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# Cytological Studies on some Species in Genus *Pennisetum*

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**Summary.** Detailed microsporogenesis in 4 species of the genus *Pennisetum* namely *P. typhoides* (n = 7), *P. longistylum* (n = 18), *P. polystachyon* (n = 27) and *P. pedicellatum* (n = 27) was studied. Nature of chromosome pairing was critically studied and pairing was regular in diploid and allotetraploid species. Some multivalents formation occurred in segmental allopolyploids. They displayed numerous meiotic irregularities. Aberrant meiosis in the material is evaluated. The role of apomixis, hybridization and polyploidy in the evolution of the genus is discussed.

## Introduction

The genus *Pennisetum*, one of the most important genera of the tribe *Paniceae* of the family *Gramineae*, embraces about 50 species widely distributed in the tropics and subtropics of both hemispheres. The key characters of the genus are: Spikelets are solitary and surrounded by an involucre of bristles that are free except at the very base. The first glume is shorter than the spikelets, the second glume is almost equal to the sterile lemma in size and the fertile lemma is smooth with a thin margin enclosing the palea. The genus is of considerable economic importance, the species studied here are highly valued forage grasses widely cultivated in this country. There are very few studies dealing with the cytology of the genus *Pennisetum*. Many chromosome counts have been made (Krishnaswamy and Raman, 1949; Hrishi, 1952; Nath and Swaminathan, 1957; Joshi et al., 1959; Singh and Godward, 1960; and Tateoka, 1965) but meiotic phenomena in these species is practically unknown. Only the papers on *P. typhoides* contain statements about meiosis. The main objective of the present cytological investigation was to gain some knowledge about the pairing relationships of the chromosomes of different *Pennisetum* species.

## Materials and Methods

The grasses listed below were used in the present investigation (1) *P. typhoides* (2) *P. longistylum* (3) *P. polystachyon* and (4) *P. pedicellatum*. The young flower buds of grasses used in the present study were fixed in acetic alcohol (1:3). A trace of ferric acetate added to the fixative was found to yield better results. The anthers were then squashed in acetocarmine. Photomicrographs were taken from temporary slides.

## Observations

*P. typhoides* Stapf et Hubb., Pearl millet.

It is an important millet of India and is widely cultivated in India from time immemorial.

Earlier prophase studies could not readily be observed due to the slender and entangled nature of chromosomes. At diakinesis and metaphase I seven bivalents are invariably observed. One bivalent is seen associated to the nucleolus at diakinesis and the bivalents appear somewhat loose and dissociated because of terminalization of chiasmata (Fig. 1). The chiasma frequency per bivalent is 1.71. All the bivalents are generally found to orient themselves at the equator. Bivalents disjoin normally at anaphase I. Further stages of meiosis are found to be regular. Pollen viability is about 97%.

*P. longistylum* Hochst.

It is a fair fodder grass (White, 1964).

At diakinesis besides bivalents, quadrivalents and univalents are observed in each P.M.C. The various types of configurations observed are presented in the table 1:

Table 1

| Types of configurations | No. of P. M. Cs observed |
|---|---|
| 3IV 1II 2I | 80 |
| 2IV 1II 6I | 13 |
| 1IV 3II 6I | 07 |
| Total: | 100 |

Mean frequency and range of associations per cell

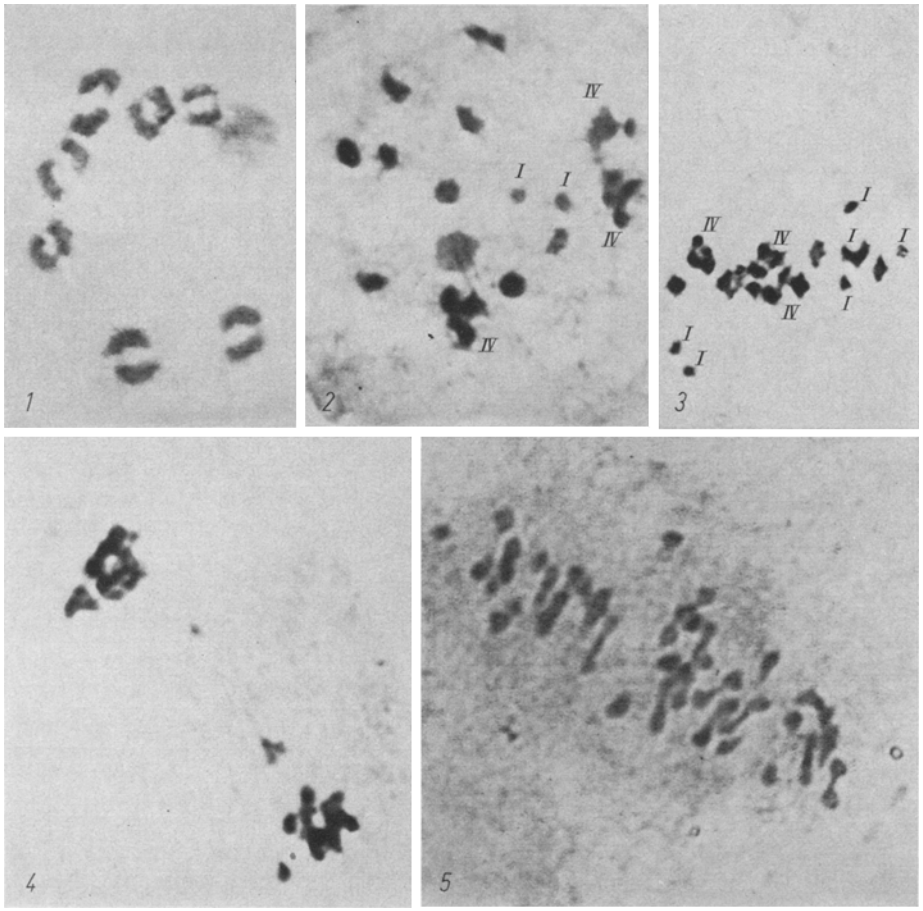
| Quadrivalents | | Bivalents | | Univalents | |
|---|---|---|---|---|---|
| Frequency | Range | Frequency | Range | Frequency | Range |
| 2.73 | 1–3 | 11.14 | 11–13 | 2.80 | 2–6 |

Quadrivalents are chain shaped (Fig. 2). The chiasma frequency per bivalent is 1.63.

The various types of configurations observed at metaphase I are presented in Table 2:

Table 2

| Types of metaphase plates | No. of P. M. Cs observed |
|---|---|
| 3IV 1II 2I | 12 |
| 2IV 1II 6I | 60 |
| 1IV 3II 6I | 20 |
| X 14II 8I | 13 |
| X 15II 6I | 09 |
| X 16II 4I | 10 |
| X 18II X | 10 |
| Total: | 134 |




Figs. 1—5. Meiotic behaviour of *Pennisetum* species

Fig. 1. Diakinesis showing 7 bivalents in *P. typhoides*, Fig. 2. Diakinesis showing $3_{IV} + 1_{II} + 2_{I}$ in *P. longistylum*, Fig. 3. Metaphase I showing $3_{IV} + 9_{II} + 6_{I}$ in equatorial view in *P. longistylum*, Fig. 4. Telophase I showing 2 laggards in *P. longistylum*, Fig. 5. Metaphase I showing anaphasic separation of some bivalents in *P. polystachyon*

Mean frequency and range of associations per cell

| Quadrivalents | | Bivalents | | Univalents | |
|---|---|---|---|---|---|
| Frequency | Range | Frequency | Range | Frequency | Range |
| 1.43 | 0—3 | 3.80 | 11—18 | 2.77 | 0—8 |

The range of quadrivalents is from zero to three. The bivalents generally orient themselves on the equator (Fig. 3) and the univalents lie either only on one side, on both sides of the equator or between the bivalents.

Anaphase I is nearly in 39% of the cases normal. In other cases it exhibits laggards which may be dividing or non-dividing (Table 3). The dividing laggards represent univalents.

Table 3

| Types of anomalies at anaphase I | No. of P. M. Cs observed |
|---|---|
| 4 non-dividing laggards | 18 |
| 3 non-dividing laggards | 05 |
| 2 non-dividing laggards | 13 |
| 1 dividing and 4 non-dividing laggards | 05 |
| Normal cases | 27 |
| Total: | 68 |

Lagging chromosomes are observed in 10% of the cases at telophase I (Table 4). They are not included in the telophasic nuclei (Fig. 4).

Table 4

| Types of anomalies at telophase I | No. of P. M. Cs observed |
|---|---|
| 3 laggards | 1 |
| 2 laggards | 4 |
| 1 laggard | 2 |
| Normal cases | 38 |
| Total: | 45 |

Anaphase II and telophase II exhibit lagging chromosomes. At the tetrad stage they form up to four micronuclei. Pollen viability is about 50%.

*P. polystachyon* (Linn.) Schult.

It is a first class fodder grass for cattle when young, and it can also be made into an excellent hay (Bor, 1960).

In a study of over 100 pollen mother cells at diakinesis and metaphase I invariably 27 bivalents are observed (Fig. 5). Chiasma frequency for bivalent is 1.80. Hrishi (1952) also observed complete 27 bivalents formation at diakinesis and metaphase I. Some

bivalents are observed precociously separated into univalents. Further stages of meiosis are found to be regular. Pollen viability is about 92%.

*P. pedicellatum* Trin.

It is a much branched leafy annual, 12 to 90 inches in height. The grass grows well in the rainy season. In India the grass is proved an ideal fodder for cattle and may well be adopted for regenerating overgrazed pastures (Khan, 1957).

At diakinesis configurations in the form of univalents, bivalents, quadrivalents and hexavalent are observed in each P.M.C. The different types of configurations met with are shown in table 5:

Table 5

| Types of configurations | No. of P. M. Cs observed |
|---|---|
| $1_{VI}\ 2_{IV}\ 18_{II}\ 4_{I}$ | 06 |
| $1_{VI}\ 2_{IV}\ 16_{II}\ 8_{I}$ | 09 |
| $1_{VI}\ 1_{IV}\ 20_{II}\ 4_{I}$ | 15 |
| $1_{VI}\ 1_{IV}\ 18_{II}\ 8_{I}$ | 20 |
| Total: | 50 |

Mean frequency and range of associations per cell

| Hexavalent | | Quadrivalents | | Bivalents | | Univalents | |
|---|---|---|---|---|---|---|---|
| Frequency | Range | Frequency | Range | Frequency | Range | Frequency | Range |
| 1.00 | 1—1 | 1.30 | 1—2 | 19.00 | 16—20 | 4.07 | 4—8 |

Invariably one chain shaped hexavalent is observed in each P.M.C. The chiasma frequency per bivalent is 1.44.

At metaphase I besides bivalents, one hexavalent, quadrivalents, trivalents and univalents are observed. An analysis of 200 P.M.Cs is presented in table 6:

Table 6

| Types of metaphase plates | No. of P. M. Cs observed |
|---|---|
| $1_{VI}\ 1_{IV}\ 1_{III}\ 19_{II}\ 3_{I}$ | 02 |
| $1_{VI}\ 3_{IV}\ X\ 17_{II}\ 2_{I}$ | 06 |
| $1_{VI}\ 3_{IV}\ X\ 16_{II}\ 4_{I}$ | 09 |
| $1_{VI}\ 3_{IV}\ X\ 14_{II}\ 8_{I}$ | 05 |
| $1_{VI}\ 3_{IV}\ X\ 13_{II}\ 10_{I}$ | 03 |
| $1_{VI}\ 2_{IV}\ X\ 12_{II}\ 16_{I}$ | 03 |
| $1_{VI}\ 1_{IV}\ X\ 21_{II}\ 2_{I}$ | 10 |
| $1_{VI}\ 1_{IV}\ X\ 20_{II}\ 4_{I}$ | 12 |
| $1_{VI}\ 1_{IV}\ X\ 19_{II}\ 6_{I}$ | 120 |
| $1_{VI}\ 1_{IV}\ X\ 18_{II}\ 8_{I}$ | 12 |
| $1_{VI}\ 1_{IV}\ X\ 17_{II}\ 10_{I}$ | 04 |
| $1_{VI}\ X\ 4_{III}\ 17_{II}\ 2_{I}$ | 06 |
| $1_{VI}\ X\ X\ 21_{II}\ 6_{I}$ | 03 |
| $1_{VI}\ X\ X\ 23_{II}\ 2_{I}$ | 05 |
| Total: | 200 |

Mean frequency and range of associations per cell

| Hexavalent | | Quadrivalents | | Trivalents | | Bivalents | | Univalents | |
|---|---|---|---|---|---|---|---|---|---|
| Frequency | Range | Frequency | Range | Frequency | Range | Frequency | Range | Frequency | Range |
| 1.00 | 1—1 | 1.17 | 0—3 | 0.13 | 0—4 | 18.58 | 12—23 | 5.74 | 2—16 |

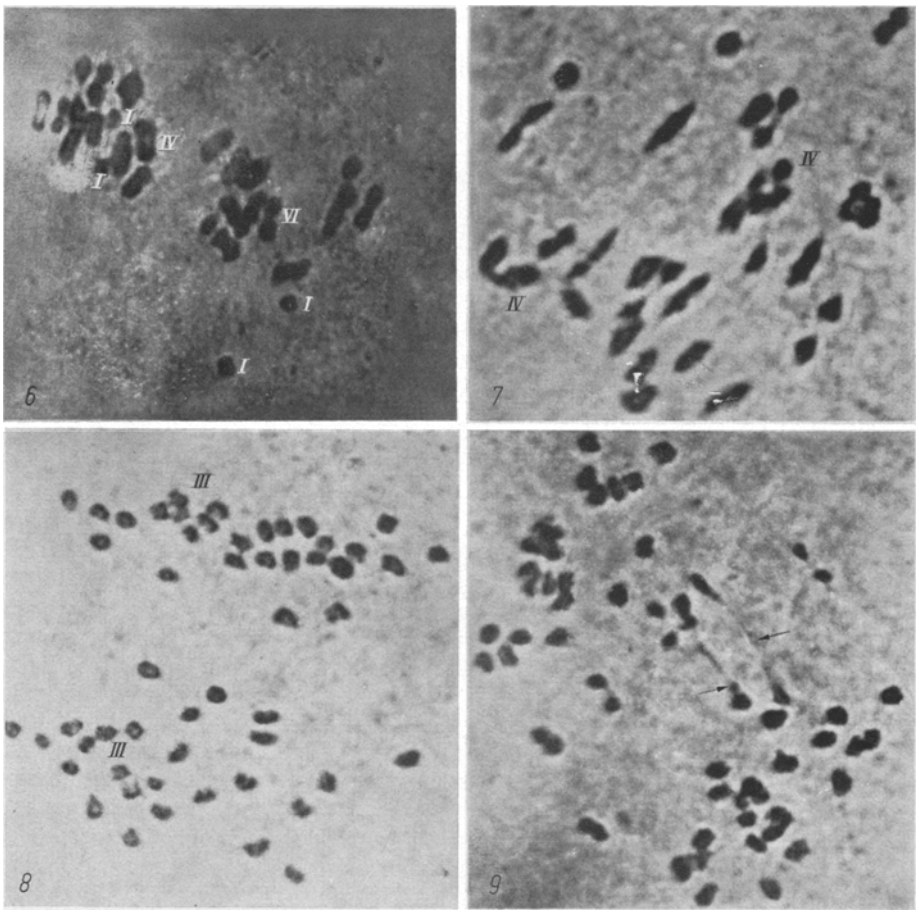
Invariably one hexavalent has also been observed in each P.M.C. at metaphase I (Fig. 6). The hexavalent is usually chain shaped, but in rare cases it appears zig-zag (Fig. 6) or U shaped. The quadrivalents are mostly chain shaped but sometimes they give an appearance of more or less ring (Fig. 6). The multivalents are more often in the form of chains probably indicating that there exists only terminal affinity between the pairing chromosomes. Univalents generally orient themselves on both sides or one side (Fig. 6) of the equator. Sometimes univalents are seen between the bivalents (Fig. 6). The first possibility of presence of many univalents (their range from 2 to 16 in most of their cells) with a few trivalents (only in 4% of P.M.Cs) indicates failure of pairing at pachytene rather than subsequent breakage of pachytene multivalents. Another possibility of precocious separation of some bivalents resulting into univalents can not be strictly ruled out.

Anaphase I in 25% of cells is regular. But in 75% of the cases it exhibits some interesting anomalies. Table 7 shows various types of anomalies observed at anaphase I.

The quadrivalents (Fig. 7) and trivalents (Fig. 8) are observed at anaphase I. The quadrivalents and trivalents may presumably be the result either of non-disjunction of the quadrivalents or trivalents or disjunction of a hexavalent into two trivalents

Table 7

| Types of anomalies | No. of P. M. Cs observed |
|---|---|
| Unequal distribution of chromosomes (28:26) | 05 |
| One trivalent seen at each pole | 10 |
| One quadrivalent seen at each pole | 15 |
| One bivalent seen at each pole | 05 |
| Two dividing laggards | 33 |
| Three dividing laggards | 05 |
| Four dividing laggards | 23 |
| Two non-dividing laggards | 13 |
| One dividing and two non-dividing laggards | 05 |
| Four non-dividing laggards | 10 |
| One univalent bridge with 2 non-dividing laggards | 07 |
| Two univalent bridges, 4 dividing laggards and two non-dividing laggards | 09 |
| Two univalent bridges and 2 dividing laggards | 10 |
| Normal cases | 50 |
| Total: | 200 |




Figs. 6—9. Meiotic behaviour of *P. pedicellatum*
Fig. 6. Metaphase I showing $1_{VI} + 1_{IV} + 20_{II} + 4_I$ in equatorial view, Fig. 7. Anaphase I showing one quadrivalent at each pole, Fig. 8. Anaphase I showing one trivalent at each pole and unequal distribution of chromosomes (28:26), Fig. 9. Anaphase I showing two univalent bridges, four dividing laggards and two non-dividing laggards (magnification approx. × 1000)

or one quadrivalent and one bivalent. Unequal disjunction of chromosomes is seen in 2.5% of cells. 28:26 chromosomes are seen at each pole (Fig. 8). Univalent bridges have also been seen (Fig. 9) and the dividing laggards divide equationally at the first meiotic system. One P.M.C. is observed where the chromosomes have failed to separate at the end of anaphase to two poles resulting in the formation of restitution nucleus.

Telophase I is found to be regular in about 78% of P.M.Cs. In 22% of P.M.Cs the laggards are seen which are presented in table 8:

Table 8

| Types of anomalies | No. of P. M. Cs observed |
|---|---|
| One laggard | 20 |
| Three laggards | 07 |
| Four laggards | 05 |
| Twelve laggards | 01 |
| Normal cases | 25 |
| Total: | 58 |

The laggards do not get included within the telophasic nuclei.

Second meiotic division exhibits laggards. One to four laggards are seen excluded from the telophasic nuclei. They form micronuclei. From two to four micronuclei are observed. Pollen viability is about 65%.

This species is also known to exist as tetraploid (2 n = 36) and as aneuploid (2 n = 48). Nath and Swaminathan (1957) reported 2 n = 36 and 54 chromosome numbers in this species. Joshi et al. (1959) recorded 2 n = 48 chromosome number. All the previous observations on this grass have been restricted to determination of chromosome numbers only.

Inspite of the aberrant meiosis and poor pollen, the good seed set and the constancy of chromosome numbers in seed-propagated progeny (although these grasses are annual) is highly suggestive of these two species namely *P. longistylum* and *P. pedicellatum* being apomicts. Patil (cited by White, 1964) found evidence of apomixis in *P. pedicellatum*.

## Discussion

A study of over 100 pollen mother cells at metaphase I of the species i.e. *P. polystachyon* (n = 27), the hexaploid, did not reveal any multivalent at metaphase I. It seems probable that there exists

very little homology between the three genomes of the hexaploid. In short the hexaploid species is allohexaploid in nature. Alternatively, the three genomes involved may be homoeologous and pairing between them being completely restricted due to some form of genotypic control (cf. Sears and Okamoto, 1958; Riley and Chapman, 1958). At present it is indeed difficult to decide one for all in favour of this possibility, however, one point is clear that the hexaploid grass shows virtually no pairing between the three genomes and is at present an obligate bivalent former.

The absence of expected number of multivalents in the hexaploid may be due to a "special genotypically control tendency to bivalent formation" as advocated by Müntzing and Prakken (1940) and Nordenskiöld (1941) for a similar lack of multivalents in *Phleum pratense*. The experimental support for this theoretical suggestion has come from the work on wheat (Sears and Okamoto, 1958; Riley and Chapman, 1958; Riley, 1960; Riley et al., 1960; Riley and Kempanna, 1963; and Riley et al., 1966). It has been shown that a genotypic basis is at work in the hexaploid wheat, what is normally an obligate bivalent former and a species in which such a mechanism was hardly suspected. In view of these findings the present writer does not outright exclude the possibility of such a basis, working for the predominant bivalent formation in the hexaploid grass.

However, the absence of multivalents in the species *P. polystachyon* does not any way preclude the possibility of their autopolyploidy at some stage in their long history. It is quite probable that in course of evolution, the multivalent pairing may be replaced by bivalent pairing because of the progressive diploidization. This could be achieved either by elimination of the duplicated regions, or by rendering such regions non-homologous, by fixation of new gene mutations. Perfect diploidization could also be brought about in a much shorter time by fixation of specific mutations for bivalent formation. Establishment of homozygous types involving mutations of any magnitude is facilitated by a sexual mode of reproduction. When a polyploid has, through a combination of mutations, established sufficient different chromosomes among originally identical chromosomes, it behaves like diploids during meiosis. What we are currently dealing with most probably represent upper members of a series whose basis have been lost, and as such we can not easily decide whether auto or allopolyploidy or a combination of the two might have been operative at different stages in their long history. Evidence from artificially produced autopolyploidy indicates that autopolyploidy is rarely, if ever, successful at higher levels than tetraploidy (Stebbins, 1950).

In *P. longistylum* and *P. pedicellatum*, the author noticed some multivalents formation. Obviously homology, homoeology, and non-homology in these materials are a matter of degree. *P. longistylum*, ($n = 18$); the chromosome number of the species is reported for the first time here, exhibits besides bivalents, quadrivalents and univalents at diakinesis and metaphase I. The mean frequency per cell of such configurations at metaphase I is $1.43_{IV}+13.80_{II}+2.77_{I}$ (average of 134 cells). The multivalents formation in comparison to bivalents is low in this species. It seems likely that the species is a segmental allotetraploid.

*P. pedicellatum* ($n = 27$) shows, besides bivalents, one hexavalent, quadrivalents, trivalents and univalents at diakinesis and metaphase I. The mean frequency of associations per cell at metaphase I is $1.00_{VI} + 1.17_{IV} + 0.13_{III} + 18.58_{II} + 5.74_{I}$ (average of 200 cells). Since the frequency of multivalents was never so high as to suggest an autopolyploid or auto-allopolyploid evolution for the species i.e. *P. pedicellatum* studied. It seems likely possible that factors favouring the accumulation of chromosome structural changes are in operation in the grass. Invariably one hexavalent has been observed in each P.M.C. at diakinesis and metaphase I. The hexavalent and other multivalents are more often in the form of chain, probably indicating that there exists only terminal affinity between the pairing chromosomes. The low multivalent frequency evidently points to the differentiation of chromosomes on one hand and to their slight homology on the other hand. The former would account for the higher bivalent ($18.58_{II}$ per cell) and univalent ($5.7_{I}$ per cell) frequency and the latter would account for the low multivalent frequency as detailed above. Naturally, therefore, the chromosomes forming multivalents do not seem to be completely homologous and this taxon is not an autopolyploid, the meiosis indicates that the present hexaploid is perhaps a segmental allohexapolyploid.

Apomixis has been reported in species like *P. pedicellatum*. Apomixis and sexuality is known to be genetically controlled in higher plants (Gustafsson 1946, 1947a and b, Stebbins 1950). They have shown that apomictic and sexual processes run concurrently in higher plants. In natural apomicts the apomictic fertility is greater than the effective sexual fertility and the apomictic fraction of the progeny is often more vigorous than the sexual, hence the apomicts tend to predominate (Clausen 1954). In apomictic groups the apomictic extend their distribution more and more at the expense of their sexual relatives (Müntzing, 1961). Gene controlling apomixis is dominant to gene controlling sexuality (Borgaonkar et al., 1962).

The prevalence of apomixis in this genus has probably been of great importance in preserving intact the more desirable genotypic combinations which might have arisen by hybridization, polyploidy or combination of both.

It appears that hybridization between taxa at the same as well as at the different chromosomal levels

has played an important role in the diversification of this complex genus. This is evident from the behaviour of the different species reported above where different chromosome numbers in the same species testify to their diverse origin. This is particularly true of *P. pedicellatum* in which chromosome numbers 36, 48, and 54 have been reported.

Further investigation on the genome analysis of the vast complex of races in this taxon with 2 n = 36, 48, and 54 should prove highly interesting both from the point of view of gaining fundamental knowledge and from that of obtaining improved strains of this highly valuable fodder grass. Crosses between various diploid and tetraploid forms following by doubling could similarly give rise to new forms with 2 n = 54. In these cases, of course, it would be necessary to reselect for apomictic reproduction so that seed propagated progeny will continue to be uniform. Though it is but to be expected that a large majority of the forms so synthesized may not be immediately desirable, a wide range of variability will be made available and biotype suited to different ecological niches could perhaps be isolated following natural and human selection.

That polyploidy has also played a prominent role in the evolution of the genus is clear from the fact that in the *Pennisetum* the increase in chromosome number has been involved in the development of species ranging from 2 n to 6 n.

The increasing importance of this genus would appear to warrant more detailed studies of the reproduction and breeding behaviour of these species and their relatives.

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### Zusammenfassung

Es wird über eingehende Untersuchungen der Mikrosporogenese in 4 Species der Gattung *Pennisetum*, nämlich *P. typhoides* (n = 7), *P. longistylum* (n = 18), *P. polystachyon* (n = 27) und *P. pedicellatum* (n = 27) berichtet. Die Art der Chromosomenpaarung wurde kritisch geprüft, sie war bei den diploiden und allotetraploiden Species regulär. Multivalentbildung trat in einigen Fällen bei Segment-Allopolyploiden auf, sie zeigten zahlreiche meiotische Unregelmäßigkeiten. In dem Material aufgetretene aberrante Meiosen wurden ausgewertet. Die Rolle von Apomixis, Hybridisation und Polyploidie bei der Evolution der Gattung wird besprochen.

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