**Chromosome Pairing in the Interspecific Hybrids: *Arachis hypogaea* L. $\times$ *Arachis chacoense* nom. nud.
Krap et Greg. and *A. hypogaea* L. $\times$
A. villosa Benth.**

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The genus *Arachis* consists of 22 published species and 40 or more unpublished and a few unnamed species. These various taxa were grouped into seven sections (Gregory *et al.* 1973). Of these, the cultivated species *A. hypogaea* belongs to, and is crossable to, only the members of the section *Arachis* (Smartt and Gregory 1967, Gregory *et al.* 1973). This section consists of other than *A. hypogaea* and *A. monticola* (another tetraploid with $2n=40$); at least seven diploid species ($2n=20$) of which six carry the A genome (*A. villosa*, PI 219554; *A. chacoense*, PI 276235; *A. correntina*, PI 262808; *A. duranensis*, PI 219823; *A. stenosperma*; *A. cardenasii*, PI 262141) and one the B genome; (*A. batizocoi*, PI 338312). The A genome species contains the classical A chromosome of Husted (1931, '33, '36) while *A. batizocoi* does not have such a chromosome. *A. hypogaea* was assumed to have been derived as an amphiploid of an A and B genome species (Smartt *et al.* 1978). However, detailed studies on pachytene chromosome morphology by Murty and his colleagues (Murty *et al.* 1980, Murty *et al.* 1981, Murty *et al.* 1982, Kirti *et al.* 1982) have indicated that the probability of *A. hypogaea* to have been derived from two A-genome carrying species is as great as that from an A and a B genome species. The present investigation was undertaken to find out precise chromosome homologies of two A genome species *A. chacoense* and *A. villosa* with those of *A. hypogaea* by studying detailed pachytene pairing in the triploid interspecific hybrids.

Plate I. Photomicrographs of the pachytene chromosomes of triploid interspecific hybrids, *A. hypogaea* (TMV-2) $\times$ *A. chacoense* ($2n=30$). Figs. 1-11. 1, long median chromosome (bivalent). 2, long submedian chromosome (bivalent). 3, euchromosome (bivalent). 4, short median chromosome (bivalent). 5, nucleolus organizing chromosome (bivalent). 6, chromosome with heterochromatic short arm (bivalent). 7, medium submedian chromosome (large unpaired regions are present). 8, medium median chromosome (bivalent). 9, short submedian chromosome (bivalent). 10, chromosome with heterochromatic short arm (bivalent). 11, A-chromosome (bivalent).

Plate II. Camera lucida drawings of the pachytene chromosomes of triploid interspecific hybrid, *A. hypogaea* (TMV-2) $\times$ *A. chacoense* ($2n=30$). Figs. 1-11. 1, long median chromosome (bivalent). 2, long submedian chromosome (bivalent). 3, euchromosome (bivalent). 4, short median chromosome (bivalent). 5, nucleolus organizing chromosome (bivalent). 6, chromosome with heterochromatic short arm (bivalent). 7, medium submedian chromosome (large unpaired regions are present). 8, medium median chromosome (bivalent). 9, short submedian chromosome (bivalent). 10, chromosome with heterochromatic short arm (bivalent). 11, A-chromosome (bivalent).

Plate I.

Plate II.

Material and methods

The material consisted of a popular variety of groundnut, TMV₂ and two diploid species *A. chacoense* PI 276235 and *A. villosa* PI 219554. *A. chacoense* was supplied by the cytogenetics section of ICRISAT and *A. villosa* by the Tamilnadu Agricultural University, Coimbatore.

Classical cytological techniques were used, details of which were given by Murty *et al.* (1980, 1982).

Results

In general, there was good amount of pairing resulting in bivalent formation. However, several chromosomes could be seen left unpaired and remaining as univalents (Pls. III and IV). Trivalents and quadrivalents also could be observed. It was not possible to analyse full chromosome complements from single pachytene nuclei. However, several thrown offs could be observed. From the pairing behaviour of the 10 chromosomes, the homologies of the 10 chromosomes of the diploid parent could be deduced. The details of the pairing behaviour of the chromosomes are given below. Details of the different chromosomes in *A. hypogaea*, *A. chacoense* and *A. villosa* are given in Murty *et al.* 1982 and Kirti *et al.* 1982.

1. Chromosome 1 of *A. chacoense*

This chromosome in *A. chacoense* is a long chromosome with a submedian centromere, measuring 63.33 μm . In the hybrid, it was seen to pair with chromosome 1 of *A. hypogaea* which is a long submedian chromosome with a total length of 60.5 μm . However, there was a small unpaired region in the heterochromatic region. (Pl. I, Fig. 2; Pl. II, Fig. 2).

2. Chromosome 2 of *A. chacoense*

This is a long median chromosome with a length of 51.80 μm . This chromosome was seen to pair with chromosome 2 of *A. hypogaea* in the hybrid. In *A. hypogaea*, this is a long median chromosome with a total length of 58.1 μm . These two chromosomes are seen to be completely homologous, pairing fully along their length except for a little unpaired region in one of the arms (Pl. I, Fig. 1; Pl. II, Fig. 1).

3. Chromosome 3 of *A. chacoense*

This is a completely euchromatic chromosome having a total length of 42.05 μm . This chromosome in the hybrid was seen to pair with chromosome 3 of *A. hypogaea* which is completely euchromatic measuring 52.1 μm (Pl. I, Fig. 3; Pl. II, Fig. 3).

4. Chromosome 4 of *A. chacoense*

This is a medium sized chromosome with a median centromere, measuring 36.83 μm . In the hybrid, it was seen to pair with chromosome 9 of *A. hypogaea* which is also a medium sized chromosome with a median centromere having a total length of 31.3 μm . However this pairing is partial, there being a long unpaired region in one of the arms (Pl. I, Fig. 8; Pl. II, Fig. 8).

5. Chromosome 5 of *A. chacoense*

This is a medium sized submedian chromosome having a total length of 35.55 μm . This chromosome in the hybrid is seen to pair with chromosome 8 of *A. hypogaea* which is a medium sized chromosome with a submedian centromere and length of 32.51 μm (Pl. I, Fig. 7; Pl. II, Fig. 7).

6. Chromosome 6 of *A. chacoense*

This is a short chromosome with a median centromere. It is having a total length of 28.55 μm . This chromosome in the hybrid was seen to pair with chromosome 15 of *A. hypogaea* (Pl. I, Fig. 4; Pl. II, Fig. 4).

7. Chromosome 7 of *A. chacoense*

This is a short submedian chromosome with a total length of 26.13 μm . In the hybrid, this chromosome was seen to pair with chromosome 16, which is short and submedian with a length of 24.0 μm in *A. hypogaea*. These two chromosomes are seen to pair completely in the hybrid (Pl. I, Fig. 9; Pl. II, Fig. 9).

8. Chromosome 8 of *A. chacoense*

This is the nucleolus organizing chromosome having a length of 24.00 μm . This chromosome is completely homologous to the 12th chromosome of *A. hypogaea* which is also a nucleolus organizing chromosome with a total length of 28.8 μm . These two chromosomes in the hybrid were seen to pair completely with each other (Pl. I, Fig. 5; Pl. II, Fig. 5).

9. Chromosome 9 of *A. chacoense*

It is a chromosome with completely heterochromatic short arm with a total length of 23.50 μm . This chromosome in the hybrid was seen to pair with chromosome 14, which is a long chromosome with completely heterochromatic short arm with a length of 25.7 μm of *A. hypogaea* (Pl. I, Fig. 10; Pl. II, Fig. 10). However, in some PMCs it was observed that this chromosome also paired with chromosome 19 of *A. hypogaea*, which also has a heterochromatic short arm with a total length of 15.4 μm . These chromosomes pair completely in the heterochromatic region, the euchromatic region, however, remained unpaired (Pl. I, Fig. 6; Pl. II, Fig. 6).

10. Chromosome 10 of *A. chacoense*

This is the shortest chromosome of the set, which is completely heterochromatic. This chromosome has a total length of 14.58 μm and represents the 'A' chromosome. This is completely homologous with chromosome 20 of *A. hypogaea*. These two chromosomes were seen to pair completely in the hybrid (Pl. I, Fig. 11; Pl. II, Fig. 11).

Although multivalents, like trivalents and quadrivalents were observed, they could not be identified accurately because of the extensive clumping of the chromosomes.

B. *A. hypogaea* $\times$ *A. villosa*

1. Chromosome 1 of *A. villosa*

This chromosome in *A. villosa* is a long submedian chromosome having a total length of 60.99 μm . In the hybrid this chromosome was seen to pair with chromosome 1 of *A. hypogaea* which is a long chromosome with a submedian centromere having a total length of 60.5 μm . However, some unpaired regions were ob-

served occasionally (Pl. V, Fig. 2; Pl. VI, Fig. 2).

2. Chromosome 2 of *A. villosa*

This is a long chromosome with a median centromere, with a total length of $46.02\ \mu\text{m}$. This chromosome in the hybrid was seen to pair with chromosome 5 of *A. hypogaea* which is a long median chromosome having a total length of $42.0\ \mu\text{m}$ (Pl. V, Fig. 1; Pl. VI, Fig. 1).

3. Chromosome 3 of *A. villosa*

This is a medium sized chromosome with a submedian centromere with a total length of $37.50\ \mu\text{m}$. This chromosome in the hybrid was seen to pair with chromosome 7 of *A. hypogaea* which is a medium submedian chromosome having a total length of $31.8\ \mu\text{m}$ (Pl. V, Fig. 3 (left); Pl. VI, Fig. 3).

4. Chromosome 4 of *A. villosa*

This is a medium sized chromosome with a median centromere. In the hybrid this chromosome was seen to pair with chromosome 9 of *A. hypogaea*. In this chromosome pair, a small unpaired region was observed in the long arm (Pl. V, Fig. 4; Pl. VI, Fig. 4).

Plate III. Photomicrographs of the pachytene chromosomes of triploid interspecific hybrid, *A. hypogaea* (TMV-2) $\times$ *A. chacoense* ($2n=30$). Figs. 1-5. 1, long submedian chromosome (I). 2, medium median chromosome (II). 3, long medium chromosome (I). 4, medium submedian chromosome (II). 5, chromosome with heterochromatic short arm (I).

5. Chromosome 5 of *A. villosa*

This is a short chromosome with a median centromere, with a total length of $25.30\ \mu\text{m}$. This chromosome in the hybrid was seen to pair with chromosome 16 of *A. hypogaea*, which is a short median chromosome measuring $24.9\ \mu\text{m}$ (Pl. V, Fig. 5; (Bottom) Pl. VI, Fig. 5).

6. Chromosome 6 of *A. villosa*

This is a short chromosome with a submedian centromere, measuring $24.0\ \mu\text{m}$. In the hybrid this chromosome was seen to pair with chromosome 15 of *A. hypogaea*. In this chromosome pair, a small unpaired region was observed in the long arm (Pl. V, Fig. 7; Pl. VI, Fig. 7).

7. Chromosome 7 of *A. villosa*

This is a euchromosome, with a total length of $23.56\ \mu\text{m}$. This chromosome in the hybrid was seen to pair with chromosome 11 of *A. hypogaea* (Pl. V, Fig. 3 (right); Pl. VI, Fig. 3).

8. Chromosome 8 of *A. villosa*

This is a chromosome with a completely heterochromatic short arm, measuring $19.83\ \mu\text{m}$. This

Plate IV. Camera lucida drawings of the pachytene chromosomes of triploid interspecific hybrid, *A. hypogaea* (TMV-2) $\times$ *A. chacoense* ($2n=30$). Figs. 1-5. 1, long submedian chromosome (I). 2, medium median chromosome (II). 3, long median chromosome (I). 4, medium submedian chromosome (I). 5, chromosome with heterochromatic short arm (I).

Plate V. Photomicrographs of the pachytene chromosomes of triploid interspecific hybrid, *A. hypogaea* (TMV-2) $\times$ *A. villosa*. Figs. 1-8. 1, long median chromosome (bivalent). 2, long submedian chromosome (bivalent). 3, euchromosome (bivalent) (right); medium submedian chromosome (bivalent) (left). 4, medium median chromosome (bivalent). 5, nucleolus organizing chromosome (bivalent) (top); short median chromosome (bivalent) (bottom). 6, chromosome with heterochromatic short arm (bivalent). 7, short submedian chromosome (bivalent). 8, A-chromosome (bivalent).

Plate VI. Camera lucida drawing of the pachytene chromosome of triploid interspecific hybrid, *A. hypogaea* (TMV-2) $\times$ *A. villosa*. Figs. 1-8. 1, long median chromosome (bivalent). 2, long submedian chromosome (bivalent). 3, euchromosome (bivalent) (right); medium submedian chromosome (bivalent) (left). 4, medium median chromosome (bivalent). 5, nucleous organizing chromosome (bivalent) (top); short median chromosome (bivalent) (bottom). 6, chromosome with heterochromatic short arm (bivalent). 7, short submedian chromosome (bivalent). 8, A-chromosome (bivalent).

chromosome in the hybrid was seen to pair with chromosome 19 of *A. hypogaea*, which is the second (short) chromosome with completely heterochromatic short arm, with a total length of $15.4\ \mu\text{m}$ (Pl. V, Fig. 6; Pl. VI, Fig. 6).

9. Chromosome 9 of *A. villosa*

This is a nucleolus organising chromosome with a total length of $15.56\ \mu\text{m}$. This chromosome has a nucleolus organizing region in the submedian position. In the hybrid, the chromosome was seen to pair with chromosome 13 of *A. hypogaea* (Pl. V, Fig. 5 (top); Pl. VI, Fig. 5).

10. Chromosome 10 of *A. villosa*

This is the A-chromosome. It has a total length of $12.14\ \mu\text{m}$. The A-chromosomes of both the species paired perfectly. The length difference measured in individual species was seen to disappear in the hybrid (Pl. V, Fig. 8; Pl. VI, Fig. 8).

Discussion

A. hypogaea contains two genomes, the A and the B. Although several A genome species were identified among the section *Arachis*, there is only one B-genome species, i.e. *A. batizocoi*. Murty *et al.* (1980) characterised the A-genome as consisting of the A-chromosome; a chromosome with completely heterochromatic short arm; a euchromosome; a nucleolus organizer; 2 long chromosomes; 2 medium and 2 short chromosomes. Each of these chromosomes could be distinguished on the basis of centromere position. The B-genome was characterized as consisting of the B-chromosome (chromosome with 2 large heterochromatin blocks in short arm); a chromosome with completely heterochromatic short arm; a euchromosome; a nucleolus organizer; the long median, the long submedian, the medium median, the medium submedian, the short median and the short submedian chromosomes. The genomes of *A. villosa* and *A. chacoense* compared more or less with the A-genome. However, *A. villosa* differs from *A. chacoense* in the morphology of the nucleolus organizer. *A. hypogaea* has two nucleolus organizer chromosomes each of them pairing with the corresponding nucleolus organizing chromosomes of *A. villosa* and *A. chacoense*.

The genomes of *A. hypogaea* have been much discussed. The presence of occasional quadrivalents and the presence of a single pair of A-chromosomes have led to the designation of *A. hypogaea* as a segmental allotetraploid (Stebbins 1957). One or the other of the 'A' genome species has been suggested as at least one of the putative parents of *A. hypogaea* by several workers from time to time (Varisai Muhammed 1973, Seetaram *et al.* 1973, Gregory and Gregory 1976, Smart *et al.* 1978). Ressler *et al.* (1981) concluded from their studies on estimations of DNA, that it may not be possible to identify the genomes of *A. hypogaea*. However, pachytene analysis has given some concrete information on this point.

Chromosome pairing results of the present investigation suggest that both *A. villosa* or *A. chacoense* although have homologous partners in *A. hypogaea*, have minor structural differences in the form of unpaired regions and heteromorphic bivalents. Reports of chromosome pairing in the hybrid between A and B genome

species (Stalker and Wynne 1979) suggest that *A. batizocoi* has at least 8 chromosomes homologous with those of the A-genome species. If the chromosomes of *A. chacoense* and *A. villosa* paired predominantly with the A-genome of *A. hypogaea* and if the other chromosomes of *A. hypogaea* originated from *A. batizocoi*, then one should expect at least 8 trivalents in such hybrids. Non occurrence of such a high frequency of trivalents suggests 3 possibilities.

1. That the B-genome of *A. hypogaea* may not be from *A. batizocoi*.
2. There is preferential pairing between homeologous chromosomes.
3. Extensive structural alterations leading to the differentiation of A and B genomes.

From this discussion it is apparent that the classification of the genomes of *A. hypogaea* into A and B is only tentative. There is extensive structural repatterning in the A-genome species. There are evidences for structural changes in the genomes of *A. hypogaea* also so as to result in predominant bivalent formation. Evidence for concluding structural alterations was obtained from the occasional presence of unpaired regions and heteromorphic bivalents.

Summary

Chromosome pairing at the pachytene stage of meiosis was studied in triploid hybrids involving *A. hypogaea*, and *A. chacoense* and *A. villosa*. There was very good pairing at least in respect of 10 chromosomes. Unpaired regions and heteromorphic bivalents were observed occasionally. Chromosome pairing indicated a close relation among the 3 species. *A. hypogaea* has 10 chromosomes in common with *A. chacoense* and *A. villosa* although the 10 chromosomes of each these species are not necessarily homologous. Evidence was obtained for the existence of structural repatterning in the A-genome species and also in the genomes of *A. hypogaea*. The information obtained was utilised in the discussion of the origin of *A. hypogaea*.

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