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A NEW SPECIES IN SECTION ARACHIS OF PEANUTS WITH A D GENOME[1]

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Arachis glandulifera Stalker is a diploid ($2n = 2x = 20$) taxon in section *Arachis* native to eastern Bolivia. Plants of *A. glandulifera* have longer lateral branches than other taxa of section *Arachis*, an upright mainstem, prostrate lateral branches, and larger flowers and seeds than other wild species in the section. The pods are greatly reticulated. Glandular trichomes are present on vegetative plant parts and the pe-. Intraspecific hybrids among four accessions are fertile and uniformly have ten bivalents in pollen mother cells. Three accessions had nearly identical karyotypes, while a fourth had subtelocentric chromosomes 6 and 9. Hybrids between *A. glandulifera* and two other diploid species of section *Arachis* were male-sterile, and chiasmata frequencies ranged between 5.8 and 12.1 per cell. Attempts to hybridize the species with *A. hypogaea* failed. A new species description and D genomic classification are proposed for *A. glandulifera*, which is different from previously described A and B genomes of section *Arachis*.

Species of *Arachis* are widely distributed throughout South America. Monographs have been published by Chevalier (1933, 1934, 1936), Hoehne (1940), and Hermann (1954). However, these works describe only a small percentage of the estimated 70 or more species in the genus (Gregory and Gregory, 1979; Stalker and Moss, 1987). Although a taxonomic revision is needed in *Arachis*, many taxa have been hybridized to better define species relationships. For example, Gregory and Gregory (1979) used 100 accessions in a diallel crossing program and found semifertile F_1s could be produced within sections, but crosses among taxa of different sections were difficult to obtain.

Taxa of section *Arachis* nom. nud. sensu Gregory et al. (1973) are of special interest because the cultivated peanut *A. hypogaea* L. ($2n = 4x = 40$) belongs in the group. Section *Arachis* is distinguished from other sections of the genus by having tap roots but no adventitious roots or rhizomes, vertical pegs (a modified gynophore which initiates as an aerial structure and grows underground where pods are formed) that do not grow in a horizontal direction after soil penetration, and flowers without prominent red veins (Gregory et al., 1973; Resslar, 1980). Because taxa of section *Arachis* have been evaluated extensively, it is the only group in which more than one genomic classification has been made (Smartt and Stalker, 1982; Stalker and Moss, 1987).

Most species in section *Arachis* are diploid ($2n = 2x = 20$), while *A. hypogaea* and its presumed progenitor, *A. monticola* Krapovickas et Rigoni, are segmental allopolyploids ($2n = 4x = 40$). Crossing data and cytological investigations indicate that most diploid species in the section will hybridize, produce semifertile F_1s, and have a high percentage of chromosome homology (Smartt, Gregory, and Gregory, 1978a, b; Resslar and Gregory, 1979; Stalker and Wynne, 1979; Singh and Moss, 1984; Stalker and Hahn, 1989). These taxa have been designated as A genome species (for review, see Stalker and Moss, 1987). On the other hand, when *A. batizocoi* Krapovickas et Gregory is hybridized with other taxa in section *Arachis*, the interspecific hybrids are sterile, due largely to lack of complete chromosome pairing and meiotic irregularities (Smartt, Gregory, and Gregory, 1978a, b; Stalker and Wynne, 1979; Singh and Moss, 1984); therefore, *A. batizocoi* has been designated as a B genome species. Further, karyotypic data indicate that most species of the section have median chromosomes (A-genome species), whereas *A. batizocoi* has several submedian to subtelocentric chromosomes (Stalker and Dalmacio, 1981; Singh and Moss, 1982).

During the past 15 years a large number of *Arachis* accessions have been obtained from collection trips to South America (Simpson and Higgins, 1984). As a result, the number of sec-

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TABLE 1. *Accessions of* A. glandulifera *analyzed morphologically and cytologically*

Accession no.	Collector*	PI	Origin		Latitude	Longitude
			State	Country		
30091	GKSSc	468336	Santa Cruz	Bolivia	16°29′	62°05′
30098	GKSSc	468341	Santa Cruz	Bolivia	16°33′	61°00′
30099	GKSSc	468342	Santa Cruz	Bolivia	16°36′	61°01′
30100	GKSSc	468343	Santa Cruz	Bolivia	16°10′	61°02′

* G = W. C. Gregory, K = A. Krapovickas, S = C. E. Simpson, and Sc = A. Schinini.

tion *Arachis* accessions available in germplasm collections has more than tripled from ca. 120 to more than 420 accessions during recent years. The objectives of this investigation are to describe the morphology and cytology of a new species and to determine its relationships to A and B genome species of section *Arachis*.

MATERIALS AND METHODS

Species accessions used in this investigation were collected by W. C. Gregory, A. Krapovickas, C. E. Simpson, and A. Schinini during a 1977 expedition in northeast Santa Cruz, Bolivia (Table 1). Seeds of accessions Gregory et al. 30091, 30098, 30099, and 30100 were subsequently introduced to the United States and forwarded to North Carolina by D. J. Banks, USDA/ARS *Arachis* Curator, Stillwater, Oklahoma. Plants of each accession were grown at the Sandhills Agricultural Experiment Station, North Carolina, for seed increase, after which morphological traits were measured during the summer of 1986. Because plant size and growth habit of *Arachis* species can change significantly when grown in different environments, plants of the following four species were also planted at the same site to be used for comparisons during 1986: *A. batizocoi* (Krapovickas 9484; Gregory et al. 30079 and 30082), *A. chacoense* Krapovickas et Gregory nom. nud. (Gregory et al. 10602), *A. monticola* (Gregory et al. 30062), and *A. villosa* Bentham var. *villosa* (Bentham 22585). Plants within each accession appeared morphologically the same, so traits were recorded from only three randomly selected plants. Average measurements for the following structures were determined for each accession: length of mainstem; length of longest lateral branch; length, width, and shape of mainstem and lateral leaves and leaflets; stipule length, number of trichomes on stems, leaves, and pegs; flower height, width, and color; hypanthium length; peg length, pod length, width, shape, and reticulation; seed length, width, and weight; and flowering pattern on mainstem and lateral stems. All measurements were made approximately 90 days after planting in the field when plants were considered to be mature.

To karyotype the species, root tips of the four *Arachis* accessions were collected from seedlings germinated in sand, pretreated 15 min in a saturated solution of paradichlorobenzene, hydrolyzed in 1 N HCl, stained in 2% aceto-orcein for 2 hr, squashed in an oil press at approximately 100 kg/cm^2, dehydrated in an alcohol series after removing coverslips, and then permanently mounted on slides with Permount. Observations were made from 15 cells of each accession in the early metaphase stage of mitosis. Photomicrographs were taken of cells and printed at ×5,000. Chromosomes were ordered from 1 to 10 (based on length and chromosome morphology, with the longest chromosome designated as number 1) and placed in four centromere-position types based on the short/long arm ratios as follows: 0.80 to 1.00 = median, 0.65 to 0.79 = slightly median, 0.33 to 0.64 = submedian, and 0 to 0.32 = subtelocentric.

Because species of section *Arachis* have previously been separated using chromosome arm ratios (Singh and Moss, 1982), a principal component analysis using a SAS computer program was conducted using short/long arm ratios of the four accessions of 30091, 30098, 30099, and 30100 plus previously collected data (Stalker and Dalmacio, 1981) from A and B genome species. Species representing the A genome included the following: *A. cardenasii* Krapovickas et Gregory nom. nud. (Gregory et al. 10017), *A. chacoense* (Gregory et al. 10602), *A. correntina* (Burkart) Krapovickas et Gregory nom. nud. (Gregory et al. 9530), *A. duranensis* Krapovickas et Gregory nom. nud. (Krapovickas 7988), *A. stenosperma* Gregory et Gregory nom. nud. (Hammons et al. 410), *A. villosa* var. *villosa* (Bentham 22585), and *A. spegazzinii* Gregory et Gregory nom. nud. (Gregory et al. 10038). The B genome species *A. batizocoi* was represented by the five accessions Krapovickas 9484 and Gregory et al. 30079, 30080, 30081, and 30082.

Intraspecific crosses were made among the four accessions in a half diallel crossing block

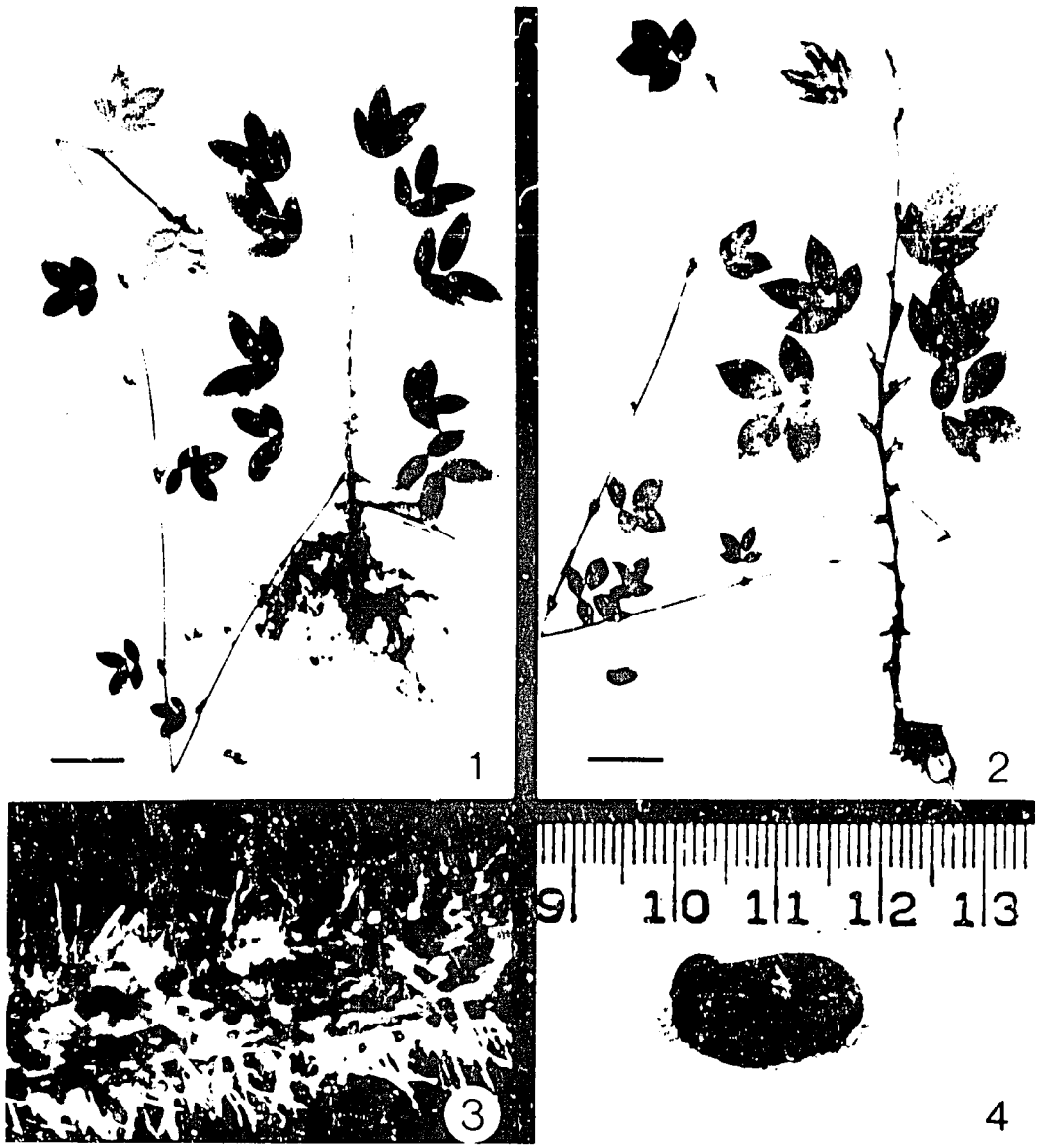
TABLE 2. *Numbers of* A. glandulifera *hybrids, pollen stained, and chromosome associations*

	No. pollinations	No. hybrids	Pollen stained (%)	Meiosis: Number of Plants	Meiosis: Number of Cells	Meiosis: Average I	Meiosis: Average II	Meiosis: Average Chiasmata
A. duranensis (7988)-A genome	—	—	98.0	6	171	0.05	9.98	19.63
A. batizocoi (9484)-B genome	—	—	99.1	3	83	0	10.00	19.06
A. glandulifera (30091)	—	—	99.4	3	150	0	10.00	19.02
A. glandulifera (30098)	—	—	99.2	2	100	0	10.00	19.34
A. glandulifera (30099)	—	—	99.0	3	150	0	10.00	19.54
A. glandulifera (30100)	—	—	99.2	2	75	0	10.00	19.61
Intraspecific hybrids								
30091 × 30098	45	4	98.8	2	115	0.02	9.91	19.71
× 30099	34	3	97.8	2	109	0	10.00	18.60
× 30100	37	2	95.3	—	—	—	—	—
30099 × 30098	40	1	—	—	—	—	—	—
× 30100	39	5	95.3	2	135	0	10.00	19.47
30100 × 30098	36	2	90.1	—	—	—	—	—
Interspecific hybrids (diploids × diploids)								
7988 × 9484	103	5	6.2	1	75	5.30	6.47	7.99
× 30091	132	4	10.8	1	75	10.00	5.10	5.78
× 30099	53	1	5.3	1	50	7.00	6.50	7.50
9484 × 7988	92	6	1.3	3	150	7.14	6.45	8.98
× 30091	233	19	1.8	6	277	3.29	8.36	12.08
× 30099	52	4	2.1	2	101	2.38	8.81	10.61
30091 × 9484	30	2	6.3	1	38	5.60	7.20	9.23
Interspecific hybrids (diploids × tetraploids)								
7988 × NC 4	113	8	0.0	—	—	—	—	—
× Argentine	150	4	0.1	—	—	—	—	—
9484 × NC 4	78	5	0.0	—	—	—	—	—
× Argentine	99	4	0.1	—	—	—	—	—
30091 × NC 4	98	0	—	—	—	—	—	—
× Argentine	84	0	—	—	—	—	—	—
30099 × NC 4	57	0	—	—	—	—	—	—
× Argentine	54	0	—	—	—	—	—	—
NC4 × 7988	141	6	0.0	—	—	—	—	—
× 9484	200	1	0.0	—	—	—	—	—
× 30091	161	0	—	—	—	—	—	—
× 30099	105	0	—	—	—	—	—	—
Argentine × 7988	137	11	0.0	—	—	—	—	—
× 9484	92	8	0.0	—	—	—	—	—
× 30091	141	0	—	—	—	—	—	—
× 30099	125	0	—	—	—	—	—	—

during the summer of 1983 (Table 2). An interspecific crossing experiment was conducted during the summers of 1983 and 1984 to hybridize the accessions with *A. duranensis* (A genome), *A. batizocoi* (B genome), and *A. hypogaea* cultivars NC 4 and Argentine (A and B genomes). As an estimate of male fertility, at least 600 pollen grains from each F_1 plant were scored for stainability with acetocarmine on at least 2 different days. Flower buds were also collected during the summers of 1985 and 1988, fixed, and stored in Carnoy's solution (six parts absolute ethanol : three parts chloroform : one part acetic acid). Anthers were squashed in acetocarmine to examine chromosome associations in the early metaphase stage of meiosis of parent accessions and F_1 hybrids.

RESULTS

The recently discovered taxon here described as *Arachis glandulifera* is an annual member of section *Arachis*. Four accessions were collected—one near Concepcion, Bolivia (coll. GKSSc 30091), and the other three near San Ignacio, Bolivia—which is ca. 100 km east of the 30091 collection site (Table 1). *Arachis glandulifera* is not cultivated. Plants grow in sandy soils and have an upright mainstem (Figs. 1, 2). They differ from other members of section *Arachis* in their long lateral branches which



Figs. 1–4. 1. Herbarium specimen of 60-day-old plant of *A. glandulifera* accession 30099 showing multiple flowers at a node. Bar = 45 mm. 2. Herbarium specimen of mature plant of *A. glandulifera* accession 30091. Bar = 45 mm. 3. Photomicrograph of *A. glandulifera* peg section showing glandular hairs (arrows), ×20 actual size. 4. Pod of *A. glandulifera* with highly reticulated pod.

extend to 2.5 m or more; large, elliptic leaflets with an acute apex; long pegs with glandular hairs (Fig. 3); and large seeds and pods (as compared to other diploid species of *Arachis*) with the pod surface highly reticulate (Fig. 4).

Arachis glandulifera Stalker, sp. nov.

Herba annua. Ramis lateralibus paucis, 2–3 m longis, prostratis. Foliolis ellipticis acutis. Floribus magnis, 17–19 mm longis, 13–17 mm latis. Gynophoris elongatis, glandulosis, ad aliquando 30 cm longis. Leguminibus magnis, reticulatovenosis, 13–17 mm longis, 8–10 mm diametis. Geminibus ovoideis ad oblongis, 11–13 mm longis, 7–8.5 mm latis.

Plants annual, tap roots. Mainstem erect, ca. 40 cm tall, with flowers. Lateral branches few, 2–3 m long, prostrate, pilose, bearing flowers. Stipules lanceolate, bristly, shorter than petiole, margins ciliate. Leaves tetrafoliate, glabrous above, villous beneath, margins ciliate. Mainstem leaves 73–105 mm long, 51–88 mm wide, leaflets 38–55 mm long, 19–25 mm wide, elliptic, apex obtuse; lateral branch leaflets 27–37 mm long, 15–23 mm wide. Flowers sessile in axillary spikes; standard 17–19 mm wide, 13–17 mm high, orange, curved at margins; wings orange and yellow; keel ca. 15 mm long. Pegs borne all along stem, up to 30 cm long,

TABLE 3. *Selected morphological traits of* A. glandulife.a *and four other species of section* Arachis *presented as averages of three plants grown at the Sandhills Research Station, NC*

Accession	$\bar{X}$ Length		$\bar{X}$ Mainstem leaf		$\bar{X}$ Mainstem leaflet		$\bar{X}$ Flower		$\bar{X}$ Seed		Pod	
	Mainstem	Longest branch	Length	Width	Length	Width	Height	Width	Length	Width	Length	Diameter
	cm		mm									
A. glandulifera												
30091	42	221	93	74	45	21	16	19	124	84	152	100
30098	58	241	81	70	43	20	13	18	132	77	170	97
30099	52	220	82	59	41	20	16	17	110	78	137	94
30100	49	250	90	64	43	21	14	19	128	74	154	87
A. batizocoi												
9484	34	127	81	60	33	24	10	11	100	48	126	61
30079	32	160	84	51	29	20	11	10	96	57	123	66
30082	29	151	104	53	34	17	11	11	99	57	118	66
A. chacoense												
10602	10	70	66	41	29	9	14	13	100	40	124	53
A. monticola												
30062	31	83	118	81	53	25	12	13	103	64	124	78
A. villosa												
22585	14	41	60	32	23	10	15	16	80	54	104	66

trichomes many, glandular. Fruit unilocular, ovoid to oblong, 13–16 mm long, 8–10 nim wide, apex beaked; pericarp with 8–10 longitudinal ribs, greatly reticulated between ribs. Seeds ovoid to oblong, 11–13 mm long, 7–8.5 mm wide. Chromosome number $2n = 20$.

Type: NORTH CAROLINA. Moore County: Sandhills Research Station, field D2, plot number 90 WSN 40; 12 Sep 1990 *H. T. Stalker 90-40* (HOLOTYPE: NCSU; ISOTYPE; NA, US).

Morphology of *Arachis* species can differ significantly between environments. For example, Krapovickas, Fernandez, and Seeligman (1974) reported that the lateral stems of *A. batizocoi* are usually 4 m long, whereas in North Carolina they are usually 1.5 m in length. A comparison of the four *A. glandulifera* accessions was thus made with other species of section *Arachis* for selected traits which will serve as a reference for future identification (Table 3). As compared to *A. batizocoi, A. chacoense, A. monticola,* and *A. villosa, A. glandulifera* accessions have a relatively long mainstem, extremely long lateral branches, and large leaves, leaflets, flowers, pods, and seeds. Variation was observed within the species, however, with plants of 30098 slightly taller than other accessions and 30100 with fewer lateral branches.

Cytological observations confirmed that ali accessions were diploid with $2n = 2x = 20$. The somatic chromosomes of *A. glandulifera* range between 2.48 and 4.47 μm in length. Even though care was taken to observe cells at the same stage of mitosis, variation was observed among cells of each accession for length of individual chromosomes. In particular, the size of consistently shorter chromosomes of accession 30098 (Table 4) was likely due to variation in penetration rates of pretreatment solutions. In addition to chromosome length, short/long arm ratios and secondary constriction location are presented in Table 4 and are believed to be a more precise measure of cytological similarities and differences among genotypes. Even though many of the chromosomes in the genome were nearly the same length, identification of each of the ten homologous chromosomes was possible by collectively considering length, arm ratios, and several unique features such as heterochromatic regions and secondary constrictions. Two unique karyotypes were observed among the four accessions. The three accessions 30098, 30099, and 30100 had seven median chromosomes (no. 1, 2, 3, 5, 6, 7, and 9), two submedian chromosomes (no. 8 and 10), and one subtelocentric chromosome (no. 4) (Fig. 5). Satellites were observed on the short arm of chromosomes 2, 3, and 6. On the other hand, accession 30091 had five median chromosomes (no. 1, 2, 3, 5, and 7), four submedian chromosomes (no. 6, 8, 9, and 10), one subtelocentric chromosome (no. 4), and satellited chromosomes 2 and 6. A large heterochromatic

TABLE 4. *Somatic chromosome length and arm ratio measurements for four* A. glandulifera accessions

Accession	Chromosome 1	2	3	4	5	6	7	8	9	10
Average chromosome length (μm)										
30091	4.46[a]	3.69	3.55	3.50	3.27	3.27	3.05	3.05	2.86	2.78
30098	3.58[a]	3.64	3.35[a]	3.21[a]	3.09[a]	3.00[a]	2.70[a]	2.64[a]	2.49[a]	2.48[a]
30099	4.15	3.65	3.53	3.42	3.33	3.33	3.10	3.10	2.81	2.76
30100	4.19	3.75	3.57	3.39	3.39	3.17	3.20	2.99	2.90	2.67
Average chromosome arm ratio (short/long)										
30091	0.80	0.82[b]	0.91	0.29	0.90	0.59[b]	0.92	0.35	0.38[b]	0.41
30098	0.88	0.91[b]	0.83[b]	0.29	0.92	0.82[b]	0.85	0.34	0.87	0.42
30099	0.88	0.90[b]	0.80[b]	0.30	0.93	0.76[b]	0.89	0.35	0.86	0.52
30100	0.84	0.86[b]	0.82[b]	0.31	0.91	0.91[b]	0.91	0.33	0.81	0.38

[a] Accessions significantly different at $P = 0.05$ as determined by Duncan's multiple range test.
[b] Chromosomes with a secondary constriction.

block was observed on the long arm of chromosome 1 of all accessions.

A principal component analysis using data from short/long chromosome arm ratios illustrated that the somatic chromosomes of *A. glandulifera* cluster as a single cytological group and are significantly different from other species of section *Arachis* (Fig. 6). Seven diploid A genome species also grouped together as a cluster. However, variation was observed for the B genome species *A. batizocoi* where accessions 9484, 30079, and 30082 were very similar; while 30081 differed slightly from other genotypes and 30080 was separate and intermediate between *A. batizocoi* and *A. glandulifera* accessions. Stalker and Hahn (1989) reported that 30080 (previously reported as 30097 because of a misidentification of seed) has multiple translocations and a highly asymmetrical karyotype as compared to other accessions of *A. batizocoi*.

Intraspecific hybrids of *A. glandulifera* were relatively difficult to produce, as shown by the overall successful pollination rate of 7.2% (Table 2). Only one hybrid was produced between accessions 30099 and 30098, but it died before cytological analyses could be completed. F_1s were highly fertile, and meiotic irregularities or multivalents were not observed in any intraspecific hybrid (Table 2).

Hybrids between either of the two species *A. duranensis* (7988) or *A. batizocoi* (9484) and *A. glandulifera* accessions 30091 and 30099 were produced at only slightly lower frequencies (5.7%) than those for intraspecific hybrids (Table 2); however, all interspecific F_1 hybrids with *A. duranensis* and *A. batizocoi* were sterile. Significant morphological differences were also observed among these hybrids. For example, *A. batizocoi* × 30091 hybrids were vigorous had lateral branches approximately 2 m long, and a mainstem 1.5 m high. Plants from the cross *A. batizocoi* × 30099 had very few short branches reaching 40 cm in length and mainstems only 2 cm tall. Chromosome associations in pollen mother cells (PMCs) averaged 10.0 I + 5.1 II and 5.8 chiasmata in the hybrid *A. duranensis* × 30091 and 7.0 I + 6.5 II and 7.5 chiasmata in the hybrid *A. duranensis* × 30099. Hybrids between *A. ba-*

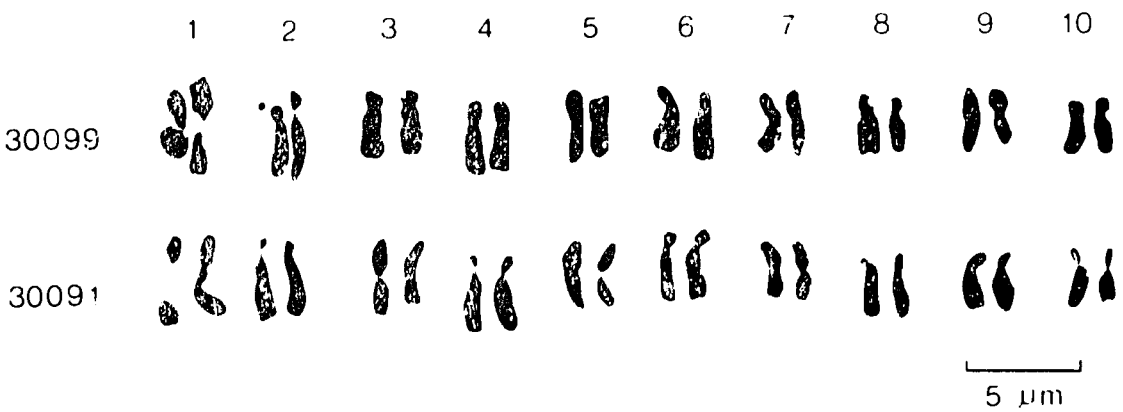


Fig. 5. Somatic chromosomes of *A. glandulifera* accessions 30098 and 30091.

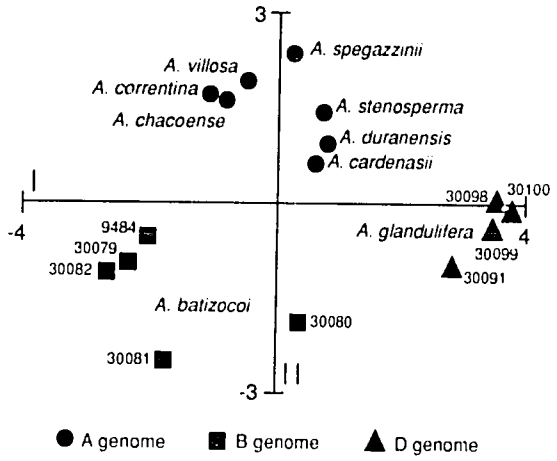


Fig. 6. Projection of nine section *Arachis* species onto the first two principal components estimated from a correlation matrix of ten short long arm ratios. A-genome species are represented by a ●, the B-genome species *A. batizocoi* by ■, and the D-genome species *A. glandulifera* by a ▲.

tizocoi and accession 30091 averaged 3.29 I + 8.36 II and 12.1 chiasmata and *A. batizocoi* × 30099 averaged 2.38 I + 8.81 II and 10.6 chiasmata per PMC (Table 2).

The two *A. hypogaea* (A and B genomes) cultivars NC 4 and Argentine were used as both male and female parents in crosses with accessions 30091 and 30099, *A. duranensis* and *A. batizocoi*. Crosses between *A. hypogaea* and *A. duranensis* (A genome) resulted in 5.3 hybrids per 100 pollinations and a slightly lower frequency of 3.8 for *A. hypogaea* × *A. batizocoi* (B genome) crosses. However, 825 pollinations failed to produce hybrids when attempts were made with the two *A. glandulifera* accessions (Table 2).

DISCUSSION

Arachis glandulifera evolved in a region of South America where many species belonging to section *Arachis* have been found. Plants have upright mainstems and have longer lateral branches than other diploid taxa. The pods and seeds are also very large as compared to other diploid species of *Arachis*, approaching the size of small-seeded genotypes of the cultivated peanut. Although several species of *Arachis* have glandular trichomes on stems or leaves, *A. glandulifera* is the only one thus far observed with glandular trichomes on pegs.

Interspecific hybrids between *A. glandulifera* and other diploid members of section *Arachis* have been obtained, but they are all sterile. Homology does exist among chromosomes of *A. glandulifera* and those of both *A. duranensis* (A genome) and *A. batizocoi* (B genome); however, the chiasmata frequencies ranged only between 10.6 and 12.1 when accessions were hybridized with *A. batizocoi*, and between 5.8 and 7.5 when the same taxa were hybridized with *A. duranensis*. These ranges can be compared to 17–20 chiasmata per cell when two species with an A genome are hybridized and 6–11 chiasmata for A × B genome hybrids (Singh and Moss, 1984). Further, analyses of the somatic chromosomes showed that *A. glandulifera* has a unique karyotype. Thus, the species *A. glandulifera* is believed to be a good biological species and is being designated as the first member of a new D genomic group.

Because the genome of *A. glandulifera* has several subtelocentric or telocentric chromosomes, it may have evolved from other members of section *Arachis* through pericentric inversions and/or translocations. However, genetic distance from other diploid species is not so great as to prevent hybridization (even though F_1s are sterile). One accession (30091), with a slightly different karyotype, indicates that cytological evolution is continuing in the species. Interestingly, 30091 was found at a location ca. 100 km from the other accessions, and additional accessions are expected to exist in Bolivia that are cytologically different from 30098, 30099, and 30100.

A comparison of the karyotype of *A. glandulifera* with the chromosomes of *A. hypogaea* and *A. monticola* (Singh and Moss, 1982; Stalker and Dalmacio, 1986) indicates that a large number of chromosome differences exist between this diploid and the two tetraploid species. Although *A. glandulifera* will hybridize with other diploid species of section *Arachis*, attempted hybridizations with the cultivated peanut have failed. Thus, *A. glandulifera* is the only species in the section for which triploid interspecific hybrids with *A. hypogaea* have not been obtained after sufficient numbers of pollinations, in reciprocal crosses, were made to give a reasonable probability of successful hybridization. The reasons for failures to obtain hybrids may be due to both pre- and postfertilization events, because very few pegs were produced after pollination, and the small percentage of pods that were observed had tiny embryos at the time of normal seed maturity. The cultivated peanut is thus assumed to be cross-incompatible with *A. glandulifera*. Based on crossing and cytological evidence, the species is not believed to have been involved in the evolution of *A. hypogaea*. Further, germplasm introgression to *A. hypogaea* will be difficult and may require specialized techniques

such as embryo rescue before germplasm from the species can be exploited.

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