

CHROMOSOME STUDIES ON AFRICAN PLANTS. 7.

The presentation of chromosome numbers in this report conforms with the outlay described in the previous publications in this series (Spies & Du Plessis 1986a & b; 1987a & b; 1988; Spies & Jonker 1987).

POACEAE

Ehrharteae

Ehrharta calycina J.E. Sm. var. *calycina*: **n = 15 + 0-4B, 24.**

CAPE.—3017 (Hondekliipbaai): 15 km east of Hondekliipbaai (-AB), *Spies* 3030 (n = 15 + 0-4B), 3031 (n = 24).

E. pusilla Nees ex Trin.: **n = 12.**

CAPE.—2917 (Springbok): 6 km east of Steinkopf (-BD), *Spies* 2989. 3018 (Kamiesberg): 16 km east of Kamieskroon (-AC), *Spies* 3059.

Pappophoreae

Enneapogon cenchroides (Roem. & Schult.) C. E. Hubb.: **n = 20.**

CAPE.—2924 (Hopetown): 31 km from Hopetown to Britstown (-DD), *Spies* 2709.

E. scaber Lehm.: **n = 20.**

SWA/NAMIBIA.—2617 (Bethanie): Seeheim (-DD), *Spies* 2892.

Eragrostideae

Diplachne fusca (L.) Beauv. ex Roem. & Schult.: **n = 19.**

CAPE.—3017 (Hondeklipbaai): 6 km east of Kamieskroon (—BB), *Spies* 2991.

Eragrostis capensis (Thunb.) Trin.: **n = 30.**

NATAL.—2832 (Mtubatuba): 34 km from Cape Vidal to St Lucia (—AD), *Spies* 2409.

E. echinochloidea Stapf: **n = 30.**

CAPE.—2822 (Glen Lyon): 93 km from Groblershoop to Kimberley (—DC), *Spies* 2869.

E. lehmanniana Nees: **n = 20.**

CAPE.—2822 (Glen Lyon): 38 km from Groblershoop to Kimberley (—CD), *Spies* 2857.

Eleusine coracana (L.) Gaertn. subsp. *africana* (K.-O'Byrne) Hilu & De Wet [= *E. indica* (L.) Gaertn. subsp. *africana* (K.-O'Byrne) S. M. Phillips]: **n = 9.**

NATAL.—2832 (Mtubatuba): near Cape Vidal (—BA), *Spies* 2365.

CAPE.—3118 (Vanhynsdorp): Koekenaap (—CB), *Spies* 2783.

Sporobolus africanus (Poir.) Robyns & Tournay: **n = 18.**

CAPE.—3028 (Matatiele): Antelope Park (—CC), *Spies* 2529.

S. pyramidalis Beauv.: **n = 12, n = 15.**

SWAZILAND.—13 km from Manzini to Siteki (—AD), *Spies* 2588 (n = 15), 2594 (n = 12).

Poeae

Poa annua L.: **n = 14.**

CAPE.—3318 (Cape Town): near Stellenbosch turnoff on road between Paarl and Franschhoek (—DD), *Spies* 3205.

Festuca scabra Vahl: **n = 21.**

CAPE.—3319 (Worcester): Franschhoek Pass (—CC), *Spies* 3219.

Lolium multiflorum Lam.: **n = 7 + 0—2B.**

CAPE.—3318 (Cape Town): 1 km east of Mamre (—BC), *Spies* 3191.

L. perenne L. × *L. multiflorum* Lam.: **n = 14.**

O.F.S.—2826 (Brandfort): Glen Agricultural College (—CD), *Spies* 2663.

L. rigidum Gaudin: **n = 7.**

CAPE.—3318 (Cape Town): 1 km east of Mamre (—BC), *Spies* 3190.

Briza maxima L.: **n = 7.**

CAPE.—3218 (Clanwilliam): Versveld Pass (—DC), *Spies* 3159. 3318 (Cape Town): Stellenbosch turnoff on road between Paarl and Franschhoek (—DD), *Spies* 3204.

Vulpia bromoides (L.) S. F. Gray: **n = 7.**

CAPE.—3018 (Kamiesberg): 16 km east of Kamieskroon (—AC), *Spies* 3060.

V. muralis (Kunth) Nees: **n = 14.**

CAPE.—3118 (Vanhynsdorp): Gifberg Pass (—DC), *Spies* 3084.

V. myuros (L.) C. C. Gmel.: **n = 7 + 2B.**

CAPE.—3126 (Queenstown): 3 km from Molteno to Steynsburg (—AD), *Spies* 1849a.

Agrostideae

Polypogon monspeliensis (L.) Desf.: **n = 14.**

CAPE.—2917 (Springbok): Wildeperdehoek Pass (—DB), *Spies* 3024.

Lophochloa pumila (Desf.) Bor: **n = 14 + 0—4B.**

CAPE.—2917 (Springbok): Wildeperdehoek Pass (—DB), *Spies* 3024.

Lagurus ovatus L.: **n = 7.**

CAPE.—3418 (Simon's Town): 1 km north of Scarborough (—AB), *Spies* 3237.

Aveneae

Anthoxanthum tongo (Trin.) Stapf: **n = 20 + 0—5B.**

CAPE.—3118 (Vanhynsdorp): Gifberg Pass (—DC), *Spies* 3083.

Koeleria capensis (Steud.) Nees: **n = 7.**

CAPE.—3320 (Montagu): 6 km north of De Hoop Nature Reserve (—AD), *Spies* 3250.

Meliceae

Melica racemosa Thunb.: **n = 9.**

CAPE.—3320 (Montagu): 6 km from Malgas to Bredasdorp (—AD), *Spies* 3253.

Phalarideae

Phalaris minor Retz.: **n = 7, n = 21.**

CAPE.—2917 (Springbok): Wildeperdehoek Pass (—DB), *Spies* 3023 (n = 21). 3118 (Vanhynsdorp): Gifberg Pass (—DC), *Spies* 3108 (n = 7).

DISCUSSION

In contrast to previous articles in this series, where the occurrence of certain phenomena, e.g. the presence of univalents, was discussed separately for all the taxa concerned, this paper will discuss the meiotic chromosome behaviour of each species individually. In this report the basic chromosome number of any taxon is taken to be the highest common denominator of the majority of specimens as described in Darlington & Wylie (1955); Ornduff (1967–1969); Fedorov (1969); Moore, R. J. (1970–1977); Moore, D. M. (1982) and Goldblatt (1981–1985).

Ehrharteae

The basic chromosome number of the Ehrharteae is considered to be 12 (Watson *et al.* 1986). In this study somatic chromosome numbers of 24, 30 and 48 were observed in specimens of the two species studied. The *Ehrharta calycina* var. *calycina* specimen (*Spies* 3030) with a somatic chromosome number of 30, indicates that this plant has a basic chromosome number of six rather than 12. This specimen therefore, represents a pentaploid form and strongly suggests that the previously described basic number of 12 actually represents a secondary basic chromosome number based on $x = (6 + 6)$.

Two specimens of *Ehrharta calycina* var. *calycina* were studied from the same locality. The one specimen (*Spies* 3031) has a somatic chromosome number of 48 and normal meiosis. A meiotic chromosome configuration of $20_{II} 2_{IV}$ was most frequently observed. The

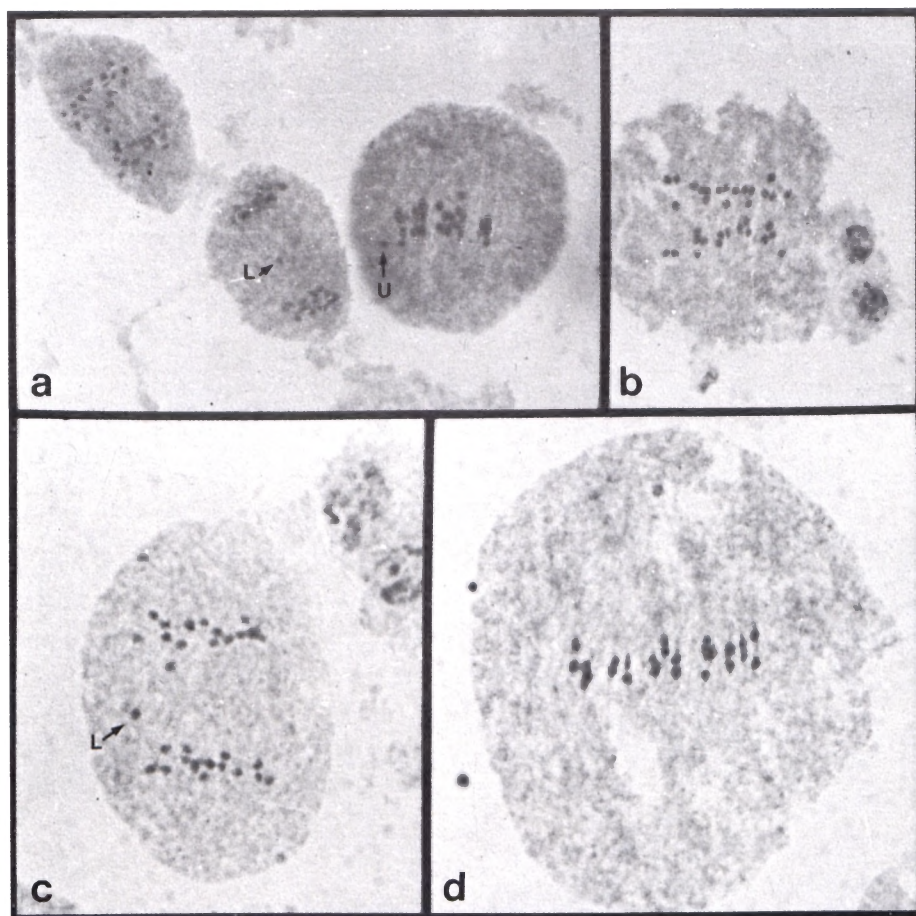


FIGURE 3.—Meiosis in *Ehrharta* species. a–c, *E. calycina* var. *calycina* (Spies 3030); d, *E. pusilla* (Spies 3059). L, chromosome laggard; U, univalents. $\times 1300$.

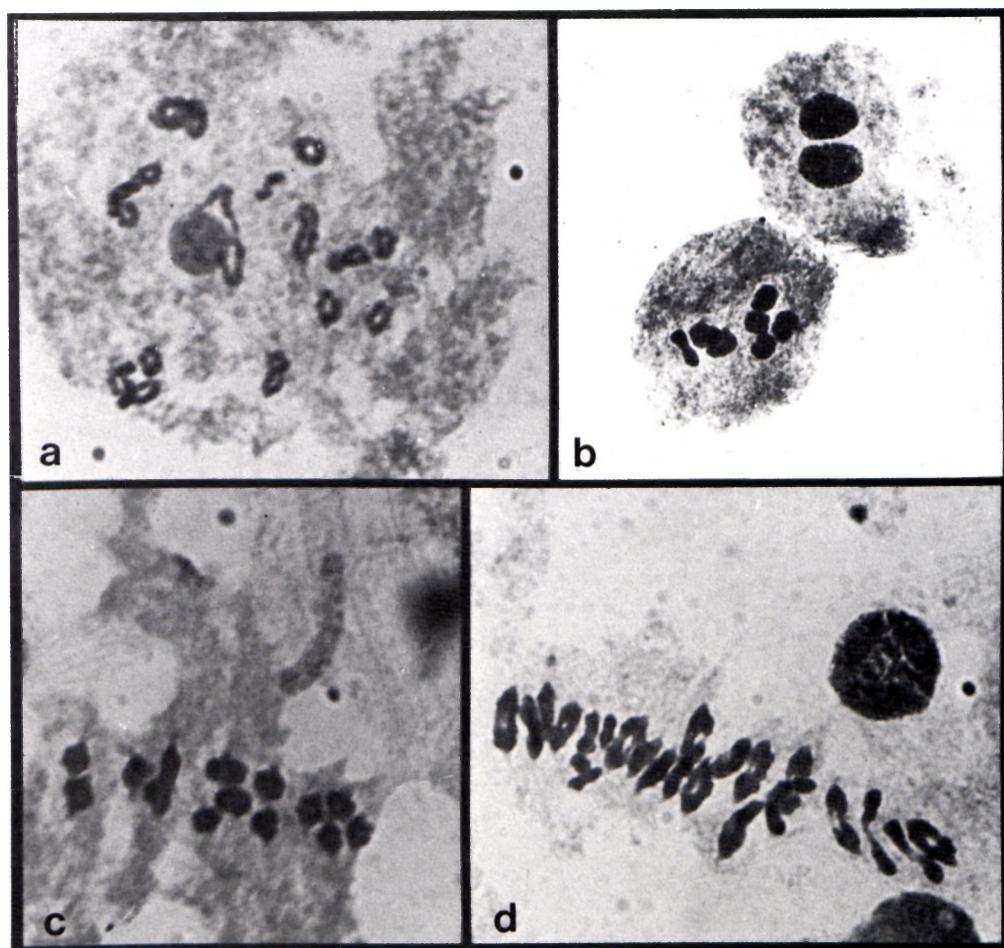


FIGURE 4.—Meiosis in specimens from the subfamily Pooideae. a, Diplotene/diakinesis in *Poa annua* (Spies 3205); b, diakinesis in *Briza maxima* (Spies 3159); c, diakinesis/metaphase in *Polypogon monspeliensis* (Spies 3014); d, metaphase I in *Anthoxanthum tongo* (Spies 3083). $\times 1200$.

second specimen (*Spies 3030*) has 30 somatic chromosomes and a very abnormal meiosis (Figure 3a–c). In this specimen nil to four B-chromosomes were observed. No size differences or differences in regard to chromosome behaviour between the A and B-chromosomes were observed. However, the number of B-chromosomes varied from cell to cell with three B-chromosomes observed in the majority of cells studied. In addition to the presence of B-chromosomes, an average of 1.7 (range from 0 to 5) univalents per cell was observed during metaphase I. Analysis of metaphase I cells indicated that chromosome configurations varied from $1_1 9_{II} 1_{III} 2_{IV}$ to $5_1 11_{II} 1_{III}$. During anaphase I the majority of cells (81.5%) had at least one chromosome laggard (Figure 3a & c). This abnormal meiosis resulted in micronuclei being present in 50% of the telophase II cells studied. The presence of multivalents and univalents in this specimen suggests at least a segmental allopolyploid origin for this specimen and it confirms that this specimen represents an uneven ploidy level.

Both *E. pusilla* specimens formed 12_{II} during meiosis and no abnormalities were observed (Figure 3d).

Pappophoreae

The results of this study confirm that the basic chromosome number of this tribe is ten.

Eragrostideae

In addition to the well known basic number of $x = 10$ in the Eragrostideae, several additional basic chromosome numbers are reported. Among these a basic chromosome number of $x = 6$ for the genus *Sporobolus* was observed. Another deviation from these basic chromosome numbers is the genus *Eleusine* with $x = 9$. This is a well known departure from the rest of the tribe (Watson *et al.* 1986). In one cell of *E. coracana* var. *africana* (*Spies 2365*), a fragment was present.

An unexpected deviation was encountered in a *Diplachne fusca* specimen (*Spies 2991*) with $n = 19$. We suggest that this specimen represents an aneuploid form of this genus which has a basic chromosome number of ten (Watson *et al.* 1986). In spite of the suggested aneuploidy present in *Diplachne fusca*, no further abnormalities were observed. The absence of univalents indicates that a homologous pair of chromosomes was somehow lost in this specimen.

Meiotic chromosome configurations revealed that up to six univalents were present in an *Eragrostis lehmanniana* specimen (*Spies 2857*). Since no multivalents were formed, the presence of univalents may be attributed to hybridization (segmental allopolyploidy). The other *Eragrostis* specimens showed bivalents only. Further investigations of this genus may reveal whether the absence of multivalents can be attributed to an allopolyploid origin or to the presence of genes inhibiting multivalent formation.

Chromosome configurations indicated that some multivalents are formed in *Sporobolus africanus*. During this

study between nil and two trivalents per cell were observed. The basic number of $x = 6$ for the genus *Sporobolus* mentioned above, is deduced from *S. africanus* ($n = 18$) and *S. pyramidalis* ($n = 12$ & 15). The basic numbers of the genus *Sporobolus* are usually considered to be 6, 9 or 10 (Davidse, Hoshino & Simon 1986), with the majority of specimens having a basic chromosome number of 9, being tetraploid ($2n = 4x = 36$) (Watson *et al.* 1986). The observation that two specimens of *S. pyramidalis* from the same locality have somatic chromosome numbers of 24 and 30 indicates that the basic number is 6 and that these specimens are respectively $2n = 4x = 24$ and $2n = 5x = 30$. The majority of the specimens studied, therefore, represent hexaploid plants and not tetraploid plants as generally accepted.

The difference between basic chromosome numbers of six and ten implies a greater phylogenetic difference than between plants with basic numbers of nine and ten. The loss of a single chromosome from a plant with a basic number of ten will result in a basic number of nine, whereas a chromosome doubling from $x = 6$ to $x = 12$, with the subsequent loss of two chromosomes, are required to produce a plant with a basic chromosome number of ten. Detailed cytogenetic studies in the genus *Sporobolus* will reveal if this dibasic group represents a single phylogenetic entity. If it is actually a single phylogenetic entity such studies may help resolve which group of species is the most primitive.

Poeae

All specimens studied confirm a basic chromosome number of seven for this tribe. Chromosome configurations were, in most instances, restricted to bivalents (Figures 4a–d). The exceptions were *Festuca scabra* with a meiotic chromosome configuration of $17_{II} 2_{IV}$. High chiasma frequencies were observed in *Lophochloa pumila*, *Briza maxima* and *Polypogon monspeliensis* where the majority of bivalents formed rings (Figure 4b & c), in contrast to the rod-bivalents usually observed. B-chromosomes were observed in several specimens, i.e. *Lolium multiflorum* (*Spies 3191*) with nil to two, *Vulpia myuros* (*Spies 1849a*) with two in every cell and *Lophochloa pumila* (*Spies 3024*) with nil to four per cell.

One of the most interesting phenomena observed during this study is a possible translocation in a *Lagurus*

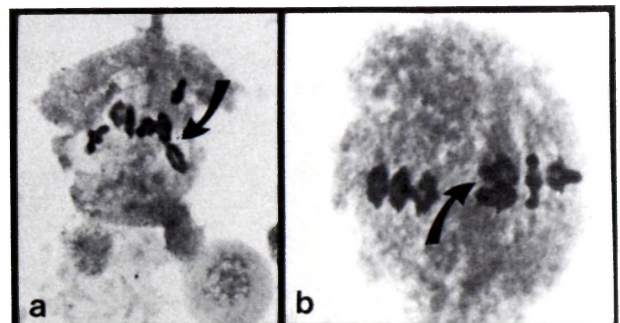


FIGURE 5.—Metaphase I in *Lagurus ovatus* (*Spies 3237*) showing only six meiotic figures of which one (indicated by arrow) is a quadrivalent (note the 90° rotation of this chromosome figure in b). $\times 1040$.

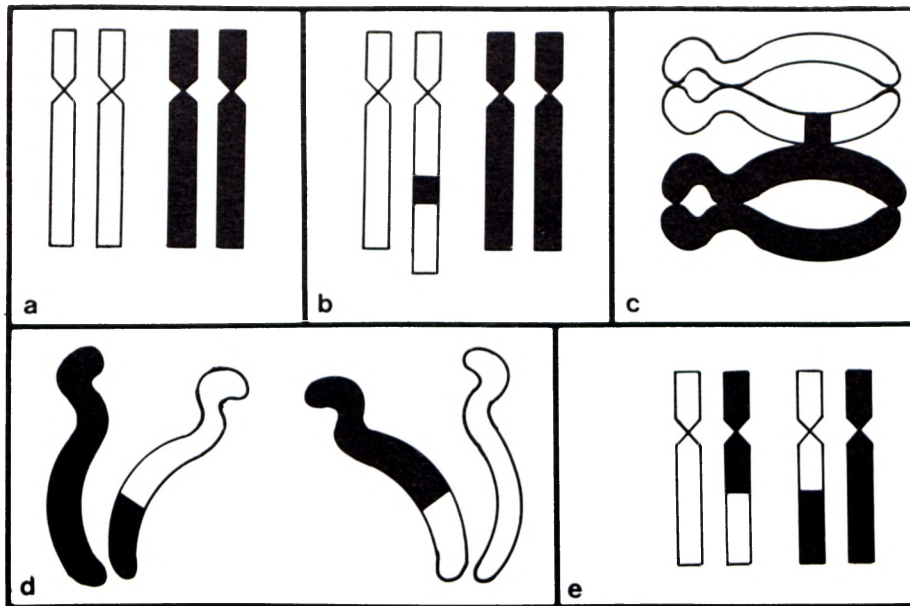


FIGURE 6.—Diagrammatic representation of possible cause for the abnormal meiosis in *Lagurus ovatus*. a, two pairs of normal homologous chromosomes; b, translocation of a portion of one chromosome to another; c, pairing of the translocated chromosome with its homologous and homoeologous partners; d, anaphase I segregation of the chromosomes after cross-over has occurred; e, recombination of chromosomal material in the offspring.

ovatus specimen, Spies 3237. This plant is a diploid ($2n = 2x = 14$) but only six meiotic figures were formed in each cell (Figures 5a & b). The one figure is much larger than the rest and is obviously a quadrivalent (Figures 5a & b). The interesting feature of this quadrivalent is its orientation. Instead of the two homoeologous chromosomes lying side by side on the metaphase plate with the duplicated part forming a chiasma, the homoeologous chromosomes are lying on top of each other (Figure 5b). The significance of this 90° rotation is not clear. It is proposed that the quadrivalent is formed by a translocation. Due to the translocation the two figure 8 homologous chromosome pairs form a chiasma in the long arms of the two homoeologous chromosomes (the parental form and the translocated form) (Figures 6a–e).

Aveneae

Anthoxanthum tongo (Spies 3083) has a basic chromosome number of ten ($2n = 40$) (Figure 4d), and the highest ploidy level so far known in the genus. Previous chromosome counts indicate that the genus *Anthoxanthum* has a basic chromosome number of 10 (or 5), in contrast to the basic number of seven usually found in the Aveneae (Watson *et al.* 1986). Between nil and five B-chromosomes were observed per cell in this specimen.

Meliceae

This study confirms that this tribe, with its basic chromosome number of nine, deviates from the expected basic chromosome number of seven for the subfamily.

Phalarideae

The chromosome numbers observed for *Phalaris minor*, $2n = 14$ and 42, confirm published results (Watson *et al.* 1986).

CONCLUSION

The presence and behaviour of accessory (or B-) chromosomes in the South African flora has been studied

inadequately. Usually B-chromosomes are somewhat smaller than A-chromosomes, they can contain more heterochromatin and their number may vary from one population to another, from one individual to another, or even from one cell to another (Stebbins 1971; Sybenga 1972; Jones 1978). This on-going study on the chromosome numbers of South African grasses, will continue to gather information on the presence and behaviour of B-chromosomes which may assist in interpreting the evolutionary importance of B-chromosomes in this family.

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J. J. SPIES* and S. P. VOGES*

* Botanical Research Institute, Department of Agriculture and Water Supply, Private Bag X101, Pretoria 0001, RSA.

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