History of *Arachis* Including Evidence of *A. hypogaea* L. Progenitors

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ABSTRACT

The genus *Arachis* L. probably originated as a geocarpic form of *Stylosanthes* Sw. on the old Brazilian Shield in what is now southwestern Mato Grosso do Sul, Brazil or northeastern Paraguay. Several mid-Tertiary uplifts followed, raising the penaplain and the ancient *Arachis* with it. The two most ancient species are still found in the area today, comprising the taxonomic section *Trierectoides* Krapov. and W.C. Gregory. From this beginning the other species and sections evolved as the shield was uplifted and eroded by the tributaries. The more advanced species, but still quite ancient, are in sections *Extranervosae* Krapov. and W.C. Gregory, *Triseminatae* Krapov. and W.C. Gregory, *Heteranthae* Krapov. and W.C. Gregory, and *Erectoides* Krapov. and W.C. Gregory. The evolution and distribution of these species was a slow process because of the geocarpic fruit, which would have limited movement to an estimated 1 m/yr. However, after several geologic uplifts, flowing water likely played a large part in the distribution of the *Arachis* species. From the early materials evolved the more advanced species in sections *Caulorrhizae* Krapov. and W.C. Gregory, *Procumbentes* Krapov. and W.C. Gregory, and *Rhizomatosae* Krapov. and W.C. Gregory. The evolution of species in the most advanced section *Arachis*, which includes the cultivated peanut, has overlapped the distribution of other sections, and the distribution of some members of section *Arachis* has been strongly affected by man. There is evidence that development of the major domesticated species, *A. hypogaea* L., did not occur in the wild, and extensive supportive data now exist on two other cultivated *Arachis* species still grown in Brazil for food and medicinal use—*A. villosulicarpa* Hoehne and *A. stenosperma* Krapov. and W.C. Gregory. *Arachis hypogaea* seeds likely moved to China and Africa with ancient mariners well before the time of Columbus. After discovery of the Western Hemisphere and the conquests, many forms of *A. hypogaea* spread to Africa and Asia. Later the cultivated peanut traveled in slave ships from Africa into the southeastern U.S., Central America, and northeast South America, thus returning modified germplasm to the Americas. No evidence has been found that native Americans brought the peanut, along with corn (*Zea mays* L), to the east coast of North America in pre-Columbian times.

Key Words: Domestication, evolution, wild species.

History and Origin of the Genus

The origins of the *Arachis* genus are not totally clear, but little doubt remains that the genus was formed in the southwestern part of Mato Grosso do Sul, Brazil or northeast Paraguay because the most ancient species of the genus, *A. guaranitica* Chodat. and Hassl. and *A. tuberosa* Bong. ex Benth., are still growing in that area. It is unclear about which of these two species is most ancient. Studies of leaflet morphology of older leaves on plants indicate that *Stylosanthes* is likely the progenitor genus, and *A. guaranitica* is the most ancient species in the genus *Arachis*. If the young (embryonic) leaflets are studied, then *Zornia* Gmel. could very well be the progenitor genus, and *A. tuberosa* would likely be the original *Arachis* species. The time frame of these origins was probably early or mid-Tertiary era, which makes the genus quite ancient. The amount of time required to distribute the genus to its present status in location (excluding man's intervention) and evolution of almost 100 species would require many thousands of years.

As the Brazilian Shield was alternately uplifted and eroded, the geocarpic fruit appears to have been the most limiting factor in distribution of the wild species, but it also has played a large role in allowing the genus to inhabit many different ecological niches. The fruit, along with the many varied root structures, has given species in the *Arachis* genus opportunities to evolve in varied environs from the northeastern desert of Brazil, across the vast flood plains of the Pantanal, to the lower Andean foothills—from sea level to 2000+ m elevation, and from the equator to 30°S. In these areas we have found the wild *Arachis* growing in deep friable sand; heavy alluvial loam; thick, gummy clay; and shiest rock out-crops with virtually no soil and the only organic matter being from decomposing vegetation. The numerous types of tuberous, tuberform, axonomorphic, and rhizomatous root systems indicate a long evolutionary history providing survival in many harsh environments.

The genus has evolved into species that fit into nine taxonomic sections (Krapovickas and Gregory, 1994) which include the most ancient section *Trierectoides* with its two species with three leaflets, *A. tuberosa* and *A. guaranitica*. From these ancient progenitors developed the sections *Erectoides*, *Extranervosae*, *Triseminatae*, and *Heteranthae*. The species of these four sections have varying affinities to the primitive section, as reported by Gregory and Gregory (1979) and Krapovickas and Gregory (1994) (Simpson, unpubl. data). The more advanced sections include the *Caulorrhizae*, *Procumbentes*, and *Rhizomatosae*. The affinities of these latter species groups are varied as well, but with very limited successes reported in crossing with species of the most advanced section, *Arachis* (Gregory and Gregory, 1979; Krapovickas and Gregory, 1994). The distribution of the *Arachis* section has overlapped that of the other sections in many areas. It is not unexpected that the most advanced species would be more adaptable to many environments and, thus, able to rapidly move to areas where the more ancient species have been adapted for

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many millennia. Also, man has played a role in the distribution of several species, most of which belong to section *Arachis*, including *A. stenosperma* and *A. hypogaea*. This latter species is the most widely cultivated member of the genus.

Origin and History of *Arachis hypogaea*

Very comprehensive accounts of the history of the peanut were presented by Hammons (1973, 1982). The cultigen, *A. hypogaea*, cannot survive for many years in nature without the aid of man (or other animals) to harvest seeds each year. Experiments conducted by the senior author (unpubl.) with a range of materials from primitive land races to improved cultivars have resulted in a natural survival of about three to five generations, but usually three or less in the accessions tested to date. The plants produce too many seed in a small area and the competition for light, moisture, and nutrients will eliminate the population.

In our plant explorations we have found the A and B genome species growing sympatrically at several locations, but we have not found tetraploid hybrid populations at or near the sites and only one obvious interspecific hybrid has been collected (GKPSBSc-30095 herb. spec. IBONE, Corrientes, Arg.).

The most convincing data to date, indicating that *A. hypogaea* originated in the gardens of primitive 'hunter/gather/cultivators', come from digs on the coast of Peru—two sites near Casma and another near Bermejo. In these locations, peanut shells which closely resemble the shells of *A. magna* Krapov., W.C. Gregory and C.E. Simpson, *A. ipaensis* Krapov. and W.C. Gregory, and/or *A. monticola* Krapov. and Rigoni were excavated from a layer where there was no indication of the presence of corn. These shells were dated at 1800 to 1500 B.C. In the next layer above these shells was found evidence of corn and cultivated peanut shells, which closely resemble peanut grown in the area today (Simpson, unpubl. data). In a dig nearby, shells were found that closely resemble *A. duranensis* Krapov. and W.C. Gregory dated at about the same time period (D.J. Banks, pers. commun.). If the native peoples were growing both A and B genome wild species, it is easy to envision a sterile bee-made hybrid that subsequently doubled in chromosome number. The hunters who became cultivators would recognize the larger fruits as something desirable, thus, establishing the cultivated peanut. We are not presenting here that the origin event had to occur on the west coast of Peru; only that, because of the large quantity of shells found, the wild peanuts were grown in the area and were preserved because of the arid climate. Other sites on the more eastern slopes of the Cordillera would more likely be the origination site because there would have been more moisture to support plant growth, a better environment for bee populations, and a better environment for a sterile hybrid to survive for a longer period which would allow more time for a doubling of the chromosomes. This doubling is a common occurrence in the genus *Arachis*. The senior author has observed the phenomena in his greenhouse on numerous occasions in triploid as well as diploid hybrids. Amphiploidization is more likely to be observed in sterile hybrids because no other seeds would be present.

Archeological evidence similar to that found in Peru has been discovered in northwest Argentina, indicating that the hunter/gatherers possessed, and possibly grew, wild peanut fruits in the high Andes of Argentina as well, although the sample sizes of excavated shells was much smaller (A. Krapovickas, unpubl. data). This Argentine site could possibly supply some data in the future to support a two-event origin of *A. hypogaea*, but additional data will be required to fully support such a theory.

Distribution of *A. hypogaea* was covered well by Hammons (1973, 1982), but some evidence has accumulated in the past 20 years indicating that peanuts were found in a Chinese dwelling dated at least 4900 yr before present, and a second group of peanuts were dug from a site in China where peanuts were laying next to charcoal dated 2335 B.C. (Mathews, 1983). Also, stones found off the coast of California and Peru closely match ballast and anchor stones from ancient Chinese marine vessels used up to and during the first millennia A.D. (Mathews, 1983). Other Chinese data indicate the presence of peanut well before the 15th century (Anon., 1993a,b).

Discussion

The *Arachis* genus originated on the old Brazilian Shield during the Tertiary era. This was a deduction made by Gregory and Gregory (1979) and, although no firm archeological data exist to confirm such a theory, it is a reasonable conclusion based on plant morphology and growth habit evidence we have on the genus. In many of the species, long, horizontal pegs have evolved; in other species long lateral branches with short pegs have evolved. In some species moderate length pegs and branches occur. In all three cases the total length of placement of the fruit away from the mother plant main axis is approximately 1 m. Thus, a species could move at the rate of an estimated 1000 km in 1 million yr. If moving water is put into the mix, seed of a species could possibly move many meters in 1 yr; but many millennia of evolution likely occurred before running water played a major role in movement, so caution must be exercised in estimating the time involved for the movement of the many species of *Arachis*.

The natural distribution of the wild *Arachis* appears to have been made well before man arrived in South America, but man has obviously played an important role in distributing some of the cultivated species, including *A. villosulicarpa, A. stenosperma,* and the man-selected species, *A. hypogaea.*

The origin of the domesticated peanut is becoming clearer with new archeological data and the use of molecular tools. Our presentation does not refute information presented by Hammons (1973, 1982), and in several instances confirms his conclusions. An exact location is still not known, but some good candidates are emerging in northwest Peru and/or northwest Argentina.

Recent archeological information supports the molecular data reported by Kochert *et al.* (1991) and Halward *et al.* (1993) that *A. duranensis* and *A. ipaensis*, or species very much like these, were the probable progenitor spe-

cies of *A. hypogaea.* Additional information regarding molecular work on peanut appears in the paper by Stalker and Mozingo (2001) of this symposium series and will not be presented here.

The future will hold some interesting developments on understanding the evolution of the genus *Arachis* and the cultigen *A. hypogaea* as more molecular data are generated and the molecular techniques become more advanced. The history of distribution of *A. hypogaea* prior to Columbus' discovery of the New World remains questionable. Recent evidence from China and along the west coast of the Americas indicate there may have been visitation by ancient Chinese mariners and a growing body of evidence exists that they did take peanut and other crops back to mainland China in the first millennia A.D. (Mathews, 1983).

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