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Chromosome studies on African plants. 11. The tribe Andropogoneae (Poaceae: Panicoideae)

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ABSTRACT

Representative specimens of various species of the genera *Andropogon* L., *Cymbopogon* Spreng., *Elionurus* Kunth ex Willd., *Hyparrhenia* Fourn. and *Hyperthelia* Clayton were cytogenetically studied. All specimens had a secondary basic chromosome number of ten. Polyploidy, either as alloploidy or segmental alloploidy, was frequent. The taxa studied represent mature polyploid complexes.

UITTREKSEL

Verteenwoordigende eksemplare van verskeie spesies van die genusse *Andropogon* L., *Cymbopogon* Spreng., *Elionurus* Kunth ex Willd., *Hyparrhenia* Fourn. en *Hyperthelia* Clayton is sitogeneties bestudeer. Die eksemplare het almal 'n sekondêre basiese chromosoomgetal van tien. Poliploïdie kom dikwels voor as alloploidie of segmentele alloploïdie. Die bestudeerde taksons verteenwoordig volwasse poliploïede komplekse.

INTRODUCTION

The tribe Andropogoneae forms part of the subfamily Panicoideae of the Poaceae. Andropogoneae is a large tribe with 85 genera and approximately 960 species (Clayton & Renvoize 1986). Although the tribe is well defined (Clayton 1986) and well represented in South Africa, few cytogenetic studies on this tribe have been completed in South Africa. Chromosome numbers obtained from miscellaneous chromosome counts in South African representatives of the Andropogoneae, indicate that the tribe has a primary basic chromosome number of five (Spies *et al.* 1991).

The aim of this paper is to present chromosome numbers obtained during routine cytogenetic investigations from our laboratories.

MATERIALS AND METHODS

For the purpose of this study, cytogenetic material was collected in two different ways. 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). The cytogenetic material was collected and fixed at both the aforementioned institutions. The material used and the collecting localities are listed in Table 1. 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. After 24–48 hours of fixation, the fixative was replaced by 70% ethanol. Anthers were squashed in 2% aceto-carmine (Darlington & La Cour 1976). Slides were made permanent by freezing them with liquid CO_2 (Bowen 1956), followed by dehydration in ethanol and mounting in Euparal. A Nikon Microphot photomicroscope and Ilford Pan-F film (ASA 50) were used for the photomicrographs. Except where otherwise indicated, at least twenty cells per specimen were studied for each meiotic stage.

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 AND DISCUSSION

The cytogenetic materials used during this study were collected between three and eight years prior to this study. Difficulty was experienced in obtaining sufficient contrast between the chromosomes and the cytoplasm. Consequently, the quality of the photos is poor.

Representatives of the Andropogoneae usually have a basic chromosome number of five (Clayton & Renvoize 1986). This basic chromosome number is confirmed by all the specimens in our study (Table 1). Ploidy levels, ranging from tetraploid (n = 2x = 10) to 16-ploid (n = 8x = 40), observed during this study, fall within the range of diploid (n = x = 5) to 24-ploid (n = 12x = 60) described by Clayton & Renvoize (1986).

The genus *Andropogon* L. comprises approximately 100 species (Clayton & Renvoize 1986), with 15 species indigenous to South Africa (Gibbs Russell *et al.* 1990). The six species studied have haploid chromosome num-

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TABLE 1.—Haploid chromosome numbers (n) of representatives of the tribe Andropogoneae (Poaceae, Panicoideae) in southern Africa with the voucher specimen numbers and their localities, arranged according to the system of Edwards & Leistner (1971)

Taxon	Voucher	n	Locality
Andropogon amethystinus Steud.	*Spies 4015*	20	EASTERN CAPE.—3028 (Matatiele): 36 km from Rhodes to Maclear via Naude's Neck, (–CC)
A. appendiculatus Nees	*Spies 1585*	30	EASTERN TRANSVAAL.—2530 (Lydenburg): Goede Hoop, on road between Dullstroom and Lydenburg, (–AC)
	Spies 4694	10	EASTERN CAPE.—3028 (Matatiele): 47 km from Rhodes to Maclear via Naude's Neck, (–CC)
	Spies 4702	10	EASTERN CAPE.—3028 (Matatiele): 69 km from Rhodes to Maclear via Naude's Neck, (–CC)
	Spies 4709	20	EASTERN CAPE.—3128 (Umtata): 38 km from Maclear to Elliot, (–AC)
	Spies 3514	10	EASTERN CAPE.—3323 (Willowmore): 9 km from Coldstream to Humansdorp, (–DD)
A. chinensis (Nees) Merr.	*Spies 3315, 3734*	20	NORTHERN TRANSVAAL.—2428 (Nylstroom): Soutpan Experimental Farm, (–CD)
	Spies 3718	10	PWV.—2627 (Potchefstroom): 12 km from Hartebeespoort turnoff, on road between Muldersdrift and Hekpoort, (–BB)
A. eucomus Nees	*Spies 1968*	10	EASTERN TRANSVAAL.—2430 (Pilgrim's Rest): 17 km from Sabie to Graskop, (–DD)
	Spies 3271	10	WESTERN CAPE.—3321 (Ladismith): 6 km from Ladismith in Seweweekspoort, (–AD)
	Spies 3510	10	EASTERN CAPE.—3424 (Humansdorp): 30 km from Humansdorp to Knysna, (–AA)
A. huillensis Rendle	*Spies 1977*	40	EASTERN TRANSVAAL.—2530 (Lydenburg): Mac-Mac Falls, (–BB)
A. schirensis A. Rich.	*Du Plessis 88*	10	ORANGE FREE STATE.—2829 (Harrismith): near Sterkfontein Dam, (–CA)
Cymbopogon excavatus (Hochst.) Stapf ex Burtt Davy	*Du Plessis 129*	10	KWAZULU/NATAL.—2930 (Pietermaritzburg): 2 km from Greytown to Colenso, (–BA)
C. marginatus (Steud.) Stapf ex Burtt Davy	*Spies 3430*	10	WESTERN CAPE.—3318 (Cape Town): Tafelberg, near cableway, (–AB)
	Spies 3887	10	WESTERN CAPE.—3319 (Worcester): 34 km from Worcester to Paarl in Du Toit's Kloof, (–CA)
	Spies 3459	10	WESTERN CAPE.—3420 (Bredasdorp): 6 km from Ouplaas to De Hoop Nature Reserve, (–AD)
	Spies 4489	10	WESTERN CAPE.—3420 (Bredasdorp): 1 km north of De Hoop Nature Reserve, (–CA)
C. plurinodis (Stapf) Stapf ex Burtt Davy	*Spies 3300*	10	NORTHERN TRANSVAAL.—2428 (Nylstroom): Soutpan Experimental Farm, (–CD)
	Spies 3322	20	NORTHERN TRANSVAAL.—2428 (Nylstroom): Soutpan Experimental Farm, (–CD)
	Spies 2026	40	PWV.—2528 (Pretoria): Sphinx Railway Station, (–CA)
	Spies 3482	10	EASTERN CAPE.—3325 (Port Elizabeth): 37 km from Rocklands to Elandsrivier, (–CA)
C. validus (Stapf) Stapf ex Burtt Davy	*Spies 2396*	30	KWAZULU/NATAL.—2832 (Mtubatuba): 12 km from Cape Vidal to St Lucia, (–AB)
	Spies 3480	10	EASTERN CAPE.—3325 (Port Elizabeth): Spring Resort Valley, (–CB)
Elionurus muticus (Spreng.) Kunth	*Spies 4707*	10	EASTERN CAPE.—3027 (Lady Grey): 78 km from Rhodes to Maclear via Naude's Neck, (–CD)
	Spies 4663	10	EASTERN CAPE.—3027 (Lady Grey): Karringmelkspruit on road between Lady Grey and Barkly East, (–CD)
	Spies 4740	10	EASTERN CAPE.—3027 (Lady Grey): 15 km from Barkly East to Lady Grey, (–CD)
	Spies 4755	10	EASTERN CAPE.—3027 (Lady Grey): 50 km from Barkly East to Lady Grey, (–CD)
	Spies 4664	10	EASTERN CAPE.—3028 (Matatiele): 10 km from Rhodes to Maclear via Naude's Neck, (–CC)
Hyparrhenia anamesa Clayton	*Spies 1969*	20	ORANGE FREE STATE.—2829 (Harrismith): Kaity Nilgeres, (–AC)
	Du Plessis 145	30	KWAZULU/NATAL.—2729 (Volksrust): 80 km from Newcastle to Ladysmith, (–BD)
	Du Plessis 103	30	KWAZULU/NATAL.—2829 (Harrismith): Cathedral Peak, (–CC)
	Spies 2567	20	SWAZILAND.—2631 (Mbabane): 22 km northeast of Mbabane, (–AA)
H. filipendula (Hochst.) Stapf var. *filipendula*	*Du Plessis 107*	20	KWAZULU/NATAL.—2931 (Stanger): Balito Bay, (–CA)
H. filipendula var. *pilosa* (Hochst.) Stapf	*Spies 3741*	20	NORTHERN TRANSVAAL.—2428 (Nylstroom): Soutpan Experimental Farm, (–CD)
H. hirta (*L.*) Stapf	*Du Plessis 148*	20	KWAZULU/NATAL.—2729 (Volksrust): O'Niels Cottage, (–BD)
	Du Plessis 128	20	KWAZULU/NATAL.—2930 (Pietermaritzburg): 2 km from Greytown to Colenso, (–BA)
	Spies 3099, 4342, 4459	20	WESTERN CAPE.—3118 (Vanrhynsdorp): Gifberg Pass, (–DC)
H. pilgeriana C.E. Hubb.	*Spies 4738*	40	EASTERN CAPE.—3027 (Lady Grey): 15 km from Barkly East to Lady Grey, (–DC)
	Spies 4603	10	WESTERN CAPE.—3319 (Worcester): Du Toit's Kloof Pass, (–CA)
	Spies 4649	10	WESTERN CAPE.—3419 (Caledon): 27 km from Villiersdorp to Caledon, (–AB)
	Spies 4635	10	WESTERN CAPE.—3420 (Bredasdorp): 3 km north of De Hoop Nature Reserve, (–AD)
H. variabilis Stapf	*Saayman 73*	20	EASTERN TRANSVAAL.—2530 (Lydenburg): 10 km from Sabie to Graskop, (–BB)
Hyperthelia dissoluta (Nees ex Steud.) Clayton	*Spies 2591*	10	SWAZILAND.—2631 (Mbabane): 13 km from Manzini to Siteki, (–AD)
	Spies 4730	10	EASTERN CAPE.—3027 (Lady Grey): 27 km from Barkly East to Rhodes, (–DC)

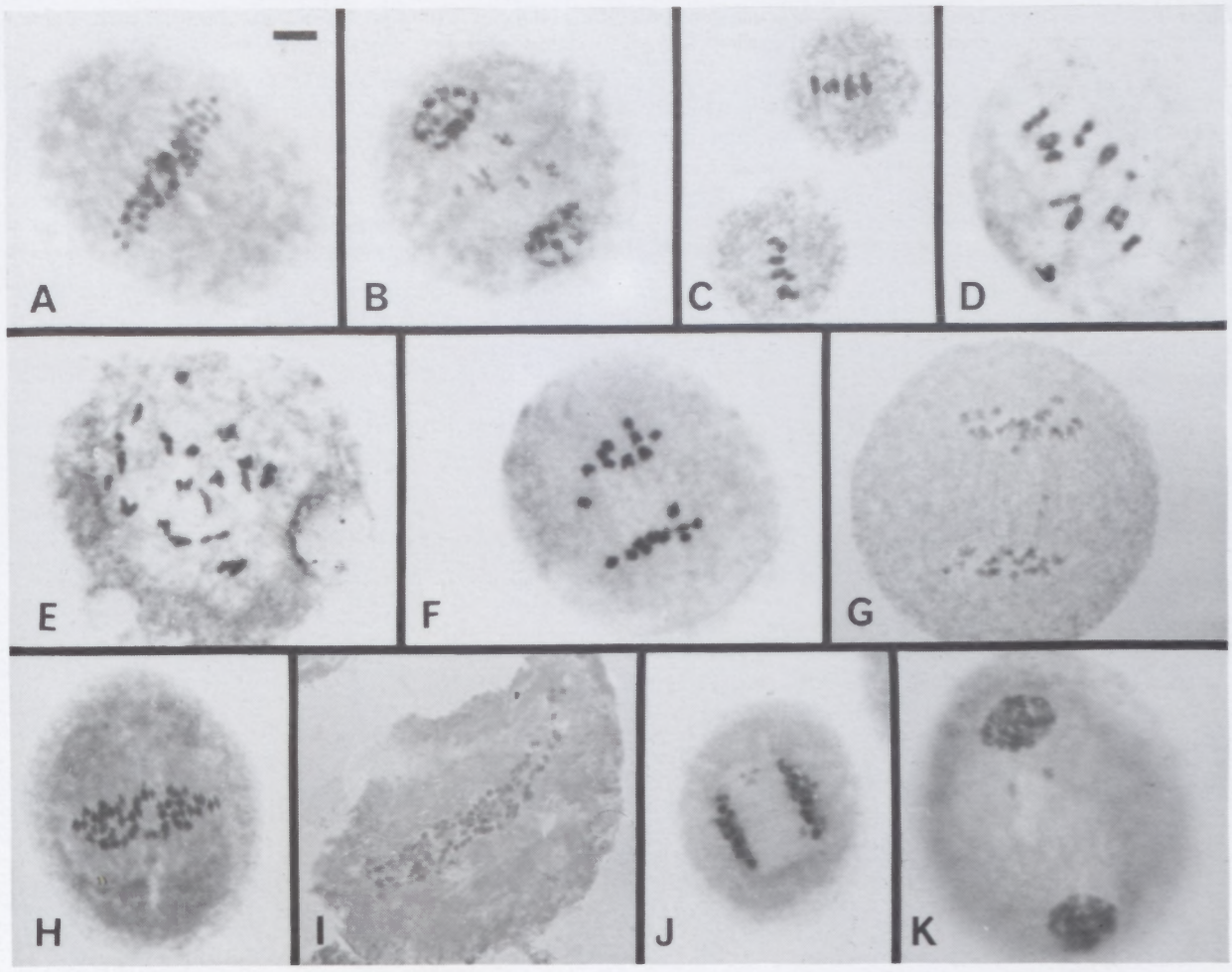

FIGURE 1.—Meiotic chromosomes in the genus *Andropogon*. A, *A. amethystinus*, *Spies 4015*, n = 4x = 20, metaphase I; B, *A. amethystinus*, *Spies 4015*, n = 4x = 20, telophase I with 8 chromosome laggards; C, *A. appendiculatus*, *Spies 3514*, n = 2x = 10, metaphase I; D, *A. appendiculatus*, *Spies 4694*, n = 2x = 10, early metaphase I; E, *A. appendiculatus*, *Spies 4709*, n = 4x = 20, diakinesis; F, *A. appendiculatus*, *Spies 4694*, n = 2x = 10, anaphase I; G, *A. chinensis*, *Spies 3315*, n = 4x = 20, anaphase I; H, *A. huillensis*, *Spies 1977*, n = 8x = 40, metaphase I; I, *A. huillensis*, *Spies 1977*, n = 8x = 40, metaphase I; J, *A. huillensis*, *Spies 1977*, anaphase I; K, *A. huillensis*, *Spies 1977*, n = 8x = 40, telophase I with 2 micronuclei. Scale bar: A–I, K, 10 µm; J, 15 µm.

bers ranging from n = 10 to n = 40. The *Andropogon amethystinus* specimen studied, had a haploid chromosome number of n = 20 (Figure 1A). This is a lower ploidy level than the n = 30 specimen described by Hoshino & Davidse (1988). Meiosis is abnormal in this specimen and between five and ten anaphase laggards are present in every anaphase cell (Figure 1B). No multivalents are formed and this specimen therefore seems to be an allopolyploid.

Three different haploid chromosome numbers are present in *A. appendiculatus*, namely n = 10, 20 and 30 (Figure 1C–F). No specimen seen formed multivalents, and all can therefore be described as alloploids. All ploidy levels are based on ten and the absence of multivalents, indicates that *A. appendiculatus* may have a secondary basic chromosome number of ten. Two different ploidy levels, n = 10 and 20, are present in *A. chinensis* (Figure 1G). All the specimens displayed a very low frequency of multivalents (with an average of 0.47 multivalents per cell). The low multivalent frequency suggests that these specimens represent segmental alloploidy. The presence of multivalents in plants with a haploid chromosome number of ten, indicates that the basic chromosome number of the genus is five, in contrast to the suggested ten described for *A. appendiculatus*.

All *A. eucomus* specimens have haploid chromosome numbers of n = 10. Haploid chromosome numbers of n = 10 and 20 have previously been described (Spies & Du Plessis 1986; 1987; Spies *et al.* 1991). Only bivalents were observed during this study, indicating that this species has an alloploid origin. *A. huillensis* is represented by a single specimen in this study. This specimen has a haploid chromosome number of n = 40 (Figure 1H), but cell fusion resulted in meiotic cells with more than 100 chromosomes (Figure 1I). Some anaphase I cells (20%) contain anaphase laggards (Figure 1J), resulting in micronuclei during telophase I (Figure 1K). Chromosome associations are restricted to bivalents, or occasionally two univalents, and *A. huillensis* is also an alloploid. In this study *A. schirensis* is represented by a single specimen. This specimen has a haploid chromosome number of n = 10 and meiosis is normal.

The genus *Andropogon* has a basic chromosome number of five, as indicated by the multivalent formation observed in n = 10 specimens of *A. chinensis* during this

study. No specimen with n = 5 has, as yet, been observed to confirm the basic chromosome number beyond doubt. The basic chromosome number for the genus is inferred from the existence of other species in the tribe with n = 5, for example *Sorghum* (Garber 1950). The basic chromosome number of a taxon is the lowest haploid chromosome number in any lower ranking taxon that does not involve aneuploidy (Stace 1980). With this definition in mind the lowest haploid chromosome number of a lower ranking taxon in this tribe is five. If n = 5 was derived through aneuploidy, various intermediate chromosome numbers are to be expected in the tribe, especially among close relatives of *Sorghum*, or even in *Sorghum* itself, since it contains species with both x = 5 and 10 as the basic number (Garber 1950; Celarier 1956, 1958; Spies *et al* 1991). The only deviation from multiples of 5 (or 10) among closely related plants, is x = 9 in *Cleistachne sorghoides* (Gibbs Russell *et al.* 1990). Therefore, it can be concluded that the tribe Andropogoneae has a primary basic chromosome number of five. However, most taxa in the Andropogoneae living today, suggest a basic chromosome number of ten. The tribe therefore has a primary basic chromosome number of five and a secondary basic chromosome number of ten.

The chromosomal behaviour during meiosis indicates that most *Andropogon* species represent mature polyploid complexes, because no diploids are found and the majority of specimens vary from tetraploid to 16-ploid. During polyploidization the species were either subjected to diploidization, or originated through hybridization (alloploidy). A more comprehensive study of this genus is urgently needed.

Cymbopogon Spreng. comprises approximately 40 species (Clayton & Renvoize 1986). Gibbs Russell *et al.* (1990) recognized an urgent need for the revision of this genus with its six southern African species. The basic chromosome number of *Cymbopogon* is five or ten (Gibbs Russell *et al.* 1990). This study included four species, and haploid chromosome numbers varied between n = 10 and 40.

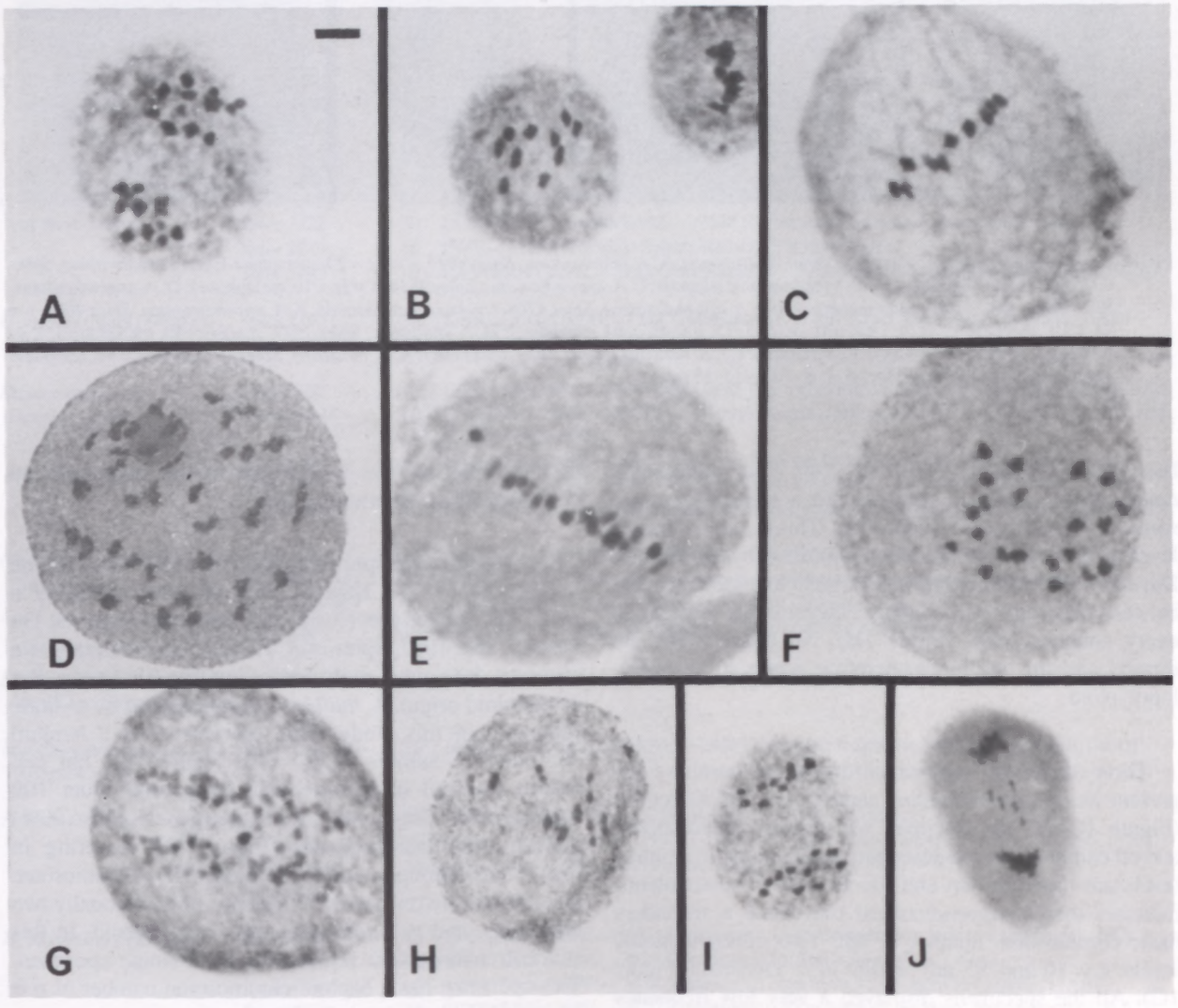

FIGURE 2.—Meiotic chromosomes in the genus *Cymbopogon*. A, *C. excavatus*, *Du Plessis 129*, n = 2x = 10, anaphase I; B, *C. marginatus*, *Spies 3887*, n = 2x =10, early metaphase I; C, *C. marginatus*, *Spies 4489*, n = 2x = 10, metaphase I; D, *C. plurinodis*, *Spies 2026*, n = 8x = 40, diakinesis; E, *C. plurinodis*, *Spies 3482*, n = 2x = 10, metaphase I; F, *C. plurinodis*, *Spies 3300*, n = 2x = 10, anaphase I; G, *C. plurinodis*, *Spies 2026*, n = 8x = 40, anaphase I; H, *C. validus*, *Spies 3480*, n = 2x = 10, early metaphase I; I, *C. validus*, *Spies 3480*, n = 2x = 10, anaphase I; J, *C. validus*, *Spies 2396*, n = 6x = 30, late anaphase I with 5 chromosome laggards. Scale bar: A–H, 10 µm; I, J, 15 µm.

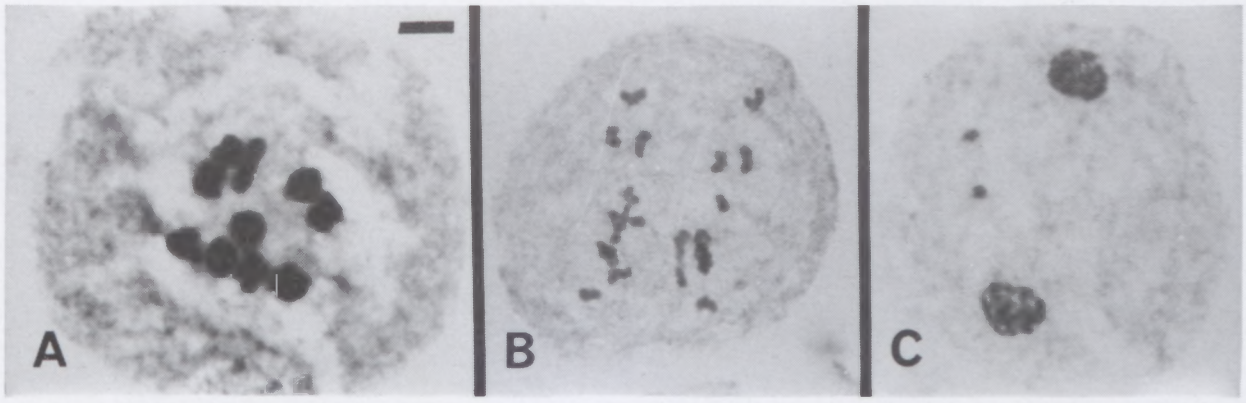

FIGURE 3.—Meiotic chromosomes in *Elionurus muticus*, all specimens with n = 2x = 10. A, *Spies 4740*, diakinesis; B, *Spies 4755*, anaphase II; C, *Spies 4755*, telophase I with 2 micronuclei. Scale bar: A–C, 10 µm.

In this study *Cymbopogon excavatus* is represented by a single specimen. The specimen has a haploid chromosome number of ten and meiosis is normal (Figure 2A), with only bivalents being formed. Normal meiosis, with a haploid chromosome number of 10 and the presence of bivalents only (Figure 2B, C), has also been observed in *C. marginatus*. Various ploidy levels are present in *C. plurinodis* and haploid chromosome numbers of n = 10, 20 and 40 have been observed (Figure 2D–G). Two different haploid chromosome numbers, n = 10 and 30, are present in different specimens of *C. validus* (Figure 2H, I). Although only bivalents are formed at the lower ploidy level, various univalents are present during metaphase I in the specimen with the higher ploidy level, resulting in chromosome laggards during anaphase I (Figure 2J).

The genus *Cymbopogon* has a secondary basic chromosome number of 10. The occurrence of polyploid specimens and the absence of multivalents suggests an alloploid origin. Alloploidy is the product of hybridization and an increase in chromosome number, and the taxonomic difficulties indicated by Gibbs Russell *et al.* (1990), may therefore be attributed to hybridization. A revision of this genus should include a thorough cytogenetic investigation.

The genus *Elionurus* Kunth ex Willd. comprises 15 species (Clayton & Renvoize 1986), with only *E. muticus* (Spreng.) Kunth being indigenous to South Africa (Gibbs Russell *et al.* 1990). All the specimens studied have a haploid chromosome number of n = 10. Meiosis is regular with only bivalents being formed (Figure 3).

The genus *Hyparrhenia* Fourn. comprises 55 species (Clayton & Renvoize 1986), with 20 indigenous species (Gibbs Russell *et al.* 1990). The basic chromosome num-

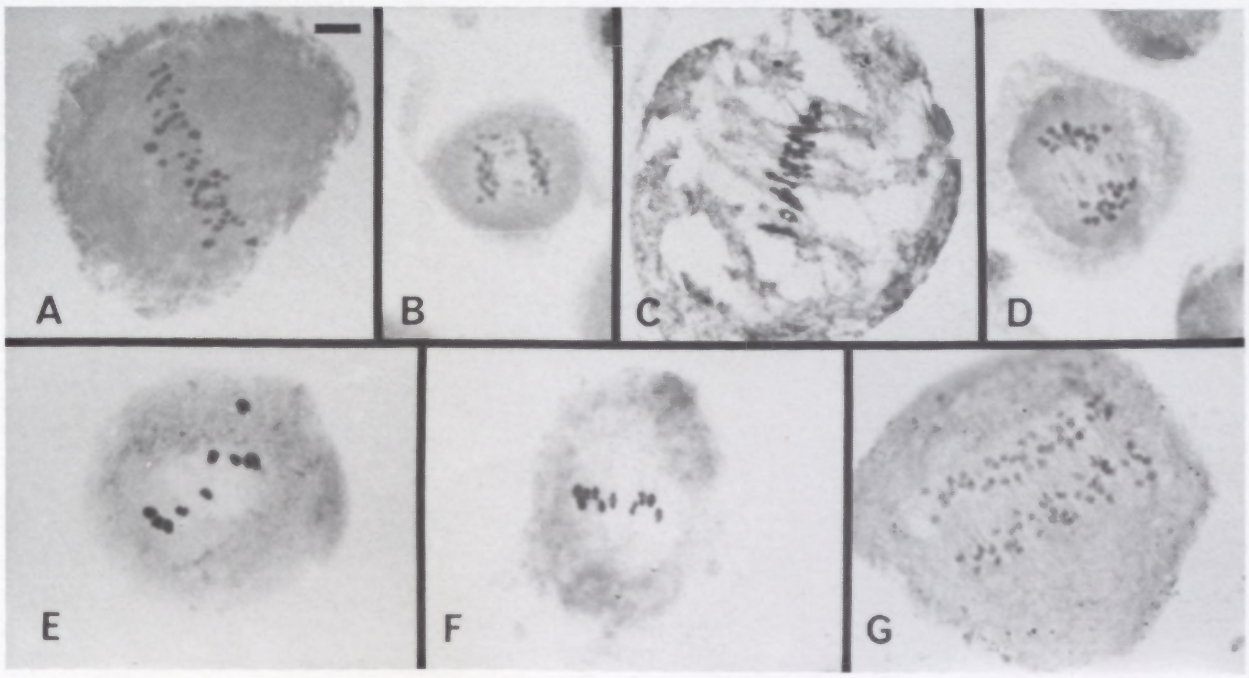

FIGURE 4.—Meiotic chromosomes in the genus *Hyparrhenia*. A, *H. anamesa*, *Spies 2567*, n = 4x = 20, metaphase I; B, *H. anamesa*, *Spies 1969*, n = 4x = 20, anaphase I with chromosome laggards; C, *H. hirta*, *Spies 4342*, n = 4x = 20, metaphase I; D, *H. hirta*, *Du Plessis 148*, n = 4x = 20, anaphase I with 4 chromosome laggards; E, *H. pilgeriana*, *Spies 4635*, n = 2x = 10, diakinesis; F, *H. pilgeriana*, *Spies 4635*, n = 2x = 10, metaphase I; G, *H. pilgeriana*, *Spies 4738*, n = 8x = 40, anaphase I. Scale bar: A, C, E–G, 10 µm; B, D, 15 µm.

ber of this genus is described as 10 and 15 (Gibbs Russell *et al.* 1990). Six taxa are included in this study.

Hyparrhenia anamesa has haploid chromosome numbers of n = 20 and 30 (Figure 4A, B). These numbers correspond to the earlier numbers obtained by Spies & Du Plessis (1988) and Du Plessis & Spies (1988). The lack of multivalents suggests that these specimens are either alloploids, or homoeologous chromosome pairing is suppressed by the action of Ph-like genes (Riley & Chapman 1958; Sears 1976). Both varieties of *H. filipendula* studied, i.e. *filipendula* and *pilosa*, have haploid chromosome numbers of 20, as does *H. hirta* (Figure 4C, D). Haploid chromosome numbers of 15, 20 and 30 have previously been described for this species (Spies & Du Plessis 1988; Hoshino & Davidse 1988). *Hyparrhenia pilgeriana* has haploid chromosome numbers of n = 10 and 40 (Figure 4E–G). The last species studied, *H. variabilis*, has a haploid chromosome number of n = 20.

The genus *Hyperthelia* Clayton is represented by a single indigenous species. This study confirms the haploid chromosome number of *Hyperthelia dissoluta* as n = 20.

The chromosome numbers of all specimens studied are multiples of ten. This evidence supports a basic chromosome number of five for the tribe (Celarier 1956). The occurrence of a few multivalents in some specimens, indicates that Ph-like genes are possibly not present. The near absence of diploids and prevalence of polyploids, suggests that these taxa represent mature polyploid complexes. The formation of mainly bivalents in all specimens indicates an alloploid or segmental alloploid origin for these specimens. This supports a hybrid origin for the taxa.

In conclusion, the Andropogoneae has a secondary basic chromosome number of ten. Polyploidy is extremely frequent. It occurs either as alloploidy or segmental alloploidy. This process of hybridization and polyploidization resulted in a number of mature polyploid complexes.

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