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An account of natural hybridization within *Luzula* sect. *Luzula* (*Juncaceae*) in Europe

Přehled přirozené hybridizace v rámci *Luzula* sect. *Luzula* (*Juncaceae*) v Evropě

Jan Kirschner

Department of Biosystematics, Institute of Botany, Czechoslovak Academy of Sciences, 252 43 Průhonice 1, Czechoslovakia

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A survey of natural hybrids within *Luzula* sect. *Luzula* (*Juncaceae*) is given. Hybrid combinations reported erroneously in the literature are analysed and veritable records are summarized. Taxonomy of the parental taxa is annotated and a new species is described from the Balkan Peninsula (*L. fallax*). Two new natural hybrids were revealed: *Luzula divulgata* × *L. multiflora* (= *L.* × *media*) and *L. fallax* × *L. campestris* subsp. *campestris* (*L.* × *bogdanii*), new localities are given for *L. campestris* × *L. sudetica* (= *L.* × *heddae*), *L. pallidula* × *L. sudetica*. (= *L.* × *hybrida*), *L. multiflora* s.str. × *L. congesta* (= *L.* × *danica*). Binomials are introduced for the above nothospecies. Other hybrids are briefly mentioned as well. Chromosome numbers, ecology and distribution of the hybrids are given and annotated, selected localities are listed. Some of the hybrid combinations were checked by means of experimental crosses (*L. campestris* s.str. × *L. pallidula*, *L.* × *bogdanii* × *L. campestris* s.str. etc.).

Introduction

Alleged or supposed hybridization has played a controversial role in treating complicated variation patterns in plants. In some cases the complex variability of hybrid swarms led the students to describe individual nothomorphs (with various modes of reproduction) as separate taxa. The genera *Mentha* and *Viola* can serve as a good example of this approach in 19th century.

On the contrary, situations when other types of variability are mistaken for results of hybridization are much less frequent and not so easily detectable.

A review of the *Luzula* hybrids reported in the literature

Luzula sect. *Luzula* obviously belongs to the group of taxa where hybridization was regarded as having much greater importance than that it has in reality. On the other hand, true hybrids usually were overlooked or misinterpreted. The greatest monographer of the genus, F. Buchenau (1890, 1906), classes most of the members of the section (as varieties) under the name of *L. campestris*, and finds a series of intermediate forms linking many taxa of this assemblage. Little attention is paid to the hybridization in the first version of his monograph (1890), and only few notes illustrate his concept of intermediates: [var. *multiflora*] "mit den meisten anderen Varietaeten durch Uebergaenge verbunden" (p. 162) and [var. *pallescens*]"zahlreiche Mittelformen, welche ihre Grenzen gegen die Varietaeten *multiflora* und *sudetica* verwischen" (p. 164). In 1906, several (not specified) intermediates are considered as hybrids, and the problem of hybrids is summarized as follows (1906: 95): "Hybridae inter varietates diversas *Luzulae campestris* (Blendlinge) certe haud raro occurrunt, sed difficile agnoscendae sunt." At the same time, some authors are of the opinion that *L. multiflora* easily hybridizes with close species. Ascherson and Graebner (1904: 525) suggest that intermediate forms between *L. multiflora* and *L. pallidula* (as *L. campestris* B. *multiflora* and *L. sudetica* B. *pallescens*) may represent hybrids (in fact, they are pale flowered specimens of *L. multiflora*). Stace (1975: 469) also lists this hybrid combination among the British hybrids but does not consider the evidence available as "sufficient to prove the existence of the hybrid". In addition, Ascherson and Graebner (l. c.) take over a personal communication concerning the occurrence of *L. multiflora* × *L. sudetica* in Bohemia. This report was repeated by Domin (1936), and later this imaginary hybrid was accorded a name *L.* × *dominii* (an invalid one) by Ciferri and Giacomini (1950: 86). Another name that has been believed to belong to the *L. multiflora* × *L.sudetica* parentage is *L.* × *hybrida* Lindb. fil. (Lindberg 1906). However, its original material represents another hybrid combination (*L. pallidula* × *L. sudetica*, see below).

In spite of the fact that *L. multiflora* subsp. *multiflora* frequently occurs at the same localities as *L. sudetica* and *L. pallescens*, I have not seen any unequivocal evidence in favour of the hypothesis that the latter two species form hybrids with *L. multiflora*. It should be pointed out that attempts to carry out these crosses under experimental conditions completely failed, and that alleged natural intermediates proved to belong to *L. multiflora* (in both cases on the basis of both karyology and morphology). Nevertheless, despite the lack of evidence both 'hybrids' are sometimes listed in Floras and Catalogues (e.g., Rothmaler 1976: 653).

A hybrid combination that is most commonly recorded in the literature is *L. campestris* s.str. × *L. multiflora* s.str. Leaving alone the 'intermediates' given in Buchenau (op. c.), the first work devoted to this supposed hybrid is that by Chabert (1896). A later description of *Luzula* × *chabertii* Rouy (1912) is based on the same material (herb. FI). A closer examination of the type collection clearly showed that it represented *Luzula campestris* subsp. *campestris* (Kirschner 1990). Another work dealing with this parental combination contains a description of *L.* × *intermedia* Figert (1897). The original material (according to Rordorff, 1926) ought to have been deposited at the Legnica Museum (=Liegnitz). However, a part of the authentical (but not type) collection is deposited at Goerlitz (GLM). The original description of *L.* × *intermedia* Figert points to *L. multiflora*; the type collection has not been traced up to now. (It is not deposited in HAL.) It should be added that the name *L.* × *intermedia* Figert represents a later homonym of *L. intermedia* Nocca et Balbis 1816 and *L. intermedia* (Thuill.)Spenner 1825, and it was given a new name, *L.* × *ambigua* Soó 1971.

L. multiflora s.str. and *L. campestris* s.str. frequently grow together in mesophilous meadows. However, karyological examination of representative samples from such localities failed to give any evidence supporting the hybridization hypothesis (Buchanan 1960, Kirschner, unpubl.). Attempts to obtain this hybrid experimentally did not give any progeny, either (Nordenskioeld 1956). It can be concluded that *L. campestris* does not hybridize with *L. multiflora*. In many Floras or accounts the hybrid between these two species is listed (usually under the name *L.* × *intermedia* Figert), e.g., Janchen 1960, Rothmaler 1976, Stace 1975. All these works, however, merely repeat the reports analysed above.

An account of more veritable records of hybrids within the section *Luzula* is short. Soon after publication of *L.* × *hybrida* Lindb. fil., the name was recognized to represent *Luzula pallidula* × *L. sudetica* (cf. Hylander 1955: 15). Another hybrid was also found in Scandinavia, *L. campestris* x *L. sudetica* (Hylander 1953, Nordenskioeld 1956). Hedda Nordenskioeld (1956) was the first to report hybrids between *L. campestris* and *L. pallidula*, and *L. multiflora* × *L. congesta*. The latter hybrid was ascertained and documented by J.Buchanan (1960) as well.

Parental taxa of natural hybrids

Luzula sect. *Luzula* as treated in the present paper corresponds to the circumscription proposed by Chrtek et Křísa (1974, 1980). This concept roughly agrees with the subsect. *Luzula* of Kovtonjuk (1987), and to the *Luzula campestris-multiflora* complex of Nordenskioeld (1956). It is an almost cosmopolitan group with a high proportion of continental endemism. Estimates of the number of species in the section vary; in my opinion the section contains at least 45-50 species. There is one particular feature characterizing the variation pattern in the section: the karyological variation mostly corresponds to the morphology of the plants but only few qualitative characters are available to document this fact. Morphological differentiation chiefly manifests itself through quantitative characters with common (although minor) overlaps.

The following survey provides brief data on the distribution, karyology and ecology of the taxa involved in natural hybridization. Notes on nomenclature are given when necessary.

A. Diploids and agmatoploids at the diploid level

1. *Luzula campestris* (L.)DC. in Lam. et DC., Fl. Franc., ed. 3, 3: 161, 1805.

a. subsp. *campestris* - 2n = 12 AL

The geographical range of this subspecies extends from W. and SW. Europe, central Scandinavia and NW. Russia to Ucraine, and the Balkan Peninsula in the southeast (the eastern limit is not known in detail). It most often grows in lawns, short-grass meadows and pastures, usually on acid (sometimes secondarily acidified) shallow soils. Its amplitude also includes mesophilous meadows where it often meets *L. multiflora* subsp. *multiflora*.

b. *L. campestris* s. l. - 2n = 12 AL

In the Balkan Peninsula, Dalmatia, Greek islands, Sicily, Corsica, S. Italy and Iberian Peninsula, a series of populations is found which is close to *L. campestris* s.str. and is characterized by darker flowers, a caespitose or laxly caespitose general habit (stolons usually absent), seeds with short (0.2-0.3 mm) caruncles. There are many names in the literature that may belong to this taxon (or taxa), and the whole problem of these populations requires further studies. This group has been considered as a (rather improbable) candidate for the role of one of the parents of *L.* × *bogdanii* (see below).

2. *Luzula pallidula* Kirschner, Taxon 39: 110, 1990. (= *L. pallescens* auct.)

A widespread Eurasian diploid (2n = 12 AL) occurring from C. Europe to the Far East. It most often grows on mineral (often sandy) soils, frequently in disturbed forest habitats, along paths and wood-clearings, more rarely in grasslands on similar soils. Similar localities were found in the Caucasus and Siberia. It often grows together with *L. divulgata*, *L. multiflora* (in C. Europe), more rarely with *L. campestris*, in the north not so seldom with *L. sudetica*.

3. *Luzula sudetica* (Willd.)Schult. Oesterr. Fl., ed.2, 1: 573, 1814.

European mountain and northern species with the 2n = 48 CL karyotype. It usually grows on deeper peaty soils, most often above the timberline but also at much lower altitudes in northern part of Europe. It occurs in Scandinavia, N. European Russia and in the mountain ranges from the Pyrenees to Greece in the south, and the Carpathians in the east. Its more frequent contacts with other members of the section are confined to Scandinavia (*L. campestris*, *L. pallidula*) and the Alps (*L. alpina*) but in greater part of its range it is found together with mountain forms of *L. multiflora*.

4. *Luzula* **fallax** Kirschner, sp. nov. (Fig. 1)

Plantae dense caespitosae sine stolonibus, rhizomate brevi. Caules erecti, tempore florendi 15-20 cm, dein usque ad 35 cm alti, tenues. Folia basalia numerosa, ± dense ciliata, plerumque usque ad 3(-4) mm lata, folia caulina plerumque numero 2, brevia [ea summa (1.5-)2.5-3.0(-4.5) cm longa] et ad 3 mm lata marginibus dense papilloso-serratis (microscopium !). Bractea infima inflorescentiae semper brevior, (1.2-)1.5- 1.8(-2.5) cm longa, angusta. Inflorescentia plerumque paucicapitulata, ex (2)3-4(6) capitulis pedunculatis et 1(2) subsessili composita, ramis inflorescentiae eramosis, dense papillosis (semper in tertia parte superiore, cf. Kirschner 1982: 28, fig. 1c), rectis vel interdum paulo flexuosis, tenuibus, tempore florendi eis longissimis ca (2.0-)2.5-3.5(- 5.5) cm longis, in fructibus interdum conspicue elongatis. Capitula parva, ovoidea vel hemisphaerica, interdum latior quam longior, pauciflora, plerumque (4.5-)5.0-6.5(-7.5) mm longa et 5.0-6.5 mm lata, capitula ramorum longissimorum (2)4- 6(8)flora. Bracteola membranacea, ovata, 1.0-1.5(-2.0) mm longa, apice ciliata. Tepala ± aequilonga, anguste lanceolata, acuminata vel breviter aristata, obscure brunnea vel castanea, ea externa florum basalium capitulorum ad ramos longissimos (2.5-)2.6-2.9(-3.0) mm longa. Stamina horum florum ca 1.1-1.3 mm longa, antheris ca 0.7-0.9 mm longis (exsiccatis ca 0.5 mm longis), filamentis ca 0.4-0.6 mm longis ca 1.2-1.5 x longior. Ovarium tempore florendi ca 0.7-0.8 mm altum, stylus (0.7-)0.8-1.0 mm longus, stigmate (1.7-)2.0-2.2 mm longo subdeciduo. Segmenta capsularum ellipsoidea, breviter mucronata, brunnea, ca 2.0-2.4 mm longa et ca 1.3 mm lata. Semina ovoidea, (0.9-)1.0 mm longa, 0.7-0.8 mm lata, cum carunculis ca 0.3 mm longis. Chromosomatum numerus diploideus, agmatoploideus 2n=24,karyotypo 2n=24BL.

Typus : Graecia septentrionalis, Mt. Pangeon, ca 0.5 km situ orientali a summo montis, alt. 1800-1850 m s.m. Planta in horto experimentali in Průhonice, Bohemia, sub no L134 a J.Kirschner culta, a. 1990 lecta. E seminibus a cl. S. Snogerup et A. Strid sub no 4934, die 12.7. 1987, lectis. HT in herb. PR asservatur, IT in PR et LD.

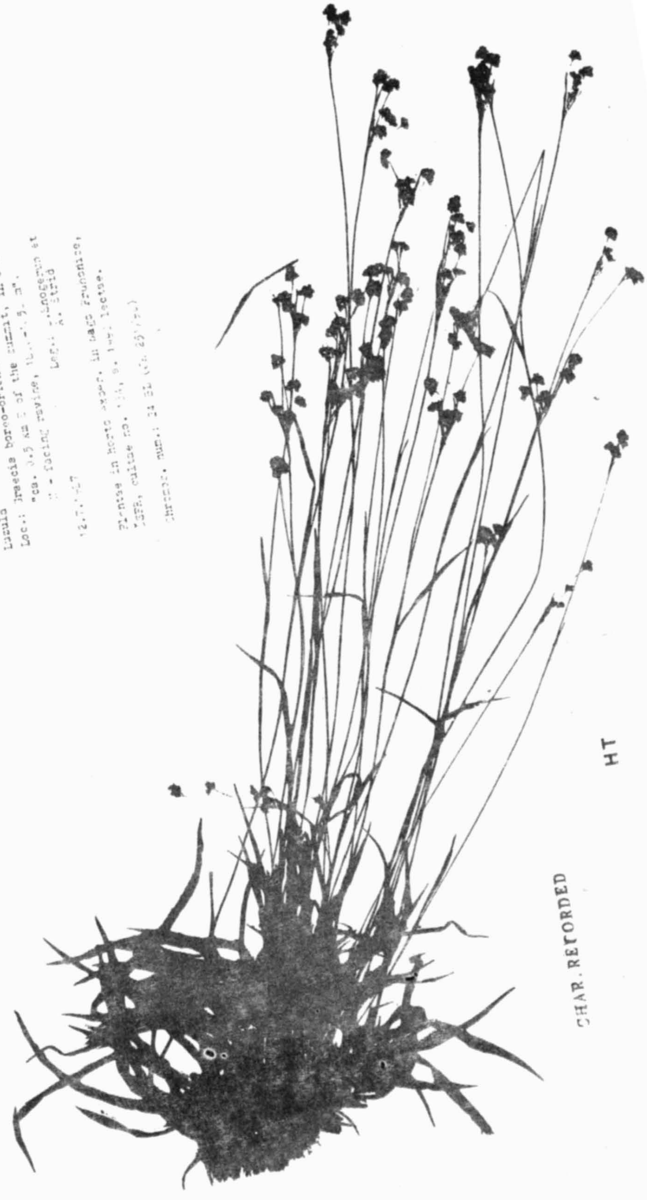


Fig. 1. - *Luzula fallax*. The holotype (PR).

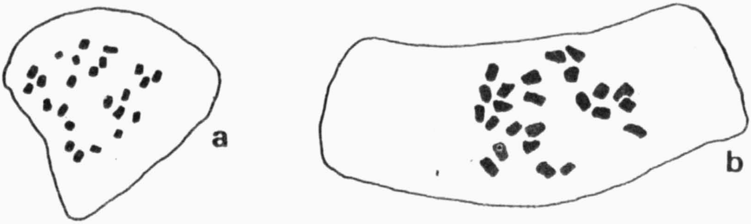


Fig. 2. - Chromosomes of *L. fallax*. a: 2n=24BL, the type. (K251-3/1, L134). b: *Luzula fallax*, an introgressant in the *L.* × *bogdanii* population. 2n=24BL (K159-2/1, L116).

The first impression made by the general appearance of *L. fallax* is that of certain slender pauciflorous forms of the common *Luzula multiflora* with smaller flowers. Although these two taxa are related only very distantly, they can be distinguished by few features. *L. fallax* has less numerous flowers in broader, often hemispherical clusters, the longest bracts are always shorter than longest branches of the inflorescence. Papillose peduncles represent an important feature characterizing *L. fallax*. In addition, caruncles of *L. fallax* are usually shorter than those of *L. multiflora*.

Chromosome number and karyotype: ***Luzula fallax*** represents the first European member of the sect. *Luzula* that proved to be tetra-agmatoploid (i.e. diploid having only BL chromosomes, as understood by H. Nordenskioeld, 1951). Thus, its karyotype is 2n=24=24BL.

Localities of chromosome counts (2n=24 BL):

1. Graecia, Mt. Pangeon (counted sub no 251/90). Fig. 2
2. Bulgaria, Melnik, Mts. Pirin, supra pagum Rožen (sub no 198/89). Fig. 2.

Geographical distribution: ***Luzula fallax*** very likely represents an endemic of Balkan peninsula. Up to now, it has been found in Greece (mountains of Pangeon and Olympos), Bulgaria (the Pirin Mts.), Albania and European Turkey.

Localities: Graecia septentrionalis, Mt. Pangeon, ca 0.5 km situ orient. a summo montis, alt. 1800-1850 m (S.Snogerup et A. Strid, no 4934, 1987 LD); plants cultivated in Bohemia and collected in 1990 as no L134 (PR, LD). - Mt. Pangeon: the SE top, 1700-1836 m (Snogerup 1971 LD). - Graecia, Macedonia, Ep. Pierias: NW foothills of Mt. Olympos, along the Ag. Dimitros - Katerini road 2 km past turn-off to Petra, 300 m. Meadow by a small stream in deciduous oak scrub (Strid et Andersen, no 8440, 1974 LD). - Bulgaria australis, montes Pirin, oppid. Melnik: graminosis in decl. (arenaceis) supra pagum Rožen (supra Solunski preslap) sec. viam in jugo Vlaškija Put. Alt. ca 1450-1550 m s.m. (Kirschner et Kuzmanov 1989 PR). - Albania: Albanisch-montenegr. Grenzgeb., "Wiesen am Kiri bei Skutari (Doerfler 1914 LD). - Turkey (A2E): Istanbul, Silivri, Sinekli: Sinekli and Saray road junction. Macquis. (Delice et Bulut 1977 LD).

B. Polyploids (rarely partial agmatoploids)

5. *Luzula divulgata* Kirschner, Folia Geobot. Phytotax. 14(1979): 431, 1980.

A tetraploid (2n = 24 AL) most common in subcontinental part of east-central Europe, its geographical range extending from Poland, eastern part of Germany, Czechoslovakia and Austria to W. Ucraine and northern Balkan Peninsula. It is confined to the forest biotopes: steep woody slopes with lowered coverage of the herb layer, along paths and wood- clearings, usually in subxerophilous to xerophilous deciduous forests, rarely in shrubby forest-steppe communities in warmer regions. It often grows together with *L. pallidula* and *L. multiflora*, rarely with *L. campestris*.

6. *Luzula multiflora* (Ehrh.)Lej., Fl. Envir. Spa 1: 169, 1811.

a. subsp. *multiflora*

An extremely variable assemblage of hexaploid populations (2n = 36 AL) with wide geographical distribution throughout the whole of Europe (substituted by subsp. *frigida* in the north, and by subsp. *sibirica* in the northeast - behind the Urals). Ecologically it is very catholic, its amplitude embracing both meadow and subalpine and various forest biotopes. It gets into contact with almost all the other European members of the section.

b. *L. multiflora* s. l.

Under this designation, a series of tetraploid (2n = 24 AL) mountain populations of *L. multiflora* is classed. These populations are relatively common in the Alps, and only scattered elsewhere. They rarely grow at same places as other taxa of the section (*L. alpina*, *L. sudetica*, *L. multiflora* subsp. *multiflora*).

7. *Luzula congesta* (Thuill.)Lej., Fl. Envir. Spa 1: 169, 1811.

A W. European and Baltic octoploid (2n = 48 AL). It usually grows on peaty soils in moist meadows and peat-bogs. Sometimes together with *L. multiflora*, rarely with *L. campestris*.

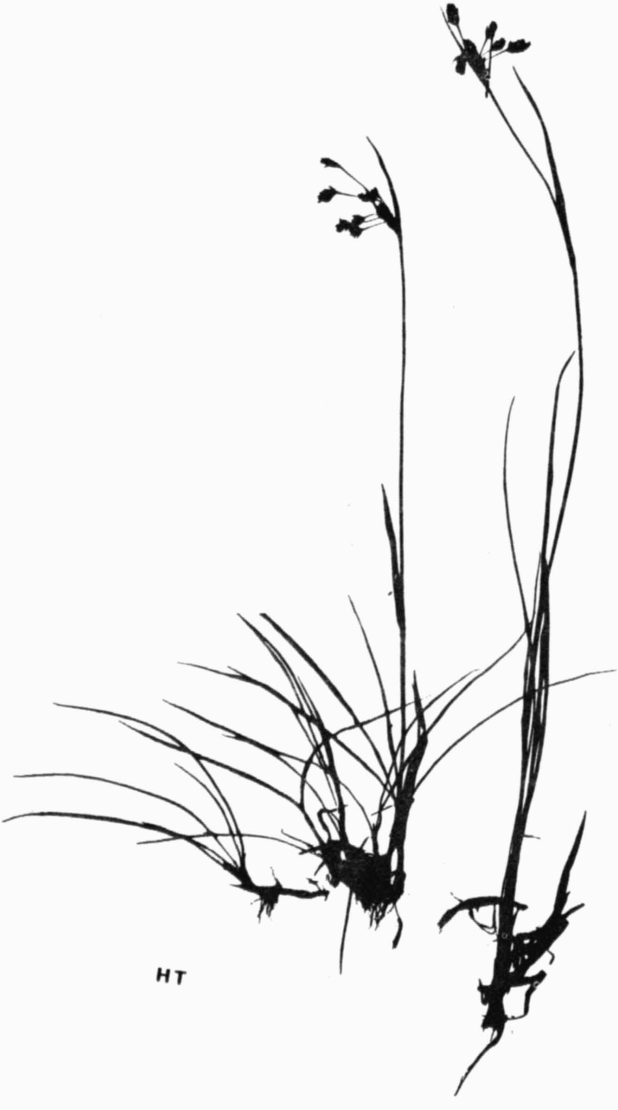
8. *Luzula alpina* Hoppe in Sturm, Deutschl. Fl. 1/77:no.6,1839.

A more detailed data concerning this partial agmatoploid (2n = 36 = 12 AL + 24 BL) is given in Kirschner, Engelskjoen et Knaben (1988). It is very likely confined to the Alps where it is sometimes found at the same localities as *L. sudetica* and *L. multiflora* s.l.

General features of hybridization in *Luzula* sect. *Luzula*

While in most genera data concerning experimental hybridization and compatibility between taxa and ploidy levels is very insufficient and fragmentary, this is not the case with *Luzula* sect. *Luzula*. Hedda Nordenskioeld in a series of excellent works (1951, 1956, 1961, 1966, 1969, 1971 etc. etc.) published results of hundreds experimental crosess among almost all members of the section known hitherto. The crosses involved geographically and taxonomically close species pairs but also very distant taxa. Thus, the few additional experimental crosses I have carried out in the course of the study presented here provide some concrete special evidence (see the special part of this study) but cannot add any new general idea. The following points summarize the Nordenskioeld experimental results and give the background for understanding the rules of natural hybridization in the section.

1. Experimental crosses between diploid taxa with the 12 AL karyotype are successful and give rise to usually fertile F1 and F2 progeny.
2. Experimental crosses between diploid species with 2n = 12 AL and agmatoploids of the diploid level give sterile F1 or a progeny with strongly suppressed fertility.
3. Experimental crosses between diploids (including the agmatoploids of the diploid level) and all polyploids fail completely.



3. - *Luzula × heddae*. The holotype (PR).

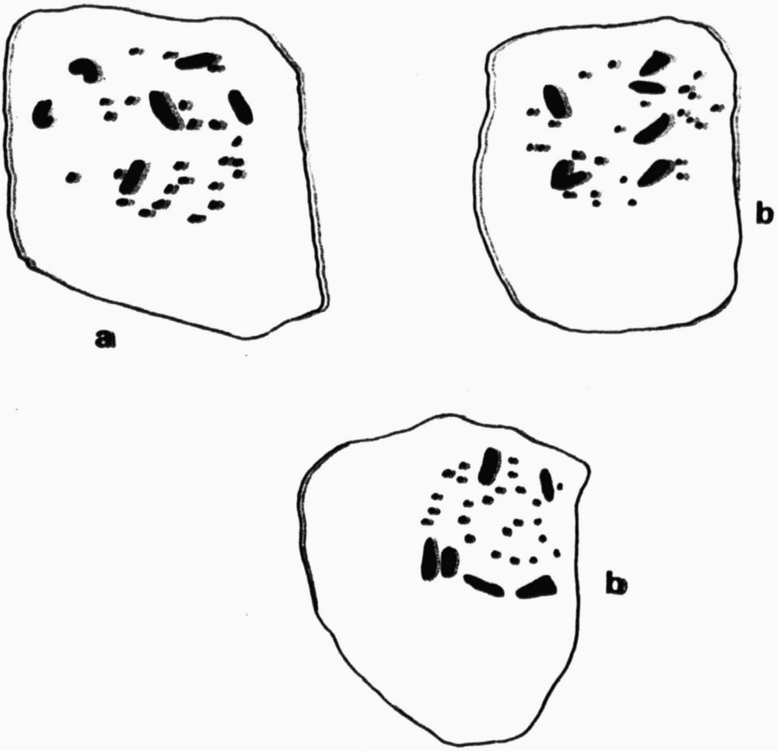


Fig. 4. Chromosomes of *L.* × *heddae*. a: 2n=6 AL+24 CL (L333/1). b: 2n=6 AL+24 CL (L384/2).

4. Experimental crosses between close tetraploids or between tetraploids and hexaploids are often successful and give at least partly fertile progeny. Some crosses between geographically distant parents fail to give fertile progeny.
5. Attempts to hybridize tetraploids with the only octoploid completely fail.
6. Experimental crosses between hexaploids and the octoploid provide partially fertile progeny.

From the above studies and from my field observations, an additional conclusion can be made: hybridization within the section (and the frequency of the hybrid plants) in the nature is very unevenly distributed. While in large territories of W. Europe only one hybrid can be found (and in the whole N. and north-central Russia none is present), in C. Europe and Scandinavia three or four hybrids are known. In New Zealand not less than six hybrids of this group were detected (Edgar 1966). In most of Europe the hybrid plants of this group are rare and scattered, in the Balkan Peninsula hybrids occupy large localities and are met with rather frequently.

In the course of analyses of my gatherings from Bulgaria, a certain proportion of the plants turned out to have very complicated karyotypes showing a complex agmatoploidy, very likely of hybrid origin. Neither in field, nor in herbarium material it was possible to find their parents or closer relatives among the taxa known from that territory. In addition, the populations were morphologically variable and were found in synanthropically disturbed vegetation. Whether or not these plants represent hybrids, and through what parentage they came into being will be studied on a more complete live material.

In the studies of H. Nordenskioeld (e.g., 1956) a great effort was given to elucidate all the experimental aspects of compatibility relationships and chromosome behaviour of the artificial hybrids. Natural hybridization in Europe was dealt with marginally in Nordenskioeld, op. c., pp.51-52. The accounts of the section in Australia and New Zealand, however, give very important information concerning natural hybrids (1966, 1969).

The survey presented therefore (1) reviews critically the hybrids within the sect. *Luzula* reported in the literature, (2) summarizes veritable literature data, (3) gives newly revealed hybrids or new localities, (4) annotates more complicated cases of taxonomic complexity, and (5) consolidates the nomenclature of those hybrids where the evidence available is adequate.

A. Diploid hybrids

1. *Luzula campestris* subsp. *campestris* × *L. sudetica* (= *L.* × *heddae*, Fig. 3)

A completely sterile hybrid of an intermediate general appearance. Both natural hybridization and experimental crosses only give rise to F1s, which is also confirmed by chromosome number of the hybrid plants (see below). In the course of meiosis six large multiassociations and a few CL univalents were observed by Hedda Nordenskioeld (1956: 33). In central Europe, the hybrid comes into being very rarely, at the marginal points of both altitudinal and ecological ranges of the parental species. Ecologically, these narrow overlaps represent (in central Europe) contact zones between mesophilous meadows or pastures and wet sedge meadows on peaty soils, always close to the parents. Another feature of this occurrence is the fact that hybrid plants are confined to disturbed sites as, for instance, spots without vegetation (e.g., tyre tracks). This also suggests lowered competitive ability of the hybrid. The altitudinal overlap is very likely narrower in C. Europe (from ca 600 to 900 m) than in Scandinavia, and, in the latter region, the common occurrence of the parental species is more frequent as well. Thus, this hybrid is not rare in Sweden.

Karyology: A very characteristic karyotype provides an excellent confirmation of hybridity in this case. As a result of sterility, the karyotype is 'F1 frozen' and remains constant. It is in a good agreement with that published by H. Nordenskioeld (1956).

$2n = 30 = 6\ AL + 24\ CL$ (Fig. 4)

Localities of the chromosome counts:

1. Bohemia, Český Herálec, Skelné Hutě (no 334/2)
2. Bohemia, Hlinsko, Rváčov (no 333/1).

Distribution: Cz, He, Su

Selected herbarium specimens: Czechoslovakia: Bohemia orientalis, opp. Hlinsko, oppidulum Český Herálec, in prato udo haud procul a casa venatoria (et vico) Skelné Hutě dicta; una cum *Carex disticha*, rare inter parent. (Kirschnerová et Kirschner 11.7.1990 PR). - Bohemia orientalis, opp. Hlinsko, ad marg. orient. pagi Rváčov (Kirschnerová et Kirschner 1990 PR). - Switzerland: Kt. Waadt, Les Mosses (Mermod 1883 LAU,cf. Samuelsson 1922: 246). - Sweden: Dalsland, Edskskog, Radane (Samuelsson 1918 LD). - Dalsland, Mo, Oejersbyn (Samuelsson 1918 LD). - Naerke, Kit, Ramskyttan (Samuelsson 1918 LD). - Vaermland, Svanskog, Graensjoen (Samuelsson 1918 LD). - Naerke, Svennevad, Zettermanstorp (Kjellmert 1941, 1942

Tab. 1. - Differences between *L. sudetica*, *L. campestris* and their hybrid.

	L. sudetica	L. x heddae	L. campestris
rhizome	oblique, branched, usu. long	creeping	creeping to oblique, long
stolons	absent	short, ascending	creeping
heigth [cm]	9-27	16-35	5-25
width of leaves [mm]	1.5-4.0	1.8-2.3	3-4
bracts	1.5-3.5 cm long, longer or equalling the inflorescence	1.5-3.5 cm long, equalling the inflorescence or shorter	1.0-1.5 cm long, shorter than the inflorescence
number of clusters	3-9	3-7	2-6
peduncles	erect (or very short)	erect, often flexuose, sometimes recurved	some of them recurved
number of flowers in a cluster	(5)7-11(15)	6-10	(3)4-7(9)
outer tepals	longer than the inner ones	subequal to longer than inner ones	equalling the inner ones
tepal length [mm]	1.9-2.7	2.8-3.0	2.8-4.1
anthers [mm]	0.5-0.7	(1.0)1.2-1.3	1.1-2.1
anther-filament ratio	1.0-1.5	2.5-3.0	(2)3-4
length of stigmas [mm]	1.0-1.4	2.5	(1.5)2.0-3.0 (4.2)
flower colour	blackish brown	blackish to dark brown	usually chestnut or brown coloured
fertility	fertile	sterile	fertile

Fig. 5. *Luzula × hybrida*. The holotype (LD).

LD). - Vaestmanland, Grythyttan, Hagen (Samuelsson 1918 LD). - Nora, Pershyttan (Samuelsson 1918 LD). - Ramsberg (Samuelsson 1935 LD). - Naerke, Kvistblo s:n, Ribbokyttan (Waldheim 1934 LD).

Nomenclature of *L. campestris* subsp. *campestris* × *L. sudetica*

Luzula × **heddae** Kirschner, nothosp. nov. (Fig. 3)

Diagnosis: Planta sterilis, a *L. sudetica* stolonibus longis, pedunculis interdum nutantibus, plerumque flexuosis, floribus majoribus, antheris multo longioribus (et eis filamentis 2.5-3.0 × longioribus) necnon stigmatibus longioribus differt. A *L. campestris* foliis et capitulis angustioribus, tepalis plerumque inaequilongis, obscurioribus, antheris brevioribus differt (cf. Tab. 1).

Typus: Bohemia orientalis, oppidum Hlinsko, solo denudato inter viam publicam et pratulum turfosum ad marg. orient. pagi Rváčov. Disperse inter parent. (Kirschnerová et Kirschner 9.7.1990) HT in herb. PR, isotypi in herb. PR et LD asservantur.

2. *Luzula pallidula* × *L. sudetica* (= *L.* × *hybrida*, Fig. 5)

Again a completely sterile product of hybridization between comparatively closely related species (*L. sudetica* seems to represent a descendant of *L. pallidula*). Both natural hybrids and progeny of experimental crosses are very homogeneous morphologically ('frozen F_1s') and karyologically. In central Europe the parents get only very rarely into contact, the most likely localities being in moist montane grassy wood-clearings (at the altitude of 800-900 m). However, the only stand of this hybrid revealed in C. Europe (Bohemia) harbours only one of the parents (*L. sudetica*) together with the hybrid plants (see also a note below). Another peculiarity of this locality consists in the fact that it lies at the western limit of the distribution of *L. pallidula*. By contrast, in Scandinavia the parental species are often found growing together, and the hybrid is not rare, either.

Karyology: Similarly as with the previous hybrid, *L. pallidula* × *L. sudetica* is characterized by F1 intermediate karyotype with chromosomes of diverse size. $2n = 30 = 6$ AL + 24 CL (Nordenskioeld 1956: 33, an artificial hybrid).

Distribution: Cz, Su, Fe

Selected herbarium specimens: Czechoslovakia: Bohemia occidentalis, montes Krušné hory, opp. Nejdek, pagus Přebuz, in prato silvatico haud procul a riv. Jelení potok, ca 400 m supra confluentem cum fl. Rolava, ca 2 km situ bor.-or. a pago Přebuz. Alt. ca 860 m s.m. (Štěpánek 1990 PR). - Sweden: Vaestmanland, Grythytte s:n, Braten (Binning 1921 LD). - Finland: Torne Lappmark, Vittangi, in sphagneto versus Taerpijaervi (Holmberg 1929 LD). - Savonia bor., par. Jorois, Lapinmaeki (Lindberg 1904 LD, PR). - Ks., Posio, Kaski-Posio, SE of Salmela hills (Marklund 1949 LD). - Ok, Paltamo and Kuusamo (H, cf. Lindberg 1906: 11).

Nomenclature of *L. pallidula* × *L. sudetica*

H. Lindberg (1906) devoted a brief report to the finding of this hybrid, and introduced a binomial, *L. hybrida* (the plants in question were mistakenly considered as *L. multiflora* × *L. sudetica)*. However, Lindberg failed to give any description and the name was published invalidly at that time. I have done an unsuccessful search to find any validating diagnosis. The name is validated in what follows.

Luzula × **hybrida** Lindb. fil. (1906) ex Kirschner, nothosp. nov. (Fig. 5)

Diagnosis : Planta sterilis, sine stolonibus, rhizomate obliquo, foliis longis angustisve. Bractea infima (=longissima) inflorescentia plerumque conspicue longior. Inflorescentia pedunculis glabris (non papillosis), rectis, ± erectis usque erecto-patentibus. Flores minimi, tepalis inaequilongis.

Fig. 6. - *Luzula campestris* subsp. *campestris* × *L. pallidula*. An F$_1$ plant from the experimental cross 150/3x151, *L. pallidula* = fem.

Tab. 2. - Differences between *L. campestris*, *L. pallidula* and their hybrid

	L.campestris	the hybrid	L.pallidula
habit	laxly caespitose	densely caespitose	densely caespitose
stolons	present	absent	absent
heigth of plants [cm]	(5)10-17(25)	20-25	(9)12-20(30)
width of basal leaves	3-4 mm	usually 2.0-2.5 mm	usually 2 mm
lower bract	shorter than inflorescence	shorter than inflorescence	usually longer than inflor.
number of clusters	2-6	8-15	6-22
peduncles	some of them recurved	erect to flexuose	erect
secondary branching of peduncles	absent	present	present
number of flowers in a cluster	usually 4-7	usually 6-8	usually 10-20
shape and size of clusters	broadly ovoid 5-8 x 4-6 mm	ellipsoidal 7-8 x 6 mm	cylindrical 4-7 x 3-4 mm
outer tepals	equalling the innner ones	+/- equalling innner ones	conspicuously longer
outer tepal length [mm]	(2.8)3.1-3.6 (4.1)	2.9-3.2	(2.0)2.2-2.5 (2.8)
anthers [mm]	(1.1)1.3-2.1	0.7-1.0	(0.4)0.5-0.6
anther/filament ratio	usually 3-4	ca 2	ca 1
styles [mm]	0.9-1.6	ca 0.7	0.2-0.3
stigmas [mm]	1.5-4.2	1.3-1.7	0.5-0.6
seed width[mm]	0.8-1.0	0.6-0.7	0.5-0.6
papillosity of the peduncles	absent	below the clusters	papillose throughout
caruncles [mm]	0.4-0.7	0.4	0.2-0.3

Tab. 3. - Characters and character states used in the PCA

A. Papillosity of the peduncles	1. Densely papillose 2. Densely papillose only in the upper 1/3-1/4 of the peduncles 3. Slightly papillose, almost smooth 4. Smooth
B. Stolons and/or creeping rhizomes	1. Present 2. Absent
C. Peduncles ('reflexed' has preference over 'flexuose')	1. All +/- straight 2. Some of them flexuose 3. Some of them reflexed
D. Length of the outer tepals (basal flowers of pedunc. clusters)	[mm]
E. Length of anthers	[mm]
F. Anther/filament length ratio	
G. Length of stigmas	[mm]
H. Length of seeds	[mm]
I. Width of seeds	[mm]
J. Length of caruncles	[mm]

Note: Differences between the measures given in the Tab. 4 and those in the description are due to the fact that live plants were measured for the descriptions while dry ones were analysed for the PCA.

Typus: Finland, Savonia borealis, par. Jorois, Lapinmaeki (H. Lindberg fil., 2.7.1904, LD).[The same material (IT) also distributed as Plantae Finlandiae Exsiccatae, no 156 ut *L. multiflora* × *L. sudetica* = *L.* × *hybrida*, e.g., LD,BP,PRC]

Description: Sterile F_1 plants. Stems (25)30-45 cm long, rhizome oblique, comparatively long, without stolons. Inflorescence composed of 5-11 pedunculate clusters (or 2-3 of them subsessile), lower bract equalling or overtopping the inflorescence. Clusters ± cylindrical, usually not wider than 4 mm, number of flowers variable, most often 5-20. Peduncles straight, erect to erecto-patent, smooth (not papillose), secondary branches frequently present. Flowers very small (of the same size as those of *L. pallidula* or a little smaller), tepals usually unequal, the outer ones 2.0-2.3 mm long, the inner ones ca 1.8-2.0 mm long, brown, pale brown to dark (blackish) brown, with broad pale margin in the upper half. Stigmas short (ca 1.0 mm long), anthers ca 0.5 mm, filaments ca 0.5-0.6 mm long.

3. *Luzula campestris* subsp. *campestris* × *L. pallidula* (Fig. 6)

This hybrid between species with the same karyotype is characterized by a relatively high fertility and conspicuous segregation in the F_2 generation. The parental species can sometimes be found growing together at their localities both in C. and N. Europe. Ecologically,

Tab. 4. - Original data used in the PCA. Letters correspond to those in Tab. 3, case numbers to those in Tab. 5

	A	B	C	D	E	F	G	H	I	J
1	4	1	3	3.6	1.3	2.4	3.2	0.95	0.85	0.50
2	4	1	3	3.3	1.2	2.4	2.9	1.05	0.90	0.55
3	3-4	1	3	3.6	1.3	2.6	2.5	1.10	0.80	0.45
4	2	2	2	3.1	1.0	2.8	1.9	0.90	0.70	0.30
5	2-3	1-2	2	3.1	0.9	2.2	1.8	0.90	0.70	0.40
6	3-4	1-2	2-3	3.3	0.85	1.9	2.2	0.95	0.70	0.40
7	4	1-2	3	3.5	1.3	2.6	2.8	1.00	0.90	0.50
8	3-4	1-2	3	3.2	1.2	2.6	2.0	0.90	0.70	0.35
9	2-3	2	2	3.0	1.1	2.2	1.8	1.00	0.80	0.40
10	2	2	2-3	3.4	1.1	2.7	2.4	0.90	0.70	0.30
11	3-4	1	2	3.4	1.1	1.8	2.3	1.10	0.80	0.50
12	2-3	2	1-2	2.8	0.9	2.0	1.9	1.00	0.70	0.40
13	3	2	2-3	3.3	1.0	2.0	2.5	1.10	1.00	0.50
14	3	2	2-3	3.4	1.1	2.25	2.9	1.10	0.90	0.30
15	3-4	2	2	3.5	1.1	2.7	2.8	1.10	0.90	0.35
16	3	2	3	3.7	1.3	2.6	3.1	1.10	0.90	0.40
17	2-3	1-2	2	3.3	1.0	2.0	2.3	1.00	0.85	0.35
18	2	2	3	3.3	1.2	2.4	2.4	1.00	0.85	0.30
19	3-4	2	2-3	3.7	1.4	2.8	3.2	1.10	1.00	0.60
20	1-2	2	2	3.1	0.9	1.8	1.8	1.05	0.80	0.35
21	3	2	1-2	3.3	1.0	1.7	2.3	1.00	0.85	0.35
22	1	2	1-2	3.0	0.9	1.8	1.8	0.95	0.75	0.35
23	2-3	2	3	3.5	1.3	2.2	2.7	1.20	0.90	0.65
24	3	2	2-3	3.5	1.2	2.6	2.8	1.10	0.90	0.50
25	2-3	2	2	2.9	0.8	1.4	1.8	1.05	0.80	0.25
26	2	2	2	2.9	0.8	1.6	1.8	1.00	0.80	0.30
27	2	2	1-2	3.2	0.9	1.8	2.6	1.00	0.85	0.40
28	2-3	2	2	3.2	1.0	2.2	2.2	1.00	0.90	0.45
29	2-3	2	2-3	3.6	1.3	2.9	2.4	1.15	0.90	0.35
30	2-3	2	2	3.3	1.0	2.0	2.2	1.00	0.90	0.30
31	1	2	1-2	2.6	0.55	1.2	1.9	0.95	0.70	0.30
32	1	2	1-2	2.7	0.75	1.6	2.1	1.00	0.70	0.35
33	3	2	2	2.8	0.8	2.0	1.8	0.95	0.80	0.30
34	1-2	2	2	2.6	0.75	1.9	2.0	1.05	0.80	0.35
35	2	2	2	3.2	1.0	2.2	2.2	1.00	0.80	0.40
36	3	2	2	2.9	0.8	2.0	1.8	0.90	0.75	0.30
37	4	1-2	3	3.4	1.4	1.8	3.5	1.20	1.00	0.65
38	3	1-2	2-3	2.9	1.2	2.4	2.8	1.15	1.00	0.60
39	4	2	1-2	3.3	0.8	1.3	3.0	1.05	0.85	0.25
40	4	2	1	3.3	1.0	1.9	2.9	1.10	0.80	0.25
41	3	2	2	3.2	0.8	1.6	2.8	1.10	0.80	0.25
42	3-4	2	2-3	3.2	0.9	1.8	2.8	1.00	0.75	0.20
43	3-4	2	2	3.3	0.8	1.6	2.6	1.05	0.85	0.25

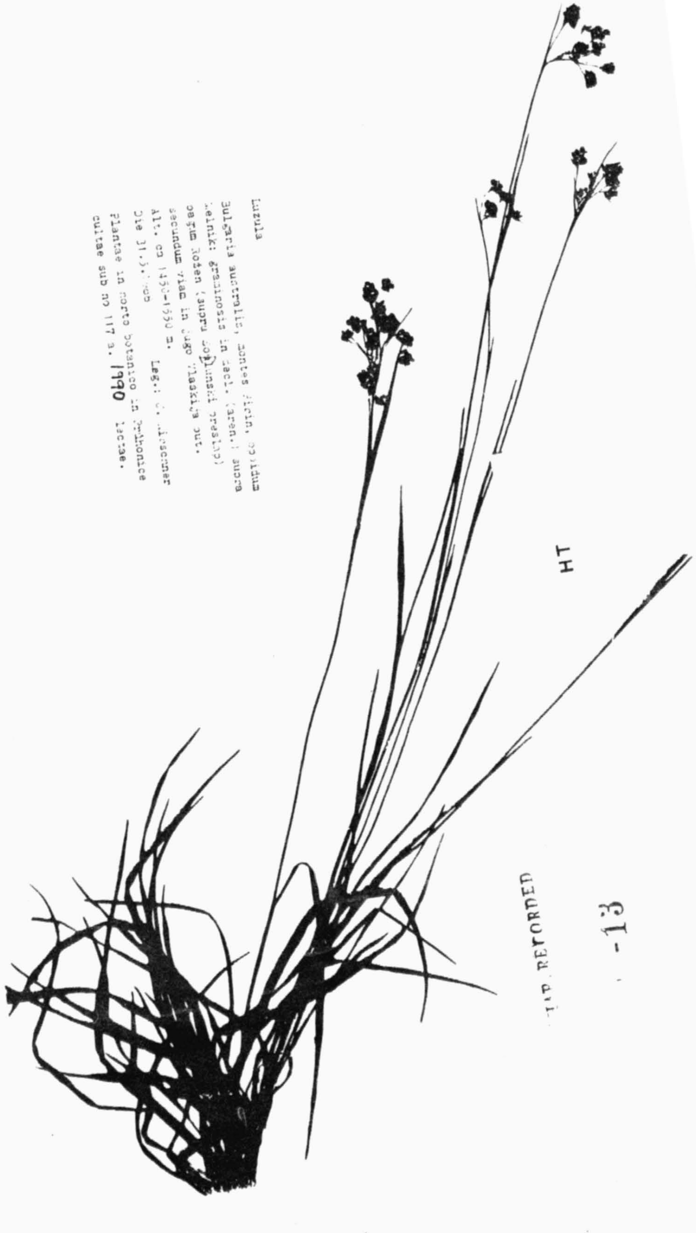


Fig. 7. - *Luzula × bogdanii*. The holotype (PR).

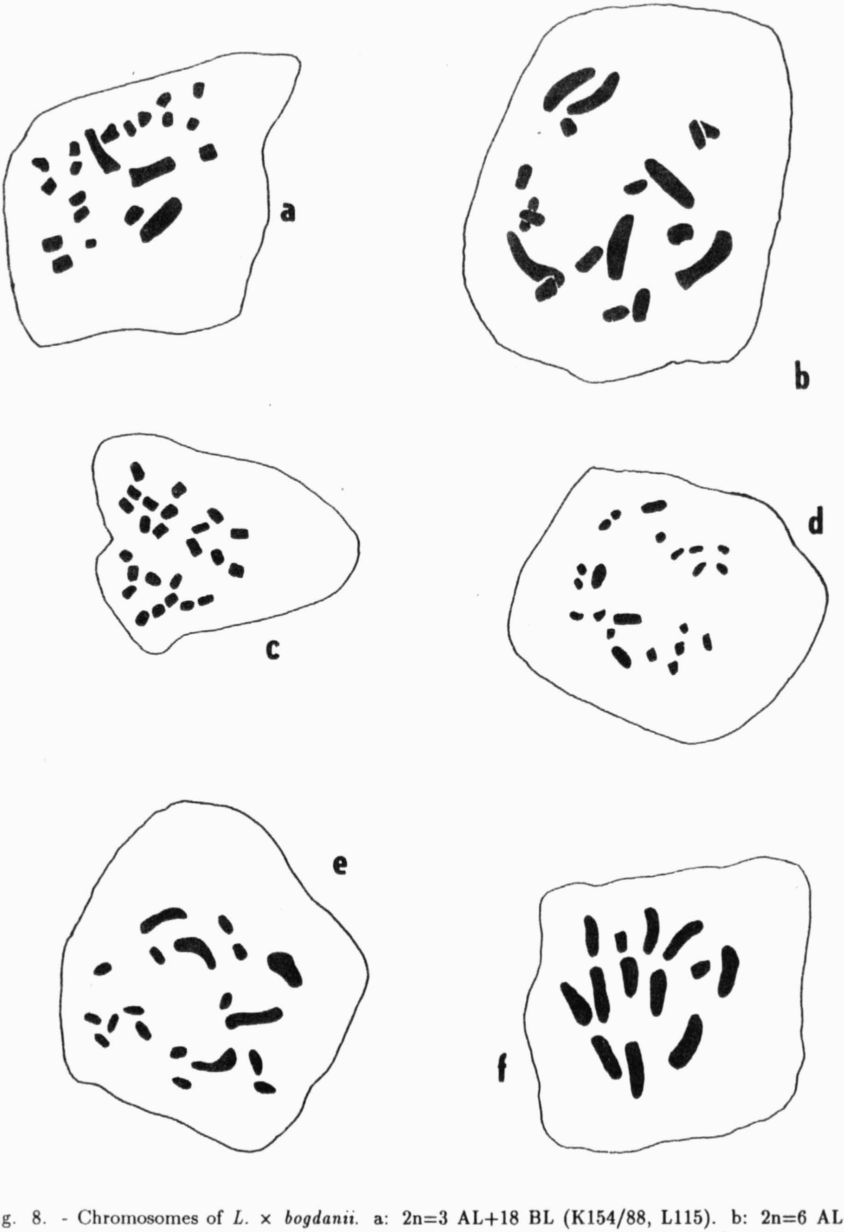


Fig. 8. - Chromosomes of *L.* × *bogdanii*. a: 2n=3 AL+18 BL (K154/88, L115). b: 2n=6 AL+12 BL (K164/88, L117, thge type). c: 2n=24 BL (K174/89). d: 2n=4 AL+18 BL (K268/90A, L233). e: 2n=5 AL+14 BL (K270/90A, L241). f: 2n=11 AL+2 BL (K270/90A, L241).

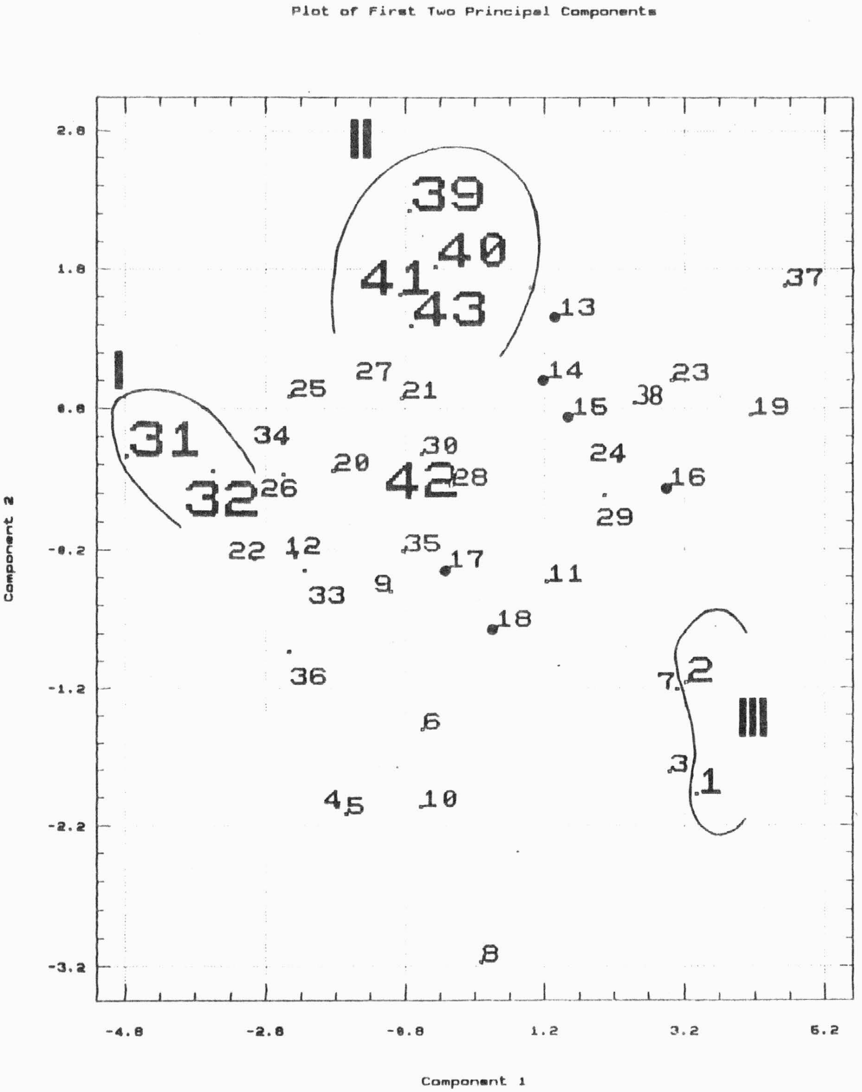


Fig. 9. - Results of PCA of the *L.* × *bogdanii* data from the Pirin population. I - *L. fallax* (31,32), II - *L.campestris* s.l.(39-43), III-*L. campestris* subsp. *campestris* (1,2). - plants with hybrid karyotypes. The figures correspond to those given in Tab. 4 and 5. X-axis (51.6%): component 1. Y-axis (15.0%): component 2. (Component 3: 10.5%; cases with highest contributions to the component 3: positive: 4, 10, 16, 18, 19, 23, 29; negative: 1,2,6,11,39,40,42,43).

Tab.5. - Material used in the PCA of the data given in Tab. 4.

no	taxon	locality	orig.no.of plant collection	chromosome number 2n
1	campestris	Bu,Gorni Lozen	-	-
2	s. str.	Cz,Vimperk	L151/1	12 AL
3	hybrid	Bu, Melnik,	-	-
4	(herbarised)	the Pirin Mts.		
5	"	"	-	-
6	"	"	-	-
7	"	"	-	-
8	"	"	-	-
9	"	"	-	-
10	"	"	-	-
11	"	"	L32A	24 BL
12	"	"	L31A	24 BL
13	hybrid	"	L117 (the type)	6AL+12BL
14	(cultivated)	"	L241	various
15	"	"	L241	hybr.
16	"	"	L115	3AL+18BL
17	"	"	L233	various
18	"	"	L233	hybr.
19	"	"	L119C	-
20	"	"	L120	24 BL
21	"	"	L121	-
22	"	"	L123	24 BL
23	"	"	L236	-
24	"	"	L236	-
25	"	"	L237	-
26	"	"	L237	-
27	"	"	L239	-
28	"	"	L239	-
29	"	"	L240	-
30	"	"	L240	-
31	L.fallax	Gr, Mt.Pangeon	L134	24 BL
32	L.fallax	"	L134	24 BL
33	hybrid	Bu, Melnik,	L230	-
34	"	the Pirin Mts.	L230	-
35	"	"	L230	24 BL
36	"	"	L230	24 BL
38	"	"	L119A	24 BL
37	an artificial hybrid between {\it L. campestris} (L151/1, 2n=12AL) and a hybrid plant from the Pirin locality (L119A, 2n=24BL). The exper. hybrid has 2n=6AL+12BL.			
39	L. camp.s.l.	Gr,Mt.Vourvoura	L135	12 AL
40	"	"	L135	-
41	"	"	L137	12 AL
42	"	"	L137	-
43	"	"	L141	12 AL

their amplitudes overlap in older dry grassy wood-clearings with sparse vegetation, in forest paths etc., usually on mineral acid soils. However, in spite of studying plants from several such localities in C. Europe (Bohemia, Poland), I failed to find hybrid plants. In Scandinavia this hybrid also seems to be rare. On the other hand this apparent rarity very likely results from the fact that the hybrid can easily be overlooked. The intermediate plants are superficially similar to *L. multiflora* (which is often found at these localities), and in subsequent generations the hybrid plants usually approach one of the parents. Thus, a more common occurrence is to be expected, and a search is made in other localities to prove this assumption.

Karyology: The hybrid retains the chromosome number and the karyotype of the parental species. $2n = 12 = 12AL$

Localities of the chromosome counts:

Natural hybrid: Sweden, Soedermanland, Kila (lit.: Nordenskioeld 1956; 51).

Progeny of experimental crosses:

1. [parents: ***L. pallidula*** - Moravia, Rohatec, L150/3 (Kirschnerová 1987 PR), 2n = 12; ***L. campestris*** subsp. ***campestris*** - Bohemia, Vimperk, N. margin of the town (Kirschnerová 1987 PR), 2n = 12. ***L. pallidula*** = fem.] Hybrid cultivated under no L220, 2n = 12 (det. JK as K-264/90A).

2. Various crosses (in both directions) carried out by H. Nordenskioeld (cf. 1956: 23-25). 2n = 12 (some of the vouchers in UPS).

Distribution: Su

Selected records: Sweden, Dalecarlia, Stora Skedevi (Samuelsson UPS). - Soedermanland, Kila (Nordenskioeld UPS [I failed to find the specimen]). Cf. Hylander 1953, 1955, 1959.

Morphology: In the present paper, binomials are only accorded to the hybrids that are known from rich material and/or were found and studied in field. ***Luzula campestris*** × ***L. pallidula*** is not the case because I have merely studied the herbarium material at UPS and results of experimental crosses (both Nordenskioeld's and mine). This hybrid is given a note in Nordenskioeld 1956: 51; contrary to her results, the intermediate (F_1) plants were found to lack stolons. In F_2, a conspicuous segregation takes place and concerns many important features (presence of stolons, heigth and colour of the plants, shape and colour of the inflorescence etc.). In order to provide a more complete information, morphology of the artificial F_1 hybrid is described in Tab. 2 (cf. Fig. 6).

4. *Luzula campestris* subsp. *campestris* × *L. fallax* (= *L.* × *bogdanii*, Fig.7)

During an expedition to southernmost Bulgaria, prof. Bogdan Kuzmanov and I visited the vicinity of Melnik. On the sandstone slopes of the Pirin Mts., we came across the locality of a variable ***Luzula*** population. As the morphology of these plants varied between two conspicuous extremes (one approaching ***L. campestris***, the other having remarkable appearance close to *L. multiflora*), the population has been subjected to a closer study. The latter extreme morphotype was studied in more detail, recognised as a distinct new species and found in other localities. It is described in the introductory part of this paper as *L. fallax.* The other plants of the Pirin population were suspected to represent members of a hybrid swarm and tested for hybridity. Plants were sampled along the transect in order to get a representative material covering all the morphotypes.

Fig. 10. - *Luzula* × *media*. The holotype (PR).

About 40 plants were sampled, ten of them were examined karyologically, seeds of seven samples were sown to obtain a richer material of possible hybrid plants, and this progeny (autogamised) again tested karyologically.

In the course of these investigations, it turned out that the population actually represents a hybrid swarm with a majority of *L. fallax*-like plants. Unfortunately, among the randomly sampled live plants, no specimens having the *L. campestris* karyotype were found (among the herbarised plants a few ones very close to *L. campestris* s.str. were present).

Thus, it was necessary to screen the morphology of the population by means of a multivariate method, taking not only the true *L. campestris* into account but also the morphologically close plants of the *L. campestris* agg. occurring in this region (see the taxonomic introduction, *L. campestris* s.l.). PCA was used to study phenetic relationships among *L. fallax* (Greece, Bulgaria), *L. campestris* subsp. *campestris* (Bohemia, Bulgaria), *L. campestris* s.l. (Greece) and the members of the hybrid Pirin population.

The material and the data used are given in Tabs. 3, 4, and 5, and results are presented in the following subchabters.

Karyology: The karyotype analysis shows that the hybrid population contains diploid and aneuploid plants both with the *L. fallax* karyotype (2n=24 BL) and with hybrid karyotypes of the 12 AL × 24 BL parentage. Three specimens of the original collection proved to show the hybrid karyotypes (L115, L117 and L118). The progeny of the original live plants also has this hybrid character (L230, L233 and L241). Most counts (except for no L233 and L241) were made on root tips of the mature plants, the others on young seedlings (higher number of roots examined).

Hybrid karyotypes ascertained in the material:

2n = 13 = 11 AL + 2 BL (L241/1, Fig. 8f)
2n = 17 = 7 AL + 10 BL (L230)
2n = 18 = 6 AL + 12 BL (L117, Fig. 8b)
2n = 20 = 6 AL + 14 BL (L233/1)
2n = 19 = 5 AL + 14 BL (L241/2, Fig. 8e)
2n = 22 = 4 AL + 18 BL (L233/2, Fig. 8d)
2n = 21 = 3 AL + 18 BL (L115, Fig. 8a)
2n = 23 = 1 AL + 22 BL (L118)

Note: The karyotype 2n = 24 BL was also found in some plants with hybrid appearance (e.g. K174/89, Fig. 8c).

Results: The population studied consists of a hybrid swarm with only one parental taxon present (*L. fallax*). There are two candidates to represent the other parental taxon. They are *L. campestris* subsp. *campestris* (plants of the 'campestroid' morphology were sampled at the Pirin locality, and included in the analysis as nos 3 and 7, see Tab.5) and a taxon close to *L. campestris*, referred to as "*L. campestris* s.l." here.

The following questions were expected to be answered by means of the analysis:

1, are the campestroid plants of this population sufficiently close to the true *L. campestris*?
2, will the 2n=24 BL plants of the hybrid population form a group close to the reference samples of *L. fallax*?
3, which of the possible parents of the hybrid plants is more likely to play this role?
4, what position is occupied by an artificial hybrid 12 AL × 24 BL (*L.campestris* s.str. × *L.* × *bogdanii*), i.e. no 37 in Fig.9 ?

Two geographically distant samples of *L. campestris* subsp. *campestris* were included in the analysis as a reference material (no 1, 2, see Tab.5 and Fig. 9). Campestroid plants from the hybrid population (particularly no 3) are very close to the true *L. campestris*.

Most of the 2n=24 BL plants are relatively close to the reference sample of *L. fallax*, one of the parents. The 2n=24 BL plants are found in Fig. 9 under nos. 12, 20, 22, 35 etc. (cf. Tab.5).

Plants with hybrid karyotypes are very unlikely to be of intermediate position between *L. fallax* and *L. campestris* s.l. On the other hand, the position of the plants with hybrid karyotypes is in a good agreement with the hypothesis that *L. campestris* subsp. *campestris* represents one of the parental taxa.

The experimental hybrid between the agmatoploid (L119A, 2n=24 BL) and the true *L. campestris* s.str. (L151/1; 2n=12 AL) occupies a rather extreme position in the plot (no 37). Leaving alone the size effect of heterosis (marginal position on the Y-axis), no 37 is among hybrid plants, somewhat closer to the cluster of *L. campestris* s.str.

Thus, I am of the opinion that the Pirin population (the exact locality is given below) is in fact a hybrid swarm containing results of hybridisation between *L. fallax* and *L. campestris* subsp. *campestris*.

Nomenclature of *L. fallax* × *L. campestris* subsp. *campestris*

Luzula × **bogdanii** Kirschner, nothosp. nov. (Fig. 7)

Descriptio: Plantae dense vel sublaxe caespitosae, sine stolonibus. Folia caulina 2-3, longa (ad 7 cm). Inflorescentia ex (4)6-10 capitulorum composita, ramis inflorescentiae (raro ramosis) rectis, flexuosis, raro nutantibus, ± glabris vel sparse papillosis, capitulis 7-8 mm longis, 6-7 mm latis, plerumque 7-8floris. Tepala 3.2-3.5 (in typo) usque ad 4.0 mm longa, antheris 1.0-1.2 mm longis, filamentum 1.5-2.0 × (in typo) vel ad 3.0 × longior. Stigmata 2.5-3.0 mm longa, capsularum segmenta ca 2.3 mm (in typo), usque 2.8 mm longa. Semina ca 1.1 mm longa, 0.9-1.0 mm lata, cum carunculis 0.3- 0.5 mm longis.

Typus: Bulgaria australis, montes Pirin, oppidum Melnik: graminosis in decl.(arenaceis) supra pagum Rožen (supra Solunski preslap) sec. viam in jugo Vlaškija Put.Alt. ca 1450- 1550 m s.m. (Kirschner 1988, planta in Bohemia culta sub no L117). HT in herb. PR, IT in LD, PR asservantur.

A very variable hybrid of slightly reduced fertility. It is only known from the type locality, and it is not to be expected to occur outside the region of south-central Balkan Peninsula.

B. Polyploid hybrids

5. *Luzula divulgata* × *L. multiflora* subsp. *multiflora* (=*L.* × *media*, Fig. 10)

Nordenskioeld (1956: 50 etc.) reports successful attempts to cross hexaploids and tetraploids, and, generally speaking, hybrids between polyploids may be expected to occur in the nature as well (except for the parental combination with 24 AL × 48 AL). That is why I carefully studied plants from the (many) localities of the common occurrence of *L. divulgata* and *L. multiflora* s.str. In several cases (particularly those with common presence of sterile or morphologically dubious plants), representative samples of live plants were examined karyologically. In spite of this effort, only one plant proved to represent the

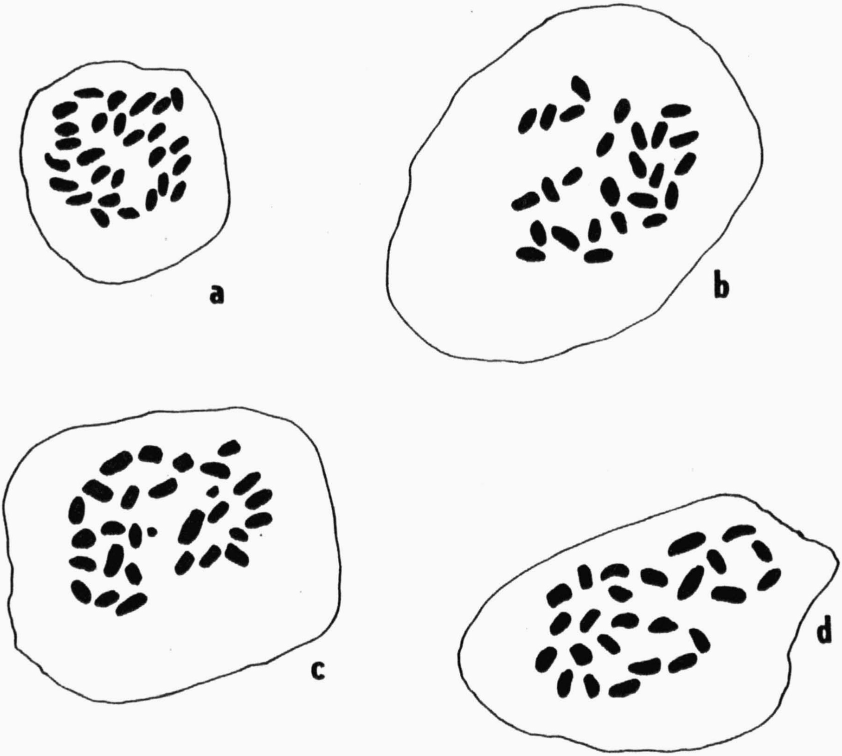


Fig. 11. - Chromosomes of *L.* × *media*. a: 2n=27AL (226/89-2/3). b: 2n=26AL (226/89-3/1). c: 2n=27AL+2 fragm. (226/89-4/2). d: ***Luzula divulgata*** or an introgressant with *L.* × ***media***. 2n=25AL (178/89-L58).

expected hybrid both morphologically and karyologically, and (at another locality) another plant showed some traces of hybridity, both of them in Czechoslovakia.

In Europe, there is a very wide geographical overlap between the ranges of ***L. divulgata*** and *L. multiflora*, and in subxerophilous to almost mesophilous forest communities, these two taxa meet relatively frequently. Three apparent isolation mechanisms act simultaneously and prevent the species from hybridization: 1, the autogamy predominating (geitonogamy), 2, phenological difference (*L. multiflora* flowers about two to three weeks later than *L. divulgata*, and their flowering periods do not overlap every year), 3, the two species inhabit different microsites at a given locality. In addition, partial sterility of the hybrid plant suggests that a genetical barrier is also involved.

The hybrid grew at the border between a wood clearing (with ***L. pallidula, L. multiflora*** and rarely ***L. divulgata*** being present) and an open secondary mixed forest (with scattered ***L. divulgata***).

The hybrid seems to be rare but there is no reason to suppose that it is absent from other regions in C. Europe (particularly, its occurrence should also be expected in Poland, Austria and Hungary).

Karyology: The hybrid seeds have a variable chromosome number intermediate between 2n=24 and 2n=36. The karyotype is only composed of the AL chromosomes, although a few small fragments were ascertained as well. The chromosome counts were made on young seedlings (in order to avoid the possibility of F_1 seeds, eleven analyses were carried out, all of them demonstrating the hybridity of the plant examined).

2n = 26 AL, 27 AL, 27 AL + 2 fragm. (Fig. 11a,b,c).

Locality: Czechoslovakia, Bohemia, Rakovnik: mixed pine forest ca 1 km sw of Nový Mlýn (counted as K225/89).

Note: Another chromosome count that may be due to hybridization or introgression between *L. divulgata* and *L. multiflora* was made on a plant from south-central Moravia (phytogeogr. distr. 68), village of Hlína (Řepka 10018, 20.6.1987, herb. Řepka), i.e. 2n=25 AL. Morphologically nothing suggests hybridization, and the count is given here for the sake of completeness only.

Nomenclature of *Luzula divulgata* × *L. multiflora* subsp. *multiflora*

Luzula × **media** Kirschner, nothosp. nov. (Fig. 10)

Diagnosis: A *Luzula divulgata* floribus minoribus, antheris brevioribus (filament. 2-3 × longioribus), seminibus ovoideis (nec subglobosis) cum carunculis brevioribus; a *L. multiflora* subsp. *multiflora* stylis longioribus, stigmatibus subpersistentibus (nec deciduis) longioribusve, bracteis inflorescentiae conspicue brevioribus differt.

Description: Stems 25-30 cm long, basal leaves usually 2.5- 3.5 mm wide. Inflorescence composed of 3-4 clusters, lower bract up to 1.5 cm long, always shorter than the inflorescence, longest peduncles 1.5-2.5 cm long, straight to slightly flexuose, clusters of 6-8 flowers. Tepals 2.9-3.5 mm long, anther/filament length ratio 2-3. Style 1.3-1.5 mm long, stigmas ca 3 mm long, subpersistent. Capsule segments 2.8-2.9 mm long, seeds ovoid, 1.0-1.1(1.2) mm long, 0.8-0.9 mm wide, caruncles 0.4-0.5 mm long.

Type: Bohemia centralis, distr. phytogeogr. 32, Křivoklátsko, oppid. Rakovník: in pinetis mixtis ad marg. austr. silvae Brabečka, ca 1.0-1.5 km situ austro-occid. a vico Nový Mlýn. Alt. ca 400 m s.m. (Haškova, Kirschner et Krahulec 16.6.1987). In herb. PR asservatur.

6. *Luzula congesta* × *L. multiflora* subsp. *multiflora* (= *L.* × *danica*, Fig. 12)

Another polyploid hybrid comes into being at some of the localities where *L. multiflora* s.str. (hexaploid cytotype) and *L. congesta* are found to grow together. Natural hybridization between these two taxa is reported to take place in Denmark (Nordenskioeld 1956: 52-53) and Britain (Buchanan 1960: 127). In both cases representative samples were gathered and examined karyologically. Although presence of hybrid swarms is considered as common "where the hexaploid *multiflora* occurs together with the octoploid *congesta*" (Nordenskioeld, l.c.), in the material examined, heptaploids predominate among hybridogenous karyotypes. In Danish populations, among 14 hybrid plants eight were heptaploids, in the British locality only heptaploids were found along with the parents. This (together with partial or rarely even complete sterility of the hybrids, indicates that backcrosses are not common in natural populations. Whenever mature plants were examined the hybrids proved to be heptaploids only.

Both ecologically and geographically, the ranges of *L. multiflora* s.str. and *L. congesta* widely overlap. The most frequent common occurrence of these two taxa is at the bog margins and in moist meadows on peaty soils (and, of course, at wet disturbed sites in the

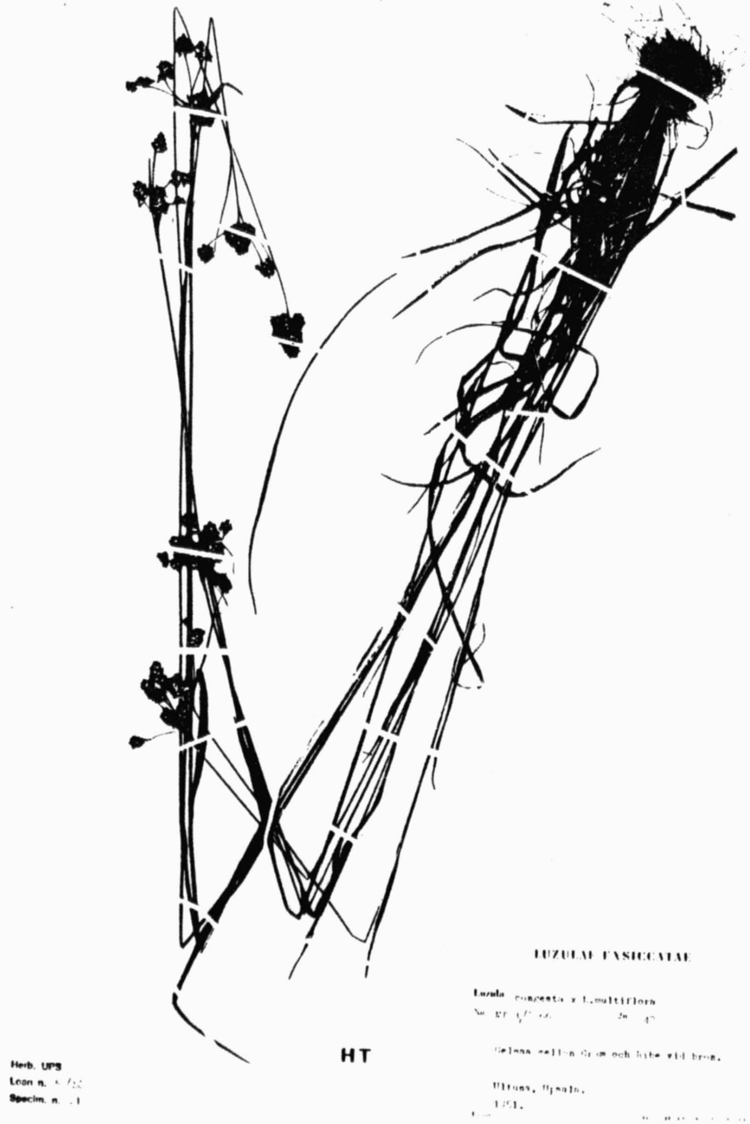


Fig. 12. - ***Luzula* × *danica*.** The holotype (UPS).

territories inhabited by both species). In spite of the fact that the hybrid has merely been recorded in Britain and Denmark, its occurrence is very likely throughout the geographical range of *L. congesta* (i.e. from Portugal through France and Germany and along the coast to S.Sweden and N.W. Poland).

Karyology: As mentioned above, heptaploids (2n=42) prevail among the hybrid karyotypes, the other counts (2n=39,40,44,47) being much rarer. All the chromosomes are of the AL size.

2n = 42 AL

Localities:

1. Britain, Glen Lyon (Buchanan 1960: 127)
2. Denmark, Gelsaa, between Gram and Ribe (H. Nordenskioeld, UPS 1951-66)
3. Denmark, Oddesund (H.Nordenskioeld, UPS 1951-77)
4. Denmark, 13 km N. of Skern (Nordenskioeld 1951 UPS)

2n=39,44,47 AL (loc. 4)
2n=39,40 (loc. 2).

Nomenclature of *L. congesta* × *L. multiflora* subsp. *multiflora*

Luzula × **danica** Nordenskioeld et Kirschner, nothosp. nov. (Fig. 12)

Diagnosis: Plantae dense caespitosae, ca 30-50 cm altae. Inflorescentia congesta, subcongesta vel congesta cum 1-2 capitulis pedunculatis, pro parte sterilis. Bractea infima plerumque pedunculorum brevior vel inflorescentia aequans, patens. Tepala 3.4-3.7 mm longa, pallide brunnea, late pallide marginata. Segmenta capsularum ca 2.9-3.0 mm longa, semina matura 1.2-1.3 mm longa, 0.8-1.0 mm lata, carunculis ca 0.4 mm longis.

Typus: Danmark, mellan Gram och Ribe (H.Nordenskioeld, culta sub no MT 3, 1951-66 in Ultuna, Uppsala, 1951). In herb. UPS asservatur.

7. *Luzula alpina* × *L. multiflora* s.l. (tetraploid cytotype)

These two taxa grow together from time to time, and both belong to the tetraploid level. Hedda Nordenskioeld (unpubl., vouchers UPS) crossed these two taxa with success; my attempts to obtain experimental hybrids gave rise to sterile plants with low viability. This indicates that the hybrid is to be expected to occur rarely between parents in the Alps.

The only plant that is likely to belong to this hybrid is deposited at UPS. The cultivated plant proved to have 2n = 28 = 20AL + 8BL. Such a karyotype either represents a tetraploid *L. multiflora* s.l. with partially fragmented chromosome set or, more probably, belongs to the hybrid of *L. alpina* × *L. multiflora* s.l.

The herbarium specimen (loc.: Grossglockner, Oesterreich, 15.6.1953 leg. M. Palm, cult as H1-1, UPS) is a dwarf plant with relatively broad basal leaves, a stout stem, a broad bract, perianth segments 2.3-2.4 mm long, and seeds 0.9 mm long, 0.7-0.8 mm wide, caruncles 0.4(-0.5) mm long. The size of caruncles indicates that *L. alpina* may be involved.The hybrid should be proved on a more extensive material.

C. Hybrids expected within *L. multiflora*

a. *L. multiflora* subsp. *multiflora* × *L. multiflora* s.l.($2n=24$)

These two cytotypes may get into contact in the Alps and other regions of the occurrence of the tetraploid race, and hybridization in such a case is very likely. Similar situation is described from Mt. Washington, New England, USA, by Nordenskioeld (1956: 52). The fertile hybrid formed a hybrid swarm there.

b. *L. multiflora* subsp. *frigida* × *L. m.* subsp. *sibirica*

According to Laščenkova (1976) and Novikov (1976), *L. multiflora* subsp. *sibirica* reaches Europe in the territory of the N. Urals. I have studied the material from that region in the herb. LE but failed to find any support for this statement. (The plants from the easternmost regions belong to *L. multiflora* subsp. *frigida* L. However, if it is the case, natural hybridization is to be expected.

My experimental crosses between these two subspecies (*L. m.* subsp. *frigida* from Pojakonda, the White Sea region, $2n=36$AL, and *L.m.* subsp. *sibirica* from the Kuraisky chrebet, the Altai, $2n=36$ AL) give rise to fully fertile progeny with the same chromosome number ($2n=36$AL, det. as no L219). Laščenkova (op.c., p. 106) reports the occurrence of intermediates between the subspecies in the Polar Urals region.

c. *L. multiflora* subsp. *multiflora* × *L. m.* subsp. *frigida*

These two subspecies can easily be crossed experimentally and the hybrids are highly fertile (Nordenskioeld 1956, 1961).They are sympatric in central Scandinavia as well. Thus, it is probable that natural hybrids are not rare in this region. However, concrete evidence is lacking, and the examination of apparent intermediates is required to solve this problem.

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Souhrn

Předmětem článku je souhrnná informace o rozsahu a projevech přirozené hybridizace mezi zástupci sekce *Luzula* rodu *Luzula* (*Juncaceae*) v Evropě. Převážná část starších literárních údajů o hybridizaci v této skupině se ukázala být mylnou interpretací proměnlivosti (např. *L. multiflora* × *L. sudetica*, *L. multiflora* x L. pallidula, *L. multiflora* × *L. campestris*). Nejspolehlivější údaje jsou v pracích skandinávských autorů (*L. pallidula* × *L. sudetica*, *L. campestris* × *L. sudetica*). Další hybridy experimentálně i karyologicky doložila Hedda Nordenskioeld (*L. multiflora* × *L. congesta*, *L. campestris* × *L. pallidula*), a navíc stanovila pravidla, jimž se hybridizace v této skupině podřizuje.

Úvodní část studie je věnována taxonomickému přehledu druhů, které se na přirozené hybridizaci účastní. Je popsán nový druh z Bulharska a Řecka (*L. fallax*). Systematický výčet hybridů s poznámkami o jejich rozšíření, ekologii, rozmnožování a nomenklatuře obsahuje sedm přirozených kříženců, z nichž dva jsou zcela nově objevení (*L. multiflora* × *L. divulgata* v Československu a *L. campestris* × *L. fallax* v Bulharsku). Další hybridi: *L. campestris* × *L. sudetica* (= *L.* × *heddae*, také v ČSFR), *L. pallidula* × *L. sudetica* (= *L.* × *hybrida*, také v ČSFR), *L. campestris* × *L. pallidula* (Švédsko), *L. congesta* × *L. multiflora* (= *L.* × *danica*, Dánsko, Británie) a *L. alpina* × *L. multiflora* s.l. (Rakousko). Některé hybridy byly potvrzovány i

experimentálním křížením (*L. campestris* × *L. pallidula*, *L.* × *bogdanii* × *L. campestris*). Zvláštní pozornost byla věnována kříženci *L.* × *bogdanii*, který byl zkoumán podrobněji karyologicky a morfologicky, a použita metoda hlavních komponent (PCA), aby byly získány doklady o rodičovství. Některé očekávané kombinace byly též získány v experimentálních podmínkách (*L. multiflora* subsp. *frigida* × *L. m.* subsp. *sibirica*).

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Ri Jong-Dzae et Hoang Ho-Dzun

Sigmulmjongsadzon (Slovník jmen rostlin - Plant Name Dictionary)

Goahakbaekgoasadzon - Tschulpansa, Pyongyang 1984, 544 str., cena vaz. 4,50 Won.

Slovník připravený v Botanickém ústavu Akademie věd KLDR splňuje několik funkcí. V prvé řadě je zmodernizovaným seznamem všech dosud poznaných vyšších rostlin severní části Korejského poloostrova. Jména, propracovanost jednotlivých rodů a užitá nomenklatura poukazují na významný pokrok v badatelském úsilí korejských botaniků (cf. Anonymus 1979, Flora Coreana, Appendix).

První část knihy je abecedním seznamem latinských jmen rodů a druhů s uvedením autorů, synonym a dále k nim přiřazeným jménům (pokud existují).v korejštině, ruštině, angličtině a japonštině. Každý rod a druh je očíslován, což je využito v odkazové části rejstříků. Další části knihy tvoří rejstříky korejských jmen s odkazy. Poslední tři stránky jsou věnovány latinským jménům čeledí a jejich korejským ekvivalentům.

Přestože slovník má shrnující charakter, je zřetelný i přínos systematický. Ve srovnání se sedmidílnou Flora Coreana (Anonymus 1972-1976, Pyongyang) a Flora of Pyongyang (Anonymus 1984, Pyongyang) jsou doplněny zvláště jména rostlin hospodářsky pěstovaných a zahradních. V mnoha případech je zřetelný moderní posun v řešení nomenklatorických otázek.

Škoda, že tato zajímavá kniha, přibližující rostlinný svět a úroveň botanické práce ve východní Asii, se vyskytuje v přírodovědných knihovnách jen sporadicky, je jen těžko dostupná a tedy i málo využívaná.

J. Kolbek