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An overview of peanut and its wild relatives

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Abstract

The legume *Arachis hypogaea*, commonly known as peanut or groundnut, is a very important food crop throughout the tropics and sub-tropics. The genus is endemic to South America being mostly associated with the savannah-like Cerrado. All species in the genus are unusual among legumes in that they produce their fruit below the ground. This profoundly influences their biology and natural distributions. The species occur in diverse habitats including grasslands, open patches of forest and even in temporarily flooded areas. Based on a number of criteria, including morphology and sexual compatibilities, the 80 described species are arranged in nine infrageneric taxonomic sections. While most wild species are diploid, cultivated peanut is a tetraploid. It is of recent origin and has an AABB-type genome. The most probable ancestral species are *Arachis duranensis* and *Arachis ipaënsis*, which contributed the A and B genome components, respectively. Although cultivated peanut is tetraploid, genetically it behaves as a diploid, the A and B chromosomes only rarely pairing during meiosis. Although morphologically variable, cultivated peanut has a very narrow genetic base. For some traits, such as disease and pest resistance, this has been a fundamental limitation to crop improvement using only cultivated germplasm. Transfer of some wild resistance genes to cultivated peanut has been achieved, for instance, the gene for resistance to root-knot nematode. However, a wider use of wild species in breeding has been hampered by ploidy and sexual incompatibility barriers, by linkage drag, and historically, by a lack of the tools needed to conveniently confirm hybrid identities and track introgressed chromosomal segments. In recent years, improved knowledge of species relationships has been gained by more detailed cytogenetic studies and molecular phylogenies. This knowledge, together with new tools for genetic and genomic analysis, will help in the more efficient use of peanut's genetic resources in crop improvement.

Keywords: Arachis; breeding; crop improvement; genetic resources; groundnut; peanut; wild species

Introduction Peanut's importance in the world, and some peculiarities of its biology

Peanut, also commonly known as groundnut (*Arachis hypogaea*), is a major food crop, grown throughout the tropics and sub-tropics. World annual production is about 38 million tonnes. Like so many other crops, it has become most important in regions of the world far from its original home. Peanut is particularly important in Asia, which accounts for 64% of the world production, and where it provides a similar number of calories to soya. In Africa, which accounts for 26% of the world production, peanut has a key role as providing protein, energy and iron; amazingly, on this continent, its production exceeds that of all other grain legumes put together. In the USA, largely due to the research efforts

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of Dr George Washington Carver, peanut became an important crop in the South. The USA now accounts for some 6% of the world production. South America currently produces only 3% of the world production, but it is there that the genus *Arachis* is endemic, and cultivated peanut originally arose (production Statistics from 2008 (FAOSTAT, 2008)).

The first written reference to peanut seems to have been published in 1535 by Gonzalo Hernández de Oviedo y Valdés in his chronicles of his travels in the Americas. He wrote that maní (peanut) 'is very common with the Indians', and, in words that ooze the historical context of colonization, that 'Christians take little comfort in them, being eaten mostly by lowly men and boys and slaves and by people who do not pardon their taste for anything'. Over 200 years later, peanut was given its scientific name by Linnaeus, in his Species Plantarum of 1753. It was the first of its genus described, and thus became the genus' type species. The species epithet *hypogaea* refers to the character that perhaps mostly calls attention to this remarkable plant. It is geocarpic, that is, its fruits develop below the ground. Geocarpy is rare among flowering plants, but it is important to note that it is not unique. It is present in a wide array of species, from monocots (Meney *et al.*, 1990) to other legumes (e.g. subterranean clover *Trifolium subterraneum* L. and bambara groundnut *Voandzeia subterranean* L.). However, these genera and species are phylogenetically scattered, and geocarpy seems to have developed many times by convergent evolution, in some cases, apparently in response to arid environments (Barker, 2005). Accordingly, it is an adaptation to heat and drought that are key to peanut's success as a crop plant in many regions of its cultivation.

The flowers of *Arachis* species appear superficially similar to other Papilionoid legumes; however, there are intriguing differences that relate to geocarpy. The ovary is not enclosed by the petals, but is at the base of what appears to be the flower stalk. In fact, this 'stalk' is a hollow structure named a hypanthium, through which runs the style. The hypanthium is typically 1–2 cm long, but in some species may be up to 15 cm. After fertilization, the embryo undergoes only a very few cell divisions and then becomes quiescent. Then, the intercalary meristem of the ovary begins to elongate forming a 'peg' structure with the ovary just behind the lignified tip. This peg grows downwards and penetrates the soil, where embryo development resumes and the pod is formed (Smith, 1950). In *A. hypogaea*, the pods develop only a centimetre or two below the soil surface, but in wild species, they develop much further down. In *A. hypogaea*, the seeds in the pods develop side by side in much the same way as pea seeds. However, in wild species, the development of an intercalary meristem between the (typically two) seeds draws out the pod between the seeds into a long thread-like isthmus. This creates a space between the seeds and, when they germinate, the competition between the seedlings is reduced (Krapovickas and Gregory, 1994).

The position of the genus *Arachis* within the legumes

The legume family (Fabaceae or Leguminosae) is divided into three very large subfamilies, Mimosoideae, Caesalpinioideae and Papilionoideae. Almost all economically important legumes fall within two sub-clades of the Papilionoideae that diverged from each other some 50 Myr ago, the Phaseoloids and Galegoids (Fig. 1; Wojciechowski *et al.*, 2004; Lewis *et al.*, 2005).

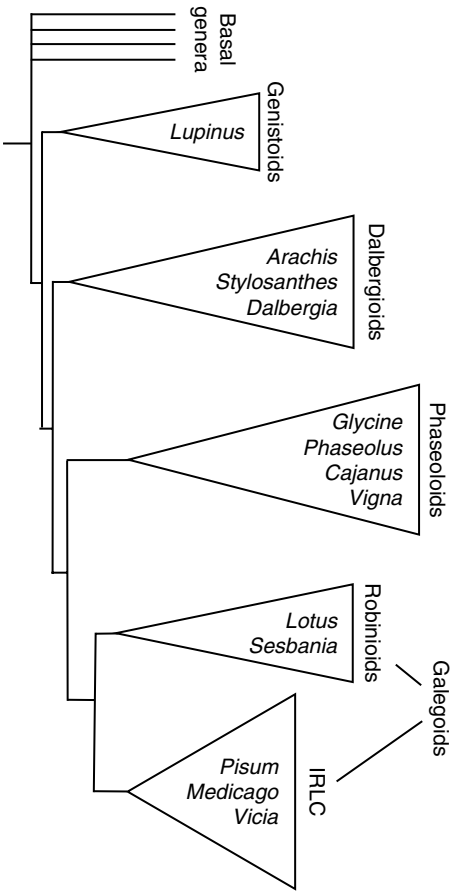

Fig. 1. A tree representation of the phylogeny of the Papilionoids with triangles representing the major clades, and the two subclades of the Galegoids; the Robinioids and the IRLC (plastid DNA inverted repeat lacking clade). Names of some notable genera are placed within the triangles. Note that *Arachis,* which is a member of the Dalbergioids, represents a more basally diverged clade than the Phaseoloid or Galegoid legumes. The figure is from Bertioli *et al.* (2009) and is a simplified and stylized phylogeny based on a tree in Wojciechowski *et al.* (2004).

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The Phaseoloids, also known as the 'warm season', 'tropical' or 'millettioid' clade, is a pan-tropical group with a base chromosome number of $1n = 11$ or 12. This clade includes bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), soya (*Glycine max*) and pigeon pea *(Cajanus cajan*).

The Galegoids, also known as the 'cool season', 'temperate' or 'Hologalegina' clade, include over 4800 species with their centre of distribution in Europe and the Mediterranean and make up the vast majority of legumes distributed in temperate regions of the world. This clade includes clover (*Trifolium* ssp.), pea (*Pisum sativum*), lentil (*Lens culinaris*), field bean (*Vicia faba*), chickpea (*Cicer arietinum*) and alfalfa (*Medicago sativa*).

However, *Arachis* falls in a different Papilionoid clade, the Dalbergioids. This clade is more basal in its divergence than the phaseoloids and galegoids (Fig. 1). The Dalbergioids are predominantly New World and tropical and have an ancestral chromosome number of $1n = 10$. All species of *Arachis* are geocarpic, but none of the species in its sister genus *Stylosanthes* have this trait. In this way, geocarpy taxonomically clearly defines the genus *Arachis*. Also, most unusually among flowering plant genera, the most significant characters that separate the species of the genus are not above ground, but below, the fruits, rhizomatous stems, root systems and hypocotyls (Krapovickas and Gregory, 1994).

Because of geocarpy, an individual plant within the genus *Arachis* can usually disperse its seed only about 1 m/year. Plausible agents of distribution over longer distances are water and in some special cases, humans. The species also show a predominance of autogamous and asexual reproduction, and a steady evolutionary drift that leads to noticeable incompatibilities between different collections of the same species. These factors are fundamental to the biology and taxonomy of the genus, and make it more complex than most.

By mid-20th century, some 10–15 species had been described, but among these, there were numerous confusions. At this point began the work of a group of researchers based within the Americas, who with systemic collections, extensive experimental crosses, morphological observations and cytogenetics would produce the first broad treatment of the genus. Their landmark monograph recognized 69 species, it was published in Spanish, and recently has been translated into English (Table 1; Krapovickas and Gregory, 1994; Krapovickas and Gregory, 2007). Subsequently, 11 new species have been described (Table 1; Valls and Simpson, 2005), also around ten more have been collected in the last decade but still have to be formally described.

Table 1. Described sections and species of the genus *Arachis* part 1 (synonyms not listed)

Sect. Arachis
Arachis batizocoi Krapov. & W.C. Greg.
Arachis benensis Krapov., W.C. Greg. & C.E. Simpson
Arachis cardenasii Krapov. & W.C. Greg.
Arachis correntina (Burkart) Krapov. & W.C. Greg.
Arachis cruziana Krapov., W.C. Greg. & C.E. Simpson
Arachis decora Krapov., W.C. Greg. & Valls
Arachis diogoi Hoehne
Arachis duranensis Krapov. & W.C. Greg.
Arachis glandulifera Stalker
Arachis gregoryi C.E. Simpson, Krapov. & Valls
Arachis helodes Mart. ex Krapov. & Rigoni
Arachis herzogii Krapov., W.C. Greg. & C.E. Simpson
Arachis hoehnei Krapov. & W.C. Greg.
Arachis hypogaea L.
Arachis ipaënsis Krapov. & W.C. Greg.
Arachis kempff-mercadoi Krapov., W.C. Greg. & C.E. Simpson
Arachis krapovickasii C.E. Simpson, D.E. Williams, Valls & I.G. Vargas
Arachis kuhlmannii Krapov. & W.C. Greg.
Arachis linearifolia Valls, Krapov. & C.E. Simpson
Arachis magna Krapov., W.C. Greg. & C.E. Simpson
Arachis microsperma Krapov., W.C. Greg. & Valls
Arachis monticola Krapov. & Rigoni
Arachis palustris Krapov., W.C. Greg. & Valls
Arachis praecox Krapov., W.C. Greg. & Valls
Arachis schininii Krapov., Valls & C.E. Simpson
Arachis simpsonii Krapov. & W.C. Greg.
Arachis stenosperma Krapov. & W.C. Greg.
Arachis trinitensis Krapov. & W.C. Greg.
Arachis valida Krapov. & W.C. Greg.
Arachis vallsii Krapov. & W.C. Greg. (see Valls (2006), Lavia *et al.* (2009))
Arachis villosa Benth.
Arachis williamsii Krapov. & W.C. Greg.
Sect. Caulorrhizae Krapov. & W.C. Greg.
Arachis pintoi Krapov. & W.C. Greg.
Arachis repens Handro
Sect. Erectoides Krapov. & W.C. Greg. (continued in Table 2)
Arachis archeri Krapov. & W.C. Greg.
Arachis benthamii Handro
Arachis brevipetiolata Krapov. & W.C. Greg.
Arachis cryptopotamica Krapov. & W.C. Greg.
Arachis douradiana Krapov. & W.C. Greg.
Arachis gracilis Krapov. & W.C. Greg.
Arachis hatschbachii Krapov. & W.C. Greg.
Arachis hermannii Krapov. & W.C. Greg.

Based on: Krapovickas and Gregory (1994), Valls and Simpson (2005), and Lavia (2009).

The distribution and ecology of the genus

The genus is distributed within a large region of South America, which extends from the eastern foothills of the Andes Mountains in Bolivia and northern Argentina to the Atlantic coast in Brazil and from the southern limit of the Amazonian rainforest towards the northern

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Table 2. Described sections and species of the genus *Arachis* part 2 (synonyms not listed)

Sect. Erectoides Krapov. & W.C. Greg. (continued)
Arachis major Krapov. & W.C. Greg.
Arachis martii Handro
Arachis oteroi Krapov. & W.C. Greg.
Arachis paraguariensis Chodat & Hassl.
Arachis porphyrocalyx Valls & C.E. Simpson
Arachis stenophylla Krapov. & W.C. Greg.
Sect. Extranervosae Krapov. & W.C. Greg.
Arachis burchellii Krapov. & W.C. Greg.
Arachis lutescens Krapov. & Rigoni
Arachis macedoi Krapov. & W.C. Greg.
Arachis marginata Gardner
Arachis pietrarellii Krapov. & W.C. Greg.
Arachis prostrata Benth.
Arachis retusa Krapov., W.C. Greg. & Valls
Arachis setinervosa Krapov. & W.C. Greg.
Arachis submarginata Valls, Krapov. & C.E. Simpson
Arachis villosulicarpa Hoehne
Sect. Heteranthae Krapov. & W.C. Greg.
Arachis dardani Krapov. & W.C. Greg.
Arachis giacomettii Krapov., W.C. Greg., Valls & C.E. Simpson
Arachis interrupta Valls & C.E. Simpson
Arachis pusilla Benth.
Arachis seridoënsis Valls, C.E. Simpson, Krapov. & R. Veiga
Arachis sylvestris (A. Chev.) A. Chev.
Sect. Procumbentes Krapov. & W.C. Greg.
Arachis appressipila Krapov. & W.C. Greg.
Arachis chiquitana Krapov., W.C. Greg. & C.E. Simpson
Arachis hassleri Krapov., Valls & C.E. Simpson
Arachis kretschmeri Krapov. & W.C. Greg.
Arachis lignosa (Chodat & Hassl.) Krapov. & W.C. Greg.
Arachis matiensis Krapov., W.C. Greg. & C.E. Simpson
Arachis pflugeae C.E. Simpson, Krapov. & Valls
Arachis rigonii Krapov. & W.C. Greg.
Arachis subcoriacea Krapov. & W.C. Greg.
Sect. Rhizomatosae Krapov. & W.C. Greg.
Arachis burkartii Handro
Arachis glabrata Benth.
Arachis nitida Valls, Krapov. & C.E. Simpson
Arachis pseudovillosa (Chodat & Hassl.) Krapov. & W.C. Greg.
Sect. Trierectoides Krapov. & W.C. Greg.
Arachis guaranitica Chodat & Hassl.
Arachis tuberosa Bong. ex Benth.
Sect. Triseminatae Krapov. & W.C. Greg.
Arachis triseminata Krapov. & W.C. Greg.

Based on: Krapovickas and Gregory (1994), Valls and Simpson (2005), and Lavia (2009).

coast of La Plata River in Uruguay (Fig. 2; Krapovickas and Gregory, 1994). Within this area, the species may either have extended ranges or be limited to only one collection site. The distribution areas of the species may overlap, but sympatric populations are rarely observed. Some of the species are composed of populations scattered throughout the entire species range, but others occur in a few small populations often separated by long distances. Reflecting the geocarpic habit, each population usually has tens to hundreds of individuals, arranged in patches of different sizes or with a more or less regular distribution.

Arachis species are adapted to a wide variety of habitats. They can be found in the xerophytic forests, in temporarily flooded areas, in grasslands and in open patches of the sub-tropical rainforest. Soil preferences are diverse ranging from rock outcrops, layers of laterite pebble, heavy soils, poorly drained areas to well drained sandy soils. They grow spontaneously from sea level on the Atlantic coast in Brazil and Uruguay to around 1450 m in the Andes Mountains of Northwestern Argentina. In spite of the ample range of ecological preferences displayed by the wild species, the genus as a whole is mainly associated with the savannah-like Cerrado biogeographical region as defined by Cabrera and Willink (1973).

According to the distribution of ancestral characters, it has been proposed that the genus originally evolved in an area that divides the Parana and Paraguay River basins in Mato Grosso do Sul State (Brazil) and northern Paraguay (Krapovickas and Gregory (1994)). However, the major centre of morphological, cytogenetic and genetic variation for the genus is around the Brazilian and Bolivian pantanal (Gregory *et al.*, 1980; Fernández and Krapovickas, 1994; Lavia, 1999).

The infrageneric taxonomy of *Arachis*

Based on morphology, cross-compatibility, viability of the hybrids, geographic distribution and cytogenetics, the *Arachis* species have been arranged in nine taxonomic sections: *Trierectoides*, *Erectoides*, *Procumbentes*, *Rhizomatosae*, *Heteranthae*, *Caulorrhizae*, *Extranervosae*, *Triseminatae* and *Arachis* (Krapovickas and Gregory, 1994; Fernández and Krapovickas, 1994; Lavia, 1999; Valls and Simpson, 2005). Among these, the section *Trierectoides* is considered to have the most ancestral characters, such as tuberous hypocotyls or roots, trifoliated leaves and vaginated stipules, the last two of these characters resembling those present in the genus *Stylosanthes*. On the other hand, the section *Arachis* is considered to be the most diverse and derived, harbouring both annual and perennial species and different chromosome numbers, ploidy levels and karyotype structures. Between these two sections, species that belong to sections *Erectoides* and *Procumbentes* seem to be the most related to those within the section *Arachis*. Some of the members of sections *Rhizomatosae, Heteranthae* and *Caulorrhizae* may produce hybrids with the most derived sections, but others show a strong genetic isolation. Sections *Extranervosae*

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and *Triseminatae* are the most isolated sections, and their evolutionary position has to be determined (Krapovickas and Gregory, 1994). Recent phylogenies of rDNA sequences that use *Stylosanthes* as outgroups generally support the grouping of the species within the sections, but do not support *Trierectoides* as the most primitive. They suggest that sections *Extranervosae*, *Heteranthae* and *Triseminatae* are most primitive, section *Arachis*

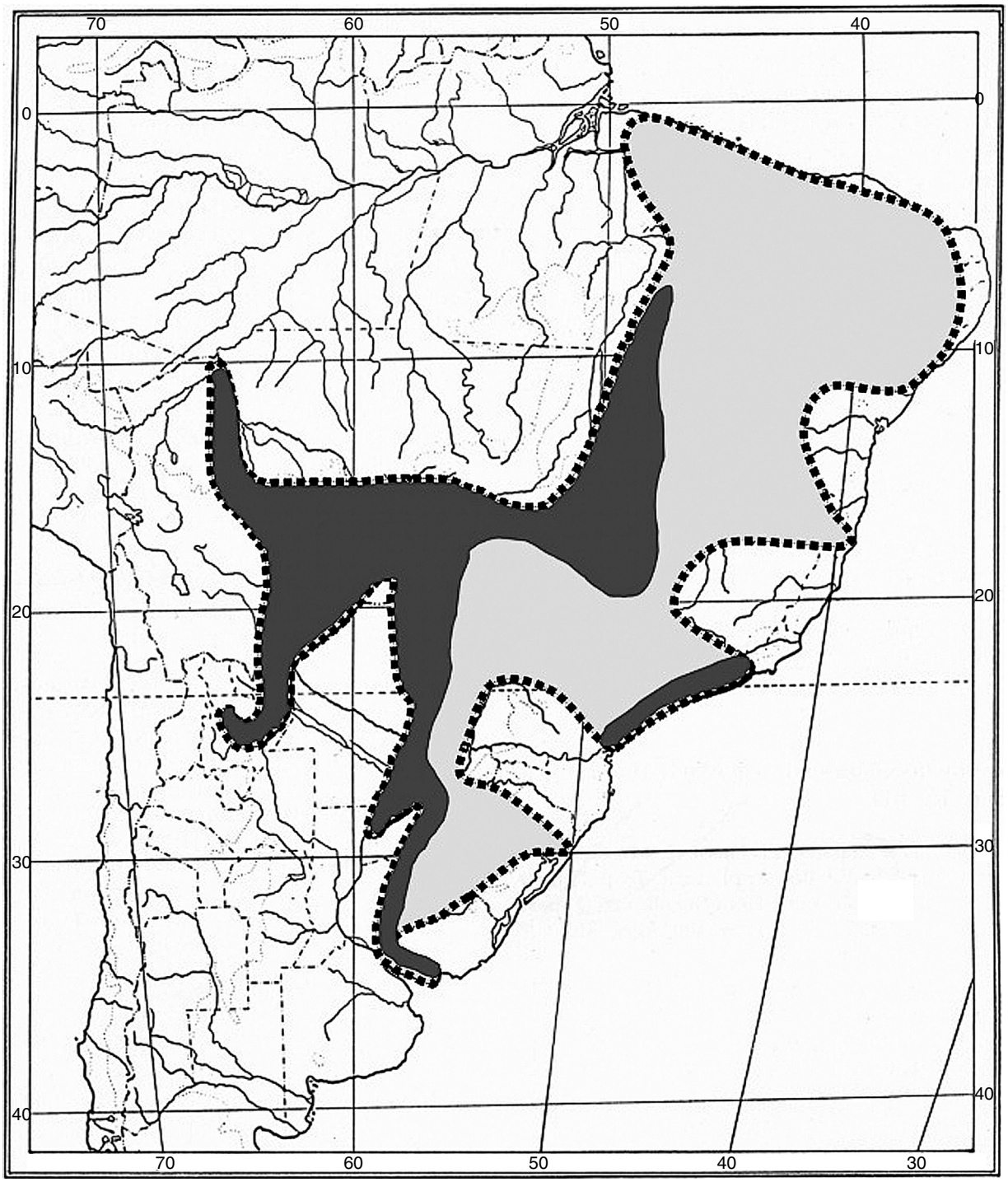

Fig. 2. Geographic distribution of all the species in the genus *Arachis* (delimitated by dashed line) and the distribution of the species in the section *Arachis* (delimitated by darker grey area). The discontinuous section *Arachis* area on the coast of Brazil is of *Arachis stenosperma*. This distribution is almost certainly not natural. This species was cultivated for food by native peoples, and it is believed that plants in this region are descendants of plants that persisted and spread in the wild after escaping from cultivation.

is the most derived, and that sections *Caulorrhizae*, *Erectoides*, *Procumbentes*, *Rhizomatosae* and *Trierectoides* are intermediate in position (Wang *et al*., 2010; Bechara *et al*., 2010).

The species relationships within the botanical section *Arachis*, and the most probable ancestors of cultivated peanut

Among the nine different sections, the type section *Arachis* has received particular attention because it contains the cultivated peanut and its putative wild progenitors. In accordance with its status as the most evolutionarily derived section, geographically it is the most widely distributed (Fig. 2). It extends in an east–west direction between the Chapada dos Parecis in the central west of Mato Grosso State (Brazil) and the northern edge of the Chacoan region. From this latitudinal central axis, in the east, the species extend towards the northeast along the Tocantins River (central Brazil) and southward along the Paraguay–Paraná and Uruguay River Basins (Paraguay, Argentina and Uruguay) reaching the northern shore of La Plata River. In the west, they are found towards the northwest along the Mamoré and Guaporé Rivers in north Bolivia and towards the southwest along the Parapetí, Pilcomayo, Bermejo, San Francisco and Juramento River Basins in southern Bolivia and northern Argentina. In its centre, the section *Arachis* overlaps with sections *Procumbentes*, *Erectoides* and *Trierectoides*, towards the southeast with section *Rhizomatosae*, and from the centre towards the northwest with section *Extranervosae*. It has parapatric distribution with sections *Caulorrhizae* and *Heteranthae* at the northwest edge of its distribution. Section *Triseminatae* is the only one with a completely separate distribution from the *Arachis* section area (Krapovickas and Gregory, 1994).

The chromosomes of the section *Arachis* species are small and mostly metacentric. In spite of this, analyses of karyotypes do provide valuable information. Diploid species with $2n = 20$ have been assigned to three different genomes, A, B and D. The species with the A genome are characterized by a small pair of chromosomes with allocyclic condensation, 'the A chromosomes' after Husted (1936) (Smartt *et al*., 1978). The remaining species with symmetric karyotypes but without A chromosomes have been considered members of the B genome (Smartt *et al*., 1978; Smartt and Stalker, 1982; but also see later in manuscript). The only species with an asymmetric karyotype (*Arachis glandulifera*) is classified as having the D genome (Stalker, 1991). Diploid species with $2n = 18$ are not well characterized, and their genome constitution still has to be determined (Lavia, 1996, 1998; Peñaloza and Valls, 1997). Cultivated peanut and the wild *Arachis monticola* are allopolyploid species ($2n = 40$) and have an AABB genome constitution (Husted, 1936; Smartt *et al*., 1978; Fernández and Krapovickas, 1994). Analysis using molecular markers corroborates the division of the section into two main groups consisting of the A and B genomes, with the D genome and the three $2n = 18$ species being closely related to the B genome species (Halward *et al*., 1992; Moretzsohn *et al*., 2004; Milla *et al*., 2005; Tallury *et al*., 2005; Bravo *et al*., 2006; Gimenes *et al*., 2007; Cunha *et al*., 2008; Tang *et al*., 2008). Further supporting these main divisions within the sections, for diploids, there is a remarkable correlation between the presence of A chromosomes and perennial growth habit. All A genome species are perennials, except *Arachis duranensis* and *Arachis schininii*. Indeed, it has been commented that without the tetraploid AABB genomes to unify them, the A and B genome species could have been placed into two distinct sections.

Because the A and B genomes are closely related to the genomic components of cultivated peanut, the fine structure of the relationships of the species with these genomes is worth considering more closely.

For the A genome species, three different karyotype subgroups could be established on the basis of the number of rDNA loci and chromosomes with centromeric heterochromatin (Robledo *et al*., 2009). Within this scheme, the A genome of *A. hypogaea* falls into the same subgroup as *A. duranensis*, *Arachis villosa*, *A. schininii* and *Arachis correntina*. Concerning molecular studies, the placement of diploid and tetraploid species in the same study is problematic, because the latter should occupy not one, but two, positions within a tree of relationships. In spite of this, *A. hypogaea* often falls closely to *A. duranensis*, which, in turn, is most closely associated with *A. villosa*, *Arachis stenosperma* and *Arachis diogoi* (Moretzsohn *et al*., 2004; Milla *et al*., 2005; Bravo *et al*., 2006; Cunha *et al*., 2008; Tang *et al*., 2008; Koppolu *et al*., 2010).

The species included within the B genome are more diverse in their karyotype formulas (Fernández and Krapovickas, 1994) and karyotype structure (Seijo *et al*., 2004). The analysis of heterochromatin distribution and rDNA loci mapping by FISH demonstrated that these species can be arranged into three different groups. Species included in each group have a strong genetic isolation with those included in the other groups. On this basis, the B genome *sensu lato* or, as they may be better termed the 'non-A genome' taxa, were segregated into three different genomes: B *sensu stricto*, F and K (Seijo *et al*., 2004; Robledo and Seijo, 2010). The B genome *s.s.* is deprived of centromeric

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heterochromatin and consists of the B component of *A. hypogaea*, *Arachis ipaënsis*, *Arachis magna*, *Arachis gregoryi*, *Arachis valida*, and *Arachis williamsii*. The other two genomes have centromeric bands on most of the chromosomes, but differ in the amount and distribution of heterochromatin. The molecular data provide strong support for the division of the B genome *s.s.* from the other non-A genomes. Often, *A. hypogaea* is associated with *A. ipaënsis*, but also to *A. magna*, *A. williamsii*, *A. gregoryi* and *A. valida* (Moretzsohn *et al.*, 2004; Milla *et al.*, 2005; Tallury *et al.*, 2005; Bravo *et al.*, 2006). The other group usually contains *Arachis batizocoi*, *Arachis benensis* and *Arachis cruziana*. The only study that included *Arachis krapovickasii* grouped it to these later three species (Moretzsohn *et al.*, 2004).

The exact genetic origin of cultivated peanut has long interested plant taxonomists, geneticists and breeders. Initially, a different origin for each subspecies (see below) was advanced based on the morphological variability and their partial reproductive isolation (Singh and Moss, 1982; Lu and Pickersgill, 1993). However, most authors now support the hypothesis that *A. hypogaea* is an allotetraploid derived from just two wild diploid species, and indeed probably between very few individuals of these diploid species. This is supported by the very limited genetic variability among landraces and commercial cultivars of *A. hypogaea*, and from its molecular cytogenetics (Halward *et al.*, 1991; Kochert *et al.*, 1996; Raina *et al.*, 2001; Seijo *et al.*, 2004, 2007; Milla *et al.*, 2005). 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 and are the same biological species. They have very high crossability, cytogenetically the species are indistinguishable, and molecular studies show they are very closely related. They could not be differentiated based on isozymes (Lu and Pickersgill, 1993), random amplified polymorphic DNA (RAPD; Hilu and Stalker, 1995; Cunha *et al.*, 2008) and some microsatellite markers (Gimenes *et al.*, 2007; Koppolu *et al.*, 2010). However, various studies, based on amplified fragment length polymorphism (AFLP), microsatellite and sequence-related amplified polymorphism markers, have shown that *A. monticola* does have enough genetic divergence to form a separate group (Gimenes *et al.*, 2002; Moretzsohn *et al.*, 2004; Milla *et al.*, 2005; Bravo *et al.*, 2006; Ren *et al.*, 2010).

Based on the evidence cited above, on whole genome *in situ* hybridization and on biogeographic information (Fig. 3; also see below), 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; Seijo *et al.*, 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 (Krapovickas, 2004).

As for the geographical origin, archaeological studies indicate the presence of *A. hypogaea* in the Huarmey Valley in Peru (5000 year BP) (Bonavia, 1982) and of pod samples that strongly resemble those of wild species, in the Casma Valley also in Peru (3500 and 3800 year BP). These locations are perfect for the preservation of archaeological 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 is even possible 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 bees that could serve as agents for cross pollination. 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 (Fig. 3; Gregory *et al.*, 1980; Krapovickas and Gregory, 1994).

The genetic behaviour of peanut

From genetic maps, it is apparent that the order of molecular markers in the A and B genomes is mostly co-linear with only a few major rearrangements that distinguish them (Burow *et al.*, 2001; Moretzsohn *et al.*, 2009). This emphasizes the similarity of the two genome components. However, the A and B genomes must have important differences because cultivated peanut is an allotetraploid that is well diploidized genetically; almost all chromosome pairing during meiosis is bivalent, and no large chromosome rearrangements between the A and B genome components seem to have occurred after the formation of the tetraploid species (Smartt, 1990; Seijo *et al.*, 2007). The nature of the differences between the genomes that prevent efficient pairing in meiosis is unknown, but recent studies

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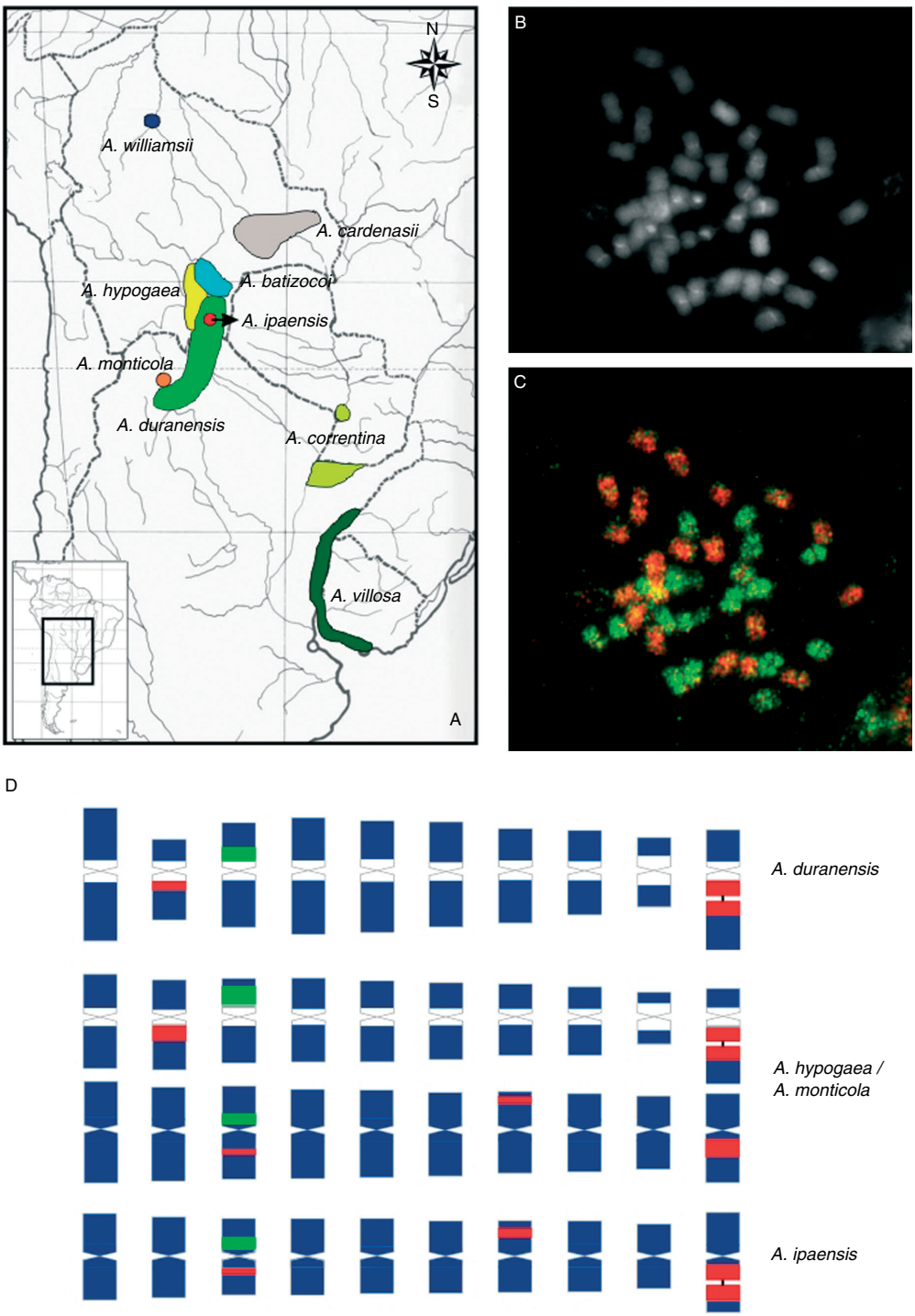

Fig. 3. (A) Geographic distribution of the putative wild progenitors of peanut and the major centre of variability of *Arachis hypogaea* var. *hypogaea* (adapted from Seijo *et al.* (2004)). (B) Somatic metaphases of *A. hypogaea* after 4-6-diamidino-2-phenylindole (DAPI) staining showing half of the chromosomes with heterochromatic bands. (C) Same metaphase after double genomic *in situ* hybridization using total DNA probes from *Arachis ipaensis* (red) and *Arachis duranensis* (green) (B and C from Seijo *et al.* (2007)). (D) Idiograms of *A. hypogaea*/*A. monticola* and their most probable wild ancestors (*A. duranensis* and *A. ipaensis*) showing the distribution of 5S (green) and 18S–25S (red) rDNA loci, and the DAPI-enhanced heterochromatic bands (white) (adapted from Seijo *et al.* (2004)).

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may have some bearing on this. *In situ* hybridization analysis performed with genomic DNA of wild species onto the chromosomes of *A. hypogaea* suggests that genome differentiation in *Arachis* section may have been accompanied by rapid divergence in the content of the repetitive elements (Seijo *et al.*, 2007). A closer analysis of the abundance, distribution and evolution of one Ty3-*gypsy* element, called FIDEL, on the A and B genomes supports this (Nielen *et al.*, 2010).

Variation within cultivated peanut

It was perhaps Charles Darwin who first noted that domesticated species accumulate a remarkable amount of variation in a short time. Peanut follows this pattern, and considering its very recent origin, it exhibits a remarkable amount of morphological variability. Based on this, two subspecies were recognized, *hypogaea* and *fastigiata*. These, in turn, have two (*hypogaea* and *hirsuta*) and four (*fastigiata*, *vulgaris*, *aequatoriana* and *peruviana*) botanical varieties, respectively (Fig. 4; Krapovickas and Gregory, 1994).

The type variety (*A. hypogaea* subsp. *hypogaea* var. *hypogaea*) has a long cycle, no flowers on the central stem, and regularly alternating vegetative and reproductive side stems. It is widely present as landraces along the tributaries to the South of the Amazon River in Brazil and Bolivia. The modern agricultural types 'Virginia' or 'Runner' exemplify this type. Also classified within subsp. *hypogaea*, but with more hirsute leaflets and even longer cycle, is the variety *hirsuta* Köhler (Peruvian Runner). Nowadays, this variety is concentrated in the coastal regions of Peru, from where it extends to Central America and Mexico, Asia and Madagascar. The variability of this variety found in the Old World even suggests the possibility of pre-Colombian contacts.

The subspecies *fastigiata* Waldron has a shorter cycle, flowers on the central stem and reproductive and vegetative stems distributed in a disorganized way. The variety *vulgaris* C. Harz has its distribution centred on the basin of the river Uruguay. Usually, the fruits are two seeded, and the varieties correspond to the agricultural type known as 'Spanish'. The variety *fastigiata* has fruits with more than two seeds and a smooth pericarp; this variety corresponds to the agricultural type 'Valencia'; centres of diversity are in Paraguay, and Central and North-Eastern Brazil extending to Peru. The other two varieties *aequatoriana* Krapov. and W.C. Gregory (Ecuador and North of Peru) and *peruviana* Krapov. and W.C. Gregory (Peru, North East of Bolivia and the Brazilian State of Acre) have fruits with more than two seeds, heavy reticulation of the pericarp and very restricted distributions.

Initially, the very limited DNA polymorphism present in *A. hypogaea* limited the information that could be gained from molecular studies. The first studies were based on isozymes and proteins (Krishna and Mitra, 1988; Grieshammer and Wynne, 1990; Lu and Pickersgill, 1993), followed by restriction fragment length polymorphism – RFLPs (Kochert *et al.*, 1991, 1996; Paik-Ro *et al.*, 1992), RAPDs (Halward *et al.*, 1991; 1992; Hilu and Stalker, 1995; Subramanian *et al.*, 2000; Dwivedi *et al.*, 2001) and AFLPs (He and Prakash, 1997, 2001; Gimenes *et al.*, 2002; Herselman, 2003; Milla *et al.*, 2005; Tallury *et al.*, 2005). None of these marker systems were very informative in cultivated germplasm. Higher levels of polymorphism were observed with microsatellites, in particular with longer TC motif repeats (Moretzsohn *et al.*, 2005). Over the last few years, many new microsatellite markers have been developed, and this has enabled the detection of moderate levels of genetic variation in *A. hypogaea* accessions and even intra-variety polymorphism (Krishna *et al.*, 2004; Barkley *et al.*, 2007; Tang *et al.*, 2007; Varshney *et al.*, 2009c). These studies have shown the grouping of accessions according to the varieties they belong to (Jiang *et al.*, 2007; Kottapalli *et al.*, 2007). In general, two main groups were observed, joining accessions of *A. hypogaea* ssp. *fastigiata* '*fastigiata*' (Valencia type) and *fastigiata* '*vulgaris*' (Spanish type) in one group, and *hypogaea* '*hypogaea*' (Virginia and

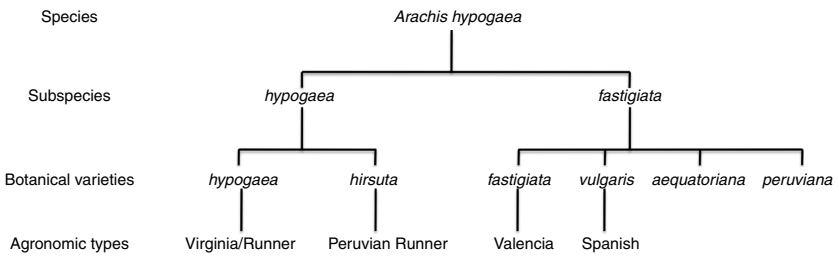

Fig. 4. The taxonomic arrangement of subspecies and botanical varieties of *Arachis hypogaea,* and their equivalence to agronomic types. It should be noted that many modern cultivars are of mixed parentage and are not good representatives of the botanical varieties.

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Runner types) and *hypogaea* '*hirsuta*' (Peruvian runner) in a second group. These results corroborated the current taxonomic status of these subspecies and varieties. Exceptions to these results may be explained by the erroneous use of modern cultivars or breeding lines to represent the varieties. Frequently, these cultivars/lines have different varieties in their pedigrees and do not represent the varieties as well as landraces do. However, in contrast, studies that included *fastigiata* '*aequatoriana*' and, especially, *fastigiata* '*peruviana*' accessions raised questions on the current classification of these varieties (He and Prakash, 2001; Raina *et al*., 2001; Ferguson *et al*., 2004a; Tallury *et al*., 2005; Freitas *et al*., 2007; Cuc *et al*., 2008). Most of them have shown that accessions of these varieties have greater similarity to subspecies *hypogaea* rather than to subspecies *fastigiata*, to which they are currently thought to belong; the exception being the study of Moretzsohn *et al*., 2004. However, only a small number of *fastigiata* '*aequatoriana*' and *fastigiata* '*peruviana*' accessions were included in these studies, and we consider that more investigation is required to reach firm conclusions.

Landraces

South America's history, past and present, is of a tapestry of peoples living in very different environments and circumstances, of displacements, and migrations. Over much of the region, where the climate is suitable, this history is intrinsically tied to the evolution and maintenance of diverse landraces and types of peanut. The changes that were initiated some 500 years ago with the discovery of the Americas by Europeans have steadily increased in impact and speed to the present day. Now South America has some of the largest urban centres in the World and some isolated communities that have never been in contact with the modern World. Many landraces must have been lost during these changes, but many survived. Numerous landraces are grown by South Americans of mixed descent, sometimes using cultivation methods such as companion planting with cassava, that were obviously used by pre-Colombian native peoples. Recently, a very interesting description of 62 distinct landraces in Bolivia has been published (Krapovickas *et al*., 2009). Almost all of these landraces are endemic to the country.

Many landraces are cultivated by more isolated communities and remain poorly characterized or unknown to science. These landraces are of particular interest because they may have new valuable characteristics. However, they are also vulnerable to extinction during the social upheavals that seem inevitable when native and modern societies meet. Below we shall give a brief description of two such cases.

Williams (1996) described the very interesting cultivation of landraces by native farmers in Eastern Bolivia. They plant in very unusual conditions, the beaches, or sandbanks of rivers that are exposed for a rather short period during the dry season. Under this cropping system, the plants suffer strong selection pressure for uniform germination and a very short cycle, because they must produce seed before the water rises again and inundates the growing area.

Another very interesting case has been coming to light recently of the Kayabi Indians who live in the Xingu Indigenous Park in the Central West of Brazil. The park was officially created in 1961 and covers 30,000 km^2, almost the size of Belgium. It is located in a transition area between biomes, with the Cerrado to the South and the Amazon to the North. Indians from a number of distinct ethnic groups originally inhabited the park, and some others, including the Kayabi, were transferred there. Now there are 14 villages of the Kayabi living in the Park, and peanut is important to them both as a food and culturally. Some villages cultivate only two or three types of peanut, but others many more, some 60 types being recognized by the Indians themselves. The types are morphologically very diverse, and their combinations of unusual characters make them unique. Some types are very large and have a very long cycle, and some have extremely large seeds. Some types have very tough pods, and others have thin pods. Seeds are purple, brown, red or white, some types having a uniform colour, others being partly coloured and partly white (Fig. 5).

The peanuts are cultivated in a slash and burn system. Within an area of forest, the smaller vegetation is cut in

Fig. 5. A selection of cultivated peanuts and their wild relatives. The groups of pods and seeds are, starting from top left and going clockwise: Of107, Of128 and Of111, three types of cultivated peanut (*Arachis hypogaea*) kindly given to Fábio de Oliveira Freitas by the Kayabi South American Indians; *Arachis cardenasii*, *Arachis stenosperma* and *Arachis duranensis* are the three wild diploid species. Note that the long thread-like isthmus, which separates the seeds in the pods, has broken during harvesting; *Arachis hypogaea* var. *fastigiata* cv. Tatu, a popular cultivar of peanut in Brazil.

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May/June. This is then left during the dry season, and the area is cleared by burning in August, just before the start of the rains. Areas with more fertile black soils are chosen, and are cultivated for several years. The different types of peanut have cycles of different lengths, and planting is programmed such that all the peanuts can be collected together. At the beginning of the season, women select the seeds and men do the planting. At the end of the season, women harvest the plants simply by pulling them from the ground. The larger runner-type plants come loose after a series of pulls starting at one edge of the plant and working over to the other edge. After harvesting, the peanuts are dried and stored all mixed together, in pod, in enormous baskets (Fig. 6). Peanuts are taken from these baskets for consumption starting at the top, and those left at the bottom are used for seed at the beginning of the next season.

Thirty samples of this material were analyzed from two Kayabi villages using microsatellite markers along with a selection of other cultivated and wild accessions. With the exception of one pair, all Kayabi samples could be distinguished, and the samples formed three deep-rooted clades within the dendrogram, reflecting their genetic distinctness. Of particular interest was an accession that, although not wild in phenotype in any obvious way, grouped closest to the wild tetraploid *A. monticola*. Amazingly, this accession had been described by the Indians as the most ancient of the peanuts, and was known to them as 'peanut of the field' (Freitas *et al.*, 2007). We hope that this story serves to illustrate the diversity of peanut landraces that still awaits discovery by science, and that it also provides a glimpse of how traditional knowledge may enhance our understanding of germplasm.

Fig. 6. A Kayabi man next to the large baskets used to store peanuts.

Germplasm banks

Important collections of germplasm are held at ICRISAT, India; the USDA-ARS, USA; INTA, Argentina; PROINPA, Bolivia; EMBRAPA–Cenargen, Brazil; IBONE, Argentina and Texas A&M, USA. The first four collections mentioned concentrate on cultivated peanut, and the latter three collections focus more on wilds. Structured core collections of cultivated peanut have been assembled of 1704 and 831 accessions, and mini-cores of 184 and 112 accessions at ICRISAT and USDA-ARS, respectively (Holbrook *et al.*, 1993; Varshney *et al.*, 2009b). These cores and mini-cores are an efficient way to access greater diversity in breeding programmes, and are being widely used. There are numerous other collections of peanut germplasm maintained around the world, most of them being focused on cultivated peanut at institutions that have, or are linked to, breeding programmes.

The use of wild germplasm in peanut breeding

As a consequence of having duplicated genomes, the tetraploid that gave rise to *A. hypogaea* would have been isolated from sharing genes with its wild relatives. Therefore, a strong genetic bottleneck was created at the origin of the tetraploid species. In spite of this, the variation that has accumulated in peanut during artificial selection over thousands of years of domestication provides a rich material for breeding for many traits. This is the case, for example, with seed and pod characteristics and growth habit. However, for other characteristics such as disease and pest resistance, the narrow genetic base presents clear limitations to crop improvement. There are also good theoretical reasons to believe that genetic limits for more complex traits such as yield and drought tolerance can be overcome by broadening the genetic base of the crop. For these reasons, for many years, peanut breeders have been interested in the introduction of new alleles from wild species.

The transfer of genes from wild species by crossing has faced three fundamental problems: fertility barriers

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caused by species incompatibilites and ploidy differences; linkage drag of desirable wild alleles with ones that confer agronomically unadapted traits; and difficulties in confirming hybrid identities and tracking introgressed segments. Together, these problems are considerable, but as the knowledge base, and tools available improve, the ability to overcome them also improves. As outlined earlier in this manuscript, research over the last few years has provided a much better understanding of the origin of cultivated peanut and the relationships of the species that are closely related to its A and B genome components. This has effectively expanded the secondary gene pool. Furthermore, considerable effort has been invested in the creation of the tools needed for hybrid identification, tracking of introgressed segments and for the genetic analysis necessary to understand linkage drag. The number of molecular markers, in particular microsatellite markers, has increased enormously over the last few years. Microsatellites are currently the markers of choice for peanut since they are co-dominant, highly polymorphic, transferable among related species, PCR-based and work easily in the tetraploid. Now more than 3000 markers are available (Hopkins *et al*., 1999; Palmieri *et al*., 2002, 2005; He *et al*., 2003, 2005; Moretzsohn *et al*., 2004, 2005, 2009; Ferguson *et al*., 2004b; Bravo *et al*., 2006; Budiman *et al*., 2006; Martins *et al*., 2006; Gimenes *et al*., 2007; Proite *et al*., 2007; Wang *et al*., 2007; Cuc *et al*., 2008; Guo *et al*., 2008; Liang *et al*., 2009; Moretzsohn MC, de Macedo SE, Leal-Bertioli SCM, Guimarães PM and Bertioli DJ, unpublished data). Furthermore, reference genetic maps, both in diploid A and B and in tetraploid genomes, have been created enabling the comparison of different peanut maps, and even allowing the alignment of maps with other legume species (Hougaard *et al*., 2008; Bertioli *et al*., 2009; Leal-Bertioli *et al*., 2009; Moretzsohn *et al*., 2009; Varshney *et al*., 2009a).

A number of methods have been used for the introgression of wild genes in cultivated peanut, with variable success, but here we shall cover two methods that have resulted in well-characterized introgressions: the hexaploid and tetraploid routes.

The hexaploid route was used by Stalker *et al*. (1979) who generated a triploid hybrid from a cross between the tetraploid *A. hypogaea* and the diploid *A. cardenasii*. The resulting hybrid was colchicine treated to create a hexaploid plant, and after five generations of selfing, all plants were tetraploid (Stalker *et al*., 1979). Selected lines were released with resistance to multiple disease resistances (Stalker and Beute, 1993; Reddy *et al*., 1996). These lines were characterized using RFLP and RAPD markers, and this showed that introgression was widespread (Garcia *et al*., 1995). Furthermore, markers linked to root-knot nematode resistance were identified (Garcia *et al*., 1996). Recently, more details on the genetics of fungal disease resistances of these lines have been obtained. A population derived from a cross of the peanut cultivar TAG24 with one of the lines (GPBD 4) was used for the identification of quantitative trait loci (QTLs) for rust and late leaf spot resistance (Khedikar *et al*., 2010).

The tetraploid route was first used by Simpson (1993) to create a wild-derived tetraploid. Firstly, an A genome hybrid was made by crossing *A. cardenasii* with *A. diogoi*. Then, the B genome *s.l.* species *A. batizocoi* was crossed with the A genome hybrid to create a sterile AB hybrid. This was treated with colchicine to double the chromosome number and restore fertility. This tetraploid $[A.\ batizocoi \times (A.\ cardenasii \times A.\ diogoi)]^{4x}$ was registered as TxAG-6 (Simpson *et al*., 1993). Because of the method used to produce it and its genetic behaviour, this hybrid is usually referred to as an amphidiploid. Hybrids between cultivated peanut and TxAG-6 have low fertility, but a BC-1 population and the first tetraploid map of peanut were developed from it using the peanut cultivar Florunner as the recurrent parent (Burow *et al*., 2001). TxAG-6 has very strong nematode resistance, but also presents very strong linkage drag to low yield. RFLP markers linked to nematode resistance were used to substantially break this linkage in the development of the nematode-resistant variety NemaTAM (Church *et al*., 2000; Simpson *et al*., 2003). Recently, a detailed study by Nagy *et al*. (2010) used microsatellite and resistance gene analogue markers, and diploid and tetraploid mapping populations to show that the introgressed chromosome segment displayed strongly suppressed recombination with cultivated peanut, and spanned an amazing one-third to one-half of an entire chromosome. Numerous co-dominant DNA markers were identified within the segment, opening up the perspective of finer mapping of the resistance gene and of shortening the introgressed segment by marker-assisted selection. A set of introgression lines from TxAG-6 that cover other parts of the genome are in the final phase of development, and are being characterized by RFLP and microsatellite markers (Dr Mark Burow, Texas A&M University, pers. commun.). These lines have great potential to serve as donors of other valuable wild genes.

Recently, also using the tetraploid route, introgression work has been done using a synthetic amphidiploid produced from the proposed ancestors of cultivated peanut, $(A.\ ipaënsis \times A.\ duranensis)^{4x}$ (Fávero *et al*., 2006). Using the cultivar Fleur 11 as the recurrent parent and the amphidiploid as donor, BC_1 plants were used to construct a microsatellite-based genetic map. To confirm linkage order, the map was aligned with diploid reference maps (Bertioli *et al*., 2009; Moretzsohn *et al*., 2009) and, using the genotyping information,

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a subset of BC_1s was selected for further backcrossing. The progeny plants were again genotyped, and a set of 59 BC_2 plants that represented the entire donor genome were again selected for backcrossing. In the BC_2F_1 plants, segment lengths ranged between 2.3 and 46.9 cM (mean of 24.5 cM), and the percentage of the recurrent background ranged between 62 and 94% (Foncéka *et al.*, 2009). In work that has run in parallel, lines have been developed using a different recurrent parent, IAC-Runner 886 (a selection of Florunner), and the same amphidiploid donor. Using a combination of genotyping and phenotyping, 12 lines have been selected at BC_1F_3 that combine agronomically adapted phenotypes with resistance to late leaf spot (Leal-Bertioli, 2010; Leal-Bertioli SCM, Moretzsohn MC, Guimarães PM and Bertioli DJ, unpublished results). These results are promising, but it is evident that the disease resistances of this amphidiploid are not as strong as in some other wild species. Recently, we have been exploring the potential of *A. stenosperma*, from which amphidiploids have been obtained (Santos SP, Leal-Bertioli SCM, Moretzsohn MC and Bertioli DJ, unpublished results). *A. stenosperma* has strong resistances against rust, leaf spots and root-knot nematodes (Proite *et al.*, 2008; Leal-Bertioli *et al.*, 2010). Apart from segregation distortion, genetically it behaves in an apparently normal way when crossed with *A. duranensis*, and QTLs for resistance against late leaf spot have been identified (Leal-Bertioli *et al.*, 2009). Presently, we are gathering phenotypic and genotypic data from hybrids between cultivated peanut and these new amphidiploids. Further analysis will reveal their potential.

Conclusions

The genus *Arachis* has a unique biology and unusually complex taxonomy. In spite of this, the overall view of the relationships of the species within the genus, while by no means completely defined, has a firm basis and is consistent and well organized. Cultivated peanut is a very important food crop throughout the tropics and sub-tropics. Because of its allotetraploid origin, it has a very narrow genetic base, and this presents fundamental limitations for the improvement of the crop. In contrast, during evolution, wild species have adapted to diverse ecological niches, and have diverse alleles with potential for use in improvement of the peanut crop. To date, various difficulties, both biological and technical, have led to this resource being underutilized. Our improved understanding of the species relationships within the genus, and improved tools for genetic and genomic studies will enable more efficient use of the genetic resources available.

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