Cytogenetic studies in the genus *Tribolium* (Poaceae: Danthonieae). V. Section *Acutiflorae*, related genera, and conclusions

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The section *Acutiflorae* of the genus *Tribolium* Desv., comprises four species [*T. acutiflorum* (Nees) Renv., *T. glomeratum sensu* Davidse, *T. obliterum sensu* Davidse and *T. obtusifolium* (Nees) Renv.]. Tetraploid (*T. acutiflorum, T. glomeratum* and *T. obliterum*) and hexaploid (*T. glomeratum*) chromosome numbers have been observed. Meiosis is mostly normal and B-chromosomes are present. The species are similar in gross morphology and hybridization occurs. The number of species in the section *Acutiflorae* should be reduced from four to two, namely *T. acutiflorum sensu stricto* and a *T. obliterum*-hybrid swarm. *Prionanthium* Desv. differs cytogenetically from *Tribolium* and *Urochlaena* Nees.

Die seksie *Acutiflorae*, wat tot die genus *Tribolium* Desv. hoort, bestaan uit vier spesies [*T. acutiflorum* (Nees) Renv., *T. glomeratum sensu* Davidse, *T. obliterum sensu* Davidse en *T. obtusifolium* (Nees) Renv.]. Tetraploïede (*T. acutiflorum, T. glomeratum* en *T. obliterum*) en heksaploïede (*T. glomeratum*) chromosoomgetalle is waargeneem. Meiose is grotendeels normaal en B-chromosome is teenwoordig. Die spesies stem morfologies ooreen en verbastering kom voor. Daar word voorgestel dat die hoeveelheid spesies in die seksie *Acutiflorae* verminder word van vier na twee, naamlik *T. acutiflorum sensu stricto* en 'n *T. obliterum*-basterkompleks. *Prionanthium* Desv. verskil sitogeneties van *Tribolium* en *Urochlaena* Nees.

Keywords: Cytogenetics, meiosis, Poaceae, *Tribolium*.

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Introduction

This is the concluding paper in a series on the genus *Tribolium* Desv. The first paper dealt with a taxonomical overview of *Tribolium* and the subdivision of the genus (Visser & Spies 1994a). Subsequently, the embryo sac development of various species was discussed (Visser & Spies 1994b), followed by reports on the meiotic chromosome behaviour of two sections of the genus (Visser & Spies 1994c,d). This paper deals with the cytogenetic aspects of the third section, *Acutiflorae* [*T. acutiflorum* (Nees) Renv., *T. glomeratum sensu* Davidse, *T. obliterum sensu* Davidse and *T. obtusifolium* (Nees) Renv.]. Not only is the information in the other papers summarized, but the position of the genus within the tribe Danthonieae Zotov is also examined. Consequently, two related genera, *Prionanthium* Desv. and *Urochlaena* Nees, are included in this study. New information presented in this paper is, therefore, limited to morphological and cytogenetic data on *Tribolium* section *Acutiflorae* and the genera *Prionanthium* and *Urochlaena*.

The genus *Prionanthium* was first described by Desvaux (1831) and is endemic to the Cape Province of South Africa. This genus comprises three annual species, namely *P. dentatum* (L. f.) Henr., *P. ecklonii* (Nees) Stapf and *P. pholiuroides* Stapf, and is one of the rarest of the grass genera in southern Africa, with two species restricted to single localities (Davidse 1988). *Prionanthium dentatum* is restricted to an area between Nieuwoudtville and Clanwilliam, whereas *P. ecklonii* can be found in sandy soil at a locality between Clanwilliam and Citrusdal in the western Cape. *Prionanthium pholiuroides* grows in three isolated areas in the western and south-western Cape.

The genus *Urochlaena* is an endemic monotypic genus, consisting of *U. pusilla* Nees (Davidse 1986). Although *U. pusilla* is regarded as an endangered species, specimens are found in abundance along roadsides in the triangle between Vanrhynsdorp, Nieuwoudtville and Clanwilliam. All the species in the section *Acutiflorae* are distributed in the western to southwestern Cape Province.

Few cytogenetic studies on these genera could be found in the literature. The genera *Tribolium* and *Urochlaena* have a basic chromosome number of six, whereas for *Prionanthium* it is seven (Davidse 1988; Spies *et al.* 1992). In addition to chromosome numbers, cytogenetic studies of meiotic chromosome behaviour can contribute to taxonomical studies. A meiotic analysis can indicate whether a specimen (or sometimes a species) is a hybrid. This indication usually attributes to the delimitation of biological species. An increased frequency of abnormalities, especially the presence of univalents during metaphase I and chromosome laggards during anaphase I, is expected in hybrids. The frequency of these abnormalities is correlated with the degree of divergence between the parental taxa. An increase in divergence reflects a decrease in the degree of homology between the chromosomes of different genomes and consequently an increase in the frequency of meiotic chromosome abnormalities in any hybrid between these taxa. The types and frequencies of abnormalities within each genus indicate the degree of homology between genomes and, therefore, aid in determining their phylogenies.

The purpose of this study was to examine some specimens of the genera *Tribolium* (section *Acutiflorae*), *Prionanthium* and *Urochlaena* morphologically, determine their haploid chromosome numbers and study their meiotic chromosome behaviour. Additionally, phylogenetic relationships within the genus *Tribolium*, and between *Tribolium* and the related genera, will be inferred from cytogenetic, embryological and morphological evidence.

Materials and Methods

The materials used were collected in the field. Voucher herbarium specimens are housed in the Geo Potts Herbarium (BLFU),

Department of Botany and Genetics, University of the Orange Free State, Bloemfontein. These specimens and their localities are listed in Table 1. Specimens were studied morphologically, anthers were squashed in aceto-carmine and meiotically analysed (Visser & Spies 1994c).

Chiasma frequencies were considered to be the average number of chiasmata per bivalent and were calculated as the total number of chiasmata per cell divided by the haploid chromosome number of the cell. This method was used because it is congruous to other calculations done, especially with determining genome homology within an individual (Kimber & Alonso 1981).

Results

This study confirmed that the species of section *Acutiflorae* are mostly found in xeric surroundings. All four species are perennial. *Tribolium glomeratum, T. obliterum* and *T. obtusifolium* are stoloniferous. *Tribolium acutiflorum* grows tufted, whereas the other species are prostrate. The leaves are glabrous and vary in length. The inflorescences are spicate with clustered, shortly stalked, spikelets. The spikelets have three to six flowers, rarely more. The glumes are firm, acute or mucronate. The lemmas generally have stout trichomes on the lower parts. The glumes of *T. acutiflorum, T. glomeratum* and *T. obliterum* specimens are glabrous and possess only a small fringe of trichomes on the lower margins of the lemma, which differ between the various species. The trichomes of *T. acutiflorum* are club-shaped, whereas those of *T. glomeratum* and *T. obliterum* are tapered.

We used the different characteristics as variables and a correlation matrix was calculated as the first step of a factor analysis [Sneath and Sokal (1973) have provided a short synopsis of the principles, use and formulae pertaining to factor analyses]. Normalized factor loadings and coefficients resulted in the scattergrams presented in Figure 1. These scattergrams revealed that no distinct groups can be identified when factors 1 vs. 2 (Figure 1A), 1 vs. 3 (Figure 1B) or 2 vs. 3 (Figure 1C) are plotted, although part of *T. acutiflorum* is grouped together. The specimens of the various species were mixed and overlapped.

Five *T. acutiflorum* specimens were studied cytogenetically (Table 1). This species has a tetraploid chromosome number of $n = 12$ (Figure 2). Meiosis is relatively normal (Table 2). The average chiasma frequency per bivalent for this species is relatively high and only bivalents have been observed (Table 2). Low percentages of the following chromosome abnormalities have been observed: anaphase bridges, anaphase I laggards and micronuclei during telophase II (Table 2). B-chromosomes were present in three specimens (Table 1). The B-chromosomes are slightly smaller than the euchromosomes. Cell fusion was observed in two specimens (Table 1). Genome analyses of three specimens revealed that the observed chromosome association concurred best with the associations expected for the 2:2-model of Kimber and Alonso (1981). The 2:2-model indicates that two sets of genomes are present. Each set consists of two genomes and the relative similarity of the genomes in a set is considered to be 0.5. The relative similarity between the sets of genomes is expressed by an x-value that may vary between 0.5 (differences between sets are similar to differences within a set) and 1 (sets differ very much). The x-values for the *T. acutiflorum* specimens vary from 0.99 to 1 (Table 3), thus indicating very little to no homology between the two sets of genomes.

Tribolium glomeratum is a very rare species and only two specimens have been studied (Table 1). This species has two polyploid levels, namely tetraploid ($n = 12$) (Figures 3A,B) and hexaploid ($n = 18$) (Figures 3C–E). The average chiasma frequency per bivalent for the hexaploid specimen is lower than that of the tetraploid specimen (Table 2). Mostly bivalent chromosome configurations were observed (Figures 3A,C) (Table 2). Almost no meiotic abnormalities were observed (Table 2), excepting for micronuclei during telophase I (Figure 3F) and cell fusion (Table 1). B-chromosomes were absent. The genome analysis of one specimen was determined. It revealed that the observed chromosome association conformed best with the associations expected for the 2:2-model of Kimber and Alonso (1981), with an x-value of 1 (Table 3).

Tribolium obliterum was cytogenetically represented by ten specimens (Table 1). This species is tetraploid ($n = 12$) (Figure 4A). Chiasma frequencies vary to a great extent (Table 2). Mostly bivalent chromosome configurations were observed (Table 2). Various chromosome abnormalities occurred, such as univalents during metaphase I (Figure 4B), precocious segregation of one or two bivalents on the metaphase plate (Figure 4C), anaphase laggards (Figure 4D), anaphase bridges (Figure 4E), cell fusion (Figure 4F) and micronuclei (Table 2).

Table 1 List of species cytogenetically studied, voucher specimen numbers and localities according to the degree reference system (Edwards & Leistner 1971)

Tribolium*, section *Acutiflorae

***T. acutiflorum* (*n* = 12 + 0 – 1B)**

—**3318** (Cape Town): 7 km from Yzerfontein to Darling (–AC), *Spies 4568* (*n* = 12); on top of Bothmaskloof (–BC), *Spies 4427*[a] (*n* = 12).

—**3420** (Bredasdorp): 2 km from Waenhuiskrans to Bredasdorp (–CA), *Spies 4618*[a] (*n* = 12 + 0 – 1B), *4619* (*n* = 12 + 0 – 1B) & *4620* (*n* = 12 + 0 – 1B).

***T. glomeratum* (*n* = 12, 18)**

—**3319** (Worcester): Du Toit's Kloof Pass (–CA), *Spies 4614*[a] (*n* = 12).

—**3320** (Montagu): 44 km from Montagu to Touwsrivier (–CC), *Spies 5059* (*n* = 18).

***T. obliterum* (*n* = 12 + 0 – 3B)**

—**3320** (Montagu): 61 km from Montagu to Touwsriver (–CD), *Spies 4539* (*n* = 12 + 0 – 3B) & *4613* (*n* = 12).

—**3419** (Caledon): 37 km from Caledon to Bredasdorp (–AB), *Spies 5032* (*n* = 12).

—**3420** (Bredasdorp): 3 km from Waenhuiskrans to Bredasdorp (–CA), *Spies 5041* (*n* = 12); De Hoop Nature Reserve (–CA), *Spies 4512* (*n* = 12 + 0 – 1B), *4631* (*n* = 12) & *5049* (*n* = 12); 67 km from Bredasdorp to Malgas (–CB), *Spies 5044* (*n* = 12); 11 km from Bredasdorp to Cape Agulhas (–CC), *Spies 5034* (*n* = 12).

Prionanthium

***P. dentatum* (*n* = 7)**

—**3119** (Calvinia): 15 km from Nieuwoudtville to Clanwilliam (–CA), *Spies 4360*.

***P. ecklonii* (*n* = 7)**

—**3218** (Clanwilliam): 13 km from Clanwilliam to Citrusdal (–BB), *Spies 4379*.

***P. pholiuroides* (*n* = 7 + 0 – 2B)**

—**3318** (Cape Town): 2 km east of Mamre Road (–BC), *Spies 4421*.

Urochlaena

***U. pusilla* (*n* = 6 + 0 – 2B)**

—**3118** (Vanrhynsdorp): Vanrhynsdorp (–DA), *Spies 4946*; Botterkloof (–DB), *Spies 4975*.

—**3218** (Clanwilliam): 1 km from Clanwilliam to Nieuwoudtville (–BB), *Spies 4378*.

[a] Presence of cell fusion, resulting in more than one haploid chromosome number per specimen.

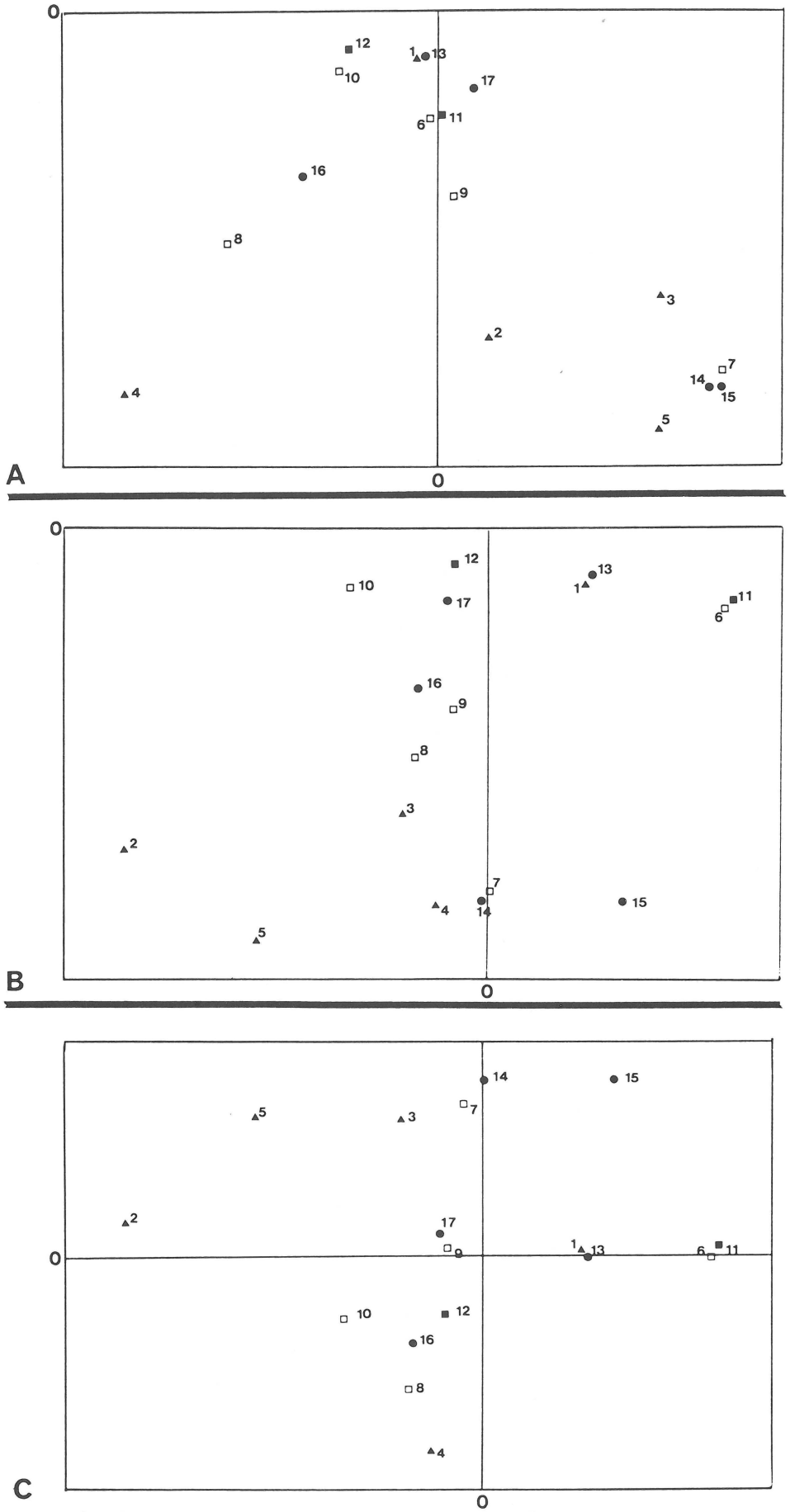

Figure 1 Factor analysis of specimens representative for section *Acutiflorae*. **A.** Factors 1 and 2. **B.** Factors 1 and 3. **C.** Factors 2 and 3. ▲, *T. acutiflorum*; □, *T. glomeratum*; ■, *T. obtusifolium*; ●, *T. obliterum*. 1, Average values for *T. acutiflorum*; 2, *Davidse 33378*; 3, *Davidse 33944*; 4, *Davidse 33984*; 5, *Spies 4620*; 6, average values for *T. glomeratum*; 7, *Davidse 34047*; 8, *Davidse 34084*; 9, *Davidse 34088A*; 10, *Spies 4614*; 11, *Duthie 1761A*; 12, *Schlechter 9483*; 13, average values for *T. obliterum*; 14, *Davidse 33797*; 15, *Davidse 33747*; 16, *Phillips 4*; 17, *Spies 4473*.

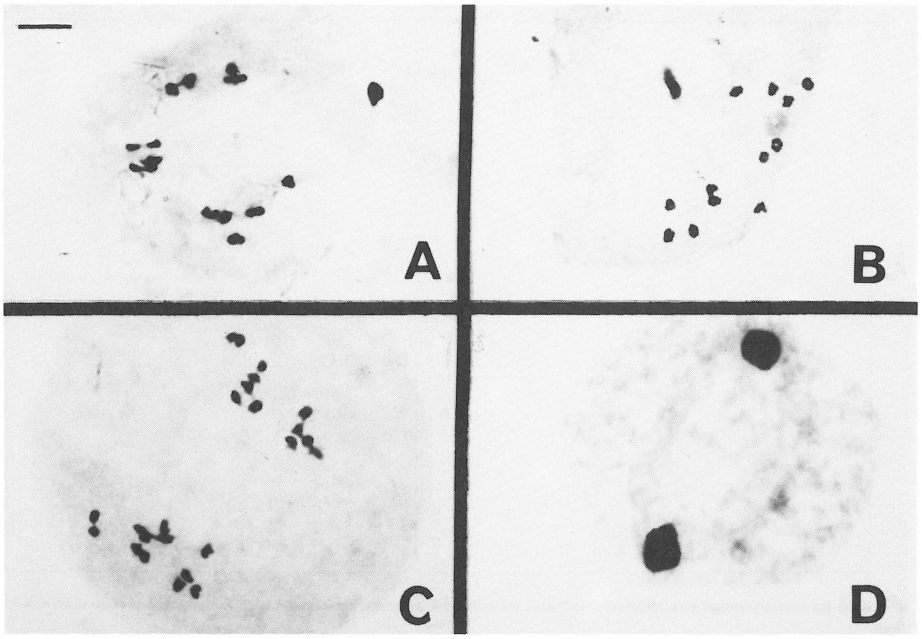

Figure 2 Meiotic chromosomes in *Tribolium acutiflorum* specimens (n = 12). **A.** *Spies 4427*, diakinesis with 12_{II}. **B.** *Spies 4618*, diakinesis with 12_{II}. **C.** *Spies 4427*, anaphase I with 12–12 segregation of chromosomes. **D.** *Spies 4618*, telophase I. Scale bars: 10 μm.

B-chromosomes were present in four specimens and varied from zero to three per cell (Figures 4B,C). Chiasma frequencies per bivalent vary from 1.05 in a specimen with zero to one B-chromosome, to 1.89 for a specimen without B-chromosomes (Table 2). These B-chromosomes may form univalents on the metaphase plate (Figures 4B,C), which may in turn form laggards during anaphase I (Figure 4D) and may result in micronuclei during telophases I and II. Genome analyses of three specimens revealed that the observed chromosome associations correspond best with the associations expected for the 2:2-model of Kimber and Alonso (1981), with x-values of 1 (Table 3).

Prionanthium dentatum was represented by one specimen, *Spies 4360*, which was diploid (n = 7) (Figures 5A,B). One small B-chromosome was present in this species (Figure 5C).

Only one representative specimen of *P. ecklonii* was studied (*Spies 4379*). This specimen was diploid with n = 7 (Figures 5D,E). The chiasma frequency per bivalent was 1.75 (Table 2). On average, 1.75 rod and 5.25 ring bivalents per cell were observed (Table 2). Meiosis is normal with the exception of micronuclei present during telophase (Table 2). B-chromosomes were absent.

Prionanthium pholiuroides was represented by *Spies 4421*.

Table 2 Meiotic analyses of some *Tribolium*, *Prionanthium* and *Urochlaena* specimens[a]

	Voucher specimen[b]								
	1	2	3	4	5	6	7	8	9
Tribolium acutiflorum									
Spies 4427	12	1.69	0	3.7	8.3	0	0	10	0
Spies 4618	12	1.67	0–1	4	8	0	10	0	0
Spies 4620	12	1.69	0–1	3.7	8.3	0	0	0	0
Average	—	1.68	—	3.8	8.2	0	3.3	3.3	0
T. glomeratum									
Spies 4614	12	1.63	—	4.4	7.6	0	0	0	0
Spies 5059	18	1.52	—	7.8	9.4	0.4	0	0	0
T. obliterum									
Spies 4511	12	1.05	0–1	5.5	6.1	0.2	10	0	50
Spies 4539	12	1.3	0–3	7	5	0	10	35	90
Spies 4631	12	1.89	0	4.1	7.9	0	10	0	10
Average	—	1.41	—	5.5	6.3	0.1	10	11.7	50
Prionanthium ecklonii									
Spies 4379	7	1.75	0	1.7	5.3	0	0	0	0
P. pholiuroides									
Spies 4421	7	1.58	0–3	2.9	4.1	0	0	50	33
Urochlaena pusilla									
Spies 4378	6	1.84	0–2	1.1	4.9	0	0	12.5	40

[a] Specimens are included only where twenty or more cells of each meiotic stage were studied.

[b] 1 Haploid chromosome number
2 Chiasma frequency per bivalent
3 Number of B-chromosomes
4 Average number of rod bivalents per cell
5 Average number of ring bivalents per cell
6 Average number of multivalents per cell
7 Percentage of cells containing anaphase bridges
8 Percentage of cells containing laggards
9 Percentage of cells containing micronuclei during telophases I & II.

Table 3 Genomic relationships in tetraploid *Tribolium acutiflorum*, *T. glomeratum* and *T. obliterum* specimens according to the models of Kimber and Alonso (1981)[a]

	4:0	3:1	2:2	2:1:1
T. acutiflorum				
Spies 4427	(7.07)	0.5 (7.331)	1 (0.12)	0.99 (0.65)
Spies 4618	(6.85)	0.5 (7.11)	0.99 (0.17)	0.98 (0.85)
Spies 4620	(7.05)	0.5 (7.31)	0.99 (0.11)	0.98 (0.64)
T. glomeratum				
Spies 4614	(6.73)	0.5 (6.99)	1 (0.2)	0.98 (1)
T. obliterum				
Spies 4511	(6.36)	0.5 (6.64)	1 (0.6)	0.97 (2.39)
Spies 4539	(5.62)	0.5 (5.84)	1 (1.75)	0.91 (4.63)
Spies 4631	(6.81)	0.5 (7.07)	1 (0.18)	0.98 (0.9)

[a] The x-value is followed by the sum of squares of the deviation between the observed and the expected values for each model, in parentheses.

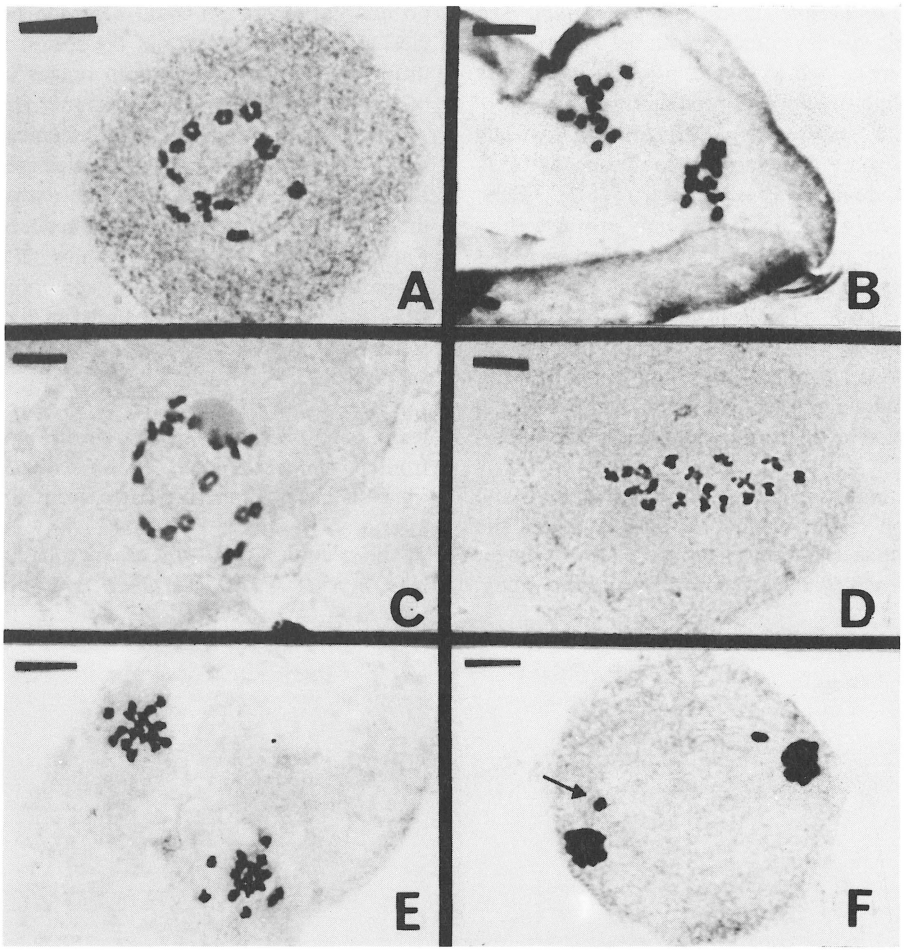

Figure 3 Meiotic chromosomes in *Tribolium glomeratum*. **A.** *Spies 4614*, n = 12, diakinesis with 12_{II}. **B.** *Spies 4614*, n = 12, anaphase I with 12–12 segregation. **C.** *Spies 5059*, n = 18, diakinesis with 18_{II}. **D.** *Spies 5059*, n = 18, metaphase II with 18_{II}. **E.** *Spies 5059*, n = 18, anaphase I with an 18–18 chromosome segregation. **F.** *Spies 4614*, n = 12, micronuclei during telophase I (indicated by arrow). Scale bars: 10 μm.

This species is diploid (n = 7) (Figures 5F–I). Only bivalents were formed during meiosis (Figures 5F,G). An average of 2.9 rod and 4.07 ring bivalents per cell resulted in a mean chiasma frequency of 1.58 per bivalent (Table 2). Meiosis is normal, unless influenced by B-chromosomes. Zero to three B-chromosomes were present (Figures 5F,H,I). The presence of B-chromosomes often led to an 8–8 or 8–9 segregation of chromosomes (Figure 5I). However, these cells still represent normal meiosis, since the euchromosomes segregate normally and the deviations in the numbers in the poles may be attributed to the presence of different numbers of B-chromosomes in each pole. Micronuclei were present in telophase I cells (Table 2).

Urochlaena pusilla was cytogenetically represented by three specimens (*Spies 4378, 4946 & 4975*). The species is diploid (n = 6), with a basic chromosome number of x = 6 (Figures 5J–L). Diakinesis chromosome configurations varied from ring bivalents only, to rod bivalents only (Figures 5J,K). The average chiasma frequency was 1.84 per bivalent (Table 2). Chromosome abnormalities included univalents during metaphase I and laggards during anaphase I. The laggards resulted in the presence of micronuclei during telophase (Table 2). Zero to two B-chromosomes were present.

Discussion

According to Gibbs Russell *et al.* (1990), the geographical distributions of the four species in the section *Acutiflorae* overlap. This is also evident from the plants collected by Spies *et al.* (1992), as the specimens of all the different species were collected in the southwestern Cape in the surroundings of Bredasdorp and Worcester.

Fifty-nine representative specimens of the section *Acutiflorae* (12 *T. acutiflorum*, 7 *T. glomeratum*, 38 *T. obliterum* and 2 *T. obtusifolium*) were included in this morphological study. The species are similar in gross morphology, excepting for the shape of the trichomes at the base of the lemma and the presence of stolons in *T. acutiflorum*. This fact is substantiated by the results of the factor analysis, which indicate that the species in the section *Acutiflorae* form a hybrid swarm. Only *T. acutiflorum* can be identified as a separate taxon (Figure 4B), although the analysis indicates hybridization with *T. obliterum*. All of the four species have ligules of trichomes at the base of their lemmas (Visser & Spies 1994a). *Tribolium acutiflorum* can be separated from the other species through its trichomes which are club-shaped (Visser & Spies 1994a) in contrast to the blunt-shaped trichomes in the other species.

Tribolium obtusifolium is a very rare species. Only two *T. obtusifolium* specimens were morphologically studied (*Duthie 1716 & Schlechter 9483*) and they differ greatly from each other concerning setaceous leaves, leaf-tip shape, the presence of stolons and rhizomes. Both specimens are short and petite. The distribution area of this species has been thoroughly searched for living specimens, but to no avail. This species may thus be extinct or can be regarded as a morpho-

logical variant of *T. obliterum* and/or *T. glomeratum*. The distribution areas of this species coincide with the extension of coastal development areas, which could have disturbed the species' habitat, excluding any possibility of survival.

The specimens of *T. glomeratum* differ morphologically from each other, with some being similar to specimens of *T. obliterum*. Seven were studied (*Davidse 34047, 34049, 34084, 34088a, 34126, Spies 4614 & 5059*). The only characteristics that are uniform, are the orientation of the inflorescence and perennial growth. Among those that vary are the presence of stolons or rhizomes, the shape of the leaf-tip, and growth form.

Thirty-eight *T. obliterum* specimens were studied. They differ greatly from one another concerning plant height, presence of stolons, leaf length, leaf-tip shape, and the length of the panicle, the latter being partly enclosed by the uppermost leaf.

Davidse (pers. commun.) separated *T. glomeratum* and *T. obliterum* mainly on anther length. He postulated that the anthers of *T. glomeratum* (>0.6 mm) are consistently longer than those of *T. obliterum* (0.2 – 0.5 mm). During this study, no definite separation could be made between these two species, as the characteristics of the specimens with longer anthers differ among themselves, with ranges corresponding to those of *T. obliterum* specimens with shorter anthers.

The existing range of morphological variation in *T. obliterum* and *T. glomeratum* indicates the existence of a single hybrid swarm. This hybrid swarm reproduces sexually, for all the species in this section form reduced embryo sacs of the *Polygonum*-type (Visser & Spies 1994b). Therefore, we suggest that anther length is an apomorphic character, resulting from the new gene combinations in the sexually reproducing swarm and that the separation of species on this basis is not supported.

Since *T. acutiflorum* has club-shaped trichomes on the lemma and no stolons, it can be distinguished morphologically from *T. glomeratum* and *T. obliterum* and should be regarded as a distinct species, separated from the *T. obliterum* hybrid swarm.

The section *Acutiflorae* has two haploid chromosome numbers, n = 12 (*T. acutiflorum*, *T. glomeratum* and *T. obliterum*)

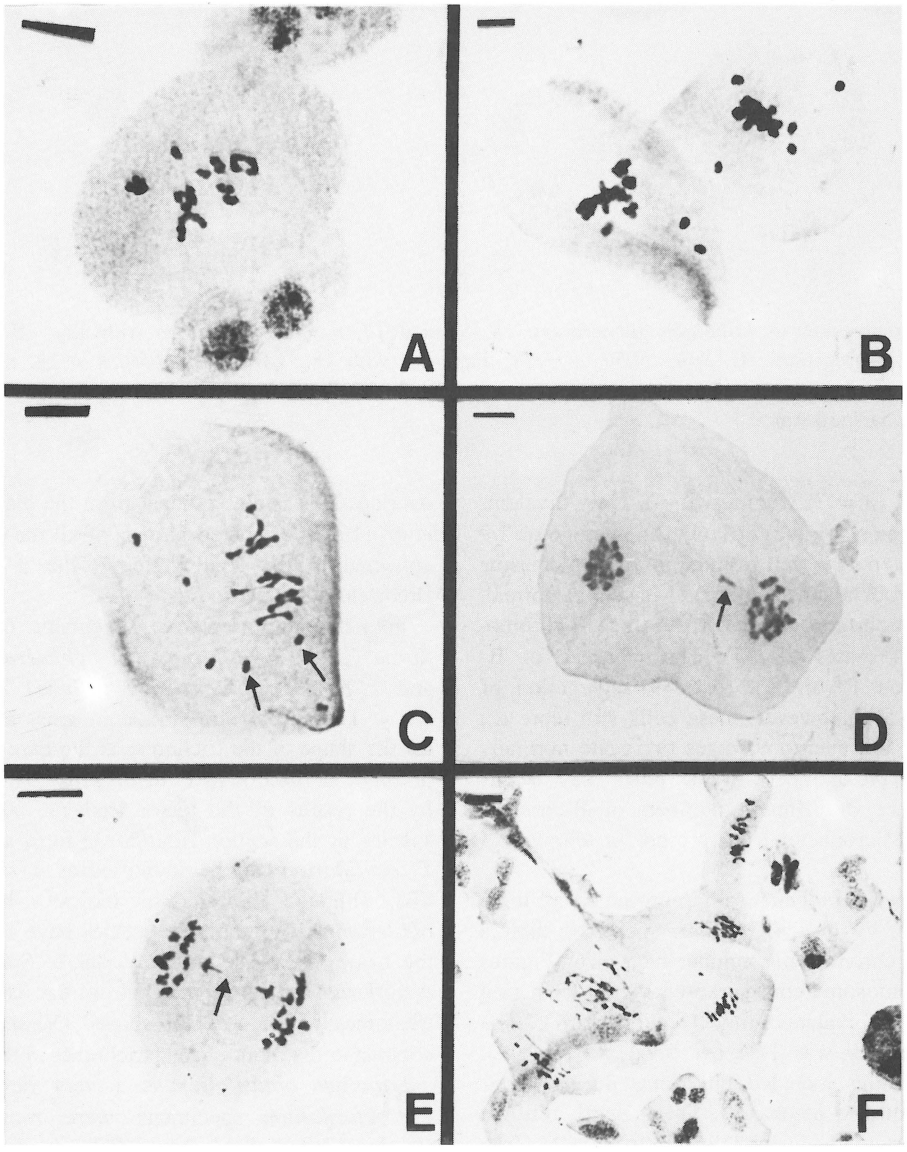

Figure 4 Meiotic chromosomes in *Tribolium obliterum* (n = 12). **A.** *Spies 4511*, diakinesis with $8_{II}2_{IV}$. **B.** *Spies 4511*, two metaphase I cells with univalents. **C.** *Spies 4539*, metaphase I with seven univalents due to precocious segregation of bivalents and the presence of B-chromosomes (the univalents and B-chromosomes cannot be categorized at this stage and are therefore combined as seven univalents; however, from the study of other cells of this specimen, it is known to have up to five B-chromosomes). **D.** *Spies 4539*, laggard during anaphase I. **E.** *Spies 4511*, anaphase bridge (indicated by arrow). **F.** *Spies 4511*, cell fusion. Scale bars: 10 μm.

and n = 18 (*T. glomeratum*). Somatic chromosome numbers of 24 and 36 indicate that the basic chromosome number of the species in this section, and thus the genus, is x = 6. This conforms with the previous findings (Spies *et al.* 1992; Visser & Spies 1994c).

This study confirms a previous report (Spies & Du Plessis 1988) that *Urochlaena pusilla* is a diploid species with a basic chromosome number of six. Meiosis is regular. All of the three species of the genus *Prionanthium* are diploid, thus confirming a basic chromosome number of seven as described by Davidse (1988). Meiosis is regular in all the species.

Polyploidy is common in the section *Acutiflorae* of the genus *Tribolium*. Spies *et al.* (1992) recorded tetraploid and hexaploid specimens for *T. obliterum*, whereas only tetraploid specimens were observed in this study. They also recorded only hexaploid chromosome numbers for *T. glomeratum*, whereas, during this study, both tetraploid and hexaploid chromosome numbers were observed.

Meiosis is mainly normal in the specimens of *T. acutiflorum* and *T. glomeratum*, whereas various abnormalities have been observed in *T. obliterum*. These abnormalities include univalents during metaphase, precocious segregation of one or two bivalents on the metaphase plate, anaphase laggards, anaphase bridges and cell fusion (Figure 3F). Micronuclei were present in 90% of the telophase cells of *Spies 4539*. Spies *et al.* (1992) reported no meiotic chromosome abnormalities for this species.

The average chiasma frequencies per bivalent for the tetraploids vary from 1.41 (*T. obliterum*) to 1.68 (*T. acutiflorum*). The frequency for *T. glomeratum* (n = 18) is 1.52 (Table 2). The relatively low frequency of quadrivalents and high frequency of bivalents indicate a low degree of homology between the genomes of these polyploid species. This corresponds with the findings of Spies *et al.* (1992).

With the aid of the models postulated by Kimber and Alonso (1981) for different types of genome homology in polyploids, the genomes of three tetraploid *T. acutiflorum*, one *T. glomeratum* and three *T. obliterum* specimens have been analysed (Table 3). The 2:2-model fits all specimens of these species best, thus indicating either segmental alloploid or alloploid origins. The x-values, varying from 0.99 to 1 (Table 3), indicate an alloploid or a segmental alloploid tending towards alloploid origin. A genomic constitution of AABB is, therefore, suggested for the species in the section *Acutiflorae*.

The occurrence of polyploidy in the form of alloploidy in all species of the section *Acutiflorae* indicates that all these species are the results of hybridization. The combination of morphological overlapping between species and the evidence that the species originated as alloploids, indicate the presence of a rather large hybrid swarm in this section. The progenitors of these hybrid species may be some representatives of the

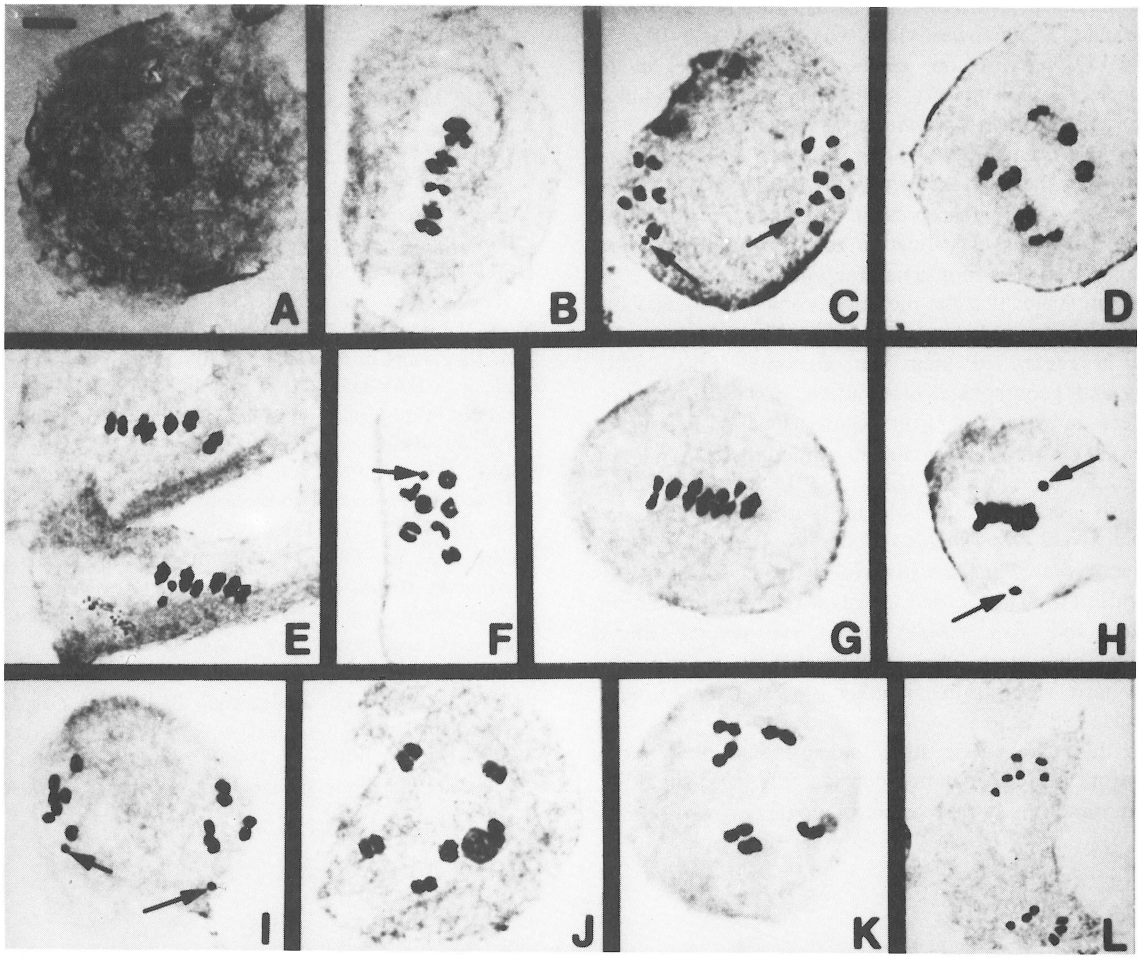

Figure 5 Meiotic chromosomes in the genera *Prionanthium* and *Urochlaena*. A–C. *P. dentatum, Spies 4360, n* = 7; A, diakinesis with 7_{II}; B, metaphase I with 7_{II}; C, anaphase I with two B-chromosomes (one in each pole — indicated by arrows). D,E. *P. ecklonii, Spies 4379, n* = 7; D, diakinesis with 7_{II}; E, two metaphase I cells, each with 7_{II}. F–I. *P. pholiuroides, Spies 4421, n* = 7; F, diakinesis with 7_{II} and a B-chromosome (indicated by arrow); G, metaphase I with 7_{II}; H, metaphase I with 7_{II} on metaphase plate, and a B-chromosome on each side (indicated by arrows); I, anaphase I with seven euchromosomes and a B-chromosome (indicated by arrows) at each pole. J–L. *U. pusilla, Spies 4378, n* = 6; J, diakinesis with 6_{II}; K, diakinesis with 6_{II}; L, anaphase I with a 6–6 chromosome segregation. Scale bars: 10 μm.

sections *Tribolium* or *Uniolae* (see Vissers & Spies 1994a). This study, however, could not determine their identities and we propose a study based on molecular markers to determine whether these progenitors are still extant.

B-chromosomes are present in *T. acutiflorum* (0 – 1), *T. obliterum* (0 – 3), *Prionanthium dentatum* and *P. pholiuroides*. Those present in *Prionanthium* are much smaller than those in *Tribolium*. The behaviour of the B-chromosomes is constant through meiosis and has been described previously (Visser & Spies 1994c). These chromosomes are known to influence and regulate the amount of genetic variability within populations occasionally, by affecting chiasma frequency during homoeologous chromosome pairing (Jones & Rees 1982). It is possible that B-chromosomes reduce the formation of chiasmata in *T. obliterum*, as chiasma frequencies vary from 1.05 per bivalent in a specimen with B-chromosomes (0 – 1) (*Spies 4511*), to 1.89 for a specimen without B-chromosomes (*Spies 4631*). An euchromosome abnormality was associated with the presence of B-chromosomes, namely precocious segregation of one or two bivalents during metaphase I [discussed elsewhere (Visser & Spies 1994c)]. This phenomenon was only observed in cells containing B-chromosomes.

As a result of our observations we conclude that *T. acutiflorum* is an allotetraploid species which is morphologically different from the *T. obliterum* hybrid complex (comprising the rest of the species in the section), although it may hybridize with the hybrid swarm. The number of species in the section *Acutiflorae* should therefore be reduced to two only, namely *T. acutiflorum* and a *T. obliterum* hybrid swarm.

The genus *Tribolium* is one of the primitive genera in the Arundinoideae. Clayton (1981) divided the tribe Arundineae into four groups, with *Prionanthium, Tribolium* (= *Lasiochloa* and *Plagiochloa*) and *Urochlaena* as the South African representatives of the primitive group 3. Although Clayton did not consider the groups to represent natural taxonomic units, we decided to use his classification as basis for determining whether the three species form a natural unit or not.

This study indicates that the meiotic chromosomal behaviour of *Tribolium* and *Urochlaena* corresponds. These species also correspond in regard to their leaf anatomy (Ellis 1988), morphology and geographical distribution. However, *Prionanthium* differs substantially from these species, having a different basic chromosome number. Although leaf anatomy corresponded in these genera (Ellis 1989), the shared characters are also present in morphologically different genera, i.e. *Chaetobromus* Nees, *Karroochloa* Conert & Tuerpe, *Schismus* P. Beauv. and some *Pentaschistis* (Nees) Spach species (Ellis 1989). Davidse (1988) proposed a distant relationship between *Prionanthium* and *Pentaschistis* based on several shared morphological characters. We support that view and also support the basic chromosome number of seven for *Prionanthium* (Davidse 1988).

Although this cytogenetic study supports the morphology and earlier work on leaf anatomy, considerably more should be done to determine finally the correct phylogenetic relationships in the Danthonieae. The additional studies should include cytogenetic studies of artificial hybrids and also molecular studies.

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