Bothalia 32,2: 233–249 (2002)

Miscellaneous notes

POACEAE

CHROMOSOME STUDIES ON AFRICAN PLANTS. 17. THE SUBFAMILIES ARUNDINOIDEAE AND DANTHONIOIDEAE

Cytogenetic studies in our laboratory focused on the former grass subfamily Arundinoideae and we have published chromosome numbers of 422 specimens, representing 12 genera and 54 species (Du Plessis & Spies 1988; Spies & Du Plessis 1988; Spies *et al.* 1990, 1992; Du Plessis & Spies 1992; Spies *et al.* 1994; Visser & Spies 1994b, d, e; Klopper *et al.* 1998; Spies & Roodt 2001). This subfamily was recently subdivided into two separate subfamilies, the Arundinoideae and Danthonioideae by the Grass Phylogeny Working Group (GPWG 2001): the Arundinoideae, represented by *Styppeiochloa* De Winter, has basic chromosome numbers of 6, 9 and 12 and the Danthonioideae, represented by *Chaetobromus* Nees, *Karroochloa* Conert & Türpe, *Merxmuellera* Conert, *Pentameris* P.Beauv., *Pentaschistis* Stapf, *Pseudopentameris* Conert, *Schismus* P.Beauv. and *Tribolium* Desv., has x = 6, 7 and 9.

This is a chromosome number report for the two subfamilies.

MATERIALS AND METHODS

Cytogenetic material of identical plants of a population was collected and fixed in the field. Voucher specimens, listed in Table 1, are housed in the Geo Potts Herbarium, Department of Botany and Genetics, University of the Free State, Bloemfontein (BLFU) or in the National Herbarium, Pretoria (PRE).

Anthers were squashed in aceto-carmine and meiotically analysed—at least 20 cells per meiotic stage were studied (Spies *et al.* 1996). Only gametic chromosome numbers are presented to conform to previous papers on chromosome numbers in this journal (Spies & Du Plessis 1986).

RESULTS AND DISCUSSION

One hundred and nineteen plants, representing 38 species and 9 genera, were studied (Table 1).

Arundinoideae

Three specimens of the monospecific genus *Styppeiochloa, S. gynoglossa,* were studied. Two specimens had n = 2x = 12, and one octaploid specimen (n = 4x = 24) was found (Figure 1A). These specimens represent the first known chromosome number reports for this genus and six is the original basic chromosome number. Twelve is probably a secondarily derived basic chromosome number.

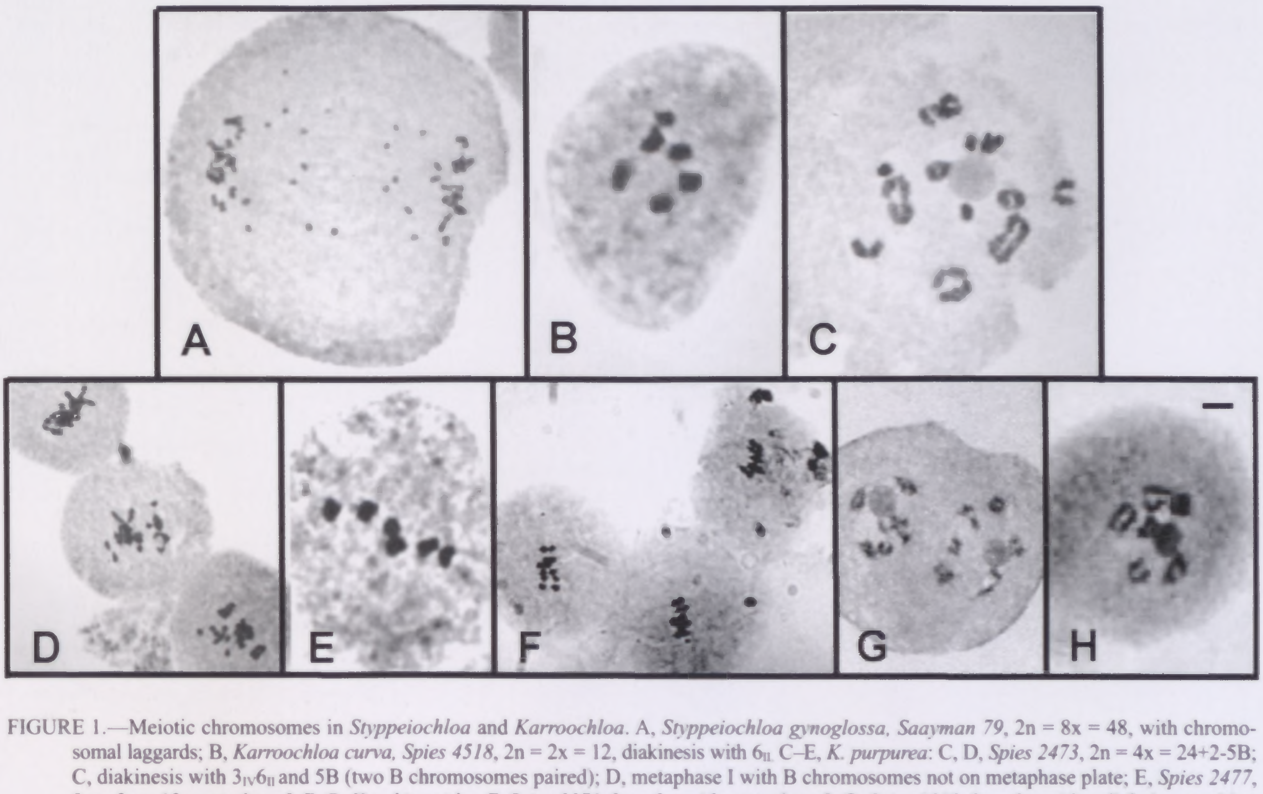

FIGURE 1.—Meiotic chromosomes in *Styppeiochloa* and *Karroochloa*. A, *Styppeiochloa gynoglossa, Saayman 79*, 2n = 8x = 48, with chromosomal laggards; B, *Karroochloa curva, Spies 4518*, 2n = 2x = 12, diakinesis with 6_{II}. C–E, *K. purpurea*: C, D, *Spies 2473*, 2n = 4x = 24+2-5B; C, diakinesis with $3_{IV}6_{II}$ and 5B (two B chromosomes paired); D, metaphase I with B chromosomes not on metaphase plate; E, *Spies 2477*, 2n = 2x = 12, metaphase I. F, G, *K. schismoides*: F, *Spies 3371*, 2n = 2x = 12, metaphase I; G, *Spies 3382*, 2n = 2x = 12, cell fusion resulting in 12 bivalents and two micronuclei during diakinesis. H, *Karroochloa* species, *Spies 5192*, 2n = 2x = 12, diakinesis with 6_{II}. Scale bar: B, 5 µm; B, C, E, H, 8 µm; D, F, G, 15 µm.

TABLE 1.—Gametic chromosome numbers (n) of representatives of subfamilies Arundinoideae and Danthonioideae (Poaceae) in southern Africa with their voucher specimen numbers and specific localities. Species are listed alphabetically and localities presented according to Edwards & Leistner (1971)

Taxon	n	Voucher	Locality
Arundinoideae			
Styppeiochloa gynoglossa (Gooss.) De Winter	12	*Spies 1485*	MPUMALANGA.—2530 (Lydenburg): in the Steenkampsberge, 6 km from Goede Hoop to Roossenekal, (–AA).
	12	*Spies 2642*	SWAZILAND.—2631 (Mbabane): Moimba beacon, 16 km from Mbabane to Oshoek, (–AD).
	24	*Saayman 79*	MPUMALANGA.—2430 (Pilgrim's Rest): 3 km from Graskop to Bosbokrand, (–DD).
Danthonioideae			
Chaetobromus involucratus (Schrad.) Nees subsp. *dregeanus* (Nees) Verboom	6	*Spies 5691*	NORTHERN CAPE.—2917 (Springbok): 78 km from Steinkopf to Port Nolloth, (–BA).
Karroochloa curva (Nees) Conert & Türpe	6	*Spies 4518*	WESTERN CAPE.—3420 (Bredasdorp): 25 km from Swellendam to Ashton, (–AB).
K. purpurea (L.f.) Conert & Türpe	6	*Spies 3370*	NORTHERN CAPE.—2918 (Gamoep): 26 km southeast from Springbok to Garies, (–CA).
	6	*Spies 4542*	WESTERN CAPE.—3319 (Worcester): 69 km from Montagu to Touwsriver, (–DB).
	6	*Spies 4536*	WESTERN CAPE.—3320 (Montagu): 61 km from Montagu to Touwsriver, (–CD).
	6+0-2B	*Spies 2473, 2477*	EASTERN CAPE.—3126 (Queenstown): Penhoek Pass, (–BC).
K. schismoides (Stapf ex Conert) Conert & Türpe	6	*Spies 2826*	NORTHERN CAPE.—2917 (Springbok): 34 km from Port Nolloth to Steinkopf, (–CA).
	6	*Spies 2976*	NORTHERN CAPE.—2917 (Springbok): 25 km east of Port Nolloth, (–AC).
	6	*Spies 3357*	NORTHERN CAPE.—2917 (Springbok): 36 km from Port Nolloth to Kleinsee, (–AC).
	6	*Spies 4276*	NORTHERN CAPE.—2917 (Springbok): 13 km from Springbok on road to Hondeklipbaai, (–DB).
	6	*Spies 3371*	NORTHERN CAPE.—2918 (Gamoep): 26 km southeast from Springbok to Garies, (–CA).
	6	*Spies 3382*	NORTHERN CAPE.—3017 (Hondeklipbaai): 42 km west of Garies to Groenrivier, (–DC).
	6	*Spies 3081*	WESTERN CAPE.—3118 (Vanrhynsdorp): 15 km north of Vanrhynsdorp, (–AD).
K. tenella (Nees.) Conert & Türpe	6	*Spies 4350*	NORTHERN CAPE.—3119 (Calvinia): 35 km from Vanrhynsdorp to Nieuwoudtville, (–AC).
Karroochloa sp.	6	*Spies 5192*	EASTERN CAPE.—3324 (Steytlerville): 25 km from Patensie to Willowmore, (–DA).
Merxmuellera cincta (Nees) Conert	18	*Spies 3504*	EASTERN CAPE.—3424 (Humansdorp): 16 km from Humansdorp to Cape St Frances, (–BB).
M. decora (Nees) Conert	24	*Spies 4407*	WESTERN CAPE.—3219 (Wuppertal): 3 km from Algeria to Citrusdal, (–AC).
	24	*Spies 4458*	WESTERN CAPE.—3419 (Caledon): 21 km from Franschoek to Villiersdorp, (–AA).
	24	*Spies 3465*	WESTERN CAPE.—3420 (Bredasdorp): 8 km south from Ouplaas to De Hoop Nature Reserve, (–AD).
M. disticha (Nees) Conert	24	*Spies 4751*	EASTERN CAPE.—3027 (Lady Grey): 43 km from Barkley East to Lady Grey, (–CA).
M. drakensbergensis (Schweick.) Conert	18	*Spies 4676*	EASTERN CAPE.—3028 (Matatiele): 12 km from Rhodes to Naude's Nek, (–CC).
	18	*Spies 4687*	EASTERN CAPE.—3028 (Matatiele): 22 km from Rhodes on road to Barkley East, (–CC).
M. lupulina (Thunb.) Conert	24	*Spies 4601*	WESTERN CAPE.—3319 (Worcester): Du Toitskloof next to tunnel, (–AC).
M. macowanii (Stapf) Conert	24	*Spies 4724*	EASTERN CAPE.—3027 (Lady Grey): 37 km from Rhodes via Luncheon's Nek, (–DD).
	24	*Spies 4727*	EASTERN CAPE.—3027 (Lady Grey): 50 km from Rhodes via Luncheon's Nek, (–DD).
	24	*Spies 4757*	EASTERN CAPE.—3027 (Lady Grey): 65 km from Barkley East to Lady Grey via Joubert's Pass, (–CA).
	24	*Spies 4682*	EASTERN CAPE—3028 (Matatiele): 16 km from Rhodes via Naude's Nek, (–CC).
M. rufa (Nees) Conert	24	*Spies 4402*	WESTERN CAPE—3219 (Wuppertal): top of Uitkyk Pass, (–AC).
M. stricta (Schrad.) Conert	12	*Spies 6288*	NORTHERN CAPE.—3119 (Calvinia): 41 km from Vanrhynsdorp on Vanrhyns Pass, (–AC).
	12	*Spies 4384*	WESTERN CAPE.—3218 (Clanwilliam): Uitkyk Pass, (–AC).
	12	*Spies 3695*	WESTERN CAPE.—3219 (Wuppertal): 22 km from Clanwilliam to Calvinia, (–AA).
	12	*Davidse 33333, 33939, 34091*	Localities unknown.
	18	*Spies 4339*	NORTHERN CAPE.—3118 (Vanrhynsdorp): Gifberg Pass, (–DC).
	18	*Spies 4351*	NORTHERN CAPE.—3119 (Calvinia): 41 km from Vanrhynsdorp on Vanrhyns Pass, (–AC).

TABLE 1.—Gametic chromosome numbers (n) of representatives of subfamilies Arundinoideae and Danthonioideae (Poaceae) in southern Africa with their voucher specimen numbers and specific localities. Species are listed alphabetically and localities presented according to Edwards & Leistner (1971) (cont.)

Taxon	n	Voucher	Locality
M. stricta (Schrad.) Conert	18	*Spies 3839*	WESTERN CAPE.—3218 (Clanwilliam): Uitkyk Pass, (–AC).
	18	*Spies 3147*	WESTERN CAPE.—3219 (Wuppertal): 2 km from Houdenbek to Katbakkies Pass, (–DC).
	18	*Spies 3637*	WESTERN CAPE.—3319 (Worcester): 4 km from Franschoek turn-off on Villiersdorp-Grabouw road, (–CC).
	18	*Spies 3469*	WESTERN CAPE.—3419 (Caledon): Swartberg Pass, (–AA).
	18	*Spies 3618*	WESTERN CAPE.—3419 (Caledon): 18 km from Botriver to Villiersdorp via Vanderstel Pass, (–AA).
	18	*Davidse 33347, 34028, 34110, 34121*	Localities unknown.
	± 26	*Spies 3140*	WESTERN CAPE.—3220 (Sutherland): 15 km from Sutherland to Matjiesfontein, (–BC).
Pentameris thuarii P.Beauv.	7	*Spies 3541*	WESTERN CAPE.—3322 (Oudtshoorn): Montagu Pass, (–CD).
Pentaschistis acinosa Stapf	7	*Spies 5981*	WESTERN CAPE.—3218 (Clanwilliam): 40 km from Clanwilliam to Lamberts Bay, (–AB).
	7	*Spies 6033, 6035*	WESTERN CAPE.—3218 (Clanwilliam): 32 km from Clanwilliam to Nieuwoudtville at Klawer turn-off, (–BB).
	7	*Spies 3650*	WESTERN CAPE.—3318 (Cape Town): Table Mountain, (–CD).
P. airoides (Nees) Stapf subsp. *airoides*	7	*Spies 5946*	NORTHERN CAPE.—3018 (Kamieskroon): 5 km from Kamieskroon to Leliehoek, (–AC).
P. airoides (Nees) Stapf subsp. *jugorum* (Stapf) H.P.Linder	14	*Linder 4862*	FREE STATE.—2828 (Bethlehem): Bethlehem, Golden Gate National Park, (–DA)
P. aristifolia Schweick.	7	*Spies 6036*	WESTERN CAPE.—3218 (Clanwilliam): 32 km from Clanwilliam to Nieuwoudtville, at Klawer turn-off, (–BB).
	28	*Spies 6002*	WESTERN CAPE.—3218 (Clanwilliam): 14 km from Clanwilliam to Nieuwoudtville, (–BB).
P. curvifolia (Schrad.) Stapf	7	*Spies 5727*	WESTERN CAPE.—3118 (Vanrhynsdorp): On top of Gifberg Pass, (–DC).
	7+1B	*Spies 6315*	WESTERN CAPE.—3218 (Clanwilliam): Uitkyk Pass, (–AC).
	7+1-2B	*Spies 4456*	WESTERN CAPE.—3319 (Worcester): 21 km from Franschoek to Villiersdorp, (–CC).
	7+0-2B	*Spies 6169*	WESTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, (–AC).
	7+0-4B	*Spies 6236*	WESTERN CAPE.—3419 (Caledon): Galgeberg, (–BA).
P. densifolia (Nees) Stapf	28	*Spies 6328*	WESTERN CAPE.—3219 (Wuppertal): on top of Nieuwoudt's Pass, (–AC).
P. galpinii (Stapf) McClean	7	*Linder 4844*	EASTERN CAPE.—3028 (Matatiele): Barkley East, Naude's Nek, (–CC).
P. pallida (Thunb.) H.P.Linder	7	*Spies 5446*	WESTERN CAPE.—3418 (Simonstown): 7 km from Betty's Bay to Onrus, (–BD).
	7+1B	*Spies 5367*	WESTERN CAPE.—3218 (Clanwilliam): 13 km from bridge over Olifants River, (–DB).
	14	*Spies 5917*	NORTHERN CAPE.—2917 (Springbok): 24 km from Springbok to Hondeklipbaai, (–DB).
	14	*Spies 5737*	WESTERN CAPE.—3119 (Calvinia): on Vanrhyns Pass, (–AC).
	14	*Spies 6208*	WESTERN CAPE.—3420 (Bredasdorp): 1 km north of De Hoop Nature Reserve, (–AD).
P. pappilosa (Steud.) H.P.Linder	7+1B	*Spies 5445*	WESTERN CAPE.—3418 (Simonstown): 7 km from Betty's Bay to Onrus, (–BD).
P. rigidisimma Pilg. ex H.P.Linder	7	*Spies 6243*	WESTERN CAPE.—3319 (Worcester): FM tower on Matroosberg, (–BC).
P. rupestris (Nees) Stapf	7	*Spies 6080*	WESTERN CAPE.—3219 (Wuppertal): 5 km from Algeria to Citrusdal, Nieuwoudt's Pass, (–AC).
	21	*Spies 4408*	WESTERN CAPE.—3219 (Wuppertal): 5 km from Algeria to Citrusdal, Nieuwoudt's Pass, (–AC).
	49/2	*Spies 4392*	WESTERN CAPE.—3219 (Wuppertal): Uitkyk Pass, (–AC).
	35	*Spies 6308*	WESTERN CAPE.—3219 (Wuppertal): Uitkyk Pass, (–AC).
	35	*Spies 6330*	WESTERN CAPE.—3219 (Wuppertal): on top of Nieuwoudt's Pass, (–AC).
	49	*Spies 6309, 6310*	WESTERN CAPE.—3219 (Wuppertal): Uitkyk Pass, (–AC).
P. tomentella Stapf	7	*Spies 4300, 6343*	NORTHERN CAPE.—3017 (Hondeklipbaai): 7 km from Kamieskroon to Leliefontein, (–BB).
	7+0-2B	*Spies 6344*	NORTHERN CAPE.—3017 (Hondeklipbaai): 7 km from Kamieskroon to Leliefontein, (–BB).
	14	*Spies 5301*	NORTHERN CAPE.—3119 (Calvinia): 7 km from Nieuwoudtville to Clanwilliam, (–AC).
	14	*Spies 5738*	NORTHERN CAPE.—3119 (Calvinia): on top of Vanrhyns Pass, (–AC).
P. tortuosa (Trin.) Stapf	7	*Spies 5425*	WESTERN CAPE.—3320 (Montagu): 24 km from Montagu to Touws River, Burger's Pass, (–AC).
	28	*Spies 6214*	WESTERN CAPE.—3420 (Bredasdorp): 5 km from Ouplaas to Malgas, (–AD).
P. veneta H.P.Linder	14	*Spies 6327*	WESTERN CAPE.—3219 (Wuppertal): on top of Nieuwoudt's Pass, (–AC).
P. viscidula (Nees) Stapf	14+0-2B	*Spies 6178*	WESTERN CAPE.—3322 (Oudtshoorn): Robinson's Pass, (–CC).
	35	*Spies 6020*	WESTERN CAPE.—3218 (Clanwilliam): 21 km from Clanwilliam to Nieuwoudtville, (–BB).
Pseudopentameris macrantha (Schrad.) Conert	7	*Spies 3431*	WESTERN CAPE.—3318 (Cape Town): Table Mountain, (–AB).

TABLE 1.—Gametic chromosome numbers (n) of representatives of subfamilies Arundinoideae and Danthonioideae (Poaceae) in southern Africa with their voucher specimen numbers and specific localities. Species are listed alphabetically and localities presented according to Edwards & Leistner (1971) (cont.)

Taxon	n	Voucher	Locality
Schismus barbatus (Loefl. ex L.) Thell.	6	*Spies 5284*	GAUTENG.—2528 (Pretoria): Pretoria, (–CA).
	6	*Spies 4273*	NORTHERN CAPE.—2917 (Springbok): 2 km from Springbok to Pofadder, (–DB).
	6	*Spies 4277, 4278, 4285*	NORTHERN CAPE.—2917 (Springbok): 13 km from Springbok to Hondeklipbaai, (–DB).
	6	*Spies 6596*	FREE STATE.—2925 (Jagersfontein): Petrusburg, (–AB).
	6	*Spies 4289*	NORTHERN CAPE.—3017 (Hondeklipbaai): 24 km from Soebatsfontein to Kamieskroon, (–BA).
	6	*Spies 4315*	NORTHERN CAPE.—3018 (Kamiesberg); 28 km from Leliefontein to Garies, (–AB).
	6	*Spies 4366*	WESTERN CAPE—3119 (Calvinia): 55 km from Nieuwoudtville to Clanwilliam, (–CC).
	6	*Davidse 34033, 34039*	WESTERN CAPE.—3219 (Wuppertal): 44 km from Clanwilliam to Calvinia, (–AA).
	6	*Spies 5342*	WESTERN CAPE.—3318 (Vanrhynsdorp): Vanrhynsdorp, (–DA).
	6	*Spies 4523*	WESTERN CAPE.—3320 (Montagu): 24 km from Montagu to Touws River, (–CC).
	6	*Spies 4524*	WESTERN CAPE—3320 (Montagu): 38 km from Montagu to Touws River, (–CC).
S. inermis (Stapf) C.E. Hubb	6	*Spies 4308*	NORTHERN CAPE.—3017 (Hondeklipbaai): 18 km from Kamieskroon to Leliefontein, (–BA).
	6	*Spies 4311*	NORTHERN CAPE.—3018 (Kamiesberg): 3 km from Leliefontein to Garies in Groenkloof, (–AB).
	6	*Spies 4575*	WESTERN CAPE.—3318 (Cape Town): Langebaan, (–DC).
	6	*Davidse 33758*	WESTERN CAPE.—3421 (Riversdale): 2 km south of Vermaaklikheid on road to Puntjie, (–AC).
	12	*Spies 4471*	WESTERN CAPE.—3420 (Bredasdorp): 1 km from Waenhuiskrans to Bredasdorp, (–CA).
	12	*Davidse 33804*	Locality unknown.
S. scaberrimus Nees	6	*Spies 4661*	NORTHERN CAPE.—3121 (Fraserburg): 55 km from Loxton to Fraserburg, (–DB).
	6	*Spies 4660*	NORTHERN CAPE.—3220 (Sutherland): 2 km from Sutherland to Calvinia, (–BC).
Tribolium acutiflorum (Nees) Renvoize	12	*Spies 3866*	WESTERN CAPE.—3319 (Worcester): 5 km from Gouda to Porterville, (–AC).
T. hispidum (Thunb.) Desv.	6	*Spies 4496*	WESTERN CAPE.—3420 (Bredasdorp): 1 km north of De Hoop Nature Reserve, (–CA).
	12	*Spies 3509*	EASTERN CAPE.—3424 (Humansdorp): 30 km from Humansdorp to Knysna, (–AA).
T. obtusifolium (Nees) Renvoize	18	*Davidse 34049*	Locality unknown.
T. pusillum (Nees) H.P.Linder & Davidse	6	*Davidse 34022*	WESTERN CAPE.—3218 (Clanwilliam): 7 km from Clanwilliam in Pakhuis Pass, (–BB).
T. uniolae (L.f.) Renvoize	12+0-2B	*Davidse 34166*	Locality unknown.

The two tetraploid specimens, *Spies 1485*, *2642*, with x-values of 0.829 and 1 respectively, agree with the 2:2 model of Kimber & Alonso (1981) (Table 2). The high x-value of *Spies 1485* indicates segmental alloploidy, with a tendency towards alloploidy. The other specimen, *Spies 2642*, has a value of 1, suggesting an alloploid origin. In both specimens mostly bivalents were observed. In *Spies 1485*, multivalent formation was rarely observed, but in *Spies 2642* only rod and ring bivalents were observed, evidence of alloploidy. The formation of mainly bivalents indicates an alloploid or segmental alloploid origin, thus suggesting a hybrid origin for this monotypic genus.

TABLE 2.—Genomic relationships in tetraploid *Styppeiochloa* specimens analysed according to Kimber & Alonso (1981). Values indicated represent the sums of squares calculated for the four possible tetraploid models. x-values are indicated in parentheses. Model best suited for each specimen is indicated in bold

Voucher no.	Chiasma frequency	4:0 1 mode	3:1 model	**2:2 model**	2:1:1 model
Spies 1485	0.86	3.688	3.973 (0.9485)	**0.416 (0.829)**	0.458 (0.9389)
Spies 2642	0.81	6.570	7.135 (0.92)	**0.000003 (1)**	1.835 (1)

Danthonoideae

A single specimen of *Chaetobromus involucratus* subsp. *dregeanus* was investigated with n = x = 6. This confirms a basic chromosome number of six for this genus, endemic to the semi-arid and arid western Cape region of South Africa and the extreme southwestern corner of Namibia (Du Plessis & Spies 1988; Spies & Du Plessis 1988; Spies *et al.* 1990; Verboom & Linder 1997). Studies of the genus *Chaetobromus* by Spies *et al.* (1990) suggested a polyploid complex, ranging from diploid to duodecaploid. Polyploidy occurs as segmental alloploidy or occasionally as alloploidy (Spies *et al.* 1990). Spies *et al.* (1990) reported on extensive morphological, cytogenetical and anatomical variation in *Chaetobromus*, indicating hybridization and polyploidy.

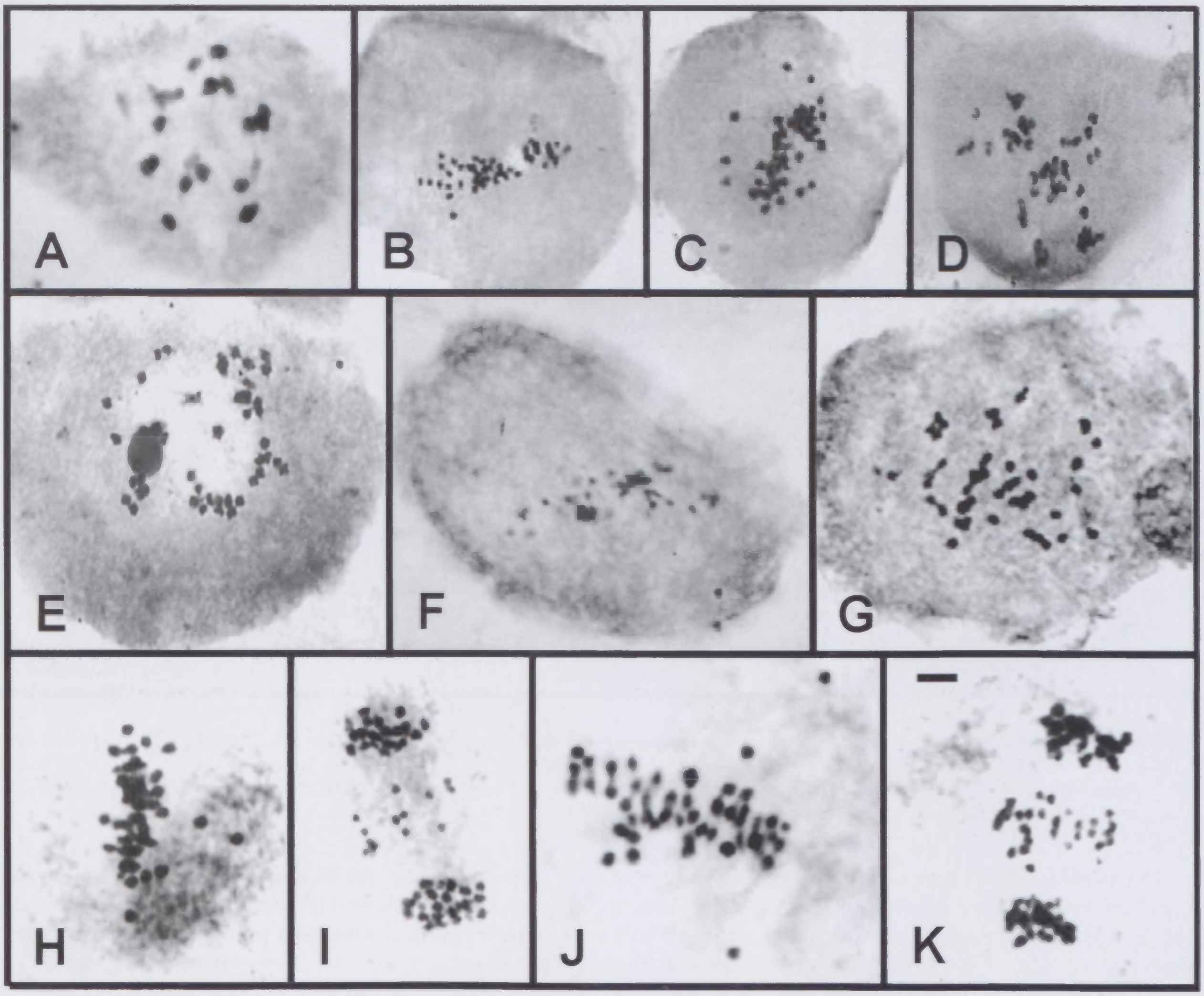

FIGURE 2.—Meiotic chromosomes in *Merxmuellera*. A, *M. cincta*, *Spies 3504*, 2n = 6x = 36, diakinesis with 18_{II}, three bivalents are not in focus on this photograph. B, C, *M. decora*: B, *Spies 4407*, 2n = 8x = 48, metaphase I; C, *Spies 4458*, 2n = 8x = 48, metaphase I. D, *M. drakensbergensis*, *Spies 4687*, 2n = 6x = 36, early anaphase I 18-18 segregation; E, *M. lupulina*, *Spies 4601*, 2n = 8x = 48, diakinesis with 24_{II}; F, *M. macowanii*, *Spies 4727*, 2n = 8x = 48, metaphase I; G, *M. rufa*, *Spies 4402*, 2n = 8x = 48, diakineses. H–K, *M. stricta*, *Spies 3140*, 2n = 9x = 54: H, J, metaphase I with various univalents; I, K, anaphase I with numerous laggards. Scale bar: A, E, F, G, J, 5 µm; B, C, D, H, I, K, 9 µm.

Diploid chromosome numbers (n = x = 6) were observed for all of the *Karroochloa* specimens studied, (Figure 1B–H) namely *Karroochloa curva*, *K. schismoides* and *K. tenella*. One *K. curva* specimen was studied cytogenetically and a low percentage of univalents (*Spies 4518*, Figure 1B) was observed. Two to five B chromosomes were observed in a single *K. purpurea* specimen (*Spies 2473*, Figure 1C, D) and this was also the only tetraploid specimen found. Further *K. purpurea* specimens exhibited normal meiosis (Figure 1E, F). In *K. chismoides* meiosis was normal (Figure 1F, H), but cell fusion was observed in some specimens (*Spies 3382*, Figure 1G) which could lead to polyploidy. The basic chromosome number of six was confirmed for this genus (Du Plessis & Spies 1988; Spies & Du Plessis 1988).

Chromosome numbers are reported for eight of the 18 southern African species of the genus *Merxmuellera*. The genus has a basic chromosome number of six (Du Plessis & Spies 1988; Spies & Du Plessis 1988). A single *M. cincta* specimen was investigated and found to be hexaploid (Figure 2A). All three *M. decora* specimens were octaploid (n = 4x = 24) (Figure 2B, C). Meiosis was abnormal with a high percentage of laggards during anaphase I (Figure 2C) and micro-nuclei during telophase I. In *M. disticha* meiosis was very abnormal with a high percentage of univalents during metaphase I, anaphase I laggards and micro-nuclei. This is the first report for *M. drakensbergensis*, both specimens being hexaploid (n = 3x = 18) (Figure 2D). Only one *M. lupulina* specimen was investigated for the first time with n = 4x = 24 (Figure 2E). All four *M. macowanii* specimens were octaploid (Figure 2F). An octaploid chromosome count for *M. rufa* is a first for this species (Figure 2G). Several multivalents are evident in various cells of this specimen. A large number of the specimens were *M. stricta*. Mostly tetraploid and hexaploid numbers, or deviations thereof, (*Spies 3140*, 2n = 6x = 51) (Figure 2H–K) were evident. Meiotic irregularities such as univalents (Figure 2H, J), laggards (Figure 2I, K) and micro-nuclei as well as cytomixis were observed. This abnormal meiotic behaviour in the genus and especially *M. stricta* would suggest these specimens to be of hybrid origin. Many *M. stricta* specimens were found to contain a high number of chromosomal laggards, and it is a variable perennial species.

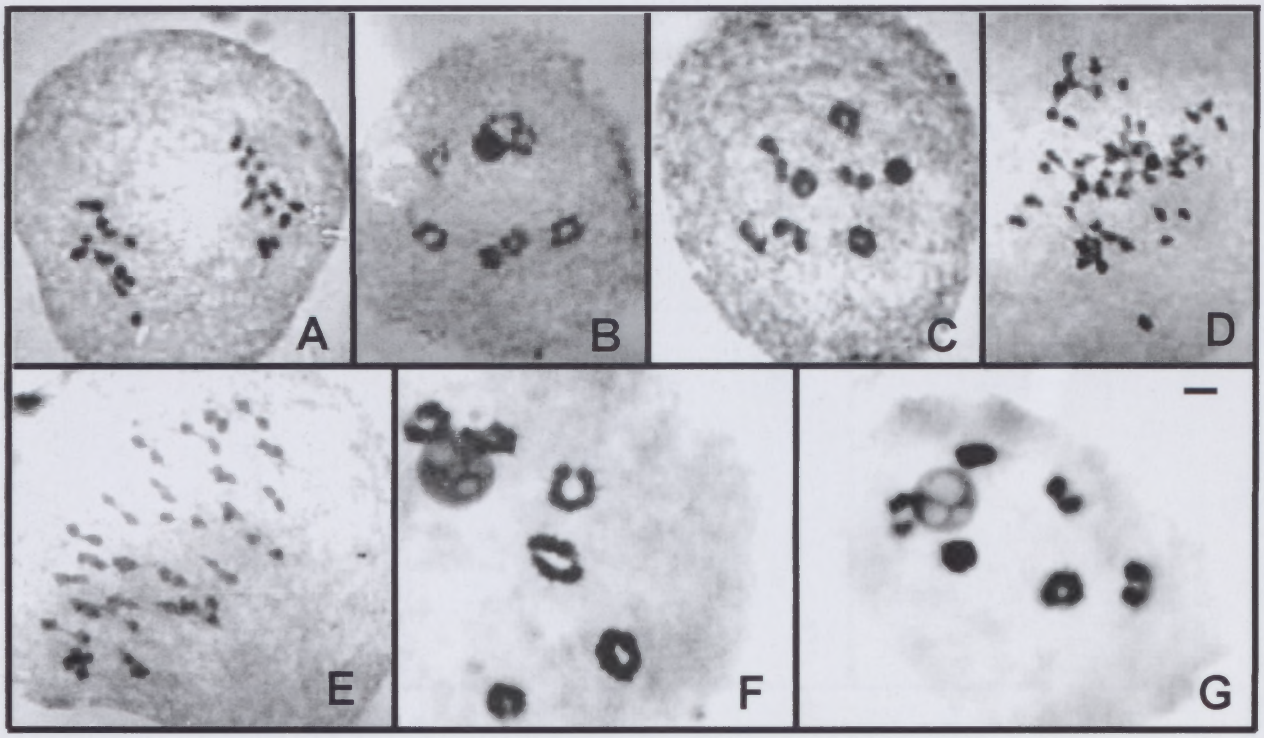

FIGURE 3.—Meiotic chromosomes in *Pentaschistis* and *Pseudopentameris*. A, *Pentaschistis pallida, Spies 6208*, 2n = 4x = 28, anaphase I with 14-14 segregation; B, *P. rigidissima, Spies 6243*, 2n = 2x = 14, diakinesis with 7_{II}; C, *P. tomentella, Spies 6344*, 2n = 2x = 14+0-2B, diakinesis with 7_{II}; D, E, *P. tortuosa, Spies 6214*, 2n = 8x = 56, early anaphase I with chromosomes starting to segregate. F, G, *Pseudopentameris macrantha, Spies 3431*, 2n = 2x = 12, diakinesis with 6_{II} in each cell. Scale bar: B, F, G, 6 µm; A, C–E, 10 µm.

Chippindall (1955) states that 'There is considerable variation in the plants referred to as *Danthonia stricta* (*M. stricta)*, and it is possible that they comprise more than one variety'. Ellis (1980) divided *M. stricta* into four 'forms': the 'typical form' (*M. stricta*), the 'Drakensberg form' (*M. stricta*), the 'Cathedral Peak form' (*M. guillarmodiae* Conert) and the 'alpine form' (*M. guillarmodiae*). Each of these forms exhibits distinct epidermal structure and leaf anatomy. In the Drakensberg region, two *Pentaschistis* species displayed remarkable anatomical similarities with *M. stricta.* These are *Pentaschistis tysonii* Stapf and an unnamed *Pentaschistis* species. Anatomically they seem to show greater affinity with the *M. stricta* group than with *Pentaschistis* (Ellis 1980). This raises the issue as to whether hybridization occurred, or is still occurring between the different *M. stricta* forms, or between the *Pentaschistis* species and *M. stricta,* and whether this could clarify the possible hybrid nature of *M. stricta.*

One diploid *Pentameris thuarii* specimen was studied (n = x = 7). This confirms a basic chromosome number of seven for the genus (Spies & Roodt 2001).

In the genus *Pentaschistis*, 14 of the 57 indigenous south African species (Gibbs Russell *et al.* 1990) were studied. This is the first report for numbers in *P. acinosa* (n = x = 7), *P. galpinii* (n = x = 7) and *P. veneta* (n = 2x = 14). Diploidy was observed in 21 of the 39 specimens (Figure 3B, C). Polyploidy is frequently encountered in *Pentaschistis*. In the study by Du Plessis & Spies (1992), 59% of the species investigated were polyploid, or had different polyploid levels. In this study tetraploidy was observed in *P. airoides*, *P. pallida* (*Spies 5737, 5917, 6208*) (Figure 3A), *P. tomentella* (*Spies 5301, 5738*), *P. veneta* and *P. viscudula*. Hexaploid (*P. rupestris*), octaploid (*P. densifolia, P. lima, P. tortuosa*) (Figure 3D, E), decaploid (*P. rupestris*, *P. viscidula*) and up to 14-ploid levels (*P. rupestris*) were also observed. Higher ploidy levels in some cells of specimens can be caused by cell fusion (Spies & Van Wyk 1995). It is not an uncommon phenomenon in this genus.

Polyploidy is frequent in *Pentaschistis*. Klopper *et al.* (1998) reported on the existence of young polyploid complexes in 17 species. Twelve species were found to be old polyploid complexes, but were not adequately studied and the age of the complexes should be verified. Furthermore, Klopper *et al.* (1998) suggest that the genus *Pentaschistis* is a young polyploid hybrid complex.

B chromosomes were mostly encountered at the diploid level (33% of the diploid specimens having 1 to 4 B chromosomes present in some cells). In *Pentaschistis*, the number of B chromosomes per cell varied within the same species and even within the same specimen. This is evident in *P. curvifolia* (*Spies 4456, 6169, 6236, 6315*) where the number of B chromosomes varied from 0–4 in the different specimens. B chromosomes were also encountered in the tetraploid *P. viscidula* specimen (0–2B) but were absent from higher polyploid levels.

Only four genera, namely *Merxmuellera, Pentameris, Pentaschistis* and *Prionanthium* Desv., share the basic chromosome number of seven. Davidse *et al.* (1986) suggested that x = 7 is a primitive number, as in the genus *Pentaschistis*, and that x = 13, which also occurs in the genus, was secondarily derived through an aneuploid reduction from x = 14. In this study no specimens with a basic chromosome number of 13 were observed.

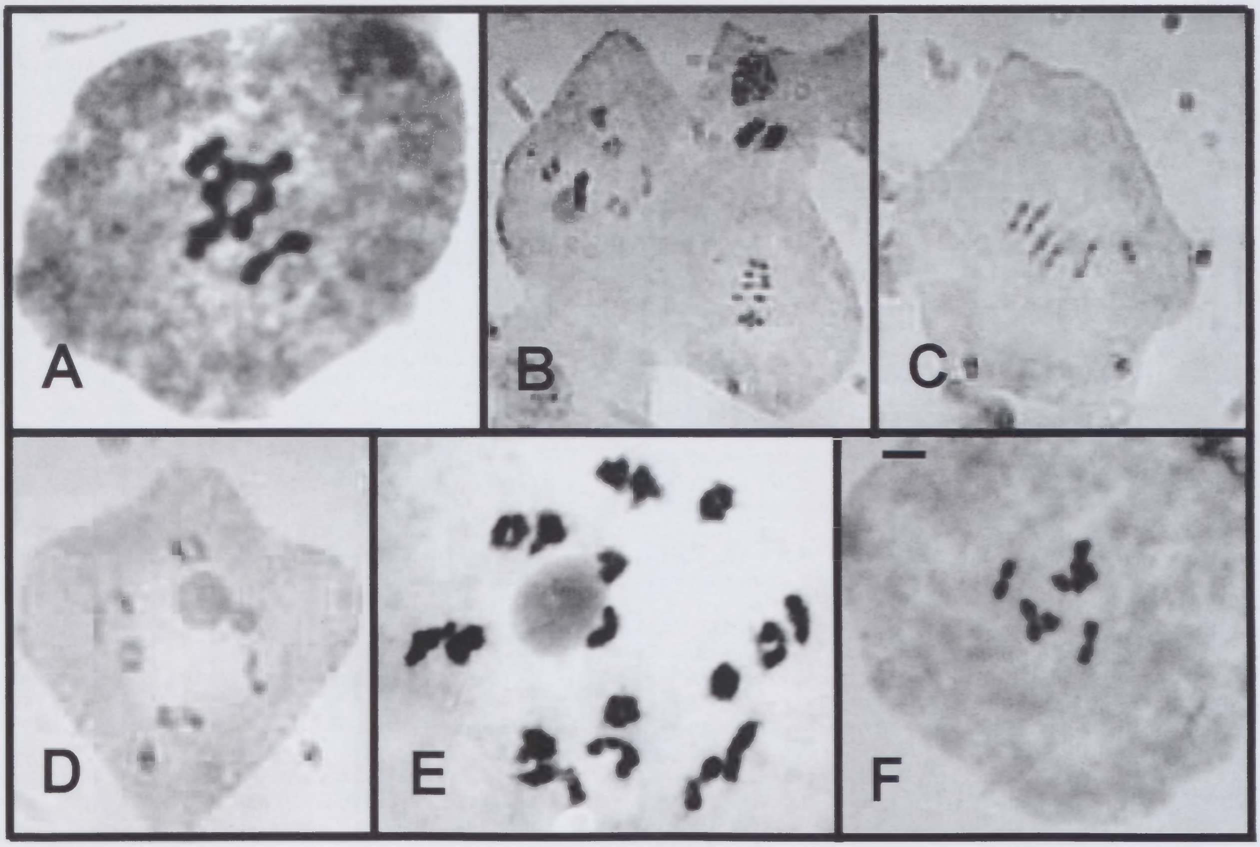

FIGURE 4.—Meiotic chromosomes in *Schismus* and *Tribolium*. A, *S. barbatus*, *Davidse 34033*, 2n = 2x = 12, early metaphase I. B–D, *S. scaberrimus*: B, C, *Spies 4660*, 2n = 2x = 12, metaphase I; D, *Spies 4661*, 2n = 2x = 12, diakinesis with 6_{II}. E, *T. obtusifolium*, *Davidse 34049*, 2n = 6x = 36, diakinesis with 18_{II}; F, *T. pusillum*, *Davidse 34022*, 2n = 2x = 12, diakinesis with 6_{II}. Scale bar: A, F, 5 µm; B–E, 10 µm.

One single specimen in the genus *Pseudopentameris* is reported here for the first time, *P. macrantha* with 2n = 2x = 12 (Figure 3F, G), and a basic chromosome number of six for the genus.

Three of the four endemic *Schismus* species were investigated cytogenetically. With the exception of a single *S. inermis* specimen (*Davidse 33804*), all the specimens were diploid, 2n = 2x = 12, (Figure 4A–D) and confirms the basic chromosome number of six for the genus (Du Plessis & Spies 1988; Spies & Du Plessis 1988).

Du Plessis & Spies (1988) reported a polyploid complex in *Schismus barbatus*, based on the meiotic behaviour of one diploid, three tetraploid and one hexaploid specimen. However, all 14 *S. barbatus* specimens of this study were diploid.

The genus *Tribolium* was thoroughly investigated cytogenetically over the last couple of years (Spies *et al.* 1992; Visser & Spies 1994a–e). It was concluded that six is the basic chromosome number for the genus. Six additional specimens representing five species were investigated. Diploidy 2n = 2x = 12 was encountered in the species *T. hispidum* and *T. pusillum* (Figure 4F). *Tribolium acutiflorum*, *T. hispidum* and *T uniolae* were found to be tetraploid and a single hexaploid specimen, *T. obtusifolium* was found (Figure 4E). We and Visser & Spies (1994b) found diploid and tetraploid specimens in *T. hispidum*. In *Tribolium* polyploidy is common. This led Visser & Spies (1994b, d, e) to conclude that the genus *Tribolium* is a polyploid complex. Visser & Spies (1994d) reported on a *T. uniolae* hybrid swarm in which polyploidy is frequent and various meiotic abnormalities occur. 0–2 B chromosomes were observed, but only in the single *T. uniolae* specimen.

The basic chromosome numbers of six and seven for the Danthonioideae and six for *Styppeiochloa* (Arundinoideae) is confirmed.

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CHROMOSOME STUDIES ON AFRICAN PLANTS. 18. THE SUBFAMILY CHLORIDOIDEAE

The subfamily Chloridoideae comprises ± 150 genera and 1 360 species and occurs mainly in arid regions (Hilu & Alice 2001). The plants probably originated in Africa (Hartley 1964), hence the great representation of the subfamily in Africa and especially southern Africa, with ± 51 genera and 235 species (Gibbs Russell *et al.* 1990). It is currently divided into five tribes by the Grass Phylogeny Working Group (GPWG 2001): Cynodonteae Dumort., Eragrostideae Stapf, Leptureae Dumort., Orcuttieae Reeder and Pappophoreae Kunth. The genus *Centropodia* Reich. and the species *Merxmuellera rangei* (Pilg.) Conert, previously included in the Arundinoideae, are now included in the Chloridoideae. They have not previously been included in any of the recognized tribes (GPWG 2001).

The aim of this study is to investigate chromosome numbers, meiotic chromosome behaviour and polyploid levels of some southern African representatives of this subfamily.

MATERIALS AND METHODS

Cytogenetic material of identical plants of a population was collected and fixed in the field. Voucher specimens, listed in Table 3, are housed in the Geo Potts Herbarium, Department of Plant Sciences, University of the Free State, Bloemfontein (BLFU), or in the National Herbarium, Pretoria (PRE).

Anthers were squashed in aceto-carmine and meiotically analysed (Spies *et al.* 1996)—at least 20 cells per meiotic stage were studied. Only gametic chromosome numbers are presented to conform to previous papers on chromosome numbers in this journal (Spies & Du Plessis 1986).

RESULTS AND DISCUSSION

Seventy-nine plants, representing 42 species and 19 genera, were studied (Table 3). They represent three of the recognized tribes, namely Cynodonteae, Eragrostideae and Pappophoreae, as well as the unplaced genus *Centropodia*.

Tribe Cynodonteae

In the genus *Chloris* Sw., a single *C. virgata* specimen was investigated and found to be diploid (n = x = 10)

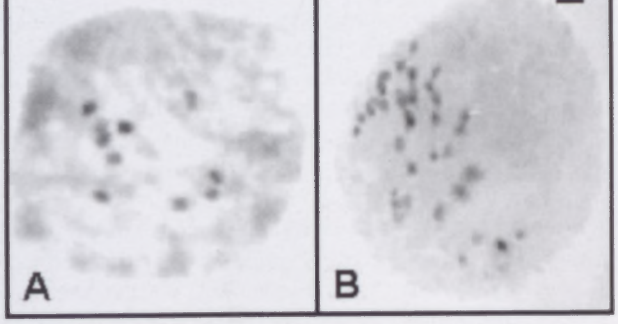

FIGURE 5.—Meiotic chromosomes. A, *Chloris virgata*, *Spies 6616*, 2n = 2x = 20, diakineses with 20_{II}; B, *Cynodon dactylon*, *Spies 2549*, 2n = 4x = 36, metaphase I. Scale bar: 5 µm.

TABLE 1.—Gametic chromosome numbers (n) of representatives of subfamily Chloridoideae (Poaceae) in southern Africa with their voucher specimen numbers and specific localities. Species listed alphabetically and localities presented according to Edwards & Leistner (1971)

Taxon	n	Voucher	Locality
Cynodonteae			
Chloris virgata Sw.	10	*Spies 6616*	FREE STATE.—2827 (Senekal): 20 km from Senekal to Rosendal, (–BD).
Cynodon dactylon (L.) Pers.	18	*Spies 2549*	SWAZILAND.—2631 (Mbabane): 18 km northeast of Mbabane, (–AC).
	18	*Spies 2966*	NORTHERN CAPE.—2816 (Oranjemund): Alexander Bay, (–DA).
Enteropogon macrostachyus (A.Rich.) Benth.	10	*Venter 9339*	NAMIBIA.—1913 (Sesfontein): Sesfontein, Kaokoland, (–BB).
Harpochloa falx (L.f.) Kuntze	18	*Spies 5113*	MPUMALANGA.—2530 (Lydenburg): 5 km from Belfast to Dullstroom, (–CA).
	18	*Spies 5065*	FREE STATE.—2729 (Volksrust): 92 km from Harrismith to Normandien Pass, (–DC).
	18	*Spies 5078*	FREE STATE.—2729 (Volksrust): 97 km from Harrismith to Normandien Pass, (–DC).
	18	*Spies 6629*	FREE STATE .—2827 (Senekal): 33 km from Senekal to Rosendal, (–BD).
	18	*Spies 3986*	EASTERN CAPE.—3027 (Lady Grey): 45 km from Barkly East to Rhodes, (–DD).
	18	*Spies 4729*	EASTERN CAPE.—3027 (Lady Grey): 52 km from Rhodes via Lundean's Neck, (–DD).
	18	*Spies 4691*	EASTERN CAPE.—3027 (Lady Grey): 47 km from Rhodes via Naude's Neck, (–CC).
	18	*Spies 4695*	EASTERN CAPE.—3027 (Lady Grey): 65 km from Rhodes to Maclear via Naude's Neck, (–CC).
	18	*Spies 6955*	EASTERN CAPE.—3027 (Lady Grey): 39 km from Barkly East to Rhodes, (–DD).
	27	*Spies 5125*	MPUMALANGA.—2530 (Lydenburg): 16 km from Dullstroom to Lydenburg via Frischgewaagd, (–AC).
	27	*Spies 5128*	MPUMALANGA.—2530 (Lydenburg): Nederhorst turn-off on Lydenburg-Roossenekal road, (–AA).
	27	*Spies 4712*	EASTERN CAPE.—3128 (Umtata): 38 km from Maclear to Elliott, (–AC).
Tragus sp.	10	*Spies 4803*	FREE STATE.—2827 (Senekal): 6 km from Clocolan to Peka bridge, (–DC).
Eragrostideae			
Bewsia biflora (Hack.) Gooss.	20	*Spies 1531*	MPUMALANGA.—2530 (Lydenburg): Steenkampsberg, (–AA).
Cladoraphis cyperoides (Thunb.) S.M.Phillips	10	*Spies 5704*	NORTHERN CAPE.—2816 (Oranjemund): 46 km from Bloeddrift to Alexander Bay, (–CB).
	10	*Spies 4894*	NORTHERN CAPE.—2917 (Springbok): 135 km from Springbok to Kleinsee, (–CA).
	10	*Spies 4889*	NORTHERN CAPE.—2917 (Springbok): 84 km from Springbok to Kleinsee, (–CA).
	10	*Spies 5356*	WESTERN CAPE.—3118 (Vanrhynsdorp): 21 km from Doorn Bay to Donkin Bay, (–CD).
C. spinosa (L.f.) S.M.Phillips	20	*Spies 4885*	NORTHERN CAPE.—2917 (Springbok): 82 km from Springbok to Kleinsee, (–CA).
Dactyloctenium aegyptium (L.) Willd.	20	*Spies 2403*	KWAZULU-NATAL.—2832 (Mtubatuba): 22 km from Cape Vidal to St Lucia, (–AD).
Eleusine coracana (L.) Gaertn. subsp. *africana* (Kenn.-O'Byrne) Hilu & De Wet	9	*Spies 2365, 2366*	KWAZULU-NATAL.—2832 (Mtubatuba): Cape Vidal, (–BA).
	18	*Spies 2783*	WESTERN CAPE.—3118 (Vanrhynsdorp): Koekenaap, irrigation scheme, (–CB).
Eragrostis barbinodis Hack.	20	*Spies 3317*	NORTHERN PROVINCE.—2428 (Nylstroom): Soutpan, (–CD).
E. capensis (Thunb.) Trin.	10	*Spies 4696*	EASTERN CAPE.—3027 (Lady Grey): 65 km from Rhodes via Naude's Neck, (–CC).
	20	*Spies 1595*	MPUMALANGA.—2530 (Lydenburg): 41 km from Lydenburg to Roossenekal, (–AB).
	20	*Spies 5069*	FREE STATE.—2729 (Volksrust): 92 km from Harrismith to Normandien Pass, (–DC).
	20	*Du Plessis 110*	KWAZULU-NATAL.—2931 (Stanger): Balito Bay to Umhlali, (–AC).
	20	*Spies 3483*	EASTERN CAPE.—3325 (Port Elizabeth): 2 km from Rocklands to Elands River, (–CD).
	20	*Spies 3498*	EASTERN CAPE.—3424 (Humansdorp): 4 km from Humansdorp to Cape St. Francis, (–BB).
	20	*Davidse 33552*	Locality unknown.
E. chloromelas Steud.	20	*Spies 6947*	EASTERN CAPE.—3027 (Lady Grey): 35 km from Aliwal North to Lady Grey, (–CA).
E. ciliaris (L.) R.Br.	10	*Du Plessis 111*	KWAZULU-NATAL.—2931 (Stanger): Balito Bay to Umhlali, (–AC).
E. curvula (Schrad.) Nees	30	*Spies 1137*	EASTERN CAPE.—3225 (Somerset East): 35 km from Somerset East to Pearston, (–CB).
E. echinochloidea Stapf	20	*Spies 2799, 2800*	NORTHERN CAPE.—3018 (Kamiesberg): 3 km from Bitterfontein to Garies, (–DB).
E. heteromera Stapf	20	*Spies 2634*	SWAZILAND.—2631 (Mbabane): 80 km from Manzini to Lomahasha, (–BA).
E. inamoena K.Schum.	20	*Spies 2392*	KWAZULU-NATAL.—2832 (Mtubatuba): 12 km from Cape Vidal to St Lucia, (–AD).
E. obtusa Munro ex Ficalho & Hiern	10	*Spies 2886*	NORTHERN CAPE.—2823 (Griekwastad): 16 km from Griekwastad to Kimberley, (–CD).
E. planiculmis Nees	30	*Spies 1116*	EASTERN CAPE.—3225 (Somerset East): Daggaboersnek Pass, Cookhouse to Cradock, (–DB).
E. racemosa (Thunb.) Steud.	20	*Spies 5066*	FREE STATE.—2729 (Volksrust): 92 km from Harrismith to Normandien Pass, (–DC).

TABLE 1.—Gametic chromosome numbers (n) of representatives of subfamily Chloridoideae (Poaceae) in southern Africa with their voucher specimen numbers and specific localities. Species listed alphabetically and localities presented according to Edwards & Leistner (1971) (cont.)

Taxon	n	Voucher	Locality
E. racemosa (Thunb.) Steud.	20	*Spies 3279*	KWAZULU-NATAL.—2829 (Harrismith): Windy Corner, Van Reenen, (–AD).
	20	*Spies 4743*	EASTERN CAPE.—3027 (Lady Grey): 15 km from Barkly East to Lady Grey, (–CD).
E. sclerantha Nees subsp. *sclerantha*	20	*Spies 4844*	FREE STATE.—2828 (Bethlehem): 19 km from Fouriesburg to Clarens, (–CA).
E. superba Peyr.	20	*Spies 3326*	NORTHERN PROVINCE.—2428 (Nylstroom): Soutpan, (–CD).
	20	*Du Plessis 136*	KWAZULU-NATAL.—2830 (Dundee): 5 km from Muden to Greytown, (–DC).
E. tef (Zucc.) Trotter	20	*Spies 2405*	KWAZULU-NATAL.—2832 (Mtubatuba): 22 km from Cape Vidal to St Lucia, (–AD).
E. tenuifolia (A.Rich.) Steud.	10	*Spies 2595*	SWAZILAND.—2631 (Mbabane): Siteki, (–BD).
E. trichophora Coss. & Dur.	20	*Spies 2774*	WESTERN CAPE.—3118 (Vanrhynsdorp): 3 km from Lutzville to Koekenaap, (–CB).
Fingerhuthia africana Lehm.	20	*Spies 2947*	NAMIBIA.—2618 (Keetmanshoop): Remshoogte, Annisfontein, (–BD).
	20	*Spies 4349*	WESTERN CAPE.—3118 (Vanrhynsdorp): 35 km from Vanrhynsdorp to Nieuwoudtville, (–DA).
Leptochloa fusca (L.) Kunth.	10	*Spies 4875*	NORTHERN CAPE.—2917 (Springbok): 7 km from Springbok to Kleinsee, (–DB).
	10	*Spies 2991A*	NORTHERN CAPE.—3017 (Hondeklipbaai): 5 km east of Kamieskroon, (–BB).
	10	*Spies 3037*	NORTHERN CAPE.—3017 (Hondeklipbaai): 12 km east of Hondeklipbaai, (–AD).
	10	*Spies 4316*	NORTHERN CAPE.—3018 (Kamiesberg): 35 km from Leliefontein to Garies, (–AB).
	10	*Spies 3794*	WESTERN CAPE.—3118 (Vanrhynsdorp): Gifberg, (–CB).
	10	*Spies 5200*	WESTERN CAPE.—3324 (Steytlerville): 34 km from Patensie to Willowmore, (–DD).
	10	*Spies 3932*	WESTERN CAPE.—3419 (Caledon): McGregor FM tower, Riviersonderend Mountain, (–BA).
	10	*Davidse 33407*	Locality unknown.
Odyssea paucinervis (Nees) Stapf	18	*Spies 3384*	NORTHERN CAPE.—3017 (Hondeklipbaai): Groen River mouth, (–DC).
Sporobolus africanus (Poir.) Robyns & Tournay	9	*Spies 4508*	WESTERN CAPE.—3420 (Bredasdorp): 1.4 km from De Hoop Nature Reserve, (–AD).
	18	*Spies 2369*	KWAZULU-NATAL.—2832 (Mtubatuba): Cape Vidal, (–BA).
S. albicans Nees	27	*Spies 3141*	WESTERN CAPE.—3220 (Sutherland): 15 km from Sutherland to Matjiesfontein, Verlatenkloof, (–BC).
S. ioclados (Trin.) Nees	9	*Spies 3171*	WESTERN CAPE.—3218 (Clanwilliam): 1 km from Sauer to Velddrif, (–DC).
S. virginicus (L.) Kunth	9	*Du Plessis 122*	KWAZULU-NATAL.—2931 (Stanger): Tongaat River, on beach near bridge, (–CA).
Stiburus alopecuroides (Hack.) Stapf	10	*Spies 1470*	MPUMALANGA.—2530 (Lydenburg): Steenkampsberg, 18 km from Dullstroom to Goede Hoop, (–AC).
S. conrathii Hack.	10	*Du Plessis 19*	MPUMALANGA.—2530 (Lydenburg): 19 km from Lydenburg to Weltevreden, (–AB).
Trichoneura sp.	10	*Spies 4833*	FREE STATE.—2827 (Senekal): 6 km from Nebo to Fouriesburg via Generaalsnek, (–DB).
Pappophoreae			
Enneapogon cenchroides (Roem. & Schult.) C.E.Hubb.	20	*Spies 3288*	NORTHERN PROVINCE.—2428 (Nylstroom): Soutpan at the crater, (–CD).
	30	*Spies 2709*	NORTHERN CAPE.—2924 (Hopetown): 31 km from Hopetown to Britstown, (–CA).
E. pretoriensis Stent	10	*Spies 3716*	NORTH-WEST.—2527 (Rustenburg): 7 km from Hartbeeshoek turn-off between Muldersdrift and Hekpoort, (–DB).
Enneapogon sp.	20	*Spies 5532*	NORTH-WEST.—2725 (Bloemhof): 31 km from Vryburg to Schweizer-Reineke, (–AB).
Schmidtia pappophoroides . Steud	18	*Du Plessis 186*	NORTHERN PROVINCE.—2329 (Pietersburg): 66 km from Pietersburg to Louis Trichardt, (–BB).
Schmidtia sp.	18+0-4B	*Spies 5536*	NORTH-WEST.—2624 (Vryburg): 36 km from Vryburg to Amalia, (–DC).
Unplaced			
Centropodia glauca (Nees) Cope	24	*Spies 5706*	NORTHERN CAPE.—2816 (Oranjemund): 46 km from Bloeddrift to Alexander Bay, (–DA).

(Figure 5A). This confirms the basic chromosome number of 10 for this genus (Darlington & Wylie 1955; Pienaar 1955; Ornduff 1967, 1968, 1969; Federov 1969; Moore 1970, 1971, 1972, 1973, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1998, 2000). Polyploid levels do occur in the genus and triploid and tetraploid numbers have been observed in South African specimens by previous authors (Moffet & Hurcombe 1949; De Wet 1954; Spies & Du Plessis 1987). The genus is known to contain many aneuploid deviations from the basic chromosome number of ten (Fish 2000), but none have been observed in South African specimens before (Hunter 1934; Moffet & Hurcombe 1949; De Wet 1954; Spies & Du Plessis 1987; Spies & Jonker 1987; Strydom & Spies 1994).

Cynodon dactylon is an introduced species in tropical and warm temperate areas throughout the world, but is indigenous to southern Africa (Gibbs Russell & Spies 1988). Two specimens were investigated, both with $2n = 4x = 36$ (Figure 5B). Tetraploidy is by far the most numerous polyploid level present in the genus (Darlington & Wylie 1955; Pienaar 1955; Ornduff 1968, 1969; Federov 1969; Moore 1970, 1972, 1973, 1974, 1977; Goldblatt

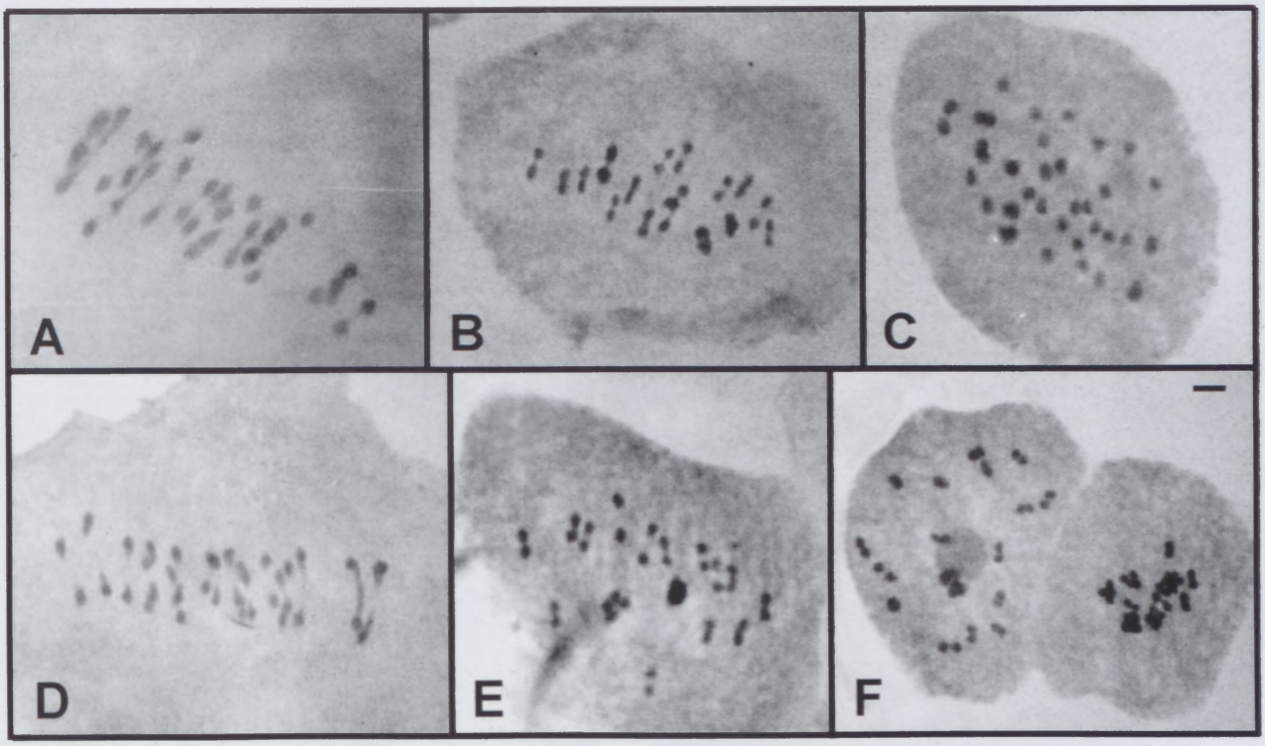

FIGURE 6.—Meiotic chromosomes in *Harpochloa falx*. A, *Spies 3986*, 2n = 4x = 36, metaphase I. B, C, *Spies 4695*, 2n = 4x = 36: B, metaphase I; C, desynapsis of bivalents during metaphase I. D, *Spies 4729*, 2n = 4x = 36, metaphase I; E, *Spies 5113*, 2n = 4x = 36, metaphase I; F, *Spies 6955*, 2n = 4x = 36, diakineses with 18_{II}. Scale bar: C, E, 8 µm; A, B, D, F, 10 µm.

1981, 1983, 1985; Goldblatt & Johnson 1990, 1994, 1996, 1998). De Silva & Snaydon (1995) concluded that the differences in the polyploid level in *C. dactylon* could be related both to different climatic regions and different ecological habitats. The populations growing in arid, dry and intermediate regions were tetraploid and those from wetter regions consisted entirely of diploid plants. De Silva & Snaydon (1995) also related these polyploid levels to soil acidity and alkalinity (tetraploid = pH > 6.5; diploid = pH < 5.0). These findings might explain the predominance of tetraploidy in South Africa with its dryer, more arid regions. A basic chromosome number of x = 9 is confirmed for this species and genus, although 10 has also been reported in a few instances (Ornduff 1968, 1969; Moore 1970, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985; Goldblatt & Johnson 1990, 1994, 1996, 1998).

Chromosome numbers for the genus *Enteropogon* Nees have only been reported once and a basic chromosome number of 10 published for the genus (Darlington & Wylie 1955). One *E. macrostachyus* specimen investigated in this study was found to be tetraploid (n = 2x = 20). This is the first report on a South African specimen in the genus, the previous one being from India.

Twelve specimens representing the species *Harpochloa falx* were studied. Nine of these were tetraploid and three were hexaploid. All specimens had multiples of nine (n = 2x = 18; n = 3x = 54) (Figure 6A–F). This represents a new basic chromosome number for this genus and could imply that *Harpochloa* also has two basic chromosome numbers (De Wet 1958; Spies & Du Plessis 1986; Spies *et al.* 1991; Strydom & Spies 1994). Furthermore, no known reports of any diploid specimens in the genus exist, which could indicate the existence of an older polyploid complex.

The genus *Tragus* Haller is widespread throughout the tropics, but mainly in Africa. It is especially common in disturbed areas (Clayton & Renvoize 1986; Fish 2000). One *Tragus* specimen was investigated and found to be diploid with n = x = 10. Only diploid, as in this study, or tetraploid chromosome numbers are known for this genus, based on a basic chromosome number of 10 (Darlington & Wylie 1955; Ornduff 1967, 1968, 1969; Federov 1969; Moore 1970, 1972, 1973, 1974, 1977; Goldblatt 1981, 1983, 1988; Goldblatt & Johnson 1990, 1994, 1998).

Tribe Eragrostideae

The genus *Bewsia* Gooss. is monotypic and a single *Bewsia biflora* specimen was investigated. This specimen was tetraploid (n = 2x = 20) (Figure 7A), which confirms a basic chromosome number of ten, based on previous reports by De Wet & Anderson (1956) of 2n = 3x = 30 and Davidse *et al.* (1986) of 2n = 45 from Zimbabwe. Davidse *et al.* (1986) reported on very irregular meiosis in the particular specimen. Results presented in this study are the third known report for this genus.

Cladoraphis Franch. comprises two species *C. cyperoides* and *C. spinosa*. De Winter (1955) included this genus in *Eragrostis* Wolf, but later authors (Phillips 1982; Clayton & Renvoize 1986; Gibbs Russell *et al.* 1990; Watson & Dallwitz 1992) retained its separate generic status. It has a very specific habitat and occurs in sandy desert (*C. spinosa*) and coastal dunes (*C. cyperoides*) (Clayton & Renvoize 1986), mainly in the western regions of Namibia and Northern and Western Cape (Fish 2000). Five specimens were investigated representing both species. All four *C. cyperoides* specimens were diploid, with *C. spinosa* being tetraploid (n = 2x = 20)

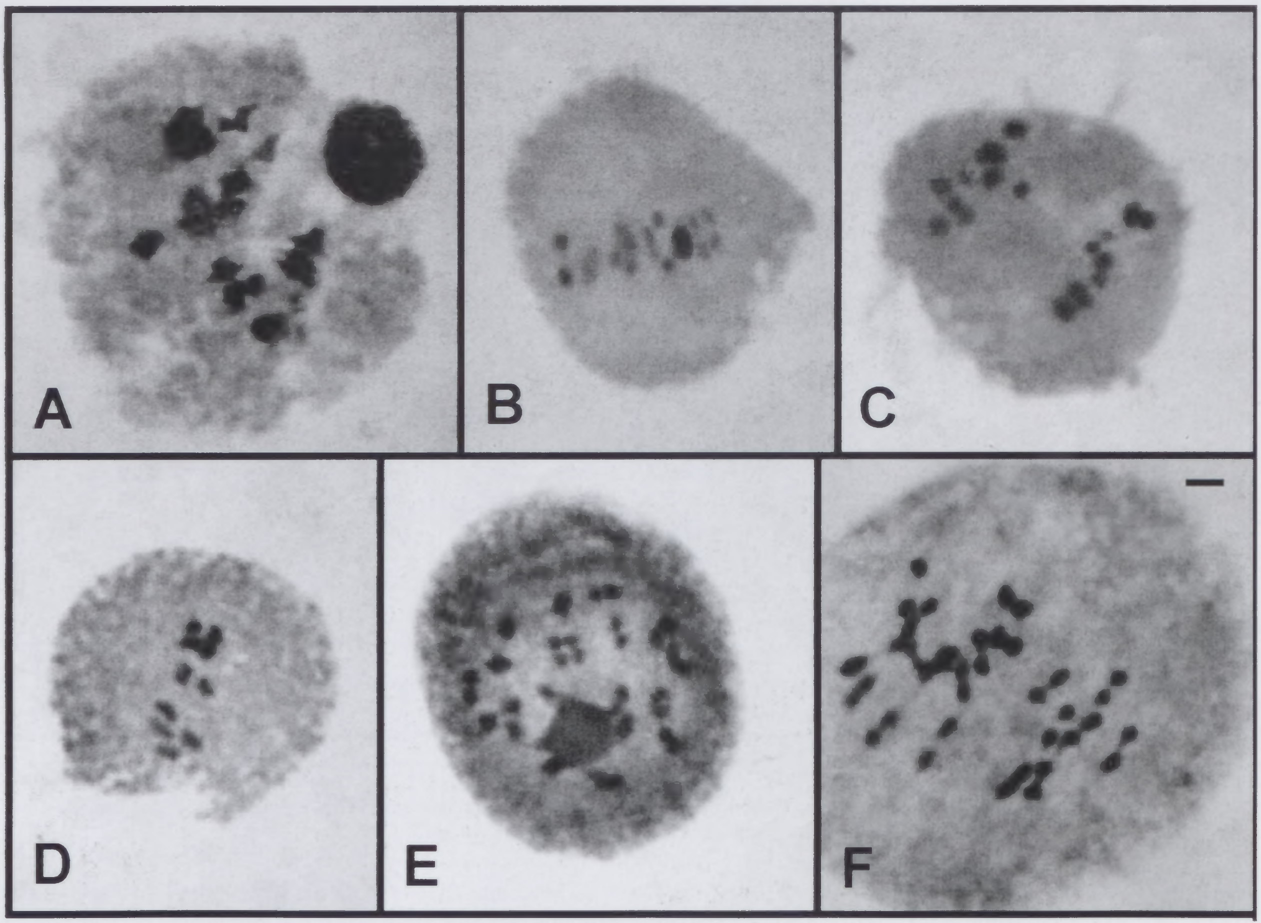

FIGURE 7.—Meiotic chromosomes. A, *Bewsia biflora*, *Spies 1531*, 2n = 4x = 40, diakineses with 20_{II}, three chromosomes are not in focus on this photograph. B, C, *Cladoraphis cyperoides*, *Spies 4894*, 2n = 2x = 20: B, metaphase I; C, anaphase I, 10-10 segregation. D, *C. cyperoides*, *Spies 5356*, 2n = 2x = 20, diakinesis; E, *C. spinosa*, *Spies 4885*, 2n = 4x = 40, diakineses with 20_{II}; F, *Dactyloctenium aegyptium*, *Spies 2403*, 2n = 4x = 40, metaphase I. Scale bar: 5 µm.

(Figure 7B–E). This is, to the best of our knowledge, the first reports for chromosome numbers in this genus.

One specimen of the widespread tropical weed (Gould & Soderstrom 1974) *Dactyloctenium aegyptium* was investigated. It was found to be tetraploid (n = 2x = 20) (Figure 7F). Three basic chromosome numbers are recorded for this genus, x = 9, 10, 12 (Darlington & Wylie 1955 (x = 10, 12); Pienaar 1955 (x = 9, 12); Ornduff 1967 (x = 10), 1968 (x = 12); Moore 1971 (x = 9), 1972 (x = 9), 1977 (x = 12); Goldblatt 1981 (x = 9, 10, 12), 1983 (x = 9, 10, 12), 1985 (x = 12), 1988 (x = 9, 10); Goldblatt & Johnson 1990 (x = 9, 10, 12), 1991 (x = 10), 1994 (x = 12), 1998 (x = 10, 12). This is one of the genera in the Chloridoideae (as is *Sporobolus*), with the most variation in basic chromosome number.

The generic status of *Diplachne* P.Beauv. has long been in doubt (McVaugh 1983; Peterson *et al.* 1997), with some authors preferring to unite this genus with the closely related genus *Leptochloa* P.Beauv. (McNeill 1979; Phillips 1982). These two genera have traditionally been kept distinct by Old World taxonomists where these genera are quite distinct, whereas the position of the genera from the Americas are very confused with intergrading taking place (Phillips 1982). For this study, the accepted name *Leptochloa* will be used.

Eight *Leptochloa fusca* specimens were investigated and all were diploid (n = x = 10) (Figure 8A–E), which confirms the basic chromosome number of ten for this genus (Darlington & Wylie 1955; Ornduff 1968; Federov 1969; Moore 1977; Goldblatt & Johnson 1990, 1991, 1994, 1998). Previous studies have mostly reported tetraploids and this is the first study with such a large number of diploids. The specimens investigated were largely from Northern and Western Cape, and due to the widespread distribution of this species, the total variation present might not be represented.

Eleusine Gaertn. is predominantly an African genus, with six of the nine species confined to tropical and subtropical Africa (Phillips 1972). *Eleusine coracana* (L.) Gaertn. is widely grown in Africa, India and China, and used as a cereal. It is derived from *E. indica* (L.) Gaertn., a diploid cosmopolitan weed (subsp. *indica*, 2n = 18), which has a tetraploid race in Africa (subsp. *africana*). The morphological characters of the two races overlap greatly, and this leads to their inclusion in a single species (Clayton & Renvoize 1986). *Eleusine coracana* subsp. *africana* (= *E. indica* subsp. *africana*) is native to Africa, where it is widespread along the eastern highlands and the highlands of the southern African plateau (Phillips 1972).

Three *E. coracana* subsp. *africana* specimens were investigated. The two specimens from Cape Vidal were

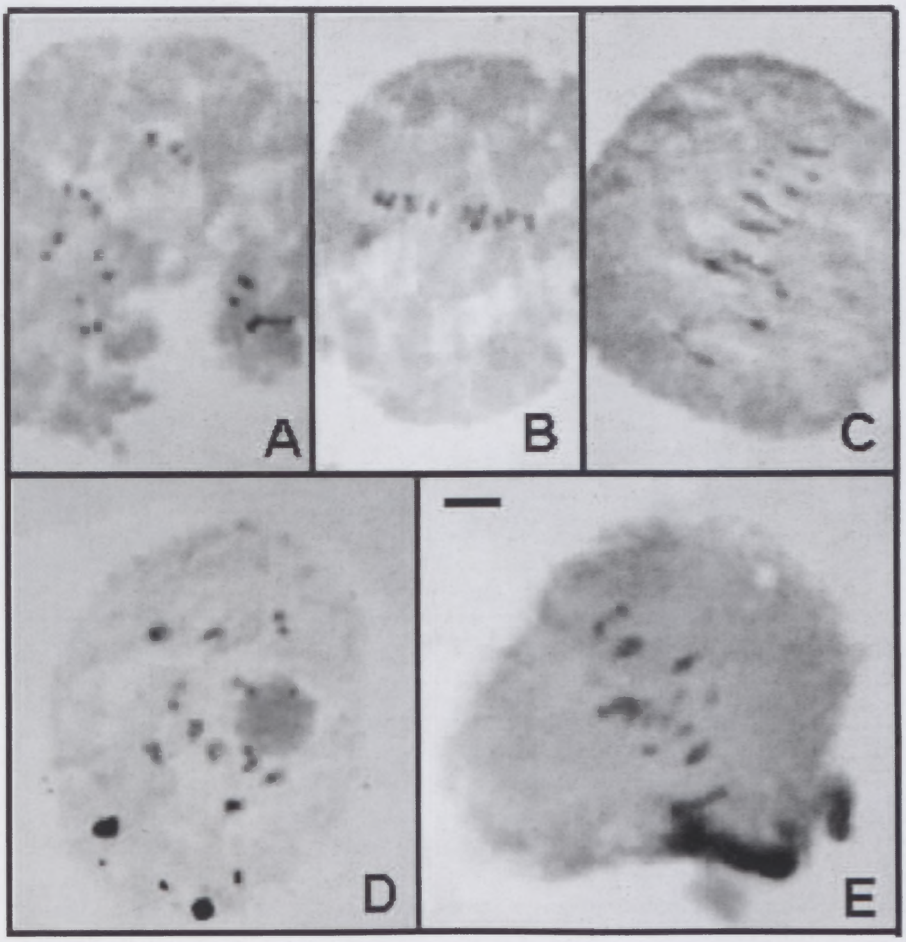

FIGURE 8.—Meiotic chromosomes in *Leptochloa fusca*. A, B, *Spies 3794*, 2n = 2x = 20: A, anaphase I with 10-10 segregation; B, metaphase I. C, *Spies 3932*, 2n = 2x = 20, metaphase I; D, *Spies 4316*, 2n = 2x = 20, diakineses with 10_{II}; E, *Spies 5200*, 2n = 2x = 20, metaphase I. Scale bar: 5 μm.

diploid (Figure 9A, B) and the specimen from Koekenaap in Western Cape was tetraploid (n = 2x = 18) (Figure 9C). This indicates that diploid and tetraploid forms of this species are present in South Africa and confirm a basic chromosome number of nine for this genus (Darlington & Wylie 1955; Pienaar 1955; Ornduff 1967, 1968, 1969; Federov 1969; Moore 1970, 1971, 1972, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994, 1998, 2000).

Eragrostis Wolf is the largest genus in the subfamily Chloridoideae. It has a worldwide occurrence in the warmer regions where it is found in most habitats, showing a preference for open sites, poor dry soil and weedy places (Clayton & Renvoize 1986). The genus exhibits the full range of morphological and anatomical variation found in the subfamily (Van den Borre & Watson 1994).

Eragrostis is the largest grass genus in southern Africa with ± 90 species. In this study 27 specimens were investigated, representing 17 species. Twenty of the specimens were tetraploid (Figure 10E, F, H). Only five specimens investigated were diploid and two were hexaploid (Figure 10D, G). Polyploidy is frequent in this genus as can be seen from the results presented. Tetraploidy, as in this study, is the most frequent polyploid level observed, followed by diploidy (Darlington & Wylie 1955; Pienaar 1955; Ornduff 1967, 1968, 1969; Moore 1970, 1971, 1972, 1973, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994, 1998, 2000).

Seven specimens were investigated for *E. capensis*. All but one was tetraploid (Figure 10A–C). *Spies 4696* was diploid and is the second report for this species (De Wet 1958) where tetraploidy (Avdulov 1931; Pienaar 1953; Davidse *et al.* 1986; Spies & Du Plessis 1986; Spies *et al.* 1991) and hexaploidy (Moffet & Hurcombe 1949; Spies & Voges 1988) have previously been observed.

De Winter (1955) regards *E. curvula* as the most variable species in the genus in southern Africa, with a great many morphological forms. This was corroborated by large-scale cytogenetic studies by Vorster & Liebenberg

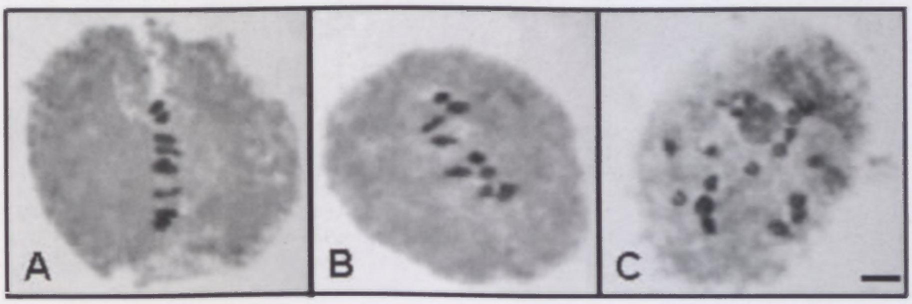

FIGURE 9.—Meiotic chromosomes in *Eleusine coracana* subsp. *africana*. A, B, *Spies 2365*, 2n = 2x = 18, metaphase I; C, *Spies 2783*, 2n = 4x = 36, diakineses with 18_{II}. Scale bar: 5 μm.

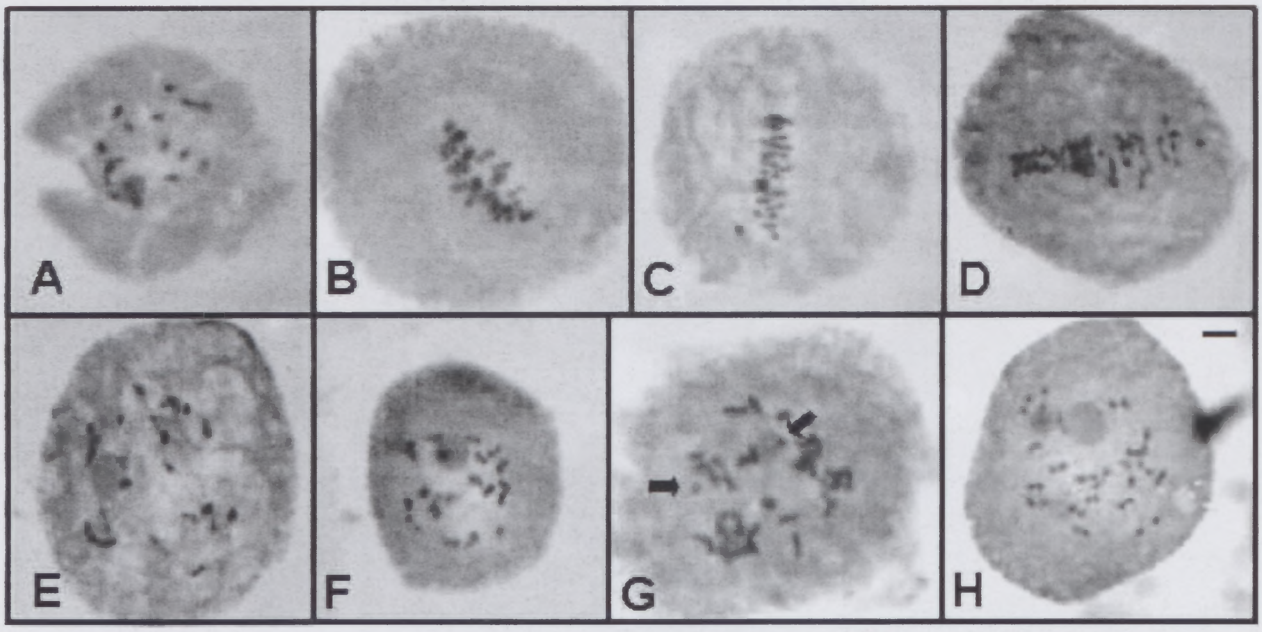

FIGURE 10.—Meiotic chromosomes. A–C, *Eragrostis capensis*: A, *Spies 3483*, 2n = 4x = 40, diakineses with 20_{II}; B, *Spies 3498*, 2n = 4x = 40, metaphase I; C, *Spies 5069*, 2n = 4x = 40, metaphase I. D, *E. curvula*, *Spies 1137*, 2n = 6x = 60; E, *E. echinocloidea*, *Spies 2799*, 2n = 4x = 40, diakineses with 20_{II}; F, *E. inamoena*, *Spies 2392*, 2n = 4x = 40, diakineses with 20_{II}; G, *E. planiculmis*, *Du Plessis 116*, 2n = 6x = 60+0-4B, diakineses with 30_{II}, two B chromosomes are indicated; H, *E. superba*, *Du Plessis 136*, 2n = 4x = 40, diakineses with 20_{II}. Scale bar: B, G, 10 μm; A, C–F, H, 12 μm.

(1977). Several species are known to intergrade with *E. curvula* through hybridization: *E. barbinodes*, *E. caesia* Stapf, *E. chloromelas*, *E. lehmaniana* Nees, *E. planiculmis* and *E. rigidor* Pilg. (Smook 1990). Proof of hybridization in this species indicates a collapse of isolating mechanisms between different species in the *Eragrostis curvula* complex, resulting in a large-scale hybrid swarm, with continuous variation of characters between parental extremes. The variation in morphological characters is an indication of the extent of hybridization (Spies 1984). Four specimens in this complex were cytogenetically investigated and tetraploid (*E. barbinodes* and *E. chloromelas*) and hexaploid (*E. curvula* and *E. planiculmis*) levels were observed (Figure 10D, G). In all but *E. barbinodes*, various univalents were observed which resulted in laggards and later formed micronuclei. According to Church (1929), the presence of unpaired or univalent chromosomes is one of the most prominent suggestions that a plant is of hybrid origin (Church 1929) and therefore, in this complex with its large-scale hybridization, these phenomena will be very prevalent.

This is the third report for the species *E. heteromera* with 2n = 4x = 40 (De Wet 1958; De Wet 1960). As far as is known only two reports for *E. tef* exist (Avdulov

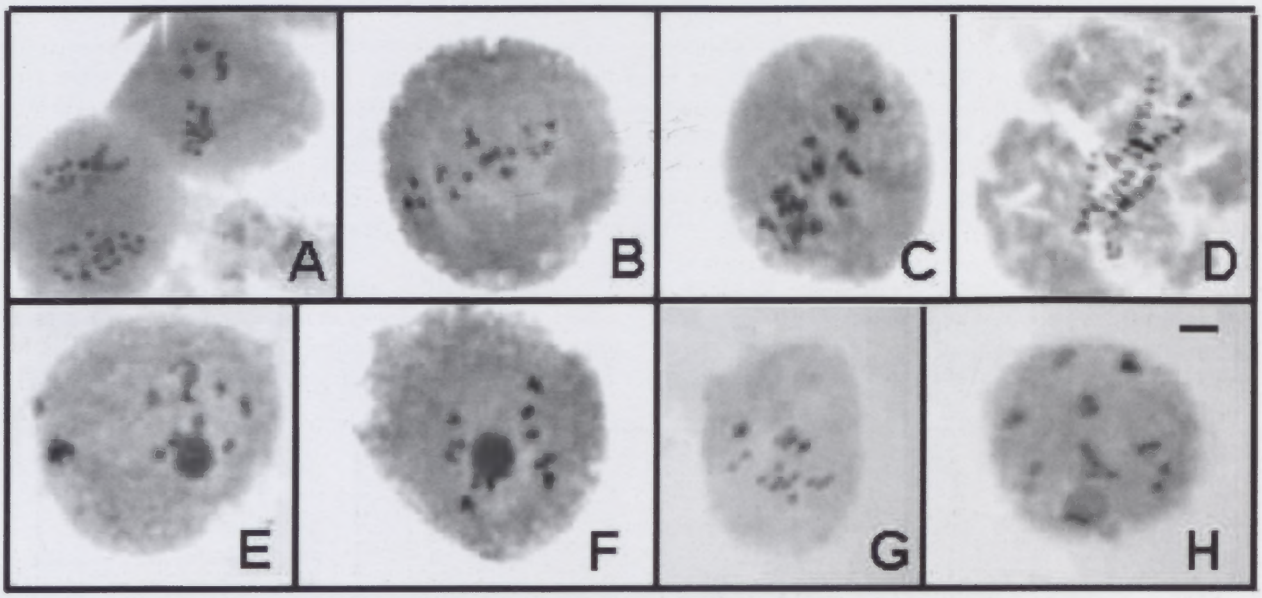

FIGURE 11.—Meiotic chromosomes. A, B, *Fingerhuthia africana*, *Spies 2947*, 2n = 4x = 40: A, late anaphase I; B, metaphase I. C, *Sporobolus albicans*, *Spies 3141*, 2n = 6x = 54, metaphase I; D, *S. africanus*, *Spies 2369*, 2n = 4x = 36, metaphase I; E, F, *S. virginicus*, *Du Plessis 122*, 2n = 2x = 18, diakineses with 10_{II}. G, H, *Stiburus conrathii*, *Du Plessis 19*, 2n = 2x = 20: G, metaphase I; H, diakineses with 10_{II}. Scale bar: 8 μm.

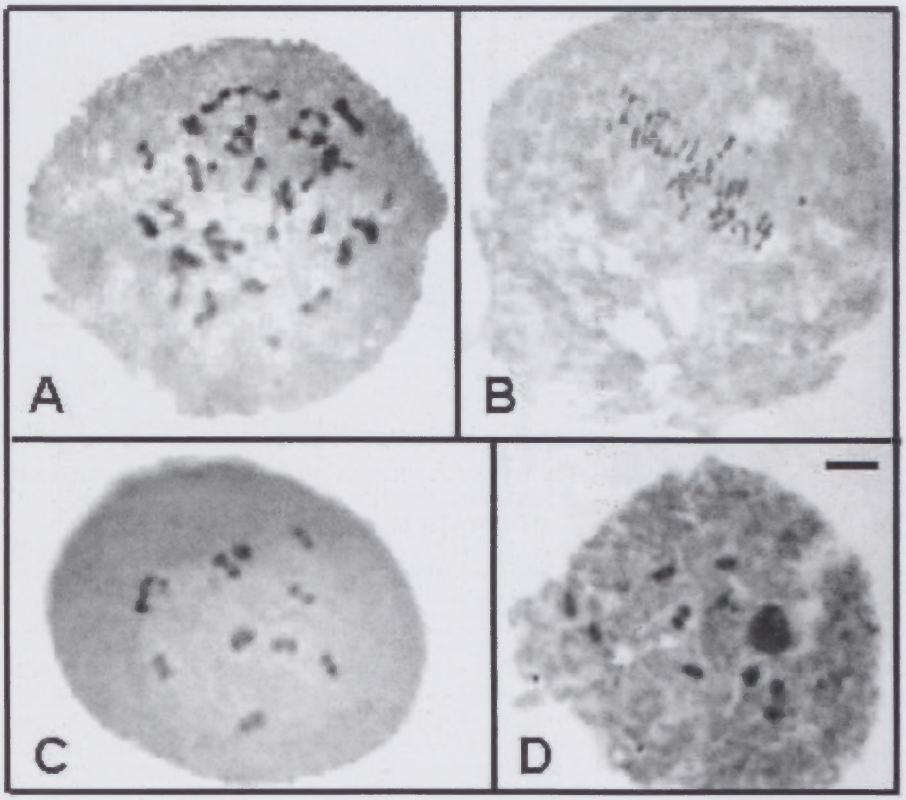

FIGURE 12.—Meiotic chromosomes in *Enneapogon*. A, B, *E. cenchroides*, *Spies 2709*, 2n = 6x = 60: A, diakinesis with 30_{II}; B, metaphase I. C, D, *E. pretoriensis*, *Spies 3716*, 2n = 2x = 20, diakinesis with 10_{II}. Scale bar: A, C, D, 5 μm; B, 8 μm.

1931; Moffet & Hurcombe 1949) and corroborates tetraploidy present in this species. Previously only tetraploid levels were observed in the species *E. tenuifolia* (Ornduff 1967; Moore 1973, 1977; Goldblatt 1983). Here we report on a diploid specimen from Siteki in Swaziland. Univalents were observed in some cells in this specimen. The tetraploid chromosome count for *E. trichophora* reported here is the second for the species (Davidse *et al.* 1986) and a hexaploid specimen was reported by Spies & Jonker (1987). One previous report of 2n = 4x = 40 for *E. racemosa* (Ornduff 1967) is confirmed in this study where three tetraploid specimens were found.

Two *Fingerhuthia africana* specimens were investigated and were tetraploid (n = 2x = 20) (Figure 11A, B). Previous reports by Spies & Du Plessis (1987) and De Wet (1958, 1960) also found tetraploidy in the genus, but diploidy has been reported (De Wet 1958, 1960) as well.

Odyssea Stapf is a xerophytic grass genus with two species, one indigenous to southern Africa (Clayton & Renvoize 1986). It has a very distinct, much-branched, spiny habit, which is an adaptation to its specialized sandy and saline habitats (Phillips 1982). This is a first report for the genus. The specimen, *O. paucinervis*, was tetraploid (n = 2x = 18) and, therefore the basic chromosome number is 9.

The genus *Sporobolus* R.Br. is cytogenetically complex and different basic chromosome numbers, x = 6, 9 and 10 may be present (Davidse *et al.* 1986). Five *Sporobolus* species were investigated. Three diploid (*S. africanus, Spies 4508, S. ioclados, S. virginicus*), one tetraploid (*S. africanus, Spies 2369*) and one hexaploid (*S. albicans*) specimen were found (Figure 11C–F). They all displayed multiples of nine and this confirms x = 9 as the basic chromosome number for the genus (Darlington & Wylie 1955; Pienaar 1955; Ornduff 1967, 1968, 1969; Federov 1969; Moore 1970, 1971, 1972, 1973, 1974, 1977; Goldblatt 1981, 1983, 1985, 1988; Goldblatt & Johnson 1990, 1991, 1994, 1996, 1998). A chromosome number for *S. albicans* has not previously been published and this is the first report for the species (Figure 11F). Large-scale studies in this genus are still necessary to investigate the different basic chromosome numbers present and their possible phylogenetic relationships.

One specimen each of the two species *Stiburus alopecuroides* and *S. conrathii* was examined. Both were diploid (n = x = 10) (Figure 11G, H) and this confirms chromosome counts based on multiples of 10 for the genus (Spies & Du Plessis 1986).

A single *Trichoneura grandiglumis* specimen was found with a chromosome count of n = x = 10. Moffet & Hurcombe (1949) and De Wet & Anderson (1956) also reported on diploid specimens.

Tribe Pappophoreae

The genus *Enneapogon* Desv. ex P.Beauv. is a very uniform genus in which most species (28 in total) closely resemble one another. Four specimens representing two species and one unidentified specimen were examined in this study (Figure 12A–D). One specimen, *Enneapogon cenchroides* was tetraploid with n = 2x = 20, but another specimen was hexaploid (Figure 12A, B). *Spies 5532*, the unidentified specimen, was also found to be tetraploid. A single *E. pretoriensis* specimen had n = x = 10 (Figure 12C, D). Two basic chromosome numbers are reported for this genus, x = 9, 10 (Darlington & Wylie (x = 9, 10); Ornduff 1968 (x = 10), 1969 (x = 10); Moore 1970 (x = 10), 1977 (x = 10);

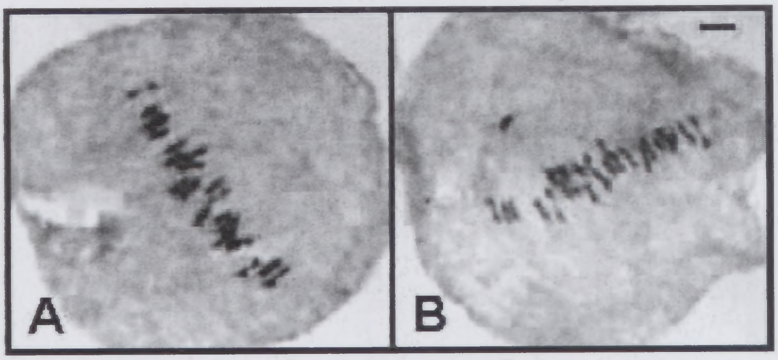

FIGURE 13.—Meiotic chromosomes in *Centropodia glauca*: A, B, *Spies 5706*, 2n = 8x = 48, metaphase I. Scale bar: 8 μm.

Goldblatt 1981 (x = 10), 1985 (x = 10); Goldblatt & Johnson 1991 (x = 10), 1998 (x = 10). The majority of the studies support a basic chromosome number of ten. Only three studies, De Wet (1954), Thomas unpublished (listed Darlington & Wylie 1955) and De Wet & Anderson (1956) ever reported x = 9. They found one diploid (De Wet & Anderson 1956) and five tetraploid (De Wet 1954; Thomas (Darlington & Wylie 1955); De Wet & Anderson 1956) specimens based on x = 9. Davidse *et al.* (1986) also reported on aneuploidy in the genus.

The genus *Schmidtia* Steud. ex J.A.Schmidt comprises only two species, both widespread in southern Africa. Two specimens were examined representing *S. pappophoroides* and an unidentified *Schmidtia* species. Both were tetraploid but *Spies 5536* had 0–4 B chromosomes present in some cells. This confirms the basic chromosome number of 9 for the genus (De Wet & Anderson 1956; De Wet 1958), although Reeder & Singh (1968) reported on a basic chromosome number of ten.

Unplaced

Centropodia Rchb. was formerly recognized as an arundinoid genus but has recently (GPWG 2001) been included in the subfamily Chloridoideae. A single specimen of this genus was investigated and found to be octaploid (n = 4x = 24) (Figure 13A, B). This confirms the basic chromosome number of the genus as six (Du Plessis & Spies 1988; Hoshino & Davidse 1988).

CONCLUSIONS

Chromosome numbers are reported for three of the five tribes of the subfamily Chloridoideae. Basic chromosome numbers of x = 9 and 10 occur in all the tribes. A basic chromosome number of six is also corroborated for the genus *Centropodia*. The high incidence of polyploidy (65% in this study) in Poaceae and especially the southern African grasses are once again confirmed by this study.

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