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Cytogenetic studies in some representatives of the subfamily Pooideae (Poaceae) in South Africa. 1. The tribe Aveneae, subtribe Aveninae

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ABSTRACT

This is a report on chromosome numbers for 14 species of the subtribe Aveninae, which is largely naturalized in South Africa. This is the first chromosome number report for *Helictotrichon longifolium* (Nees) Schweick. (n = 14), *H. longum* (Stapf) Schweick. (n = 14), *H. namaquensis* Schweick. (n = 14) and *Lophochloa cristata* (L.) Hyl. (n = 7, 21/2, 14). The subtribe has a basic chromosome number of seven, and fewer ploidy levels occur in the naturalized species in South Africa than in the same species in other parts of the world. All tetraploid specimens were alloploids.

INTRODUCTION

Polyploidy is one of the most important forms of chromosomal evolution in plants (Stebbins 1971). Preliminary studies on chromosome numbers of South African grasses revealed over 80% polyploid specimens (Moffett & Hurcombe 1949; De Wet 1954; De Wet & Anderson 1956; Pienaar 1955; De Wet 1960; Davidse *et al.* 1986; Spies & Du Plessis 1986a & b, 1987a & b; Spies & Jonker 1987; Du Plessis & Spies 1988; Spies & Du Plessis 1988; Spies & Voges 1988; Spies *et al.* 1989, 1990, 1991, 1992; Du Plessis & Spies 1992; Strydom & Spies 1994; Visser & Spies 1994a–c). The present article corroborates these findings.

The Pooideae is, for the largest part, introduced to southern Africa. The majority of species belonging to this subfamily is restricted to either the winter rainfall area of South Africa or to high altitude areas. The tribe Aveneae Dumort. comprises 57 genera and approximately 1 050 species in the world (Clayton & Renvoize 1986). Most South African representatives (18 genera and 59 species) are naturalized (Gibbs Russell *et al.* 1990). Clayton & Renvoize (1986) subdivided the tribe into four subtribes, i.e. Duthieinae Potztal, Aveninae Presl, Phalaridinae Rchb. and Alopecurinae Dumort. The genera representing these subtribes are listed in Table 1.

The aim of this study is to determine the chromosome numbers, polyploid levels and meiotic chromosome behaviour of the South African representatives of the tribe Aveninae. These results will eventually be compared with results of indigenous and endemic taxa to compare the frequency of polyploidy between indigenous and introduced grasses.

MATERIALS AND METHODS

Cytogenetic material was collected in two different ways for the purpose of this study. The material was either collected and fixed in the field, or living material was collected in the field and transplanted in the nurseries of either the National Botanical Institute (Pretoria) or the Department of Botany and Genetics, University of the Orange Free State (Bloemfontein), where cytogenetic material was collected and fixed. The material used and their localities are listed in Table 2. Voucher specimens are housed in the Geo Potts Herbarium, Department of Botany and Genetics, University of the Orange Free State, Bloemfontein (BLFU) or the National Herbarium, Pretoria (PRE).

Young inflorescences were fixed in Carnoy's fixative (Carnoy 1886). The fixative was replaced by 70% ethanol after 24–48 hours of fixation. Anthers were squashed in 2% aceto-carmine (Darlington & LaCour 1976). Slides were made permanent by freezing them with liquid CO_2 (Bowen 1956), followed by dehydration in ethanol and mounting in Euparal. An Olympus Vanox-S or Nikon Microphot photomicroscope and Ilford Pan-F film (ASA 50) were used for the photomicrographs. At least ten cells

TABLE 1.—List of subdivisions of the tribe Aveneae, indicating the genera and number of species present in southern Africa

Subtribe	Genus	No. of species
Alopecurinae Dumort.	*Agrostis* L.	11
	Ammophila Host	1
	Calamagrostis Adans.	1
	Gastridium P.Beauv.	1
	Lagurus L.	1
	Polypogon Desf.	4
Aveninae Presl	*Aira* L.	2
	Arrhenatherum P.Beauv.	1
	Avena L.	5
	Corynephorus P.Beauv.	1
	Deschampsia P.Beauv.	2
	Helictotrichon Schult.	12
	Holcus L.	2
	Koeleria Pers.	1
	Lophochloa Rchb.	2
	Periballia Trin.	1
Duthieinae Potztal	Not represented in South Africa	
Phalaridinae Rchb.	*Anthoxanthum* L.	5
	Phalaris L.	6

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TABLE 2.—Haploid chromosome numbers of representatives of the subtribe Aveninae (Poaceae, Pooideae, Aveneae) in southern Africa with the voucher specimen numbers and their specific localities, arranged according to the system of Edwards & Leistner (1971)

Taxon	Voucher	n	Locality
Aira caryophyllea L.	*Spies 3438*	7	WESTERN CAPE.—3418 (Simonstown): Silvermine Nature Reserve, (–AB)
A. cupaniana Guss.	*Spies 3797,4950*	7	WESTERN CAPE.—3118 (Vanrhynsdorp): Gifberg, (–DC)
	Spies 4964	7	NORTHERN CAPE.—3119 (Calvinia): 5 km from Nieuwoudtville to Clanwilliam, (–CA)
	Spies 4597	7	WESTERN CAPE.—3319 (Worcester): Du Toit's Kloof Pass, (–AC)
	Spies 4623	7	WESTERN CAPE.—3420 (Bredasdorp): 3 km north of De Hoop Nature Reserve, (–AD)
	Spies 3464	7	WESTERN CAPE.—3420 (Bredasdorp): 8 km from Ouplaas to De Hoop Nature Reserve, (–AD)
	Spies 4643	7	WESTERN CAPE.—3420 (Bredasdorp): 4 km north of De Hoop Nature Reserve, (–AD)
Avena barbata Brot.	*Spies 4837*	14	(ORANGE) FREE STATE.—2827 (Senekal): 6 km from Nebo to Fouriesburg via Generaalsnek, (–DB)
	Spies 4808	14	(ORANGE) FREE STATE.—2827 (Senekal): 25 km from Clocolan to Ficksburg, (–DC)
	Spies 5302	14	NORTHERN CAPE.—3119 (Calvinia): 7 km from Nieuwoudtville to Clanwilliam, (–CA)
	Spies 5287	14	NORTHERN CAPE.—3119 (Calvinia): 56 km from Calvinia to Nieuwoudtville, (–CC)
A. byzanthina K.Koch.	*Spies 2481*	21	EASTERN CAPE.—3127 (Lady Frere): 24 km from Dordrecht to Lady Grey, (–AA)
A. fatua L.	*Spies 4899*	21	NORTHERN CAPE.—2917 (Springbok): 14 km from Springbok to Hondeklipbaai, (–DB)
	Spies 4915	21	NORTHERN CAPE.—3017 (Hondeklipbaai): 88 km from Springbok to Kamieskroon via Soebatsfontein, (–BA)
Corynephorus fasciculatus Boiss. & Reut.	*Spies 3690*	7	WESTERN CAPE.—3218 (Clanwilliam): 11 km from Piquetberg in Versveld Pass, (–DC)
Helictotrichon longifolium (Nees) Schweick.	*Spsies 3982*	14	EASTERN CAPE.—3127 (Lady Frere): 9 km from Dordrecht to Barkly East, (–AC)
H. longum (Stapf) Schweick.	*Spies 3428*	14	WESTERN CAPE.—3218 (Clanwilliam): Roche Nature Reserve, (–AB)
H. namaquense Schweick.	*Spies 3137*	14	NORTHERN CAPE.—3220 (Sutherland): 10 km from Sutherland to Matjiesfontein, (–BC)
H. turgidulum (Stapf) Schweick.	*Saayman 75*	14	MPUMALANGA (EASTERN TRANSVAAL).—2430 (Pilgrim's Rest): 14 km from Sabie to Graskop, (–DD)
	Saayman 102	14	MPUMALANGA (EASTERN TRANSVAAL).—2530 (Lydenburg): 39 km from Lydenburg to Roossenekal, (–AA)
	Spies 5103	14	MPUMALANGA (EASTERN TRANSVAAL).—2630 (Carolina): 46 km from Ermelo to Breyten, (–AA)
	Spies 5097	28	MPUMALANGA (EASTERN TRANSVAAL).— 2630 (Carolina): 9 km from Ermelo to Breyten, (–AC)
	Spies 2355	14	MPUMALANGA (EASTERN TRANSVAAL).—2730 (Vryheid): near Piet Retief, (–BB)
	Spies 2654	14+0–2B	SWAZILAND.—2631 (Mbabane): 16 km from Mbabane to Oshoek, (–AC)
	Spies 4775	21	(ORANGE) FREE STATE.—2926 (Bloemfontein): 19 km from Dewetsdorp to Hobhouse, (–DB)
	Spies 4776	14	(ORANGE) FREE STATE.—2926 (Bloemfontein): 19 km from Dewetsdorp to Hobhouse, (–DB)
	Spies 4763	14	EASTERN CAPE.—3027 (Lady Grey): 82 km from Barkly East to Lady Grey via Joubert's Pass, (–CB)
	Spies 4753	14	EASTERN CAPE.—3027 (Lady Grey): 47 km from Barkly East to Lady Grey via Joubert's Pass, (–CD)
	Spies 4721	14	EASTERN CAPE.—3027 (Lady Grey): 34 km from Rhodes to Lundean's Neck, (–DD)
	Spies 4678	14	EASTERN CAPE.—3028 (Matatiele): 12 km from Rhodes to Naude's Neck, (–CC)
	Spies 2476	14	EASTERN CAPE.—3126 (Queenstown): Penhoek Pass, (–BC)
	Davidse 34079	14	WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (–AD)
	Spies 4507	14+0–4B	WESTERN CAPE.—3420 (Bredasdorp): 1 km north of De Hoop Nature Reserve, (–CA)
	Davidse 33456	14	WESTERN CAPE.—3218 (Clanwilliam): Rocher Nature Reserve, (–AB)
Holcus lanatus L.	*Saayman 124*	7+0–1B	MPUMALANGA (EASTERN TRANSVAAL).—2530 (Lydenburg): 27 km from Dullstroom to Belfast, (–CA)
	Spies 4675	7+1B	EASTERN CAPE.—3028 (Matatiele): 12 km from Rhodes to Naude's Pass, (–CC)
Koeleria capensis (Steud.) Nees	*Spies 5119*	7	MPUMALANGA (EASTERN TRANSVAAL).—2530 (Lydenburg): 11 km from Dullstroom to Lydenburg via Frischgewaagd, (–AC)
	Spies 5094	7	MPUMALANGA (EASTERN TRANSVAAL).—2630 (Carolina): 9 km from Ermelo to Breyten, (–AC)
	Spies 5102	7	MPUMALANGA (EASTERN TRANSVAAL).—2630 (Carolina): 46 km from Ermelo to Breyten, (–AA)
	Spies 4749	7	EASTERN CAPE.—3027 (Lady Grey): 31 km from Barkly East to Lady Grey, (–CD)
	Spies 4716	7	EASTERN CAPE.—3128 (Umtata): 38 km from Maclear to Elliot, (–AC)
	Spies 3250	14	WESTERN CAPE.—3420 (Bredasdorp): 6 km north of De Hoop Nature Reserve, (–CA)
	Spies 4855	14	WESTERN CAPE.—3420 (Bredasdorp): 3 km from De Hoop turnoff to Ouplaas on road between Bredasdorp and Malgas, (–CA)

TABLE 2.—Haploid chromosome numbers of representatives of the subtribe Aveninae (Poaceae, Pooideae, Aveneae) in southern Africa with the voucher specimen numbers and their specific localities (arranged according to the system of Edwards & Leistner (1971) (continued)

Taxon	Voucher	n	Locality
Lophochloa cristata (L.) Hyl.	*Spies 4965*	21/2	NORTHERN CAPE.—3119 (Calvinia): 5 km from Nieuwoudtville to Clanwilliam, (–CA)
	Spies 4365	7	WESTERN CAPE.—3119 (Calvinia): 55 km from Nieuwoudtville to Clanwilliam, (–CC)
	Spies 4567	14	WESTERN CAPE.—3318 (Cape Town): 7 km from Yzerfontein to Darling, (–AC
	Spies 3855	14	WESTERN CAPE.—3319 (Worcester): Mitchell's Pass, (–AD)
	Spies 4499	14	WESTERN CAPE.—3420 (Bredasdorp): 1 km north of De Hoop Nature Reserve, (–CA)
L. pumila (Desf.) Bor	*Spies 3424*	7	WESTERN CAPE.—3218 (Clanwilliam): 5 km south of Eland's Bay, (–AB)
	Spies 3143	7	NORTHERN CAPE.—3219 (Wuppertal): in Hartnekskloof, (–DC)
	Davidse 33272a	7	NORTHERN CAPE.—2917 (Springbok): 36 km SE of Port Nolloth on road to Kleinsee, (–AC)

per specimen were studied for each meiotic stage, except where otherwise indicated.

Meiotic chromosome counts are given as haploid (n) numbers to conform to the style set out by the editors of the Index to plant chromosome numbers series, published by the Missouri Botanical Garden.

RESULTS

All studied specimens of *Aira* L. were diploid (Table 2) and all meiotic cells appear normal. Seven bivalents were present during diakinesis (Figure 1A).

Two different ploidy levels, based on seven, were present in the *Avena* L. specimens studied. The species cor-

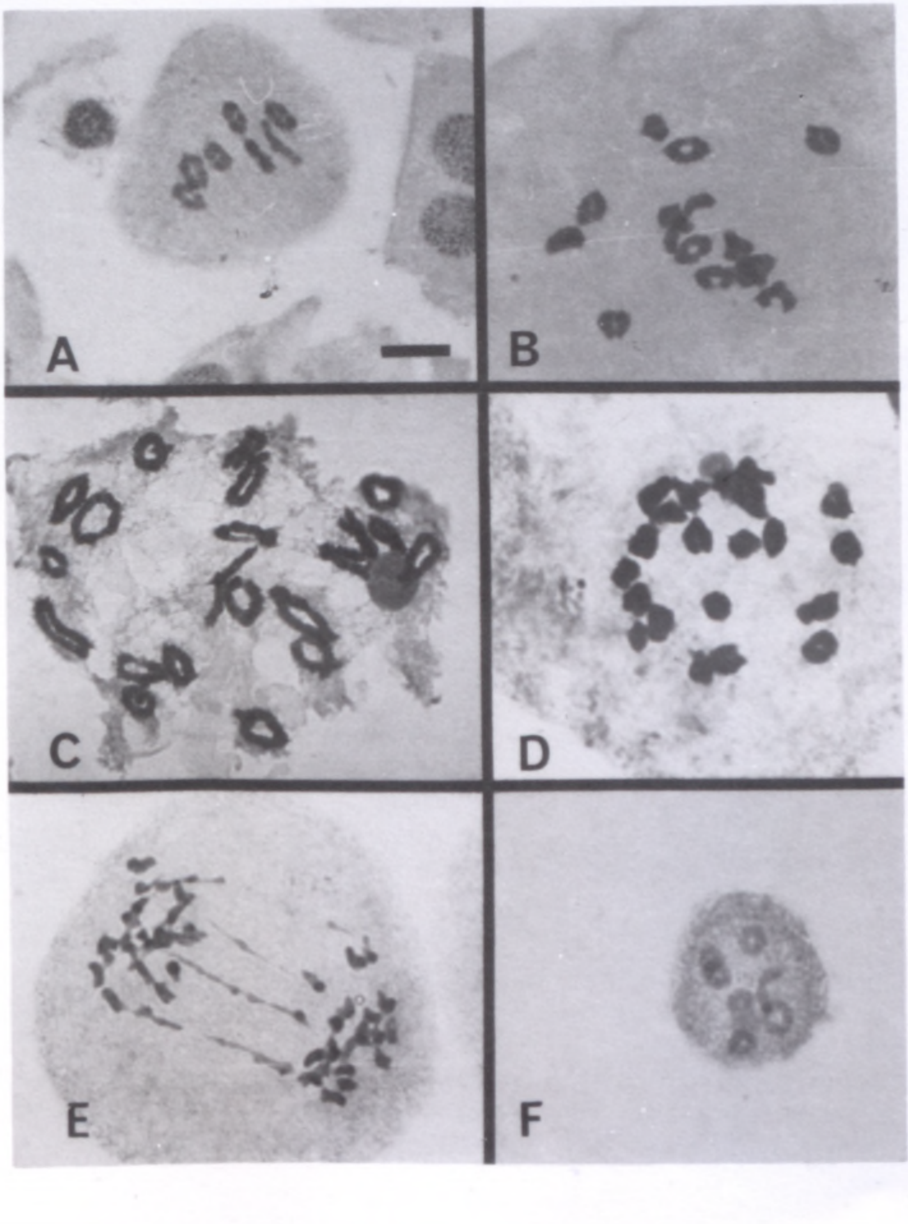

FIGURE 1.—Photomicrographs of meiotic chromosomes in some representatives of the genera *Aira, Avena* and *Corynophorus*. A, *Aira cupaniana, Spies 4597*, early metaphase I with 7_{II}; B, *Avena barbata, Spies 5287*, early metaphase I with 14_{II}; C, *A. byzanthina, Spies 2481*, diplotene with 21_{II}; D, *A. fatua, Spies 4899*, diakinesis with 21_{II}. E; *A. fatua, Spies 4915*, anaphase I with chromatid bridges; F, *Corynephorus fasciculatus, Spies 3690*, diakinesis with 7_{II}. Scale bar: A & F, 35 μm; B, D & E, 30 μm; C, 28 μm.

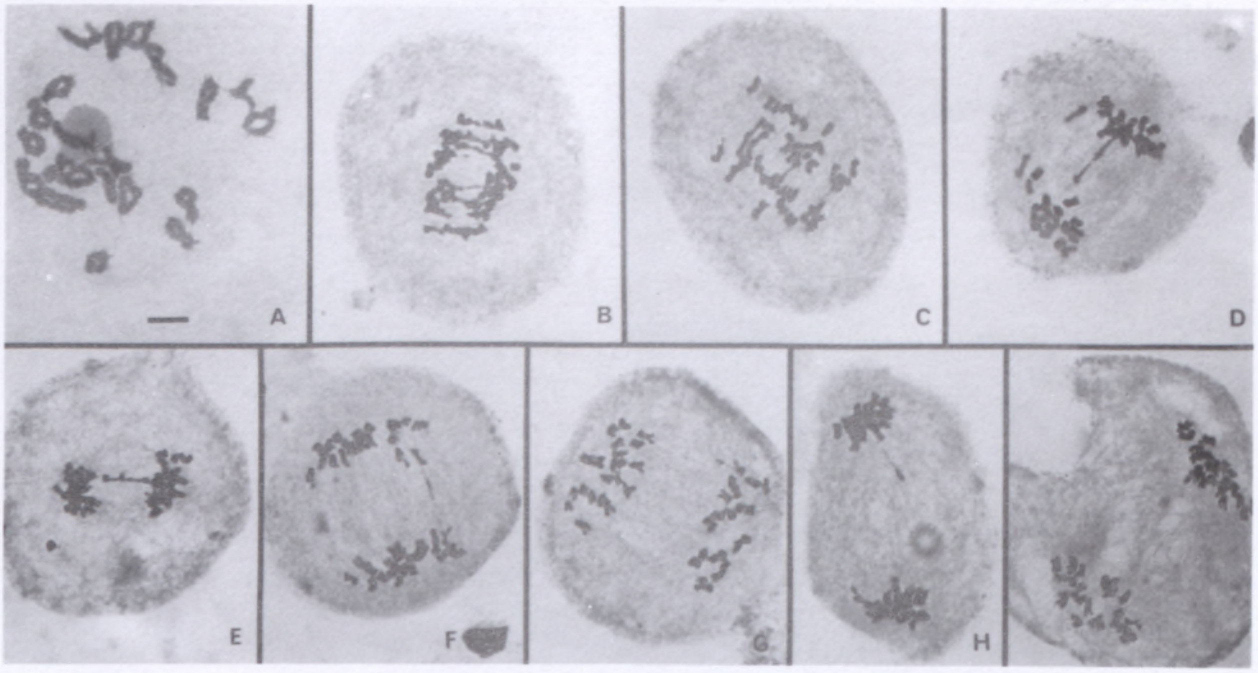

FIGURE 2.—Photomicrographs of meiotic chromosomes in *Avena fatua, Spies 4915*. A, diakinesis, with 21_{II}; B–I, anaphases with various numbers of chromatid bridges. Scale bar: A–I, 10 μm.

responded morphologically and separation of species was sometimes doubtful. According to the classification we received for our specimens, *A. barbata* Pott ex Link is tetraploid (Figure 1B), whereas *A. byzanthina* K.Koch (Figure 1C) and *A. fatua* L. (Figure 1D; 2A) are hexaploid. The majority of bivalents were ring bivalents and no multivalents were present. Up to four chromatid bridges per cell have been observed in the three *Avena* species mentioned in *Spies 2481, 4808, 4899* and *4915*) (Figure 1E; 2). The frequent occurrence of this phenomenon suggests that this specimen is heterozygotic for a high number of paracentric inversions.

The only *Corynephorus fasciculatus* Boiss. & Reut. specimen studied, proved to be a diploid (Figure 1F), with normal meiosis.

Haploid chromosome numbers in the genus *Helictotrichon* ranged from diploid to octaploid (Figure 3A–E). A similar range was observed in *H. turgidulum*. The

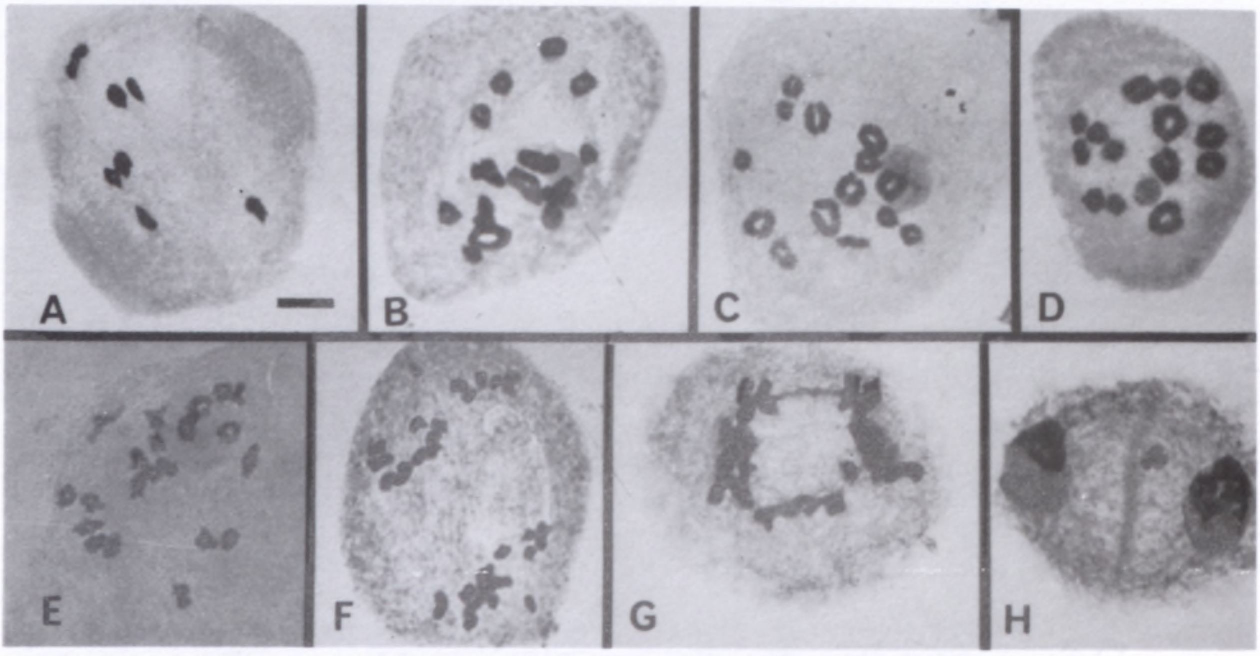

FIGURE 3.—Photomicrographs of meiotic chromosomes in some representatives of *Helictotrichon turgidulum*. A, *Spies 4721*, diakinesis with 7_{II}, B, *Spies 4763*, diakinesis with 14_{II}; C, *Spies 4678*, diakinesis with 14_{II}; D, *Spies 2355*, diakinesis with 14_{II}; E, *Spies 4775*, diakinesis with 21_{II}; F, *Spies 4507*, anaphase with 16-16 segregation of chromosomes, thus indicating the presence of B-chromosomes; G, *Spies 3137*, anaphase I with a chromatid bridge and a chromosome bridge; H, *Spies 3137*, telophase I with a micronucleus. Scale bar: 30 μm.

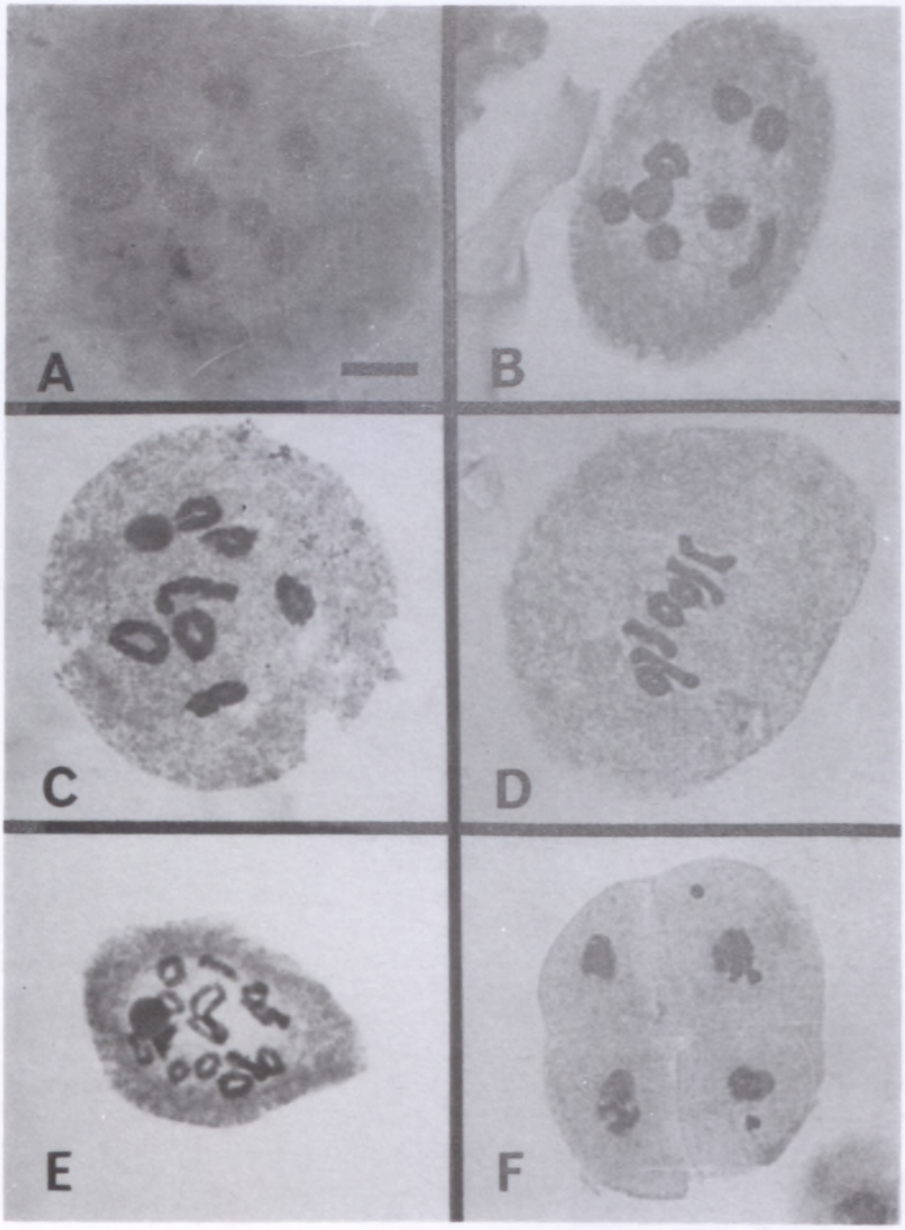

FIGURE 4.—Photomicrographs of meiotic chromosomes in some representatives of the genera *Holcus* and *Koeleria*. A, *Holcus lanatus, Saayman 124*, diakinesis with 7_{II}; B, *Koeleria capensis, Spies 5119*, diakinesis with 7_{II}; C, *K. capensis, Spies 5094*, diakinesis with 7_{II}; D, *K. capensis, Spies 5119*, metaphase I with 7_{II}; E, *K. capensis, Spies 4855*, diakinesis with 14_{II}; F, *K. capensis, Spies 5111*, telophase II with two micronuclei. Scale bar: A–D, 30 μm; E & F, 27 μm.

other species were all tetraploid. All the tetraploid specimens were alloploids, with the observed chromosome configurations concurring best with the expected configurations for the 2:2 model of Kimber & Alonso (1981). All specimens had x-values of 1. The 2:2 model indicates the presence of two sets of genomes, both consisting of two genomes. The x-value can vary from 0.5 (relative distance between the sets of genomes equals the relative distance between the genomes within a set) to 1 (relative distance between sets much larger than the distance within a set). The x-value of one, therefore, indicates that the specimens are alloploid. Two specimens had B-chromosomes (0–4B) (Figure 3F). Chromosomes were regarded as B-chromosomes if additional chromosomes were observed in some cells of an individual, or if the behaviour of the additional chromosomes deviated from the expected behaviour of euchromosomes. Occasionally meiotic abnormalities of euchromosomes during anaphase I have been observed. These abnormalities included chromatid bridges (Figure 3G), anaphase laggards and micronuclei during telophase I (Figure 3H).

Holcus lanatus was diploid (Figure 4A), with regular chromosome behaviour. *Koeleria capensis* encompassed both diploid and tetraploid specimens (Figure 4B–E). Occasionally chromosome laggards during anaphase I and micronuclei during telophases I and/or II (Figure 4F) have been observed. *Lophochloa pumila* was diploid (Figure 5A), whereas *L. cristata* varied from diploid to tetraploid (Figure 5B–G). One *L. cristata* specimen was either triploid or it contained up to seven B-chromosomes (Figure 5F, G; 6).

DISCUSSION

Aira is naturalized in South Africa and two species are recognized in this country, i.e. *A. caryophyllea* and *A. cupaniana* (Gibbs Russell *et al.* 1990). Both species are diploid, n = x = 7 (Table 2), with normal meiosis. This deviates from the somatic chromosome number of 28 usually reported for *A. caryophyllea* (Albers & Albers 1973; Queiros 1974; Albers 1978; 1980; Kirschner *et al.* 1982). However, a diploid specimen has been reported by Romero Zarco (1988). This study confirms the chromo-

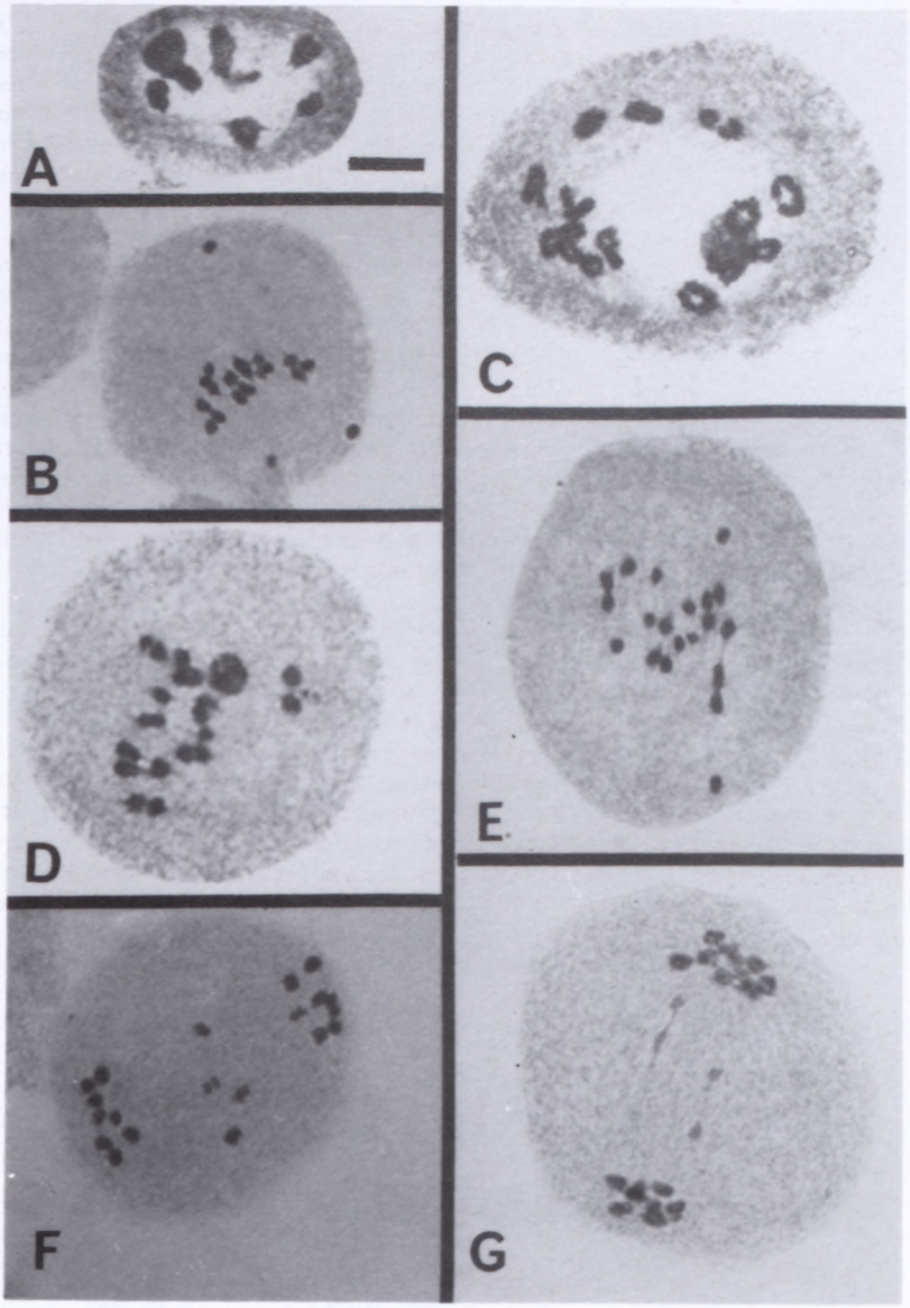

FIGURE 5.—Photomicrographs of meiotic chromosomes in some representatives of the genus *Lophochloa*. A, *Lophochloa pumila, Davidse 33272*, diakinesis with 7_{II}; B, *L. cristata, Spies 4965*, metaphase I with $7_{II}7_{I}$; C, *L. cristata, Spies 4567*, diakinesis with 14_{II}; D, *L. cristata, Spies 4965*, metaphase I; E, *L. cristata, Spies 4965*, early anaphase I; F, *L. cristata, Spies 4965*, late anaphase I with 4 laggards; G, *L. cristata, Spies 4965*, late anaphase I with laggards. Scale bar: A, C–G, 30 μm; B, 27 μm.

some numbers previously described for *A. cupaniana* (Albers & Albers 1973; Albers 1980). Although polyploidy is frequently observed in Europe, it seems absent in the naturalized species.

Arrhenatherum P.Beauv. is represented by one naturalized species in South Africa, *A. elatius* (L.) Presl (Gibbs Russell *et al.* 1990). No specimen could be obtained for this study. However, published results indicate that diploid (n = 7 or 2n = 14), tetraploid (n = 14 or 2n = 28) and hexaploid (n = 28) specimens of *A. elatius* have been observed elsewhere (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991).

Avena consists of four naturalized and a cultivated species in South Africa (Gibbs Russell *et al.* 1990). All *A. barbata* specimens studied, are tetraploid. This supports the different ploidy levels, ranging from diploid to hexaploid, previously described (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991). These results may indicate that a single introduction, or several introductions from the same ploidy level, of *A. barbata*, occurred.

Avena byzantina is hexaploid, thus supporting the chromosome number previously described (Morikawa 1982). The high frequency of ring bivalents and the absence of any multivalent suggests an alloploid origin for both species. This alloploid origin is confirmed by the corresponding values obtained during this study and when the expected chromosome associations for the 2:2 model of Kimber & Alonso (1981) is determined. The x-value of 1 indicates no relationship between the chromosomes of the two different genomes.

The hexaploid chromosome number determined for *A. fatua* supports the published chromosome number of this species (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991). The absence of multivalents in the studied specimens, suggests an alloploid origin for this species.

The naturalized *Corynophoris fasciculatus* is the only representative of this genus in South Africa (Gibbs Russell *et al.* 1990). Our study confirmed the diploid chromosome number previously described for this species (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991).

Deschampsia P.Beauv. is represented by two naturalized species in South Africa, *D. caespitosa* (L.) P.Beauv. and *D. flexuosa* (L.) Trin. (Gibbs Russell *et al.* 1990). In Europe *D. caespitosa* has haploid chromosome numbers of 9, 12, 13 and 26 (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991), whereas *D. flexuosa* has haploid chromosome numbers of 7 and 14 (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991). It would be very interesting to study the South African species cytogenetically to determine whether we have both basic chromosome numbers of 7 and 13 present, as suggested by chromosome numbers of other members of this genus.

Helictotrichon is represented by 13 indigenous species in South Africa (Gibbs Russell *et al.* 1990). Four species were included in this study, *H. longifolium*, *H. longum*, *H. namaquensis* and *H. turgidulum*. This is, to the best of our knowledge, the first report of chromosome numbers for *H. longifolium, H. longum* and *H. namaquensis*, which are all tetraploid. Additionally to the tetraploid chromosome number described for *H. turgidulum* (Hoshino & Davidse 1988), diploid, hexaploid and octaploid specimens were studied. All tetraploid specimens (from the four species) conform with the expected chromosome configurations for the 2:2 model of Kimber & Alonso (1981). The x-values of 1 indicate alloploid origins for all these specimens.

Holcus is represented by one indigenous species, *H. setiger* Nees, and a naturalized species, *H. lanatus* (Gibbs Russell *et al.* 1990). Only the latter species has been studied and the species seems to be diploid in South Africa, in contrast to the diploid and tetraploid species described in other countries (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991).

Koeleria capensis is indigenous and the only representative of the genus *Koeleria* in South Africa (Gibbs Russell *et al.* 1990). This study revealed two ploidy levels for this species, diploid and tetraploid, thus confirming previous results (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991). The tetraploid specimens were restricted to the southern Cape, near Bredasdorp. Their chromosome configurations concurred with the expected configurations for the 2:2 model with an x-value of 1. These specimens are consequently alloploids.

Lophochloa is represented by two naturalized species in South Africa, *L. cristata* and *L. pumila (Desf.) Bor* (Gibbs Russell *et al.* 1990). This is, to the best of our knowledge, the first report on chromosome numbers for *L. cristata*, which has at least two different ploidy levels, diploid and tetraploid. One specimen (*Spies 4965*) with abnormal chromosomal behaviour was observed. This specimen is either a triploid or it contains up to seven B-chromosomes. The additional chromosomes do not differ morphologically from the 'normal' chromosomes. However, since the number of additional chromosomes seems to differ from one cell to another (Figure 6), we suggest that they are B-chromosomes. The chromosome configurations harmonized best with the expected values obtained from the 2:2 model of Kimber & Alonso (1981). An x-value of 1 indicated that the tetraploid specimens

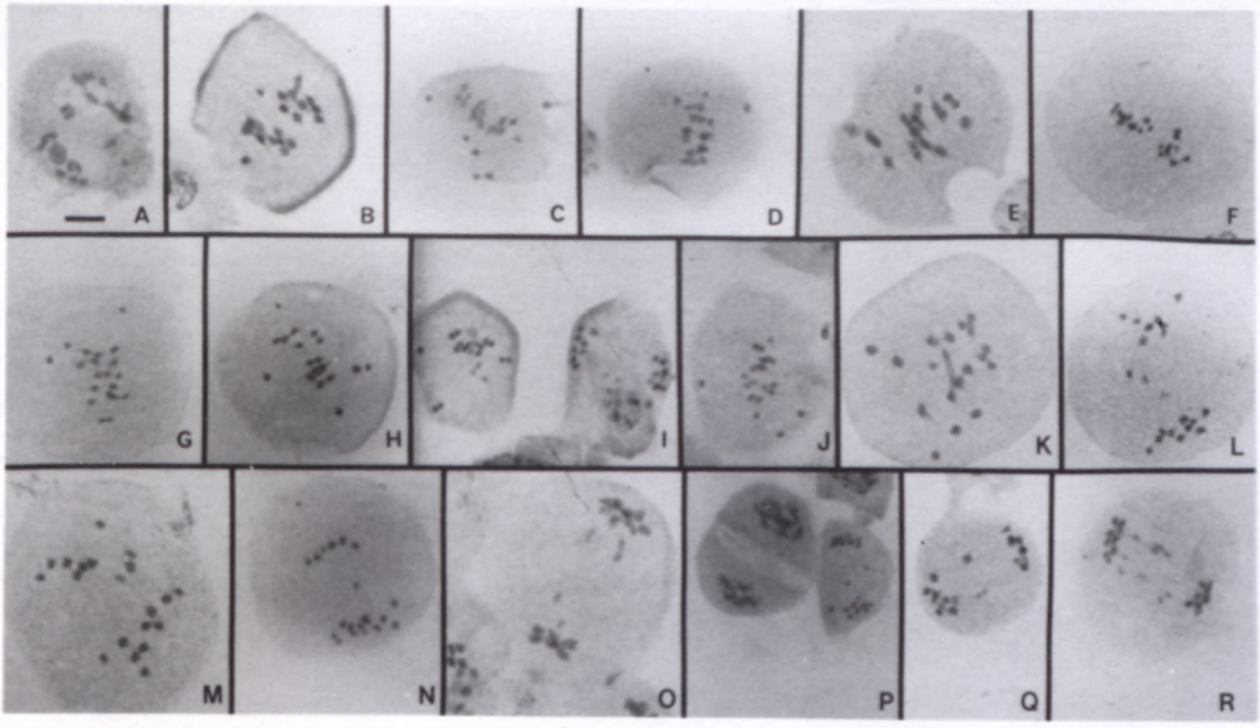

FIGURE 6.—Photomicrographs of meiotic chromosomes in *Lophochloa cristata*, *Spies 4965*. A–R, various cells indicating the difficulty to determine whether the additional chromosomes are B-chromosomes or whether they represent a third genome. Scale bar: A–R, 10 μm.

are alloploids. This study confirms the diploid status already described for *L. pumila* (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991). However, we found no confirmation for a basic chromosome number of 13 for *Lophochloa* as often reported (Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991).

The genus *Periballia* Trin. comprises a single naturalized species in South Africa, *P. minuta* (L.) Asch. & Graebn. (Gibbs Russell *et al.* 1990). Reports indicate that this species has a haploid chromosome number of 4 (Goldblatt 1981, 1983, 1985 1988; Goldblatt & Johnson 1990, 1991).

The subtribe Aveninae is largely naturalized in South Africa. The exceptions are the genus *Helictotrichon* and the species *Holcus setiger* and *Koeleria capensis*. The subtribe has a basic chromosome number of seven, and less ploidy levels occur in the naturalized species in South Africa in comparison to the same species in other parts of the world. This may be attributed to the introduction of these species. The species deviating from the basic chromosome number of the subtribe need to be investigated thoroughly.

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