Chapter 2

SPECIATION AND CYTOGENETICS IN *ARACHIS*

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The value of evolutionary and cytogenetic studies in the improvement of crop plants is established, but biosystematic and taxonomic studies are less generally appreciated. This is frequently because economic plants have often been neglected by taxonomists. Fortunately this situation is now changing and many biosystematists who investigate taxonomic problems of cultigens and their relatives are performing a valuable service for the plant breeder.

At the present time, data and observations from several sources can be integrated in the production of taxonomic systems. Still paramount is morphological evidence, but this can be supplemented by studies of experimental hybridization and comparative cytology and biochemistry with considerable advantage. This has been done in the case of *Arachis* L. to an almost unparalleled degree, and a satisfactory taxonomic synthesis is emerging.

THE TAXONOMIC SYNTHESIS IN *ARACHIS*

The genus *Arachis* is morphologically well defined and clearly delimited from its closest relatives by the development of a peg and by geocarpy. *Arachis* is placed with its relatives *Stylosanthes, Chapmannia, Arthrocarpum* and *Pachecoa* in the subtribe Stylosanthinae of the tribe Aeschynumeneae on the basis of the shared morpological characters of a staminal tube with alternately attached basal and dorsal anthers, with flowers in terminal or axillary spikes or small heads (which are sometimes raceme-like), pinnate leaves, and leaflets few without stipels (*vide* Taubert, 1894).

Although a recent monograph of the genus has not been published, Gregory et al. (1973, 1980) and Krapovickas (1973) have outlined a taxonomic scheme which provides a useful basis for biosystematic discussion. The problems and difficulties in producing a satisfactory classification of the genus have been discussed by Gregory et al. (1973) and the following is a brief summary of their views and conclusions. Prior to Bentham's (1841) description of 5 wild species -*A. glabrata, A. pusilla, A. villosa, A. prostrata,* and *A. tuberosa* - the only member of the genus known to science was *A. hypogaea* described by Linnaeus (1753). Although 23 species of the genus have been described and diagnoses published, it seems probable that at least an equal number remains to be described. Recognized species are *A. hypogaea* L. (1753), *A. villosa* Benth. (1841), *A. tuberosa* Benth. (1841), *A. glabrata* Benth. (1841), *A. prostrata* Benth. (1841), *A. pusilla* Benth. (1841), *A. marginata* Gard. (1842), *A. hagenbeckii* Harms (1898), *A. paraguariensis* Chod. et Hassl. (1904), *A. guaranitica* Chod. et Hassl. (1904), *A. diogoi* Hoehne (1919), *A. nambyquarae* Hoehne (1922), *A. angustifolia* (Chod. et Hasl.) Killip (in Hoehne, 1940), *A. vil-*

losulicarpa Hoehne (1944), *A. lutescens* Krap. et Rig. (1957), *A. helodes* (Martius) Krap. et Rig. (1957) (material of this species was collected by Martius in 1839), *A. monticola* Krap. et Rig. (1957), *A. burkartii* Handro (1958), *A. benthamii* Handro (1958), *A. martii* Handro (1958), *A. repens* Handro (1958), *A. rigonii* Krap. et Greg. (1960), and *A. batizocoi* Krap. et Greg. (in Krapovickas et al., 1974).

While the status of most validly described species is unquestioned, *A. nambyquarae* should probably be regarded as a form of *A. hypogaea*. The status of *A. monticola* as a distinct species might also be questioned. If this species is regarded as a wild form conspecific with *A. hypogaea* as breeding experiments suggest (Hammons, 1970), then *A. monticola* may be more correctly regarded as a subspecies or perhaps a botanical variety of *A. hypogaea*.

Chevalier (1933), Hoehne (1940), and Hermann (1954) have all published monographs of the genus which Gregory et al. (1980) considered to be unsatisfactory, largely because of deficiencies in herbarium material which had been collected prior to 1950. It was not until entire plants of a wide range of species were collected from type localities and other areas of South America that Krapovickas and Gregory were able to propose taxonomic subdivisions of the genus (Table 1). This classification has not been validly published according to the International Code of Botanical Nomenclature and therefore all subgeneric epithets are *nomina nuda* (Resslar, 1980). However, their scheme is workable and of considerable practical value.

Table 1. Taxonomic subdivision of the genus *Arachis* (after Gregory et al., 1973; Resslar, 1980).

Section *Arachis nom. nud.* - Plant tap-rooted with vertical pegs, flowers without red veins on back of standard.

Series *Annuae* Krap. et Greg. *nom. nud.* - Flowers medium to small, standard 14 mm wide x 12 mm high; short-lived, usually annual $2n = 2x = 20$.

1. *A. batizocoi* Krap. et Greg. (K 9484*)
2. *A. duranensis* Krap. et Greg. *nom. nud.* (K 7988)
3. *A. spegazzinii* Greg. et Greg. *nom. nud.* (GKP 10038)
4. *A. stenosperma* Greg. et Greg. *nom. nud.* (HLK 410)
5. *A. ipaensis* Greg. et Greg. *nom. nud.* (19455)

Series *Perennes* Krap. et Greg. *nom. nud.* - Flowers medium to large, standard 14 mm wide x 12 mm high; perennial $2n = 2x = 20$.

6. *A. helodes* Martius ex Krap. et Rig. (GKP 9926)
7a. *A. villosa* Benth. var. *villosa* (B 22585)
7b. *A. villosa* var. *correntina* Burkart (GKP 9530-31)
{A. correntina (Burk) Krap. et Greg. *nom. nud.}*
8. *A. diogoi* Hoehne
9. *A. cardenasii* Krap. et Greg. *nom. nud.* (GKP 10017)
10. *A. chacoense* Krap. et Greg. *nom. nud.* (GKP 10602)

Series *Amphiploides* Krap. et Greg. *nom. nud.* - Flowers small to large, standard 10-21 mm wide x 8-14 mm high; shortlived $2n = 4x = 40$.

11. *A. hypogaea* L.
12. *A. monticola* Krap. et Rig. (K 7264)
13. *A.* x *batizogaea* Krap. et Fern. (of experimental hybrid origin)

Section *Erectoides* Krap. et Greg. *nom. nud.* - Plants tap-rooted or with tuberiform hypocotyl; plants erect or prostrate; pegs horizontal or nearly so, flowers medium to large 16-24 mm x 12-20 mm $2n = 2x = 20$.

Series *Trifoliolatae* Krap. et Greg. *nom. nud.* - Hypocotyl tuberiform; leaves trifoliolate.

14. *A. guaranitica* Chod. et Hassl. (GK 10568)

Table 1 (Continued)

15. *A. tuberosa* Benth (GKP 9837)

Series *Tetrafoliatae* Krap. et Greg. *nom. nud.* - Plants erect or prostrate; hypocotyls not tuberiform; leaves tetrafoliolate; standard orange.

16. *A. benthamii* Handro (GKP 9764)
17. *A. martii* Handro (HLKHe 526)
18. *A. paraguariensis* Chod. et Hassl. (GKP 9646)
19. *A. oteroi* Krap. et Greg. *nom. nud.* (GK 10545)

Series *Procumbensae* Krap. et Greg. *nom. nud.* - Plants prostrate- standard yellow.

20. *A. rigonii* Krap. et Greg.
21. *A. lignosa* (Chod. et Hassl.) Krap. et Greg. *nom. nud.*

Section Caulorhizae Krap. et Greg. *nom. nud.* - Plants with hollow stems, rooting at nodes; pegs vertical, standard yellow. $2n = 2x = 20$.

22. *A. repens* Handro (GKP 10538)
23. *A. pintoi* Krap. et Greg. *nom. nud.* (GK 12787)

Section *Rhizomatosae* Krap. et Greg. *nom. nud.* - Plants rhizomatous, solid stems; flowers large.

Series *Prorhizomatosae* Krap. et Greg. *nom. nud.* - Plants delicate; flowers large, red veins on both faces of standard. $2n = 2x = 20$.

24. *A. burkartii* Handro (HLP 17)

Series *Eurhizomatosae* Krap. et Greg. *nom. nud.* - Plants usually robust; flowers large, without red veins on back of standard. $2n = 4x = 40$.

25. *A. glabrata* Benth. (GKP 9830)
26. *A. hagenbeckii* Harms

Section *Extranervosae* Krap. et Greg. *nom. nud.* - Plants with thickened lomentiform tuberoid roots; pegs vertical, sometimes producing adventitious roots; flowers small to medium, with red veins on back. $2n = 2x = 20$.

27. *A. marginata* Gard. (GKP 10406)
28. *A. lutescens* Krap. et Rig. (GKP 9898)
29. *A. villosulicarpa* Hoehne (KHe 14446)
30. *A. macedoi* Krap. et Greg. *nom. nud.* (GKP 10127)
31. *A. prostrata* Benth. (GKP 10234)

Section *Ambinervosae* Krap. et Greg. *nom. nud.* - Plants tap-rooted; pegs vertical; flowers very small 8 mm x 6 mm, standard with red veins on front and back. $2n = 2x = 20$. (No species names, valid or invalid, have been given to forms in this section.)

Section *Triseminalae* Krap. et Greg. *nom. nud.* - Plants tap-rooted; pegs horizontal; flowers small 10 - 12 mm wide x 8 - 10 mm high, purple mark inside orange standard; fruits often three-segmented. $2n = 2x = 20$.

32. *A. pusilla* Benth. (GK 12881)

*** Only the most commonly used collection number is listed with each species.**

The unsatisfactory nature of taxonomic schemes advanced prior to the works of Krapovickas and Gregory is illustrated by the treatment accorded to the genus by successive monographers. Chevalier (1933) recognized 8 species, although descriptions of 11 were validly published at the time. Hoehne (1940) increased this to 11 species, while Hermann (1954) reduced the number to 9, although 13 valid descriptions had been published of which only 1 (*A. nambyquarae* Hoehne) would be challenged now. The present tally of validly described botanical species is about 20; satisfactorily distinctive but undescribed forms comprise another 11 species. It is a matter of conjecture as to how many more species will be described from the materials listed by Gregory et al. (1973) and which have been and may yet be collected (Gregory et al., 1980).

THE MORPHOLOGICAL SPECIES CONCEPT IN *ARACHIS*

As has been noted, the entirely unsatisfactory quality of much *Arachis* plant material deposited in the major herbaria of the world has been a major stumbling block in developing a sound morphological basis for species recognition in *Arachis*. A major classification problem arising from the sparse and incomplete herbarium material is due to the fact that strong morphological convergence has occurred in the aerial vegetative parts of taxa which are not closely related. For example, a strong morphological resemblance exists between *A. hagenbeckii, A. chacoense,* and some species of section *Erectoides* erroneously identified as *A. diogoi*. Similar close resemblances are apparent betwen *A. pusilla* and *A. duranensis; A. rigonii* and *A. cardenasii; A. lignosa* and *A. helodes*. Only when morphological studies are made of reproductive and subterranean vegetative parts can a sensible basis for distinctions among taxa emerge and confusion between some members of different sections be avoided. Collections by Krapovickas and Rigoni (1957), Krapovickas and Gregory (1960), and subsequent plant explorations (*vide* Gregory et al., 1973) have now produced adequate plant material on which a sound taxonomic system can be based.

The morphological characters with the greatest diagnostic value are enumerated briefly. Based on the root system, an important distinction among taxa is possible. The major peanut root types found are taprooted (axonomorphic) and tuberous rooted; the latter can be subdivided further into those in which both the hypocotyl and primary root become tuberous and those in which lateral roots are so affected. The production of rhizomes or the spontaneous production of adventitious roots at stem nodes are characters of high diagnostic value. Behavior of the peg during its growth phase, whether it is vertical or mainly horizontal, delimits important taxa within the genus. Although usually regarded as trivial characters in other plant groups, size of flowers, pigmentation, and presence and location of red venation on the standard are of considerable importance in *Arachis* taxonomy.

A morphological scheme of classification had developed sufficiently by 1964 to have been made use of by Smartt (1965) in his study of interspecific hybridization. Subsequently it has been developed and expanded until the broad lines of the classification have now been confirmed by experimental studies (Gregory and Gregory, 1979).

THE BIOLOGICAL SPECIES CONCEPT IN *ARACHIS*

From the plant breeder's point of view, the biological species concept is of greatest significance for plant improvement, since this comprises all populations which actually or potentially can interbreed freely. Sharp demarcation between biological species does not always exist, in which case genetic introgression can be of great practical value in improving the cultivated species.

The biological species approach to taxonomic classification is concerned with the evolution of isolating mechanisms. Where genetical isolation is complete, we have no difficulty in distinguishing taxa at the species level or above. In the absence of complete isolation, species delimitation is more subjective. The evolution of isolating mechanisms cannot be considered apart from the

evolution of the genus as a whole. Other things being equal, the more ancient evolutionary lineages tend to be more isolated genetically from each other than those of relatively recent origin. This is likely to be true in a genus such as *Arachis* which is predominantly self-pollinated (although cross-pollination does occur) and where selection pressures tending to establish isolating mechanisms by suppressing interspecific cross-pollination are expected to be low. In these circumstances, genetic isolation might be expected to evolve rather slowly by gradual and progressive accumulation of genetic differences. Therefore, where genetic isolation is incomplete between taxa, there is a high probability that evolutionary divergence is of comparatively recent origin.

Gregory et al. (1980) and Gregory and Gregory (1979) reviewed evolutionary trends in the genus and presented a definitive treatment of species relationships as determined by actual or attempted interspecific hybrid production. The treatment of evolution in *Arachis* by Gregory et al. (1980) attempted to bring together geographical, geomorphological, and ecological evidence to produce a reasoned synthesis and establish a credible evolutionary hypothesis.

In South America the genus ranges geographically from the equator near the mouth of the Amazon to 34° S on the northern bank of the Rio de la Plata in Uruguay. From the Atlantic coast it ranges westward to the Parana and the eastern foothills of the Andes. The northern boundary is marked by the southern extent of the Amazonian rain forest. In this area a great diversity of extreme climatic and ecological conditions (e.g., soil type) occur. The geocarpic habit of peanuts is advantageous from the standpoint of survival in harsh environments, but imposes considerable restrictions on distribution. The geocarpic fruit of *Arachis* can only be effectively distributed over long distances by agents which can physically move soil plus fruits, and therefore the only plausible natural agent is water. The effectiveness of moving water in the distribution of *Arachis* is apparently supported by distributions of taxa which are closely associated with specific drainage basins of both recent and ancient times.

From these considerations Gregory et al. (1980) inferred that the center from which the present distribution has been achieved is the "planaltine ellipse" demarcated by plotting distributions of *Arachis* collections from above 550 m on the Brazilian shield. Geomorphological changes have produced changes in drainage patterns which have isolated taxa in distinct drainage basins (Figures 1-4). These isolated taxa have evolved unique patterns of variation and genetic isolation from taxa in other isolated areas. This has been a major factor in the differentiation of the major subgeneric groups.

Studies of Interspecific Hybridization in *Arachis*

Initial studies of interspecific hybridization in *Arachis* involved the use of *A. hypogaea* as seed parent. Subsequently, Gregory and Gregory (1967, 1979) crossed wild species as both pollen and seed parents and extensively elucidated taxonomic relationships between species.

The first recorded attempt at interspecific hybridization was reported by Hull and Carver (1938) between *A. hypogaea* and *A. glabrata* but no hybrid seed were recovered. A similar attempt by Gregory (1946) was also unsuccessful as were the crosses *A. hypogaea x A. villosulicarpa* and *A. hypogaea x A. "diogoi."* The first reported viable interspecific hybrid was produced by

Fig. 1. The rivers of South America important in the distribution of the subgeneric sections of *Arachis*.

Fig. 2. Geographic distribution of *Arachis* which shows the association of botanical group with drainage system. From south to north: the *Prorhizomatosae* (R_1) in the basin of the Uruguay; *Caulorhizae* (C) in the basin of the Jequitinhonha; *Triseminalae* (T) in the São Francisco; *Extranervosae* (EX) around the headwaters of Tocantins, Araguaia, Xingu, Juruena, Paraguay and Paranaiba; series of section *Erectoides* (E_1, E_2, E_3) in the basins of the Paraguay and Paranaiba; *Eurhizomatosae* (R_2) in the Paraguay, Paranaiba, and Paraná; section *Arachis* (A) mainly in the Paraguay and headwaters of the Madeira; and section *Ambinervosae* (Am) in the Parnaiba. Stippled areas denote recently established centers of diversity (Adapted from Gregory and Gregory, 1979).

Fig. 3. Distribution of botanical groups of *Arachis* above 550 m on the Planalto (blackened areas). *Erectoides* and *Eurhizomatosae* to the southwest and *Extranervosae* to the northeast. When inscribed in a common area, these two figures describe the 'planaltine ellipse' (Adapted from Gregory et al., 1980).

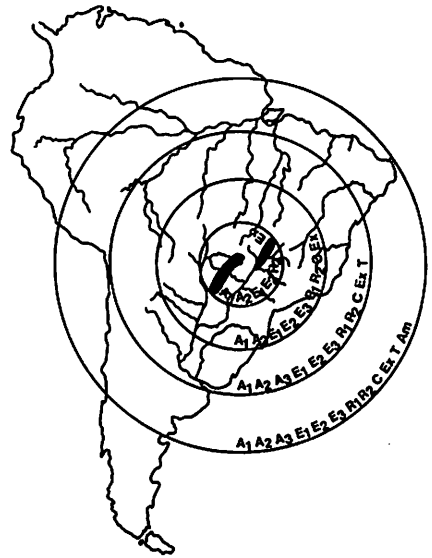

Fig. 4. The center of distribution of the genus *Arachis*. This area, the 'planaltine ellipse', does not represent the area of the greatest profusion of the genus *Arachis* but is simply the inferred center, given that *Arachis* was lifted by the mid-Tertiary uplift of the old Brazilian peneplane and that migration of *Arachis* is mostly dependent on the downward flows of soil and water. Each successive concentric circle incorporates additional botanical groups, their totals are respectively 4, 6, 9, 11 and 12. As one moves outward from the center, fewer special features adaptive to the Planalto are encountered (Adapted from Gregory et al., 1980).

Krapovickas and Rigoni (1951) between *A. hypogaea* and *A. villosa* var. *correntina* and subsequently by Kumar et al. (1957) and Raman (1959a). Johansen and Smith (1956) made a study of embryo development in the unsuccessful crosses *A. hypogaea x A. "diogoi"* (this material was apparently not authentic *A. diogoi* Hoehne, *vide* Gregory and Gregory, 1979). Fertilization apparently occurred, but growth of embryo and endosperm were retarded, and hypertrophy of the testa was noted in the *A. hypogaea x A. "diogoi"* hybrid. Hybrid embryos then died before differentiation. Johansen and Smith (1956) found that mature pods arising from interspecific hybridization were empty except for the shrivelled remains of aborted embryos and testas as had been observed previously by Gregory (1946), researchers at the East African Agricultural and Forestry Research Organization (1954-56) and subsequently by Tuchlenski (1958) and Smartt (1964). Johansen and Smith (1956) also reported failure of fertilization in *A. hypogaea x A. glabrata* crosses. The first attempt to study systematically the cross-compatibility relationships between *A. hypogaea* and a broad cross-section of wild species was reported by Smartt (1965) and Smartt and Gregory (1967). Seven viable interspecific hybrid combinations were reported between *A. hypogaea* and the wild species *A. villosa, A. villosa* var. *correntina, A. duranensis, A. cardenasii, A. chacoense, A. helodes,* and A. sp. 9901 GKP. The cross *A. spegazzinii x A. hypogaea* succeeded only with the wild species as seed parent. Additional crosses between the cultigen and wild species *A. batizocoi, A. stenosperma,* and *A. ipaensis* have been obtained by Gregory and Gregory (1979). Morphologically, all species which cross successfully with *A. hypogaea* are included in the section *Arachis*.

Gopinathan Nair et al. (1964) produced a viable *A. hypogaea x A. glabrata* var. *hagenbeckii* hybrid. Raman (1976) and Varisai Muhammad (1973a, b, c, d) have reported viable hybrids between *A. hypogaea* as seed parent with *A. "diogoi"* (see Johansen and Smith, 1956), *A. glabrata,* and *A. villosulicarpa,* and also between *A. monticola* and the species *A. "diogoi"* and *A. marginata* as well as *A. villosa x A. hagenbeckii* and *A. duranensis x A. villosulicarpa*. Pompeu (1977) was unable to obtain hybrids using materials from the same sources. Gregory and Gregory (1979), who have examined material of putative hybrid origin (*A. hypogaea x A. glabrata*), believe that it is pure *A. hypogaea*. Possibly this material could have arisen through selfing or perhaps by sporadic apomixis (Smartt, 1979). Gregory and Gregory (1979) remain convinced that all successful interspecific crosses to date involving *A. hypogaea* are with closely related species only, i.e., within section *Arachis*.

Crosses between wild species are of particular interest because they might reveal which diploid species are progenitors of the tetraploid *A. hypogaea*. The first reported interspecific hybrid between wild species was produced by Raman and Kesavan (1962). Gibbons and Turley (1967) produced hybrids *A. batizocoi x A. duranensis, x A. villosa, x A. villosa* var. *correntina; A. spegazzinii x A. duranensis, x A. batizocoi;* and *A. villosa x A. villosa* var. *correntina*. The most interesting feature of these crosses is that F_1 progeny were fertile except where *A. batizocoi* was 1 of the parents. Resslar and Gregory (1979) and Stalker and Wynne (1979) have reported additional hybrids between species of section *Arachis* in which only those involving *A. batizocoi* were completely pollen sterile. Gregory and Gregory (1979) published a comprehensive listing of viable interspecific hybirds.

CHEMOTAXONOMY

Three different groups of chemical compounds have been studied chemotaxonomically in *Arachis*. These are seed proteins, nucleic acids, and flavonoids.

Proteins

Seed proteins have been studied using the techniques of both immuno-electrophoresis and disc eletrophoresis. Daussant et al. (1969a, b) produced the first immunoelectrophoretic characterization of *A. hypogaea* seed proteins. The use of the technique was applied to other species of *Arachis* by Neucere and Cherry (1975). Their immunoelectrophoretic analyses suggested interspecific relationships which were consistent with the taxonomic scheme of Krapovickas and Gregory (Gregory et al., 1980). A similar conclusion regarding species relationships was reached by Cherry (1975) using disc electrophoresis. Tombs and Lowe (1967) identified 3 forms of arachin, 1 of the major seed storage proteins. The nature and extent of seed protein polymorphisms will need to be established in *A. hypogaea* before fully effective use can be made of disc electrophoretic and immunoelectrophoretic data. A project similar to that conducted by Kloz and Klozová (1968) on *Phaseolus* is needed.

Cytophotometric Studies of Cell DNA Contents

Resslar et al. (1981) determined 2C amounts of DNA for 12 taxa in section *Arachis*. He found a range from 4.92 to 5.98 pg DNA per cell in diploid species and 10.36 to 11.35 pg DNA in the tetraploids. Annual diploids (series *Annuae*) averaged 1 pg less per cell than the diploid perennials (series *Perennes*). Variation was found in the tetraploids (series *Amphiploides*) between the species *A. monticola* and *A. hypogaea* and between the *A. hypogaea* subspecies *hypogaea* and *fastigiata* Waldron.

Flavonoids

Flavonoid chromatography of leaf extracts has been undertaken by Krapovickas and Seeligmann (Krapovickas, 1973; Krapovickas et al., 1974). More than 20 compounds have been detected in the genus *Arachis* as a whole with no more than 12 of these, and usually fewer, found in any 1 taxon. The data obtained are difficult to interpret and considerable variation exists within the species *A. hypogaea*. Additive inheritance of flavonoids has been shown in an interspecific hybrid derivative, *A. batizogaea* Krap. et Fern. (Krapovickas et al., 1974). Krapovickas (1973) has generally found the centers of variation for chemical and morphological characters coincide reasonably well.

The Role of Studies on Chemical Variation

Published work indicates that interesting and potentially useful variation exists for chemical characters in the genus. The data are not so extensive to supplement greatly the volume of taxonomically useful information. Flavonoids

derived from leaf tissue could potentially be of value in resolving the problems of classifying largely clonal material in the section *Rhizomatosae*. Such studies might also be useful in establishing affinities betwen incomplete herbarium specimens and material from living collections.

The preferred source of material for protein chemotaxonomic studies is the seed. Rhizomatous forms produce seed very sparingly and alternative sources of proteins such as leaves could be investigated with possible taxonomic advantage.

Studies of nucleic acids are clearly in a preliminary phase. The differences in nuclear DNA contents observed between the series of section *Arachis* by Resslar et al. (1981) suggest that a comprehensive study of the whole genus would be worthwhile.

CYTOLOGY AND CYTOGENETICS OF *ARACHIS*

Chromosome Number

The earliest comprehensive reports on chromosome number, morphology and behavior were those of Husted (1933, 1936) on *A. hypogaea*. Kawakami (1930) had earlier reported a somatic complement $2n = 40$ and a gametic number $n = 20$, while Husted (1931) had confirmed the somatic complements of *A. nambyquarae* and 6 cultivars of *A. hypogaea* to be $2n = 40$. These reports contradicted the finding of Badami (1928) of complements $2n = 20$, $n = 10$, in some lines of cultivated peanuts.

The first chromosome count reported for a wild species was $2n = 40$ for *A. glabrata* (Gregory, 1946). This count was confirmed by Conagin (1962) and Smartt and Gregory (1967). Mendes (1947) published counts of $2n = 20$ chromosomes for *A. diogoi, A. marginata, A. prostrata,* and *A. villosulicarpa*; this gave the first indication of the existence of 2 chromosome series in the genus of $2n = 20$ and $2n = 40$. While the nomenclature of some of Mendes' material can be questioned (Gregory et al., 1973, 1980), it does appear that at least 4 clearly distinct wild species were studied. Table 2 lists those species for which chromosome numbers have been reported in the genus.

From these data it became clear that 2 series of chromosome numbers occur in the genus $2n = 2x = 20$ and $2n = 4x = 40$. Polyploidy has apparently arisen independently at least twice in the genus, in the immediate ancestor of the cultivated peanut itself and in the section *Rhizomatosae*. Primitive rhizomatous forms are diploid, and the more abundant and robust forms are tetraploids (Gregory et al., 1973). These authors also reported chromosome complements of $2n = 20$ for species of sections *Ambinervosae (Pseudoaxonomorphae)* and *Triseminalae*, the latter including the true *A. pusilla*.

Aneuploidy

Aneuploid complements have been reported in *A. hypogaea* sporadically since Husted (1936) first reported a plant showing $2n = 41$ plus a chromosome fragment. The most extensive reports of aneuploidy in the genus have arisen as a result of interspecific hybridization. Kumar and D'Cruz (1957) obtained a plant with $2n = 41$ from the backcross (*A. hypogaea* x *A. villosa*) x *A. hypogaea*.

Table 2. Reported chromosome numbers of named *Arachis* species in chronological order.

Species	2n	Reference
A. hypogaea	40	Kawakami, 1930
A. glabrata	40	Gregory, 1946
A. diogoi	20	Mendes, 1947
A. marginata	20	"
A. prostrata	20	"
A. villosulicarpa	20	"
A. villosa ("typica" and var. *correntina*)	20	Krapovickas & Rigoni, 1949
A. pusilla (correctly *A. monticola*)	40	"
A. hagenbeckii	40	Krapovickas & Rigoni, 1957
A. monticola	40	"
A. pusilla (correctly *A. duranensis*)	20	"
A. rigonii	20	Krapovickas & Gregory, 1960
A. lutescens	20	Conagin, 1963
A. repens	20	"
A. helodes	20	Smartt & Gregory, 1967
A. macedoi	20	"
A. benthamii	20	"
A. paraguariensis (*A.* sp. 9646, 10585)	20	"
A. cardenasii (*A.* sp. 10017)	20	"
A. chacoense (*A.* sp. 10602)	20	"
A. lignosa (*A.* sp. 10598)	20	"
A. batizocoi	20	"
A. oteroi (*A.* sp. 10541)	20	"
A. spegazzinii (*A.* sp. 10038)	20	"
A. ipaensis	20	Gregory & Gregory, 1979
A. stenosperma	20	"

Cytologically, the extra chromosome behaved as a trisomic. Smartt (1965) and Smartt and Gregory (1967) reported material with aneuploid complements ranging from $2n = 38$ to 60 arising from *A. hypogaea* x section *Arachis* diploid species hybrids. Davis and Simpson (1976) report aneuploid chromosome complements in the ranges 32-43 and 32-48 in the F_7 generation of allohexaploids derived from the F_1 hybrids *A. hypogaea* x *A. cardenasii* produced by Smartt (1965). The origin of these aneuploids is unclear; they could have arisen through crosses with the cultivated peanut, thus producing pentaploids, the meiosis of which would tend to produce aneuploids at the subpentaploid level. Alternatively they could have arisen through erosion of the hexaploid complement by univalent or multivalent formation and unequal chromosome segregation in meiosis. It is interesting to note that all selections made by Stalker et al. (1979) for good agronomic characters from material of the same origin as that of Davis and Simpson (1976) had chromosome complements of $2n = 40$. Aneuploidy in *A. hypogaea* can be found by selecting small seeds (Spielman et al., 1979) and can also arise from the effects of ionizing radiation on cells in division (Madhava Menen et al., 1970; Patil, 1968; Patil and Bora, 1961).

Chromosome Morphology

Ghimpu (1930) in his study of *A. hypogaea* chromosomes noted in addition to the complement being $2n = \pm 40$, that the centromeres were median and that the chromosomes of bunch and runner types were similar (see Figure 5). Husted (1933, 1936) identified 2 distinctive chromosome pairs; one he termed "A" chromosomes which were distinctly smaller than any other pair; the other, termed the "B" chromosomes, showed a secondary constriction. These observations were confirmed by Babu (1955) and D'Cruz and Tankasale (1961). Raman (1959b) observed the presence of 1 pair of "A" chromosomes in *A. villosa* var. *correntina* and suggested a relationship between this genome and 1 of the presumably distinct genomes of *A. hypogaea*.

Smartt (1965) confirmed Raman's observation on the occurrence of "A" chromosomes in *A. villosa* var. *correntina* and noted that all species of section *Arachis* in which he had been able to examine karyotypes had an "A" chromosome pair. He also noted the apparent absence of this distinctive chromosome pair in the section *Erectoides* species *A. paraguariensis* (A. sp 9646). The suggestion was made that the origin of the cultivated peanut from diploid ancestors could have occurred by the hybridization of a form with a karyotype like that of *A. villosa* and another with a karyotype like that of *A. paraguariensis*. This suggestion raised some difficulties in that hybrids between sections *Arachis* and

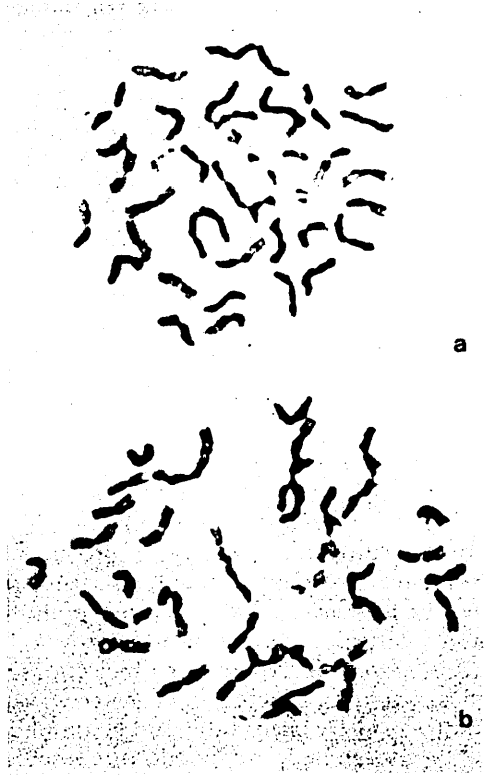

Fig. 5. Mitotic chromosomes of *A. monticola* (a) and *A. hypogaea* var. Argentine (b).

Erectoides are difficult to produce experimentally, only 2 examples being confirmed (Gregory and Gregory, 1979), and are probably not formed naturally. The publication of the description, chromosome counts, and photomicrographs of chromosomes of *A. batizocoi* by Krapovickas et al. (1974) showed that cytological differentiation is present within section *Arachis*. Although Krapovickas et al. (1974) did not comment on the general karyotype of this species, it is clearly apparent that no identifiable "A" chromosome pair is present. Subsequently, Smartt et al. (1978a, b) confirmed the absence of an "A" chromosome pair in *A. batizocoi* and its presence in all other examined material of section *Arachis*. They inferred that the chromosome complement of *A. batizocoi* differed largely from that of other species in section *Arachis* in structural changes; at the genic level no greater differentiation seems to have occurred between *A. batizocoi* and the other species of section *Arachis* than is apparent between other species of the section. Furthermore, hybrids between *A. batizocoi* and other species in the section are obtained readily. By inference, genic differentiation is probably a major factor which severely restricts the success of intersectional crosses. Smartt et al. (1978a, b) suggested a model of interspecific hybridization events that could have produced the cultivated peanut from diploid progenitors within section *Arachis*. The most eligible species ar collected are *A. batizocoi* and *A. cardenasii* (A. sp. 10017). The reciproc ploid F_1 hybrids between these forms are sterile and have not yet

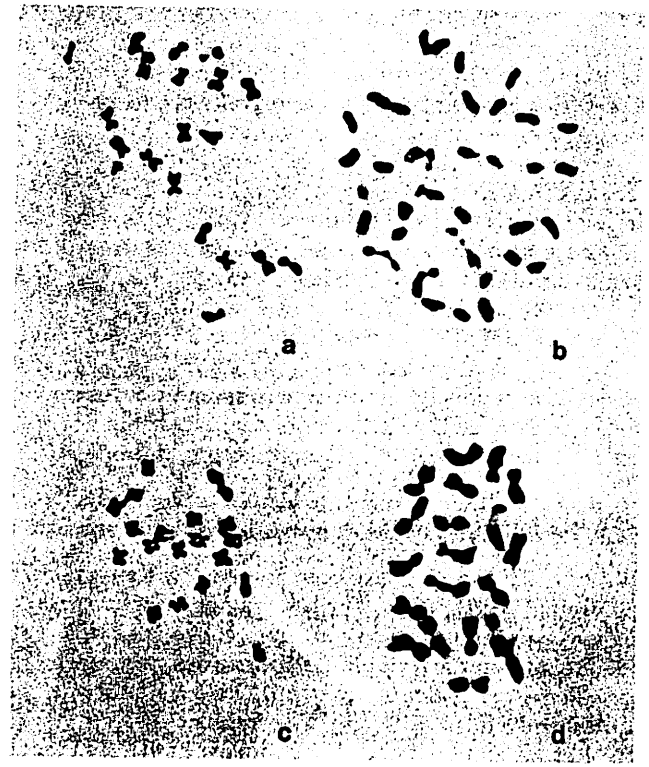

Fig. 6. Contracted (a) and noncontracted (b) mitotic chromosomes of *A. cardenasii* and contracted (c) and noncontracted (d) chromosomes of *A. batizocoi*.

been induced to produce amphidiploids. It is possible, however, that more recently collected taxa could be the true genome donors of the cultivated peanut. The above studies have made use of the presence or absence of 1 chromosome pair as markers of genomes (Figure 6). It is clear that other recognizable karyotype differences exist, for example, in the morphology of nucleolar organizer chromosomes.

Chromosome Behavior

The first detailed study of chromosome behavior in *Arachis* was conducted by Husted (1936). The material studied was all *A. hypogaea* (this included forms such as *A. rasteiro* and *A. nambyquarae* now regarded as being synonymous with *A. hypogaea*). In most metaphase I cells studied, pairing was 20II (see Figure 7) (ranging from 88.2% in White Spanish to 97.1% in Pearl, another bunch form). The runner cultivar Improved Virginia showed 94.0% normal bivalent pairing. Departures from this pattern included formation of univalents and trivalents in addition to bivalents as follows: 1I + 18II + 1III and 2I + 19II. Other cultivars had 18II + 1IV chromosome associations. In "Nhambiquaras" Husted (1936) reported 11II + 2III + 3IV; and in hybrids Improved Virginia x White Spanish configurations observed were mostly 20II, but 18II + 1IV, 2I + 17II + 1IV, 14II + 2III + 1VI, 14II + 2VI, 17II + 2III and 17II + 1VI were also observed. Because of the low frequencies of multivalent configurations, it can be inferred that the cultivated peanut is an effectively diploidized tetraploid. Multivalent association can be due to homoeologous pairing (the formation of quadrivalents or a trivalent plus a univalent) between chromosomes of the 2 genomes. When pairs of trivalents or hexavalents were observed, the probability of segmental interchanges having occurred in the differentiation of the genomes is high. The enhanced production of such associations in the virginia x spanish F_1 hybrid discussed by Husted (1936) suggests that there may be chromosome structural differences between different subspecies of the cultigen, a suggestion made more recently by Gregory et al. (1980) on the basis of reduced fertility in hybrids between sequentially branching and alternatively branching forms. Subsequent studies by Raman (1976) also confirm Husted's conclusions. In these studies aneuploidy was observed occasionally in addition to sporadic occurrence of chromatin fragments in meiotic cells. The authors suggested that aneuploids could have originated as a result of departures from normal diploid pairing.

Wild Species Meiosis

Meiotic studies in wild species have been reported by Raman (1976) for both tetraploid and diploid wild species. The behavior of *A. monticola* is comparable to that of *A. hypogaea* with normally 20II but occasionally with 18II + 1IV. Meiosis was less regular in the tetraploid rhizomatous species which may form up to 4 quadrivalents per pollen mother cell. Pollen mother cells in diploid wild species uniformly form 10II and have regular meiosis (Smartt, 1965; Raman, 1976; Resslar and Gregory, 1979; Smartt et al., 1978a; Stalker and Wynne, 1979) (Figure 7).

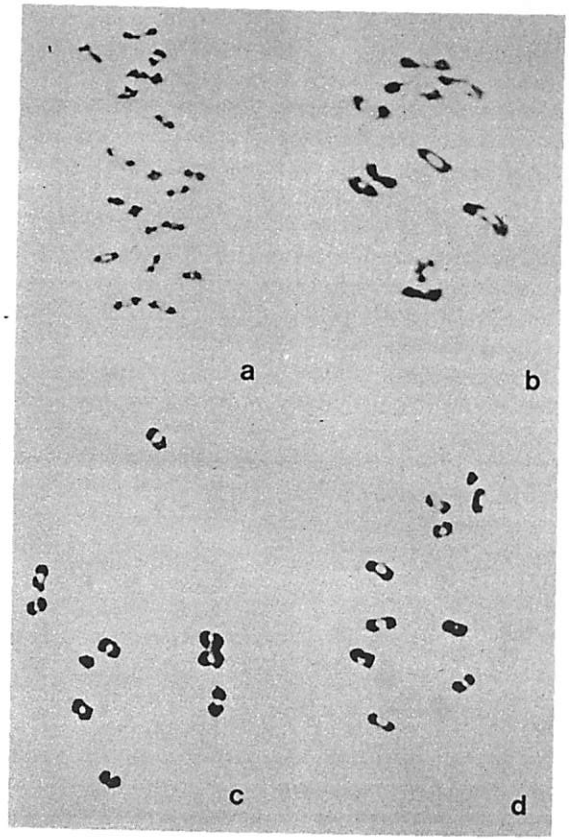

Fig. 7. Metaphase I of *A. hypogaea* (a), *A. villosa* (b), *A. cardenasii* (c), and *A. duranensis* (d). Note that each species has one distinctively smaller bivalent (photomicrographs c&d by P. M. Resslar).

Meiosis in Interspecific Hybrids

The authenticity of some interspecific hybrids reported by Raman (1976) and Varisai Muhammad (1973a, b, c, d) has been questioned (Gregory and Gregory, 1979; Smartt, 1979). For this reason, only the meiotic behavior of interspecific hybrids of unquestioned authenticity will be reviewed. The first interspecific hybrids obtained in *Arachis* were produced with *A. hypogaea* as seed parent. These were between the tetraploid cultigen and diploid species of section *Arachis*, and as a result, functionally sterile triploids were produced. Natural or artificially induced hexaploidy usually restored fertility (Kumar et al., 1957; Raman, 1959b; D'Cruz and Chakravarty, 1961; Smartt and Gregory, 1967.)

The first interspecific hybrid reported between diploid *Arachis* species was produced by Raman and Kesavan (1962) between *A. duranensis* and *A. villosa* var. *correntina*. These authors found meiosis to be regular, a conclusion which has been confirmed and amplified by Resslar and Gregory (1979) and Stalker and Wynne (1979) (Figure 8). Regular meiotic pairing has been found in all

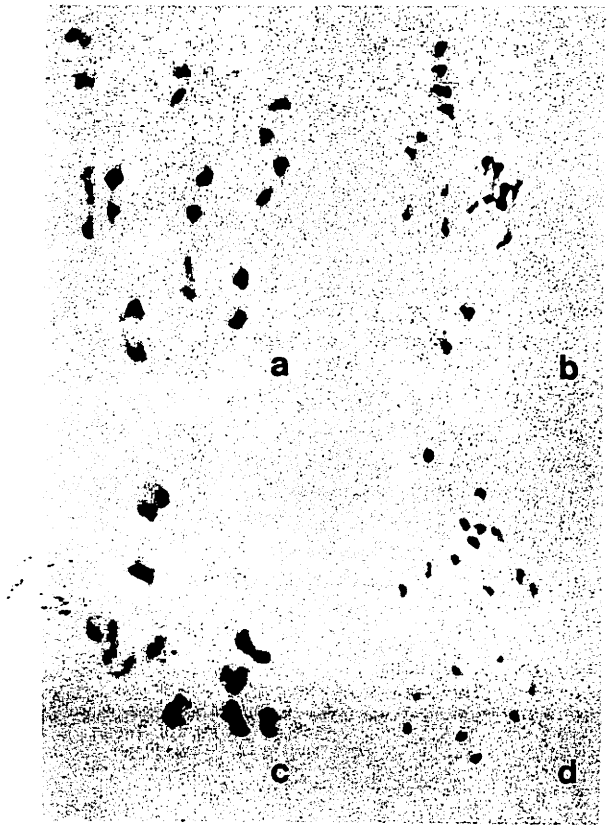

Fig. 8. Metaphase I of *A. cardenasii* x *A. correntina* F_1 with 10 bivalents (a), *A. cardenasii* x *A. batizocoi* F_1 with 6 bivalents and 8 univalents (b), *A. spegazzinii* x *A. correntina* F_1 with 10 bivalents (c), and anaphase I of *A. spegazzinii* x *A. batizocoi* F_1 with 12 chromosomes segregating to one pole and 8 to the other.

interspecific hybrids between species within section *Arachis* except for those involving *A. batizocoi* (Smartt et al., 1978a, b; Stalker and Wynne, 1979). In F_1 interspecific hybrids involving the latter species, meiosis is extremely irregular and sterility virtually complete (Gibbons and Turley, 1967; Smartt et al., 1978a, b; Stalker and Wynne, 1979) (Figure 8). Irregular meiosis appears to be due to extensive rearrangement of structural elements between *A. batizocoi* and other species in the section.

Stalker (1981) reported meiotic behavior in complex triploid hybrids between section *Erectoides* (4*x*) and section *Arachis* (2*x*). The *Erectoides* (4*x*) parent was an amphidiploid derived from the F_1 hybrid between *A. rigonii* and A. sp. GKP 9841. This was crossed successfully with the 2 accessions *A. stenosperma* (HLK 410) and *A. duranensis* from section *Arachis*. The resulting hybrids were sterile and either euploid $2n = 30$ or aneuploids $2n = 31, 32$. Trivalents were observed at low frequencies, suggesting that at least some homology exists between the chromosomes of the *Arachis* and *Erectoides* species involved.

Further meiotic studies of intersectional hybrids could yield valuable information on genomic homologies. The difficulty with which such hybrids are

produced suggests that within each section the genome or genomes are genetically isolated from those of other sections. The most numerous intersectional hybrids have arisen from combinations *Erectoides* x *Rhizomatosae* and *Arachis* x *Rhizomatosae*. Considerably fewer have arisen from other combinations such as *Erectoides* x *Arachis* and *Erectoides* x *Caulorhizae* and none have been produced by the great majority of intersectional combinations (Gregory and Gregory, 1979). Application of techniques such as protoplast fusion or *in vitro* culture of immature F_1 hybrid embryos may possibly produce further interspecific combinations. The pattern of intersectional cross-compatibility observed has led Gregory and Gregory (1979) to suggest that members of both sections *Arachis* and *Erectoides* have some affinity with the 4x *Rhizomatosae*. It is possible that since sections *Arachis* and *Erectoides* are almost completely cross-incompatible, 1 of the 2 *Rhizomatosae* genomes confers compatibility with the *Erectoides* and the other with species of section *Arachis*. In section *Arachis*, only members of the series *Annuae* have demonstrated intersectional cross-compatibility. Neither the perennials nor the tetraploids of this section have produced intersectional hybrids. The presumed presence of a genome from a perennial species (Smartt et al., 1978a, b) may explain the lack of cross-compatibility between *A. hypogaea* (and *A. monticola*) and any other section (Gregory and Gregory, 1979).

Technical and Interpretative Aspects

The chromosomes of *Arachis* species are far from ideal material for cytological study. The chromosomes are small, 1-4 μ (the actual lengths observed in preparation vary according to duration of pretreatment) and are prone to stickiness in both mitotic and meiotic preparations. This latter problem can be overcome by taking precautions in making preparations (Fernandez, 1973) and avoiding conditions of stress (Stalker, unpubl.).

Somatic Chromosomes

The chromosomes of *Arachis* species generally have median centromeres and are difficult to karyotype, but as Smartt et al. (1978a, b) have shown, the few distinctive features among species can be of value. It seems highly probable that different technical approaches to the preparation of chromosomes for examination could be of value in different ways. The simplest procedure would be to reduce either pretreatment times or concentration of spindle inhibitor reagents to minimize the degree of chromosome contraction while retaining effective spindle inhibition. This could maximize expression of differences in chromosome morphology and ensure consistent expression of features such as secondary constrictions and satellites which are frequently lost in preparation of strongly contracted chromosomes. The second and potentially much more valuable approach is that of chromosome banding. Resslar (1979) showed that the technique has promise, but production of high quality material in adequate quantity is difficult. Banding patterns could be of value in characterization of the genomes in different sections of the genus and tracing chromosome homologies between species.

Stalker and Dalmacio (1981) observed that the chromosomes of section

Arachis species ranged from 1.5 to 3.8 μ in length. Chromosomes 1 to 3 were generally near the same length, chromosomes 4 to 7 were of median length, and chromosomes 8 to 10 were distinctly shorter. Each of the 10 homologous pairs was identified based on centromere position, satellited chromosomes and differential staining between heterochromatic and euchromatic regions and ordered from number 1 = longest to chromosome 10 = shortest (Figure 9). *Arachis batizocoi* had many slightly submedian and one submedian chromosome plus a satellited chromosome 2. *Arachis cardenasii* also had many slightly submedian chromosomes and satellites on chromosomes 5 and 10. *Arachis chacoense, A. duranensis,* and *A. stenosperma* had similar karyotypes with one of the median chromosomes with a satellite. A satellite was not observed for the species *A. correntina, A. spegazzinii,* nor *A. villosa* and the species all had a submedian chromosome 9. Although each of the above species can be cytologically identified, *A. correntina, A. spegazzinii,* and *A. villosa* have very similar karyotypes.

The quotient of arm ratios for chromosome 10/1 was 0.64 and 0.63 for *A. batizocoi* and *A. cardenasii,* respectively, 0.56 for *A. chacoense,* 0.51 for *A. correntina* and the other species had a ratio of 0.50 or less. No distinctly short "A" chromosome was observed for *A. batizocoi* or *A. cardenasii* in cell preparations with only slightly condensed chromosomes (Figure 9). However, in highly contracted mitotic cells, Smartt et al. (1978a, b) reported a distinctly small "A" chromosome in all section *Arachis* species except *A. batizocoi,* and they concluded that the presence or absence of the "A" chromosome could be used as a genome marker. The differences in observation may be due to the tendency of the shortest chromosome to stain lighter than other chromosomes, thus appearing smaller than is actually the case, or possibly different species have varying rates of condensation when exposed to paradichlorobenzene or 8-hydroxyquinoline. The actual size of any specific chromosome in relation to the other chromosomes in the genome can be deceptive unless measurements are made.

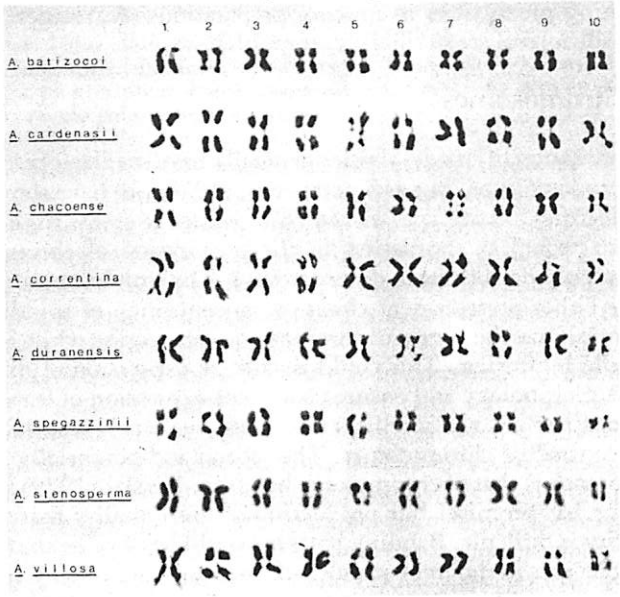

Fig. 9. Karyotypes of somatic chromosomes of eight section *Arachis* species. Reprinted from J. Heredity 72:403 (1981). Copyright 1981 by American Genetic Assoc.

Meiotic Chromosomes

On the whole, production of high quality meiotic preparations is not excessively difficult and satisfactory preparations for cytogenetic analysis can be obtained in most species. Polyploidy is a feature of species in the genus for both sections *Arachis* and *Rhizomatosae* as well as amphidiploidy following colchicine treatment of F_1 interspecific hybrids. Colchicine treatment often, but not invariably, improves fertility of F_1 hybrids. Interpretation of meiosis in polyploids is thus of considerable importance.

The interpretation of pairing relationships in diploid interspecific hybrids is quite simple and straightforward. In instances where meiotic pairing is high, fertility is also high (Raman and Kesavan, 1962; Resslar and Gregory, 1979; Stalker and Wynne, 1979). Where it is reduced, fertility is also low (Smartt et al., 1978a, b; Stalker and Wynne, 1979). Pairing relationships in triploids are more difficult to interpret and evidence to support inferences is sometimes lacking. In triploids and higher polyploids the extent to which multivalents form is determined by chromosome homology, length, and chiasma frequency. In an autotriploid, pairing may be entirely (I + II) due to low chiasma frequency combined with short arm length. Similarly in an autotetraploid, pairing could be exclusively (II + II). In allopolyploids the situation is more complex. Smartt (1965) observed that in triploid F_1 hybrids the frequency of trivalents varied according to the wild species used as pollen parent with *A. hypogaea*. In *A. hypogaea* x *A. villosa* var. *correntina* a mean of 0.95 trivalents (range 0-2) per cell was recorded, in *A. hypogaea* x *A. duranensis* this was 2.15 (range 0-5), and in *A. hypogaea* x *A. helodes* 3.40 (range 0-6) trivalents per cell. The major variable in these 3 hybrids is the wild species genome. It is reasonable to assume that within limits, the more homologous the wild species genome and 1 of the *A. hypogaea* genomes, the more rapidly synapsis will occur and thus tend to exclude the second *A. hypogaea* genome. A lower level of homology could reduce the rate and extent of synapsis and permit more multivalent associations. The homology between the genomes of *A. hypogaea,* as indicated by meiotic pairing relationships, would be best exemplified in a haploid *A. hypogaea,* but a haploid plant has never been found. Anther culture might eventually produce such haploids, which would be extremely valuable for cytological analysis. Raman's (1959a, b) interpretation of genomic homology between *A. villosa* var. *correntina* and *A. hypogaea* is probably correct. However, he could not know that all incoming chromosomes of *A. villosa* var. *correntina* were pairing with 1 genome of *A. hypogaea* as he assumed. *Arachis villosa* var. *correntina* chromosomes could have been paired with members of both *A. hypogaea* genomes or the 2 *A. hypogaea* genomes could have been paired with each other.

Similar caution is advisable in the interpretation of chromosome pairing situations in artificially produced allotetraploids and allohexaploids as to the implications of both production and nonproduction of multivalent associations. An example from another leguminous amphidiploid is instructive. Smartt and Haq (1972) produced an amphidiploid from the F_1 hybrid

Phaseolus vulgaris L. x *P. coccineus* L. and observed in successive generations a reduced frequency of multivalent associations in meiosis. Spielman et al. (1979) reported many univalents and irregular meiosis in 6x (*A. hypogaea* x *A. cardenasii*) hybrids. Propagation by seed imposes selection for a more regular and diploidized meiosis through selection for high levels of seed production. In amphidiploids, genomic homologies would be indicated by meiotic associations of (I + III) and (IV), but these would not necessarily exclude interchange heterozygosity. Higher multivalent associations (III + III), (I + V), or (VI), etc. would, however, indicate genomic differentiation by segmental interchange. Allohexaploid associations of (I + V) or (VI) would indicate some homology of all 3 genomes present. The formation of quadrivalents only could indicate that 2 of the genomes had sufficient homology to pair, but would not definitely exclude the possibility of homology between all 3 genomes. Conversely, normal diploid pairing patterns in allopolyploids do not necessarily indicate lack of the capability for homoeologous pairing between genomes.

Genomic Divergence in *Arachis*

Divergence between evolving genomes can occur through changes at individual genetic loci and also through rearrangement of chromosome segments. In the long-standing differentiation between genomes of different sections in the genus it is probable that the lack of interspecific cross-compatibility is primarily due to genetic divergence and perhaps to a lesser extent to plasmon differentiation (Ashri, 1976). This may be accompanied by chromosome structural rearrangement although its extent has not been measured. Differentiation of genomes within a section has occurred, for example, in section *Arachis*. However, even though *A. batizocoi* hybrids are sterile, its genome has not diverged genetically from other members of this section to the point where it can no longer hybridize. Smartt et al. (1978a) and Stalker and Wynne (1979) ascribe this to chromosome structural rather than genetical divergence. Smartt et al. (1978a) designated 1 genome as A (typical of the section *Arachis*) and another as B (typified by *A. batizocoi*). Perhaps designation of genomes A_1 (typical of the section) and A_2 (atypical of the section) would better convey both the genetical homology and the cytological differentiation among the species. The very low level of fertility and the highly disrupted meiosis in interspecific hybrids suggests more structural differentiation than in just 2 chromosome pairs as suggested by Stalker and Wynne (1979). This is apparent visually in the absence of the "A" chromosome in *A. batizocoi* and in morphological differences between nucleolar organizer chromosomes (Smartt, unpubl.; Stalker and Dalmacio, 1981). Much structural differentiation could involve small segments and be cryptic and undetectable from pairing relationship studies in meiosis, but might occasionally be manifested in bridge and fragment formation in anaphase I and II.

Evolution of the Cultivated Peanut

The production of structural divergence in genomes within section *Arachis* provides an insight into a probable mode of evolution for the cultivated peanut. Extensive chromosome structural changes such as those which have occurred in the divergence between *A. batizocoi* and other diploid species of section *Arachis*, effectively reduce and perhaps inhibit gene exchange between diverging forms. Extreme structural heterozygosity would render sterile any interspecific hybrids carrying both structurally differentiated genomes. Doubling of the chromosome complement would provide structurally congruent chromosome pairs in meiosis and fertility might improve. Selection for fertility would then tend to reduce multivalent formation.

Since the genus *Arachis* is largely autogamous, a relatively high chiasma frequency is likely to be favored by selection. This would create no fertility problems in diploids, but in tetraploids a high chiasma frequency could increase multivalent formation unless crossing-over was suppressed or eliminated by chromosome structural reorganization or a genetic mechanism similar to that in *Triticum aestivum* L. Reduced chiasma frequency would establish a diploid meiotic pairing pattern while still permitting high rates of recombination of linked genes following occasional hybridization. This is important in the contexts of both evolution and practical plant breeding.

Genome Evolution in Different Sections of the Genus

From the Gregory and Gregory (1979) studies of interspecific cross-compatibility, it is possible to establish tentatively a series of genomes. Some of the taxa concerned represent only a single or a pair of species, i.e., series *Procumbensae* (section *Erectoides*)- *A. rigonii, A. lignosa;* series *Prorhizomatosae* (section *Rhizomatosae*) - *A. burkartii;* section *Triseminalae* - *A. pusilla;* and section *Caulorhizae* - *A. repens* and *A. pintoi*. This narrow range of species provides a very restricted base for inference. However, the sections with more species provide reasonably satisfactory basis from which to draw conclusions.

On the basis of crossing relationships established by Gregory and Gregory (1979), it seems probable that the following distinct genomes have evolved:

1. Am - *Ambinervosae*
2. T - *Triseminalae*
3. C - *Caulorhizae*
4. Ex - *Extranervosae*
5. E - *Erectoides* (subgenomes E_1, E_2, E_3 corresponding to series?)

These sections are all diploid and raise few problems. Section *Erectoides* does comprise 3 series and there may be corresponding subgenomes. The situation considered in section *Arachis* is rather different; here designated subgenomes do not conform with the delimitation of series. The series *Annuae* embraces species possessing 1 or other subgenomes (A or B), the series *Amphiploides* species probably contain both (A and B), while all known series *Perennes* species possess the same subgenome (A). The *Rhizomatosae* pose a particular set of problems. Compatibilities of sections *Erectoides* x *Rhizomatosae* and *Arachis* x *Rhizomatosae* are high for intersectional crosses; this suggests that the tetraploid rhizomatous species have 1 genome with *Erectoides* affinities, the other perhaps closer to section *Arachis*. In terms of apparent evolutionary age, *Rhizomatosae* is older than *Arachis*, but it is very unlikely that section *Arachis* evolved from *Rhizomatosae*. The diploid rhizomatous *A. burkartii* is genetically isolated from all other *Arachis* species and its affinities remain uncertain. Even within a species, such as *A. hypogaea*, some genotypes are extremely poor par-

ents in both intra- and inter-specific crosses (Smartt, 1965). The failure of *A. burkartii* to cross successfully may be a reflection of the genotypes used in the crossing program rather than of fundamental cross-incompatibility.

The genomes in the 2 sections *Rhizomatosae* and *Arachis* could be designated R_1 (*Prorhizomatosae*), R_2 and R_3 (*Eurhizomatosae*), and A, B, or A_1, A_2 for section *Arachis*. These suggestions are tentative and could be modified as plant exploration and experimental hybridization studies proceed.

PRACTICAL APPLICATIONS

While the information obtained by biosystematic investigators of the genus *Arachis* is of considerable scientific interest, it is of even greater importance to those seeking to improve the cultivated peanut. Taxonomic characterization using morphological characters establishes the affinities of the cultigen with other species, and indicates the taxa most likely to be accessible to the breeder. Investigations to establish biological species by the study of cross-compatibility patterns and hybrid behavior are also important. It is fortunate that section *Arachis*, to which the cultivated peanut belongs, is probably one of the more recently evolved and most rapidly evolving taxa within the genus. As a result, barriers to interspecific gene flow are less than they appear to be in more ancient sections such as the *Extranervosae* and *Erectoides*.

The general position of germplasm accessibility to *A. hypogaea* can be summed up by a definition of ordered gene pools which are available for peanut improvement (Figure 10). We can consider a first-order gene pool which consists of all cultivated varieties and landraces, together with all breeding lines derived from them. A second-order gene pool would be constituted by *A. monticola* and any other wild tetraploid forms (as yet unknown) with a similarly high level of cross-compatibility with *A. hypogaea*. The wild diploid species of section *Arachis* would comprise a third-order gene pool which should be

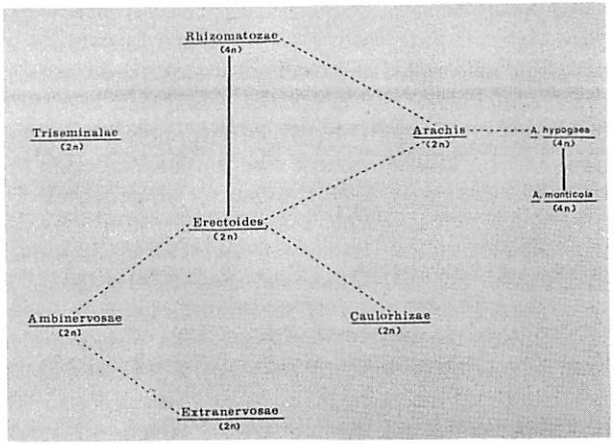

Fig. 10. Cross compatibilities among sections of *Arachis* where solid lines represent crosses where fertile hybrids have been obtained and broken lines represent crosses where only sterile hybrids have been obtained. Varieties of *A. hypogaea* represent the primary gene pool, *A. monticola* the secondary gene pool, diploid section *Arachis* the third-order gene pool, and other species of the genus the fourth-order gene pool, for improvement of cultivated peanuts.

reasonably accessible to breeders. A fourth-order gene pool of low accessibility is constituted by remaining sections of the genus. Some exploitation of this large resource may be possible through the use of bridging intersectional crosses, for example, section *Arachis* x section *Erectoides* (Banks, 1974). Gene pools of the fourth order will probably be exploited only in rather exceptional circumstances and that such efforts will be expensive, with little chance of ultimate success. A desirable gene from a species in section *Erectoides*, for example, will not necessarily be equally effective when transferred to a species (e.g., *A. hypogaea*) in section *Arachis*. Genetic resources in section *Arachis* will obviously be the most heavily exploited and their actual breeding value is likely to be more predictable.

The characters of wild species which have the most immediate attraction to peanut breeders concern immunity, resistance, and tolerance to pests and diseases. A considerable effort has been devoted to the evaluation of the pest and disease resistance of wild *Arachis* species, and most notably leafspot resistance has been identified in 3 species within section *Arachis* (Abdou, 1966; Gibbons and Bailey, 1967; Abdou et al., 1974; Seetharam et al., 1974; Nevill, 1978; Foster et al., 1981). Resistance to nematodes, lesser cornstalk borer, spider mites, rosette virus, stunt virus, peanut rust, tobacco thrips, web blotch, and tolerance of southern blight have been reported (Leuck and Hammons, 1968; Kousalya et al., 1972; Kamal, 1976; Simpson, 1976; Banks, 1976; Johnson et al., 1977; Hassan and Beute, 1977; Moss, 1980; Hebert and Stalker, 1981).

Another area which has attracted some attention is the possible use of wild species to improve the protein and oil composition of the cultivated peanut (Cherry, 1977). Peanut seed protein is unusually low in lysine and, more typically, it is low in sulfur amino acids and tryptophan. Amaya et al. (1977) were able to demonstrate a range in protein content of 21.35-33.35% in the wild species. Tryptophan content in *A. villosulicarpa* varied between 1.44 and 1.66 mg per 100 mg protein, somewhat in excess of the best *A. hypogaea* line tested at 1.41%. It is apparent that further detailed study of protein content and composition is required both in the cultigen and related wild species to determine the nature and extent of protein polymorphisms for selection. In addition, some cost benefit analysis would be necessary before a breeding effort would be justified.

Some physiological features such as drought tolerance might be transferred from the wild species to cultivated peanuts. Improved general vigor and growth rate, or photosynthetic efficiency are additional characters which might possibly be improved by introgression. Furthermore, structural and anatomical changes in vegetative and reproductive parts, e.g., pod and pegs, could effect useful improvement. A full realization of the potential breeding value of wild species will not be possible until their hybrids and progenies are subjected to intensive study. The biochemical and physiological behavior of peanuts are not well understood, nor is the range of feasible phenotypic manipulation known. Present efforts have been minimal and a more comprehensive evaluation of the breeding value of *Arachis* germplasm resources is an urgent necessity. Conservation of resources is futile without their exploitation and utilization. Germplasm resources are perhaps unique among our human resources in that their utilization and exploitation do not necessarily exhaust them, and should in practice never do so.

In order to reap the benefit of our germplasm resources in the improvement of the peanut crop, it is essential that effective breeding strategies are developed. It is here that cytogenetic studies fulfill a very important role. As Smartt et al. (1978a, b) have pointed out, since *A. hypogaea* is an allotetraploid which is effectively diploidized, the existence of 2 more or less distinct genomes must be acknowledged. One genome, held in common with most diploid species of section *Arachis*, is more easily subjected to introgression from most species than the other genome. Genetic improvement of characters controlled by duplicated loci in both genomes is complicated, if as suggested the 2 genomes differ substantially as a result of chromosome structural change. If as further suggested by Smartt et al. (1978a, b), species similar in chromosome structure to *A. cardenasii* and *A. batizocoi* (but not necessarily these species themselves) are involved in the ancestry of *A. hypogaea*, extensive recombination between the genomes is unlikely. It may therefore be necessary to induce segmental interchanges to effect specific gene transfers. It might also be possible to produce chromosome addition or substitution lines involving more remote germplasm. Exploitation of wild species germplasm can now be considered.

Breeding Strategies for the Exploitation of Wild Species Germplasm

In devising breeding strategies for the incorporation of exotic germplasm in the cultivated peanut, the following must be considered. The probable presence of 2 structurally differentiated genomes in *A. hypogaea* has dual implications. Firstly, that the arrangement of chromosome segments in the 2 genomes will determine the ease with which the necessary introgression can be achieved. Secondly, the high level of genetic homology which probably exists between the 2 genomes implies that many qualitative characters may be under the control of duplicate loci. Transferring a desirable dominant character may present few problems for the breeder. However, if the trait is recessive and duplicate inheritance occurred, producing homozygosity at homologous loci in both genomes would be difficult. A less serious problem could be encountered where the genes had additive effects; however, maximum expression could not be achieved unless both genomes were introgressed.

Ploidy Level Manipulation

It is fortunate that differences in the ploidy level of *Arachis* species are not in themselves barriers to hybridization and may not be great barriers to gene flow. Operating effectively at different ploidy levels despite the problem of reduced fertility is possible. This is important when breeding materials can range from diploid to hexaploid levels as is the case in *Arachis*.

The question of breeding for improved leafspot resistance provides a good illustration of the nature of the germplasm introgression problems. Leafspot is incited by 2 species of fungi, *Cercosporidium personatum* (Berk. & Curt.) Deighton and *Cercospora arachidicola* Hori (late and early leafspots, respectively). *Arachis cardenasii* has been reported as immune to *C. personatum*, *A. chacoense* as resistant to *C. arachidicola* (Abdou, 1966), and *A. stenosperma* as resistant to both pathogens (Kolawole, 1976; Sharief et al., 1978). In most peanut-growing areas, resistance to both pathogens is desirable. It would, therefore, be pertinent to consider whether each resistance would be bred into the cultigen separately or whether as Smartt et al. (1978b) suggest, it would be more efficient to combine both resistances at the diploid level and then cross a doubly resistant segregate to the cultigen. Such a cross would be triploid and more or less sterile. It is frequently possible to produce hexaploids from such triploids, either artificially and/or spontaneously (Smartt and Gregory, 1967; Spielman and Moss, 1976) and backcross these to the cultigen to produce pentaploid progeny. Pentaploids in *Arachis* vary in fertility but those capable of reproduction would probably lose chromosomes in meiosis and tend to produce progeny whose chromosome number would stabilize at the tetraploid level. Selection for both resistances could be practiced and a doubly resistant tetraploid breeding line produced. Moss (1980) suggested an alternative strategy of crossing 1 diploid species to *A. hypogaea*, doubling the chromosome complement of this F_1 hybrid and crossing the resulting hexaploid to a second diploid species to produce a tetraploid. However, this tetraploid could have 3 A_1 + 1 A_2 genomes and might, as Smartt et al. (1978b) suggested, be of reduced fertility. Both these alternative strategies, and the modification of inducing polyploidy before hybridization with *A. hypogaea* suggested by Stalker and Wynne (1978), are probably worthy of trial.

Sharief et al. (1978) conclude that leafspot resistances are controlled multifactorially. It would appear that some improvement in the level of leafspot resistance in the cultivated peanut might therefore be achieved by introgression of the A_1 genome. However, maximum resistance levels would probably not be achieved until both genomes were effectively introgressed.

The basic strategy suggested here could be employed with diploid species within section *Arachis* for a range of possible improvements. Results obtained to date suggest that this approach could be productive. Bridging the intersectional gaps is a very different problem and one likely to prove difficult. It would probably involve further development of techniques for anther, embryo, and tissue culture as well as investigation of the physiology of differentiation in cultured cells and tissues. Where conventional hybridization fails, protoplast fusion may yet succeed. However, it must be remembered that genomes from different sections may be developmentally antagonistic and preclude both normal reproduction processes and normal growth and development. Similar considerations may also apply to single chromosome pairs if these are substituted for homoeologues in the *A. hypogaea* genome or added to it. Obviously, wide crosses in *Arachis* from the standpoint of peanut improvement are a last resort.

In conclusion, we consider ourselves fortunate that the cultivated peanut, *A. hypogaea*, is a member of a recently evolved section of the genus unlike *A. villosulicarpa*, the only other cultigen of long standing in the genus. Within the section *Arachis*, most of the genetic resources should be accessible to the breeders. It is possible that more remote genetic resources than these might be utilized, but the difficulties are expected to be greater and the results less certain. Nevertheless, all the genetic resources within the genus should be properly evaluated.

ACKNOWLEDGMENTS

The authors wish to acknowledge the assistance and constructive criticism of the manuscript by Drs. W. C. Gregory, M. P. Gregory, P. M. Resslar, J. P. Moss, D. J. Banks and C. E. Simpson. Also, to Drs. W. C. Gregory, M. P. Gregory, P. M. Resslar and the Director of the Royal Botanic Gardens, Kew, for permission to reproduce figures used in this chapter.

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