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THE GENOMES OF *ARACHIS HYPOGAEA*. 1. CYTOGENETIC STUDIES OF PUTATIVE GENOME DONORS[1]

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SUMMARY

Cytological studies of wild diploid *Arachis* species in the same section of the genus (sect. *Arachis*) as the cultivated peanut *A. hypogaea* L. show, with one exception, a karyotype characterized by the presence of 9 pairs of larger chromosomes and one pair of small ('A') chromosomes. The exceptional species *A. batozocoi* KRAP. et GREG. has a more uniform karyotype. Interspecific hybrids between diploid species of similar karyotype have moderate to high pollen stainability, those involving *A. batizocoi* have zero pollen stainability and a very irregular PMC meiosis. Such infertile hybrids are the most likely to produce fertile, stable amphidiploids on doubling the chromosome complement. It is suggested that the cultivated peanut could have originated from such a sterile interspecific hybrid and on morphological and phytogeographic grounds the most likely genome donors are *A. cardenasii* (nomen nudum) and *A. batizocoi* of the species within section *Arachis*, which have been collected up to the present time.

INTRODUCTION

HUSTED (1933, 1936) reported a chromosome complement of 2n = 40 in the cultivated peanut *Arachis hypogaea* L. Chromosome complements of 2n = 40 and 20 have been reported from wild species (MENDES, 1947; KRAPOVICKAS & RIGONI, 1952; SMARTT, 1964). The occurrence of two such series of chromosome numbers indicates that the cultigen is a polyploid. This evidence supports the suggestion made initially by HUSTED (1936) who observed multivalents in meiosis of *A. hypogaea*. He was also able to recognize two distinct chromosome pairs, one he termed 'A' chromosomes, which were distinctly smaller than any others and 'B' chromosomes which had a secondary constriction and were satellited. SMARTT (1964) suggested that the occurrence of only a single pair of 'A' chromosomes in the complement was indicative of cytological differentiation between two genomes present in *A. hypogaea*. He reported that he was able to find 'A' chromosomes in the genome of several diploid species which were cross-compatible with the cultivated form but unable to find them in a representative of the erectoid section, *A. paraguariensis* CHOD. et HASSL. (9646 GKP, PI 262842 and PI 262874). The latter

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cannot, however, be crossed with *A. hypogaea*. Despite the reports by RAMAN (1976) to the contrary, we have not been able to cross *A. hypogaea* with any species of section ERECTOIDES or with any species outside of section ARACHIS to which *A. hypogaea* belongs. RAMAN (1976) and other members of his laboratory are alone in reporting hybrids between *A. hypogaea* and any wild species of *Arachis* outside of section ARACHIS. Meantime, GREGORY & GREGORY (1976) postulated that *A. hypogaea* arose from the chromosome doubling of an intrasectional species hybrid within section ARACHIS.They suggested that some species such as the perennial *A. cardenasii*[4] and the annual species *A. duranensis*[4] may have been involved in the initial hybrid. The present account records an investigation of those genomes which can be characterized by the presence of a single pair of 'A' chromosomes and those in which they are absent. All of the species studied are known to be cross-compatible with the cultivated peanut. These species are in section ARACHIS of the genus as are *A. hypogaea* and *A. monticola* KRAP. et RIG., the only known 4x wild counterpart of *A. hypogaea* (KRAPOVICKAS, 1973).

MATERIALS AND METHODS

The materials used were perennial and annual species of section ARACHIS (syn. AXONOMORPHAE) collected variously by Gregory (G), Hammons (H), Krapovickas (K), Langford (L), and Pietrarelli (P). These are listed in Table 1; this information is summarized and abstracted from GREGORY et al. (1973). All forms examined are morphologically distinct types, not all of which have been taxonomically described.

Mitotic chromosome preparations were made according to the technique of TJIO & LEVAN (1950) in the periods 1962–64 and 1976. In the latter period paradichlorobenzene was used as a spindle inhibitor in place of 8-hydroxyquinoline. When this material was used, there was less tendency for chromosomes to stick together; as a result, rather better squashes were obtained and a better presentation of chromosomes was achieved. Considerable attention had to be paid to obtaining a satisfactory spread of chromosomes by careful tapping out of particular cells after squashing. It was particularly important to apply sufficient pressure on individual cells to spread not only the larger chromosomes (ca. 2.5 μm in length), but also the 'A' chromosomes which were approximately one-half the length (ca. 1 μm) of the larger.

Meiotic studies were carried out on a selected range of parental species and interspecific hybrids. Flower buds 2 mm in length were selected and fixed in 3:1 absolute alcohol:glacial acetic acid for 24 hours and then stored in 70% alcohol until required. Anthers were dissected out and PMCs removed by extrusion from pollen sacs after the anther tips were removed. Chromosomes were stained in propionocarmine without mordant.

Stainability of pollen in parental species and interspecific hybrids was studied in extracted pollen after staining in a mixture of 1:1, 2%aceto-carmine:glycerine and warming. Five hundred grains in randomly selected plantes were counted.

[4] *Nomina nuda*

Table 1. List of species used and their provenance.

Collectors	Collection No.	U.S. Plant Intro. No.	Date	Name	Life form	Locality
K		210554	?	*A. villosa* BENTH.	Perennial	Colonia, Uruguay
K	7988	219823	1953	*A. duranensis** KRAP. et Greg. (unpub.)	Annual	Campo Duran, Argentina
K	9484	338312	1958	*A. batizocoi* KRAP. et GREG.	Annual	Parapetí, Bolivia
GKP	9530–31	262808 262809 262880	1959	*A. correntina* (BURK.) KRAP. et GREG. (unpub.)	Perennial	Corrientes, Argentina
GKP	9901	262270 262290	1959	*A.* sp.	Perennial	Cuiabá, Mato Grosso, Brazil
GKP	8826	262275 263200	1959	*A. helodes* (MART.) KRAP. et RIG.	Perennial	Cuiabá, Mato Grosso, Brazil
GKP	10017	262141	1959	*A. cardenasii** KRAP. et GREG. (unpub.)	Perennial	Roboré, Bolivia
GKP	10038	263133	1959	*A.* sp.	Annual	Salta, Argentina
GKP	10602	276235	1961	*A. chacoense** KRAP. et GREG. (unpub.)	Perennial	Puerto Casado, Paraguay
HL	410	338280	1968	*A.* sp.	Annual	Porto Dom Pedro II, Paraná, Brazil

* *Nomina nuda.*

RESULTS AND DISCUSSION

The chromosome complements of the species within section ARACHIS were characterized as far as possible. Characteristic 'A' chromosomes were found in all species of the section examined with the exception of *A. batizocoi*. Photomicrographs of the chromosome complements of *A. cardenasii* and *A. batizocoi* are presented in Figures 1–2. The presence of 'A' chromosomes in the complement of *A. cardenasii* is also apparent in meiotic metaphase I chromosomes (Figure 3).

The choice of hybrids for meiotic study was made after a preliminary investigation of pollen stainability in all available interspecific hybrid combinations. Following the axiom that sterile F_1 hybrids are likely to produce the more fertile and stable

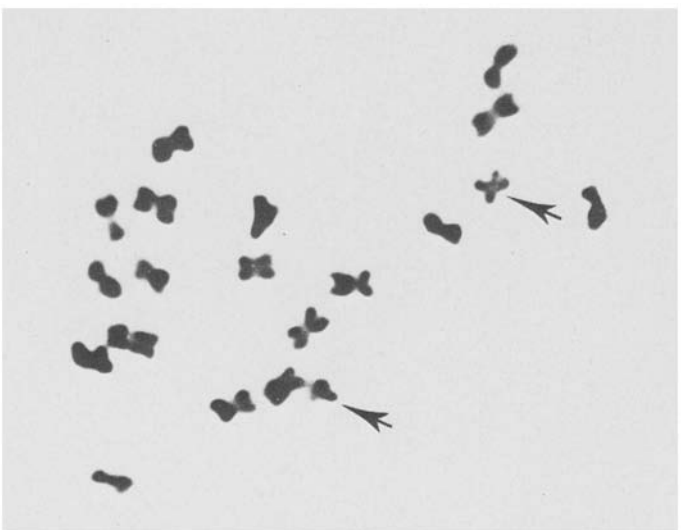

Fig. 1. *Arachis cardenasii*. Somatic (root-tip) chromosomes (note presence of 'A' chromosomes – arrowed). (× 2000; stained acetic orcein).

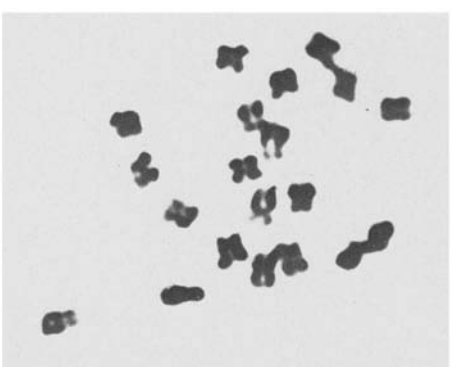

Fig. 2. *Arachis batizocoi*. Somatic (root-tip) chromosomes (note relative uniformity in size of chromosomes). (× 2000; stained acetic orcein).

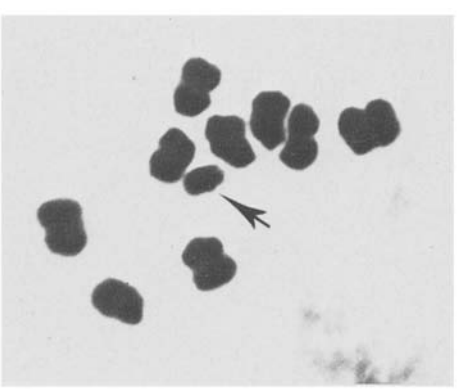

Fig. 3. *Arachis cardenasii*. PMC meiosis–metaphase I (note 'A' bivalent arrowed). (× 2500; stained propiono carmine). Preparation courtesy P. M. Resslar.

amphidiploids, particular attention was paid to interspecific hybrids producing low stainable pollen counts. GIBBONS & TURLEY (1967) reported results of attempted hybridization between diploid species of section ARACHIS and noted that hybrids involving *A. batizocoi* were highly sterile whereas those with others were appreciably more fertile. GREGORY & GREGORY (unpublished) have made an extensive range of crosses involving species of all sections and have observed that crosses involving *A. batizocoi* and other members of section ARACHIS are mostly sterile, whereas crosses between other species within section ARACHIS are of varying fertility. In the present study the lowest counts (near zero) were produced by hybrids involving *A. batizocoi* (Table 2). The few stainable pollen grains produced by these hybrids were large and may have contained unreduced chromosome complements. Some remarkably high counts (>90%) were also produced in, e.g., *A. correntina* × *A. villosa*, *A. villosa* × *A. cardenasii* and *A.* sp. 410 × *A. chacoense* which were not greatly different from the high percentages produced by parental species. Some caution is necessary in interpreting pollen stainability data. Although different environmental conditions may alter stainabilities, the level of 2% stainable pollen recorded for some samples from *A. batizocoi* × *A. cardenasii* is unusually high. It is also noteworthy that certain reciprocal hybrids differ quite markedly in pollen stainability, e.g., *A. villoda* × *A. cardenasii* and *A. cardenasii* × *A. villosa*. Where such differences occur, this can be seen to be due to a rather late onset of pollen grain degeneration producing rather irregular staining in one F_1 and more normal development in its reciprocal.

Meiotic studies of F_1 hybrids were concentrated on the hybrid *A. cardenasii* × *A. batizocoi* of which abundant material was available. Meiosis in this hybrid was extremely irregular (Figure 4), the maximum number of bivalents observed in any plate was six, disjunction was highly irregular and unequal distribution of chromosomes occurred more often than not (Table 3). Anaphase I bridges were seen in approximately

Table 2. Pollen stainability of interspecific F_1 hybrids within section ARACHIS (% stained grains).

	Pollen parents							
Seed parents	*A. villosa*	*A.* sp. 10038	*A. batizocoi*	*A. correntina*	*A. cardenasii*	*A. chacoense*	*A. duranensis*	*A.* sp. 410
A. villosa	---	23.7	–	82.6	90.1	68.1	–	30.0
A. sp. 100038	–	---	0.4	34.8	15.2	–	–	33.0
A. batizocoi	–	–	---	0.2	2.0	0.0	0.0	
A. correntina	95.7	34.4	0.5	---	52.7	43.1	36.0	19.8
A. cardenasii	40.4	47.5	0.0	63.5	---	25.5	62.0	60.8
A. chacoense	25.8	38.8	–	26.7	39.1	---	35.5	91.4
A. duranensis	–	25.8	–	78.3	73.7	–	---	22.9
A. sp. 410	28.1	–	–	44.3	62.8	83.7	22.6	---

Table 3. Meiotic irregularieties in the hybrid *A. cardenasii* × *A. batizocoi*.

Anaphase 1 bridges	0	1	2	3	4	5	6	Total
Frequency	125	7	12	12	10	1	1	168

Metaphase 2 complements	13+7	12+8	11+8+1	11+9	10+10	10+9+1	Total
Frequency	3	6	2	21	8	2	42

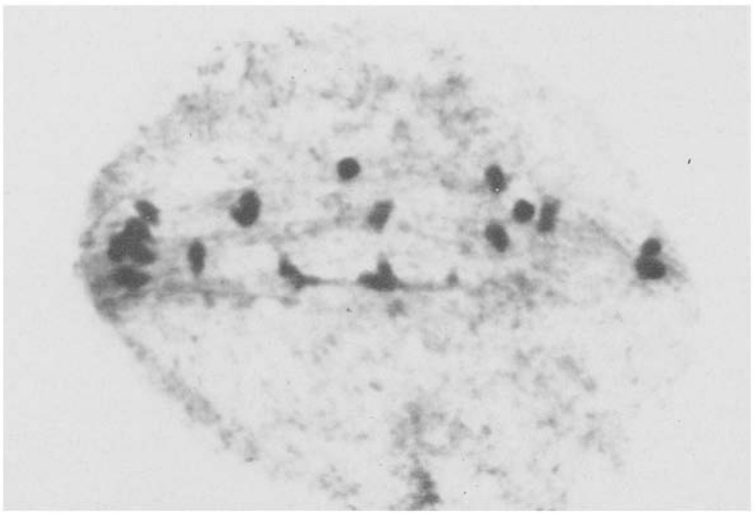

Fig. 4. *A. cardenasii* × *A. batizocoi.* PMC meiosis–anaphase I (note irregular disjunction). (×2000; stained propiono carmine).

one quarter of the plates observed (Figure 4). Irregularities in quartet production took the form either of microcytes or of micronuclei (Figures 5 and 6).

The observations by HUSTED (1936) of the occurrence of a single pair of 'A' chromosomes in *A. hypogaea* and the production in meiosis of occasional quadrivalents in this species carried important implications. First, a detectable divergence of the two genomes in their karyotype has occurred and second, the two genomes are still sufficiently homologous to pair to some extent. The single pair of 'A' chromosomes can be con-

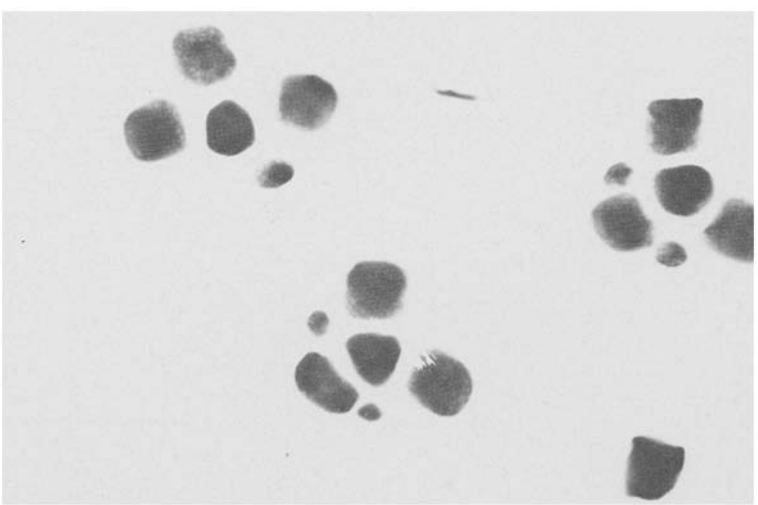

Fig. 5. *A. cardenasii* × *A. batizocoi.* PMC meiosis–quartet fomation with additional microcytes. (×300; stained aceto carmine).

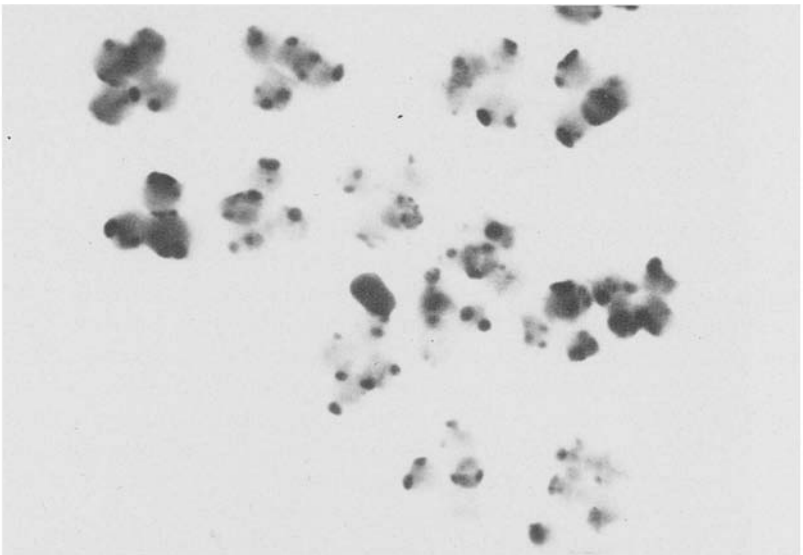

Fig. 6. *A. cardenasii* × *A. batizocoi*. PMC meiosis–quartet fomation with micronuclei. (× 200; stained aceto carmine).

sidered as a genome marker since it is characteristic of some species and absent in others (SMARTT, 1964). The results here reported indicate that there are a number of potential donor species of the 'A' chromosome or 'A' genome from section ARACHIS, while only a single species, namely *A. batizocoi* could have been the donor of the 'B' genome (i.e., that without the small 'A' chromosome). The choice of the most likely 'A' genome donor can be made on morphological and phytogeographical considerations. The species which most closely resembles *A. hypogaea* among the wild diploids is *A. cardenasii* which was collected in Bolivia 18°20'S, 59°46'W at Roboré, a locality not very far removed from that from which *A. batizocoi* was collected in the same country at 20°5'S, 63°14'W. It is therefore quite possible that the actual present distribution of these forms overlaps or has in the past overlapped and also that these species could actually have come into contact and hybridized.

While it is possible that the production of an amphidiploid from the F_1 interspecific hybrid *A. cardenasii* × *A. batizocoi* might in effect be a recapitulation of events in the evolution of *A. hypogaea*, there are good prospects of producing a whole series of new amphidiploids betweeen *A. batizocoi* and all 'A' genome-carrying species of section ARACHIS.

SMARTT (1964) noted the production of a near-tetraploid (2n = 38) spontaneously by the F_1 hybrid *A. hypogaea* × *A. cardenasii*, while KRAPOVICKAS et al. (1974) have observed tetraploid progeny from the hybrid *A. hypogaea* × *A. batizocoi*.It has subsequently been observed that the progenies of the colchicine-induced hexaploid, produced from the F_1 hybrid *A. hypogaea* × *A. cardenasii*, tend to regress to the tetraploid level. Known cytogenetic systems can explain how these events could come about. Tetraploids or near-tetraploids could arise in three different ways from triploid

F_1 hybrids. If pairing was predominantly II + I and all univalents were included in the same nucleus, a diploid and a haploid chromosome complement would arise from meiosis I. Fusion of two diploid nuclei arising in this way would give a tetraploid. Alternatively, the haploid nucleus produced could fuse with an unreduced gametic nucleus. However, this would give rise to an unbalanced tetraploid with 3A + B genomes, only the first alternative would give a balanced tetraploid with 2A + 2B genomes.

The origin of tetraploids from hexaploids can be explained by a tendency to quadrivalent formation, since genomic constitution would be AAAABB, progressive loss of 'A' genome chromosomes could continue by unequal chromosome segregation until stability was achieved at the tetraploid level (AABB). Aneuploidy is apparently tolerated well in *Arachis* between the tetraploid and hexaploid levels (SMARTT & GREGORY, 1967). Pentaploids, near pentaploids, hexaploids and near hexaploids have all arisen spontaneously from the F_1 *A. hypogaea* × *A. cardenasii*, *A. hypogaea* × *A. villosa* and *A. hypogaea* × *A. correntina* hybrids, all of which presumably could be unstable and tend as the colchicine-induced hexaploid to regress to tetraploids.

'A' genomes are found in at least nine species of section ARACHIS. The specific divergence is apparent in the pollen stainability figures of GIBBONS & TURLEY (1967) and in Table 2. In *A. villosa* × *A. correntina* pollen stainabilities of 96.5% and 82.6%, respectively, were recorded, while in *A.* sp. 10038 × *A. duranensis* and its reciprocal it was 50.9% and 25.8%, respectively. This indicates relatively little genetic divergence between the first pair of species and appreciably more between the second. Further studies along these lines are indicated as well as concurrent studies of meiosis in parent species and their hybrids.

Preliminary studies (SMARTT, 1964) have been carried out on meiosis in some triploid F_1 hybrids – *A. hypogaea* × *A. correntina*, *A. hypogaea* × *A. duranensis* and *A. hypogaea* × *A. helodes* – in which trivalent counts for 20 cells in each were 0.95 (range 0–2), 2.15 (range 0–5) and 3.40 (range 0–6), respectively. These figures indicate diminishing homology of the 'A' genomes of the diploid wild species with that of *A. hypogaea*, *A. helodes* < *A. duranensis* < *A. correntina*. The argument in support of this contention is that the more homologous the chromosomes of the introduced 'A' genome are with those of the 'A' genome of *A. hypogaea*, the more these will tend to pair to the exclusion of chromosomes of the third genome present (the 'B' genome of *A. hypogaea*).

On the basis of the present hypothesis the hybridization between the putative parental species followed by doubling of chromosome complement should give a form rather similar to *A. monticola*. This wild peanut is perfectly cross-compatible with cultivated *A. hypogaea* and the two can reasonably be regarded as constituting a single biological species. GIBBONS (1966) made a study of branching patterns in *A. monticola* and found that the same two branching patterns, sequential and alternate, occurred as in *A. hypogaea*. These branching patterns can be related to those of the putative parental species. In *A. cardenasii* an occasional vegetative branch interrupts the otherwise sequential system, whereas in *A. batizocoi* branching is mostly sequential. The characteristic branching of these forms does not find expression in subsp. *hypogaea* (alternate) but resembles that of subsp. *fastigiata* (sequential) of the cultigen. Segregation for these characters could have been initiated by mutation and exchange of

segments between homoeologues from the 'A' and 'B' genomes and subsequent segregation. Subsequent diversification within the cultigen in South America has been considered by KRAPOVICKAS (1968) and in Africa by GIBBONS et al. (1972).

The origin of cultivated peanuts (KRAPOVICKAS & RIGONI, 1957; RAMAN, 1958 et seq.; VARISAI MUHAMMAD, 1973; GREGORY & GREGORY, 1976) is still moot, despite the behaviour of *A. batizocoi* and *A. cardenasii* genomes. An objection against the hypothesis presented here is that the standards of both *A. batizocoi* and its hybrid with *A. cardenasii* are yellow while those of *A. hypogaea* and *A. monticola* are orange. If no polymorphism for flower color occurs in *A. batizocoi*, the dominant yellow allele must be assumed either to have mutated to the recessive orange form or to have been lost.

There are other points which cast some doubt upon *A. batizocoi* as a parental species. Most of the diploid species of section ARACHIS have secondary constrictions which are very close to the distal end of the arm of Husted's 'B' chromosome. The associated satellites are very small and are seldom observed in mitotic material. In *A. batizocoi*, the secondary constriction is more proximal to the centromere and the satellites are very large when compared to those of the other members of the section. In the genome of *A. hypogaea* only one pair of chromosomes has been described which has satellites. These satellites are small. Since *A. hypogaea* is believed to be a tetraploid, one would expect at least two pairs of chromosomes with satellites. There are at least three ways to explain this: (a) the secondary constriction and satellites of one pair of chromosomes has been lost, (b) the secondary constriction is masked by an amphiplastic interaction, or (c) there are two very similar pairs of chromosomes present, and because of the rarity with which the satellites are seen, only one 'pair' has been described.

If the presumptive ancestral role of *A. batizocoi* is correct, then one of the first two explanations should be true. If the third explanation is correct, then both of the satellited pairs have come from a genome other than *A. batizocoi* and *A. batizocoi* is not one of the ancestral species. The answers to these questions lie only in further investigation. The final test is obviously to produce amphidiploids from appropriate diploid F_1 interspecific hybrids, to hybridize these with the tetraploid cultigen (and *A. monticola*) and to investigate the fertility and meiosis of these tetraploid hybrids.

CONCLUSIONS

The suggestion of GREGORY & GREGORY (1976), that the genomes present in *A. monticola* and *A. hypogaea* could have originated within section ARACHIS of the genus is supported. Of forms at present known, it is supposed likely that the genome donors may be *A. cardenasii*, a diploid perennial supplying the 'A' genome and *A. batizocoi*, a diploid annual furnishing the non-'A' or 'B' genome. The combination of these two chromosome complements would produce one which would be difficult to distinguish from that of *A. hypogaea*. Hybridization is possible between *A. batizocoi* and other members of section ARACHIS but all hybrids are sterile. Meiotic studies indicate that the 'B' genome is structurally differentiated from the 'A' genome, but not necessarily very different in genetic content since *A. batizocoi* is morphologically somewhat similar to forms of *A. hypogaea* and to *A. duranensis*. Furthermore, since interspecific hybridization between *A. batizocoi* and other members of the same section can be carried out without undue difficulty, evolutionary divergence at the genetic level does not seem to be very advanced.

However, the structural differentiation between 'A' and 'B' genomes is likely to result in a diploid pattern of chromosome pairing (although occasional multivalent formation could occur) and a very stable amphidiploid could result from doubling of chromosome number in an F_1 interspecific hybrid *A. cardenasii* × *A. batizocoi*. Geographically, this hypothesis is tenable since both putative parents are found in reasonable proximity in Bolivia. Further exploration may produce new forms for which a better claim could be substantiated as potential donors of the 'A' and 'B' genomes of *A. hypogaea*, but at the present time on morphological, cytogenetic and phytogeographic grounds the claims of *A. cardenasii* and *A. batizocoi* seem to be compelling.

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