

A Comparative study on *Dactylis slovenica* Dom. and *D. glomerata* L.

A. DOROSZEWSKA

The great morphological variability in the genus *Dactylis* makes the study of the systematics of this economically important genus of grasses very difficult. In most cases the variability is continuous and there are no traits clearly distinguishing the particular forms. Neither are there any sterility barriers so that the various formes can cross with each other giving fertile hybrids. The lack of clearly marked interspecific differences has been the cause of much inconsistency in the systematic treatment of this genus by various workers. The *Dactylis* forms which have been discriminated are defined by some florists as separate species and by others merely as subspecies. Cytological investigations have revealed two chromosome levels within the genus *Dactylis*: one diploid with $2n=14$ and the other tetraploid with $2n=28$ (Levan 1930, Katterman 1931, Müntzing 1933 and 1937). In the course of an investigation on *Dactylis* Stebbins and Zahory (1959) reached the conclusion that the genus consists of one common species *Dactylis glomerata* L. in which two groups are discernable, one diploid the other tetraploid. They studied in detail the group of 11 diploid subspecies growing mainly in the Mediterranean area and in South Europe.

The tetraploid forms of *Dactylis* spreading in Europe and Asia from the polar to the subtropical regions have a much wider distribution than the diploids. The tetraploids are a very numerous and variable group of plants which as yet is little known, though the first steps towards a detailed investigation have already been made. In 1961 Borrill distinguished the new tetraploid species *Dactylis marina* Borrill occurring along the Atlantic and Mediterranean coasts of Europe. The present investigation on *D. slovenica* may also add some details to the knowledge of the tetraploid forms of *Dactylis*.

Dactylis slovenica was described by Domin in 1923 (Domin 1929) as a new species occurring in the Carpathians on lime and dolomite substrata. At that time four main forms of *Dactylis* with distinctly different distributional areas were distinguished in Europe.

These forms were *Dactylis glomerata* L., *D. Aschersoniana* Graebn.,

D. hispanica Roth., and *D. slovenica* Dom. In 1943 Domin published a monography of the genus *Dactylis* in which he defined *D. slovenica* and all other above-mentioned forms as subspecies of *D. glomerata* L. In this way *D. slovenica* was degraded by its discoverer to the rank of a subspecies, but treated on equal terms with *D. Ascher-soniana* and *D. hispanica*.

Domin discovered *D. slovenica* for the first time in the Belanske Tatry massif, which forms part of the Slovenian Tatras, whence the name *D. slovenica*. In further observations Domin found that *D. slovenica* was a montane plant growing in the Carpathian Mts. to the East Carpathian massif in the East and to the Karkonosze and Moravia in the West. In this area it occur together with *D. glomerata*.

On the slopes of the Belanske Tatry massif *D. slovenica* grows in dense high tufts together with such species as *Cimicifuga foetida*, *Aruncus silvester*, *Aconitum firmum*, *Digitalis ambigua*, *Senecio Fuchsii*, *Mulgedium alpinum* etc. The plants of *D. slovenica* are conspicuous by their vigorous growth habit. Their widely outspread and drooping panicles differ so much from the appearance of *D. glomerata* that at first sight they seem to constitute a very distant form. However, on closer examination the differences between *D. glomerata* and *D. slovenica* are seen to be less clearly marked and, therefore, the question arises whether *D. slovenica* is in fact a separate species, a subspecies or only one of the numerous modifications of *D. glomerata*. The investigation of the differences and the similarities between the two forms has been the aim of this work.

MATERIAL AND METHODS

The examinations of *D. slovenica* and *D. glomerata* were carried out on plants growing in their natural habitats and on plants transferred from their natural stands and cultivated in the Botanical Garden of the Warsaw University. The plants described by Domin as *D. slovenica* grew in the Belanske Tatry massif in the valley of the stream Regliany Potok near a locality called Siroke Pole. The altitude of the valley was about 1250 m. above sea level and the soil limy. The plants for this investigation were collected in 1956 in the Belanske Tatry massif in the Holubyho Dolina valley the altitude of which was approximately the same as of the Regliany Potok valley. In his list of stands of *D. slovenica* in the Tatras Domin in 1943 also mentioned the Holubyho Dolina valley. Somewhat below the mountain shelter in this valley there is a small dell called the Dolina Sedmi Promenov where there are stands of typical *D. slovenica*. The living specimens of *D. slovenica* for this investigation were collected from four stands situated not far from each other in Holubyho Dolina valley. The first of these stands was situated near the parth runnig just

above the Sedmi Promenov waterfall at the altitude of 1350 m, above sea level. On this stand besides the typical *D. slovenica* specimens there were also *D. glomerata* plants and natural hybrids between these two forms. The second stand was in the Dolina Sedmi Promenov dell near the waterfall at the altitude of 1275 m. This stand was the dampest of all and *D. slovenica* plants growing there were very vigorous and morphologically uniform. The third stand was situated at the bottom of the Dolina Sedmi Promenov dell at the altitude of 1225 m. Here, similarly as on the first stand, *D. slovenica* was growing together with *D. glomerata* and their hybrids. The fourth stand was situated in the Holubyho Dolina valley above the Dolina Sedmi Promenov dell at the altitude 1370 m., on the south-east slope cleared of the forest which had once grown there. This stand was the driest of the four stands described here: the plants growing there abundantly were morphologically uniform.

The *D. glomerata* plants used as the comparative material for this investigation were collected from various lowland and mountain stands in Poland.

The list of these plants cultivated in our Botanical Garden used for the investigation was as follows:

D. slovenica:

- no. 55 from stand 1 in the Tatras,
- no. 56 to 60 from stand 2 in the Tatras,
- no. 49 from stand 3 in the Tatras,
- no. 43 to 45 from stand 4 in the Tatras,
- no. 1 from Dolina Sedmi Promenov dell in the Tatras,

Natural hybrids *D. slovenica* × *D. glomerata*:

- no. 52, 53, 54 from stand 1 in the Tatras,
- no. 46, 47, 50 from stand 3 in the Tatras,

D. glomerata from mountains stands:

- no. 51, stand 1 in the Tatras,
- no. 49, stand 3 in the Tatras,
- no. 63, 64, 65, a rocky stand sparsely covered with mountain pine in the Morskie Oko valley in the Tatras,
- no. 21 to 30, a meadow near the Droga Pod Reglami road in Kiry near Zakopane,
- no. 31 to 40, a meadow near the stream in Bukowina Tatrzańska Dolna,

D. glomerata from lowland stands:

- no. 4, 5, 6, 7, open roadside stands in Salomea near Warsaw,
- no. 11 to 20, stands in a this mixed forest in Zalesie near Warsaw,
- no. 41, 42, 61, 62, the Puszcza Białowieńska forest,
- no. 2, 3, seaside, thinly forested sand dunes in Łeba on the Baltic Sea coast.

In the Botanical Garden all the *Dactylis* plants were grown side by side under the same conditions, on clayey-soil beds with strong insolation. The plants were grown from 1956 to 1960. Every year they were measured, their blooming seasons were recorded, and they were examined with regard to their vigour, pollen fertility etc.

The crosses were made by the methods of castration and of additional pollination.

The material for cytological examinations was fixed in 1:3 aceto-alcohol and stained in propiocrarmine. Pollen fertility counts were made on smears stained in 1:1 acetocarmine with glycerine.

THE MORPHOLOGY OF *D. SLOVENICA* AND *D. GLOMERATA*

Dactylis slovenica is a montane species of the Carpathians occurring most abundantly on lime substrata in the Tatras. It grows in thin forests, on pastures, and on meadows reaching from the sub-Alpine to the sub-mountain stage. In its mountain distribution *D. slovenica* meets with *D. glomerata*, the latter species being able to grow at considerable alti-

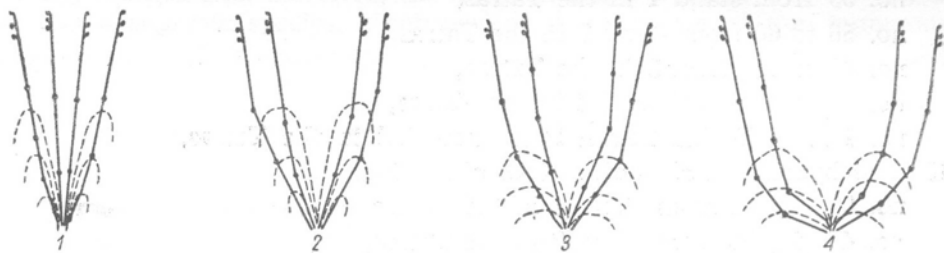


Fig. 1. Schematic diagrams showing the growth habits of *Dactylis glomerata* tufts: 1 — culms almost straight, leaves growing almost vertically with only the tips drooping; 2 — culms slightly bent in the nodes, leaves of the same kind as in 1; 3 — culms same as in 2, leaves bending outward; 4 — culms strongly arched, leaves bending outward

tudes in spite of its lowland origin. The highest altitude at which Kotula (1889—90) found *D. glomerata* was 1707 m. near Zimne Źródła in the Tatras. In the Alps *D. glomerata* was found at the altitude of 2320 m. (Hegi 1907). A characteristic trait of *D. glomerata* is its great morphological variability and, therefore, to establish the systematic position of *D. slovenica* the morphology of the latter is here compared to the characteristic traits of the former. For this purpose many plants of *D. glomerata* coming from various parts of Poland were examined but in the compara-

tive tables only the most typical individuals from the particular stands are described.

Growth habit. The plants of *D. slovenica* are vigorous, the culms are strong, thick, and slightly bent at the nodes so that the flower culms are arched.

In the case of *D. glomerata* four main types of the growth habit have been discriminated in the course of comparative examinations. The schematic diagrams of these four types are shown in fig. 1. The growth habit of the tufts, as shown by these diagrams, depends on the magnitude of the bend in the nodes and on the position of the basal leaves which are either almost vertically upright with only the ends drooping or curved towards the ground. Between the four main types there are continuous series of intermediate forms.

The distribution of the growth habit types in *D. glomerata* and *D. slovenica* is shown in Table 1. As is to be seen the variation of the growth habit of *D. slovenica* ranges between types 3 and 4 and is not as wide as the variation of *D. glomerata*.

Table 1

The types of the growth habit of tufts according to fig. 1

No. of plants	The types of the growth habit			
	1	2	3	4
<i>D. slovenica</i>			44 56 57 58 59	1 43 45 48 55
<i>D. glomerata</i>				
from lowland stands	2 3 4 5 6	61 62	18	41 42
from mountain stands	51	31 32 33 36 37 40 63 64 65 49	34 35 38 39	

The size of culms and leaves. The plants of *D. slovenica* are somewhat larger than the plants of *D. glomerata*, but the difference is not significant. The height of the culms in *D. slovenica* is about 1.5 m., whereas among the *D. glomerata* plants there are much lower individuals, some of them less than one metre tall, e.g. plants no. 41 and 42 from the Puszcza Białowieska forest, and individuals of the same size as *D. slovenica*, e.g. plants no. 2 and 3 from Leba. The basal leaves of *D. slovenica* are about one metre long and their widths range 7 to 13 mm., whereas the widths of the leaves on the culms range up to 15 mm. In the most vigorous specimens of *D. glomerata* the length of the basal leaves is not

more than 80 cm. and the widths of these leaves range 4 to 12 mm. This means that the basal leaves in *D. slovenica* are somewhat larger than in *D. glomerata*. However, in *D. slovenica* plants grown in the Botanical Garden in Warsaw the length of leaves gradually decreased and after three years of cultivation it was of the same order as in *D. glomerata*. On the other hand, the height of the culms did not decrease and after five years of cultivation the maximum height of the culms in *D. slovenica* was 1.91 m.

The length of the ligule ranges 3 to 8 mm. in *D. glomerata* and 4 to 7 mm. in *D. slovenica*.

The colour of plants. The plants of *D. slovenica* are usually bright green similarly as many specimens of *D. glomerata* from both mountain and lowland stands. In *D. glomerata* the colour of plants ranges from pale green — e.g. specimens no. 61 and 62 from the Puszcza Białowieska forest — through bright green, to bluish-green and even grayish green as in the plants no. 2 and 3 from Łeba. (Table 2).

Table 2
The colour of plants

No. of plants	Pale green	Bright green	Bluish green	Grayish green
<i>D. slovenica</i>	57 60	1 43 44 45 55 56 58 59	48	
<i>D. glomerata</i> from lowland stands	61 62	41 42	20 29	2 3
from mountain stands	31	32 33 40 63, 64 65	34 35 36 37 38 39 49 51	

The stiffness and the harshness of plants. The stiffer plants usually are also harsher, since both these traits depend on the content of silica. Lackamp (1955) demonstrated that the *D. glomerata* plants containing more silica had more sharp toothlets on the margins and the ribs of leaves and were thus harsher to the touch.

Among the plants of *D. glomerata* four degrees of harshness have been discriminated: smooth, slightly harsh, harsh, and very harsh.

The plants of *D. slovenica* are smooth or slightly harsh (Table 3).

The swelling of the culm base. The base of culms in *D. slovenica* is distinctly bulbed. The swelling is caused by a thick reduced stem inside the base of the culm. Being hard and lignified these reduced stems act in a way a reinforcement of the culm bases, thus improving the attach-

ment of the plants to the substratum. According to Domin (1929, 1943) the swelling at the base of culms is the main morphological trait distinguishing *D. slovenica* from the other *Dactylis* species.

The bulb-like swelling at the culm bases in *D. slovenica* is well developed in old culms growing separately outside the tufts. The young

Table 3
The harshness of plants

No. of plants	Smooth	Slightly harsh	Harsh	Very harsh
<i>D. slovenica</i>	1 43 44 45 57 60	48 55 56 59		
<i>D. glomerata</i>				
from lowland stands	61 62	41 42	18	2 3
from mountain stands	31 32 33 34 35 56 38 40 63 64 65	37	49 51	39

culms and the culms growing inside the compact tufts are not bulbed. The reason for this may simply be the mechanical pressure of the neighbouring tightly packed culms which do not allow the swelling to develop.

The swellings on the culms of *D. slovenica* are up to 2 cm. long and about 1.2 cm in diameter.

The plants of *D. glomerata* also have such a lignified culm, but it is much smaller than in *D. slovenica*. Its diameter is not more than 0.5 cm. and, therefore, the culm base is usually even or only slightly swollen.

In connection with the presence of the swelling on the culm base in *D. glomerata*, though much smaller than in *D. slovenica*, the question had to be considered whether the difference between the two forms in the development of this trait was not caused by the greater thickness of the whole culms in *D. slovenica*. In order to obtain quantitative data on this trait the thickness of the culms and of the swellings on them was measured. Accepting the diameter of the culm directly above the swelling as the independent variable X and the diameter of the swelling as the dependent variable Y, the regression coefficient for both forms was calculated. The ten thickest culms were measured in ten individuals of *D. slovenica* and in ten of *D. glomerata*.

The calculated regression coefficient was $b = 1.88$ for *D. slovenica* and $b = 1.19$ for *D. glomerata*. The differences between these coefficients are represented graphically in fig. 2.

The measurements and the calculated regression coefficients show that the swelling of the culm bases is much more developed in *D. slovenica* than in *D. glomerata* and that this trait does not depend on the difference in the thickness of the culms. The swelling of the culm base is certainly one of the most characteristic traits of *D. slovenica*.

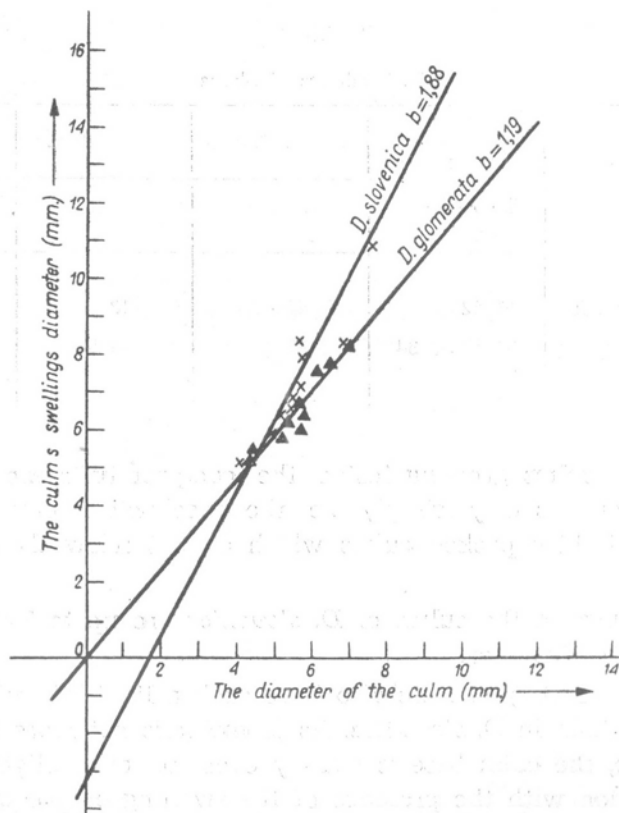


Fig. 2. Graph showing the regression of bulb diameter to culm diameter for *D. slovenica* and *D. glomerata*

The panicle. The differences in the structure of the panicles between *D. slovenica* and *D. glomerata* are considerable. The differences include the size, the proportions, and the drooping of the panicles.

The drooping of the panicle is caused primarily by the bend of the main axis and to a lesser degree by the downward recurving of the panicle branches appearing only in the large panicles with long branches.

The main axes of panicles in *D. glomerata* are differently curved. So far as the bend of the axis is concerned five types of panicles have been distinguished. They are shown schematically in fig. 3. The first diagram shows the upright type of the panicle, the second an upright panicle with

only the end drooping, the third a semi-drooping panicle, the fourth a drooping panicle, and the fifth a strongly drooping panicle. Besides the five main types shown in fig. 3 there are all kinds of intermediate forms. The drooping of the panicles in the particular tufts is not uniform and in each tuft there can be differently drooping panicles according to two or even three neighbouring types illustrated in fig. 3. Therefore, in the case of this trait only its range of variation can be considered.

The panicles in *D. slovenica* are always drooping according to the types 3 to 5 in fig. 3, though at the time of blooming they are somewhat more erect.

The panicles in *D. glomerata* are erect varying within the range of types 1 to 3. They usually are of type 1, especially before and at the time of blooming. After blooming the most common panicles are of types 1 and 2 or even 3. Panicles of type 1 after blooming are very rare. Table 4 shows the distribution of the *D. slovenica* and *D. glomerata* individuals according to the degree of drooping after anthesis.

From what has been said above it is apparent that both forms have drooping panicles, but in *D. slovenica* the trait is much more strongly marked. Although, the ranges of variation of this trait in *D. slovenica* and

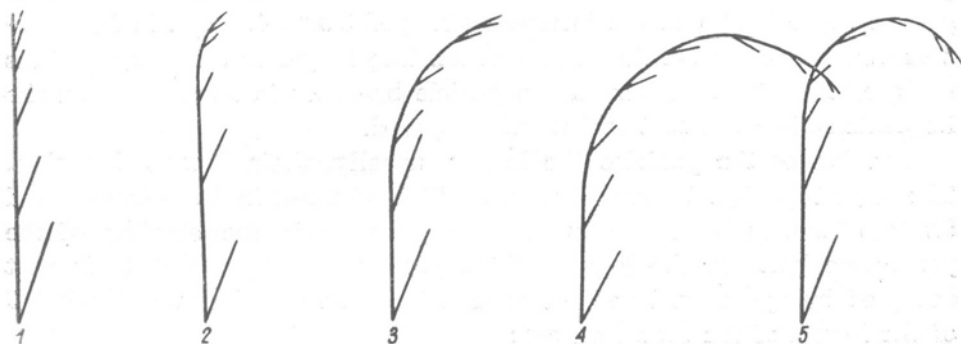


Fig. 3. Schematic diagrams showing the panicles in *D. slovenica* and *D. glomerata*: 1 and 2 — erect culms; 3 — semidrooping culm; 4 — drooping culm; 5 — strongly drooping culm

D. glomerata overlap, the drooping of the panicles can be accepted as one of the main traits distinguishing the two forms. The differences in this trait is the most distinct before anthesis, since then the panicles in *D. glomerata* are always erect and the panicles in *D. slovenica* are always drooping.

The size of panicles. The length of panicles in *D. slovenica* ranged 14.8 to 36.4 cm., the average values for the particular individuals being 18.0 to 28.7 cm.

Table 4

The drooping of the panicles according to fig. 3

No.	The types of the drooping panicles				
	1	2	3	4	5
<i>D. slovenica</i>			43 44 59	1 45 55 56 57 58 60	48
<i>D. glomerata</i> from lowland stands	2 3 41 42	18 61 62			
from mountain stands	33 34 37 49 51	32 35 38 39 40	31 35 63 63 64 65		

In *D. glomerata* the length of panicles ranged 9.3 to 23.0 cm. and the average length for the particular individuals was 11.6 to 19.3 cm. (Table 5).

The number of panicle branches was 5 to 7 in *D. slovenica* and 4.8 to 6.3 in *D. glomerata*. This small difference in the number of panicle branches coupled with the considerable differences in the length of panicles gives rise to an appreciable difference in the length of the internodes in panicles. The length of the internodes ranged 3.3 to 4.11 cm. in *D. slovenica* and 2.3 to 3.3 cm. in *D. glomerata*. The longer internodes and thus the greater distances between the panicle branches in *D. slovenica* make its panicles less compact and more outspread.

The longer the panicles the longer usually their lowest branches. The lowest panicle branches ranged 7.7 to 16.2 cm. in *D. slovenica* and 5.7 to 7.9 cm. in *D. glomerata*. Very interesting is the stability of the proportion between the length of the panicle branches and their part occupied by spikelets. The part occupied by the spikelets usually is 1/3 of the length of the branches, e.g.:

No. of plant	Length of the lowest panicle branch cm	Length of part with spikelets cm
65	12.4	3.8
1	7.7	2.7
55	10.0	3.8
59	16.6	5.2
18	5.7	2.2

The panicles in *D. slovenica* are distinctly longer than in *D. glomerata* and owing to their longer internodes they are less compact. Often the panicles of *D. slovenica* have numerous secondary branchings and two

or even three branches growing from one internode. The branching of the panicles in *D. glomerata* is never so profuse.

The spikelets. The differences between *D. slovenica* and *D. glomerata* in the structure of spikelets are not important. The spikelets are arranged in small bunches usually of four spikelets and the small bunches join together forming larger ones.

The length of spikelets ranged 6 to 8 mm. in *D. slovenica* and 5 to 9 mm. in *D. glomerata*. The number of flowers in a spikelet was 1 to 6 in *D. slovenica* and 1 to 7 in *D. glomerata*. As is to be seen in Table 5 one plant can have spikelets with a different number of flowers. This variation differs in the particular plants. The greatest difference was found in plant no. 49 which had six kinds of spikelets with 1, 2, 3, 4, 5, and 6 flowers. The variation was smallest in plant no. 1 which had five flowers in all the spikelets. No significant difference was observed between *D. slovenica* and *D. glomerata* in the number of flowers in the spikelets. In both forms spikelets with three or four flowers predominated.

The ciliation of the spikelets is considered to be an important systematic trait of *Dactylis glomerata* (Müntzig 1937 p. 191 and 1943 p. 136). In the course of this investigation it was found that ciliation could be entirely absent or could occur in various degrees. Discrimination has been made between individuals which were glabrous slightly ciliated, ciliated, and very strongly ciliated (Table 5).

In *D. slovenica* individuals with glabrous or slightly ciliated spikelets are the most common. This is in agreement with Domin's (1943) report in which on the ground of the ciliation of spikelets he defined *D. slovenica* from the Belanske Tatry massif as var. *subglabra* with two forms: f. *atrichosantha* having glabrous spikelets and f. *trichosantha* having slightly ciliated ones.

In the spikelets the cilia grow on the main rib of the glumes and sometimes also on the main rib of the lower lemma. The presence of the ciliation depending on the position of the spikelet in the bunch. Only the glumes and the lemmas situated on the outside of the bunches and not covered by other spikelets are ciliated.

The position of the spikelets in a bunch also affects the structure of the glumes: those lying on the outside of the bunches are always well developed, long, sometimes awned at the tip, with 1 to 5 ribs and the midrib ciliated, all green, and with only the margins membranous and sometimes frayed. The glumes covered by other spikelets are always badly developed, small and thin, without chlorophyll, and all membranous. The midrib often is difficult to distinguish.

The panicles and the spikelets in *D. slo*

No. of plants	Length of panicles cm	A Average length of panicles cm	Length of lowest panicle branches cm	Average length of lowest panicle branches cm
<i>D. slovenica</i>				
1	18,4—25,7	20,1	6,2—11,5	7,7
48	16,0—20,8	18,1	6,0—9,7	7,7
55	16,1—22,2	20,4	6,6—12,0	10,0
56	14,8—22,5	19,3	6,4—11,3	9,5
57	15,2—36,8	26,6	6,0—18,7	13,4
59	23,1—38,2	28,7	14,1—20,0	16,2
60	18,9—30,3	25,3	9,4—16,9	13,7
<i>D. glomerata</i> from lowland stands				
2	12,9—18,0	14,9	6,1—8,2	7,2
18	9,3—14,0	11,6	4,2—8,0	5,7
41	10,1—19,3	14,8	5,2—9,5	7,9
42	10,6—16,0	13,5	4,5—8,6	7,1
61	14,1—23,0	19,3	4,5—10,3	7,2
62	14,0—19,7	17,2	5,4—9,3	6,9
from Bukowina				
35	17,0—23,5	19,3	8,5—11,7	10,1
from Morskie Oko				
63—65	19,1—30,3	22,6	10,3—14,7	12,4
Natural hybrids				
52	13,6—23,0	18,5	5,8—12,5	9,0
53	13,9—24,4	17,6	6,6—12,0	8,4
54	14,6—17,3	15,8	7,0—9,2	8,5
Artificial hybrids				
107	17,5—23,7	21,0	8,8—12,8	11,2
106/2	7,2—16,6	12,9	3,7—7,9	6,1
106/3	11,0—16,5	14,2	5,4—9,0	7,0
106/4	11,4—16,5	14,1	5,2—8,1	6,5

le 5

venica, *D. glomerata* and their hybrids

B Average number of panicle branches	A : B Average length of panicle internode cm	Length of spikelet mm	Number of flowers in spikelets	Ciliation of spikelets
6,0	3,3	7—8	5	glabrous
5,0	3,6	6—9	2 3 4 5 6	„
6,0	3,4	7—8	2 3 4 5	„
5,5	3,5	7—8	4 3	slightly ciliated
6,9	3,8	6—7	2 3	ciliated
7,0	4,1	7—8	1 2 3	glabrous
6,0	4,3	6—8	3 4	slightly ciliated
5,0	2,9	7	3 4 5	very ciliated
5,0	2,3	6—7	1 2 3	slightly cil- iated
5,1	2,9	6—7	3 4	glabrous
4,8	2,8	6—7	3 4	„
6,3	3,0	7—8	6 7	„
5,2	3,3	7—8	4 5	„
5,0	4,4	6—7	1 2 3 4	slightly cil- iated
6,0	3,4	8—9	3 4	glabrous
5,3	3,5	5—8	1 2 3 4	slightly cil- iated
5,3	3,3	5—7	1 3 4 5	„
4,9	3,2	5—8	3 4 5	„
6,0	3,5	6—7	3 4 5	„
5,4	2,3	6—7	3 4 5	„
5,0	2,8	7	4 5	glabrous
4,8	2,9	7	3 4 5	„

The different possibilities in the development of the glumes according to the position of spikelets in the bunch are as follows:

1. in spikelets covering the bunch from the top both glumes are well developed and of the same length,
2. in spikelets with one side in and one out of the bunch the glumes are asymmetrical; the outside glume is well developed and the inner one covered by the other spikelets is reduced,
3. the spikelets inside the bunch covered on all sides by other spikelets have both glumes reduced,

The spikelets inside the bunch are always glabrous even in strongly ciliated plants.

Contrary to the glumes the structure of the lemmas in *Dactylis* is always uniform.

The structure of the glumes and the lemmas in *D. slovenica* and *D. glomerata* is the same.

EXPERIMENTS WITH THE CULTIVATED PLANTS

The *Dactylis* plants were cultivated in the Botanical Garden in Warsaw from 1956 to 1960. The observations and measurements carried out through all those years have shown that the individuals of *D. slovenica* have retained their original growth habit and size during the five years of cultivation. This also applies to other traits, such as the harshness of the culms, the ciliation of the spikelets, the colour, the swelling at the culm base, the drooping of the panicles etc. The behaviour of the cultivated individuals of *D. glomerata*, whether brought from the lowlands or from the mountains, was the same.

The blooming season. The developmental cycle in *D. glomerata* is not uniform. There are races which flower early and races which flower late: this variability was already described by Turesson (1929), Oldemeyer and Hanson (1955), Lackamp (1955), Kalton and Laffel (1955), and others. The blooming season is an important trait for the cultivation of grasses. The blooming of the lowland plants of *D. glomerata* cultivated in the Botanical Garden in Warsaw began at the end of May. The differences in the time of blooming between the particular tufts did not exceed ten days.

The blooming of *D. slovenica* in the Tatras begins during the first half of July, the actual date depending on the local ecological conditions and the altitude of the stand. In the Botanical Garden in Warsaw the blooming season of *D. slovenica* was in the middle of June, i.e. a month earlier than in the Tatras but almost three weeks later than *D. glomerata* from the lowlands.

The specimens of *D. glomerata* brought from the Morskie Oko valley

in the Tatras and some specimens brought from the mountain stands in Bukowina Tatrzańska flowered in the middle of June, similarly as *D. slovenica*. This means that the late blooming of *D. slovenica* is a trait characteristic of the montane plants in general and results from their somewhat later development than of the lowland plants. The slower rate of development is retained by the *Dactylis* individuals even when they are cultivated for five years in the lowlands under different climatic conditions.

The *D. glomerata* plants no. 49 and 59 brought to the Botanical Garden in Warsaw from the Holubyho Dolina valley in the Tatras flowered simultaneously with the other individuals of *D. glomerata* from the lowlands. They must have been newcomers in the mountains and had still retained in their development the rhythm of the lowlands. This result confirms Professor Hádač's personal communication that *D. glomerata* is not one of the natural constituents of the flora in the Holubyho Dolina valley and that the isolated individuals found in this valley must have been brought there by men and sheep.

The following plants were used for the crosses: *D. slovenica* plants no. 45 and 55, and the *D. glomerata* plant no. 41 from the Puszcz Białowieska forest. All the three plants were typical representatives of their forms. The chromosome number of these plants was 28. For the crosses the flowers were castrated or additionally pollinated: the latter method was mostly used because castration in *Dactylis* plants is very difficult and ineffective. In additional pollination the panicles of both plants were placed under one isolator and in this way F₁ seeds and selfs were simultaneously obtained from one panicle. The morphological traits of the hybrids and the selfs were sufficiently different to distinguish between them.

The following crosses were carried out by the castration method:

No. 106 = 55 × 41 giving 4 seeds and 3 seedlings.

No. 107 = 41 × 55 giving 4 seeds and 1 seedling.

The plants from these crosses were unquestionable hybrids. Their chromosome number was 28.

The additional pollination method was used for three crosses the results being as follows:

No. of cross	Number of seedlings obtained from the cross		
	total	selfs	hybrids
108 = 41 × 55	24	9	15
105 = 55 × 41	22	9	13
109 = 45 × 41	16	3	13
Total	62	21	41

As is to be seen the number of hybrids obtained with this method is twice the number of selfs, the reason being the partial self-sterility of the parental plants. The partial self-sterility in *D. glomerata* was reported by Nilsson (1934), Myers and Hill (1943), Oldemeyer and Hanson (1955), and others. The results of the crosses in this investigation indicate that partial self-sterility occurs also in *D. slovenica*.

The morphology of the F_1 generation. Morphologically the F_1 generation was not uniform regardless of whether it was obtained by the method of castration or by the method of additional pollination. In the classification of the plants only the most characteristic traits of the parental plants were considered. These traits were: the swelling at the culm base, the date of blooming, the drooping of the panicles before and after blooming, and the appearance of the panicles outspread as in *D. slovenica* or compact as in *D. glomerata*.

The manner in which these traits occur in the parental plants and in the F_1 individuals is compared in Table 6. The table list all the F_1 individuals obtained by the method of castration and some obtained by additional pollination, the individuals with different combinations of traits being selected in the latter case.

The data in the table show that the F_1 plants may have either a phenotype intermediate between the parental forms or some traits identical with one of the parental forms. The culm base may have no swelling or the swelling may be as thick as or smaller than in *D. slovenica*. In the hydrids the blooming season is retarded as in *D. slovenica* and semi-drooping panicles predominate. The semi-drooping panicles before anthesis may be erect or drooping after anthesis. The panicles may be outspread, compact, or intermediate. Various combinations of traits are also possible e.g. the plants with no swelling of the culm base may have drooping or semi-drooping and outspread panicles and on the contrary plants with a distinctly bulbed culm base may have erect and compact panicles as in *D. glomerata*.

This lack of uniformity in the F_1 generation points to the possibility of the independent inheritance of the particular traits and at the same time reflects the great phenotypic plasticity within the particular individuals.

The plants from the natural stands used for the crosses must have been heterozygotes with regard to the traits here considered.

The progeny obtained by selfing the two *D. slovenica* parent plants were uniform and identical with the parental plants. On the other hand the selfs of the *D. glomerata* parental plant differed from each other. It seems, therefore, that the main source of the lack of uniformity in the F_1 generation was the *D. glomerata* plant no. 41 used in the crosses.

Table 6

The comparison the parental plants with the artificial and natural hybrids

No of plants		Swelling of the culm base	Beginn- ing of the blooming season 1960	Drooping of the panicles*		General habit of panicles
				before anthesis	after anthesis	
Parental plants						
<i>D. glomerata</i>	41	without bulb	25.V.	1	1	compact
<i>D. slovenica</i>	45	bulbed	10.VI.	4	4	outspread
<i>D. slovenica</i>	55	bulbed	10.VI.	4	4	outspread
Artificial hybrids F ₁						
	107	bulbed		3	3 4	outspread
	106/1	bulbed		1	1 2	compact
	106/2	intermediate		1 2	3 2	intermediate
	106/3	intermediate		4	4 3	outspread
	108/4	intermediate	8.VI.	3 4	3 4	outspread
	108/6	bulbed	8.VI.	3	1 2	outspread
	108/8	intermediate	8.VI.	1 2	3	outspread
	108/12	bulbed	12.VI.	1	1	compact
	108/13	without bulb	8.VI.	4	4	outspread
	108/15	without bulb	7.VI.	3	3	outspread
	108/16	without bulb	8.VI.	3	3	compact
Natural hybrids						
	46	intermediate	5.VI.	3	1 2 3	outspread
	47	bulbed	10.VI.	3	2 3	intermediate
	50	bulbed	5.VI.	4	1 2 3	outspread
	52	intermediate	5.VI.	1	1 2	outspread
	53	intermediate	7.VI.	2 3	2 3	compact
	54	without bulb	7.VI.	2 3	2 3 4	compact
<i>D. glomerata</i>						
from Morskie Oko						
	63—65	intermediate	10.VI.	3	2 3	outspread
from Bukowina						
	31	without bulb	13.VI.	3	1 2 3	compact
	35	bulbed	13.VI.	3	2 3	outspread
	39	intermediate	13.VI.	2 3	1 2 3	outspread
	40	without bulb	13.VI.	3	1 2 3	intermediate

* According to fig. 3.

Natural hybrids. The natural hybrids found in Holubyho Dolina in the Tatras closely resemble the F₁ hybrids obtained experimentally (Table 6). In the natural hybrids the swelling of the culm base may be small, intermediate, or well developed as in *D. slovenica*. Their blooming season is distinctly retarded with regard to *D. glomerata*, but earlier than of *D. slovenica*. The panicles are usually semi-drooping and similarly as

in the experimental F_1 plants the panicles may be semi-drooping before anthesis and erect or drooping after anthesis. The natural hybrids manifest a similar phenotypic plasticity within an individual as the F_1 hybrids (Table 6).

The *D. glomerata* plants from mountain stands. The plants of *D. glomerata* from the Morskie Oko valley and from Bukowina Tatrzańska manifest some similarity with the natural and the experimental hybrids. The plants from the Morskie Oko valley are morphologically uniform, but have some traits of *D. slovenica* expressed in a small degree. They all have slightly bulbed culm bases and panicles semi-drooping before anthesis and semi-drooping or erect after anthesis. The size of the panicles is similar as in *D. slovenica*, whereas the growth habit of the plants is that of *D. glomerata* (Table 6).

Some plants from Bukowina Tatrzańska also are somewhat like *D. slovenica*. The most similar is the plant no. 35: it has a distinctly bulbed culm base, semi-drooping panicles of almost the same size as in *D. slovenica* and the vigorous growth habit characteristic for *D. slovenica*. In the other plants from this stand the swelling of the culm bases is intermediate, sometimes the panicles are semi-drooping and some plants have the vigorous growth habit (Table 6).

Although the plants in the Morskie Oko valley and in Bukowina Tatrzańska do not meet directly with specimens of *D. slovenica*, since its distribution in the Tatras is restricted to the Belanske Tatry massif, nevertheless, there are among them individuals which morphologically resemble the hybrids. The possibility that *D. slovenica* genes were transferred from the distributional areas of this forms in the Belanske Tatry massif to such neighbouring areas as the Morskie Oko valley and Bukowina Tatrzańska cannot be discarded as improbable.

CYTOLOGICAL EXAMINATIONS

D. slovenica is a tetraploid plant with the chromosome number $2n=28$. In the course of meiotic divisions there may be tetravalents in diakinesis and in metaphase I. The tetravalents may form regular rings, rings twisted into the figure 8, or disrupted circles or chains. A similar occurrence of tetravalents was reported by Müntzing (1937) for *D. glomerata*. Only in one instance the Y arrangement of the chromosomes in a tetravalent was found.

The number of tetravalents in one cell in *D. slovenica* ranges 0 to 6. Not one cell was found in which all the chromosomes would form tetravalents, but in all the plants an appreciable proportion of cells contained 14 regular bivalents. The proportion of cells in *D. slovenica* with 14 bi-

valents in diakinesis ranged 16.9 to 24.5 per cent, whereas the average number of tetravalents in one cell was 0.97 to 1.43. Besides the tetravalents and the bivalents the cells of *D. slovenica* may contain a few univalents and very rarely single trivalents (Table 7).

For comparison cytological examinations were also carried out on the *D. glomerata* plants no. 18, 41, 42, 61, and 62. Similar chromosome arrangements were found in diakinesis. The average number of tetravalents in one cell was 0.96 to 1.28 and the proportion of cells with bivalents only ranged 20.0 to 33.3 per cent. Only the plant no. 2 from Leba strongly diverged from these average values: the average number of tetravalents to one cell in this plant was 1.89 and only four cells with 14 bivalents were found in it. It is possible that these four cells were wrongly classified, because the distance between the chromosomes in late diakinesis is already considerable and the pairs are connected by one chiasma which often is almost invisible.

In the experimental F_1 hybrids (plants no. 105/18, 106/1, 106/2, and 106/3) and in the natural hybrid (plant no. 47) the average number of tetravalents in one cell ranged 1.01 to 1.28, whereas the proportion of cells with bivalents only was 15.0 to 33.3 per cent. These values were approximately the same as in the parental forms. Table 7 lists the numbers of tetravalents found in diakinesis of the pollen mother cells in *D. slovenica*, *D. glomerata*, and their hybrids. The table only lists the figure for euploid plants with 28 chromosomes.

The meiotic divisions in *D. slovenica* have an entirely regular course similarly as in *D. glomerata*. The meiotic divisions in all the pollen sacks of one flower are accurately synchronized.

However, deviations from the regular course of meiotic divisions have also been observed. In the 1st meiotic division there were occasionally 1 or 2 univalents in a cell, but more than two univalents were never found. In anaphase of the 1st division the univalents could either remain on the equatorial plate and not be included in the telophase nuclei or they moved to the poles and were then included in the telophase nuclei. When each of two univalents moved to a different pole then each telophase nucleus contained 14 chromosomes. The chromosomes were counted in the metaphase of the 2nd division. In one instance at this stage the arrangement of 13 and 15 chromosomes was found: this arrangement was probably the result of the inclusion of two univalents in one telophase nucleus of the 1st division.

In the 1st meiotic division dividing univalents were quite often found. Their division usually was retarded with regard to the bivalents separating in anaphase. In metaphase of the 2nd division 14 and 15 chromosomes were found in some instances. This distribution must have been the result

Tab

The chromosome

No. of plants	2n	Number of counted PMC	Chromosome				
			14 _{II}	13 _{II} + 2 _I	12 _{II} + 1 _{III} + 1 _I	1 _{IV} + 12 _{II}	1 _{IV} + 11 _{II} + 2 _I
<i>D. slovenica</i>							
45	28	115	19	1	—	50	—
48	28	101	24	—	—	42	1
55	28	100	19	5	—	53	2
55 S ₁	28	199	49	—	—	62	3
<i>D. glomerata</i>							
2	28	101	4	—	—	35	—
18	28	141	48	—	—	62	2
41	28	101	18	2	1	44	2
42	28	101	26	—	—	37	2
61	28	100	22	—	—	46	—
62	28	100	27	—	—	51	—
Natural hybrid							
47	28	60	16	1	—	29	—
Artificial hybrids F ₁							
105/18	28	110	37	2	—	38	—
106/2	28	102	22	3	1	50	1
106/3	28	100	21	2	—	34	—
106/4	28	100	15	—	—	49	1

of the division of one univalent in the first meiotic division. The simultaneous division of both univalents was also often observed.

In the 2nd meiotic division chromosomes left on the plate and not included in the telophase nuclei were frequent. The number of such chromosomes could be one or more and they were found in one as well as in both dividing cells.

In the tetrads additional micronuclei were sometimes found and they must have been formed from the chromosomes rejected in the 2nd division.

The same irregularities in the meiotic divisions as those caused by the presence of univalents in *D. slovenica* — i.e. chromosomes lagging on the plate in the 2nd division and the formation of micro-nuclei in the tetrads — were also found in *D. glomerata*. This means that the deviations from the regular course of meiosis in *D. slovenica* are of the same kind as the irregularities in *D. glomerata*.

The pollen fertility counts in the *Dactylis* individuals grown in the Botanical Garden in Warsaw were made in three consecutive years (1958, 1959, and 1960). The differences between the particular years were rather

le 7

conjugation in diakinesis

conjugation in diakinesis							Average number of tetravalents per one PMC	PMC with bivalents only %
$1_{IV} + 1_{III} + 10_{II} + 1_I$	$2_{IV} + 10_{II}$	$3_{IV} + 8_{II}$	$3_{IV} + 7_{II} + 2_I$	$4_{IV} + 6_{II}$	$5_{IV} + 4_{II}$	$6_{IV} + 2_{II}$		
—	38	6	—	1	—	—	1,29	16,9
—	28	6	—	—	—	—	1,15	24,0
—	21	—	—	—	—	—	0,97	24,0
1	51	18	1	12	1	1	1,43	24,5
—	39	15	—	7	1	—	1,89	4,0
1	16	10	—	1	—	1	0,96	33,3
—	22	10	—	2	—	—	1,28	20,0
—	28	7	—	1	—	—	1,18	25,7
—	24	7	—	1	—	—	1,18	22,0
—	18	4	—	—	—	—	0,99	27,0
—	10	4	—	—	—	—	1,01	28,3
—	23	9	—	1	—	—	1,04	33,6
—	22	3	—	—	—	—	1,28	15,0
—	33	10	—	—	—	—	1,02	24,8
—	28	5	1	1	—	—	1,20	23,0

small, i.e. of the order of two per cent. Pollen fertility in the individuals of *D. slovenica* ranged 77 to 95 per cent and the pollen fertility range of *D. glomerata* plants from the lowlands and from the mountains was the same. The pollen fertility in the natural and the experimental hybrids was in no way reduced and was about 90 per cent.

DISCUSSION

In the polyploid complex of *Dactylis* the tetraploid forms are much more common than the diploid ones. The tetraploids are characterized by great expansivity and a much greater morphological variability than the diploids.

This is primarily caused by the lack of sterility barriers which allows the exchange of genes between the differentiated forms thus inhibiting the differentiation processes within the genus. The exchange of genes may take place even between the diploid and the tetraploid populations (Müntzing 1937, Zahory and Nur 1959).

The other reason for the great variability of the tetraploids is their tetraploid condition owing to which some genes can occur four times. This has been demonstrated by Brix and Quadt (1953) for the gene *g* determining the colour of leaves.

Many traits forming in *D. glomerata* continuous variation series — e.g. the growth habit of plants and the drooping of the panicles — must be determined by numerous genes. An interesting characteristic of the genus *Dactylis* is the presence in this genus of diploid and tetraploid individuals which are morphologically undistinguishable (Stebbins and Zahory 1959). This characteristic makes the classification of the genus very difficult. According to Domin's (1943) classification the whole genus *Dactylis* is one compound species with seven subspecies and numerous forms. Domin's classification is based on morphological traits and disregards the cytological differences although, already in 1930 Levan reported that *D. Aschersoniana* is a diploid plant as distinguished from the tetraploid *D. glomerata*. Domin, on the ground of morphological traits, assumed that the distribution of *D. Aschersoniana* extended over the whole of Poland. In the course of the present investigation plants morphologically identical with *D. Aschersoniana* were often found in central Poland, but they always had 28 chromosomes, whereas the diploid *D. Aschersoniana* probably occurs only in the beech forests of West Poland. In Domin's classification the plants with different chromosome numbers but morphologically identical are classified together as one subspecies.

Stebbins and Zahory (1959) also consider the genus *Dactylis* to be one compound species *D. glomerata*, but unlike Domin's classification their's is based on the chromosome number. Within the species *D. glomerata* they distinguish diploid and tetraploid subspecies. In this approach morphologically identical plants may be assigned to two different subspecies and the difficulties arising in this connection were pointed out by Stebbins and Zahory themselves (1959).

All that has been said above clearly shows how differently the different workers approach the same phenomenon and what deplorable effects this has on the systematics of the genus *Dactylis*. The question thus arises what criterion should be given priority in the classification of the genus *Dactylis*, the morphology of the plants or the chromosome number?

The discrimination between diploid and tetraploid plants greatly facilitates the classification, but it seems illogical to assign to different systematic units plants morphologically identical, when within the diploid or the tetraploid forms the taxonomic units are discriminated according to the morphological traits alone.

All this makes the studies on the genus *Dactylis* a very difficult, but at the same time a very interesting problem, all the more so as the group of plants covered by the genus is still in the course of the gradual differentiation of the particular forms.

An example of this differentiation is provided by *D. slovenica* related with *D. glomerata* by many common traits. The morphological traits of both these forms are compared in Table 8. As is to be seen from this table *D. glomerata* has a much wider range of variation than *D. slovenica*.

The data assembled in Table 8 can be divided into three groups:

In the first group are the traits manifesting a continuous variation; in *D. glomerata* the range of variation is wide and in *D. slovenica* much narrower and contained within the limits of *D. glomerata*. These traits are the growth habit of the tufts, the colour and the harshness of the plants, the ciliation of the spikelets, the length of the ligule, and the number of flowers in a spikelet.

The second group also consists of traits with a continuous variation, but the overlapping of the variation ranges in *D. glomerata* and in *D. slovenica* is only partial and may differ in various degrees. The overlapping is wide in the case of the leaf widths and the maximum culm lengths, and narrow in the case of the average panicle lengths; the ranges of variation of the average lengths of internodes and of the drooping of panicles only contact.

The third group includes the contrasting traits, i.e. the swelling of the culm base or its absence and early or late blooming season. In the case of these traits the variation is discontinuous.

The late blooming of *D. slovenica* cannot be regarded as a systematic trait, since it is characteristic for all montane plants, but it is useful in the classification of plants.

The most important for distinguishing between the particular forms are the contrasting traits and for this reason the swelling of the culm base is the most characteristic trait of *D. slovenica*.

The drooping of the panicles and the length of the internodes also are useful traits for distinguishing between the two forms, because their ranges of variation are different, but these traits do not occur only in *D. slovenica*.

D. Aschersoniana has drooping and outspread panicles similarly as *D. slovenica*, however, the differences between these two forms are very great. *D. Aschersoniana* is a small frail plant, whereas *D. slovenica* is remarkable for its strong and vigorous growth habit. Szafran (1933) in the report on his investigations on the grasses of the pastures in the East Carpathians gives a detailed description and the measurements of

Table 8

The morphological traits of *D. slovenica* and *D. glomerata* from lowland stands

A. The qualitative traits

	Types of the growth habit*	Colour of plants	Harshness of plants	Swelling of the culm base	Drooping of panicles**	Ciliation of spikelets	Blooming season in Botanical Garden in Warsaw
<i>D. slovenica</i>	3—4	pale green bright green	smooth slightly harsh	bulbed	3—5	glabrous slightly ciliated	middle of Juli
<i>D. glomerata</i>	1—4	pale green bright green bluish green grayish green	smooth slightly harsh harsh very harsh	without bulb	1—3	glabrous slightly ciliated very ciliated	end of May

B. The quantitative traits

	Maximum length of culms cm	Width leaves mm	Length ligule leaves mm	Average length of panicles cm	Average number of panicle branches	Average length of panicle internodes cm	Length of spikelets mm	Number of flowers in spikelets
<i>D. slovenica</i>	124—190	6—1	4—7	11,6—19,3	5,0—7,0	3,3—4,3	6—9	2—6
<i>D. glomerata</i>	96—136	4—12	3—8	18,1—28,7	4,8—6,3	2,3—3,3	5—8	1—7

* According to fig. 1.

** According to fig. 3.

what he believed to be *D. Aschersoniana*, but the data in his report indicate that the plants he described could not have been *D. Aschersoniana*. They probably were *D. slovenica* which by its outspread and drooping panicles resembled *D. Aschersoniana*.

The analysis of morphological traits seems to indicate that *D. slovenica* has developed from *D. glomerata*. The two forms are connected by series of continuous variations indicating that *D. slovenica* is a relatively young form still in the course of differentiation out of the *D. glomerata* population.

On the other hand *D. Aschersoniana* is believed to be one of the ancestors of *D. glomerata* (Müntzing 1937, Myers 1948, Stebbins and Zahory 1959) and therefore the genes determining the drooping of panicles could have been transferred from *D. Aschersoniana* through *D. glomerata* to *D. slovenica*.

Another alternative is that *D. slovenica* appeared in the Tatras as a result of a cross between *D. glomerata* and *D. Aschersoniana* and if this was the case the exchange of genes between these two species could have taken place through triploid hybrids. An exchange of genes of this kind was observed by Zahory and Nur (1959) in Palestine where they found numerous triploids on the stands where the tetraploid and diploid *Dactylis* populations contacted. The chromosome number of some individuals in the progeny of these triploids was 28.

Whichever of these possibilities is more accurate, *D. glomerata* is certainly the main ancestor of *D. slovenica* and the Tatra Mountains undoubtedly constituted a convenient ecological niche in which the new form could develop. The conditions prevailing in the mountains must have had a decisive influence on this process.

D. slovenica certainly arose as a Carpathian ecotype of *D. glomerata*, but its morphological uniformity and the rather well marked differentiation are sufficient to classify it as a distinct systematic unit. Domin (1943) was fully justified when he classified *D. slovenica* as a systematic unit of equal rank with *D. Aschersoniana* and *D. hispanica*.

The question whether *D. slovenica* is to be treated as an independent species or as a subspecies of *D. glomerata* depends on what systematic approach to the genus *Dactylis* is chosen. If Domin's and Stebbin's opinion that the genus only consists of the compound species *D. glomerata* is accepted, then *D. slovenica* must be treated as a subspecies. But if other species than *D. glomerata* are discriminated in the genus, such as e.g. *D. marina* Borill, then *D. slovenica* also fully deserves the rank of an independent species.

Cytological examinations have revealed no differences between *D. slovenica*, *D. glomerata*, and their hybrids. In all instances the course of

meiosis was similar and the average number of tetravalents in one cell was about one, which means that the level of tetravalents in *D. slovenica* is the same as in *D. glomerata*. These results confirm the earlier supposition that *D. slovenica* is a young form developed from the *D. glomerata* population and that it did not have time to become cytologically differentiated.

The values obtained in the course of this investigation for the level of tetravalents in *D. slovenica* and *D. glomerata* are very different from the data reported by other workers. The average number of tetravalents in one P.M.C. in *D. glomerata* was 3.5 according to Müntzing (1937), 2.8—4.4 according to Myers and Hill (1942), and 3.5 according to McCollum (1958). The values reported by those workers are about three times the values obtained in this investigation. The difference probably arose owing to the high proportion of cells, more than 20 per cent, with bivalents only in the examined plants from the Tatras and the Polish lowland. This means that the differences in the level of tetravalents between the particular population of *D. glomerata* may be considerable.

McCollum (1958) found that the distribution of tetravalents in the tetraploid forms of the genus *Dactylis* follows a binomial curve. The result of this kind of distribution would be a constant level of about 3.5 tetravalents to one cell. McCollum found the same level of tetravalents in natural hybrids and in hybrids obtained experimentally by crossing two different forms. Nevertheless, in a few instances a lower average number of tetravalents in one cell was recorded.

It seems, therefore, that the average number of 3.5 tetravalents in one P.M.C. is the initial number for the tetraploid *Dactylis* plants. In some populations a reduction in the number of tetravalents and a corresponding rise in the number of bivalents takes place. This kind of chromosome behaviour is characteristic for segmental allopolyploids and makes possible further evolutionary changes in the genus *Dactylis*.

CONCLUSIONS

1. *Dactylis slovenica* is a tetraploid with the chromosome number $2n=28$ growing on limy substrata in the Carpathians.
2. *D. slovenica* crosses easily with *D. glomerata* giving fertile hybrids.
3. The course of meiosis in *D. slovenica*, *D. glomerata*, and their hybrids is the same. The average number of tetravalents in one P.M.C. in *D. slovenica* ranges 0.97 to 1.29. Similar numbers of tetravalents were found in *D. glomerata* and in the hybrids of the two forms.

4. *D. slovenica* must have developed out of *D. glomerata* the two forms being related by many common traits which differ only by their range of variation.

5. The main traits distinguishing *D. slovenica* from *D. glomerata* are the bulbed culm base and the drooping outspread panicles of the former form.

6. The plants of *D. slovenica* are morphologically rather uniform: they can be classified as a subspecies of *D. glomerata* on equal terms with the other already distinguished diploid and tetraploid subspecies.

The author is much indebted to Professor Dr. W. Gajewski for his generous help and guidance in the course of this work.

Department of Genetics

Warsaw University

Varsaw, Poland, Al. Ujazdowskie 4

(Entered: 30.3.1961)

REFERENCES

- Borrill M., 1961, *Dactylis marina* Borrill, sp. nov., a natural group of related tetraploid forms, J. Linn. Soc. (Bot.) 56: 431—439.
- Brix K. und Quadt F., 1953, Experimentell genetische Untersuchungen über die Natur einer natürlichen Polyploiden, Z. Pflanzenzucht. 32: 402—420.
- Domin K., 1929, Schedae ad floram Českoslovenicam exsiccatur, Acta Bot. Bohem. 8: 50—51.
- Domin K., 1943, Monografická studie o rodu *Dactylis* L., Acta Botanica Bohemica 14: 3—147.
- Dostal J., 1950, Kwětena ČSR, Praha.
- Hegi G., 1907, Illustrierte Flora von Mittel-Europa, 1: 294—296.
- Kalton R. R. and Leffel R. C., 1955, Evaluation of combining ability in *Dactylis glomerata* L., III. General and specific effects, Agron. Journ. 47: 370—373.
- Kattermann G., 1931, Über die Bildung polyvalenter Chromosomenverbände bei einigen Gramineen, Zeitsch. f. wiss. Biol. Abt. E., Planta 12: 732—774.
- Kotula B., 1889—1890, Rozmieszczenie roślin naczyniowych w Tatrach, Kraków.
- Lackamp J. W., 1955, On the determination of harshness in plants of cocksfoot, Euphytica 4: 31—33.
- Levan A., 1930, Beitrag zur Kenntnis der Chromosomen in der Gattung *Dactylis* L., Botan. Notiser: 95—104.
- McCollum, 1958, Comparative studies of chromosome pairing in natural and induced tetraploid *Dactylis*, Chromosoma (Berl.) 9: 571—605.
- Müntzing A., 1933, Quadrivalent formation and aneuploidy in *Dactylis glomerata*, Botan. Notiser: 198—205.
- Müntzing A., 1937, The effects of chromosomal variation in *Dactylis*, Hereditas, 23: 112—235.
- Müntzing A., 1943, Characteristic of two haploid twins in *Dactylis glomerata*, Hereditas 29: 134—140.

- Myers W. M., 1943, Analysis of variance and covariance of chromosomal association and behavior during meiosis in clones of *Dactylis glomerata*, Bot. Gaz. 104: 541—552.
- Myers W. M., 1948, Studies on the origin of *Dactylis glomerata* L., Genetics 33: 117.
- Myers W. M. and Hill H. D., 1942, Variation in chromosomal association and behavior during meiosis among plants from open pollinated populations of *Dactylis glomerata* L., Bot. Gaz. 104: 171—177.
- Myers W. M. and Hill H. D., 1943, Increased meiotic irregularity accompanying inbreeding in *Dactylis glomerata* L., Genetics 28: 383—397.
- Nilsson-Leissner G., 1942, A case of increased vitality in sibpollinated later generations of self-fertilised *Dactylis glomerata* strains, Hereditas 28: 222—224.
- Oldemeyer D. L. and Hanson A. A., 1955, Evolution of combining ability in orchard grass *Dactylis glomerata* L., Agron. Journ. 47: 158—162.
- Stebbins G. L., 1956, Cytogenetics and evolution of the grass family, Am. Journ. of Botany 43: 890—905.
- Stebbins G. L. and Zahory D., 1959, Cytogenetic and evolutionary studies in the genus *Dactylis*. I: Morphology, distribution and interrelationships of diploid subspecies, Univ. Calif. Publ. Bot. 31: 1—40.
- Turesson G., 1929, Ecotypical selection in siberian *Dactylis glomerata*, Hereditas 12: 335—351.
- Szafran B., 1933, Badania nad trawami pastewnymi Karpat Wschodnich. I. Kupkówka Aschersona (*Dactylis Aschersoniana* Graebn.), Puławy.
- Zahory D. and Nur U., 1959, Natural triploids in the orchard grass *Dactylis glomerata* L., polyploid complex and their significance for gene flow from diploid to tetraploid levels, Evolution 13: 311—317.