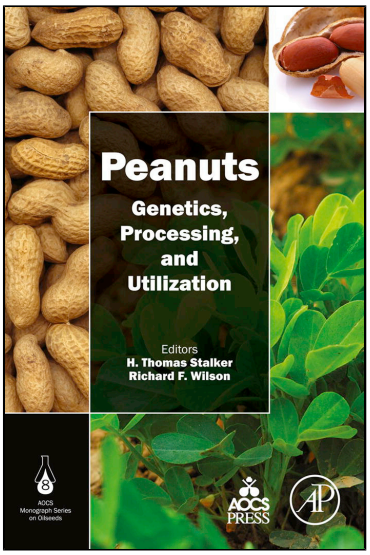




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Chapter 2

# Biology, Speciation, and Utilization of Peanut Species

**H. Thomas Stalker[1], Shyamalrau P. Tallury[2], Guillermo R. Seijo[3], Soraya C. Leal-Bertioli[4]**

*[1]Department of Crop Science, North Carolina State University, Raleigh, NC, USA; [2]Pee Dee Research and Education Center, Clemson University, Florence, SC, USA; [3]Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; [4]Embrapa Genetic Resources and Biotechnology, Brasília, Brazil*

## OVERVIEW

Peanut, also known as groundnut (*Arachis hypogaea* L.), is a native new world crop. *Arachis* species originated in South America and are found in tropical and subtropical areas. Eighty-one species have been named (Krapovickas and Gregory, 1994; Valls and Simpson, 2005; Valls et al., 2013), including the domesticated peanut, *A. hypogaea* L. Species have evolved in highly diverse habitats and both annual and perennial types exist. New species are being discovered in areas that previously were very difficult to reach because of poor roads and transportation. It is likely that the genus originated in the highlands in the southwestern Mato Grosso do Sul region of Brazil close to Gran Pantanal where the most ancient species of the genus (*Arachis guaranitica* Chodat. and Hassl. and *Arachis tuberosa* Bong. Ex Benth.) are found (Gregory et al., 1980; Simpson and Faries, 2001). Subsequently, as the planalto continued to be uplifted coupled with water flow, the genus spread into the drier lowlands of South America (Gregory and Gregory, 1979; Stalker and Simpson, 1995; Simpson et al., 2001). The genus likely originated in tropical wetland areas and subsequently adapted for survival in dry environments.

Species in the genus *Arachis* are widely distributed in South America from Northeast Brazil to southern Uruguay and from the Andean lowlands in the west to the eastern Atlantic coast, and the distribution is continuous across this region (Valls et al., 1985). Species grow in deep friable sand to thick, gummy clay and on schist rocks with virtually no soil, suggesting that species have adapted to highly diverse and harsh environments (Simpson et al., 2001). Fruiting below ground likely protected the seeds from predators and the many root adaptations (e.g., rhizomes, tuberous roots) likely helped species to adapt to new habitats. Conversely, the geocarpic fruit impeded rapid spread into new environments.

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Krapovickas and Gregory (1994) indicated that the most defining morphological features of the genus are underground plant parts, including the fruits, rhizomatous structures, root systems, and hypocotyls.

The center of origin for the cultivated species *A. hypogaea* is believed to be southern Bolivia to northwestern Argentina based on the occurrence of the two progenitor species *Arachis duranensis* and *Arachis ipaënsis*, and archaeological evidence gathered in this region (Hammons, 1982; Stalker and Simpson, 1995). Simpson et al. (2001) also suggested that the eastern slopes of Cordillera may be a possible area for origin of *A. hypogaea* because of the favorable environment for peanut growth. Advances in the peanut genome sequence and the availability of new genomic tools will help clarify the origin and evolution of the cultivated and wild species of the genus *Arachis.*

Wild peanut species were important as sources of food in pre-Columbian times and several taxa are still widely used as forages or for their aesthetic value as a ground cover. *Arachis glabrata* and *Arachis pintoi* are utilized for grazing and *Arachis repens* is used as a ground cover in residential areas and roadsides in tropical regions (Mathews et al., 2000; Hernandez-Garay et al., 2004). Two wild species (*Arachis villosulicarpa* Hoehne and *Arachis stenosperma* Krapov. and W.C. Gregory) were cultivated by indigenous people in Brazil for food and medicinal use, albeit on a limited scale (Gregory et al., 1973; Simpson et al., 2001), but only *A. hypogaea* is economically important today as a human food source. Importantly, many *Arachis* species have extremely high levels of disease and insect resistances that are not present in cultivated peanut.

## DISCUSSION

### Vegetative Growth

The peanut seed is a dormant plant in itself containing the shoot (plumule/leaf primordia) and the root initials (radicle). The seed consists of two cotyledons which are the first seed leaves and contain stored food reserves that supply energy and nutrition for the young seedling to grow and establish. The seed is enclosed by a papery seed coat that acts as a protective layer from soil microbes. It varies in color from white to tan to black and different shades of red or pink. When a peanut seed is planted under favorable environments the radicle starts to grow, forming the upper hypocotyl and the lower primary root. The hypocotyl elongates rapidly to push the cotyledons above ground in four to seven days. The cotyledons are the first foliar structures and split open to expose the shoot primordia which extends to form the epicotyl. The epicotyl contains the first true leaves and forms the main stem, whereas the lower hypocotyl elongates to form the tap root. The point of transition from stem to root is the "collar" region which is at base of the hypocotyl (Gregory et al., 1973). Lateral roots generally appear within two to three days after germination and are extensively developed by about five days (Moss and Ramanatha Rao, 1995). Tajima et al. (2008) observed three different root categories in germinating peanut: the thick

primary seminal root with extensive secondary thickening; the first-order lateral roots which were long and thin with limited secondary thickening; and second- and higher-order lateral roots, which were anatomically simple and thin, with little or no secondary growth. They suggested that the first-order lateral roots formed the skeleton of the root system and the second- and higher-order lateral roots are the feeder roots. Adventitious roots are commonly seen when stems come in contact with soil (Moss and Ramanatha Rao, 1995).

Peanut leaves are tetrafoliate and occur alternately on the main stem and lateral branches. The exceptions are the three trifoliate species *A. guaranitica*, *A. tuberosa*, and *Arachis sesquijuga* from section Trierectoides. The leaves are subtended by a partially adnate stipule. The leaflets are usually oblong to lanceolate and occur in two opposite pairs. Several naturally occurring or induced mutants with different leaf shapes and colors also occur in the germplasm collection. The stems are angular, can be pubescent or glabrous, and are usually green but can be pigmented as in Valencia-types which are dark purple. Stem pigmentation and pubescence on stems and leaves have been shown to limit damage from leaf feeding insect pests (Sharma et al., 2003).

Peanut plants are usually about 1–1.5 ft (0.30–0.46 m) tall with lateral branches of about one foot (0.30 m) wide. However, lateral branches of many *Arachis* wild species can be up to several meters in length. Based on visually vegetative and reproductive events from seedling emergence to pod maturity, Boote (1982) developed a set of uniform growth stage descriptors for Spanish and Virginia-type peanuts that are useful for management of peanut under production. Plant habit and branching patterns have been used to define the two subspecies and the six botanical varieties, and market types (Krapovickas and Gregory, 1994; Table 1). All botanical varieties except *aequatoriana* Krapov. & W.C. Gregory and *peruviana* Krapov. & W.C. Gregory are cultivated in the United States. Detailed descriptors have been published by Pittman (1995) and IBPGR and ICRISAT (1992).

## Reproductive Growth

### *Flower*

Peanut belongs to the tribe Dalbergieae, subfamily Papilionoideae in the family Fabaceae. It is a herbaceous legume with indeterminate flowering pattern and is day-neutral with respect to flower initiation (Ketring, 1979). Peanut is self-pollinating and thus the flowers are perfect/hermaphroditic containing both male and female reproductive parts. Flowers arise in leaf axils on branches and also on mainstems in subspecies *fastigiata* types. The inflorescence is a raceme and commonly contains up to three flowers. The flowers are papilionaceous with five brightly colored petals one of which is the large standard, two wing petals and two fused keel petals. The calyx is five-lobed with one lobe opposite the keel, whereas the other four are fused except at their tips on the back side of the standard. The standard varies in color from light yellow to deep orange

**TABLE 1** Subspecies and Varieties of *Arachis hypogaea*

| Variety | Market Type | South American Location | Characteristics |
|---|---|---|---|
| **Subspecies *hypogaea*** | | | |
| *hypogaea* | | Bolivia, Amazon | No floral axes on main stem; alternating pairs of floral and reproductive axes on branches; branches short; less hairy |
| | Virginia | | Less hairy; large seeded |
| | Runner | | Less hairy; small seeded |
| *hirsute* | Peruvian runner | Peru | More hairy |
| **Subspecies *fastigiata*** | | | |
| *fastigiata* | | | Floral axes on main stem; alternating pairs of floral and vegetative axes on branches |
| | Valencia | Brazil<br>Guaranian<br>Goias<br>Minas Gerais<br>Paraguay<br>Peru<br>Uruguay | |
| *peruviana* | | Peru,<br>N.W. Bolivia | Less hairy; deep pod reticulation |
| *aequatoriana* | | Ecuador | Very hairy; deep pod reticulation; purple stems; more branched, erect |
| *vulgaris* | Spanish | Brazil<br>Guaranian<br>Goias<br>Minas Gerais<br>Paraguay<br>Uruguay | More branched; upright branches |

After Stalker and Simpson (1995).

and occasionally white, and they may also have red veins on the inner face. The wings are usually yellow surrounding the keel. The keel is almost colorless and encloses the anthers and the stigma. The androecium is monadelphous with filaments fused for two-thirds of their length and contains eight functional stamens and two, small sterile ones. The flowers are subtended by a bract and are

sessile although they appear as pedicillate due to the elongated tubular hypanthium or the "calyx tube." The calyx tube contains a hollow style that is attached to the ovary at the base (Periasamy and Sampoornam, 1984). The tip of the style, called a stigma, is usually at the same level or protrudes slightly above the anthers. The stigma of *A. hypogaea* is of the dry papillate type and has no hairs, and likely accommodates up to 15 pollen grains (Moss and Ramanatha Rao, 1995). However, differences in stigma morphology exist between annual and perennial *Arachis* species, where annual species contain a large stigmatic surface but perennial species have smaller stigmas with cuticularized, unicellular hairs (Lu et al., 1990). These authors inferred that the stigmatic surfaces of many *Arachis* species accommodate only a maximum of three pollen grains. Thus, the small stigmatic surface of perennial species likely contributes to low seed set and difficulty in serving as female parents for interspecific hybridization (Moss and Ramanatha Rao, 1995). The ovary is superior, unilocular, and commonly contains two ovules, however, up to three to four ovules are present within the ovary in the Valencia market type peanuts. Following fertilization, each ovule develops into a peanut kernel or seed and the ovary becomes the pod.

### *Fertilization*

Pattee et al. (1991) indicated that pollen matures approximately 6–8 h before anthesis, which occurs within a few hours after sunrise. Generally, only one flower at an axil reaches anthesis on any given day. The mature pollen grain is two-celled with two generative nuclei (Xi, 1991); one fuses with the egg cell to form the embryo and the other participates in double fertilization to form endosperm. With the onset of anthesis the space between the anthers and the stigma within the enclosed keel becomes packed with pollen grains, thus ensuring natural self-pollination. However, Banks (1990) reported that in the species *Arachis lignosa*, there is a truncated stigma in an elevated position relative to the anthers that restricts natural self-pollination. Under field conditions there may be up to 10% outcrossing when bee populations are high (Knauft et al., 1992).

Each ovule has a mature embryo sac that contains a well differentiated egg cell at the micropylar end and the polar nucleus is surrounded by starch grains. The process of fertilization is initiated at the time of anthesis when pollen lands on the receptive stigmatic surface (pollination) followed by germination and growth of the pollen tube containing the male gamete (pollen grain) through style and eventually leading to the union with egg cell (syngamy). The pollen grain enters through the micropyle and fuses with the egg cell. The entire process of fertilization usually takes about 18–24 h from anthesis to syngamy (Pattee et al., 1991). Following syngamy, the starch grains dissolve and provide nutrition for the proembryo to grow and eventually develop into a mature seed.

### *Pod Development*

Peanut pod development is unique in that fertilization occurs in the flowers above ground but the pods develop below ground. During early embryo growth and development (between 24 and 72 h following fertilization), an intercalary

meristem at the base of the ovary undergoes active division leading to a pointed stalk-like structure called the "peg" (Smith, 1950). The fertilized ovules are at the tip of the peg. Pegs are usually observed between four and seven days after pollination, are positively geotropic (Zamski and Ziv, 1976), and require darkness for pod formation (Ziv, 1981). As the peg is elongating to enter the soil (aerial phase) the fertilized egg divides to become an 8–16 celled proembryo embryo and then remains quiescent until after soil penetration and pod development begins (Pattee and Mohapatra, 1987). After soil penetration, peg elongation is arrested and the end of the peg expands to form the pod. The peg becomes diageotropic after soil penetration such that the ovules are always located on the upper wall of the pod, with the pod tip pointing away from the plant (Moss and Ramanatha Rao, 1995). The first sign of pod development involves the swelling of the peg tip along with the horizontal turning of the peg. Pod enlargement occurs from the base toward the tip with simultaneous faster development of the basal ovule (Smith, 1950). Descriptions of peanut embryo growth and development have been published by Periasamy and Smapoornam (1984), Pattee and Mohapatra (1987), and Xi (1991). Normally, a mature peanut pod is developed within 60–80 days after fertilization. However, because plants are indeterminate and flowering occurs over an extended period of time, at the time of harvest a plant will contain pods at multiple maturity levels.

## Evolution of *Arachis*

Peanut species originated in the Mato Grosso region in the highlands of Brazil (Gregory et al., 1980) and most likely were distributed by water to lowland areas. They now occupy a large region of South America. The first *Arachis* species was described by Benthan in 1841 and several monographs were published during the 1930 and 1940s, but systematic collections were not made until the 1950s when A. Krapovickas and W.C. Gregory initiated a series of trips over a 25 year period. They published a monograph with 69 species that are grouped into nine sections (Figure 1). Additional collections by C.E. Simpson, J.F.M Valls, and G. Siejo and coworkers led to other new species and the number of named taxa has risen to 81 (Table 2), with additional ones currently being described. Jarvis et al. (2003) concluded that large areas of South America still need to be collected, so additional species are expected to be discovered in the future.

Early cytological research identified one pair of significantly smaller chromosomes (termed "A" chromosomes) in species of section *Arachis* and a unique chromosome pair that had a large secondary constriction (termed "B" chromosomes) in the species *Arachis batizocoi* (Husted, 1936). Hybridization between diploid species was first reported between *A. duranensis* and *Arachis villosa* var. *correntina* (Raman and Kesavan, 1962) and meiosis was regular. Later studies indicated that hybrids between species having the small chromosome pair are partially to fully fertile; however, hybrids between the species with the small

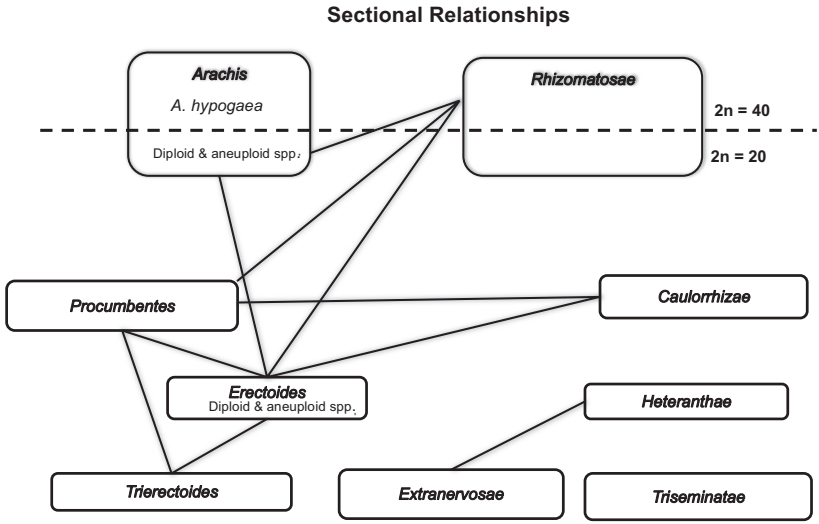


**FIGURE 1** Sectional designations of *Arachis* and crossing relationships. *After Krapovickas and Gregory (1994).*

chromosome and *A. batizocoi* are sterile and $F_1$s have many univalents (Stalker et al., 1991). Thus, the terminology "A" and "B" genome has been used in peanut to describe the two cytological groups (genomes). Because the cultivated peanut has one pair of smaller chromosomes and one pair of chromosomes with a large secondary constriction, it is an allotetraploid with AABB genomes. Hybrids between either A or B genome species with *Arachis glandulifera* (D genome) also have many univalents and are sterile (Stalker et al., 1991). Thus, there is a considerable amount of cytological differentiation among species.

Gregory and Gregory (1979) conducted an extensive hybridization program using 91 species accessions and reported cross-compatibility relationships in *Arachis*. Hybridization between species within the same section was more successful than crosses between sections, and $F_1$s of intersectional crosses were highly sterile. To overcome crossing barriers, complex hybrids have been attempted (Gregory and Gregory, 1979; Stalker, 1981), but fertility has not been restored. Thus, introgression from wild *Arachis* species to *A. hypogaea* by conventional hybridization is believed to be restricted to members of section *Arachis*. Even within section *Arachis*, hybrids may be difficult to obtain because of genomic and/or ploidy differences.

Based on cross-compatibility data, Smartt and Stalker (1982) and Stalker (1991) concluded that genomic groups have evolved in the genus which mostly follow sectional designations (Am, *Ambinervosae*; T, *Triseminatae*; C, *Caulorrhizae*; EX, *Extranervosae*; E, *Erectoides*; R, *Rhizomatosae*; and A, B, and D, *Arachis*). The B genome was divided into B, F, and K genomes by Seijo et al. (2004) and Robledo and Seijo (2010). Based on ribosomal DNA loci

**TABLE 2** *Arachis* Species Identities and Associated Type Specimens

| Section and Species | 2*n* | Genome | Collector[a] | Identification No. |
|---|---|---|---|---|
| **Section *Arachis*** | | | | |
| *Arachis batizocoi* Krapov. & W.C. Gregory | 20 | K | K | 9505 |
| *Arachis benensis* Krapov., W.C. Gregory & C.E. Simpson | 20 | F | KGSPSc | 35005 |
| *Arachis cardenasii* Krapov. & W.C. Gregory | 20 | A | KSSc | 36015 |
| *Arachis correntina* (Burkart) Krapov. & W.C. Gregory | 20 | A | Clos | 5930 |
| *Arachis cruziana* Krapov., W.C. Gregory & C.E. Simpson | 20 | K | KSSc | 36024 |
| *Arachis decora* Krapov., W.C. Gregory & Valls | 18 | – | VSW | 9955 |
| *Arachis diogoi* Hoehne | 20 | A | Diogo | 317 |
| *Arachis duranensis* Krapov. & W.C. Gregory | 20 | A | K | 8010 |
| *Arachis glandulifera* Stalker | 20 | D | St | 90-40 |
| *Arachis gregoryi* C.E. Simpson, Krapov, & Valls | 20 | B | VS | 14960 |
| *Arachis helodes* Martius ex Krapov. & Rigoni | 20 | A | Manso | 588 |
| *Arachis herzogii* Krapov., W.C. Gregory and C.E. Simpson | 20 | A | KSSc | 36030 |
| *Arachis hoehnei* Krapov. & W.C. Gregory | 20 | A | KG | 30006 |
| *Arachis hypogaea* L. | 40 | AB | Linn. | 9091 |
| *Arachis ipaënsis* Krapov., W.C. Gregory | 20 | B | KMrFr | 19455 |
| *Arachis kempff-mercadoi* Krapov., W.C. Gregory & C.E. Simpson | 20 | A | KGPBSSc | 30085 |

| | | | | |
|---|---|---|---|---|
| *Arachis krapovickasii* C.E. Simpson, D.E. Williams, Valls & I.G. Vargas | 20 | K | WiSVa | 1291 |
| *Arachis kuhlmannii* Krapov. & W.C. Gregory | 20 | A | KG | 30034 |
| *Arachis linearifolia* Valls, Krapov, & C.E. Simpson | 20 | A | VPoBi | 9401 |
| *Arachis magna* Krapov., W.C. Gregory & C.E. Simpson | 20 | B | KGSSc | 30097 |
| *Arachis microsperma* Krapov., W.C. Gregory & Valls | 20 | A | VKRSv | 7681 |
| *Arachis monticola* Krapov. & Rigoni | 40 | AB | K | 8012 |
| *Arachis palustris* Krapov., W.C. Gregory & Valls | 18 | – | VKRSv | 6536 |
| *Arachis praecox* Krapov., W.C. Gregory & Valls | 18 | – | VS | 6416 |
| *Arachis schininii* Valls & C.E. Simpson | 20 | A | VSW | 9923 |
| *Arachis simpsonii* Krapov. & W.C. Gregory | 20 | A | KSSc | 36009 |
| *Arachis stenosperma* Krapov. & W.C. Gregory | 20 | A | HLK | 410 |
| *Arachis trinitensis* Krapov. & W.C. Gregory | 20 | F | Wi | 866 |
| *Arachis valida* Krapov. & W.C. Gregory | 20 | B | KG | 30011 |
| *Arachis villosa* Benth. | 20 | A | Tweedi | 1837 |
| *Arachis williamsii* Krapov. & W.C. Gregory | 20 | B | WiCl | 1118 |
| **Section *Caulorrhizae*** | | | | |
| *Arachis pintoi* Krapov. & W.C. Gregory | 20 | C | GK | 12787 |
| *Arachis repens* Handro | 20 | C | Otero | 2999 |

*Continued*

**TABLE 2** *Arachis* Species Identities and Associated Type Specimens—cont'd

| Section and Species | 2*n* | Genome | Collector[a] | Identification No. |
|---|---|---|---|---|
| **Section *Erectoides*** | | | | |
| *Arachis archeri* Krapov. & W.C. Gregory | 20 | E | KCr | 34340 |
| *Arachis benthamii* Handro | 20 | E | Handro | 682 |
| *Arachis brevipetiolata* Krapov. & W.C. Gregory | 20 | E | GKP | 10138 |
| *Arachis cryptopotamica* Krapov. & W.C. Gregory | 20 | E | KG | 30026 |
| *Arachis douradiana* Krapov. & W.C. Gregory | 20 | E | GK | 10556 |
| *Arachis gracilis* Krapov. & W.C. Gregory | 20 | E | GKP | 9788 |
| *Arachis hatschbachii* Krapov. & W.C. Gregory | 20 | E | GKP | 9848 |
| *Arachis hermannii* Krapov. & W.C. Gregory | 20 | E | GKP | 9841 |
| *Arachis major* Krapov. & W.C. Gregory | 20 | E | Otero | 423 |
| *Arachis martii* Handro | 20 | E | Otero | 174 |
| *Arachis oteroi* Krapov. & W.C. Gregory | 20 | E | Otero | 194 |
| *Arachis paraguariensis* | 20 | | | |
| ssp. *paraguariensis* Chodat & Hassl. | | E | Hassler | 6358 |
| ssp. *capibarensis* Krapov. & W.C. Gregory | | E | HLKHe | 565 |
| *Arachis porphyrocalyx* Valls & C.E. Simpson | 18 | E | VSPtWiSv | 7307 |
| *Arachis stenophylla* Krapov. & W.C. Gregory | 20 | E | KHe | 572 |

| | | | | |
|---|---|---|---|---|
| **Section *Extranervosae*** | | | | |
| *Arachis burchellii* Krapov. & W.C. Gregory | 20 | EX | Irwin et al. | 21163 |
| *Arachis lutescens* Krapov. & Rigoni | 20 | EX | Stephens | 255 |
| *Arachis macedoi* Krapov. & W.C. Gregory | 20 | EX | GKP | 10127 |
| *Arachis marginata* Gardner | 20 | EX | Gardner | 3103 |
| *Arachis pietrarellii* Krapov. & W.C. Gregory | 20 | EX | GKP | 9923 |
| *Arachis prostrata* Benth. | 20 | EX | Pohl | 1836 |
| *Arachis retusa* Krapov., W.C. Gregory & Valls | 20 | EX | VPtSv | 12883 |
| *Arachis setinervosa* Krapov. & W.C. Gregory | 20 | EX | Eiten and Eiten | 9904 |
| *Arachis submarginata* Valls, Krapov. & C.E. Simpson | 20 | EX | SiW | 3729 |
| *Arachis villosulicarpa* Hoehne | 20 | EX | Gehrt | SP47535 |
| **Section *Heteranthae*** | | | | |
| *Arachis dardani* Krapov. & W.C. Gregory | 20 | H | GK | 12946 |
| *Arachis giacomettii* Krapov., W.C. Gregory, Valls & C.E. Simpson | 20 | H | VPzV1W | 13202 |
| *Arachis interrupta* Valls & C.E. Simpson | 20 | H | VPiFaSv | 13082 |
| *Arachis pusilla* Benth. | 20 | H | Blanchet | 2669 |
| *Arachis seridoensis* Valls, C.E. Simpson, Krapov, & R. Veiga | 20 | H | VRSv | 10969 |
| *Arachis sylvestris* (A. Chev.) A. Chev. | 20 | H | Chevalier | 486 |

*Continued*

**TABLE 2** *Arachis* **Species Identities and Associated Type Specimens—cont'd**

| Section and Species | 2*n* | Genome | Collector[a] | Identification No. |
|---|---|---|---|---|
| **Section *Procumbentes*** | | | | |
| *Arachis appressipila* Krapov. & W.C. Gregory | 20 | PR | GKP | 9990 |
| *Arachis chiquitana* Krapov., W.C. Gregory & C.E. Simpson | 20 | PR | KSSc | 36027 |
| *Arachis hassleri* Valls & C.E. Simpson | 20 | PR | SvPiHn | 3818 |
| *Arachis kretschmeri* Krapov. & W.C. Gregory | 20 | PR | KrRa | 2273 |
| *Arachis lignosa* (Chodat and Hassl.) Krapov. & W.C. Gregory | 20 | PR | Hassler | 7476 |
| *Arachis matiensis* Krapov., W.C. Gregory & C.E. Simpson | 20 | PR | KSSc | 36014 |
| *Arachis pflugeae* C.E. Simpson, Krapov, & Valls | 20 | PR | VOlSiS | 13589 |
| *Arachis rigonii* Krapov. & W.C. Gregory | 20 | PR | K | 9459 |
| *Arachis subcoriacea* Krapov. & W.C. Gregory | 20 | PR | KG | 30037 |
| *Arachis vallsii* Krapov. & W.C. Gregory | 20 | PR | VRGeSv | 7635 |
| **Section *Rhizomatosae*** | | | | |
| Ser. *Prorhizomatosae* | | | | |
| *Arachis burkartii* Handro | 20 | $R_1$ | Archer | 4439 |

| | | | | |
|---|---|---|---|---|
| Ser. *Rhizomatosae* | | | | |
| *Arachis glabrata* | 40 | | | |
| var. *glabrata* Benth. | | $R_2$ | Riedel | 1837 |
| var. *hagenbeckii* Benth. (Harms ex. Kuntze) F.J. Herm. | | $R_2$ | Hagenbeck | 2255 |
| *Arachis nitida* Valls, Krapov, & C.E. Simpson | 40 | $R_2$ | VMPiW | 14040 |
| *Arachis pseudovillosa* (Chodat & Hassl.) Krapov. & W.C. Gregory | 40 | $R_2$ | Hassler | 5069 |
| **Section *Trierectoides*** | | | | |
| *Arachis guaranitica* Chodat & Hassl. | 20 | TE | Hassler | 4975 |
| *Arachis tuberosa* Bong. Ex Benth | 20 | TE | Riedel | 605 |
| *Arachis sesquijuga* Valls, L.C. Costa & Custodio | 20 | TE | VOlEd | 15487 |
| **Section *Triseminatae*** | | | | |
| *Arachis triseminata* Krapov. & W.C. Gregory | 20 | T | GK | 12881 |

[a]*Collectors: B, Banks; Bi, Bianchetti; Cl, Claure; Cr, Cristobal; Ed, Edward; Fa, Faraco; Fr, Fernandez; G, Gregory; Ge, Gerin; H, Hammons; He, Hemsy; Hy and Hn, Heyn; K, Krapovickas; Kr, Kretchmere; L, Langford; M, Moss; Mr, Mroginski; Ol, Oliveira; P, Pietrarelli; Pi, Pizarro; Po, Pott; Pt, Pittman; R, Rao; Ra, Raymon; S, Simpson; Sc, Schinini; Si, Singh; St, Stalker; Sv, Silva; V, Valls; Va, Vargas; Ve, Veiga; Vl, Valente; W, Werneck; Wi, Williams; Others, as listed.*
From Krapovickas and Gregory (1994), Valls and Simpson (2005), and Valls et al. (2013).

and chromosomes with centromeric heterochromatin, Robledo et al. (2009) described three karyotypic subgroups within the A genome and grouped the cultivated peanut with *A. duranensis*, *A. villosa*, *Arachis schininii,* and *A. correntina*. Other studies support placing *A. hypogaea* closely with *A. duranensis* (Bravo et al., 2006; Calbrix et al., 2012; Koppolu et al., 2010; Milla et al., 2005a; Moretzsohn et al., 2004). The chromosomes of B genome species are karyologically more diverse than those with an A genome (Fernández and Krapovickas, 1994; Seijo et al., 2004). The B genome species (as opposed to the F and K genomes) do not have centromeric heterochromatin and include *A. ipaënsis* (the B component of *A. hypogaea*), *Arachis magna, Arachis gregoryi, Arachis valida,* and *Arachis williamsii* (Robledo and Seijo, 2010; Seijo et al., 2004). The D genome species *A. glandulifera* is more distantly related to *A. hypogaea* than other species of section *Arachis* (Stalker, 1991). Molecular analysis also indicated that the aneuploids in section *Arachis* are more closely related to the B (now classified as the B, F, and K genomes) and D genome species than to A genome species (Tallury et al., 2005). Evolution is apparently continuing in section *Arachis* at a rapid pace and multiple translocations have been observed in diploid accessions of *A. duranensis* (Stalker et al., 1995) and *A. batizocoi* (Guo et al., 2012; Stalker et al., 1991). At least five different secondary constriction types are present in *A. hypogaea*, which were likely from translocation events (Stalker and Dalmacio, 1986). Thus, the cultivated species also is evolving cytologically.

Analyses of species outside section *Arachis* have been infrequent. Stalker (1985) reported that hybrids of the two diploid section *Erectoides* species *Arachis rigonii* and *Arachis paraguariensis* had many univalents, and Krapovickas and Gregory (1994) later placed these species in different sections. Intersectional hybrids also were reported by Mallikarjuna (2005) who used in vitro techniques to obtain $F_1$s.

Krapovickas and Gregory (1994) concluded that *Erectoides*, *Extranervosae*, *Heteranthae*, *Trierectoides*, and *Triseminatae* are "older" sections, while *Arachis*, *Caulorrhizae*, *Procumbentes*, and *Rhizomatosae* are more "recent" in origin. The largest subgeneric group is section *Arachis*, which includes the cultivated species, one other tetraploid (*Arachis monticola*), 26 diploid ($2n=2x=20$), and three aneuploid ($2n=2x=18$) species. These species are highly variable, and especially the annual species are rapidly differentiating. For example, *A. duranensis* has northern and southern groups which can be distinguished morphologically and with molecular markers (Stalker et al., 1995).

Gregory (1946) reported the first chromosome number of a wild species (*A. glabrata*) as $2n=4x=40$ and a year later Mendes (1947) reported diploid species ($2n=2x=20$). Not until 2005 were species with 18 chromosomes discovered (Peñaloza and Valls, 2005). Most species in the genus are diploid, but tetraploids exist in sections *Arachis* and *Rhizomatosae*; and several species in sections *Arachis* and *Erectoides* are aneuploid ($2n=2x=18$) (Table 2; Figure 1). Polyploidy evolved independently in sections *Arachis* and *Rhizomatosae*

(Smartt and Stalker, 1982) and multiple times within the latter group (Nelson et al., 2006). Tallury et al. (2005) reported molecular evidence that the diploid section *Rhizomatosae* species (only one known) did not give rise to the tetraploids. Because *A. glabrata* will hybridize with species of both sections *Erectoides* and *Arachis*, Smartt and Stalker (1982) concluded that diploids from sections *Erectoides* and *Arachis* likely hybridized and spontaneously doubled in chromosome number to evolve into the present day tetraploid species of section *Rhizomatosae.*

The first published attempt at interspecific hybridization in the genus was between the two tetraploids *A. hypogaea* (section *Arachis*) and *A. glabrata* (section *Rhizomatosae*) (Hull and Carver, 1938), but no hybrids were obtained. Krapovickas and Rigoni (1951) later hybridized *A. hypogaea* with *A. villosa* var. *correntina* and the $F_1$s were vigorous, but sterile. The cultivated peanut has since been hybridized with most A and B genome species in section *Arachis*. Similar to other genera that have a polyploid series, crosses are usually more successful when the species at the higher ploidy level (in this case *A. hypogaea*) is used as the female parent. Triploid interspecific hybrids generally have 10 bivalents and 10 univalents, but trivalents also are observed in pollen mother cells which indicates that some chromosome homology exists between the A and B genomes (Stalker, 1985). This was later confirmed by comparing molecular maps from *Arachis* populations of A and B genomes (Moretzsohn et al., 2009), which showed high levels of synteny between both genomes.

In addition to morphological and cross-compatibility studies, molecular investigations have been used to better clarify the phylogenetic relationships among peanut species. Most investigations have been with species in section *Arachis* because of their close association with *A. hypogaea*. Many molecular systems have been utilized, including isozymes (Lu and Pickersgill, 1993; Stalker et al., 1994), seed storage proteins (Bianchi-Hall et al., 1993; Liang et al., 2006; Singh et al., 1991), restriction fragment length polymorphisms (RFLPs) (Kochert et al., 1991; Paik-Ro et al., 1992), amplified fragment length polymorphisms (AFLPs) (Milla et al., 2005b); simple sequence repeats (SSRs) (Guo et al., 2012; He et al., 2005; Hong et al., 2010; Hopkins et al., 1999; Moretzsohn et al., 2013; Nagy et al., 2012), randomly amplified polymorphic DNA (Halward et al., 1992; Hilu and Stalker, 1995; Lanham et al., 1992), and in situ hybridization (Raina and Mukai, 1999; Seijo et al., 2004). All of the studies have indicated that the cultivated peanut has significantly less molecular variation than diploid species, which supports the hypothesis that *A. hypogaea* originated from a single hybridization event. Additionally, there has been little or no apparent introgression from diploid species to *A. hypogaea* since its inception (Kochert et al., 1996).

As opposed to the cultivated species, large amounts of molecular variation have been documented among wild species of the genus. Although differences have been observed among marker systems regarding species relationships, and there remain questions about species positions within sectional groupings

(Friend et al., 2010), the molecular data generally fits the sectional relationship model proposed by Krapovickas and Gregory (1994). For example, Hoshino et al. (2006) used microsatellites to evaluate species in the nine peanut sections, and while most species grouped as expected, several species in the *Procumbentes* grouped with species from section *Erectoides*, and others clustered into sections *Trierectoides* and *Heteranthae*. Galgaro et al. (1997) also indicated that species in section *Heteranthae* did not group together. Friend et al. (2010) conducted a more comprehensive investigation of *Arachis* species and found that sections *Extranervosae*, *Triseminatae*, and *Caulorrhizae* each separated into distinct groups based on trnT-trnF sequences; but species in sections *Erectoides*, *Heteranthae*, *Procumbentes*, *Rhizomatosae*, and *Trierectoides* formed a major lineage. Species in section *Arachis* grouped into two major clades, with (1) the B (renamed the B, F, and K genomes), the D genome species, and 18-chromosome aneuploids in one group; and (2) the A genome species in the second group.

### *Genetic and Geographical Origin of the Domesticated Peanut*

*Arachis hypogaea* is an allotetraploid species ($2n=4x=40$, AABB) with a very large and complex genome. Cytologically, it behaves mostly as a diploid, but multivalents can result in skewed genetic ratios and likely account for many of the "off types" observed in farmers' fields. This was explained by Leal-Bertioli et al. (2015) who, using both genetic and gene expression data, demonstrated that peanut display both disomic and tetrasomic genetics recombination. The domesticated peanut has been placed into section *Arachis* based on morphology and cross-compatibility relationships with other species. Botanical varieties are characterized morphologically based on branching and flowering patterns and pod and seed traits (Krapovickas and Gregory, 1994; Table 1). Based on the same characters, many landraces have been described (Krapovickas et al., 2009, 2013).

The exact genetic origin of cultivated peanut has long interested plant taxonomists, geneticists, and breeders. Initially, a different origin for each subspecies was advanced based on the morphological variability and their partial reproductive isolation (Lu and Pickersgill, 1993; Singh and Moss, 1982). However, most authors now support the hypothesis that *A. hypogaea* was derived from just two wild diploid species, and indeed probably between very few or one individual of each diploid species. This is supported by the very limited genetic variability among landraces and commercial cultivars of *A. hypogaea* and from its molecular cytogenetics (Grabiele et al., 2012; Halward et al., 1991; Kochert et al., 1996; Milla et al., 2005a; Raina et al., 2001; Seijo et al., 2004, 2007). It is also apparent that the wild tetraploid *A. monticola* is very closely related to *A. hypogaea*, indeed they most probably share the same origin (Grabiele et al., 2012). They have very high crossability, cytogenetically the species are indistinguishable, and molecular studies show they are very closely related and the same biological species. They cannot be differentiated based on isozymes (Lu and Pickersgill, 1993), Random Amplified Polymorphic DNA (RAPD) (Cunha et al., 2008; Hilu and

Stalker, 1995), or microsatellite markers (Gimenes et al., 2007; Koppolu et al., 2010). However, various studies based on AFLP, microsatellite, or Sequence-Related Amplified Polymorphism (SRAP) markers have shown that *A. monticola* does have enough genetic divergence to form a separate group (Bravo et al., 2006; Gimenes et al., 2002; Milla et al., 2005a; Moretzsohn et al., 2004) and can be considered the same biological species.

Based on the evidence cited above, on whole genome in situ hybridization, and on biogeographic information, it is currently accepted that *A. duranensis* (AA genome) and *A. ipaënsis* (BB genome) are the most probable ancestors of *A. monticola* and *A. hypogaea* (Fernández and Krapovickas, 1994; Kochert et al., 1996; Seijo et al., 2004, 2007). These species, either by hybridization followed by chromosome duplication or by fusion of unreduced gametes, produced an AABB genome individual, probably *A. monticola* or a similar wild tetraploid. This event may have occurred in the wild or spontaneously when the two diploids were cultivated in close proximity by ancient inhabitants of South America. Morphologically diverse landraces of peanut could then have arisen by artificial selection of the polyploid in different agroecological environments by ancient South American itinerant farmers (Seijo et al., 2007).

As for the geographical origin, archeological studies indicate the presence of *A. hypogaea* in the Huarmey Valley in Peru (5000 years before present) (Bonavia, 1982), and pod samples strongly resemble those of wild species in the Casma Valley, Peru (3500 and 3800 years before present). More recently, radiocarbon-dated macrobotanical remains dating from approximately 7840 years before present, which seem to correspond morphologically to a wild *Arachis* species or to peanut fruits in the early stages of domestication, were recovered from sealed house floors and hearths in buried preceramic sites in a tropical dry forest of the Ñanchoc Valley located on the lower western slopes of the Andes in northern Peru (Dillehay et al., 2007). These locations are perfect for the preservation of archeological specimens because of their dry climates, but are far from the present day natural distribution of wild *Arachis*. This strongly suggests that ancient peoples were cultivating *Arachis* in northwest Peru, and it was once considered that these sites were the location of origin of *A. hypogaea* (Simpson and Faries, 2001). However, it seems more likely that this occurred in moister environments where there are more abundant populations of insects that could serve as agents for cross-pollination. Moreover, the morphological variability of the landraces, the distributions of the putative A and B genome donors, and the location of *A. monticola* place the most likely location origin of the domesticated peanut in northern Argentina and southern Bolivia, in a transition area between the Tucumano–Bolivian forest and the Chaco lowlands (Gregory et al., 1980; Krapovickas and Gregory, 1994). Recent molecular analyses based on the combination of chloroplast DNA and non-transcribed spacer (NTS) 5S rDNA genes identified the population of *A. duranensis* from Río Seco, Salta, Argentina, and the only known population of *A. ipaënsis* from Villa Montes, Tarija, Bolivia, as those to which the genome donors of the peanut could have belonged (Grabiele et al., 2012).

### Speciation and Evolutionary Trends

According to the estimates of divergence dates calculated based on intron sequences, the diversification rate of section *Arachis* is the highest estimated so far for legume species (Moretzsohn et al., 2013). According to the comparisons made, the diversification rate has been estimated to be about 0.95 speciation events per million years. The high rate of speciation observed in the genus may be linked to geocarpy and to the fact that most species are autogamous (Krapovickas and Gregory, 1994; Seijo et al., 2012). These two characteristics favor the success of foundational events of new fertile populations after long distance dispersal of seeds. The occurrence of multiple events of speciation may explain the species arrangement of cospecific populations in more or less disjoint patches. The combination of multiple recurrent genetic bottlenecks, small population sizes, and a typically high rate of self-fertilization provide the perfect conditions for genetic drift and the evolution of genetic mechanisms for reproductive isolation. These evolutionary dynamics may explain the high speciation rate detected in *Arachis*.

Different degrees of sexual incompatibility have been detected at interspecific levels but also between cospecific populations (Gregory and Gregory, 1979; Krapovickas and Gregory, 1994; Stalker et al., 1991). For instance, inter population hybrids of *A. duranensis* may have fallen from almost 90% of pollen viability to less than 10% (Stalker et al., 1995). Moreover, these authors demonstrated that a large amount of genetic diversity, as measured by morphological, cytological, molecular, and intercrossing data, exists among the various accessions of *A. duranensis*. Although two groups of affinities were detected, the variability observed in the characters analyzed and the sexual compatibility did not have a good correspondence with geographic variation. This inconsistency also may be explained by the occurrence of the same combination of evolutionary forces cited above to explain the high rates of speciation (Krapovickas and Gregory, 1994).

Evolutionary trends in *Arachis* are still difficult to identify since the available phylogenetic treatments of the genus are not completely concordant. However, considering the whole amount of available data some evolutionary trends can be deduced. Concerning the chromosome numbers, two base numbers and two ploidy levels have been identified within the genus. The base number $x=10$ is the most widespread and it is present in all the sections, while the $x=9$ is only present in three species of section *Arachis* and in one species probably belonging to section *Erectoides* (Lavia, 1996, 1998; Peñaloza and Valls, 1997, 2005; Silvestri et al., 2015). Considering that, it has been proposed that the $x=9$ would be a derived character that appeared at least twice in the genus by aneuploidy or disploidy (Lavia et al., 2008; Seijo et al., 2014).

Spontaneous polyploids are very rare in the genus. Species with $2n=4x=40$ are restricted to *A. hypogaea* and *A. monticola* of section *Arachis*, and to *Arachis glabrata*, *Arachis pseudovillosa* and *Arachis nitida* of section Rhizomatosae (Fernández and Krapovickas, 1994; Gregory et al., 1973; Peñaloza and Valls, 2005).

*Arachis pintoi* (section *Caulorrhizae*) is the only known species of the genus with both diploid and triploid cytotypes (Lavia et al., 2011). The two spontaneous polyploids (*A. monticola* and *A. hypogaea*) of section *Arachis* are allopolyploids (Seijo et al., 2004; Smartt et al., 1978) while the other polyploids are autopolyploids or segmental allopolyploids (Lavia et al., 2011; Ortiz et al., 2011). The available data suggest that polyploids have arisen several times in the genus either by chromosome doubling or meiotic nonreduction of interspecific hybrids.

The annual character occurs only in few species of sections *Heteranthae* and *Arachis* that live in the northeast and in the west extremes of the genus, respectively. The four constituents of section *Heteranthae* grow in the northeast of Brazil where the drought climate is proverbial. Similarly, in section *Arachis*, the annual species live in seasonally dry or cold environments. Evidently, this biological type has shown itself to be an adaptive advantage that has made possible the occupation of new areas with extreme conditions of drought or to altitude where species are found at 1500 m above sea level. Moreover, it is clear that the annual life cycle appeared in parallel in different sections as a derived character.

Another character that seems to have appeared more than once in the evolutionary history of *Arachis* is fruits with highly reticulate pericarps. This character is exclusive to section *Arachis* and is present in a few perennial species of the A genome (e.g., *A. villosa*) from the Uruguay River, in the extreme southern part of the range of the genus, and in *Arachis microsperma* from the Apa River which is on the border of Mato Grosso do Sul with Paraguay. On the other hand, there is a greater number of annual species (including all of the B or D genome taxa) with this type of fruit. For example, *A. valida* from Corumbá in the Mato Grosso Pantanal; *A. glandulifera, A. magna, A. ipaënsis*, and *A. williamsii* from Bolivia; and in the tetraploid species *A. monticola* from northwestern Argentina.

An interesting aspect of the evolution within *Arachis* is that concerning the domestication of cultivated peanut. The peanut is highly diverse morphologically as man has selected individual plants and seed types and cultivated them in very different agroecological environments. Adaptations to cultivation have followed the same types of evolutionary trends as in other domesticated crops where a few major genetic mutations were necessary to transform the wild species progenitors into land races and cultivars that we have today (Table 3). These alterations include shortening and strengthening of pegs to retain pods during harvest; suppressing the meristems between seeds in a single pod, selecting more upright growth habit and shorter branches that allow easier harvesting; selecting nondormant types to enhance plant stands; and increased seed size (Stalker and Simpson, 1995).

## Maintenance of Genetic Resources

Seeds of the cultivated peanut will remain viable for 15–20 years if they are stored in a −20 °C freezer under low moisture conditions. The two largest peanut

**TABLE 3** Evolution of *Arachis* and the Domesticated Peanut, *A. hypogaea*[a]

| More Primitive Trait | Group | More Advanced Trait | Group |
|---|---|---|---|
| **Genus—General** | | | |
| Trifoliate leaves | Sect. *Trierectoides* | Tetrafoliate leaves | |
| Diploid | | Tetraploid | |
| Perennial | | Annual | |
| Tuberiform hypocotyl | Sects. *Erectoides, Trierectoides* | Nontuberiform hypocotyl | |
| Tuberous roots | Sect. *Extranervosae* | Fibrous roots | |
| No rhizomes | | Rhizomes | Sect. *Rhizomatosae* |
| Symmetrical karyotype | Most sect. *Arachis* | Asymmetrical karyotype | *A. batizocoi* |
| **Domestication** | | | |
| Weak peg | Wild species | Stronger peg | *A. hypogaea* |
| Long peg | Wild species | Short peg | *A. hypogaea* |
| Long hypanthium | Wild species | Shorter hypanthium | *A. hypogaea* |
| Prostrate growth | Wild species | Upright growth | *A. hypogaea* |
| Long branches | Wild species | Shorter branches | *A. hypogaea* |
| Long internode between seeds | Wild species | Pod/peg internode suppressed | *A. hypogaea* |
| ***A. Hypogaea*** | | | |
| Alternating inflorescences | Subsp. *hypogaea* | Sequential inflorescences | Subsp. *fastigiata* |
| Mainstem w/o flowers | Subsp. *hypogaea* | Mainstem with flowers | Subsp. *fastigiata* |
| Simple (unbranched) | Var. *fastigiata* | Compound inflorescence | Var. *vulgaris* |
| Prostrate habit | Var. *hirsuta* | More upright | Var. *hypogaea* |
| | | Very upright | Subsp. *fastigiata* |
| Late maturing | Subsp. *hypogaea,* esp. var. *hirsuta* | Early maturing | Subsp. *fastigiata* |
| Very hairy | Var. *hirsuta* | Less hairy | Var. *hypogaea* |

**TABLE 3** Evolution of *Arachis* and the Domesticated Peanut, *A. hypogaea*[a]—cont'd

| More Primitive Trait | Group | More Advanced Trait | Group |
|---|---|---|---|
| | Var. *aequatoriana* | | Var. *peruviana* |
| 2-seeded pods | Var. *hypogaea* | 2+ seeds/pod | Var. *hirsuta* |
| | Var. *vulgaris* | 4-seeded pods | Var. *fastigiata* |
| Pod beak | | Beak absent | |
| Small seeds | Var. *vulgaris*, some var. *hypogaea* | Large seeds | Some var. *hypogaea* |
| Long lateral branches | Var. *hypogaea* | Shorter branches | Subsp. *fastigiata* |
| | –runners | | |
| Long dormancy | Var. *hypogaea* | Short dormancy | Subsp. *fastigiata* |

[a]*After Stalker and Simpson (1995).*

collections are maintained by the International Crops Research Institute for the Semiarid Tropics (ICRISAT) where 15,445 accessions are held from 93 countries and by the National Bureau of Plant Genetic Resources in India (14,585 accessions) (Upadhyaya et al., 2001). Other large collections are maintained by the Directorate of Groundnut Research (9024 accessions) in India; The Oil Crops Research Institute in China (8083 accessions); and the US Department of Agriculture (9917 accessions), of which approximately 50% are unimproved South American landraces (Holbrook, 2001). Additional germplasm collections also exist in Brazil, Argentina, Bolivia, and other locations. Many accessions were obtained in local markets where seeds vary in size, shape, color, and other characteristics, and many introductions are seed mixtures which are evident in seed colors, plant size, and growth habit. Thus, regeneration plots need to be of sufficient size to assure all variation is maintained. Maintaining the cultivated species collection is rather straight forward, with the biggest problem being extreme susceptibility to diseases, especially accessions of var. *vulgaris*, and seed reproduction may be severely limited at some locations.

The largest wild germplasm collection is placed in Embrapa Genetic Resources and Biotechnology, Brasilia, Brazil, with over 1200 accessions, representing all species described to date (J.F.M. Valls, personal communication). The wild *Arachis* species collection is significantly more difficult to maintain than cultivated peanut. About 25% of the wild species are propagated in greenhouses because they

produce very few or no seeds under cultivation. Species in section *Rhizomatosae* are all maintained vegetatively. Approximately 50% of wild species accessions have fewer than 50 seeds in storage at the major sites where they are maintained; and these accessions also are maintained vegetatively. Because of the spreading habit of most species, branches have a tendency to grow into adjacent containers and there must be separation of plants to maintain purity in the greenhouse.

Although propagation of wild peanut species is generally done in a greenhouse to prevent outcrossing, greenhouse propagation restricts the numbers of seeds that a plant will produce and is both labor-intensive and expensive. An alternative is to plant field nurseries so that sufficiently large numbers of seeds can be obtained for germplasm preservation and evaluation research. At NC State University, the field system used is to transplant seedlings into 2×3 m blocks that had not previously been planted with peanut. A minimum distance of 5 m separates adjacent plots in all directions to restrict outcrossing and seed contamination. Additionally, species in different taxonomic sections are planted adjacent to one another because they are reproductively incompatible, and if an outcross does occur, the plants will be sterile. Upon maturity, the soil in the 2×3 m block are sifted to recover seeds. Many wild species accessions will produce large numbers of seeds under field conditions.

Seeds of most wild species accessions can be maintained in a −20 °C freezer for 10 or more years, while others lose viability more rapidly. Under short-day conditions many species produce very few to no flowers, but most of these flowers self-pollinate and set pegs (Stalker and Wynne, 1983); under long days many of the same accessions will produce large numbers of flowers, but produce few pegs and seeds. Seeds of *A. tuberosa* and *A. guaranitica* enter a permanent dormancy upon drying, which prevents long-term seed storage (Stalker and Simpson, 1995).

## Desirable Traits in *Arachis* Species for Crop Improvement

Compared with lines of *A. hypogaea*, extremely high levels of resistance have been identified in wild *Arachis* species for many important peanut pathogens (Dwivedi et al., 2007; Stalker and Moss, 1987; Stalker et al., 2013). For example, Mehan et al. (1986) identified four *Arachis* species that are resistant to aflatoxin production and Xue et al. (2004) found preharvest aflatoxin resistance in *A. duranensis.* Subrahmanyam et al. (2001) found 12 *Arachis* species accessions to be immune to groundnut rosette virus as opposed to none in the cultivated species. *Arachis diogoi* is the only species identified with no infection to peanut bud necrosis virus (Subrahmanyam et al., 1985); this species is also the only one with immunity to tomato spotted wilt virus (Lyerly et al., 2002). None of 7000 *A. hypogaea* accessions screened for peanut clump virus had useful resistance, whereas four accessions of *Arachis kuhlmannii*, *A. duranensis*, and *A. ipaënsis* were immune (Dwivedi et al., 2007). ICRISAT scientists also have evaluated *Arachis* species for late and early leaf spots and they identified highly resistant

germplasm (Dwivedi et al., 2007). Many *Arachis* species also have been evaluated for insect pests and extremely high levels of resistance were observed as compared to the cultivated peanut (Stalker et al., 2013). *Arachis batizocoi* and *Arachis cardenasii* were found to be resistant to root-knot nematode (RKN), *Meloidogyne arenaria* (Nelson et al., 1990), the latter being extensively used for peanut improvement (Chu et al., 2011; Simpson et al., 2003). *Arachis stenosperma* was also found to be highly resistant to RKN, late leaf spot and rust (Leal-Bertioli et al., 2010; Proite et al., 2008).

## Interspecific Hybridization

Incompatibility occurs among *Arachis* species at several stages of reproductive development and may have physiological or genetic causes. The first barrier to interspecific hybridization, however, is at the stigmatic surface of the pistil. Akromah (2001) and Lu et al. (1990) observed several types of stigmas in species of sections *Arachis* and *Rhizomatosae* species. Annuals have large globular stigmas and no hairs whereas perennials have small stigmas with hairs that bend over the stigma surface and result in poor adhesion of pollen grains. This may explain why annuals generally produce greater numbers of seeds when selfed than perennials and why annuals are generally more successful female parents when attempting interspecific hybridization.

Another source of incompatibility is restricted pollen tube growth after pollen germination. This was observed by Halward and Stalker (1987) when crossed 6*x* interspecific *A. hypogaea* hybrids with the two diploid species *A. batizocoi* and *A. cardenasii*. This phenomenon prevented hybridization. When *A. stenosperma* was crossed with *A. hypogaea* then fertilization was delayed (Pattee and Stalker, 1992). Murty et al. (1980) reported that it took eight times longer for fertilization to occur in *A. hypogaea* × *A. glabrata* hybrids as compared to compatible crosses. Delayed pollen germination also occurs in *A. hypogaea* × *A. glabrata* crosses because of callose plugs in the pollen tubes (Shastri and Moss, 1982).

Interspecific hybridization between *A. hypogaea* and diploid species generally is more successful when the tetraploid species is used as the female parent, which may be due to a higher starch concentration in the embryo sac of the cultivated peanut (Pattee and Stalker, 1991). Pattee and Stalker (1992) analyzed reciprocal hybrids of *A. hypogaea* × *A. duranensis* and *A. stenosperma* and found that embryos aborted when *A. duranensis* was used as a female parent due to endosperm degradation. In additional studies, Singh (1998) crossed species of sections *Arachis* and *Erectoides* and observed normal peg and pod development, but no endosperm development. Wang et al. (2012) attributed the cause of embryo abortion to hormone imbalances, where abscisic acid (ABA) levels were high and indole acetic acid, gibberellic acid, and zeatin riboside, and dihydrozeatin riboside levels were lower than in normally developing tissues.

Mallikarjuna and Sastri (2002) obtained intersectional hybrids by using a combination of hormone treatments to the flower and then embryo rescue procedures. Mallikarjuna and coworkers treated the base of the flower pistil with 87.5 mg $L^{-1}$ of gibberellic acid and harvested pods 30–35 days later (which is about half the time to normal maturity). They then cultured the embryos until shoots and then roots formed. However, they obtained a very low percentage of plants from intersectional crosses and they were all sterile. Peg tip culture also has been used to obtain intersectional hybrids between cultivated peanut and species in other sections (Wang et al., 2014).

One of the most successful cases of interspecific hybridization as yet reported was by Fávero et al. (2006) who hybridized *A. ipaënsis* and *A. duranensis*. The derived hybrids had their chromosome doubled by colchicine and the resulting allotetraploid was compatible with all six botanical varieties of peanut. The successful hybridization between the diploid species and also between *A. hypogaea* and the synthetic allotetraploid support the theory that these two diploids are the progenitors of the cultivated peanut.

## Introgressing Genes from *Arachis* Species to *A. hypogaea*

Because the domesticated peanut is an allotetraploid with AABB genomes and the species being utilized for introgression are diploids with only one of the two genomes, sterility barriers result from ploidy differences and for genomic incompatibilities. Thus, traits of interest from *Arachis* species have been difficult to select in interspecific hybrid progenies because of small population sizes and little recombination between genomes. The problem of selecting disease or insect resistant progenies is made more difficult because phenotyping methods for single plants in peanut are not reliable and others are destructive. Utilizing molecular markers associated with traits of interest may enhance selection methodologies but to date, few markers have been associated with traits of interest. Molecular research indicates that introgression from *Arachis* species to *A. hypogaea* is in large blocks (Garcia et al., 1995; Nagy et al., 2010). Thus, linkage drag of undesirable traits also restricts the use of genetic resources.

The first peanut cultivars released from interspecific hybridization were from a cross between *A. hypogaea* and the second tetraploid species in section *Arachis, A. monticola* which is biologically a weedy subspecies of *A. hypogaea*. Spancross was released by Hammons (1970) and Tamnut 74 was later released by Simpson and Smith (1975). Neither of these cultivars had phenotypic traits that could be identified as being derived from the wild species *A. monticola*. Although *A. monticola* is compatible with cultivated peanut since it is tetraploid, it is not considered useful for not being significantly more resistant to the main pests and diseases.

Utilizing diploid species for cultivar improvement has more potential than crosses between the tetraploid species in section *Arachis*, but at the same time hybridization is time-consuming and difficult. Several methods have been utilized to create populations of fertile *A. hypogaea* interspecific hybrids and to

restore plants to the tetraploid level. First, crosses can be made by hybridizing *A. hypogaea* with diploids to produce triploid ($3x=30$) $F_1$s, after which seeds (or more commonly cuttings) can be colchicine-treated to restore fertility at the hexaploid ($6x=60$) level. Triploids also may produce a few seeds through fusion of unreduced gametes if they are allowed to grow in the field or greenhouse for long periods of time to increase the numbers of flowers and possible polyploidization events (Singsit and Ozias-Akins, 1992). Backcrossing hexaploids with *A. hypogaea* results in vigorous but semisterile pentaploids ($5x=50$) that produce few flowers and are difficult to use in crossing programs. The pentaploids may produce a few seeds if allowed to self-pollinate and the ploidy level stabilizes after one or several generations at the tetraploid level. Because only a few seeds are produced at the hexaploid and pentaploid levels, selection for specific traits based on phenotypes has thus far not been possible; and the many hundreds of tetraploid lines produced have lost the traits of interest. To date, no useful germplasm has resulted from backcrossing hexaploids with *A. hypogaea*. Although backcrossing hexaploids with diploids will theoretically drop the chromosome number to the tetraploid level in one generation, these $6x\times2x$ crosses (or reciprocals) have not produced viable progenies (Stalker, unpublished data).

An alternative method to backcrossing hexaploids with the cultivated species is to allow $6x$ plants to self-pollinate and, by selecting fertile progenies for several generations, a few plants may spontaneously lose chromosomes and stabilize at the 40-chromosome level. The loss of chromosomes appears to be infrequent and random, but the advantage of this procedure is more chromosome recombination at the high ploidy level. For example, hexaploids derived from *A. hypogaea* ($4n$)$\times$*A. cardenasii* ($2n$) were selfed for five generations after which they produced 40-chromosome progenies that were highly variable for seed size, color and other morphological traits (Company et al., 1982). Garcia et al. (1995) analyzed introgression from *A. cardenasii* to *A. hypogaea* with RFLPs and found wild species-specific markers in 10 of 11 linkage groups on the diploid RFLP map developed by Halward et al. (1993). Most of the introgression (88%) was apparently in the A genome of *A. hypogaea*, with the remaining 12% in the B genome, suggesting partial tetrasomic recombination. Germplasm lines have been released from this cross with resistance to early leaf spot, nematodes, and several insect pests (Isleib et al., 2006; Stalker et al., 2002a,b; Stalker and Lynch, 2002), and also the cultivar Bailey, with multiple resistances (Isleib et al., 2010). The "CS lines" were also incorporated into the ICRISAT germplasm collection and distributed to plant breeders who have used them for sources of disease resistance, especially for rust and leaf spots.

A second method to introgress germplasm from diploid species to *A. hypogaea* is to first double the chromosome number of the diploid species to the tetraploid level. This method has the advantage of avoiding several generations of mostly sterile hybrids and recovering tetraploids is much faster than by going through the triploid–hexaploid procedure; however, autotetraploids generally have low vigor, and when annual species are used as parents, they are short-lived. A third

method is the hybridization of A and B genome species at the diploid level and then double the chromosomes to produce AABB genome allopolyploids, which are compatible with the cultivated species. Examples of success with this methodology are TXAg-6 and TXAg-7 (Simpson et al., 1993) which originated from the complex hybrid (*A. batizocoi* (K genome)×(*A. cardenasii* (A genome)×*A. diogoi* (A genome)))$^{4x}$. TxAG-6 had very good nematode resistance, but also significant linkage drag which resulted in low yields and poor seed and pod quality. RFLP markers linked to the resistance nematode gene were used to select favorable genotypes (Church et al., 2000). The nematode-resistant cultivars COAN (Simpson and Starr, 2001), NemaTAM (Simpson et al., 2003), and Tifguard (Holbrook et al., 2008) were released after introgressing genes from TXAg-6 to *A. hypogaea*. By using SSR markers, Nagy et al. (2010) showed that recombination was greatly reduced in the chromosome region where the nematode-resistance gene is located because a large introgressed segment from the wild species that comprised a third to half of a chromosome. This method was also used to "resynthesize" peanut using its progenitors *A. ipaënsis* and *A. duranensis* (Fávero et al., 2006) and to produce peanut-compatible synthetic allotetraploids using the K-genome *A. batizocoi* as female parent (Leal-Bertioli et al., 2014).

Alleles from wild species show a clear potential for peanut improvement. However, the use of wild species in peanut breeding has been hindered by the ploidy differences between the cultivated and wild species, linkage drag of undesirable wild alleles with desirable ones, and difficulties of tracking introgressed fragments from wild genomes. Some wild introgression have been incorporated into commercial cultivars in the USA: strong resistance to root-knot nematode (Holbrook et al., 2008; Simpson and Starr, 2001; Simpson et al., 2006) and insects and diseases (Isleib et al., 2010) from the wild species *A. cardenasii*. A number of rust and late leaf spot resistant cultivars have been developed from a line known as GPBD 4 which in turn has a parent ICGV 86855 that is derived from an *A. hypogaea*×*A. cardenasii* cross (Gowda et al., 2002). These examples show the potential for the use of wild species in cultivar development.

Molecular markers offer a method for following introgression from *Arachis* species to *A. hypogaea* and could greatly facilitate selection of desirable progenies in advanced generations of interspecific hybrids. Different DNA marker systems can be used to monitor chromosome segments. Microsatellite or SSR markers have become the assay of choice for genetic studies in *Arachis* because they are multiallelic, codominant, transferable among related species, polymerase chain reaction-based markers, and usable in tetraploid genomes. Efforts by several research groups to develop microsatellite markers for peanut have resulted in more than 15,000 SSRs (Pandey et al., 2012). These markers have been used to study diversity in the genus *Arachis* (Barkley et al., 2007; Krishna et al., 2004; Moretzsohn et al., 2013; Tang et al., 2007; Varshney et al., 2009b) and moderately dense genetic maps of diploid and tetraploid species have been produced (Bertioli et al., 2009; Foncéka et al., 2009, 2012; Gautami et al., 2012;

Hong et al., 2008, 2010; Leal-Bertioli et al., 2009; Moretzsohn et al., 2005, 2009; Shirasawa et al., 2013; Varshney et al., 2009a).

Single nucleotide polymorphism (SNP) markers constitute the most abundant molecular markers in the genome and can be carried out with high throughput genotyping methods. SNP markers have been widely used in many plant species. However, they have had limited use in peanut because separation of A and B genome sequences is required. An SNP-based map of diploid *Arachis* was developed by Nagy et al. (2012) wherein a high-density genetic map of the A genome was developed from an *A. duranensis* intraspecies cross, and 598 SSRs, 37 single-stranded DNA conformation polymorphism markers, and 1054 SNPs were mapped. Using the same assay, Bertioli et al. (2014), by correcting the data calling, were able to score SNPs on diploid and tetraploid genotypes. This opened up the opportunity for use of SNPs separately on the two different A and B genomes. A large set of SNP data is currently available and is being mined from tetraploid (26 diverse genotypes) and diploid (four species) genome and transcriptome sequences. SNP identification using all of these sequence data currently is underway using a pipeline (SWEEP) (Clevenger et al., 2015).

To date, the number of genes associated with molecular markers in peanut is relatively small, but the large number of molecular markers becoming available has great potential for utilization in crop improvement programs. Bertioli et al. (2003) described numerous resistance gene analogues in *Arachis*, some of which were later found to be linked to resistance to late leaf spot (LLS) (Leal-Bertioli et al., 2009). Pandey et al. (2012) listed quantitative trait loci (QTLs) for several of the important traits found in the cultivated peanut. Chu et al. (2011) outlined a breeding scheme to utilize marker-assisted selection to pyramid nematode resistance and the high oleic acid trait in peanut cultivars, and the system has greatly increased efficiency for developing breeding lines. A few examples will be presented in the following paragraphs.

### *Root-Knot Nematode (*Meloidogyne *spp.)*

The first markers for an agronomically useful, wild species-derived trait in peanut were for resistance to RKN (*M. arenaria*) from *A. cardenasii*. Two closely linked sequence characterized amplified region (SCAR) markers were identified for genes for reduced galling and egg number (Garcia et al., 1996). Simultaneously, three RAPD markers were associated with nematode resistance in several backcross breeding populations derived from the interspecific hybrid TxAG-6 (*A. batizocoi* × (*A. cardenasii* × *Arachis diogoi*))$^{4x}$ (Burow et al., 1996). Marker-assisted selection then was used to develop several high yielding, nematode-resistant cultivars. In this case, it was demonstrated that use of markers was more efficient than phenotypic selection because plants selected with markers for the homozygous resistance gene have fewer escapes compared to plants from phenotypic selection. Marker-assisted selection and an accelerated backcross breeding program were also used in development of high-oleic cultivars with nematode and tomato spotted wilt virus resistances,

called high O/L Tifguard (Holbrook et al., 2008). Burow et al. (2014) found another seven QTLs that could account for part of the resistance to RKN. In spite of the success of this work, it is now thought that the use of a single gene trait that confers near immunity may be subject to breakdown of resistance under high selection pressure and is cause for concern. Therefore, new sources of resistance to nematodes are needed. The A genome species *A. stenosperma* has been found to have near-immunity to RKN (Proite et al., 2008). Induced allotetraploids were produced using *A. stenosperma* as parent, nematode-QTL linked markers were developed for RKN and are being used for marker-assisted selection (MAS) in a breeding program (Leal-Bertioli et al., 2014). It is expected that introgression of these alleles into peanut will give rise to nematode-resistant cultivars.

### *Late Leaf Spot Resistance*

Resistance to LLS (*Cercosporidium personatum*) has multiple components, including percent defoliation, incubation period, latency period, lesion number and diameter, sporulation, and pod yield (Anderson et al., 1993; Chiteka et al., 1988a,b; Green and Wynne, 1986; Waliyar et al., 1993, 1995). High levels of resistance also have been associated with low yield which suggests linkage or pleiotropic effects (Iroume and Knauft, 1987), thus breeding for high yielding cultivars with resistance requires that this linkage be broken. Stalker and Mozingo (2001) identified three RAPD markers associated with early leaf spot lesion diameter in a peanut population derived from a cross between an *A. hypogaea*×*A. cardenasii* introgression line crossed with NC 7. Mapping RFLP markers onto $BC_3F_1$ lines in greenhouse studies identified five markers for leaf spot resistance (Burow et al., 2008), including three QTLs for incubation period, one each for latency period, and lesion number and diameter. Those QTLs for latency period and lesion number were overlapping, suggesting either linkage between the two or a QTL with pleiotropic effects.

Additionally, Leal-Bertioli et al. (2009) identified five QTLs for LLS resistance on an SSR-based map using an $F_2$ population derived from the cross *A. duranensis*×*A. stenosperma*. The results suggested additive or partial dominance gene action. One QTL explained almost half of the phenotypic variance observed and some QTLs mapped near resistance gene analogues-based markers. In another QTL study based on cultivated genotypes hybridized with cultivar GPBD 4 (derived from "CS" interspecific lines), Khedikar et al. (2010) reported 11 QTLs for LLS; each QTL explained 2–7% of phenotypic variation in three environments, suggesting that the genes controlling LLS resistance in this cross are relatively minor. In maps from two other populations, again using GPBD 4 and a larger number of markers, a major QTL for LLS was reported that explained from 10–62% of phenotypic variance depending on the environment in which it was tested (Sujay et al., 2011). These QTLs are being used for marker assisted selection breeding at ICRISAT in India (Varshney et al. (2012), personal communication).

### Rust

QTL analysis using a partial genetic map of a mapping population with 67 marker loci derived from the two peanut varieties cross TAG 24×GPBD 4, based on multiple season phenotyping data for both rust and LLS detected 12 QTLs explaining between 1.70 and 55.20% of the phenotypic variation for each disease, respectively (Khedikar et al., 2010). The SSR marker tightly linked to the major QTL (IPAHM103; QTLrust01) was then validated among a diverse set of genotypes as well as in another mapping population (Sarvamangala et al., 2011) derived from the cross TG 26×GPBD 4. An SSR marker (IPAHM 103) was deployed to introgress the rust resistance QTL into three elite groundnut varieties (ICGV 91114, JL 24 and TAG 24) using the donor GPBD 4 through marker-assisted backcrossing (Varshney et al., 2014). GPBD 4 was a common parent in all of these crosses, and since it was derived from the wild species *A. cardenasii,* resistance incorporated into cultivars was likely derived from this species.

### Groundnut Rosette Virus

The aphid-transmitted groundnut rosette virus is an important pathogen of peanut in Africa and Asia, causing severe stunting and loss of yield. Herselman et al. (2004) tested 308 AFLP primer combinations and were able to devise five linkage groups consisting of 12 markers with one marker linked to aphid resistance.

### Tomato Spotted Wilt Virus (TSWV)

Tomato spotted wilt virus is transmitted by tobacco thrips (*Frankliniella* spp.) and causes serious yield losses in the US. A segregating population of $F_2$ plants of the A genome diploid cross *A. kuhlmannii*×*A. diogoi* was screened for resistance to TSWV, and five linked AFLP markers on one chromosome were associated with resistance at a high statistical threshold (Milla et al., 2003, 2004). In Brazil, interspecific populations and wild species also have been found as promising for introgression of resistance to the thrips, *Enneothrips flavens* (Janini et al., 2010).

### Agronomic Traits

Mapping of RFLP markers on $BC_3F_2$ lines of the cross *A. hypogaea*×*A. cardenasii* (Burow et al., 2011) identified 29 markers for the domestication-related traits of main stem length, number of lateral branches, pod size, and seed size. Foncéka et al. (2012) produced populations derived from crosses of cultivar Fleur 11 and an amphidiploid (*A. ipaënsis*×*A. duranensis*)$^{4x}$ (Fávero et al., 2006) and investigated introgression of wild segments. A population composed of a mixture of $BC_3F_1$ and $BC_2F_2$ individuals, each self-pollinated to produce $BC_3F_2$ and $BC_2F_3$ families, was used for phenotyping and QTL detection. Domestication-related trait QTLs were found, including some associated

with days to flowering, plant architecture, pod and seed morphology, and yield components. It was shown that wild alleles contributed positive variation to several agronomic traits such as flowering precocity; seed and pod number per plant; and length, size and maturity of pods. Moreover, the comparison of QTLs obtained under well-watered and water-limited conditions revealed that QTLs for stress tolerance indices for pod and seed numbers with favorable alleles could be attributed to the wild parents. These could be involved in reproductive trade-offs between producing large seeds versus producing more, but smaller, seeds under water stress. Twelve lines produced are now being tested in different African countries and so far have shown better phenotypes than the best elite varieties (Foncéka, personal communication).

## CONCLUSIONS

The genus *Arachis* has a large number of highly diverse species. Large collections of cultivated peanut exist at multiple locations and several hundreds of wild species are maintained in germplasm banks. Many of the species have been characterized for agronomic traits, but much of the germplasm collection remains to be evaluated for disease and insect resistances. The incorporation of wild alleles into crops is a proven strategy to develop improved varieties with pest and disease resistance. However, the extent of utilization of the useful allele reservoir in wild species and its impact on peanut breeding has been relatively limited because of restrictions to crossability, multiplication rate, and, until recently, to the lack of appropriate molecular tools to analyze and follow traits in hybrids. *Arachis cardenasii* has been one of the most useful sources of genes from wild species to date, but crosses involving other species are being produced, in particular *A. stenosperma* and *A. diogoi*. The recent use of the two most probable ancestors of peanut *A. duranensis* and *A. ipaënsis* in a systematic introgression program opens the way for extensive and detailed characterization of the peanut genome and wild allele interactions for a wide range of traits. As new materials are being created and genotyping strategies are becoming more advanced, variability from the wild species is being harnessed to the benefit of world agriculture.

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