CHROMOSOME ASSOCIATION IN TRIPLOID *CYNODON* HYBRIDS

By

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INTRODUCTION

The genus Cynodon Rich. belongs to the tribe Chlorideae Kunth, subfamily Eragrostoideae Pilger of the family Gramineae. The genus is widely distributed in the Old World with C. dactylon becoming, through the help of man, almost cosmopolitan.

It was suggested by Hartley and Slater (1960) that the subfamily is perhaps an old one because of the close relationship between climatic factors and distribution which characterizes its members. They feel that the subfamily probably had its origin in Africa at least by the Oligocene. Forbes and Burton (1963) suggested that Africa is probably the center of origin for Cynodon because of the large diversity of types found there.

The genus itself has undergone a rather confused taxonomy with some 23 species being described by various workers. It is clear that not all of these are good species, and Harlan et al. (1966) tentatively recognized 11 species and 5 varietal subdivisions.

A biosystematic study should reveal more about the genetic nature of the genus and the phylogenetic relationships between the various species. Interspecific hybridization followed by analysis of the F_1 hybrid cytology has proven a valuable tool in clarifying species relationships in many genera (Clausen, Keck and Hiesey, 1945). It is hoped that such cytological analysis of interspecific hybrids in Cynodon will

also reveal something of the evolutionary mechanisms at work in this genus.

REVIEW OF LITERATURE

In ancient times Cynodon was celebrated in the sacred Vedas as the shield of India around which a flourishing civilization, religion and culture were developed (Moore, 1960). It is still considered the sacred Durva grass of the Hindus. The widely distributed C. dactylon is known in America as Bermuda grass, in South Africa as Kweek grass, and in Australia as Couch grass.

The genus Cynodon is not native to America, and according to official records of the United States Department of Agriculture (Wilson, 1961), was first brought to the United States in 1888. However, further study has shown that Cynodon was perhaps brought to Georgia as early as 1751 by Governor Ellis (Kneebone, 1966) or even earlier in ballast on boats. It has proven to be a rapid colonizer and weed and is now widely distributed in the southern states extending as far north as Michigan (Abrams, 1940). It is extensively cultivated in Argentina and is one of the most important pasture grasses in the southern United States (Spillman, 1905 and Kneebone, 1966).

Cytology

The use of cytology and cytogenetics to establish evolutionary mechanisms and phylogenetic relationships in plants has proven to be of invaluable service. Morphological characters alone can be used to classify and differentiate plants, but morphology and cytology in

conjunction can do much more to establish a natural order into systematic botany than can either of these disciplines by itself.

Chromosome morphology and basic number are often good systematic characters. Avdulov (1931) first attempted to correlate karyological data with certain morphological and anatomical characters in an attempt to subdivide the Gramineae. On this basis, Avdulov divided the family into 2 subfamilies, the Sacchariferae and Poateae. The latter was further subdivided into the Phragmitiformes and Festuciformes. The members of the Sacchariferae are characterized by having small chromosomes in multiples of 9 or 10. The Phragmitiformes are characterized by having small chromosomes in multiples of 12, while the members of the Festuciformes have large chromosomes in multiples of 7 or less.

Tateoka (1953, 1954) presented data on chromosome number and morphology in the Gramineae and divided the family into 3 major groups; the Festucoid group with large chromosomes in multiples of 7, the Panicoid-chloridoid group with small chromosomes in multiples of 9 or 10 and the Arundinoid-danthonioid group with medium small chromosomes mostly in multiples of 12. This system is strikingly similar to that of Avdulov.

The classical studies of Navashin (1912), Newton (1921), Taylor (1924), Hunter (1934) and Krishnaswamy (1940) showed that a fairly constant chromosome number and morphology exists in each genus. Hunter feels that the first place in taxonomic significance is taken by the basic number, and size of chromosomes in idiogram types, characterized by changes in length and structure of the arms of the chromosomes, being of next importance. Levitsky (1931) and Levitsky and Araratian (1931) showed that different species of a genus are usually character-

ized by different and constant karyotypes, and a constancy of karyotype is generally maintained in each genus, with different genera having completely different karyotypes.

Karyotype analysis does have certain limitations as pointed out by Babcock (1942). Morphologically similar chromosomes in diverse species may not be homologous, and variations in chromosome shape and size may occur in strains of some species. This latter characteristic is known to be under genetic control in some instances (Darlington, 1937). Sharma and Sharma (1959) concluded that with the use of improved techniques for examining karyotypes, more species are now characterized by recognizable karyotypes. It was also concluded that perhaps eventually all species can be identified on this basis.

Another cytological characteristic which was found useful in grass systematics is the presence or absence of persistent nucleoli during mitosis in root tips. In examining 45 species of 40 genera in 30 tribes of the Gramineae, Brown and Emery (1957) concluded that all members of the subfamily Panicoideae have persistent nucleoli in some but not all cells. On the other hand, the Festucoideae have no persistent nucleoli. Among the groups designated Phragmitiformes by Avdulov, some species showed persistent nucleoli while in others they were lacking. However, this last group was expected to show variation since it is inconsistent for other characteristics. It is also known that there is a correlation between presence or absence of persistent nucleoli and cytological and anatomical characters (de Wet 1954, 1956).

There has been some confusion regarding the basic chromosome number in Cynodon. Avdulov (1931) reported a somatic chromosome number of $2n=36$ for C. dactylon, and this was substantiated by Brown (1950),

Burton (1951) and Forbes in Carnahan and Hill (1961). From a meiotic study of C. dactylon, Forbes and Burton (1963) supported the conclusion that the chromosome number is 2n=36. Darlington and Janaki Ammal (1945) lists the chromosome number of a species referred to as C. diploideum to be 2n=18, and this is supported by Delay (1950). Both Hurcombe (1946) and Forbes and Burton (1963) reported the chromosome number of C. bradleyi to be 2n=18. Forbes and Burton further reported the chromosome number of 2n=18 in one or more accessions of C. incompletus, C. transvaalensis, and C. plectostachyus. Moffet and Hurcombe (1949) reported the chromosome number of a plant identified as C. plectostachyus to be 2n=54, further suggesting a basic number of 9 in the genus. However, reports of species of Cynodon with a basic number of n=10 do occur in the literature. Hurcombe (1946, 1947, 1948) and Moffet and Hurcombe (1949) reported the somatic number of C. hirsutus, C. plectostachyus and C. transvaalensis to be 2n=20 and C. dactylon to be 2n=40. Hurcombe feels that the basic number of the genus is 10 with C. bradleyi being the result of a union of two n-1 gametes produced by an aneuploid progenitor. Hurcombe (1946) reported a species, C. magennisii, which was found to be a triploid, natural hybrid between C. dactylon and C. transvaalensis with a chromosome number of 2n=30. Forbes and Burton (1963), however, reported the chromosome number as being 2n=27. They also observed that in C. plectostachyus, C. incompletus, and C. magennisii large satellites frequently break off and are large enough to resemble whole chromosomes. These satellites apparently account for the reports of 10 as the basic number in the genus, and the correct basic number appears to be n=9.

Little is reported on the size and morphology of Cynodon chromo-

somes. Ourecky (1963) studied pachytene chromosome morphology in C. dactylon reporting the length of the chromosome arms, arm ratios, overall chromosome length, relative length of individual chromosomes, and chromomere number per chromosome. The average chromomere number per chromosome was found to vary from 14.0 to 28.8 while the size of the chromosomes varied from 16.8 μ to 36.3 μ.

Hybridization and polyploidy have evidently played a major, yet conservative, role in the evolution of the grasses (Stebbins, 1956). Nearly all genera of the grasses contain species with chromosome numbers which are multiples of the original basic number. Carnahan and Hill (1961) reported that of the 2300 species of grasses whose chromosome number is known, about 80% are probably polyploid with approximately 7% of these being aneuploid. The percentage of species with intraspecific variation in chromosome number appears to be increasing with the cytological information being added each year. Myers (1957) listed 99 and Carnahan and Hill listed 345 species with aneuploid chromosome numbers.

Polyploids may have several modes of origin from their diploid ancestors, and on this basis Stebbins (1947) recognized four types of polyploids; autopolyploids, segmental polyploids, true or genomic allopolyploids, and autoallopolyploids. According to this system, autopolyploids are defined as arising from chromosome doubling of a fertile diploid. The presence of four homologous chromosomes at meiosis in the autoploid should result in multivalent formation and sterility. True allopolyploids are the result of hybridization and chromosome doubling. The two parental genomes must be completely non-homologous and form only a few loose bivalents at meiotic prophase. Doubling of

the chromosome number gives each chromosome an exactly homologous partner and the allopolyploids are characterized strictly by bivalent formation. A segmental allopolyploid is derived from parental genomes with varying degrees of homology. The newly formed polyploid should, therefore, form some multivalent configurations during meiosis. Auto-allopolyploids arise through chromosomes doubling of an allopolyploid. Polyploids may either arise through somatic doubling of the chromosomes or functioning of unreduced gametes. Love (1964) feels that situations intermediate between auto- and allopolyploids are the most frequently found among successful polyploids. He suggests the use of the terms hemialloploid to describe polyploids formed from not fully sterile species hybrids and hemiautoploids which are produced from more or less fertile intraspecific hybrids or by differentiation of the chromosome set of successful autoploids which he terms panautoploids. In this system, allopolyploids are termed panalloploids.

Newly formed polyploids are usually partially sterile or completely so. Grasses are well adapted for overcoming this "bottleneck" of partial sterility since they often can reproduce vegetatively or apomictically (Stebbins, 1956). Stebbins (1950) feels that through segregation and selection in polyploids, the non-homologous segments can be eliminated and the polyploids will become diploidized with time.

The strict diploid-like behavior of some polyploid species is known or suspected to be under genotypic control. The classic example is hexaploid wheat which shows only bivalent formation during meiotic prophase of microsporogenesis even though its three parental genomes show considerable homology. This diploid-like behavior is shown to be under the control of a single gene or a few genes (Sears, 1954; Riley,

Kimber and Chapman, 1961). Chheda and Harlan (1962) also demonstrated the occurrence in Bothriochloa of a gene which controls strict 2 x 2 pairing. Kimber (1961) suggested that tetraploid cotton may have a diploidizing gene, pointing out that such cytological behavior can perhaps arise through a mutation which rapidly passes newly formed polyploids through the barriers of partial sterility.

Within the genus Saccharum, chromosome numbers may be increased through the functioning of unreduced gametes (Price, 1963, 1965) often without a significant increase in multivalent frequency even though more than two homologous chromosomes are present. However, it is not known whether this is under genetic control.

The actual cause of chromosome pairing at meiosis is unknown (see Rhoades, 1961 for review). It is known, however, that both major and minor genes can affect pairing of chromosomes. Most of the examples of variations in chromosome pairing which are under genetic control are reviewed by Rees (1961), and by Riley and Law (1965).

Interspecific hybrids have provided valuable information dealing with systematic and phylogenetic relationships within the Gramineae. Carnahan and Hill (1961) listed 256 interspecific grass hybrids that were then known to be cytogenetically studied. The relative ease of making such hybrids in the Gramineae suggests that the accepted systems of classification places undue emphasis upon easily observed character differences (Stebbins, 1952). However, many interspecific hybrids are sterile, and Stebbins (1958) has reviewed the evidence concerning the theories of hybrid inviability, sterility and breakdown in plants.

Very little is known about cytological analysis of interspecific hybrid in Cynodon. In a C. transvaalensis -x- C. dactylon hybrid,

Forbes and Burton (1963) observed as many as nine trivalents at diakinesis indicating that the genomes of the parents are at least partially homologous. They also reported a high rate of trivalent frequency in triploid hybrids between diploid and tetraploid strains of C. dactylon. The authors suggested, however, that all genomes of Cynodon could not be considered homologous until more hybrids are studied.

Morphology

Several authors have classified Cynodon, strictly on the basis of morphological characters, into a number of species and varieties (Hurcombe, 1948; Bogdan, 1949; Chippindale, 1955). Hurcombe found that the only reliable and constant characters to distinguish between the African species of Cynodon are the veination of the leaves, presence or absence of rhizomes, the nature of the rachilla, number of primary nerves, and the length of the glumes in relation to the spikelet. In addition, the length, width and hairiness of the leaves, the number of spikes, the nature of the ligule and size were found to be important morphological characters considered in conjunction with the first mentioned ones. Bogdan (1949) published an account of how to diffentiate C. plectostachyus from C. dactylon. According to this treatment, plants described by Hurcombe as C. plectostachyus can be classified as C. dactylon.

In a numerical taxonomical treatment of the genus, Carpena (1965) used some 38 morphological characters to describe the various species. This study indicated that on a morphological basis, some previously recognized species perhaps belong to only one taxon, while some variants within C. dactylon may deserve specific rank. The study showed C.

plectostachyus to be quite distinct morphologically from the rest, while C. hirsutus and C. incompletus form a single species complex and C. leptochloides should be combined with C. arcuatus. Morphological characteristics of the Cynodon species recognized in the biosystematic laboratory of the Oklahoma State University are discussed by Harlan et al. (1966).

In the present study, triploid Cynodon hybrids were analyzed cytologically at microsporogenesis to determine the degree of relationship, based on homology between the genomic constitutions, of the parental diploids and tetraploids. A cytogenetic study of the triploid hybrids should prove to be of some value in making some preliminary decisions about the taxonomy of the genus.

MATERIALS AND METHODS

The parents of the interspecific hybrids reported in this study consist of a collection from various parts of the Old World, grown at the Oklahoma experiment station at Stillwater. Hybridization attempts were made by W. L. Richardson in the greenhouse using the emasculation technique described by him (1958). Seeds obtained from such crossing attempts were germinated and grown in a uniform nursery as outlined by Celarier and Harlan (1958).

Bud material for sporocyte analysis was collected on warm, sunny days between 8 a.m. and 11 a.m. The material was placed in bottles containing Carnoy's fluid in the proportion of 6 parts 95% alcohol: 3 parts glacial acetic acid: 1 part chloroform (Smith, 1947) and stored in a refrigerator.

When the material was to be analyzed, a raceme was placed in a petri dish containing a small amount of Carnoy's fluid. Using a sharp pointed iron needle and small scapel, a spikelet was removed from the raceme and the 3 anthers dissected out from the floret. A small drop of acetocarmine stain was placed on a 25 x 75 mm. slide, and one anther was then placed in the stain. The iron needle was used to squash the pollen mother cells from the anther and to add iron to the stain. The slide was placed under the microscope and using low power, the sporocytes were observed to see if they were in the proper stage of meiotic division. If the sporocytes were not at the metaphase stage of meiosis

I, another spikelet was selected from nearer the center or end of the raceme, depending upon whether the sporocytes were too young or old, respectively. When the proper stage was found, an 18 sq. mm. cover slip was placed over the material, and the slide was gently warmed using a small alcohol burner. The slide was then squashed between folded blotter or filter paper to flatten the cells and give better spreading of the chromosomes. The slide was sealed using a mixture of equal parts of gum arabic and gum mastic and stored in the refrigerator for 2 or 3 days to allow for better staining and greater contrast between the chromosomes and cytoplasm.

The slides were analyzed using oil emersion objective at a magnification of 1425 X and scored for the number of univalents, bivalents, trivalents and tetravalents in the microspore mother cells. The sporocytes were analyzed further for any cytological abnormalities such as inversion bridges, fragments and laggards during the separation of the chromosomes at anaphase I. Averages are based on a study of at least 25 cells.

Mature specimens were collected from the field and placed in the grass herbarium at Oklahoma State University. Both parents and hybrids were scored for the following morphological characters: length of the longest raceme, number of nodes in the inflorescense, hairiness of the lemma, length of the glumes in proportion to length of the lemma, length and width of the peduncle leaf, and hairiness of the leaves. Ten specimens were studied for each parent and hybrid.

RESULTS

The cytology of the parents used in crossing attempts is summarized in Table I. The diploids ($2n=18$) are usually characterized by nine chromosome pairs during first metaphase of microsporogenesis. Rarely, two or four univalents were observed during late metaphase, but these resulted from very early falling apart of bivalents. The chromosomes of the tetraploids ($2n=36$) formed as many as 18 bivalents during meiotic metaphase, but two to four chromosomes sometimes fail to pair or associate into multivalents. Where no meiotic behavior is listed, the chromosome numbers were determined from root tip squashes (Harlan et al., 1966).

Both average and range of chromosome association are listed in Table II for all the hybrids studied. Photomicrographs demonstrating the cytological behavior of the hybrids are reproduced in Plates I, II and III. Distinguishing morphological characteristics of parents and their hybrids are summarized in the form of pictoralized scatter diagrams, as described by Anderson (1949), in Plates IV, V, VI and VII. The species are classified according to an unpublished system followed in the biosystematic laboratory.

Hybrids were easy to recognize as they exhibited characteristics of both parents. As could be expected in triploid hybrids, some offspring resembled the tetraploid parent more closely than the diploid parent in some characteristics. In a few hybrids, some characteristics

TABLE I

CYTOLOGICAL DATA OF HYBRID PARENTS

Species	Origin	Accession No.	2n	Chromosome Association I	II	III	IV
C. afghanus	Afghanistan	8151	18	1.0 0-2	8.5 8-9	1 0	0 0
	Afghanistan	8152	18				
	Afghanistan	8800	36				
	Afghanistan	9951	18				
C. coursii							
var. africanus	Rhodesia	10287	18	0	9	0	0
var. coursii	Malagasy	10125	36	0	18	0	0
	Malagasy	10127	36	0	18	0	0
	Malagasy	10128	36	0	18	0	0
C. dactylon							
var. aridus	India	10312	18	0.5 0-2	8.7 8-9	0 0	0 0
	India	10323	18	0	9	0	0
	India	10324	18	0	9	0	0
var. dactylon	Afghanistan	8150	36	0	18	0	0
	Afghanistan	8153	36				
	Afghanistan	9943	36	0	18	0	0
	Turkey	9945a	36	0	18	0	0
	Afghanistan	9949	36	0	18	0	0
	Afghanistan	9953	36	0	18	0	0

TABLE I, continued

Species	Origin	Accession No.	2n	Chromosome Association I	II	III	IV
	Kenya	9961	36	0	18	0	0
	India	10163	36	0	18	0	0
	South Africa	10194	36	0	18	0	0
	South Africa	10196	36				
	South Africa	10200	36	0	18	0	0
	Malagasy	10321	36	0	18	0	0
	Phillipines	10442	36	0.28 0-2	17.0 16-18	0 0	0.43 0-1
	Ghana	10448	36				
C. dactylon							
var. laxus	South Africa	10246	36	0	15.6	0	1.2
	South Africa	10357a	36				
C. dactylon							
var. palustrious	India	10447	18	0	19	0	0
C. dactylon							
var. seleucidus	Yugoslavia	9957	36				
	Yugoslavia	9959	36				
C. incompletus	South Africa	10272	18	0.3 0-2	8.8 8-9	0 0	0 0
	South Africa	10273	18	1.16 0-4	8.42 7-9	0 0	0 0
	South Africa	10274	18	0.2 1-2	8.9 8-9	0 0	0 0
	South Africa	10275	18	0	9	0	0
	South Africa	10277	18	0	9	0	0

TABLE I, continued

Species	Origin	Accession No.	2n	Chromosome Association I	II	III	IV
C. plectostachyus	Nigeria	10229	18	0	9	0	0
C. transvaalensis	South Africa	10143	18				
	South Africa	10151	18	0.4 0-2	8.8 8-9	0 0	0 0
	South Africa	10190	18				

TABLE II

CYTOLOGICAL DATA OF HYBRIDS

Parents	2n	No. Hybrids	Chromosome Association I	II	III	IV
C. dactylon var. dactylon (2n=36) -x- *C. dactylon var. aridus* (2n=18)						
9953 (2n=36) 10323 (2n=18)	27	1	5.95 3-9	9.65 7-12	0.25 0-2	0.25 0-2
8150 (2n=36) 10324 (2n=18)	27	1	8.48 6-9	9.20 9-10	0.04 0-1	0 0
C. dactylon var. aridus (2n=18) -x- *C. dactylon var. dactylon* (2n=36)						
10323 (2n=18) 8153 (2n=36)	27	1	7.0 5-11	9.4 8-11	0 0	0.3 0-1
C. dactylon var. palustrius (2n=18) -x- *C. dactylon var. dactylon* (2n=36)						
10477 (2n=18) 10321 (2n=36)	27	3	6.93 3-9	9.58 7-12	0.07 0-1	0.05 0-1
C. dactylon var. palustrius (2n=18) -x- *C. dactylon var. seleucidus* (2n=36)						
10477 (2n=18) 9959 (2n=36)	27	3	8.13 3-9	9.18 7-12	0.05 0-1	0.09 0-1
C. transvaalensis (2n=18) -x- *C. dactylon var. dactylon* (2n=36)						
10190 (2n=18) 10163 (2n=36)	27	1	10.36 7.15	8.32 6-10	0 0	0 0
10143 (2n=18) 10163 (2n=36)	27	1	4.18 1-7	9.25 6-10	1.0 0-2	0.33 0-1
C. afghanus (2n=18) -x- *C. dactylon var. dactylon* (2n=36)						
9951 (2n=18) 10442 (2n=36)	36	1	0.76 0-4	15.92 14-17	0 0	0.85 0-1

TABLE II, continued

Parents		2n	No. Hybrids	Chromosome Association I	II	III	IV
8152 (2n=18)	9961 (2n=36)	36	2	1.0 0-4	15.90 12-18	0.04 0-1	0.77 0-3
C. dactylon var. dactylon (2n=36) -x- *C. afghanus* (2n=18)							
10194 (2n=36)	8151 (2n=18)	36	2	3.54	14.56	0.22	0167
C. dactylon var. dactylon (2n=36) -x- *C. incompletus* (2n=18)							
10163 (2n=36)	10273 (2n=18)	27	6	7.74	8.70	0.38	0.18
9945a (2n=36)	10277 (2n=18)	27	1	7.00	8.50	0	0.75
C. incompletus (2n=18) -x- *C. dactylon var. dactylon* (2n=36)							
10274 (2n=18)	9943 (2n=36)	27	1	4.03 2-5	9.50 7-11	0.77 0-3	0.44 0-2
10273 (2n=18)	9949 (2n=36)	36	2	1.74 0-4	16.67 16-18	0 0	0.23 0-1
C. incompletus (2n=18) -x- *C. dactylon var. seleucidus* (2n=36)							
10274 (2n=18)	9957 (2n=36)	27	1	5.00	11.00	0	0
C. afghanus (2n=36) -x- *C. incompletus* (2n=18)							
8800 (2n=36)	10273 (2n=18)	27	7	7.18 3-13	9.58 7-12	0.22 0-1	0 0
8800 (2n=36)	10274 (2n=18)	27	14	7.24 1-15	9.59 6-13	0.06 0-3	0.10 0-1
8800 (2n=36)	10275 (2n=18)	27	3	8.36 3-13	9.18 7-12	0 0	0.07 0-1
C. coursii var. africanus (2n=18) -x- *C. dactylon var. dactylon* (2n=36)							

TABLE II, continued

Parents		2n	No. Hybrids	Chromosome Association I	II	III	IV
10287 (2n=18)	10163 (2n=36)	27	6	5.59 1-13	10.00 5-12	0.21 0-2	0.20 1-3
C. dactylon var. aridus (2n=18) -x- C. coursii var. coursii (2n=36)							
10323 (2n=18)	10128 (2n=36)	27	3	6.94 1-10	9.31 7-13	0.42 0-3	0.12 0-1
C. transvaalensis (2n=18) -x- C. coursii var. coursii (2n=36)							
10151 (2n=18)	10128 (2n=36)	27	3	7.26 3-11	9.66 4-12	0.02 0-1	0.09 0-1
C. incompletus (2n=18) -s- C. coursii var. coursii (2n=36)							
10277 (2n=18)	10128 (2n=36)	27	1	9.30 7-13	8.85 7-10	0 0	0 0
C. coursii var. coursii (2n=36) -x- C. incompletus (2n=18)							
10125 (2n=36)	10274 (2n=18)	27	1	4.80 2-7	10.00 8-11	0.44 0-1	0.22 0-2
10127 (2n=36)	10272 (2n=18)	27	2	7.74 5-11	9.55 8-11	0 0	0.04 0-1
10128 (2n=36)	10273 (2n=18)	27	1	5.24 3-9	7.33 4-11	2.22 1-5	0.11 0-1
C. dactylon var. dactylon (2n=36)							
10200 (2n=36)	selfed	54	1	1.12 0-4	24.06 23-27	0 0	0.69 0-1
C. dactylon var. aridus (2n=18) -x- C. transvaalensis (2n=18)							
10312 (2n=18)	10151 (2n=18)	18	8	0	9	0	0
		27	1	11.10 8-15	7.75 6-9	0.08 0-1	0.04 0-1

LEGEND TO PLATE I

Cytology of microsporogenesis.

Figure 1. *C. dactylon var. dactylon* (2n=36) -x- *C. dactylon var. aridus* (2n=18): metaphase with 9 II, 9 I.

Figure 2. *C. dactylon var. aridus* (2n=18) -x- *C. dactylon var. dactylon* (2n=36): metaphase with 9 II, 9 I

Figure 3. *C. dactylon var. aridus* (2n=18) -x- *C. dactylon var. dactylon* (2n=36): late anaphase showing laggards

Figure 4. *C. dactylon var. aridus* (2n=18) -x- *C. dactylon var. dactylon* (2n=36): early anaphase showing 27 chromosomes.

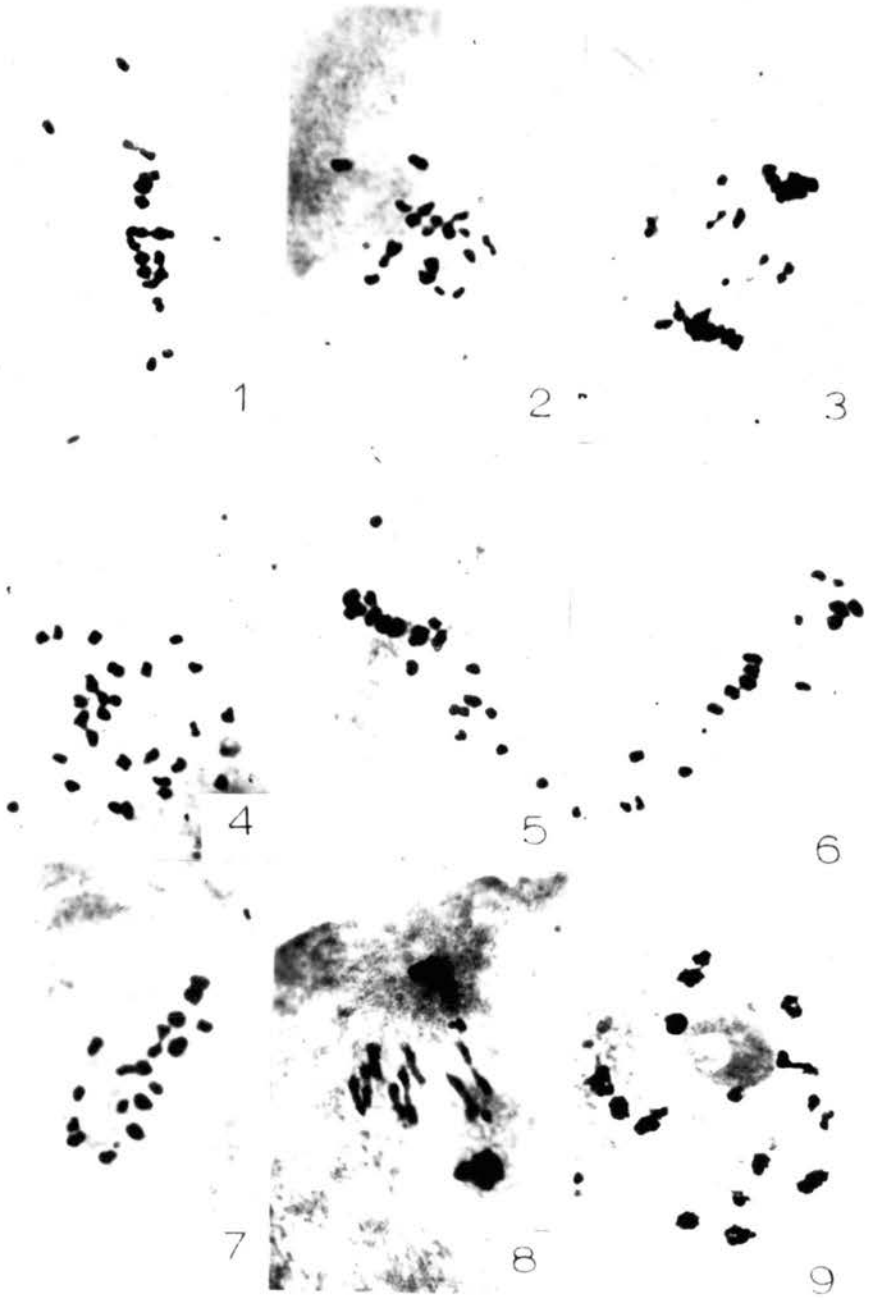
Figure 5. *C. palustrius* (2n=18) -x- *C. seleucidus* (2n=36): metaphase showing 9 II, 9 I.

Figure 6. *C. coursii var. coursii* (2n=36) -x- *C. incompletus* (2n=18): metaphase showing 11 II, 5 I.

Figure 7. *C. coursii var. coursii* (2n=36) -x- *C. incompletus* (2n=18): metaphase showing 10 II, 7 I.

Figure 8. *C. coursii var. coursii* (2n=36) -x- *C. incompletus* (2n=18): anaphase showing dividing laggards.

Figure 9. *C. transvaalensis* (2n=18) -x- *C. dactylon var. dactylon* (2n=36): diakinesis showing 10 II, 7 I.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LEGEND TO PLATE II

Cytology of microsporogenesis.

Figure 10. *C. transvaalensis* (2*n*=18) -x- *C. dactylon* var. *dactylon* (2*n*=36): seven lagging chromosomes on metaphase plate.

Figure 11. *C. transvaalensis* (2*n*=18) -x- *C. dactylon* var. *dactylon* (2*n*=36): 27 chromosomes at anaphase.

Figure 12. *C. transvaalensis* (2*n*=18) -x- *C. coursii* var. *coursii* (2*n*=36): metaphase with 9 II, 9 I.

Figure 13. *C. coursii* var. *africanus* (2*n*=18) -x- *C. dactylon* var. *dactylon* (2*n*=36): metaphase with 9 II, 9 I. One II hidden by badly stained cytoplasm.

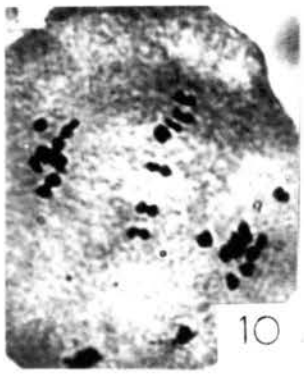
Figure 14. *C. afghanus* (2*n*=36) -x- *C. incompletus* (2*n*=18): metaphase with 10 II, 7 I, and 1 fragment.

Figure 15. *C. afghanus* (2*n*=36) -x- *C. incompletus* (2*n*=18): early anaphase showing 4 II, 19 I, and the 1 fragment.

Figure 16. *C. afghanus* (2*n*=36) -x- *C. incompletus* (2*n*=18): metaphase with 9 II, 9 I.

Figure 17. *C. afghanus* (2*n*=36) -x- *C. incompletus* (2*n*=18): 27 univalents at anaphase with 2 small chromosomes.

Figure 18. *C. afghanus* (2*n*=36) -x- *C. incompletus* (2*n*=18): metaphase with 7 II, 13 I.



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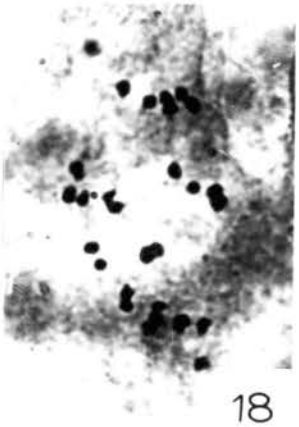

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LEGEND TO PLATE III

Cytology of microsporogenesis.

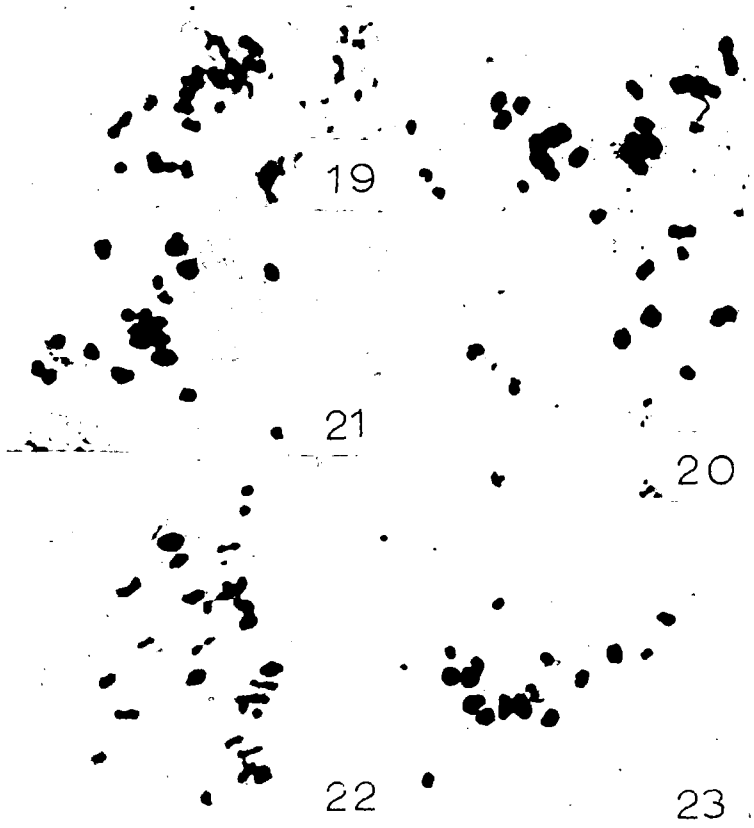
Figure 19. *C. afghanus* (2n=18) -x- *C. incompletus* (2n=36): metaphase with 10 II, 7 I.

Figure 20. A cell from the same slide with 22 II and 10 I.

Figure 21. *C. dactylon var. aridus* (2n=18) -x- *C. transvaalensis* (2n=18): metaphase with 10 II, 7 I.

Figure 22. *C. dactylon var. dactylon* (2n=54): Autohexaploid with 25 II, 4 I and 2 fragments.

Figure 23. *C. dactylon var. aridus* (2n=18) -x- *C. coursii var. coursii* (2n=36): metaphase with 9 II, 9 I and 1 fragment.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LEGEND TO PLATE IV

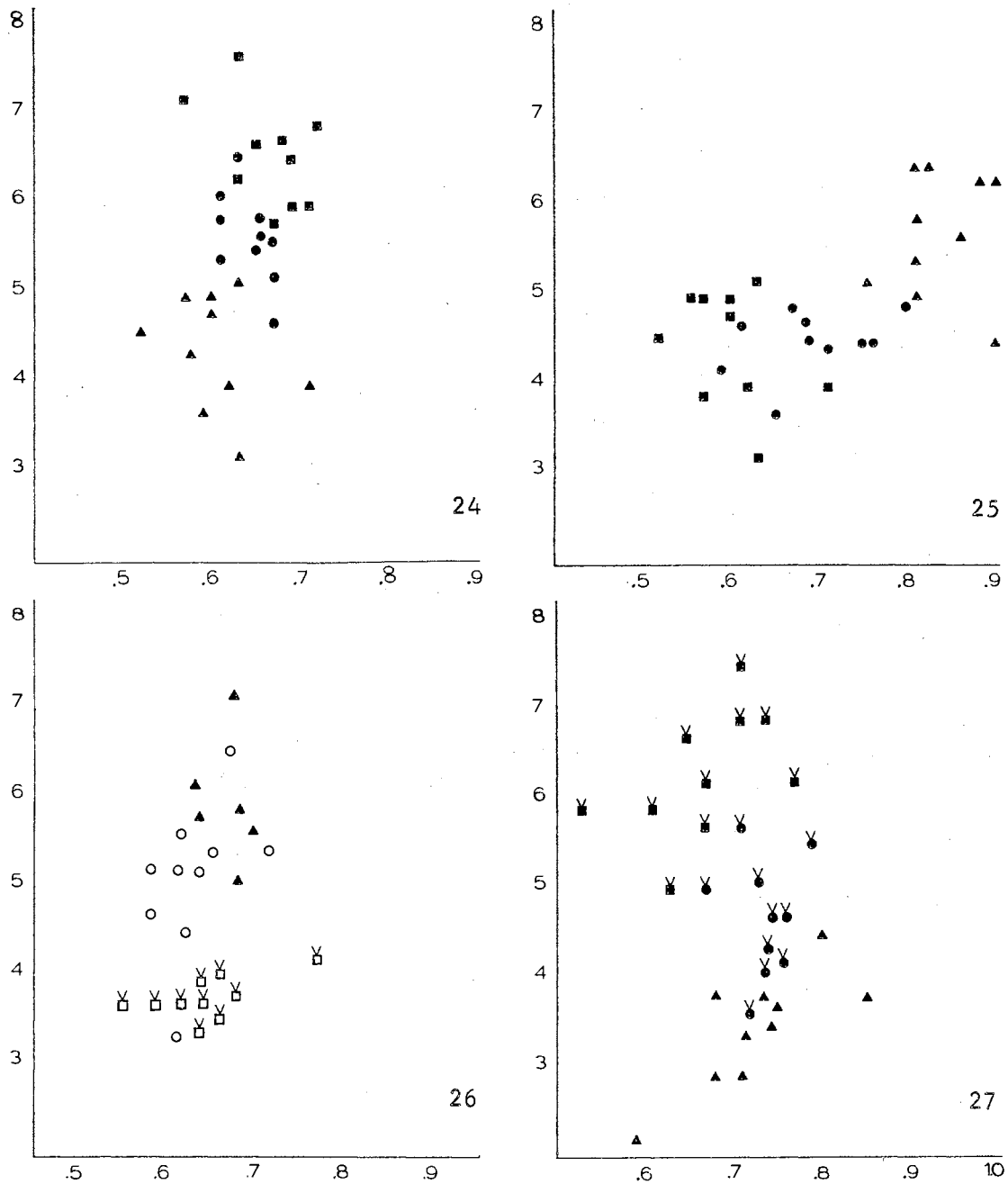
Pictoralized scatter diagrams. Vertical axis indicates length of longest raceme; horizontal axis represents glume/floret ratio. Circles represent hybrids, squares female parent, and triangles represent the male parent. Whiskers indicate pubescense of leaves and shaded symbols indicate some hair on margin of lemma as opposed to hair only on the keel.

Figure 24. *C. dactylon var. dactylon* ($2n=36$) -x- *C. dactylon var. aridus* ($2n=18$).

Figure 25. *C. dactylon var. aridus* ($2n=18$) -x- *C. dactylon var. dactylon* ($2n=36$).

Figure 26. *C. dactylon var. dactylon* ($2n=36$) -x- *C. afghanus* ($2n=18$).

Figure 27. *C. afghanus* ($2n=18$) -x- *C. dactylon var. dactylon* ($2n=36$).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LEGEND TO PLATE V

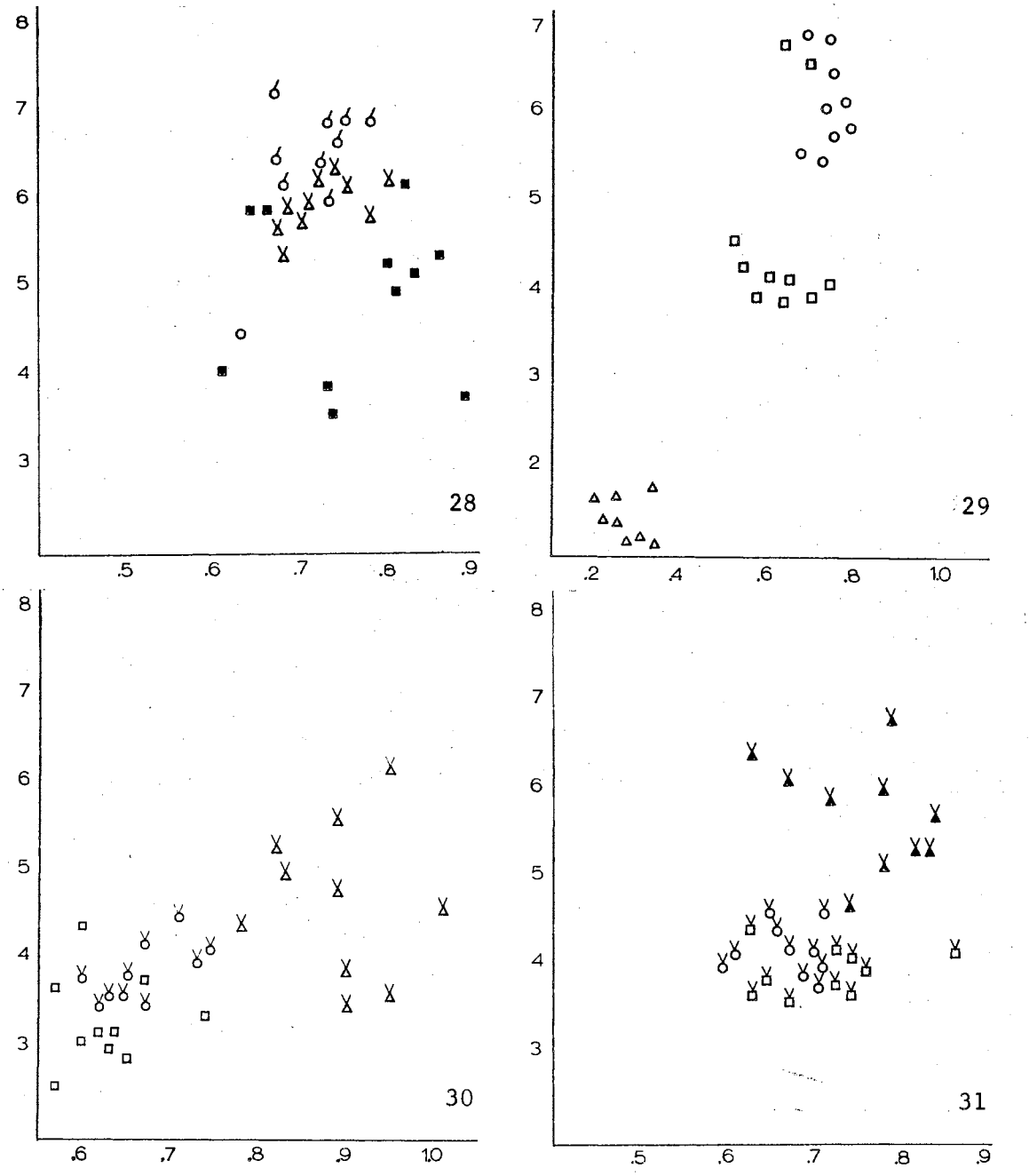
Pictoralized scatter diagrams. Vertical axis indicates length of longest raceme; horizontal axis represents glume/floret ratio. Circles represent hybrids, squares female parent, and triangles represent the male parent. Whiskers indicate pubescense of leaves and shaded symbols indicate some hair on margin of lemma as opposed to hair only on the keel.

Figure 28. *C. afghanus* ($2n=18$) -x- *C. dactylon* var. *dactylon* ($2n=36$).

Figure 29. *C. dactylon* var. *aridus* ($2n=18$) -x- *C. transvaalensis* ($2n=18$).

Figure 30. *C. dactylon* var. *dactylon* ($2n=36$) -x- *C. incompletus* ($2n=18$).

Figure 31. *C. incompletus* ($2n=18$) -x- *C. dactylon* var. *seleucidus* ($2n=36$).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LEGEND TO PLATE VI

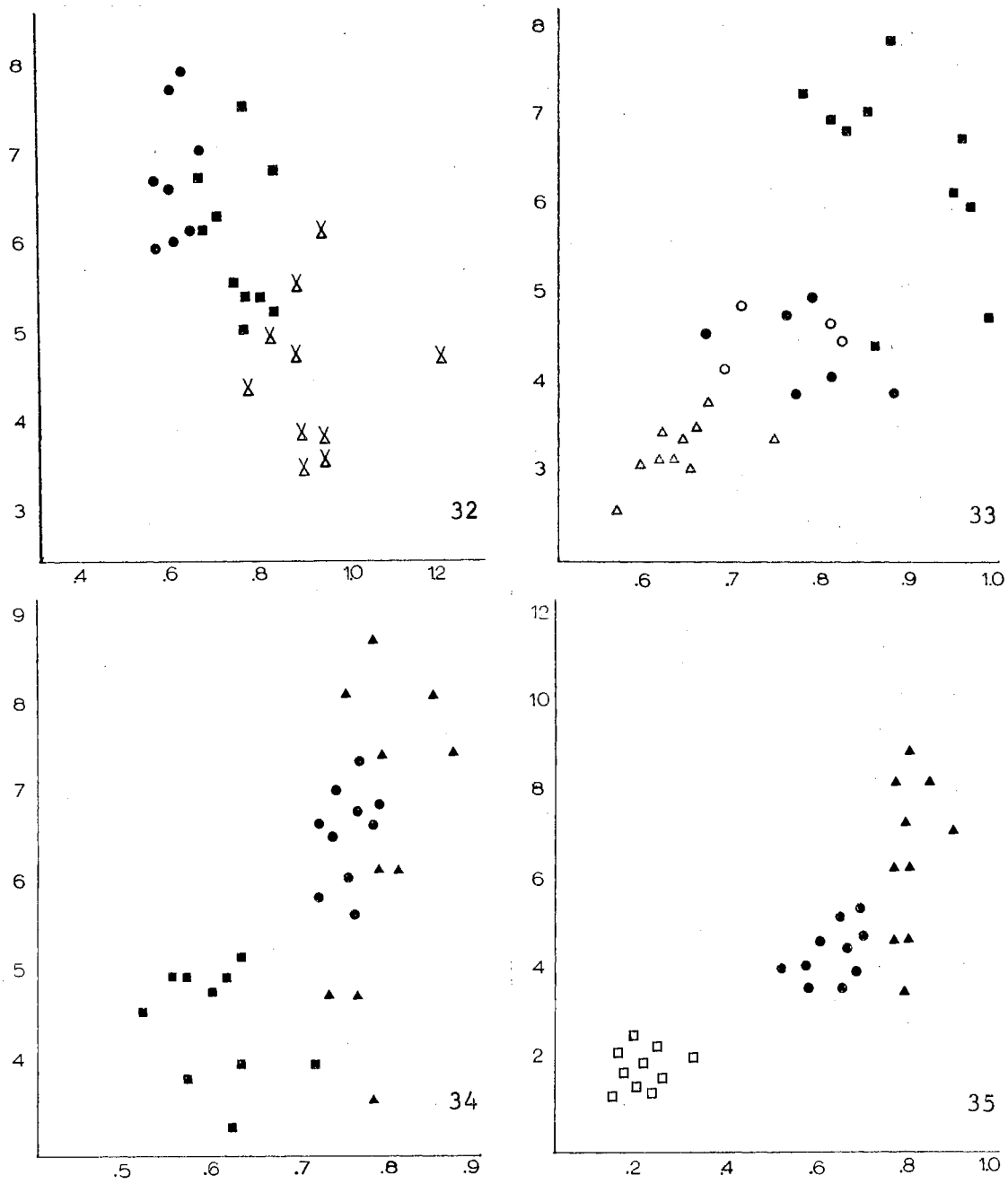
Pictoralized scatter diagrams. Vertical axis indicates length of longest raceme; horizontal axis represents glume/floret ratio. Circles represent hybrids, squares female parent, and triangles represent male parent. Whiskers indicate pubescense of leaves and shaded symbols indicate some hair on margin of lemma as opposed to hair only on the keel.

Figure 32. *C. afghanus* ($2n=36$) -x- *C. incompletus* ($2n=18$).

Figure 33. *C. coursii var. africanus* ($2n=18$) -x- *C. dactylon var. dactylon* ($2n=36$).

Figure 34. *C. dactylon var. aridus* ($2n=18$) -x- *C. coursii var. coursii* ($2n=36$).

Figure 35. *C. transvaalensis* ($2n=18$) -x- *C. coursii var. coursii* ($2n=36$).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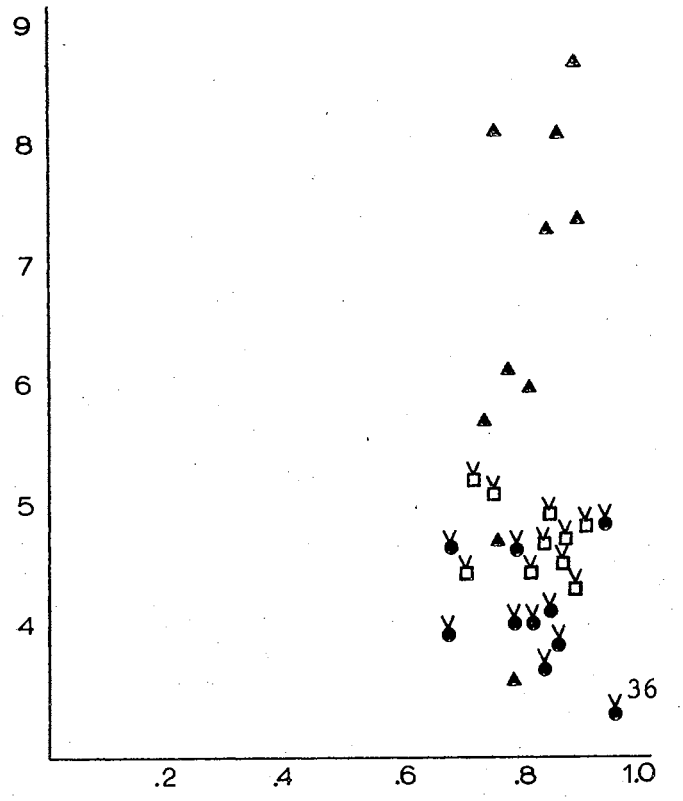
LEGEND TO PLATE VII

Pictoralized scatter diagrams. Vertical axis indicates length of longest raceme; horizontal axis represents glume/floret ratio. Circles represent hybrids, squares female parent, and triangles represent the male parent. Whiskers indicate pubescense of leaves and shaded symbols indicate some hair on margin of lemma as opposed to hair only on the keel.

Figure 36. *C. incompletus* ($2n=18$) -x- *C. coursii var. coursii* ($2n=36$).

Figure 37. *C. coursii var. coursii* ($2n=36$) -x- *C. incompletus* ($2n=18$).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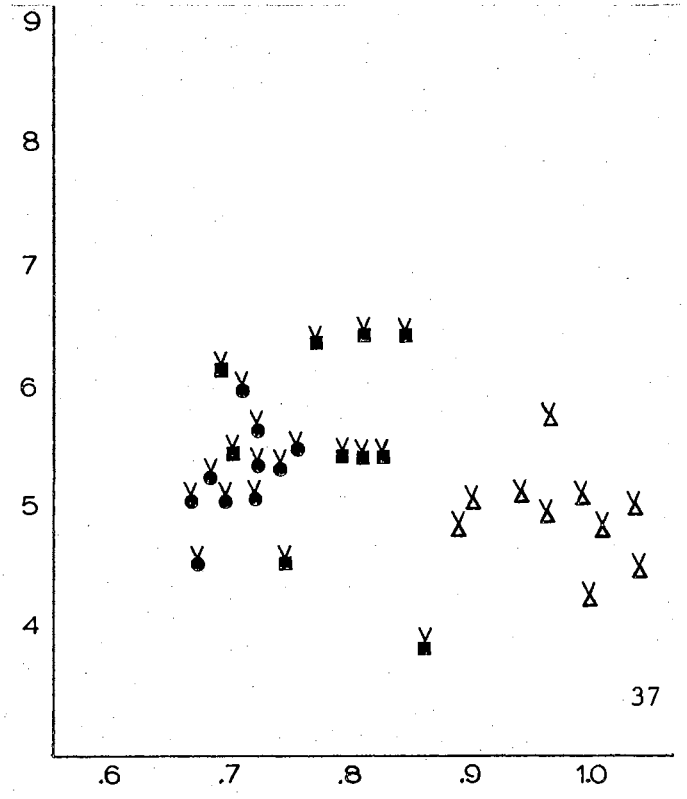
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showed heterosis. The easiest way to determine whether an offspring was a hybrid or resulted from self-fertilization was to determine its chromosome number. However, the diploid C. afghanus (2n=18) crossed with C. dactylon var. dactylon (2n=36) only when the cytologically unreduced gamete functioned. Only unreduced female gametes of C. afghanus could be fertilized by C. dactylon var. dactylon pollen, and only cytologically unreduced pollen of C. afghanus could fertilize the female gamete of tetraploid C. dactylon. One such tetraploid hybrid was also obtained when a diploid C. incompletus was fertilized by pollen from a tetraploid C. dactylon. Attempted crosses between diploid C. plectostachyus and any tetraploid C. dactylon always failed. However, out of one such an attempted cross, using C. dactylon as the female parent, a 2n=54 offspring was obtained. Comparative morphological studies indicated that this plant represents an autohexaploid C. dactylon.

Cytology of the auto-hexaploid C. dactylon: The parental tetraploid is characterized strictly by bivalent formation during meiotic prophase of microsporogenesis. The hexaploid, although combining two sets of three homologous genomes, is surprisingly regular in its meiotic behavior. Never more than one tetravalent was observed during meiotic prophase, and on an average about every other microspore mother cell was characterized strictly by bivalent formation. Four univalents together with a tetravalent was the most severe deviation from normal bivalent formation observed in this hexaploid. During early metaphase, the single tetravalent usually fell apart into two bivalents, and normal chromosome distribution during anaphase almost always took place. These cytological observations seem to indicate that the two extra

genomes pair with each other rather than entering into multivalent formation with the normal chromosome complement.

Cytology of the tetraploid hybrids: These hybrids combine the cytologically unreduced gamete of the diploid parent and the cytologically reduced gamete of the tetraploid parent. Hybrids of this nature were always obtained when tetraploid C. dactylon was crossed with the diploid C. afghanus, and once when C. incompletus ($2n=18$) was used as the female parent. In these hybrids it could be expected that if little or no homology exists between the genomes of the diploid and tetraploid, the hybrids will be characterized by nine bivalents and 18 univalents during meiotic prophase. If the basic genome of the diploid is partially homologous with one basic genome of the tetraploid, trivalents should be frequently encountered while most of the chromosomes belonging to the other basic genome from the tetraploid could be expected to remain as univalents. Actually, the chromosomes usually associate into 18 bivalents during meiotic prophase. Not more than four chromosomes were ever observed as univalents, trivalents were extremely rare, and one tetravalent was observed on an average in about every second developing microspore mother cell. These cytological observations seem to suggest that the two basic genomes derived from the tetraploid parent pair autosyndetically, while the normal complement from the diploid parent pairs normally. However, it seems equally likely that the chromosomes of the diploid can pair with either basic genome of the tetraploid. Presence of tetravalents, rather than trivalents, may indicate that the latter explanation is the most likely one.

Cytology of triploid hybrids: Two tetraploid varieties, C. dactylon var. dactylon and C. dactylon var. seleucidus, and tetraploid C.

afghanus were crossed with various, usually recognized, diploid species and varieties. These include the diploids C. dactylon var. palustrius var. aridus, C. transvaalensis and C. incompletus. All triploid hybrid combinations behave essentially alike cytologically (Table II). As many as 12 bivalents were occasionally observed in the microsporocytes, but usually about nine bivalents and nine univalents were characteristic of microsporogenesis in these triploids. Multivalents, usually either one trivalent or one tetravalent, were sometimes observed, but these often fall apart by early metaphase and were then seen as bivalents or a bivalent and univalent.

One triploid hybrid was obtained from a cross between diploid C. dactylon var. aridus and diploid C. transvaalensis. This cross gave a progeny of nine hybrids, eight of which were diploid and one was the triploid. Although these two taxa are morphologically very distinct (Harlan et al., 1966), the diploid hybrids were characterized strictly by bivalent formation during prophase of microsporogenesis. The triploid was characterized essentially by nine chromosome pairs and nine univalents during meiotic prophase.

DISCUSSION

The genus Cynodon is widely distributed in the Old World. Its species are primarily tropical and sub tropical in distribution, but the widely distributed C. dactylon also extends into the cool-temperate areas of Europe and Asia. No species is endemic to Australia, however, the South East Asian C. arcuatus extends into its northern tropics. Various species, C. dactylon, C. incompletus, C. transvaalensis, and others, were introduced into the New World, and are now widely distributed as weeds or as cultigens.

The genus is extremely variable morphologically, and is characterized by an amazing number of morphologically distinct taxa. However, comparative morphological studies suggested to Harlan et al. (1966) that many of the usually recognized species could perhaps best be combined into more complex taxa, while other unnamed ones perhaps deserve specific rank. This led to the construction of the provisional classification summarized in Table III. Detailed cytogenetic studies are now underway to determine the validity of the taxa recognized.

The South East Asian tetraploid C. arcuatus is morphologically very distinct from the other species of Cynodon and so far also seems to be genetically isolated from them. The diploids C. barberi, C. plectostachyus, and C. aethiopicus also could so far not be crossed with the other species. The limited cytogenetical data available suggest that the remaining species, C. afghanus, C. coursii, C. incom-

TABLE III

CLASSIFICATION AND DISTRIBUTION OF *CYNODON*

Species	2n	Distribution
C. arcuatus	36	Malagasy and South India to Northern Australia
C. barberi	18	South India
C. plectostachyus	18	Tropical East and Central Africa
C. aethiopicus	18	Ethiopia
C. afghanus	18, 36	Afghanistan
C. coursii		
var. coursii	36	Malagasy
var. africanus	18	Ethiopia to Rhodesia
C. incompletus	18	Southern Africa
C. robustus	18, 36	Ethiopia to Zambia
C. transvaalensis	18	South Africa
C. dactylon		
var. dactylon	36	Old World
var. aridus	18	India, Israel, and South Africa
var. laxus	36	Southern Africa
var. palustrius	18	Tropical South India
var. polevansii	36	South Africa
var. seleucidus	36	Eastern Europe and Asia Minor

pletus, C. robustus, C. transvaalensis, and C. datylon with its numerous varieties, form one large genetic complex. Hybrids were produced between various diploids within this complex, and all those studied are characterized by normal bivalent formation during meiosis of microsporogenesis. Similarly, tetraploids seem to cross in all possible combinations under experimental conditions, and diploid -x- tetraploid crosses are relatively easy to make.

These cytogenetic observations suggest that this large complex is characterized by a common genome. Further, that some tetraploids are segmental allopolyploids while others may be essentially autoploids. At least under experimental conditions, unreduced gametes frequently functioned to produce autotetraploids directly from a single diploid parent. Cytologically, the diploids in this complex, be they different specific or subspecific taxa of the same species, seem to be characterized by the same genome constitution (DD). All the tetraploids in the complex behave essentially like segmental allopolyploids derived from this basic genome, and for this reason are assigned a genome constitution of DDD'D'. All triploid hybrids will then be characterized essentially by nine bivalents and nine univalents during prophase of meiosis. Hybrids which combine the cytologically unreduced gamete of a diploid and the normal gamete of the tetraploid (DDDD') were expected to be characterized by consistent multivalent formation. However, the predominant association of the chromosomes into bivalents during meiotic prophase indicates homology between the D and D' genomes, and suggests that bivalent formation in the natural tetraploids must be due to preferential pairing. The extent to which bivalent formation can be actually induced through preferential chromosome pairing became further

obvious in the 2n=54 chromosome plant with a genome constitution of DDD'D'DD'. The essentially normal bivalent formation in such an autohexaploid also further indicates close homology between the D and D' genomes. Such a preferential pairing probably is the result of the small chromosomes which characterize Cynodon, combined with diploidizing genes as was demonstrated for other polyploids (Riley and Law, (1965).

The question now arises whether, from a biosystematic point of view, these taxa should be included in a single species. Morphological variation within C. dactylon, as recognized in Table III, is already so large that six varieties were required to indicate this variability. This species differs from the others, except for C. transvaalensis and tetraploid C. afghanus, conspicuously in having well developed rhizomes. The non-rhizomatous species of the genomic-complex, C. afghanus (diploid), C. coursii, C. incompletus, and C. robustus, are almost completely isolated from each other geographically and each taxon is morphologically distinct. For convenience, the rhizomatous C. transvaalensis may be included in C. dactylon as a variety, and tetraploid C. afghanus may be combined with the somewhat related C. dactylon var. seleucidus.

Final revision of the taxonomy must await a detailed cytogenetic study of hybrids between diploids and between tetraploids. Morphological data suggest that, although the chromosomes pair regularly in these hybrids, they may still be isolated from each other genetically. No data on degree of sterility in diploid hybrids are as yet available, but it is predicted that many hybrids will be characterized by a strong reduction in percentage seed set. Preliminary studies of hybrids

between tetraploids suggest numerous structural differences between the genomes of morphologically distinct tetraploids. The extreme morphological differences which characterize some diploid taxa seem to suggest an ancient separation into numerous isolated groups. Cytological differentiation almost certainly must have accompanied the gentical differentiation. These cytological differences may not be obvious in the hybrids because of the small chromosomes which characterize Cynodon. Chromosomes either pair or they do not pair, and the cytological variation between genomes that form bivalents may be sufficiently well established to cause extensive sterility in some interspecific hybrids.

SUMMARY

Attempts were made to produce interspecific and intervarietal crosses in the genus Cynodon. Hybridization attempts between C. arcuatus, C. barberi, and C. aethiopicus always failed. When any of these three species were used as one parent and anyone of the other recognized species of Cynodon were used as the other parent, hybrids could also not be produced, suggesting that they are genetically well isolated species.

The remaining species, C. afghanus, C. coursii, C. incompletus, C. robustus, C. transvaalensis, and C. dactylon, were crossed in various combinations with varying degrees of difficulty. This would suggest that they represent one large genetic complex.

Chromosome pairing is normal at meiotic prophase in diploid hybrids that were studied in this complex. This suggested that all the diploids in the complex are characterized by a common genome consitution (DD).

Triploid hybrids derived from diploid -x- tetraploid crosses within the complex, be they interspecific or intergeneric, are characterized by the chromosomes forming up to 12 bivalent configurations at meiotic prophase. A single multivalent was often observed, but on an average the chromosomes associated into nine bivalents and nine univalents.

Tetraploids sometimes arose from attempted crosses between diploids and tetraploids indicating that unreduced gametes can function.

Morphological data indicated that the unreduced egg usually functioned, but occasionally the normal egg was fertilized by unreduced pollen of the diploid parent. The tetraploid hybrids showed predominant bivalent chromosome association at meiotic prophase indicating close homology between the D and D^1 genomes.

Essentially strict bivalent formation during meiotic prophase in the natural tetraploids must be due to preferential pairing. The predominant bivalent formation in an artificially produced autohexaploid C. dactylon (2n=54) further substantiates this conclusion.

Although the complex seems to be characterized by a common genome, no revision of the taxonomy of the genus should be undertaken until more cytogenetical data are available.

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