Biosystematic studies on *Dactylis* L.

1. Review of the previous studies.

1.2. Cytology, genetics, experimental studies, and evolution

MARTA MIZIANTY

Wł. Szafer Institute of Botany, Polish Academy of Science,
Lubicz 46, 31-512 Kraków, Poland

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Abstract

In this paper the author presents a review of the previous studies on *Dactylis* L., dealing with cytology, genetics, experimental studies and evolution. Following cytotypes of *Dactylis* are distributed mostly in Central Europe: 16 diploids, 7 tetraploids and also 2 hexaploids in North Africa. Some aneuploids and accessory chromosomes were also found in this genus. Data dealing with karyotypes of some taxa, and geographical distribution of cytotypes are also listed. Selected problems concerning crossing within diploids as well as tetraploids and also between diploids and tetraploids were presented. Some opinions regarding the evolution in the genus *Dactylis* were also demonstrated. In all these hypotheses the following diploids are considered to be the oldest: *D. smithii* Link subsp. *smithii*, *D. g.* subsp. *aschersoniana* (Greabn.) Thell. and *D. g.* subsp. *himalayensis* Dom.

Key words: *Dactylis*, review, cytology, genetics, experimental studies, evolution

INTRODUCTION

The present paper is based on the analysis of numerous studies in which the same taxa of the genus *Dactylis* were considered as different taxonomical ranks. To avoid confusion in nomenclature, on the subsequent pages of the present study, the nomenclature and systematic treatment of the author cited were preserved. Each time, taxonomical rank according to Jones et al. (1961) and Borrell and Carroll (1969) were put in brackets. In the above studies, all taxa, except for *D. marina* Borrell, were treated as subspecies of *D. glomerata*.

Later studies by Parker (1972) revealed that *D. g.* subsp. *hylodes* Borrell (Borrell and Carroll 1969) is the subspecies of *D. smithii* Link. The author of the present study shares the above view and on the pages that follow she

distinguishes species *D. smithii* Link together with its two subspecies: subsp. *hylodes* Parker and subsp. *smithii*.

The taxa not considered in the papers mentioned above, retain the rank attributed to them by the authors cited. These are: *D. rigida* Boiss. et Heldr., and four subspecies of *D. glomerata*: subsp. *oceanica* Guignard, subsp. *reichenbachii* (Hausm.) Stebbins et Zohary, subsp. *slovenica* (Dom.) Dom. and subsp. *himalayensis* Dom.

CHROMOSOME NUMBERS

The first data on the chromosome numbers for the genus *Dactylis* were the records by Davies (1927) and Avdulov (1931) for *D. glomerata* L. (*D. glomerata* L. subsp. *glomerata*) $2n = 28$ and by Levan (1930) and Kattermann (1930) for *D. aschersoniana* Graebn., *D. glomerata* subsp. *aschersoniana* (Graebn.) Thell., $2n = 14$.

A voluminous atlas, in two parts, including chromosome numbers of the genus *Dactylis* from 391 localities in Europe and North Africa (including only one locality of *D. g.* subsp. *glomerata* recorded from Poland) was compiled by Jones et al. (1961) as well as by Borrill and Carroll (1969). The atlas registers the number $2n = 28$ for the following tetraploids: *D. g.* subsp. *glomerata*, subsp. *hispanica* (Roth) Nym., subsp. *hylodes* Borrill (*D. smithii* Link subsp. *hylodes* Parker), *D. marina* Borrill, and also the number $2n = 14$ for numerous diploids: *D. g.* subsp. *lusitanica* Stebbins et Zohary, subsp. *aschersoniana* (Graebn.) Thell., subsp. *woronowii* (Ovczinn.) Stebbins et Zohary, subsp. *santai* Stebbins et Zohary, subsp. *judaica* Stebbins et Zohary, subsp. *parthiana* Borrill et Parker, subsp. *castellata* Borrill et Parker and subsp. *lebanotica* Borrill et Parker.

Numerous former and later records of the chromosome numbers (diploids, tetraploids and triploids) of the genus *Dactylis* supplement the above mentioned atlas. They pertain to: Czechoslovakia (Májovský et al. 1974a and b, Májovský and Murin 1987), Yugoslavia (Löve and Löve 1974), Hungary (Felföldy 1949, Pólya 1949), Bulgaria (Popova 1963, Kožuharov and Nicolova 1975), Portugal (Fernandes and Queiros 1969, Queiros 1973 and Dalgaard 1985 – Madeira), Italy (Speranza and Cristofolini 1986, 1987), Israel (Nur and Zohary 1959), Soviet Union (Sokolovskaya and Probatova 1976, 1979), Japan (Moriya and Kondo 1950, Tateoka 1954a and b), Canada (Bowden 1960), Costa Rica (Pohl and Davidse 1971) and also to other territories. For Poland the chromosome number for *D. g.* subsp. *aschersoniana* ($2n = 14$) was given by Rurka (1974), Żukowski and Słowińska (1979), Mizianty (1985) and for *D. g.* subsp. *glomerata* ($2n = 28$) by Doroszevska (1961).

The results of the research carried out by Borrill and Jones (1961) who found a hexaploid chromosome number ($2n = 42$) in the representatives of

Dactylis from two localities in northern Africa (Libia-Cyrenaica and Egypt) deserve particular attention. According to the same authors, the above hexaploids are morphologically compatible with the tetraploid subsp. *hispanica*.

Müntzing (1937) found in natural localities not only diploids and tetraploids ($2n = 14$ and $2n = 28$) but aneuploids ($2n = 27, 29, 30$) as well. As he claims, 10% of *D. glomerata* populations (*D. g.* subsp. *glomerata*) is aneuploid.

Müntzing (1943) reports also a haploid *D. glomerata* (*D. g.* subsp. *glomerata*), $2n = 14$. Two such specimens were found among 198 investigated plants. These two haploid specimens were characterized by their declining vitality (their anthers were degenerating) and, moreover, they were much differentiated in respect of morphology. Such a differentiation of two haploids can be explained (as the author maintains) by the fact that numerous recessive mutations occur in the chromosomes of *Dactylis* which can reveal themselves just on the haploid level.

ACCESSORY CHROMOSOMES

1 to 12 accessory chromosomes (so called chromosomes B) are found in *Dactylis*. These chromosomes by their nature are not homologous to the normal chromosomes. They are usually half the size of the smallest regular chromosomes and they are all submedian chromosomes.

The existence of accessory chromosomes in *D. glomerata* was detected both in diploids: subsp. *lusitanica*, subsp. *judaica*, subsp. *castellata* (Jones 1962, Jones and Borrill 1962, Shah 1963, 1964a and b, 1965, 1967, Carroll and Borrill 1965, Borrill and Carroll 1969, Puteyevsky and Zohary 1970) and in tetraploids: subsp. *glomerata* and subsp. *hispanica* (Zohary and Nur 1959, Jones et al. 1961, Jones 1962, Borrill and Carroll 1969, Kožuharov and Nicolova 1975).

Puteyevsky and Zohary (1970) investigated the behavior of accessory chromosomes in *D. g.* subsp. *judaica* and they found out that they are characterized by a somatic instability (different number in different roots) and by a "non disjunction" phenomenon (ie. by a transference of a bivalent to the daughter cell without the splitting of the former). Consequently the number of accessory chromosomes shows a tendency to increase from generation to generation. According to the authors mentioned above, the transmission of B chromosomes is not a simple phenomenon. Most of the accessory chromosomes are transmitted to the offspring if they belong to a male parent. The authors point out, too, that offspring with an even number of accessory chromosomes is most frequent. Zohary and Ashkenazi (1958), when investigating the diploid populations of *Dactylis* in Israel, found that the populations occupying various habitats differ in the number of accessory chromosomes.

Accessory chromosomes can contribute to the variability of the genus in which they occur, and thus they can increase its adaptability. As it was revealed by Darlington (1963), accessory chromosomes are more effective in diploids than in tetraploids. The influence of B chromosomes is twofold. It is harmful when they appear in great number (they reduce the vitality and fertility of the population), and neutral, or even profitable, if they are not numerous (Williams and Barclay 1968). According to the authors mentioned above, the effect of the accessory chromosomes activity depends also, to a great extent, on the environmental conditions.

ANALYSIS OF THE KARYOTYPE

The chromosomes of *Dactylis* are different in size measure from about 3 to 9 μm . Their morphology has been examined in a few taxa only. Out of tetraploids only four subspecies of *D. glomerata* have been investigated so far: subsp. *glomerata* (Wetschnig 1983, 1984, and Guignard 1987), subsp. *woronowii* and subsp. *hispanica* (Fernandes and Queiros 1969, Kožuhařov and Nicolova 1975, Wetschnig 1983), subsp. *oceanica* as well as *D. marina* (Guignard 1987). Out of diploids only three subspecies of *D. glomerata* have been examined: subsp. *aschersoniana* (Wetschnig 1983, 1984, Mizianty 1985), subsp. *lusitanica* (Fernandes and Queiros 1969) and subsp. *reichenbachii* (Wetschnig 1983).

The chromosomes of *Dactylis* are mostly median and submedian. The diploids possess two pairs of chromosomes with satellites, while tetraploids — four pairs.

The next step in the cytogenetic studies on this species concerns the differential staining of the chromosomes. That method has been applied so far only to *D. g.* subsp. *glomerata* (Wetschnig 1983, 1984), *D. g.* subsp. *aschersoniana* (Wetschnig 1983, 1984, Mizianty 1985) and to *D. g.* subsp. *reichenbachii* (Wetschnig 1983).

GEOGRAPHICAL DISTRIBUTION OF CYTOTYPES

After comparing the cytological with taxonomical studies and with geographical distribution (Mizianty 1986), it can be noted that the diploids are markedly separated from one another both geographically and in respect of their morphological features, and they also have different ecological requirements. These are the taxa of a small geographical range, considerably distant from one another, often endemics. *D. g.* subsp. *aschersoniana* is the only diploid which has a relatively broad range of distribution (central Europe). As far as the area is concerned, the diploids occupy a small part of the area of distribution of the genus *Dactylis*, nevertheless, they are very numerous,

Fig. 1. The primary distribution of *Dactylis* (according to: Borrill 1961c, Doroszevska 1963, Borrill and Carroll 1969, Sokolovskaya and Probatova 1979, Lumaret 1984, Guignard 1985, Mizianty 1986 and 1988b, Speranza and Cristofolini 1987). Explanations in Table 1

contrary to some tetraploids, which occupy vast areas and their ranges of distribution frequently overlap (Fig. 1).

So far, the following tetraploids of *D. glomerata* are known (the studies dealing with the distribution of given taxa were put in brackets): subsp. *glomerata*, subsp. *hispanica* (Roth) Nym. (Mizianty 1986), subsp. *slovenica* (Dom.) Dom. (Mizianty 1988b), subsp. *oceanica* Guignard (Guignard 1985). To tetraploids there belong also: *D. rigida* Boiss, et Heldr. (Domin 1943, Stebbins and Zohary 1959, Borrill 1961c), *D. smithii* Link subsp. *hylodes* Parker (Borrill and Carroll 1969, Parker 1972) and *D. marina* Borrill (Borrill 1961a, Mizianty 1986).

To the diploids with *D. glomerata* known so far there belong: subsp. *aschersoniana* (Graebn.) Thell., subsp. *himalayensis* Dom., subsp. *woronowii* (Ovczinn.) Stebbins et Zohary, subsp. *judaica* Stebbins et Zohary, subsp. *santai* Stebbins et Zohary, subsp. *lusitanica* Stebbins et Zohary, subsp. *juncinella* (Bory) Boiss, subsp. *ibizensis* Stebbins et Zohary, subsp. *reichenbachii* (Hausm.) Stebbins et Zohary, subsp. *mairei* Stebbins et Zohary (Stebbins and Zohary 1959, Grigoryev 1962, Doroszevska 1963, Sokolovskaya

Table 1

The primary distribution of *Dactylis* (explanation to Fig. 1)

TETRAPLOIDS	
A	— limit of tetraploids
B	— zone of contact between <i>D. g.</i> subsp. <i>hispanica</i> (Roth) Nym. — south and <i>D. g.</i> subsp. <i>glomerata</i> — north
a	— locality of <i>D. g.</i> subsp. <i>hispanica</i> in Ireland
C	— limit of <i>D. marina</i> Borrill
D	— limit of:
	I. <i>D. g.</i> subsp. <i>slovenica</i> (Dom.) Dom.
	II. <i>D. g.</i> subsp. <i>oceanica</i> Guignard
	III. <i>D. rigida</i> Boiss. et Heldr.
	IV. <i>D. smithii</i> Link subsp. <i>hylodes</i> Parker
DIPLOIDS	
E	— limit of:
	1* <i>D. g.</i> subsp. <i>aschersoniana</i> (Graebner) Thell.
	2* <i>D. g.</i> subsp. <i>reichenbachii</i> (Hausm.) Stebbins et Zohary
	3. <i>D. g.</i> subsp. "galician"
	4. <i>D. g.</i> subsp. <i>lusitanica</i> Stebbins et Zohary
	5. <i>D. g.</i> subsp. <i>juncinella</i> (Bory) Boiss.
	6. <i>D. g.</i> subsp. <i>ibizensis</i> Stebbins et Zohary
	7. <i>D. g.</i> subsp. <i>santai</i> Stebbins et Zohary
	8. <i>D. g.</i> subsp. <i>castellata</i> Borrill et Parker
	9* <i>D. g.</i> subsp. <i>mairei</i> Stebbins et Zohary
	10. <i>D. g.</i> subsp. <i>lebanotica</i> Borrill et Parker
	11* <i>D. g.</i> subsp. <i>judaica</i> Stebbins et Zohary
	12. <i>D. g.</i> subsp. <i>hyrcana</i> Tzvel.
	13. <i>D. g.</i> subsp. <i>parthiana</i> Borrill et Parker
	14* <i>D. g.</i> subsp. <i>woronowii</i> (Ovczinn.) Stebbins et Zohary
	15. <i>D. g.</i> subsp. <i>himalayensis</i> Dom.
	16. <i>D. smithii</i> Link subsp. <i>smithii</i>
HEXAPLOID	
F	— limit of hexaploid

* — subspecies also includes a tetraploid cytotype

and Probatova 1979, Lumaret 1984), subsp. *hyrcana* Tzvel. (Tzvelev 1976, Sokolovskaya and Probatova 1979), subsp. *parthiana* Borrill et Parker, subsp. *castellata* Borrill et Parker, subsp. *lebanotica* Borrill et Parker (Borrill and Carroll 1969), subsp. "galician" (Borrill 1977), and *D. smithii* Link subsp. *smithii* (Stebbins and Zohary 1959, Parker 1972).

THE FORMS IDENTICAL MORPHOLOGICALLY BUT DIFFERING
IN THE LEVEL OF PLOIDY

The occurrence of specimens different as to the level of ploidy but morphologically similar to such an extent that they are indistinguishable unless their chromosomes are counted, appears to be a separate problem concerning the genus *Dactylis*. The occurrence of such forms was observed in various taxa of *Dactylis*. Tetraploids morphologically corresponding to diploid subsp. *aschersoniana* were found in the following countries: Poland (Doroszevska 1961, Rurka 1974), Yugoslavia (Böcher 1961), Finland (Jones et al. 1961), and the ones corresponding to the diploid subsp. *woronowii* in the Soviet Union — Armenia, Kazakhstan (Doroszevska 1963, Sokolovskaya and Probatova 1979), corresponding to the diploid subsp. *judaica* in Israel (Zohary and Nur 1959). As it has already been mentioned, Borrill and Jones (1961) found a hexaploid in Libia and Egypt corresponding to the tetraploid subsp. *hispanica*.

According to the authors of the above works, the occurrence of morphologically identical specimens but differing in the level of ploidy can be caused by the creation of autopolyploids, which continue to grow in the habitat of diploids, or by crossing of the diploids and tetraploids as a result of the change of the original habitat. The studies conducted by Williams and Barklay (1968), who by means of colchicine obtained artificially autotetraploids of subsp. *lusitanica*, support the first thesis, whereas the results obtained by Jones and Borrill (1962) support the second one. They crossed diploids with tetraploids and the triploid thus produced was backcrossed to the diploid. Finally, they obtained a tetraploid. They used subsp. *lusitanica*, subsp. *aschersoniana*, subsp. *woronowii*, and subsp. *santai* as diploids, and subsp. *glomerata*, subsp. *hispanica* and *D. marina* as tetraploids in their experiments.

Detailed morphological studies on the tetraploid subsp. *aschersoniana* in Poland (Mizianty 1988a) induced the author of the present study to draw the following conclusion: subsp. *aschersoniana* which occurs in Poland is only and exclusively a diploid. Tetraploid forms, resembling subsp. *aschersoniana*, differ slightly from diploid subsp. *aschersoniana* if carefully examined morphologically. These are either hybrids of diploid subsp. *aschersoniana* and tetraploid subsp. *glomerata*, or of diploid subsp. *aschersoniana* and tetraploid subsp. *slovenica*, or these are tetraploids (subsp. *glomerata* or subsp. *slovenica*) changed by modification.

To date, there has been no unanimous scientific opinion on whether the similarity of diploids and tetraploids is caused by the derivation of tetraploids from diploids (by autopolyploidy or crossing), or by the adaptation of the diploids and tetraploids to similar environmental conditions.

HYBRIDS

As it ensues from the analysis of the distribution of all the taxa of *Dactylis* (Fig. 1), diploids (except for subsp. *himalayensis*) occur within the area of the distribution of tetraploids. Generally, in nature, diploids are not in contact, because they are separated by geographical and ecological barriers. However, the possibility of contact between diploids cannot be ruled out. For example, the existence of the hybrid of subsp. *parthiana* and subsp. *woronowii* in nature was confirmed by Borrill and Carroll (1969). As far as the crossing of diploids is concerned, the following principle can be observed: fertile hybrids can be produced by the diploids between which there are no geographical and morphological barriers. The diploids which are isolated from one another for a long time produce and concentrate great genetic differences, which, in turn, do not allow the formation of fertile hybrids. This is the case with e.g. *D. g.* subsp. *smithii* (*D. smithii* Link subsp. *smithii* Parker 1972), which is supposed to be both a relic of the Tertiary and a subtropical endemic (Borrill 1961a, Parker and Borrill 1968).

In nature tetraploids cross more easily, producing fertile hybrids (Stebbins and Zohary 1959). Frequently, there appear contacts between tetraploids subsp. *glomerata* and subsp. *hispanica* as their areas of distribution adjoin, or even overlap (Fig. 1).

The contacts between diploids and tetraploids are quite frequent, too. Holmberg (1923) and Levan (1930) were the first to determine the chromosome number $2n = 21$ for the natural hybrids of *D. glomerata* and *D. aschersoniana* Graebner (*D. g.* subsp. *glomerata* and *D. g.* subsp. *aschersoniana*). Müntzing (1937) also examined natural hybrids of *D. glomerata* L. and *D. aschersoniana* Graebner. (*D. g.* subsp. *glomerata* and *D. g.* subsp. *aschersoniana*) occurring in Sweden. The triploids $2n = 21$ and pentaploids $2n = 35$, the outcome of the crossing, however, had a limited fertility. Lowered fertility of triploids coming from the crossing between *D. glomerata* and *D. aschersoniana* (*D. g.* subsp. *glomerata* and *D. g.* subsp. *aschersoniana*) was confirmed by the studies conducted by Weibull (1964). Fertile (tetraploid) offspring is produced yet by triploids in backcrosses with diploids. The occurrence of natural hybrids (triploids) between diploid and tetraploid subsp. *judaica* in Israel was also found by Zohary and Nur (1959). A series of studies by Borrill and his collaborators (Borrill 1961b and 1966, Jones 1962, Jones and Borrill 1962, Carroll and Borrill 1965, Parker and Borrill 1968, Borrill and Linder 1971) dealing with the transfer of genes between diploids and tetraploids of that genus, deserves particular attention.

Investigations on the artificial crossing in the genus *Dactylis* were also carried out (Borrill 1961b, Weibull 1964, Parker and Borrill 1968, Hu and Timothy 1971). As a result, the hybrids of different diploid taxa were obtained. The fertility of hybrids was different and depended on the extent of

geographical and ecological barriers or on morphological differences between parental taxa. Borrill (1961b) produced artificially hybrids of tetraploids (*D. g.* subsp. *glomerata*, *D. g.* subsp. *hispanica* and *D. marina*). *D. g.* subsp. *glomerata* with its extensive area of distribution is not cytologically homogenous, which was confirmed by the investigations conducted by Myers (1941, 1943) and by Myers and Hill (1942, 1943), who crossed the specimens of *D. glomerata* (*D. g.* subsp. *glomerata*). Then they analyzed thoroughly the behaviour of the offspring chromosomes in the meiosis. The differentiation of cytotypes revealed itself through the appearance of univalents in the metaphase.

The differentiation of cytotypes in *D. g.* subsp. *aschersoniana* was also demonstrated by Mizianty (1985).

Meiotic abnormalities (non-homologous chromosome associations, chromosome divisions not synchronized with the cytokinesis) in *D. g.* subsp. *lusitanica* were indicated by Shah (1964b).

EVOLUTION

At present, the genus *Dactylis* constitutes a polyploid complex to which there belong mostly diploids and tetraploids, between which there are incomplete genetic barriers. The possibility of the gene exchange between certain taxa of that genus is of a great evolutionary significance.

When considering the evolution of *Dactylis*, it should be assumed that in the past the distribution of diploids was, more or less, compact and that they occurred in the temperate and subtropical zone.

Stebbins (1956), distinguishes three phases of the evolution of *Dactylis*: the first (the Tertiary) – differentiation of diploids and the occupation of various ecological niches by them, the second (the Quaternary, the Pleistocene) – the crossing of diploids and the occupation of further ecological niches by them, the origination of tetraploids as a result of the crossing of diploids, or as a result of autopoloidization. Generally, it can be stated that the Pleistocene is the period of polyploidization in the genus *Dactylis*. The third, (connected with human activity) – the crossing of diploids with tetraploids and a further differentiation of the genus as the result of the change in natural habitats caused by man and by the rise of new ecological niches.

A similar evolutionary scheme of this genus is given by Borrill (1977) on the basis of morphological features and geographical distribution, by Luma-ret (1984) on the basis of enzyme analysis, and by Fiasson et al. (1987) on the basis of flavonoid analysis.

In all hypotheses, the following diploids are considered to be the oldest: *D. smithii* subsp. *smithii* (occurring presently on the Canary Islands), *D. g.* subsp. *aschersoniana* (occurring in the forests of central Europe) and *D. g.* subsp. *himalayensis* (with a scattered distribution: the Himalayas – Nepal and

south-east China). Subsp. *aschersoniana* and subsp. *himalayensis* originated probably in the Tertiary (the Miocen) from a common ancestor.

The origin of the tetraploid subsp. *glomerata* is explained in different ways. Müntzing (1936, 1937), Myers (1947), Stebbins (1947 and 1950) maintained that it is an autotetraploid which started its existence by the doubling of the chromosomes of subsp. *aschersoniana*. The above authors point out that in spite of a close relation, the present subsp. *aschersoniana* is not an immediate ancestor of subsp. *glomerata* in spite of the fact that they are closely related. Stebbins (1971) supposed subsp. *glomerata* to be an allopolyploid, whose both diploid ancestors can be identified (these are: subsp. *aschersoniana* and subsp. *woronowii*). On the other hand, Hanson and Carnahan (1956) claim that subsp. *glomerata* appears to be an intermediate form between an autopolyploid and allopolyploid, namely that it is the segmental allopolyploid.

Future biosystematic studies on the genus *Dactylis* will undoubtedly throw a new light on the systematics and evolution of that genus.

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Biosystematyczne studia Dactylis L. 1. Przegląd dotychczasowych badań.

1.2. Cytologia, genetyka, badania eksperymentalne i ewolucja

Streszczenie

Niniejsza praca składa się z części zatytułowanych następująco: liczby chromosomów, chromosomy dodatkowe, analiza kariotypu, geograficzne rozmieszczenie cytotypów, formy morfologicznie jednakowe a zróżnicowane cytologicznie, mieszańce, ewolucja.

W rodzaju *Dactylis* występują diploidy ($2n = 14$), tetraploidy ($2n = 28$) i hexaploidy ($2n = 42$). Spotyka się również aneuploidy ($2n = 27, 29, 30$ itp.), oraz chromosomy dodatkowe (1-12). Chromosomy *Dactylis* są zróżnicowane w wielkości od 3 do 9 μm . U nielicznych taksonów jest zbadana ich morfologia. W pracy zamieszczono mapę przedstawiającą rozmieszczenie następujących cytotypów *Dactylis*: 16 diploidów, 7 tetraploidów (głównie w centralnej Europie) oraz także hexaploida (w północnej Afryce).

Odrębny problem w rodzaju *Dactylis* stanowią diploidy i tetraploidy bardzo podobne do siebie pod względem morfologicznym. Do tej pory nie wyjaśniono, czy podobieństwo to jest spowodowane pochodzeniem tetraploidów od diploidów (przez autoploidię), czy adaptacją diploidów i tetraploidów do jednakowych warunków środowiska.

Zaprezentowano również dane dotyczące krzyżowania się między sobą diploidów jak też i możliwości wymiany genów pomiędzy tetraploidami. Zestawiono także dane odnośnie mieszańców między diploidami i tetraploidami.

W ewolucji *Dactylis* (a jest na jej temat kilka teorii, niektóre w niniejszej pracy przedstawiono), we wszystkich teoriach za najstarsze uważa się następujące diploidy: *D. smithii* Link subsp. *smithii*, *D. g.* subsp. *aschersoniana* (Graebn.) Thell. i *D. g.* subsp. *himalayensis* Dom.