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A preliminary pachytene analysis of two species of *Arachis* L.

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Summary. The morphology of pachytene chromosomes was studied in *A. glabrata* Benth. and *A. pusilla* Benth. belonging respectively to the sections Rhizomatosae and Triseminale. These two species can not be crossed with the cultivated groundnut *A. hypogaea* L. All 20 chromosomes of *A. glabrata* could be identified individually and further classified into 5 basic types. The features that enabled the identification of chromosomes were: total length, arm ratios, nucleolus attachment and position and extent of heterochromatin. A simple key has been proposed for classifying different chromosomes to facilitate their easy identification. The genomes of *A. glabrata* did not resemble those of *A. hypogaea* except for the presence of an 'A' chromosome, 2 euchromosomes and 2 nucleolus organisers. *A. glabrata* did not appear to be an amphidiploid but rather an allopolyploid hybrid. The genome of *A. pusilla* contained chromosomes unlike those of any other species of section *Arachis*. It was concluded that both these species are quite unrelated to other species of the section *Arachis*.

Key words: *A. glabrata* – *A. pusilla* – Rhizomatosae – Triseminale – Pachytene chromosome morphology

Introduction

Knowledge of the morphology of the pachytene chromosomes is useful in cytogenetic studies for the identification of chromosomes in different genetic stocks and in the proper understanding of the degree of chromosomal homology and problems of chromosomal aberrations. Such information is necessary for successful cytogenetic research involving alien transfers of genes and genomes. In groundnut *A. hypogaea* L., numerous attempts are currently being made in transferring disease, insect and virus resistance from wild species to the cultivated species (Gregory et al. 1973; Abdou et al. 1974; Smartt et al. 1982 b; Stalker 1978; Stalker 1980; Singh and Moss 1982; Peters et al. 1982). The genus *Arachis* contains 22 published species which have been divided into 7 sections (Gregory et al. 1973). Groundnut belongs to the section *Arachis*. Detailed studies of cross compatibility studies in the genus have revealed that only species of section *Arachis* can be crossed successfully with *A. hypogaea* L. (Gregory et al. 1973; Smartt et al. 1978 b; Gregory and Gregory 1979; Stalker 1981; Singh and Moss 1982). The mitotic chromosomes of *Arachis* species belonging to the section *Arachis* have been well documented (Husted 1931, 1933, 1936; Babu 1955; D'cruz and Tankasale 1961; Gregory et al. 1973; Raman 1976; Moss 1979; Singh et al. 1980; Stalker 1980; Singh and Moss 1982). Studies on the morphology of chromosomes at pachytene, however, have only recently been initiated. Morphology of the chromosomes at pachytene has been studied in *A. hypogaea* (Murty et al. 1982), in *A. villosa, A. chacoense* and *A. batizocoi* (Kirti et al. 1982), in F_1 hybrids of *A. hypogaea* × *A. monticola* (Kirti et al. 1982) and in triploid intrasectional hybrids (Bharathi et al. 1982 c). All of these studies were confined to the section *Arachis*. No such information is available for other sectional species.

The objectives of the present investigation were to gather diagnostic features of the pachytene chromosomes of two species, *A. glabrata* Benth. and *A. pusilla* Benth., belonging to the sections Rhizomatosae and Triseminale respectively, and to compare them with those of section *Arachis*.

Materials and methods

A. glabrata Benth. was obtained in the form of vegetative cuttings from Tamilnadu, Agricultural University, Coimbatore, and *A. pusilla* Benth. (PI No. 33448) was collected from the cytogenetics section of ICRISAT. Herbarium specimens were deposited at Kew Botanical gardens and at Calcutta. The plants were grown in a greenhouse in large cement pots. Material was collected in the summer season of 1981.

Young flower buds were fixed in 1:3 acetic alcohol, the acetic acid fraction being saturated with ferric acetate. After 6 h of fixation, the material was transferred to freshly mixed acetic alcohol without iron-acetate. After fixation for a total period of 24 h, the material was transferred to 70% alcohol and stored at 10 °C. Anthers were squashed in 2% propiono-carmine. Warming in propiono-carmine repeatedly resulted in overstaining. The preparations were destained in 45% acetic acid. In the case of *A. glabrata,* the preparations were examined under the ordinary light microscope but in the case of *A. pusilla,* the preparations could be studied only under the phase contrast microscope. The Leitz ortholux phase contrast system was used. Camera-lucida drawings were made at bench level with Spencer's camera-lucida. Total lengths, lengths of arms and heterochromatin segments were measured with the help of a map measurer. Total length was measured from one end of the chromosome to the other end, excluding the centromere length. Lengths of the arms were also measured similarly. Chromosome pairing was studied at meiosis in both species, at metaphase in at least 30 PMC's. Post metaphase stages were also studied in a varying number of PMC's.

Results

Pachytene chromosomes

A. glabrata

Chromosomes could be distinguished from each other by visual observations and by the varying lengths of various constituents. Morphologically, some of the chromosomes were differentiated into euchromatic and heterochromatic portions. The centromere was generally flanked by prominent heterochromatic blocks. Some chromosomes were completely euchromatic except for the small heterochromatic segments flanking the centromere. The length differences between the chromosomes were progressive, there being no sudden sharp decreases. Seventeen chromosomes had a submedian centromere, two had a subterminal centromere, and one had a median centromere. Surprisingly all 20 chromosomes (Figs. 1–20) could be distinguished from each other individually by the following diagnostic features: 1. total length; 2. arm ratio; 3. nucleous attachment, and 4. proportion and position of heterochromatin. Data on total lengths arm ratios etc. are given in Table 1.

Basically there were five types of chromosomes: 1. completely euchromatic chromosomes; 2. completely or nearly completely heterochromatic chromosomes; 3. chromosomes with terminal heterochromatic segments; 4. chromosomes associated with the nucleolus, and 5. others which did not have any such diagnostic features but were differentiated into eu- and heterochromatic segments.

1 Completely euchromatic chromosomes. Two of the chromosomes were completely euchromatic. Extremely small regions proximal to the centromere gave a heterochromatic reaction enabling the identification of the location of the centromere. One of these is much larger (5, 39.2 μM) than the other (16, 21.4 μM).

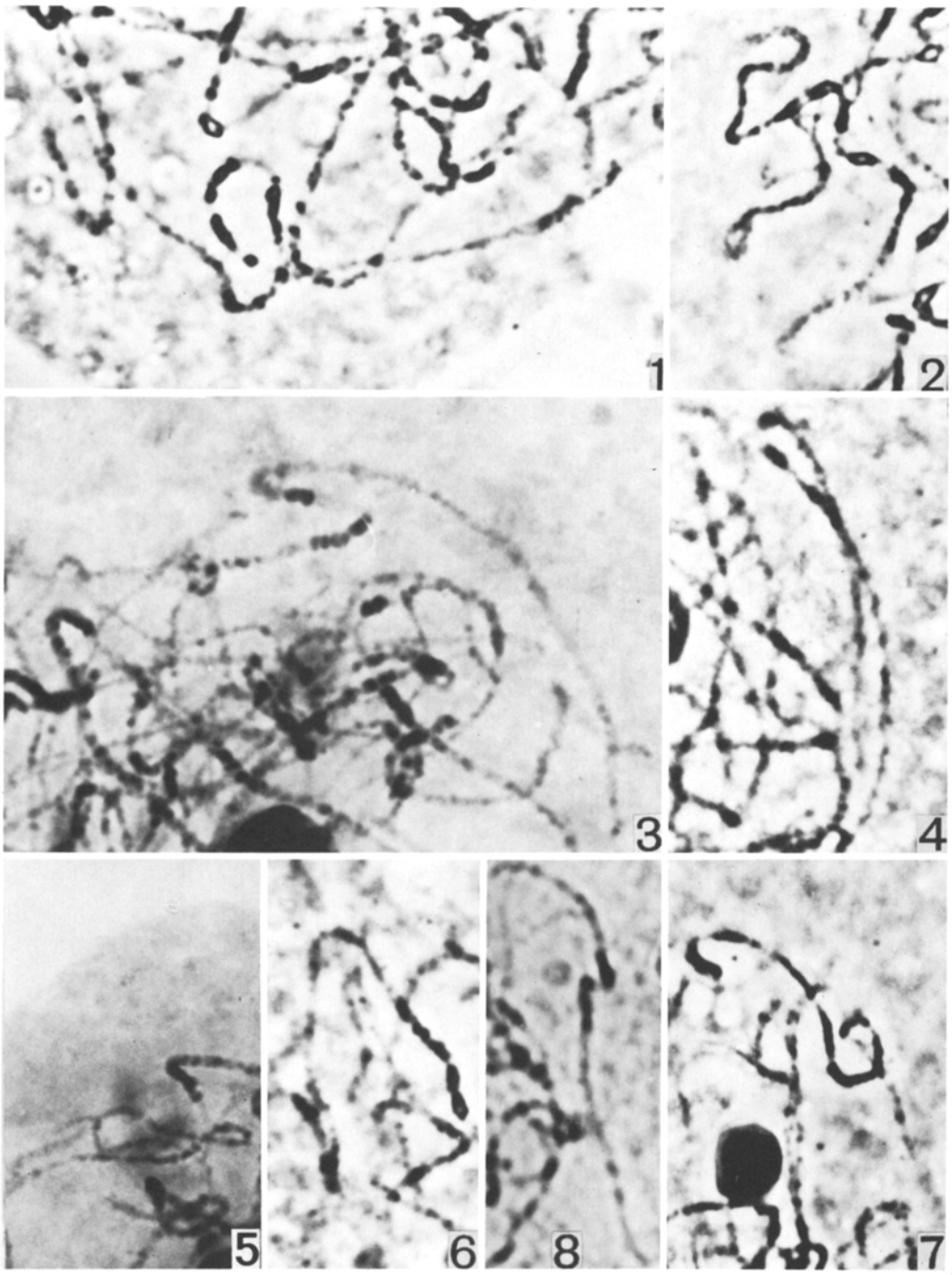
2 Completely or nearly completely heterochromatic chromosomes. Two of these chromosomes were completely heterochromatic or nearly completely heterochromatic. One of these chromosomes is completely heterochromatic; it is also the smallest of the set (20; 8 μM) and corresponds to the 'A' chromosome described in section *Arachis* species (Husted 1933; Murty et al. 1982). The last but one chromosome (19; 17.5 μM) is similar to the 'A' chromosome except that it is slightly longer and has small euchromatic segments in both arms.

3 Chromosomes with terminal heterochromatic segments. Four chromosomes had terminal heterochromatic segments. One of these had such segments in both the long and short arms (chromosome 6; 36.0 μM). In the rest of the three chromosomes only one arm had such a terminal heterochromatic segment. In chromosome 9 (31.5 μM) and chromosome 18 (17.7 μM) the short arms were completely heterochromatic. The former was much longer than the later. Chromosome 12 (28.7 μM) had a terminal heterochromatic segment in the long arm.

4 Chromosomes associated with the nucleolus. Two of the chromosomes were nucleolus organising chromosomes. Both had a similar morphology but one of them had a small heterochromatic segment distal to the short arm (chromosome 13, 28.2 μM) and this could be distinguished from the second nucleolus organising chromosome (11: 29.3 μM) which had a euchromatic segment distal to the short arm.

5 Others. The 10 chromosomes described above could be distinguished visually without making a karyotype analysis. The remainder of the ten chromosomes (1 to 4, 7, 8, 10, 14, 15 and 17) however, not be identified so readily. However, an examination of their lengths and arm ratios enabled a distinction to be made between them without any difficulty.

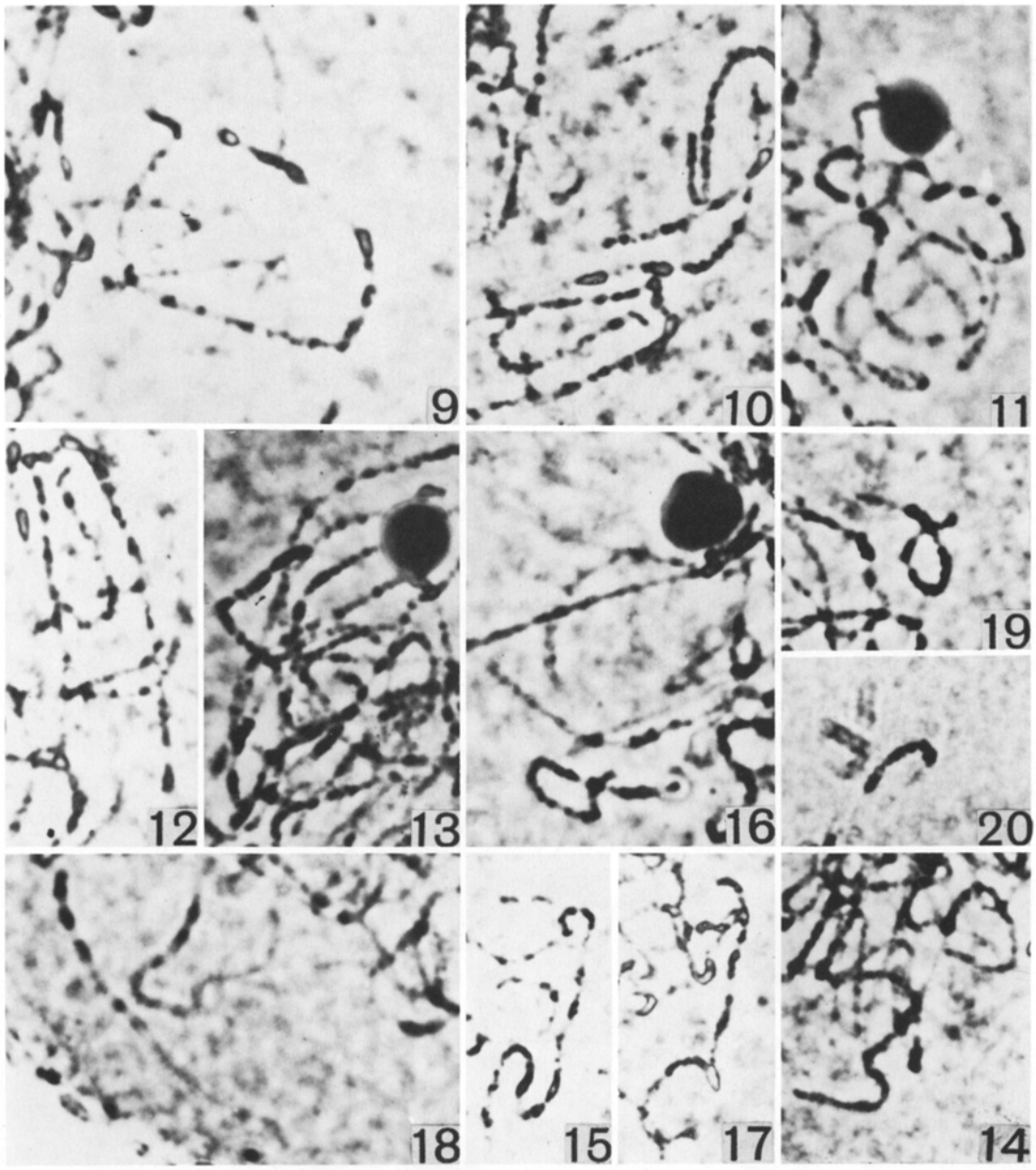
These ten chromosomes were classified into three groups: long chromosomes (40 μM); medium sized chromosomes (40–25 μM) and short chromosomes (25 μM).



Figs. 1 – 8. Pachytene chromosomes of *A. glabrata.* Figure numbers correspond with chromosome numbers

Chromosomes 1 to 4 were long chromosomes, chromosomes 7, 8 and 10 were medium chromosomes and chromosomes 14, 15 and 17 were short chromosomes. The four long chromosomes could be distinguished from each other by the presence or absence of heterochromatic segments other than those flanking the centromere. Chromosome 1 had such segments in both arms, chromosome 2, only in the long arm, chromosome 3 had no such segments and chromosome 4 had such a segment only in the short arm.

Chromosomes 7, 8 and 10 could also be distinguished very easily using the same criterion. Chromo-



Figs. 9 – 20. Pachytene chromosomes of *A. glabrata.* Figure numbers correspond with chromosome numbers

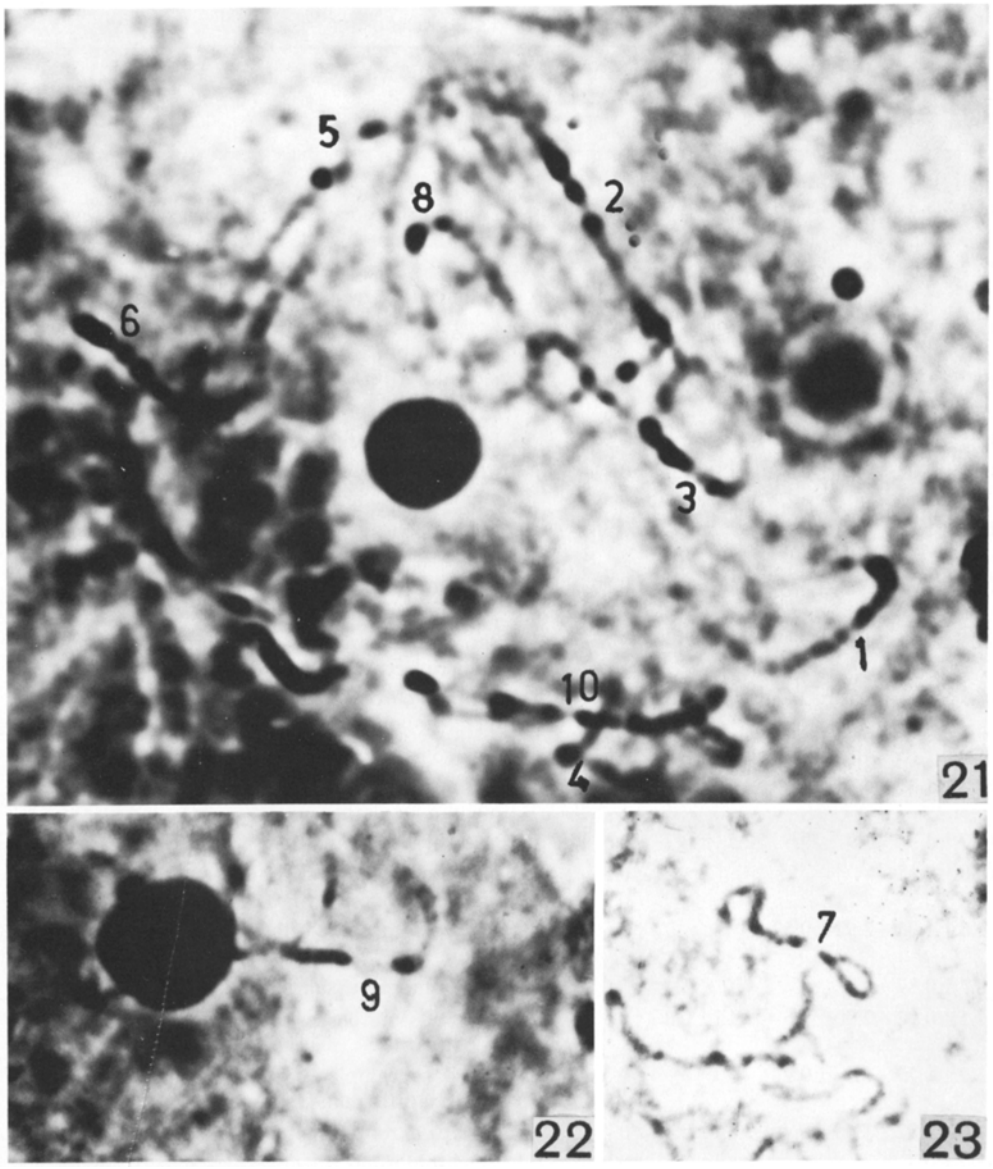
some 7 had heterochromatic segments in the long arm, and chromosome 10 had heterochromatic segments in both the arms while chromosome 8 had no such segments.

The short chromosomes 14, 15, and 17 could be similarly distinguished. The heterochromatic segments were present in the long arm of chromosome 15, in both arms of chromosome 17 and in none of the arms of chromosome 14.

Based on these observations, a key could be devised for the classification and identification of each of the twenty chromosomes.

Table 1. Data on pachytene chromosomes

S. no.	Total	Length (μM)		Heterochromatin (μM)		Arm ratio S.A./L.A.	Diagnostic features
		L.A.	S.A.	L.A.H.	S.A.H.		
I. *A. glabrata*							
1.	48.2±1.97	28.7±1.82	19.5±1.27	4.15±0.57	2.75±0.35	0.67	Long chromosome with heterochromatic segments in both arms
2.	46.8±2.57	30.1±1.80	16.7±1.60	5.8 ±1.15	–	0.54	Long chromosome with heterochromatic segments in long arm
3.	46.7±2.27	29.0±2.12	17.7±1.45	–	–	0.5	Long chromosome without heterochromatic segment in both arms
4.	42.7±1.42	25.0±0.73	17.7±1.45	–	4.4 ±0.5	0.75	Long chromosome with heterochromatic segment in short arm
5.	39.2±4.47	26.7±4.2	12.5±2.25	–	–	0.5	Euchromosome (longer than No. 16)
6.	36.0±	25.0±3.9	11.0±2.02	2.75±0.57	1.75±1.0	0.4	Chromosome with terminal heterochromatic segments in both arms
7.	35.4±0.6	25.2±1.37	10.2±1.25	4.15±0.57	–	0.36	Medium chromosome with heterochromatic segments in long arm
8.	34.2±1.92	21.5±2.25	12.7±1.37	–	–	0.50	Medium chromosome without heterochromatic segments in both arms
9.	31.5±1.72	26.5±1.4	5.0±0.8	1.8 ±0.47	–	0.17	Short arm completely heterochromatic chromosome (longer than No. 18)
10.	30.7±1.32	19.2±1.12	11.5±1.15	3.12±0.6	2.0 ±0.52	0.5	Medium chromosome with heterochromatic segments in both arms
11.	29.3±1.87	16.8±0.62	12.5±1.25	4.3 ±0.5	2.25±0.2	0.6	Nucleolus organiser-I
12.	28.7±2.6	18.2±1.57	10.5±1.3	4.17±1.6	2.67±0.92	0.5	Chromosome with terminal heterochromatic segment in long arm
13.	28.2±5.25	16.5±0.87	11.7±4.3	1.9 ±0.5	2.5 ±0.7	0.6	Nucleolus organiser-2
14.	25.0±0.7	15.0±1.2	10.0±0.87	–	–	0.5	Short chromosome without the heterochromatic segments in both arms
15.	23.6±1.0	14.6±1.27	9.0±1.05	2.92±0.57	–	0.6	Short chromosome with heterochromatic segments in long arm
16.	21.4±2.37	12.7±1.6	8.7±0.87	–	–	0.6	Euchromosome (shorter than No. 5)
17.	20.4±1.62	12.9±1.17	7.5±0.92	2.90±0.6	2.15±0.6	0.5	Short chromosome with heterochromatic segments in both arms
18.	17.7±1.32	14.5±1.27	3.2±0.25	0.5 ±0.2	–	0.2	Short arm completely heterochromatic chromosome (shorter than No. 9)
19.	17.5±0.7	12.5±1.42	5.0±1.92	1.65±0.7	1.65±0.7	0.4	'A' type chromosome
20.	8.0±0.5	4.8±0.3	33.2±0.3	–	–	0.5	'A' chromosome
II. *A. pusilla*							
1.	41.2±0.7	22.2±0.6	18.7±1.3	–	–	0.8	Long median chromosome
2.	39.5±1.0	22.7±1.8	16.8±1.5	0.4 ±0.2	–	0.6	Long sub-median chromosome
3.	31.0±0.4	16.7±0.3	14.2±0.3	0.5 ±0.2	–	0.8	Medium median chromosome
4.	30.5±0.3	20.0±0.2	10.5±1.0	–	–	0.5	Medium sub-median chromosome
5.	30.0±0.8	18.5±0.6	11.5±0.5	–	–	0.5	Euchromosome
6.	26.2±0.5	22.5±0.5	3.75±0.3	0.3 ±0.2	–	0.1	Short arm heterochromatic
7.	25.5±0.3	13.7±0.3	11.7±0.5	–	–	0.8	Short median chromosome
8.	24.7±0.4	16.0±1.07	8.7±1.0	–	–	0.5	Short sub-median chromosome
9	21.5±1.2	12.5±0.5	9.0±0.6	0.2 ±0.2	–	0.6	Nucleolus organiser
10.	21.2±0.6	13.5±1.0	8.7±0.4	1.4 ±1.6	0.8 ±0.2	0.5	'A' type chromosome



Figs. 21 – 23. Pachytene chromosomes of *A. pusilla.* **21** a PMC showing chromosomes 1 – 6, 8 and 10; **22** chromosome 9; **23** chromosome 7

Table 2. Chromosome associations at MI, and laggards and bridges at AI, in *A. glabrata* and *A. pusilla*

S. no.	Species	No. cells analysed	Chromosome associations					Mean no. of half chiasmata chromosome	No. of laggards	No. of bridges
			I	Rod II	Ring II	III	IV			
1.	*A. glabrata*	40	0.5	12.2	5.19	0.2	1.25	1.35	2.24	0.08
2.	*A. pusilla*	40	–	5.09	4.7	–	0.1	1.41	–	–

Key to the identification of the chromosomes in A. glabrata

1.1 Chromosomes completely euchromatic
  1.1.1 Longer chromosome (5, 39.2 μM)
  1.1.2 Shorter chromosome (16, 21.4 μM)
1.2 Chromosomes completely or nearly completely heterochromatic
  1.2.1 'A' chromosome (20, 8 μM)
  1.2.2 'A' type chromosome (19, 17.5 μM)
1.3 Chromosomes with terminal heterochromatic segments
  1.3.1 Chromosomes with terminal heterochromatic segments only
    1.3.1.1 Heterochromatic segments in both arms (6, 36.0 μM)
    1.3.1.2 Heterochromatic segment in the long arm (12, 28.7 μM)
  1.3.2 Chromosomes with completely heterochromatic short arms
    1.3.2.1 Longer chromosome (9, 31.5 μM)
    1.3.2.2 Shorter chromosome (18, 17.7 μM)
1.4 Chromosomes associated with the nucleolus
  1.4.1 Short arm with terminal heterochromatin (13, 28.2 μM)
  1.4.2 Short arm with terminal euchromatin (11, 29.3 μM)
1.5 Chromosomes not falling into any of the above classes
  1.5.1 Long chromosomes
    1.5.1.1 Heterochromatic segments in both arms (1, 48.2 μM)
    1.5.1.2 Heterochromatic segments in the long arm (2, 46.8 μM)
    1.5.1.3 No heterochromatin in either arm (3, 46.7 μM)
    1.5.1.4 Heterochromatic segment in short arm (4, 42.7 μM)
  1.5.2 Medium chromosomes
    1.5.2.1 Heterochromatic segments in long arm (7, 35.4 μM)
    1.5.2.2 No heterochromatic segment in either arm (8, 34.2 μM)
    1.5.2.3 Heterochromatic segments in both the arms (10, 30.7 μM)
  1.5.3 Short chromosomes
    1.5.3.1 No heterochromatic segment in either arm (14, 25.0 μM)
    1.5.3.2 Heterochromatic segments in long arm (15, 23.6 μM)
    1.5.3.3 Heterochromatic segments in both arms (17, 20.4 μM)

Although pairing was good, occasionally unpaired regions were encountered. Large unpaired regions were frequently encountered in chromosome 1.

A. pusilla

Pachytene chromosomes of *A. pusilla* were not condensed and did not stain well. All the chromosomes were to a greater extent, euchromatic. The centromere could be located by the presence of minute deeply staining regions on either side. The karyotype consisted of three metacentric (1, 3, 7) and 6 sub-metacentric (2, 4, 5, 8, 9, 10) chromosomes and one sub telocentric (6) chromosome (Figs. 21–23). A single nucleolus

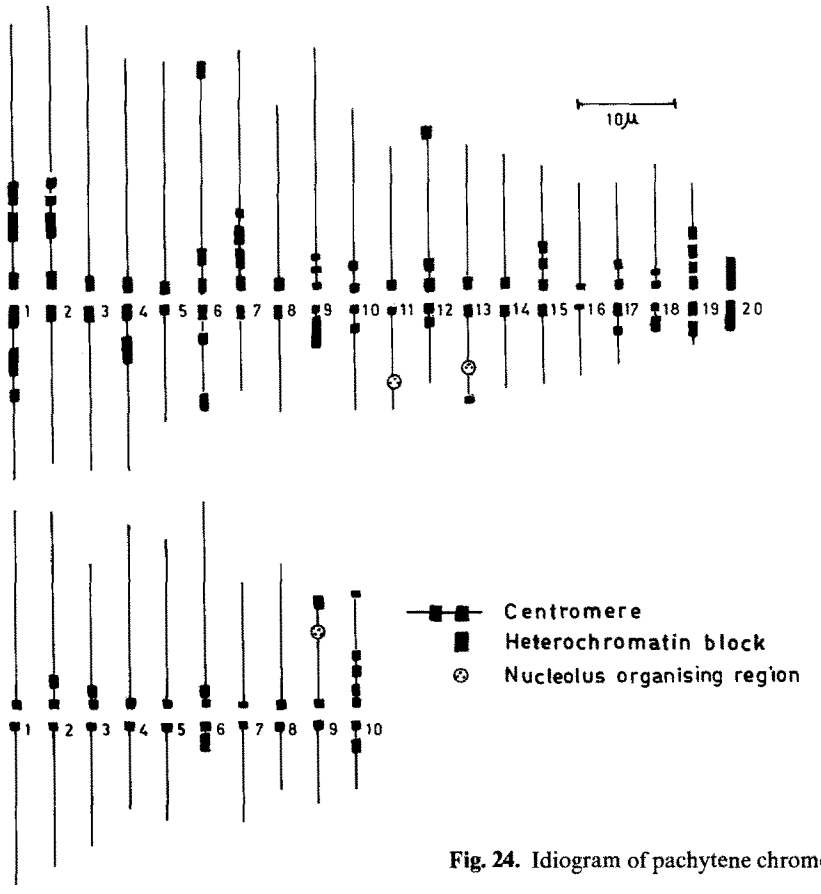


Fig. 24. Idiogram of pachytene chromosomes, *A. glabrata* (*top*) and *A. pusilla* (*bottom*)

organiser was present (9). The chromosomes were medium sized or short. Very long chromosomes were not present although the condensation was less. The total length varied from 21.2 μM to 41.2 μM. Only three chromosomes could be visually distinguished: chromosome 6, which had a completely heterochromatic short arm and a sub-terminal centromere; chromosome 9, the nucleolus organiser, and chromosome 10, which had a greater proportion of heterochromatin and also a terminal heterochromatic segment in the short arm. The remainder of the chromosomes only differed in their total length and arm ratios. Data on total length, arm ratios etc. are given in Table 1 and the karyotypes in Fig. 24.

Post pachytene stages

Meiosis was regular in *A. pusilla,* with complete bivalent formation. The mean chiasma frequency per bivalent was 1.41. Slight irregularities in meiosis could be noted in *A. glabrata.* Out of 40 cells examined at MI, 36 cells contained one or two quadrivalents. A low frequency of univalents and trivalents was also encoutered (Table 2). The mean half chiasma frequency per chromosome was 1.35.

Discussion

Since the classical studies of Husted (1931, 1933, 1936) no attempts have been made until recently to study the chromosomes of *Arachis.* Even in recent times most of the studies have been concentrated on the mitotic chromosomes. The difficult nature of the material and the smaller size of the chromosomes have generally been cited as the difficulties for the meagre studies in the species of *Arachis.* However, Murty and his colleagues were able to successfully study the pachytene chromosomes of *A. hypogaea, A. batizocoi, A. villosa, A. chacoense,* of the hybrid *A. hypogaea* L. × *A. monticola* and of three triploid hybrids (Murty et al. 1982; Kirti et al. 1982; Bharathi et al. 1982 c).

These studies have shown that the identification of pachytene chromosomes of *A. hypogaea* is possible, that the karyotype of *A. hypogaea* L. is composed of two more or less similar genomes and that the genome of section *Arachis* diploid species exhibited a great degree of similarity.

These attempts have been extended in the present study to *A. glabrata* and *A. pusilla* which belong to sections with whose species hybrids have not been frequently reported. Intersectional hybrids of *Arachis* could not be obtained by several authors (Hull and Carver 1938; Gregory 1946; Smartt and Gregory 1967; Pompeu 1977). However, Gopinathan Nair et al. (1964) Raman (1958, 1959a, b, c, 1976) and Varisai Mohammad reported such hybrids (1973 a, b, c).

Pachytene chromosomes of *A. pusilla* were unlike those of section *Arachis* sp. Most of the chromosomes were euchromosomes and did not correspond with those of any other diploid section *Arachis* sp. There was no 'A' chromosome characteristic of section *Arachis* sps. except *A. batizocoi* (Smartt et al. 1978 a); therefore, *A. pusilla* does not seem to have contributed to the origin of groundnut.

Chromosomes of *A. glabrata* were also dissimilar from those of *A. hypogaea* or *A. monticola.* The similarities include only the presence of the A chromosome, two euchromosomes and two nucleolus organizing chromosomes. The dissimilarities are many. The chromosomes of *A. hypogaea* were readily distinguishable into two more or less similar genomes, A and B, confirming the segmental allotetraploid of *A. hypogaea.* Such a genomic differentiation could not be seen in *A. glabrata.*

Chromosomes appeared to have undergone a high degree of differentiation and the species does not appear to be an amphidiploid or allotetraploid. The frequent presence of unpaired regions showed that it is probably a hybrid between two tetraploid species which have yet to be identified. *A. glabrata* is mostly seed sterile and is usually propagated vegetatively by rhizomes. The embryology of *A. glabrata* shows some irregularities (Bharthi et al. 1981, 1982 b). Some atypical embryo sacs, suggestive of apospory, have recently been reported in this species (Bharathi et al. 1982 a). Although fertilization takes place normally, the embryo gets aborted sooner or later. All this evidence suggests that *A. glabrata* probably has a hybrid origin.

In the light of pachytene chromosome morphology, it appears that successful hybridization between *A. hypogaea* and *A. glabrata* will be limited and that even if successful hybrids are obtained, the hybrids will be sterile. The transfer of desirable features, therefore, will be difficult through conventional methods. Successful transfers can be made only through bridge crosses (Stalker 1981), through partial genetic transfer using irradiated pollen, or through genetic engineering techniques.

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