
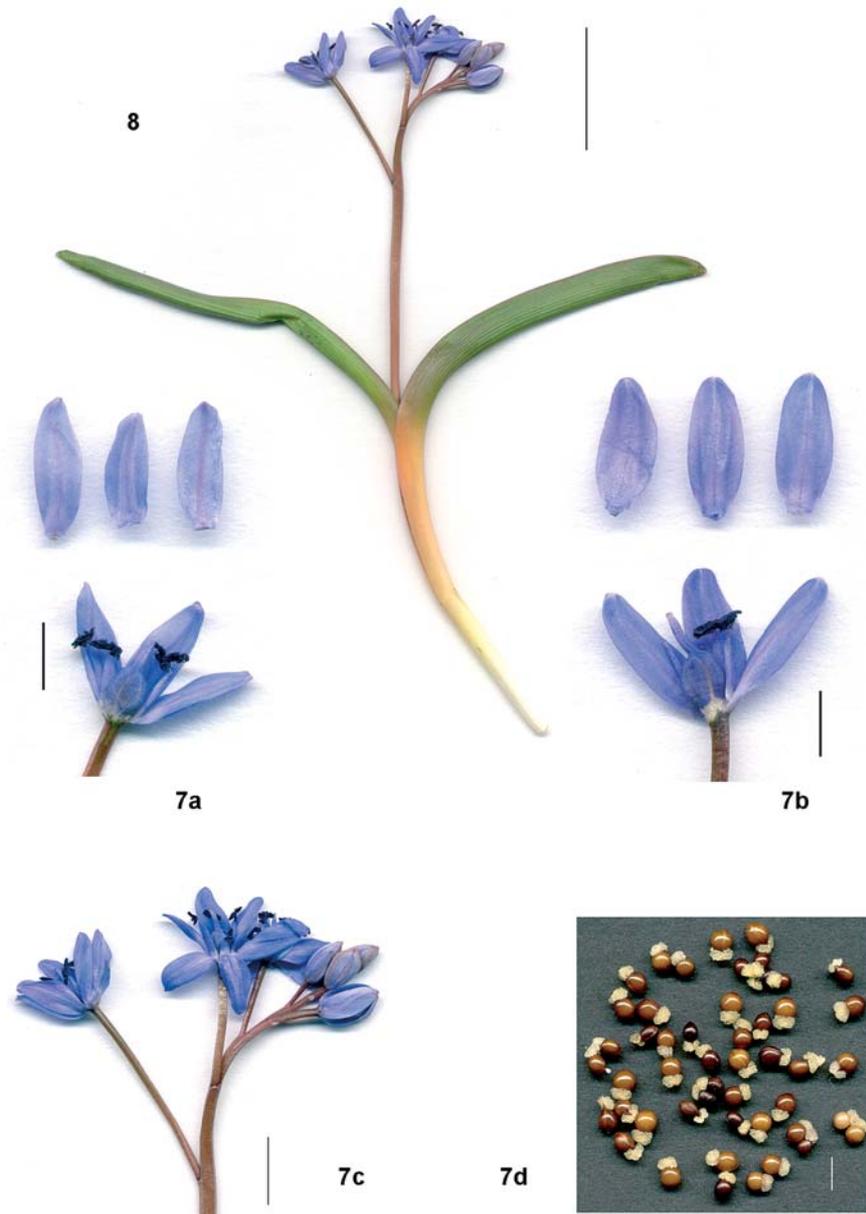
Figs 7–8. 7 – a: *Scilla bifolia* subsp. *bifolia* var. *drunensis*: flower (above left – inside of tepals, above right – outside of tepal, locality: central Moravia, Náměšť na Hané village near Olomouc), scale bar = 5 mm; b–d – *S. bifolia* subsp. *buekkensis* (locality: South Moravia, Vlčnov village near Uherské Hradiště, Vlčnovský háj Wood): b – flower (above left – inside of tepals, above right – outside of tepal), scale bar = 5 mm, c – inflorescence, live plant, scale bar = 1 cm, d – seeds, scale bar = 5 mm. 8 – *Scilla bifolia* subsp. *buekkensis*: general habit, live plant (locality: South Moravia, Vlčnov village, near Uherské Hradiště, Vlčnovský háj Wood), scale bar = 3 cm.
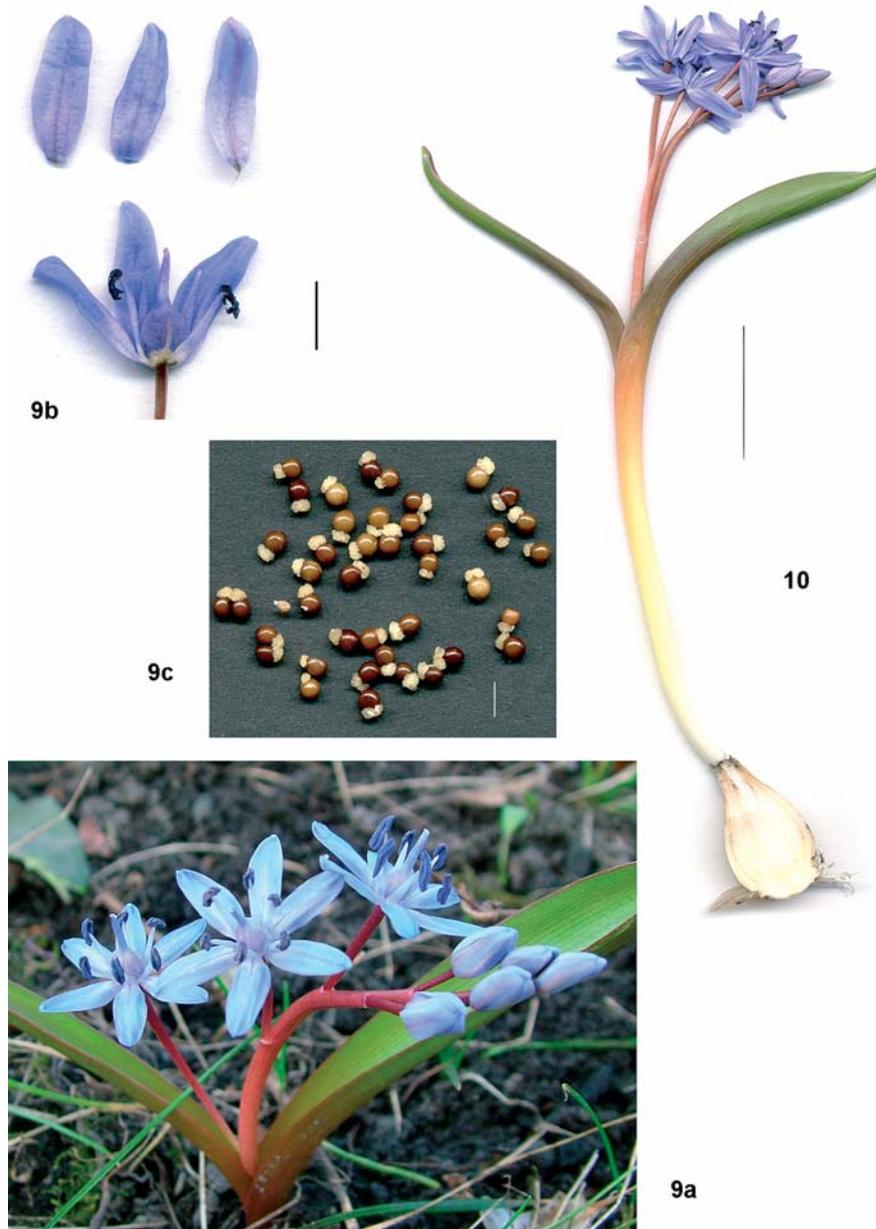
Figs 9–10. 9 – *Scilla bifolia* subsp. *spetana* var. *spetana*: a – photo of inflorescence (locality: south-western Slovakia, Malé Karpaty mountains, Pezinok town), b – flower (above left – inside of tepals, above right – outside of tepal; locality: central Moravia, Troubky village near Kroměříž), scale bar = 5 mm, c – seeds (locality: South Moravia, Lanžhot village near Břeclav), scale bar = 5 mm. 10 – *Scilla bifolia* subsp. *spetana* var. *magnomoravica*: general habit, live plant of the holotype specimen (locality: South Moravia, Mikulčice village near Hodonín), scale bar = 3 cm.
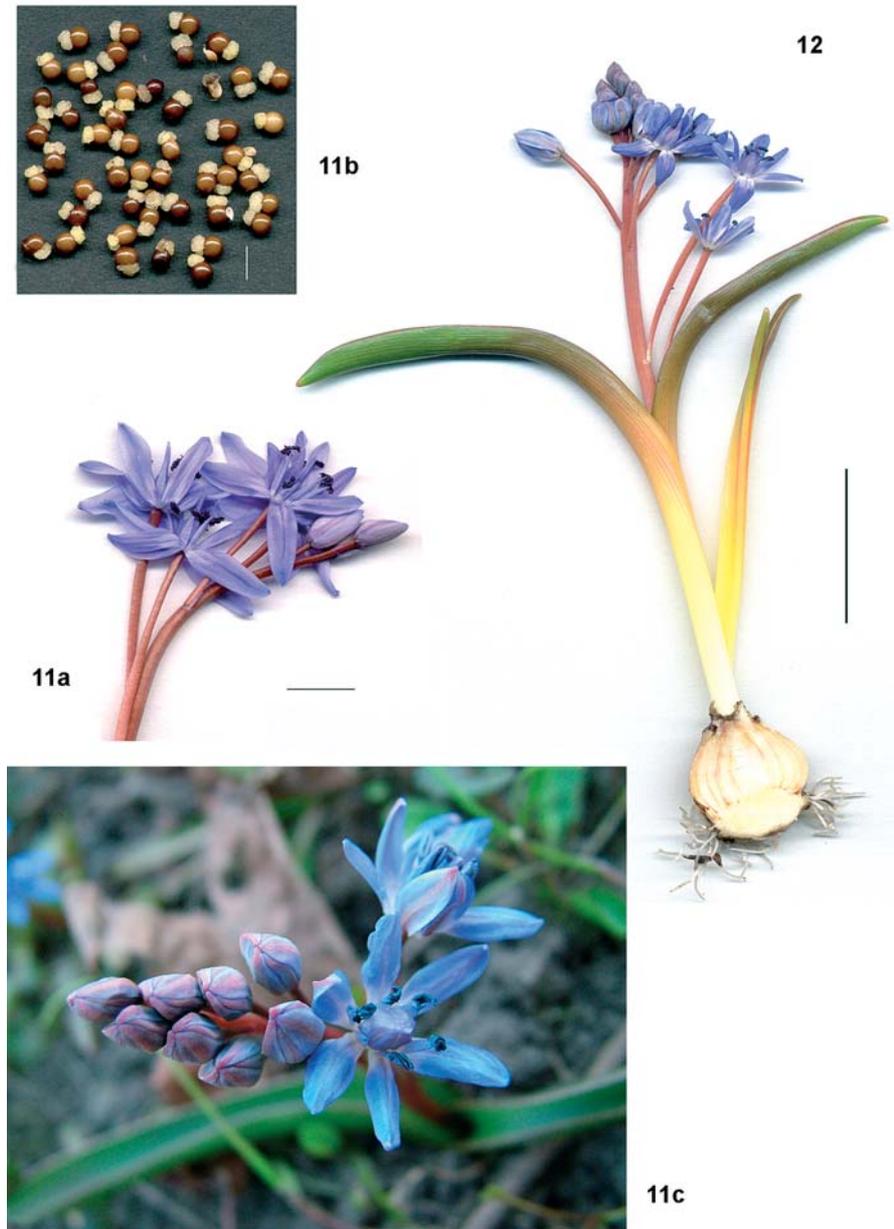
Figs 11–12. 11 – a, b: *Scilla bifolia* subsp. *spetana* var. *magnomoravica* (locality: South Moravia, Mikulčice village near Hodonín): a – inflorescence, live plant of the holotype specimen, scale bar = 1 cm, b – seeds, scale bar = 5 mm; c – *S. bifolia* subsp. *rara*: photo of inflorescence (locality: S Moravia, Suchohrdly village near Znojmo, Purkrábka Wood). 12 – *Scilla bifolia* subsp. *rara*: general habit, live plant of the holotype specimen (locality: South Moravia, Suchohrdly village near Znojmo, Purkrábka Wood), scale bar = 3 cm.

13a

13b

13c

13d

13e
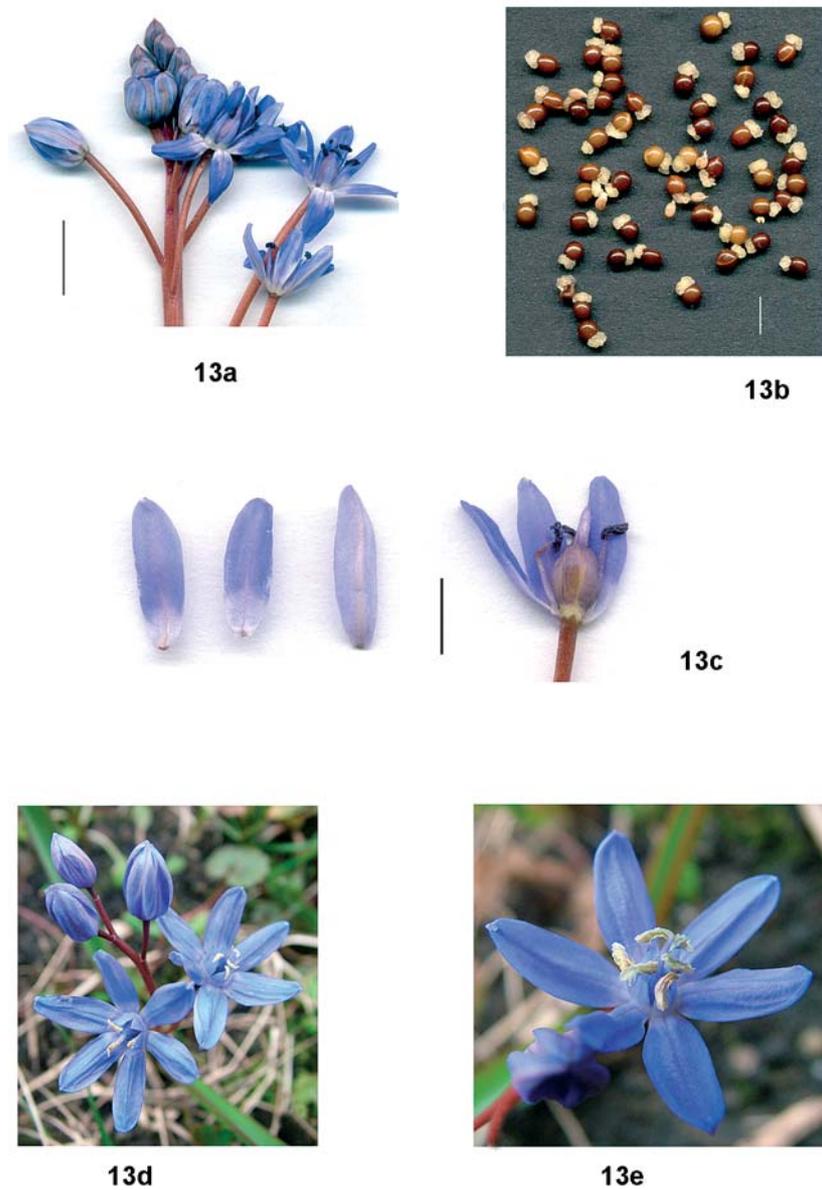
Fig. 13. a–c – *Scilla bifolia* subsp. *rara* (locality: South Moravia, Suchohrdly village near Znojmo, Purkrábka Wood): a – inflorescence, live plant of the holotype specimen, scale bar = 1 cm, b – seeds, scale bar = 5 mm, c – flower (left – inside of tepals, centre – outside of tepal), scale bar = 5 mm; d, e – *S. bifolia* subsp. *bifolia* × *S. luciliae* agg.: photos of inflorescence and flower.