Chapter 3

Structures and Genetic Resources of Peanuts

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Seed and Seedling of A. hypogaea L.

All of the leaves and above-ground parts which the peanut seedling will have for the first 2-3 weeks of its life are already present in the dormant seed. The seed of *Arachis hypogaea* is made up of two seed leaves (cotyledons) upper stem axis and young leaf primordia (epicotyl) and lower stem axis (hypocotyl) and primary root. Hypocotyl and primary root jointly make up the radicle. The epicotyl, hypocotyl, and primary root make up the peanut "hearts" of commerce. The whole of all these structures, including the cotyledons, makes up the peanut embryo which in peanuts is straight rather than curved as in beans and peas. Thus except for the variously colored outer covering (seed coat), the peanut seed is an entire peanut plant with two of its leaves (cotyledons) stuffed with stored food and all out of proportion in size to the remaining plant parts, the whole dried down to a low moisture content and in resting or dormant state. Figure 1 shows one of the seed leaves with attached embryonic axis (heart) (Gregory *et al.,* 1951).

The morphological descriptions of the growth and development of the seedling follow those of Bouffil (1947), Yarbrough (1949), Prevot (1950), and Yarbrough (1957a,b). Isolated papers dealing with specialized investigations in plant nutrition,

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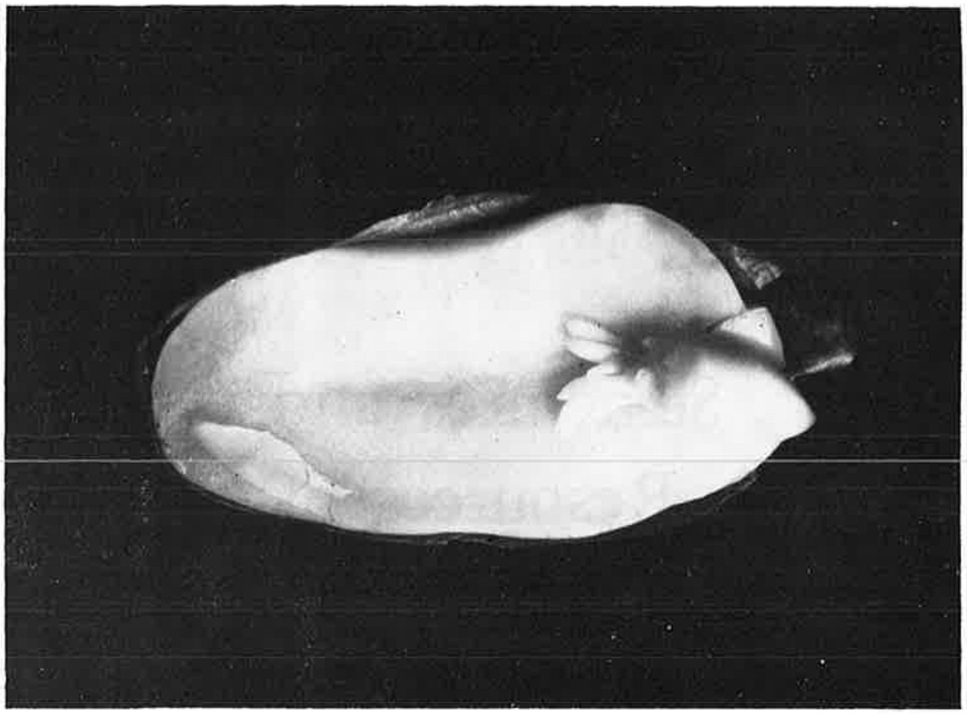

Figure 1. Peanut seed with one cotyledon removed revealing the plumule and radicle of the young peanut plant (after Gregory *et al.,* 1951).

pathology or physiology, which refer to developing structures in the peanut plant, will be found in references in other chapters of this volume.

Petit (1895) observed that the outer layers of the primary root of a peanut seedling slough off as the growth of the root proceeds. Thus the structural base for root hairs is destroyed in peanuts. Petit noted that the peanut seedling lacked root hairs. Richter (1899) confirmed Petit's observations. However, under certain conditions, root hairs may form (Waldron, 1919; Reed, 1924; Badami, 1935). The primary root elongates rapidly upon germination of the seed, reaching 4-5 inches before lateral roots begin to appear (Figure 2). Yarbrough (1949) cites Bruner (1932) as having observed peanut roots to a depth of 3-4 feet. Yarbrough measured root systems up to 20 inches in length in sand on plants a little over one month of age. He also observed tap roots 12 inches in length in seedlings 11 1/2 days old (Figure 3). Some of the lateral roots (100-116 in number) in the same seedlings had lengths as great as 7 inches. Yarbrough's peanuts were Virginia Bunch, alternate type. Bouffil (1947) illustrated the germinating seedling through successive stages of its development as did Prévot (1950). Bouffil's illustrations were probably of alternate type (African), while Prévot's may have been sequential, at any rate, varieties "la rose Loudima" and "la rouge Loudima."

Yarbrough (1949) described the internal structural organization of the primary root. By showing the exact point where the epidermis of the hypocotyl gives way to the sloughing outer layer of root cells, he was able to establish the precise external beginning point of transition from stem to root as approximately the center of the "collar" at the base of the hypocotyl (Figure 2). Microscopic examination further showed transition to be completed through 4-5 mm down into the primary root. The

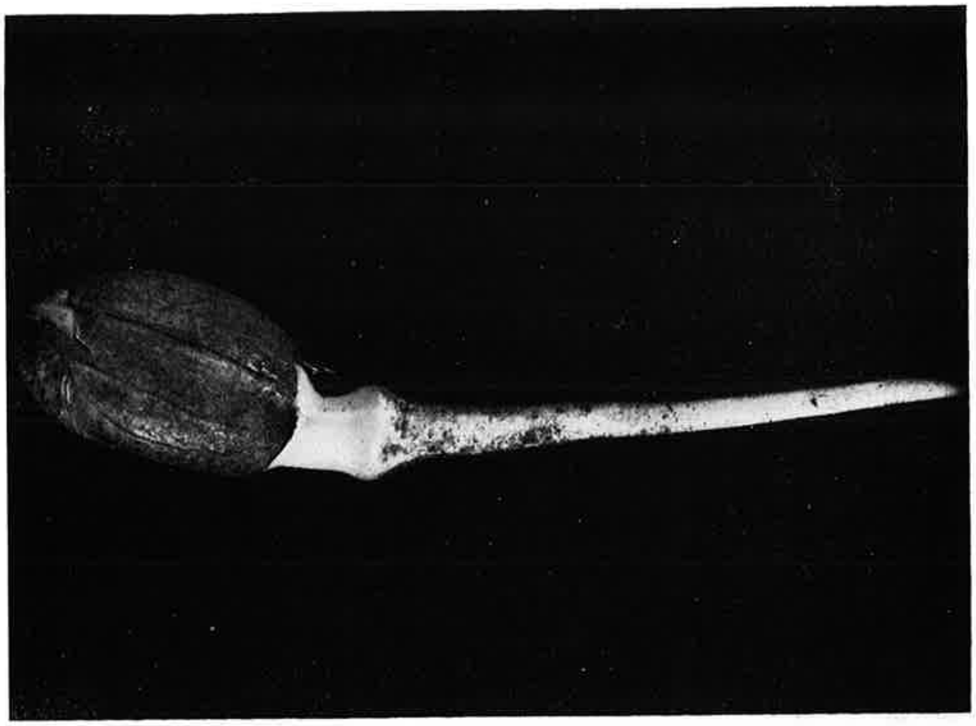

Figure 2. Germinating peanut seed. Note the prominent collar and the clearly marked union of stem (hypocotyl) and primary root with soil clinging (after Yarbrough, 1949).

endodermis and pericycle of the root extend up through the transition zone into the lower hypocotyl. During the first hours of germination, the radicle consists of about half hypocotyl and half primary root. In practice, the relative lengths of hypocotyl and primary root depend upon depth of seeding. It is the elongation of the hypocotyl which pushes the cotyledonary node and the young epicotyl to the surface of the soil [Bouffil (Figure 1), 1947]. With increasing depth of planting and increasing length of hypocotyl, there is a corresponding shortening of the primary root until at from 15-20 cm of depth of seeding there may be no primary root development whatever. In *A. monticola* [see Krapovickas and Rigoni (Figure 1), 1960], in artificial cultures, fruit set may occur on the plough sole, thus requiring extensive hypocotyl elongation.

Figures 4 and 5 illustrate the basic microscopical anatomy of the young primary root. These figures show the massive root cap, the root initial cells generating root proximally and root cap distally, the development of the stele and young vascular tissues, cortex and meristematic ring or sleeve just underneath the sloughing cells of the root exterior. The 4-partite organization of the vascular tissues corresponds to the 4-spirally arranged lines of secondary roots. Yarbrough (1949) repeated Richter's (1899) dye experiment to test the absorbing capabilities of the external sloughing layer of cells and found concentration of the dye in the hypodermal region of small, meristematically active cells indicated in his Figure 14 (Figure 5).

The lateral roots are diarch in contrast to the tetrarch primary root. They are without pith but otherwise are similar to the primary root.

The hypocotyl, as the name implies, is that portion of stem which lies between the primary root and the first leaf, one of the cotyledons. Reference in the literature to

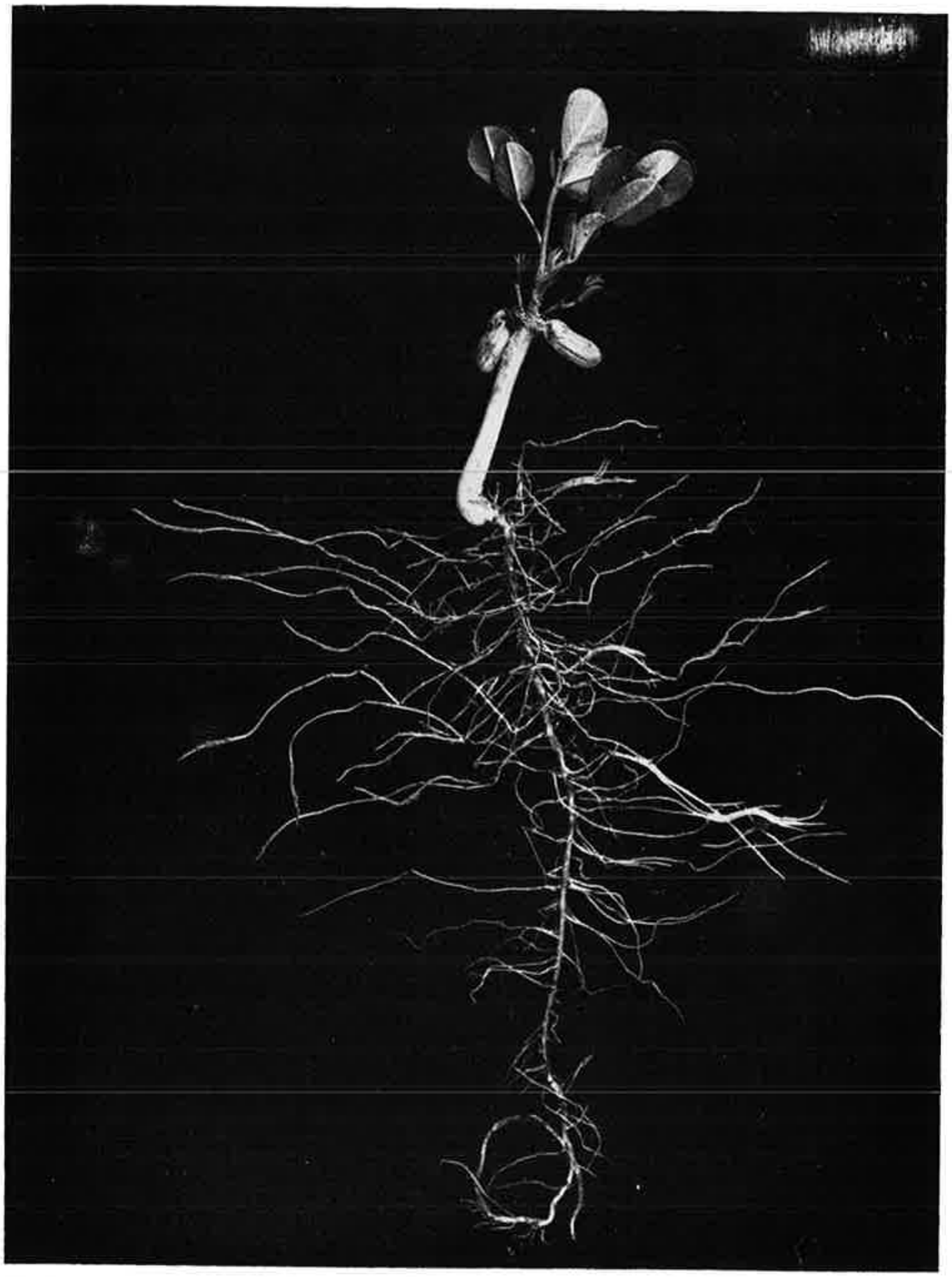

Figure 3. Young peanut seedling 11 1/2 days old (after Yarbrough, 1949).

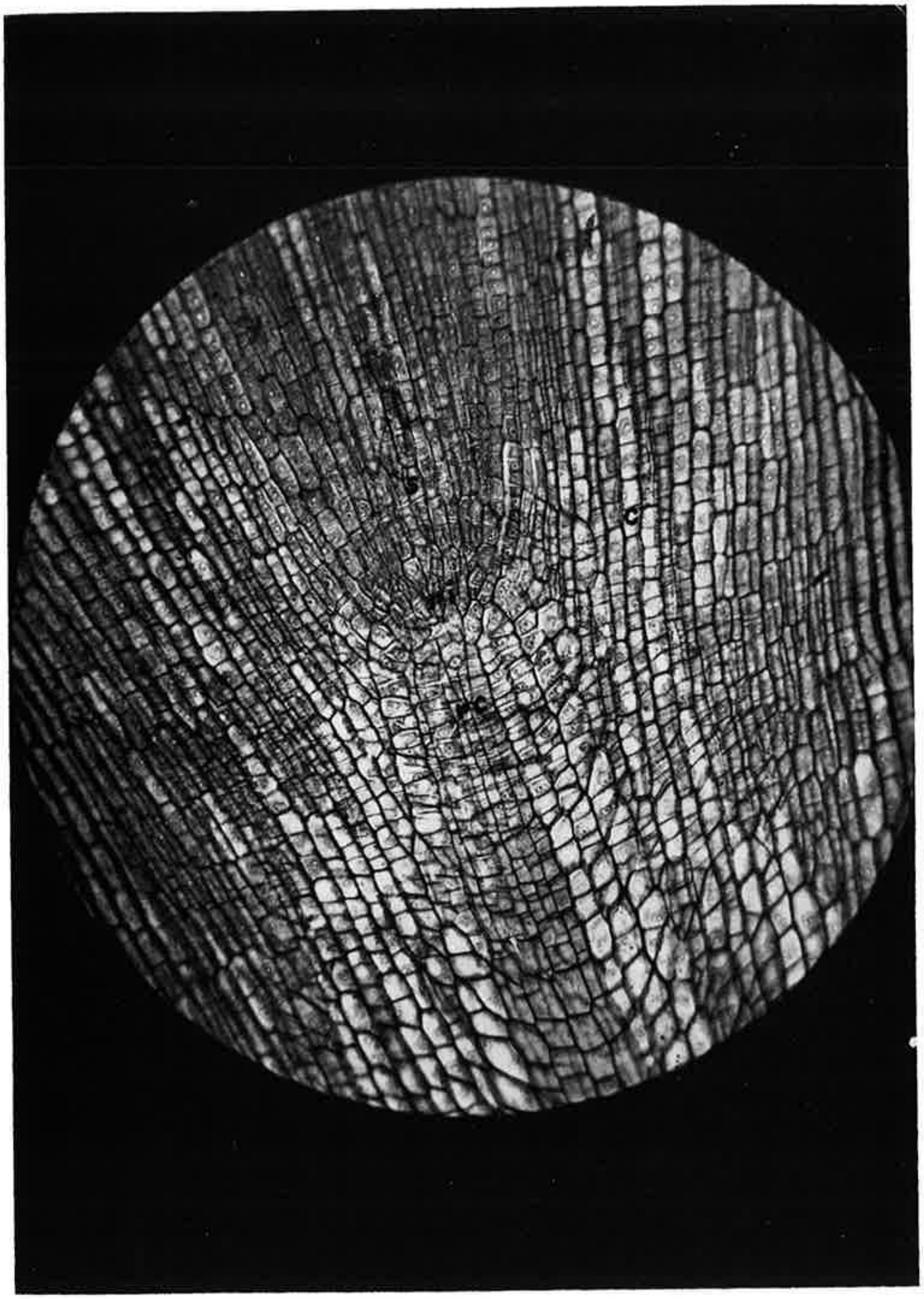

Figure 4. Longitudinal section through the tip of the primary root of a young peanut seedling showing the root initials generating root (proximally) and root cap (distally); s, stele; c, cortex; ri, root initials; rc, root cap (after Yarbrough, 1949).

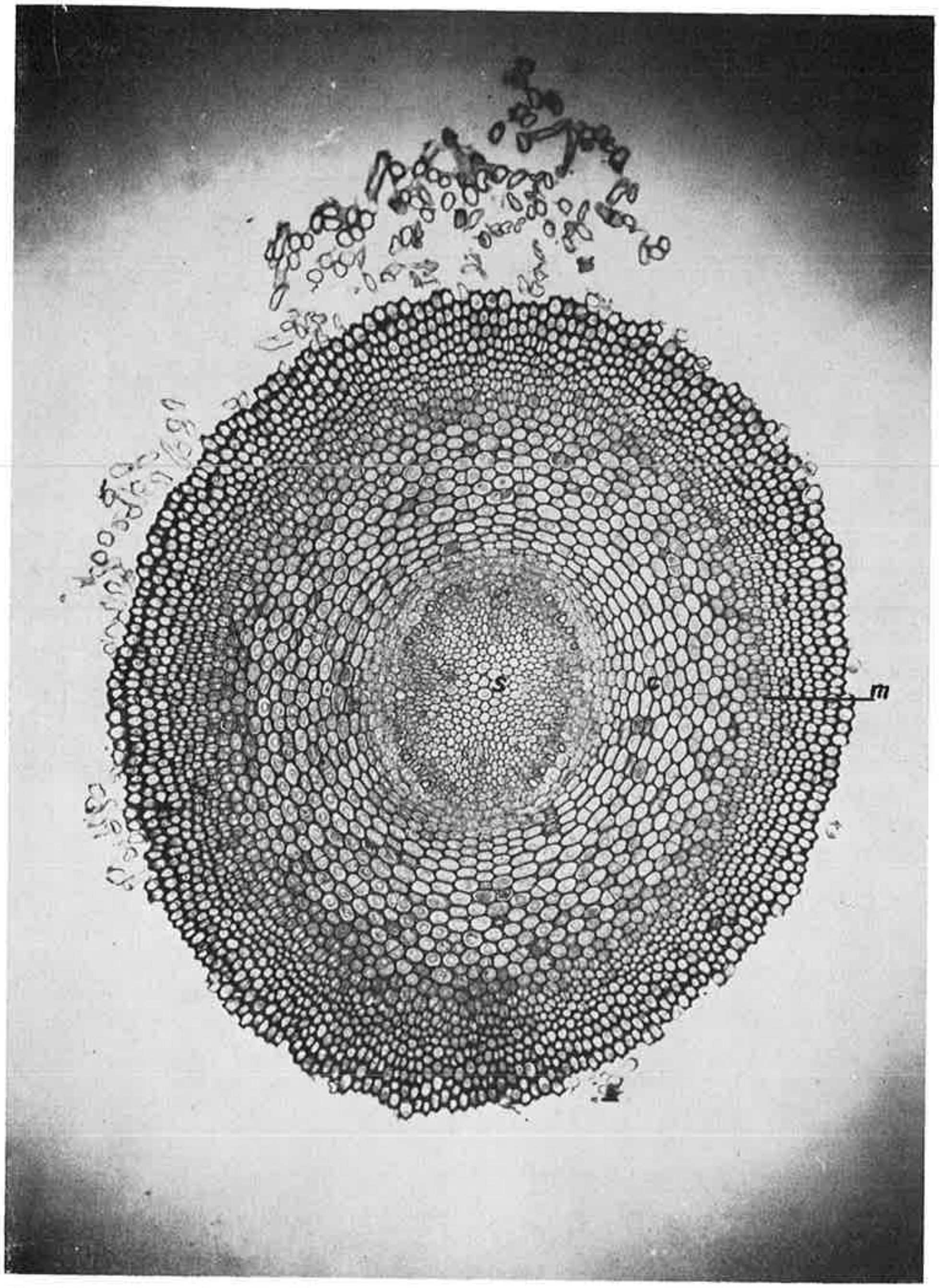

Figure 5. Cross section of primary root of peanut seedling about 2 mm back of tip; c, cortex; s, stele; m, meristematic zone. Note loose cellular organization of outer layer showing no epidermis (after Yarbrough, 1949).

the "cotyledonary node" is a misnomer since there are in fact two cotyledonary nodes in alternate positions characteristic of the rest of the leaf-bearing nodes of the stem. These offset positions of the cotyledons can easily be seen in seedlings grown in the dark or from deeply planted seed. The cotyledonary branches usually begin growth at slightly different times, the basal one first, followed closely by the next. Often a difference in size and sometimes in other characters may be seen to accompany this time discrepance.

The young hypocotyl is a very succulent structure up to 1 cm in diameter with a large cortex surrounding a small central cylinder 1.5 to 3 mm in diameter. Yarbrough has discussed the significance of the cortex as a way station and transport medium for the extensive movement of food materials from the cotyledons to the expanding root system of the young seedling. Even in the dormant seed the hypocotylar tissue is charged with stored concentrates. Conducting strands in the lower hypocotyl, the central elliptic cylindric stele, are continuous with conducting strands in the primary root which upward bifurcate into two large strands in each cotyledon. Numerous other conducting elements pass the cotyledons and enter the epicotyl. As the central conducting cylinder increases in size, its central pith breaks down. Simultaneously, the stored products of the cotyledons disappear and the cortex of the hypocotyl begins to collapse. Eventually the cortex disintegrates and the cylinder of cork cambium and outer sloughing tissues is complete from root to cotyledon. The central cylinder grows, becomes woody, and, in alternate branching forms, takes on diameters of up to 3/4 of an inch or more. It is this structure that the farmers refer to when they speak of cutting the tap root during harvesting, and it is this structure with its crown of adventitious buds around the cotyledonary nodes which provides the basis for the perennial habit in some of the wild axonomorphic relatives of peanuts.

The epicotyl consists of three major branches, the mainstem and the two cotyledonary axes. All vegetative axes arising from the main axis are characterized by the presence of scale leaves called cataphylls subtending the first two nodes of the stem. According to Yarbrough (1957a), the first nodes of all vegetative axes, except the mainstem in *A. hypogaea,* are subtended by cataphylls. It is tempting to think of the two cotyledons as being only highly specialized cataphylls subtending as they do the first two nodes of the main axis, thus making complete the essential identity of all vegetative axes of this species. However, the main axis is distinctive in other ways, having its leaves spirally arranged in a 2/5 phyllotaxy *vs* the distichous arrangement of leaves on $n + 1$ vegetative axes (Yarbrough, 1957a; Krapovickas and Rigoni, 1960). In alternate types, $n + 1$ reproductive axes are not usually formed (Gregory *et al.,* 1951; Bunting, 1955). The main axis appears to exert no dominant influence over the sprouting of the cotyledonary and other axillary buds. In fact, quite the contrary seems to occur in spreading alternate types where few additional axillaries appear above the cotyledonary axes which make almost the whole plant in these types. Furthermore, in these varieties, the mainstem usually is somewhat reduced (Yarbrough, 1957a). Harvey and Schultz (1943) and Gregory *et al.* (1951) observed that the prostrate polarity of the cotyledonary branches is maintained even after the tips are excised and rooted independently. In erect types (alternate or sequential), the growth in length of the $n + 1$ and n branches is approximately the same.

The leaves of peanuts are 4-foliolate and are not dissimilar to other dicotyledonous leaves in the anatomy of their laminae and petioles. Detailed descriptions of these structures may be found in Yarbrough (1957a). Earlier work by Reed (1924) reported similar results (see also Waldron, 1919; Badami, 1935). With regard to surface features, Yarbrough states, "In my observations stomates averaged about 150-175 per square mm." This is in striking contrast with the figure of 15-20 per square mm given by Waldron (1919).

The internal structure of the peanut stem is described in Yarbrough (1957b). Yarbrough points out its unique features and illustrates its vascular anatomy. The branching organization of the different sub-species and varieties of *A. hypogaea,* alluded to again in the discussion of the morphological basis for the classification of the various types of the cultivated peanut, is distinguished by two basic kinds of branches, reproductive and vegetative. The reproductive axis or inflorescence is in fact a reduced and telescoped replica of the ordinary vegetative branch designed to perform the special function of producing flowers and fruits. Kurtz (1875) described the peanut inflorescence as 2-3 flowered. Richter (1899) described the inflorescence as an axillary head or compressed spike with a 2/5 phyllotaxy of its reduced scale leaves and bracts similar to that of the mainstem of the vegetative axis. Reproductive branches occur normally as axillary shoots in both cataphyllar and ordinary leaf axils. The typical inflorescence or reproductive branch is schematically illustrated in Figure 6. As can be seen from the figure, short side (axillary) branches develop in the axils of the simple bracts which occur along the central axis of the inflorescence much as the leaves occur along an ordinary branch. These axillary branches of the inflorescence normally terminate after the production of one leaf, the bifid bract, in the axil of which the flower is borne. The terminal bud of this axillary, represented in *A. hypogaea hypogaea* and in *A. hypogaea fastigiata fastigiata* by a tuft of reduced scales, may grow and produce compound inflorescences in *A. hypogaea fastigiata vulgaris* varieties. The inflorescence never occurs in the same leaf axil as a vegetative branch (even though it may appear to when arising in the cataphyllar nodes of such a branch) and form with the latter the branching patterns characteristic of the sub-taxons of *A. hypogaea* (Gregory *et al.,* 1951). The internodes of the inflorescence may elongate subsequent to flowering, producing a much expanded fruiting structure. Occasionally the terminal bud of the inflorescence will revert to vegetative phase giving rise to what we have called reproductive-vegetative axes.

Flower and Fruit

The uniqueness and strangeness of flower and fruit in peanuts have led to much botanical confusion about their relationship in past times. This story, told by Smith, partly in Gregory *et al.,* (1951), but more fully in Smith (1950), finally clarified, in detailed sketches, the relationship of flower to fruit in peanuts. Excerpts with interspersed comment by the authors are repeated here verbatim from Smith's "Discussion: Aerial flower, subterranean fruit" *et seq:* "That Marggraf (1648) should have described and figured *Arachis* with the pods attached to the root system is understandable;" [but that Hoehne (1940) and Poehlman (1969) should figure them as arising from the stem and leaf rachis must be regarded as carelessness]. "Ray (1636) and Sloane (1696) appreciated the leguminous nature of the plant. Sloane cited pre-Linnean literature comprehensively. Linnaeus (1737) coined the name *Arachis* from *Arachidna* of earlier authors and included *A. hypogaea* in *Species Plantarum* (1753). Linnaeus apparently mistook the thickened style in the region of the staminal tube for the ovary *(Germen oblongum,* 1764) but said nothing of the relation of flower to fruit. Jussieu (1789) mentions many male flowers as did the various editors of Linnaeus' works (Kurtz, 1875). The showy flowers were thought to be functionally male and sterile; naked female flowers (actually pegs), more abundant in the lower axils, produced the fruits. By 1800, systematists generally accepted the existence of sexually dimorphic flowers in *Arachis.*"

Figure 6. Schematic diagram of peanut inflorescence following fruit set at its first three nodes; (b) simple bract subtending a floral branch; (f) bifid bract subtending the flower; (p) peg (after Gregory *et al.,* 1951).

"Poiteau (1806) described in 1802 before l'Institut de France the relation of flower to fruit in *Arachis* much as we understand it today . . . He insisted, correctly, that all the flowers of *Arachis* are hermaphroditic and fertile." Smith's own flower removal experiments (1954) clearly demonstrated that when the yellow showy flowers were removed, no fruits developed. This in itself did not rule out possible post pollination parthenogenesis in *Arachis* but the later extensive examinations of the embryo sac by Smith did not disclose any evidence of such behavior, nor do genetic studies support any but typical sexual reproduction for the cultivated peanut. The work of Poiteau was followed by recognition (Richard, 1823). Nevertheless, Smith goes on to show how errors committed by the scientifically prominent can overshadow the correct work of other men, even handing them down to their prominent successors. For example, Smith continues, "Aware of Poiteau's work, Bentham (1839)" (actually 1841) "ignored it when he came to write new generic characters . . . . . Bentham concluded for *Arachis:* 'The perfect flowers . . . . . have indeed a perfect ovarium with two or three ovules, but I have always observed it to fall off with the calyx, and the legumes, as far as I am able to ascertain from dried specimens of several species in various states, arise constantly from female flowers of a very different structure. These have neither calyx, corolla, nor stamina . . . . . ' " Of course, Bentham was describing the peg which normally begins its elongation several days after the ephemeral flower has wilted and has sometimes fallen away. By the time the peg is visibly exerted from between the two scale leaves subtending the flowering branch and flower, the floral parts may be lost. Corrections were quickly in order (Hasskarl, 1842, 1858; Poiteau's reiteration, 1853; and Neisler, 1855). Bentham, himself, after stoutly defending sexual dimorphism in *Arachis* (1855), retracted his error (Gray, 1856). Nevertheless, the deed was done. Smith's description follows: "Corbett perpetuated the concept of floral dimorphism in *Arachis* (Bailey, 1907). His contribution has been edited so it now includes a more ancient error (Bailey, 1944): 'The roots with the nuts attached are placed next to the stake . . . ' . . . . . (Taylor, 1948): 'Flowers of two kinds: one showy, yellow pea-like and sterile; the others also yellow but fertile' . . . . . Bailey (1924 reprinted 1938) stated in the MANUAL OF CULTIVATED PLANTS: '*A. hypogaea* L. PEANUT . . . . . showy flowers, yellow and sterile, soon withering, fertile flowers on stout recurving stipes without envelopes, soon entering the ground . . . . .' " Smith cites many similar instances in prominent works and indicates that there are many more which he did not cite.

Another kind of floral dimorphism in *A. hypogaea* persists in the literature; *i.e.,* showy aerial flowers and cleistogamous underground flowers with abnormal floral envelopes (Meisner, 1836; Kurtz, 1875; Richter, 1899; Theune, 1916; Bouffil, 1947). Smith (1950) points out that all of these observations are based upon abnormal cultural conditions, either low temperatures, high latitudes, or "the environment created by the farmer's plow." So far as we can ascertain at present, Smith's conclusions that subterranean flowers are absent naturally in *A. hypogaea* may be correct. They certainly do not include members of *Arachis* species, section Rhizomatosae, where we have photographed underground but not cleistogamous flowers on the rhizomes, nor *Arachis guaranitica,* section Erectoides, the flowers of which normally arise below the soil surface, thrusting the corolla and calyx tube into the air but developing the fruit totally underground, or the unusual case of inflorescence development on the pegs 4-5 inches below ground in *A. tuberosa,* also section Erectoides, when the original ovules are accidentally destroyed.

The peanut flower has been illustrated in various works, but the two most satisfying sketches are shown in Bouffil (1947) and Smith (1950). As can be seen from the sketches shown in Figure 7, the typically papilionaceous floral envelope is inserted at the top of the hypanthium surrounding the staminal column. The calyx is 5-lobed, one lobe separate and opposite the keel, the other four fused except for their tips and

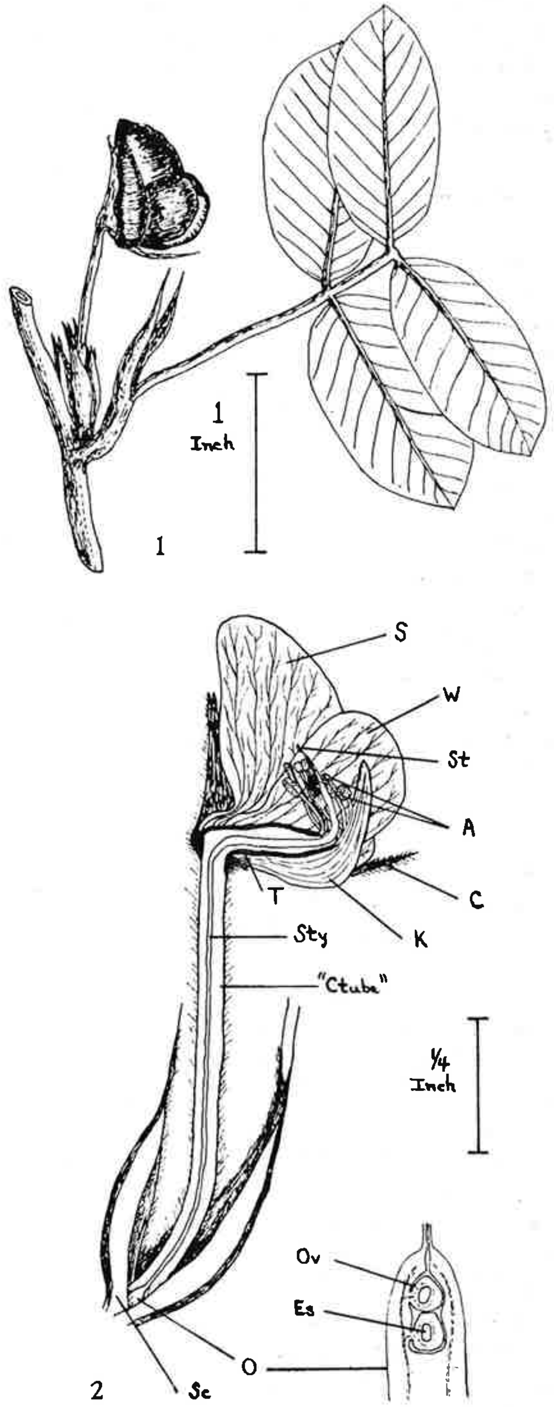

Figure 7. Showing inflorescence with flower in leaf axil (1) and longitudinal schematic drawing of peanut flower (2); S, standard; W, wing; K, keel; C, lower lip of the calyx; Ctube, hypanthium ("calyx tube"); Sc, cataphyll-like bracts; St, stigma; A, anthers; below, the filaments are fused forming a fleshy staminal tube; T, fleshy staminal tube; Sty, style; O, ovary; Ov, ovule; Es, embryo sac (bracts, keel and stamens somewhat displaced for clarity) (after Smith, 1950).

back of the standard. The keel is somewhat hyaline, almost colorless, and closely embraces the stamens and style. The wings are usually a uniform yellow but occasionally marked by a diffuse band of somewhat deeper yellow or orange across the distal portion. The standard is orange with yellow central and basal area, marked variously on its inner face by red veins. Sometimes the red color is prominent enough to make the flowers appear burnt orange to orange red in color. The size of the flowers varies with the conditions under which they are produced, but normal flowers under good conditions are about 4 to 5 cm in length and the standards are 10-21 mm wide and 8-14 mm high. Each wing is about 1/4 the width of the standard, but about the same length. The keel is even more narrow proportionately (Figure 8). The explanations accompanying Figure 8 tell the rest of the story, showing the small ovary at the base of the style and the curved style passing through the flower among the eight anthers, four globose, dorsifixed, uniloculate alternating with four adnate introrse oblong, three of which are biloculate and one, opposite the standard, uniloculate. There are normally two sterile filaments (Smith, 1950), but there are occasionally nine and sometimes 10 anthers (Maeda, 1961). The relationship of the young peg and the wilted flower is graphically illustrated.

The flowers and fruits of other species deviate considerably in size, orientation, color and markings from *A. hypogaea,* but their basic morphology is essentially the same. Many of the problems that beset the early history of *A. hypogaea* must be resolved for each of its related species.

During and after World War II, it became apparent that the world-wide yields of peanuts attained levels of approximately 1200 lbs/acre. It appeared that a base genetic capability was being expressed under some universal environmental restriction. It was also obvious that flowering was abundant, perhaps more abundant, under low-yielding conditions than otherwise. Under poor environmental conditions of climate and latitude, flowering and growth were greatly affected. These conditions have given rise to a number of studies designed to explore the ontogeny and ecology of flowering in *A. hypogaea,* with a view to its experimental control. Some of the earliest of these were Umen (1933), Shibuya (1935), Bouffil (1947), Bouyer (1949), Prevot (1950), and Smith (1954). These have been followed more recently by Fortanier (1954, 1957), Tétényi (1957a, b), Bolhuis (1958-59), Bolhuis and de Groot (1959), De Beer (1963), Gupton and Emery (1968), and Nicholaides *et al.* (1969). Wood (1968) had available environmental controls of a phytotron with correspondingly more nearly perfect control of variables and constants of the environment. All of these works are directed essentially at discovering those environmental stimuli which promote differences in what one might refer to as the normal progression of flowering. Of course, we already knew that external conditions in the extreme affected the quantitative as well as the qualitative aspects of flowering. If the temperature was too low, flowering slowed down, styles remained recessed (Richter, 1899), and if the temperatures were too high, fertility and growth were reduced.

We had also observed that unknown, but very real, environmental factors associated with the normal ontogeny and maturation of the plant, accentuated or modified by varietal differences, could transform reproductive axes into vegetative axes. The converse which happens in numerous racemose day-sensitive herbaceous perennials, giving rise to terminal spicate inflorescences, has never been observed to occur in peanuts. This, despite the fact that its close relative *Stylosanthes* tends to develop capitate spicate inflorescences terminally. The only peanut which we have observed to approximate the situation in *Stylosanthes* was a class of X-ray-induced mutants which we

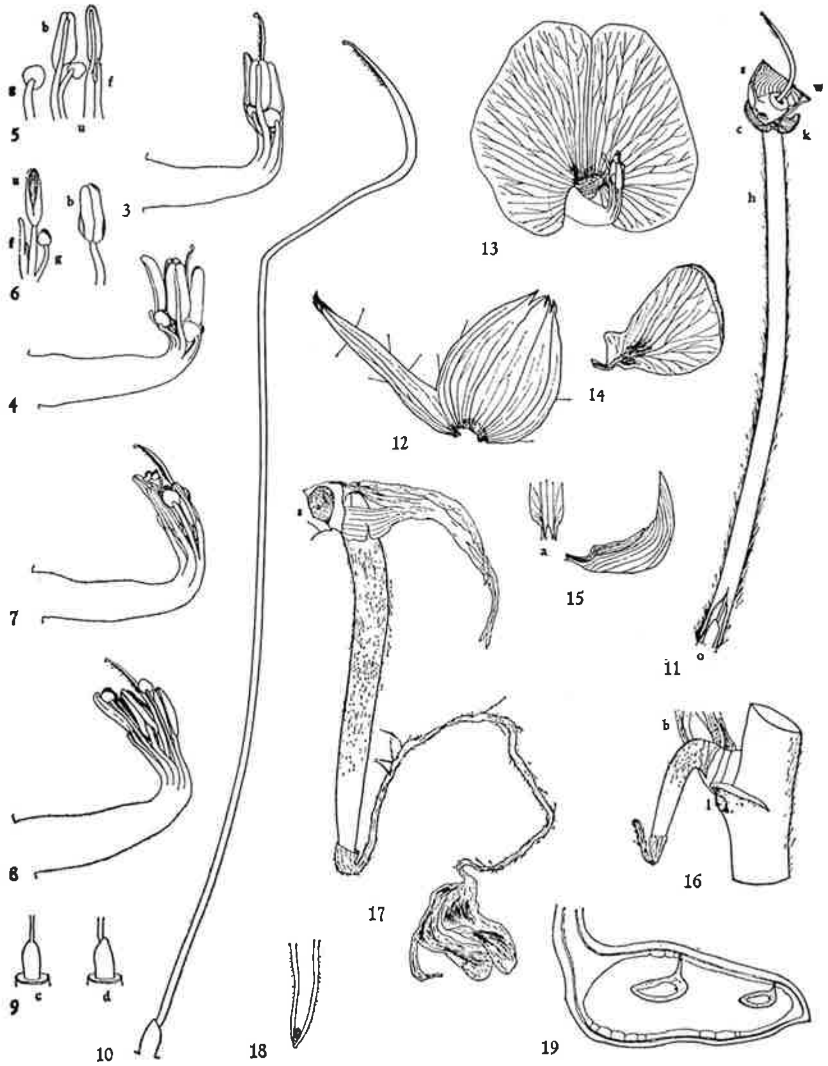

Figure 8. The reproductive structures of *Arachis hypogaea* L. (3) androecium in relation to style and stigma, 12 hours before anthesis (7:00 p.m.); (4) androecium at the time of anthesis (7:00 a.m.); (5-6) the four stamen types; g, with globose anther, dorsifixed; b, with biloculate, oblong anther, adnate, introrse; u, with uniloculate, oblong anther, adnate, introrse; f, the two sterile filaments (5, dorsal; 6, ventral at time of dehiscence); (7) androecium shortly after pollination (9:30 a.m.); (8) androecium several hours after pollination (11:30 a.m.), filament elongation complete; (9) ovary and base of style; c, dorsal view; d, side view; (10) gynoecium at time of anthesis; (11) flower, dissected to show insertion of parts; o, ovary; h, tubular hypanthium; c, calyx; s, standard; w, wing; k, keel; (12) bilabiate calyx, inferior lobe to left, five major veins; (13) notched standard in relation to androecium; (14) wing; (15) keel; a, base of keel with the four major veins; (16) early peg showing geotropic bend, base of hypanthium adhering to the tip; b, remaining buds of the same inflorescence; l, leaf and stipule scars; (17) later stage in aerial peg elongation with subtending bracts, marcescent flower still adhering to the peg tip; s, position of an earlier peg of same inflorescence which has been cut away; (18) apex of aerial peg (*cf.* 16, 17), median longitudinal section showing relative size and position of the ovules; (19) median longitudinal section of early stage in fruit development about one month after anthesis (camera lucida drawings) (after Smith, 1950).

named "Stylosanthine" because of the highly brachytic terminal nodes of its branches and the clustered inflorescences therein. We also noted that normal peanuts sometimes develop similar characteristics when severely attacked by leafhoppers. However, none of these variants assumed the complete conversion to terminal inflorescences in the sense that the reproductive axes were observed to convert to vegetative axes.

One cannot but suspect that the commitment to geocarpy and its concomitant and successive biological reinforcements driving the flowering process proximally against the "current," so to speak, of the natural vegetative ontogeny, common to plants generally, has been responsible for this inverted state of reproductivity in peanuts. Notwithstanding the natural lag in flower production at the beginning of the life of every peanut plant, Bouffil's "progression lente," there is no true juvenile phase in the peanut comparable to the vegetative phase of other plants. In the sequential types, Van Rossem and Bolhuis (1954) reported that flowers with their essential parts were in fact preformed in the seed.

The natural tendency appears to have been to compromise the forces loosed by the geocarpic commitment, where evolution should proceed from vegetative to reproductive on the lower nodes, and from bearing vegetative axes continuously to bearing reproductive axes continuously. The only peanut we know that has not compromised with these forces is *A. guaranitica* which, in plants of one year, consists of a single central vegetative axis, the lateral buds of which are all suppressed except the cotyledonary laterals which are completely telescoped into fully reproductive axes beneath the soil and consist solely of flower-bearing nodes subtended by bracts forming a collar surrounding the single central stalk just above the cotyledons. The extreme sequential varieties of *A. hypogaea* are seen to continue to subvert this reproductive tendency by the loss of control over the tips of the older reproductive axes through their conversion to reproductive-vegetative branches. In the alternate types, a balanced compromise appears to have been reached in the tendency for successive pairs of vegetative and reproductive axes. In another section of the genus, Rhizomatosae, the escape to vegetatism has been to bypass the need to produce seed in abundance. In another, the Extranervosae, shoots occur in conjunction with the peg itself. Only in the replete reproductive section containing *A. guaranitica* have adventitious inflorescenses been seen on the pegs. It is as though the natural thrust to produce vegetative shoots were breaking out in its struggle against the proximal movement of flowering necessitated by the geocarpic commitment and those environmental forces which made its adoption an advantage, the breaking out of the vegetative state at the tips of inflorescences, the conversion to rhizomatous habit, the bursting of shoots from pegs and roots of Extranervosae, and shoots from the roots of Tetrafoliolatae. It is to this problem that the modifier of environmental variables is addressing himself with respect to the initiation and progression of flowering in the peanut.

The normal course of flowering was determined by Shibuya (1935), Bouffil (1947), and Smith (1954) by counting the flowers appearing on a number of plants by days throughout the season. Bolhuis (1958a) and Tétényi (1957b) also counted the daily production of flowers. The kinds of results obtained by these investigations are illustrated in Figure 9. Smith (1954) showed that the total production of flowers was increased tremendously by keeping the fruits removed. This was corroborated by Bolhuis (1958b, 1959a). It is obvious that fruit setting affected the production of flowering and that even the fact of fertilization had such effects. Bouffil (1947), Smith (1950), and Bolhuis (1958a) all noticed the large variations in flowers per day and ascribed this periodicity to some internal rhythm in the plants. Smith noted that flower production was much affected by changes in temperature, but still concluded that within the "normal" range of environments, the periodicity in flowering was little affected. Bouffil and Bolhuis both reached Smith's conclusion that the environment had little to do with the periodicity of flowering in peanuts. Nicholaides *et al.* (1969), however, showed that a delayed reaction (2-3 days) to low temperature was expressed sharply in reduced flowering. Weather cycles passing over the culture area with a periodicity of several days would thus be reflected in flowering periodicity. Nicholaides *et al.* noted that there was a temperature-independent component of flowering periodicity and concluded that some internal factors were contributing to the periods. This observation is not unexpected since Bouffil's observations at M'Bambey station and Bolhuis' observations at Buitenzorg would not be accompanied by any marked weather cycle phenomena. This was brought out by Tardieu (1954) in Senegal who found only weak effects of the weather.

Nevertheless, there are obvious temperature extremes which will adversely affect flowering, the metabolism of the plant, and the set of fruit. Somewhere between these extremes lies a temperature or small range of temperatures under which flowering or fruiting of a given variety will be best. Appropriate measurements and standards of temperature relative to production could conceivably be utilized in strain selection and cultural management of peanut crops throughout areas where they are grown, or in the case of nonadaptive areas, as an aide in the discovery of types and cultural practices suited to adverse conditions.

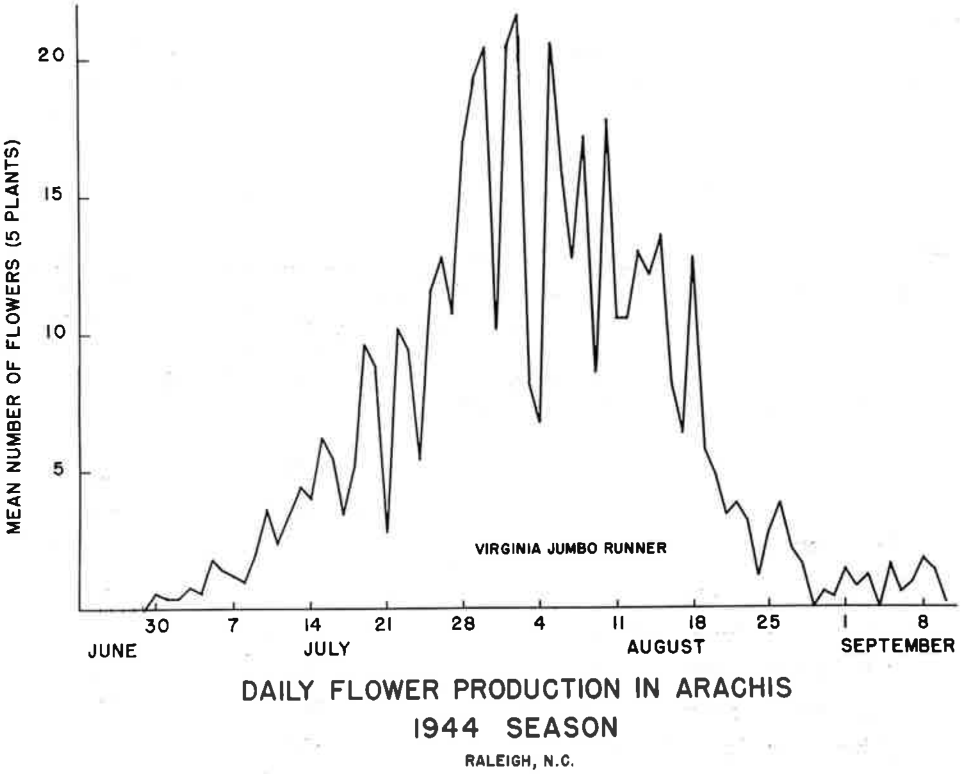

Figure 9. Frequency distribution of mean number of flowers per day (after Smith, 1954).

We will now review some of the efforts which have been made along these lines in the future of which the phytotron as an instrument of research will provide highly precise situations under which the behavior of growth, flowering, and fruiting may be observed. Jacobs (1951b) reported one of the early temperature-controlled experiments conducted on peanuts. He found that the first flower on a Valencia variety appeared after about 6 weeks (early September to October 17) on a 26°C day 30°C night treatment. However, by November 7 the 26°C day and 27°C night treatments had an average of 4 pegs per plant compared to 1 peg per plant for 26°C day 30°C night treatment. No flowers ever appeared on the 18°C day 16°C night plants. A few flowers appeared on 18°C day 22°C night plants, but no pegs. Fortanier (1954) showed that flower elongation and opening were light-dependent, in the latter case wave-length-dependent (white and blue light). He also showed that the time of opening of the flower was regulated by a light stimulus received by the bud three days earlier. In 1957, he showed that the initiation of flowers was independent of photoperiodism as well as thermoperiodism. Since flower bud initiation, at least in the sequential types, may have already taken place in the seed, it may well be that Fortanier's treatments were *ex post facto.* He indicated that numbers of flowers produced and the number open at any given time could be brought under control, at least under laboratory conditions. With night temperatures held to 20°C, a daytime temperature of 30°C was optimum. A temperature of 35°C resulted in greater stem elongation but 40°C reduced growth as much as the low temperature of 15°C. A rise in night temperature to 35°C increased stem elongation remarkably in all daytime temperature treatments. At 40°C daytime and 35°C night, no flowers opened (Fortanier, 1957).

With respect to the influence of daylength, one of the earliest efforts made was that of Umen (1933) who concluded that the peanut was photoperiod-insensitive under constant temperatures but showed light period sensitivity under variable temperatures. Tétényi (1957a,b), on the other hand, cites Tshelyadynova and Masyuk as having shown that a 10-hour day in contrast to a 14-hour day hastened the onset of flowering and increased crop weight per plant. He suggested from his own experiments that such a photosensitivity lasts only a short while, 6 days, and is temperature-dependent.

> Alegre (1957) conducted a daylength temperature interaction experiment with peanuts in the environment of Paris. He treated the peanuts with daylength of 9 hours and natural daylength (approximately 15 hours) and 3 temperatures for each light period for a total of six treatments. He recorded cumulative total flowers produced under each treatment from May 25 until September 5. His results were as follows:

Treatments	$\overline{X}$ temperature °C	Mean No. flowers per plant
15 hrs warm at night, ambient in day	17-20	172
15 hrs warm day and night	22-25	171
15 hrs ambient day and night	13-15	13
9 hrs warm at night, ambient in day	19-21	157
9 hrs warm day and night	25-27	87
9 hrs ambient day and night	15-16	48

Alegre also showed remarkable effects on the seasonal distribution of flower production for the different treatments. In a later study, Bolhuis and de Groot (1959) reported varietal differences in the temperature response of flowering. They studied three varieties — Schwarz 21, Mallorca, and Ukraine — adapted to Indonesia 6°-7° South, Mallorca 39° North, and Kiev 51° North, respectively. The following were taken from their Table 2 (p. 319):

	Number of days from date of sowing to flowering		
Temps.	Schwarz 21	Mallorca	Ukraine
21°C	Never flowered	81	Never flowered
24°C	64	48	42
27°C	42	31	32
30°C	33	24	27
33°C	51	30	24

De Beer (1963) reported the following results on the same three varieties for days to first flower:

Temps.	Schwarz 21	Mallorca	Ukraine
24°C	35	32	34
28°C	28	25	26
33°C	25	43	25

Bolhuis and de Groot (1959) and de Beer (1963) obtained similar results on flowers per day for Mallorca, but de Beer indicated high production in Schwarz 21 and Ukraine in contrast to the depressing effect of 33°C in Schwarz 21 and Ukraine reported by Bolhuis and de Groot. De Beer makes no effort to explain the obvious discrepancies in these two sets of data. His contention that at 33°C, flowering is continuous and indefinite and that this somehow negates the notion of a bell-shaped flowering curve resulted almost surely from the fact that at 33°C, practically no fruits were formed in Schwarz 21, none were formed in Mallorca, and virtually none in Ukraine. Smith (1954) and Bolhuis (1958b, 1959a,b) had already shown that flowering tends to become continuous when fertilization is prevented.

Wood (1968), reporting on phytotron-grown peanuts, showed that with a constant night temperature of 25°C, flowers per plant by days were successively depressed during the treatment period 34-47 days after sowing, beginning with a daylight temperature of 20°C and proceeding to 25°C, 30°C, and 35°C. The depressed condition persisted after the treatments were withdrawn. The data on constant day temperatures of 30°C and variable night temperatures of 20°C, 25°C, 30°C, and 35°C were not consistent. Just at the end of the treatment period, the flowers per plant, as might have been expected, were in decreasing order as follows: 20°C, 25°C, 30°C, and 35°C. After the treatments were discontinued, the 20°C and 30°C treatments recovered almost the pretreatment rate, but the 25°C (take note) and 35°C treatments remained depressed.

Tétényi concluded that there was no direct relation between the progression of flowering and ultimate fruit production (cf. Shear and Miller, 1955). Shear and Miller showed that the peanut plant quickly restores the number of fruits it will bear in case fruits are artificially removed. Thus it appears that the over-production of

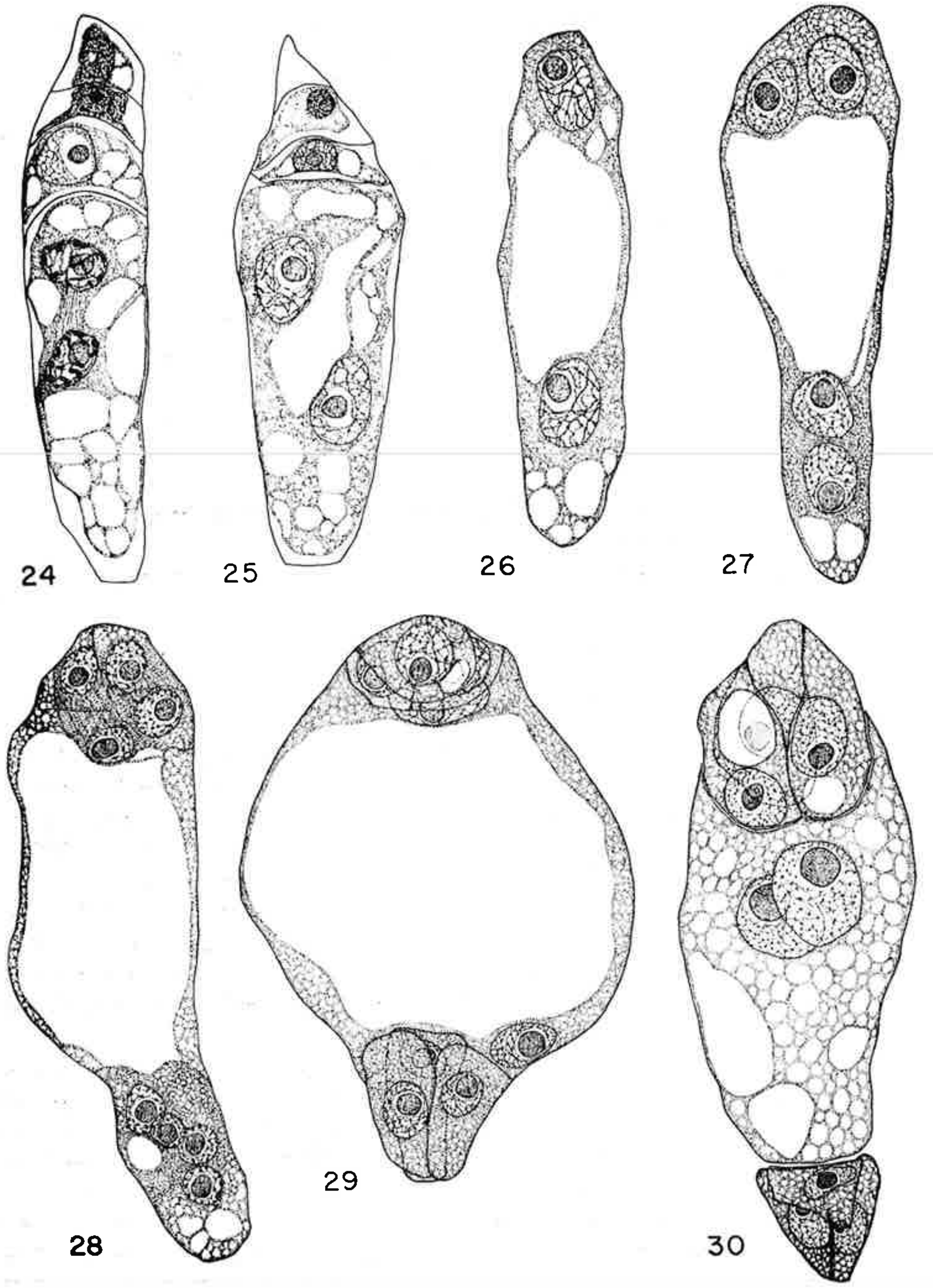

Figure 10. Megagametogenesis in *Arachis hypogaea* L. — (24-26) development of the two-nucleate embryo sac; degeneration of the three micropylar megaspores; (27) four-nucleate embryo sac; (28) eight-nucleate embryo sac at the beginning of cytokinesis; (29) early seven-celled embryo sac; (30) fully developed eight-nucleate, seven-celled megagametophyte (camera lucida drawings) (after Smith, 1956a).

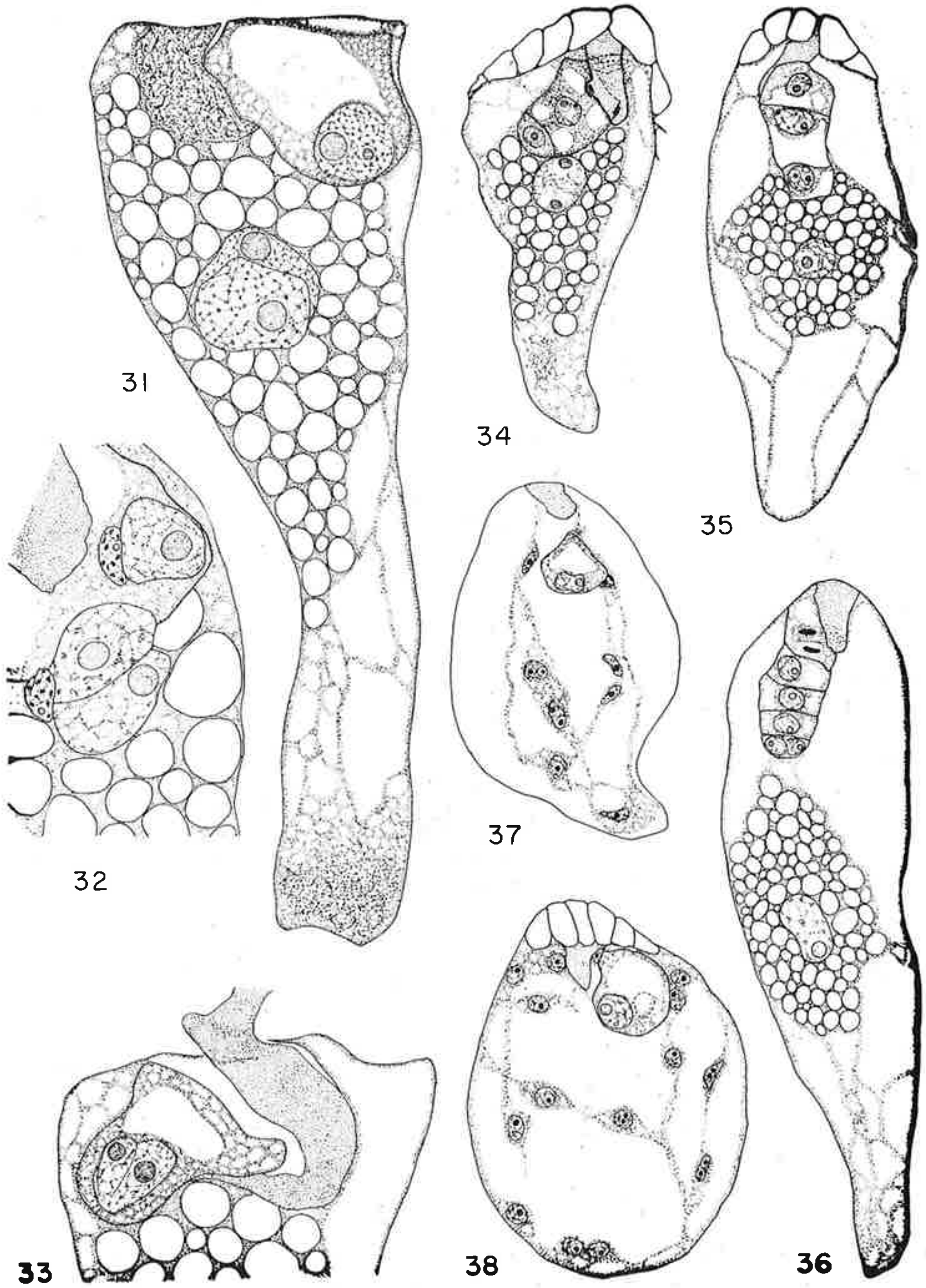

Figure 11. Fertilization in *Arachis hypogaea* L. — (31) mature embryo sac at the time of anthesis; polar nuclei surrounded by starch grains; synergids and antipodals have degenerated; (32) double fertilization; (33) pollen tube in the embryo sac, syngamy; (34-36) embryo development following syngamy although triple fusion failed; pollen tubes adjacent to the embryos, but central cells contain the fused polar nuclei and starch at 2 (34) and at 14 (35 and 36) days after pollination; (37-38) endosperm development although syngamy has failed; (37) *A. hypogaea* x *A. diogoi*, 16 days; (38) *A. hypogaea*, 7 days (camera lucida drawings) (after Smith, 1956a).

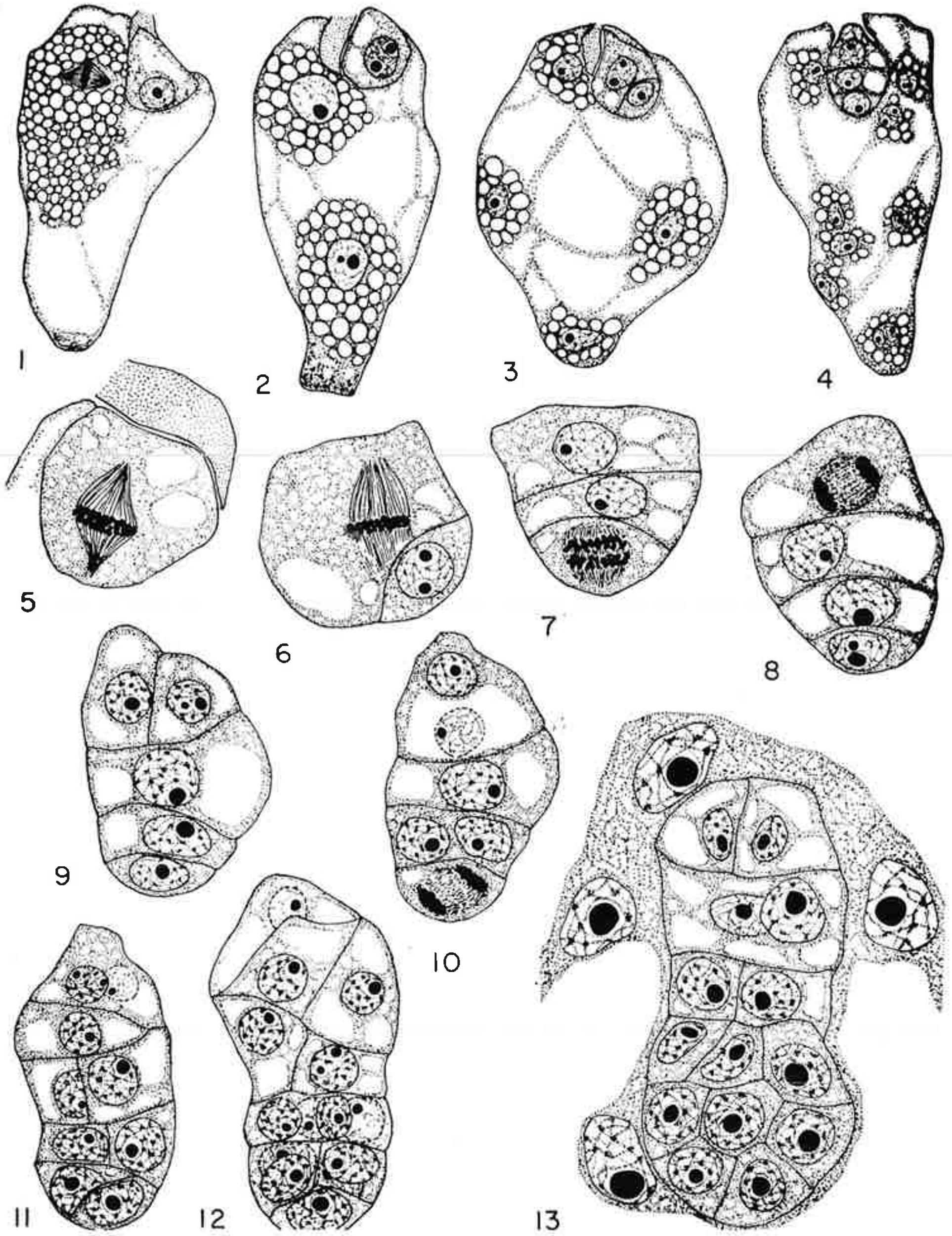

Figure 12. Early embryogeny in *Arachis hypogaea* L. — (1-4) Embryo and endosperm at 14, 23, 27, and 72 hours after anthesis (note close association of starch grains with the endosperm nuclei); (5-9) embryos of 1, 2, 3, 4, and 5 cells which show the order and orientation of the mitoses which produce the linear, proembryonic tetrad (1-3 days after anthesis); (10-12) embryos of 6, 9, and 14 cells, differentiation of the suspensor from the two basal tiers, embryo proper from the two terminal tiers of cells at the end of the third cell generation (5-9 days); (13) optical section of a 16-day embryo consisting of 8 suspensor cells and 21 cells in the embryo proper, and a portion of the associated endosperm (camera lucida drawing) (after Smith, 1956b).

flowers is related to a survival mechanism coming down from pre-cultivation times and does not necessarily represent the stupendous opportunity for production, "if we only knew how to use it," commonly implied in some discussions of this subject. It is more likely that it is evolutionally related to the frequent depredations of wild pigs and climatic disasters, possible in the long season of growth in the tropics.

The fruit of the peanut begins its life at the moment of fertilization, the union of the male and female germ cells in each of the several ovules located in the young ovary at the base of the calyx tube. At the first light of morning, under natural conditions of summer where peanuts grow, the flowers open. Shortly before or simultaneously, or sometimes afterward, the anther sacs burst and self-pollination takes place. Meantime, the female sexual apparatus has been preparing to receive the pollen tube. The preparation of the egg, the polar nuclei and the remainder of the 8-nucleate, 7-celled embryo sac are shown in Figure 10. During the next 12 hours or so, according to Smith (1956a), the pollen tube grows down through the long style, enters the embryo sac deep in the ovule and releases its two sperm nuclei, one of which fuses with the egg to begin the life of a new peanut plant. The other sperm unites with the two polar nuclei in a joint triple fusion to form the endosperm nucleus, beginning the tissue which nourishes the young embryo through its early stages (Figure 11, No. 32). Figure 11 shows the gametic union (No's. 34-38 show some abnormal cases as described). Banerji (1938) and Conagin (1957) have also described the early growth of the embryo in peanuts (Figure 12). The agreement of the descriptions of Banerji, Smith, and Conagin, together with the typical behavior of peanut embryogenesis, make further detailed description of the development process unnecessary. Figure 13 illustrates a somewhat later stage in the growth of the embryo, showing the differ-

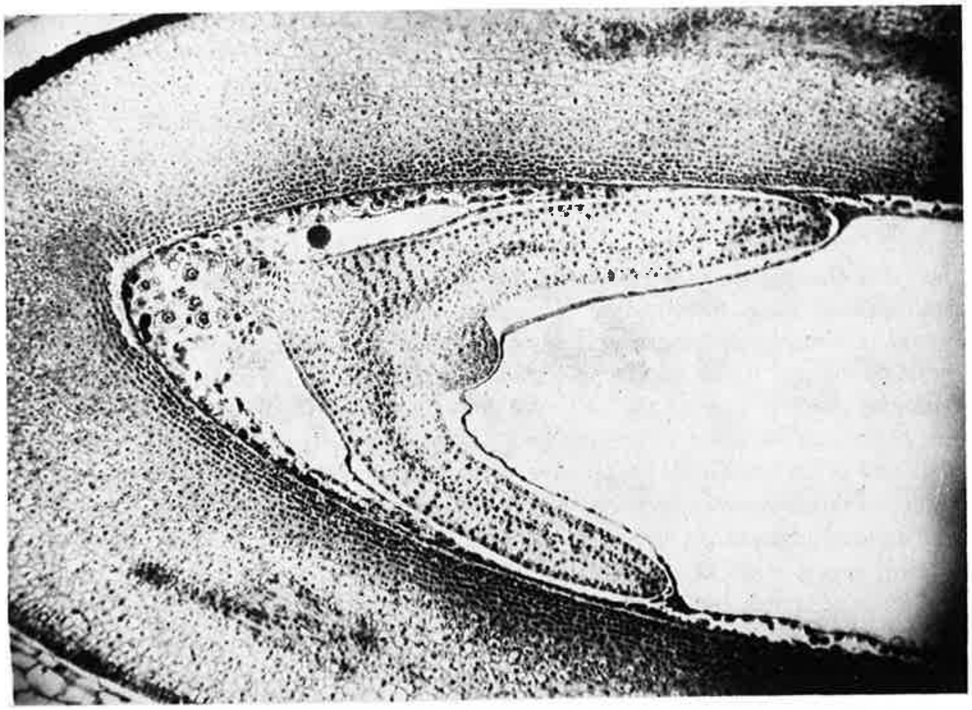

Figure 13. Longitudinal section through maturing embryo with 1st and 2nd cotyledons, young epicotyl, and suspensor. Note thin envelope of endosperm surrounding the embryo.

entiated embryo with suspensor, cotyledons, and epicotyl between the cotyledons. As growth proceeds, the cotyledons grow in length filling the embryo sac, become gorged with concentrates, and generally take on the form to be seen in the mature seed. The endosperm changes from plasmodial to cellular form and eventually may be seen as a thin, dry film, fragments of which may still be found as a veil over the plumule or between the cotyledons of the young seed.

During the early development of the young embryo, the ovary at the bottom of the calyx tube becomes mobilized for growth and within a week (sometimes less and occasionally much longer) makes its appearance from between the floral bracts and turns down toward the soil (Figure 8). Smith (1950) plotted the relative growth rates of peg, endosperm and embryo and showed that in the material he examined, while the peg was executing the first portion of a normal sigmoid curve of growth, both the endosperm and embryo relatively withheld growth. This period corresponded to the aerial phase of the peg's development. Schenk (1961) reported that pegs from underground flowers lack the light-induced inhibition to fruit enlargement. It is probable, therefore, that when the peg starts off already underground, there is no pause in embryo or endosperm growth, but that growth of peg, embryo, and endosperm are both rapid and simultaneous. After about the 10th day of peg growth, the curves for both endosperm and embryo shot upward rapidly (Figure 14).

The peg itself has been investigated by Jacobs (1947, 1951a) and by Brennan (1969). Jacobs noted that prior to fertilization a group of epidermal cells to one side of the style becomes radially elongated and that after fertilization they push the style aside at the base and form a pointed, firm protecting cap. Changes in lignification and increase in radial diameter complete the formation of this cap which is the advance structure just in front of the ovules as the peg grows toward and enters the ground. The anatomy of the above-ground portion has been described by Petit (1895). Additional descriptions may be found in Richter (1899), Waldron (1919), Reed (1924). The progressive development of peg to young mature fruit is shown in Figure 15. Pegs with fruits attached to the plants are shown in Figures 16 and 17.

The peg reaches the ground by growth mediated through an intercalary meristem located in the ovary proximal to the ovules. The meristem, according to Jacobs, is H-shaped. Vascularization extends over the ovules eventually providing a venous net over the pod. In the wild species, a meristematic zone occurs between the ovules such that the pod becomes distinctly lomentiform. In one section of the genus, the Triseminalae, there are three such segments often separated from one another by several centimeters of intercalary peg. In the cultivated peanut, the lomentiform condition of the pod has become suppressed but under various conditions intercalary meristem may develop between the basal and apical segments. In the cultivated peanut, the peg penetrates the soil a certain distance highly dependent upon undetermined conditions and at pod formation turns more or less horizontally. In many wild species, the peg turns horizontally and grows some distance, up to a meter, before setting the first or basal segment. In the wild species, as in the wild wheats, the fragility of the segment attachments causes them to break away easily when disturbed. Cultivated peanuts vary in this respect; those of the Guaraní region, where the common method of harvest in the past was to pull the plants by hand, have very tough pegs and the pods adhere tightly to them. In *A. nambyquarae* Hoehne, the pods are frequently taken individually from the plant and adhere much less tightly to the peg. The number of seeds per pod in *A. hypogaea* varies from 1-5. The colors of the seed coats may be

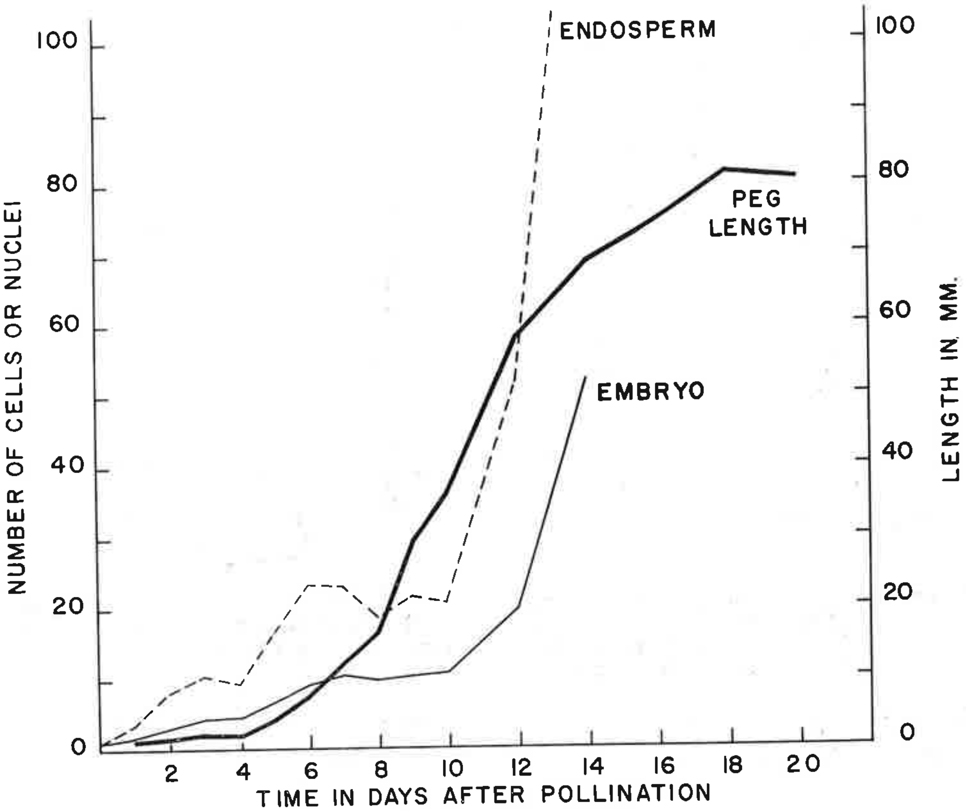

Figure 14. Embryo and endosperm growth in relation to elongation of geotropic peg. After 16-20 days the pegs have entered the soil and underground pod enlargement begins (after Smith, 1956b).

white, yellow, tan, brown, pink, red, or purple. They may be variegated variously with large or small spots (see color plate 1).

Schenk (1961) has presented observations on the development of the peanut fruit from peg elongation to maturity of an alternately branched (Virginia Bunch 67) and a sequentially branched form (Dixie Spanish). Observations were made at weekly intervals from 1 through 8 and at 9-12. He describes the morphological changes, respiratory changes, and changes in the individual constituents during development. These latter studies are more properly discussed elsewhere but were related by Schenk to the morphological changes occurring. In general, the pod expands rapidly underground by the development of a large parenchymatous tissue (endocarp) lying between the ovules and the shell layers. In normally developing fruits, the endocarp recedes in front of the advancing growth of the ovules and disappears almost completely when the seeds have matured. Meantime, the inner face of the "shell" has become progressively colored brown associated with increased tannin content and by the time the seed is fully mature, may be a very dark brown. This progressive coloration of the inner shell surface, easily seen but measured with some difficulty, has been used to estimate degree of maturity. When compared to other criteria of maturation, inner shell color still is one of the best criteria under which to make an estimate for either economic or experimental purposes. Smith (1954) has also illustrated changes in peanut fruits upon maturation and under conditions of limiting calcium

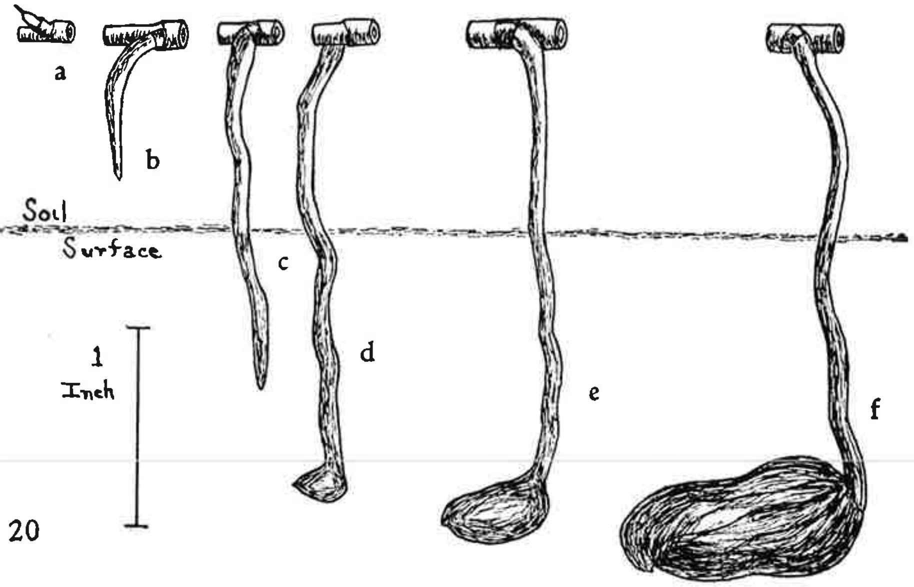

Figure 15. Successive stages of fruit development in *Arachis hypogaea* L. — (a) ovary at time of syngamy; (b) aerial peg, 5-7 days; (c) soil penetration, 8-12 days; (d) the beginning of fruit enlargement, 14-21 days; (e) early stage in fruit development; (f) immature fruit (after Smith, 1950).

in the fruiting zone. Chemical methods applied to problems of maturity may be expected to replace this practical approach in experimental analysis.

Axonomorphae, Series Amphiploides A. hypogaea L.

The subspecific classification of the cultivated peanut on the basis of its morphology merits special attention for the proper understanding of varietal development through hybridization and selection. This statement would be of little significance had it not been that the different populations of cultivated peanuts associated with the different indigenous people who grew them were effectively isolated from one another genetically, by means of small populations and autogamy, and geographically, by the great rivers and mountains of South America. If the species problem is difficult, the varietal problem is even more so, occasioned by the inter-grading of forms. Yet, as certain species grade into one another, the varietal clusters of peanuts have tended to assume sufficient distinctness to approximate subspecific rank. Gregory *et al.* (1951), discussing this problem, assessed it at that time in terms of the varieties commercially grown in the United States. Despite the limitations imposed by this incomplete sample of peanuts growing in a foreign land, these authors discovered the fundamental basis for subspecific differentiation in *A. hypogaea.* Unknown to them, Bigi (*In* Baldrati, 1950) had discovered the same relationship of characters to varietal differentiation in the peanuts at his disposal. The classification of cultivated peanuts is based on the morphological description of peanuts given by Richter (1899). He defined the branches of peanuts as (1) vegetative (*i.e.,* bearing normal green leaves) and (2) reproductive (bearing only scale leaves in the axils of which the flower-bearing axes develop). The main vegetative axis was designated *n* by Richter. The axes developing from the axils of the leaves of the *n* axis were designated $n + 1$. The next order arising from the $n + 1$ axes, Richter designated as $n + 2$ and so on for successive orders of branching. The $n+1$ and successive orders of branching may be either reproductive or vegetative. Richter pointed out that reproductive branches terminate all further branching. We, however, noted that reproductive branches may become vegetative with age and eventually assume the role of typical vegetative branches. These branches were designated as reproductive-vegetative. This condition necessitated a more explicit definition of a reproductive branch. Since the reproductive-vegetative branch initially bears only scale leaves, it may be arbitrarily defined as reproductive if its first four nodes are subtended by scale leaves in the axils of which flower-bearing axes occur. The basis for this definition is the fact that in peanuts the first two nodes of every vegetative branch are subtended by scale leaves (cataphylls). Occasionally, a vegetative branch will have its first three nodes subtended by scale leaves—hence the lower limit of four scale leaves for defining a branch as reproductive. Gregory and Gregory (1967) noticed that as the order of branching within the plant increased, the ratio of reproductive to vegetative branches increased until on the higher orders of branching every leaf subtended a reproductive branch. It was the natural variability of this phenomenon which Richter had observed and which Bigi and Gregory *et al.* had recognized as fundamental to the varietal classification of peanuts.

Earlier, as well as some very recent, classifications ignored the basic position of branching system in the subordination of forms under the species *A. hypogaea.* These classifications were based largely on plant habit and fruit characters which, important as they are in the understanding of agronomic strains and cultures (see Gibbons *et al.*, 1972) of peanuts, require to be subordinated to branching system for a proper understanding of the problem. Illustrations of efforts at peanut classification can be found in Dubard (1906), Bois (1927), Chevalier (1929a, 1933), Hayes (1933), John and Seshadri (1936), Clos (1939), Burkart (1939), Hoehne (1940), Bouffil (1947), Kumazawa and Nishimura (1952), John *et al.* (1954), Seshadri *et al.* (1958), Tétényi (1960), and Seshadri (1962).

Bunting (1955, 1958), Mazzani and Cabo (1957), Krapovickas and Rigoni (1960), and Smartt (1961) each developed systems of classification similar to the ones employed by Gregory *et al.* (1951) with results for the peanuts of Africa, Venezuela, and Argentina similar to those obtained in North America. Gibbons (1966) reported that *A. monticola,* unlike the man-restricted populations of cultivated types, varied from extreme reproductive or sequential type to a modified "Virginia" or alternate branching pattern. It should be noted that Krapovickas and Rigoni (1957) characterized *A. monticola* as "Virginia" in branching pattern but noted that reproductive axes appeared in the axils of leaves on the main axis. These will indeed be interesting observations if sustained by branching pattern analyses in the native habitat of *A. monticola,* possibly providing some evolutionary clue to the preservation of branching pattern variation in the wild. Unfortunately, however, the original description of the species was made from plants cultivated at Manfredi Station, Cordoba, Argentina, and Gibbons' material of the species proceeded from Campinas, Sao Paulo, Brazil, and was grown in Malawi prior to analysis. In North Carolina, *A. monticola* cannot maintain its integrity as a species when grown in the presence of *A. hypogaea.*

However illuminating these more recent classifications of the intraspecific variation of *A. hypogaea* and a similar study of *A. monticola* may be each of them suffered from the same difficulty that accompanied the works of Bigi and Gregory *et al.;* namely, either (1) the material classified was incomplete with respect to original centers of variation or (2) the presentations failed to associate fully prior classical taxonomic nomenclature of Harz (1885), Köhler (1898), Dubard (1906), and Waldron (1919.

In 1968, however, there appeared a work which not only tied the above works together, but successfully associated the latin names of earlier authors with the subspecific variation and the ethnic, linguistic, and geographic centers of origin of the cultivated peanut (Krapovickas, 1968). This work, appearing as it did before the wave of modern hybrid varieties now rolling back over the important areas of peanut production in South America, will be reviewed here in detail. Krapovickas and Rigoni (1960) had attempted the resolution of this problem, but at that time our collections did not represent the important secondary center of the Gé language and the Peruvian material was not well understood. Finally in 1967, our collections in Bahía, Pernambuco, and Ceará demonstrated that we had moved far afield from the mainstream of peanut variability.

An earlier work of Krapovickas and Rigoni (1960) on introgressive hybridization of peanuts in the Guaraní region: *i.e.,* in the basins of the Paraguay and Paraná Rivers, had shown that the great variability of the peanuts in this region was due to a hybrid swarm of original prototypes which hybridize freely *inter se.* Krapovickas (1968) remarks, "Similar processes but with the participation of different prototypes had occurred in the rest of South America giving origin to the patterns of variability which permit the delimitation of distinct gene centers." The centers recognized by Krapovickas are as follows:

1. Guaraní—Basin of the Paraguay and Paraná Rivers.
2. Goiás and Minas Gerais, Brazil.
3. Rondonia and N. W. Mato Grosso, Brazil.
4. The eastern slopes of the Andes, Bolivia.
5. Peru

In the Guaraní region peanuts with sequential branching systems are grown, corresponding to Krapovickas and Rigoni's subspecies *fastigiata.* Peanuts with alternate branching systems are practically unknown, being represented only by the varieties Guaycurú and Rasteiro, both probably having come from the West as the name Guaycurú implies. Since the hybrid swarm found by these authors in the Guaraní region does not contain elements of these two alternate branching varieties, it may be presumed that they are not only rare, but are of recent introduction to the region. The reliability of this inference is not impaired by the lower out-crossing rate normally observed among varieties of the alternate branching type since fastigiate x alternate occurs readily in the presence of bees even though natural hybrids of the alternate x fastigiate peanuts are rare, at least in breeding nurseries. Both varieties, *fastigiata* and *vulgaris,* of fastigiate peanuts occur in the Guaraní region, each in two forms: Valencia and Porto Alegre *(fastigiata fastigiata)* and Spanish and "negrito" *(fastigiata vulgaris),* the Spanish being restricted to the Guaraní region.

The region of Goiás and Minas Gerais includes the basins of the Tocantins and São Francisco Rivers. Here only one representative of the alternate branching pattern was found (Rasteiro) and the variety *vulgaris* contained no Spanish representatives. Obviously, Krapovickas' conclusion is correct that this region associated with the Gé language is a secondary center of variability derived from the Guaraní region.

The region of Rondonia and northwest Mato Grosso was ill-defined by Krapovickas (1968) and he himself said that the data were scarce and the region required more study. It is characterized at present by a single peanut, *A. nambyquarae* Hoehne (1922), which is closely allied to the peanuts of Bolivia and other upper Amazon drainage.[2]

The region of the eastern slopes of the Andes in Bolivia lies in the upper south basin of the Amazon. This is the center of variation for the alternate branching systems of peanuts and contains elements common to all other centers of variation. In characterization of the region Krapovickas states: "There is a great variability in regard to habit, size of plants, as well as in the fruits and in the color of the seed coats." The fastigiate peanuts found in this region differ from those of the Guaraní region. Krapovickas suggests that these fastigiate forms could be the result of introgressive hybridization.

The Peruvian region was found to be characterized by peanuts from the "selva" and peanuts from "la costa." Krapovickas notes that the coastal form is similar to peanuts found in the pre-Colombian tombs and has an alternate branching pattern. The peanut from the "selva" is sequential in branching system and corresponds to the Venezuelan variety of Mazzani and Cabo (1957), "Tingo Maria."

Krapovickas summarizes the variation from the five regions taxonomically as follows:

Arachis hypogaea L. (1753)

1. Subspecies *hypogaea* Krap. *et* Rig. (1960).[3]
    - (a) Variety *hypogaea* [= *A. africana* Lour.; type "Brasileño" (see Figure 16) Dubard (1906); type "Virginia" Gregory *et al.* (1951)].
    - (b) Variety *hirsuta* Köhler (1898) [= *A. asiatica* Lour.; type "Peruano" Dubard (1906), in part].
2. Subspecies *fastigiata* Waldron (1919).
    - (a) Variety *fastigiata* [= type "Peruano" Dubard (1906) (see Figure 16), in part; type "Valencia" Gregory *et al.* (1951)].
    - (b) Variety *vulgaris* Harz (1885) [= type "Spanish" Gregory *et al.* (1951)].

One might suppose that the above papers on the within-species variation would perhaps have satisfied the problem with peanuts. Not so. Gibbons *et al.* (1972), having added significant forms from West Africa to the total African collection, have reassessed the African peanut variability and have offered interesting and more detailed classification of the many forms which have been introduced to that continent or perhaps have evolved there, according to them, over the last 475 years. Gibbons *et al.* (1972) emphasize the fact that each of the general subdivisions of Krapovickas' classifications contains a large array of local varieties in the African and other peanut-growing areas. Some of this variation undoubtedly was present in the original seed lots introduced, some no doubt has arisen from subsequent chance and willful hybridization, but some has arisen from occasional high rates of natural genetic instability best illustrated by Smartt (1960) in Maní Pintar derived from the center of origin in Bolivia. Less pronounced, but no less real, is the natural instability in highly selected cultivated strains (Gregory, 1957).

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[2] We propose here that Hoehne's *A. nambyquarae* is no more distinct than Kohler's variety *hirsuta* and that *A. nambyquarac* = *A. hypogaea hypogaea* var. *nambyquarae*.

[3] See footnote 2.

Figure 16. Profile view of *A. hypogaea hypogaea nambyquarae* alternate branching type.

Figure 17. Profile view of *A. hypogaea fastigiata fastigiata* (Peruano) sequential type from the "selva."

Gibbons *et al.* (1972) describe four cultivar groups of the variety *hypogaea.* Each of these is subdivided into cultivar clusters on the basis of plant habit and pod and seed characters. The variation is considerable. Variety *hirsuta* is not well represented in the African collection. They found only one cultivar group of variety *fastigiata,* which was represented by two varietal clusters. In the variety *vulgaris,* however, they found three cultivar groups each represented by two varietal clusters. It is obvious that both the Guaraní region and the region of the eastern slopes of the Andes in Bolivia and parts of western Brazil are represented in the African collection. It is also fairly plain that the peanuts of the eastern slopes of the Andes must have reached Africa from Portuguese boats plying the Amazon and not from the immediate interior back of the northeast coast of Brazil, a hypothesis which was liquidated by the explorations of Gregory, Krapovickas, and Pietrarelli in Minas Gerais, Goiás, and western Bahía (Brazil) and of Gregory and Krapovickas in Bahía, Pernambuco, and Ceará (Brazil). This raises two very interesting questions which cannot be resolved without further work. One of these is the route to and original destination of the Guaraní peanuts of Africa. The other and more interesting one is brought out by the chance that the *hypogaea* varieties of peanuts reached Africa from material coming from the northern interior of the Bolivian center of origin, while our modern view of the center has come from Krapovickas and his associates' explorations coming up from the South and the East to the upper reaches of the Amazon drainage in Bolivia, but not penetrating it very far. Thus, Krapovickas explored the origin but not the areas of most natural human communications which flowed north and north-northeast with the rivers pouring off the Amazon rim. Gibbons *et al.* (1972) and Krapovickas (1968) state that the "Virginia" type of peanuts do not occur in South America except as recent introductions. Since the Virginia type seems to have reached North America from Africa (Higgins, 1951), the supposition has been that it evolved in that continent from material introduced from South America. This observation has led to the further supposition by Gibbons *et al.* that the variation observed by them in the African collection has arisen in that area by hybridization and subsequent selection in Africa, thus making of it a very important secondary center of variation of both the Guaraní and Bolivian peanuts of South America. Undoubtedly they are correct in part. To what extent further exploration in the Beni and northward to other extensions of the Amazon basin will uncover prototypes of the African forms is at present unknown. We do know that the peanuts of the tombs of Peru are remarkably similar to those of the variety *hirsuta* now growing on the Peruvian coast and this similarity has persisted for as long as 2800 years. Also, except for the products of recent hybridizations, the introductions from Africa to the United States have remained remarkably uniform for at least 150 years. And yet, the Maní Pintar story and the persistent low level of natural hybridization lay the genetic foundations for the hypothesis of an important subcenter of variation based on the great areas of peanut production of Africa.

In order to establish a sample of reference numbers traceable to the centers of origin, we have provided the following list of plant introductions from the centers. These collections were made by the authors themselves and although they are a very small fraction of the total collections of *Arachis hypogaea* available to breeders throughout the world, they will furnish to the breeder a foundation of varietal features characteristic of the centers and subcenters presented by Krapovickas (1968). Therefore, if any considerable fraction of the present listing of P.I. numbers and associated collection data should come into the breeding nursery containing a large number of introductions from all over the world, some assessment may be made by the breeder of which center a given entry in his collection represents and possibly which centers are involved in some advanced selections originating in crosses of plants from different centers. Furthermore, current studies being made of biochemical differences in commercial varieties of peanuts represented by selections from hybrids might conceivably be made more intelligible by a set of standards derived from a preliminary analysis of samples representing the primary centers of origin in South America. Brücher, H. (Erdkunde, Vol. 25, pp. 25-28, 1971) failed to see Krapovickas' work and as a consequence presented a less complete view of the gene centers of *A. hypogaea* L. According to Brücher, the geographic origin of peanuts was probably the Guaraní region of Krapovickas. As we know them today, the gene centers of Krapovickas may all be of secondary origin from a primary one along the eastern slopes of the Andes in Bolivia (Krapovickas, 1968). The present centers are associated primarily with civilizations while the geographic origin almost surely was associated with the geographic distribution of the wild progenitors of cultivated peanuts. Whether this event or these events coincided geographically with any of the present gene centers is not known.

Centers of origin—*A. hypogaea* L.

Guaraní region

Manfredi RCM No.	P. I. No.	Locality
		(Walton C. Gregory, Antonio Krapovickas, and José Pietrarelli, 1959)
446	261913	[4]"Guanaco" or "Guaycurú." Paso de la Patria, Corrientes, Argentina.
447-1	261914	Guanaco or Guaycurú. Paso de la Patria, Corrientes, Argentina. Fruit of a single plant.
447-2	261915	"
447-3	261916	"
447-4	261917	"
449-1	261918	"Negro." Paso de la Patria, Corrientes, Argentina. Fruit of a single plant.
449-2	261919	"
449-3	261920	"
449-4	261921	"
449-5	261922	"
449-6	261923	"
449-7	261924	"
450	261925	Negro. San Cosme, Corrientes, Argentina. Fruit of a single plant.
453-1	261926	Negro. Farm of V. M. Moyol, Ramada Paso, Corrientes, Argentina. Plants of great size. Fruit of a single plant.
453-2	261927	"
453-3	261928	"
453-4	261929	"
454	261930	Mixture. Farm of J. A. Román, Ruta 12, road to Loreto, Corrientes, Argentina. Fruits of several plants.

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[4] Local name enclosed in quotation marks the first time only.

Guaraní region (cont.)

Manfredi RCM No.	P. I. No.	Locality
455-1	261931	"Pálido." From a farm in Colonia Presidente Chavez, Encarnación, Paraguay. Fruit of a single plant. From a very non-uniform culture.
455-2	261932	"
455-3	261933	"
455-4	261934	"
455-5	261935	"
456-1	261936	"Colorado." From a farm in Colonia Presidente Chavez, Encarnación, Paraguay. Fruit of a single plant. From a very non-uniform culture.
456-2	261937	"
456-3	261938	"
456-4	261939	"
456-5	261940	"
456-6	261941	"
457-1	261942	"Violáceo." From a farm in Colonia Presidente Chavez, Encarnación, Paraguay. Fruit from a single plant. From a very non-uniform culture.
457-2	261943	"
458-1	261944	Pálido. Farm of Antonio Flores in Colonia Presidente Chavez, Encarnación, Paraguay. Fruit from a single plant. From a very non-uniform culture.
458-2	261945	"
459	261946	Violáceo. Nobro farm in Colonia Presidente Chavez, Encarnación, Paraguay. Fruits of two plants. From a uniform culture.
460	261947	Violáceo. Kokichi Hiraga farm in Colonia Presidente Chavez, Encarnación, Paraguay. Fruit from several plants. From a uniform culture.
461	261948	Pálido. Farm of Tomas Suarez, Trinidad-Encarnación, Paraguay. Fruit from three plants. From a uniform culture.
462	261949	Pálido. Collected from a processing plant "Fabril Paraguaya, S. A." Encarnación, Paraguay. Grown in red soil. Large fruits.
463	261950	"
464	261951	Colorado. Collected from a processing plant "Fabril Paraguaya, S. A." Encarnación, Paraguay. Grown in red soil. Large fruits.
465	261952	Violáceo. Collected from a processing plant "Fabril Paraguaya, S. A." Encarnación, Paraguay. Grown in red soil. Fruits of various sizes.
466	261953	"
467	261954	"
469	261955	Pálido. Collected from a processing plant "Fabril Paraguaya, S. A." Encarnación, Paraguay. Grown in sandy soil. Large fruits.
470	261956	Colorado. Collected from a processing plant "Fabril Paraguaya, S. A." Encarnación, Paraguay. Grown in sandy soil. Fruits of various sizes.
471	261957	"
472	261958	Colorado. Collected from a processing plant "Fabril Paraguaya, S. A." Encarnación, Paraguay. Grown in sandy soil. Fruits small to medium size.
473	261959	Violáceo. Collected from a processing plant "Fabril Paraguaya, S. A." Encarnación, Paraguay. Grown in sandy soil. Large fruits.

Guaraní region (cont.)

Manfredi RCM No.	P. I. No.	Locality
475	261960	Violáceo. Collected at a processing plant "Fabril Paraguaya, S. A." Encarnación, Paraguay. Grown in sandy soil. Fruits very small.
476	261961	Violáceo. Bought in the market, Encarnación, Paraguay. Large fruits.
477	261962	Violáceo. Farm of José Godoy, San Ignacio, Paraguay. Large fruit from a culture already harvested (mixed).
478	261963	Violáceo. Farm of José Godoy, San Ignacio, Paraguay. Small fruits from several uniform plants.
479-1	261964	Violáceo. Farm of José Godoy, San Ignacio, Paraguay. Small fruit from an atypical plant.
479-2	261965	"
479-3	261966	"
479-4	261967	"
479-5	261968	"
479-6	261969	"
480	261970	Violáceo. Farm of Ramón Rodriguez, San Ignacio, Paraguay. Large fruit taken from a non-uniform culture.
481-1	261971	Violáceo. Farm of Ramón Rodriguez, San Ignacio, Paraguay. Medium size fruits from a non-uniform culture.
481-2	261972	Violáceo. Farm of Ramón Rodriguez, San Ignacio, Paraguay. Small fruits from a non-uniform culture.
481-3	261973	Violáceo. Farm of Ramón Rodriguez, San Ignacio, Paraguay. Medium size fruits from a non-uniform culture.
482	261974	Colorado. Farm of Ramón Rodriguez, San Ignacio, Paraguay. Medium size fruits without constriction, from several plants.
483	261975	Colorado. Farm of Ramón Rodriguez, San Ignacio, Paraguay. Medium size fruit with constriction and beaked, from two plants.
484	261976	Violáceo. Farm of Felipe Villalba, road to Caaguazú, Salida de Coronel Oviedo, Paraguay. Large fruit from a culture already harvested.
485	261977	Colorado (possibly Colorado Fassardi). Farm of Felipe Villalba, road to Caaguazú, Salida de Coronel Oviedo, Paraguay. Medium to large fruits from one culture already harvested.
486	261978	Violáceo. Farm of Seferino Barreto, Colonia Balbina (15 kms from Coronel Oviedo, road to Caaguazú), Paraguay. Large fruits from a culture already harvested.
487	261979	Pálido. Farm of Seferino Barreto, Colonia Balbina (15 kms from Coronel Oviedo, road to Caaguazú), Paraguay. Fruits medium to large size from a single culture.
488	261980	Colorado. Farm of Clemente. 23 kms from Coronel Oviedo, road to Caaguazú, Paraguay. Large fruits from a single culture already harvested.
489	261981	Violáceo. Farm of Carlos Benitez, Puerto Embalse (Hernandarias), Paraguay. Large fruits.
490	261982	Rosado Salmón y Colorado (Guaycurú?). Farm of Carlos Benitez, Puerto Embalse (Hernandarias), Paraguay.
491	261983	Colorado. Farm of Antonio Ifran near Arroyos y Esteros, Paraguay. Fruits of several sizes already pulled up.

Guaraní region (cont.)

Manfredi RCM No.	P.I. No.	Locality
492	261984	Pálido. Farm of Antonio Ifran near Arroyos y Esteros, Paraguay. Fruits of several sizes already pulled up.
493-1	261985	Pálido. Farm of Antonio Ifran near Arroyos y Esteros, Paraguay. Small fruits of a single plant already pulled up.
493-2	261986	〃
493-3	261987	〃
494	261988	Violáceo. Farm of Alejandro Páez, Isla Guazú, Paraguay. Small fruits from several plants after harvest.
495	261989	Pálido. Farm of Alejandro Páez, Isla Guazú, Paraguay. Fruits of various sizes, already harvested.
496	261990	Violáceo. Farm of Alejandro Páez, Isla Guazú, Paraguay. Fruits medium to large already harvested.
497	261991	Colorado. Farm of Alejandro Páez, Isla Guazú, Paraguay. Medium size fruits already harvested.
498	261992	Pálido. Farm of Brigido Páez. Maintained by this farmer since 1934. Isla Guazú, 30 kms from Caacupé, Paraguay. Fruits slender and long from several plants already harvested.
499	261993	Colorado. Farm of Ana Maria de Figuerero, near Arroyos y Esteros, Paraguay. Fruits medium size from several plants already harvested.
500	261994	Pálido. Farm of Ana Maria de Figuerero, near Arroyos y Esteros, Paraguay. Medium size fruits from several plants already harvested.
501	261995	Violáceo. Farm of Ana Maria de Figuerero, near Arroyos y Esteros, Paraguay. Medium size fruits from several plants already harvested.
502	261996	Pálido y Colorado. Arroyos y Esteros, Paraguay. Bought at a store. Medium size fruits.
503	261997	Pálido y Colorado. Bought in the market in Caacupé, Paraguay.
504	261998	"Negrito." A culture at the Instituto Agronomico at Caacupé, Paraguay. Small fruits.
505	261999	Colorado. A culture at the Instituto Agronomico at Caacupé, Paraguay. Medium size fruits.
507	262001	Colorado. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L.," Asunción, Paraguay. Grown in sandy soil. Large fruits.
508	262002	Colorado. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L.," Asunción, Paraguay. Grown in sandy soil. Large fruits.
509	262003	Colorado. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Large fruits. Grown in sandy soil.
510	262004	〃
511	262005	〃
512	262006	Colorado. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Fruits of various sizes. Grown in sandy soil.
513	262007	Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Mixture of colors and sizes of fruit. From sandy soil.
514	262008	〃

Guaraní region (cont.)

Manfredi RCM No.	P.I. No.	Locality
515	262009	Violáceo. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Small and medium size fruits. From sandy soil.
516	262010	Violáceo. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Small size fruits. From sandy soil.
517	262011	〃
518	262012	Pálido. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Large fruits. Grown in sandy soil.
519	262013	Pálido. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Fruits medium size. Grown in sandy soil.
520	262014	Pálido. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Large fruits. Grown in sandy soil.
521	262015	Mixture. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Fruits of several sizes. Grown in red soil.
522	262016	〃
523	262017	Violáceo. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Fruits of several sizes. Grown in red soil.
524	262018	Violáceo. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Small fruits. Grown in sandy soil.
525	262019	Colorado. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción. Paraguay. Large fruits. Grown in red soil.
526	262020	〃
527	262021	〃
528	262022	Colorado. Collected from a bag stored at the "Compañia Oleaginosa Paraguaya S. R. L." Asunción, Paraguay. Fruits of various sizes. Grown in red soil.
529	262023	〃
530	262024	〃
531	262025	Violáceo. From Portera Ortiz at Rosario de Morel de Florenciano farm, Pedro Juan Caballero, Paraguay. Medium size fruits from a single culture already harvested.
532	262026	Colorado. Farm of Miguel Colman, Cerró Corá, Pedro Juan Caballero, Paraguay. (Possibly seed brought from Misiones Paraguaya.) Medium size fruits.
533	262027	Violáceo. From Fazenda Mangai between Antonio Joa and Capitán Bado, Mato Grosso, Brazil. Fruits small and medium size.
534	262028	Colorado. Sample bought at a store in Sanga-Pitay, Ponta Porá, Mato Grosso, Brazil. Fruits medium size.
535	262029	Colorado. Seed collected by Dr. Green from Daniel Tevera Diaz at Fazenda Barra Azul. P. Prudente, São Paulo, Brazil.
536	262030	Colorado. Seed collected by Dr. Green from Carrego da Onca, Fazenda de Joao Fagunde. P. Prudente, São Paulo, Brazil.
537	262031	Colorado. Seed collected by Dr. Green, Fazenda de Marikazu Ito. Bairo Matadouro, 5 km from P. Prudente, São Paulo, Brazil.

Guaraní region (cont.)

Manfredi RCM No.	P.I. No.	Locality
538	262032	Colorado. Seed collected by Dr. Green from Joao Alveno at Fazenda Santa Antonio, P. Prudente, São Paulo, Brazil.
539	262033	Colorado. Seed collected by Dr. Green from Olimpio Gomez at Fazenda Estrela da Marte, P. Prudente, São Paulo, Brazil.
540	262034	Colorado. Seed collected by Dr. Green from Emilio Bisrolo, Fazenda Floresta, P. Prudente, São Paulo, Brazil.
541	262035	Pálido. Seed collected by Dr. Green, Fazenda de Saniramo Sanchez Delgado, 7 km from Pirapé, São Paulo, Brazil.
542	262036	Colorado. Seed collected by Dr. Green, Fazenda Santa Antonio from Paulo Andrea W. Castella, São Paulo, Brazil.
543	262037	Colorado. Seed collected by Dr. Green, Fazenda de Amaneio José da Lima. 18 km from Monte Alvao, São Paulo, Brazil.
544	262038	Colorado. Seed collected by Dr. Green, Fazenda de Clemente Nunez, Agua Espalhada, São Paulo, Brazil.
545	262039	Pálido. Seed collected by Dr. Green, Fazenda de Manoel Sanchez Carion, Sitio Manoel. Monte Alvao, São Paulo, Brazil.
546	262040	Colorado. Seed collected by Dr. Green, Fazenda Guaruja de Carayi Massuda. P. Prudente, São Paulo, Brazil.
547	262041	"
548	262042	Pálido. Seed collected by Dr. Green, Fazenda de Choei Caira, Gleba Iatuzinho, P. Prudente, São Paulo, Brazil.
549	262043	Colorado. Seed collected by Dr. Green, Fazenda de Hideo Kitagato, Ameliapolis, P. Prudente, São Paulo, Brazil.
550	262044	Colorado. Seed collected by Dr. Green, Fazenda Jimoeiro Jaco de Hiroshi Jashio, P. Prudente, São Paulo, Brazil.
551	262045	Pálido. Seed collected by Dr. Green, Fazenda de Sadao, Oro Branco, P. Prudente, São Paulo, Brazil.
552	262046	Colorado. Seed collected by Dr. Green, Fazenda Sitio Luiz Cantinho, Bairo Cristalia, P. Prudente, São Paulo, Brazil.
553	262047	Pálido. Sample taken at random from one of several bags at the oil mill of Anderson-Clayton, Paraguaçú Paulista, São Paulo, Brazil. Small to medium size fruits. From red soil.
554	262048	"
555	262049	Pálido. Sample taken at random from one of several bags at the oil mill of Anderson-Clayton, Paraguaçú Paulista, São Paulo, Brazil. Medium size fruits. From red soil.
556	262050	"
557	262051	Pálido. Sample taken at random from one of several bags at the oil mill of Anderson-Clayton, Paraguaçú Paulista, São Paulo, Brazil. Medium to large fruits. From red soil.
558	262052	Colorado. Sample taken at random from one of several bags at the oil mill of Anderson-Clayton, Paraguaçú Paulista, São Paulo, Brazil. Large fruits. From sandy soil.
559	262053	"
560	262054	"
561	262055	Pálido. Sample taken at random from one of several bags at the oil mill of Anderson-Clayton, Paraguaçú Paulista, São Paulo, Brazil. Small peanuts. From sandy soil.

Guaraní region (cont.)

Manfredi RCM No.	P. I. No.	Locality
562	262056	Colorado. Anderson-Clayton Oil Mill, Paraguaçú Paulista, São Paulo, Brazil. Large fruits. From red soil. Taken at random from different portions of the mill process.
563	262057	Colorado. Anderson-Clayton Oil Mill, Paraguaçú Paulista, São Paulo, Brazil. Fruit larger than RCM 562. From red soil. Taken at random from different portions of the mill process.
564	262058	Colorado. Anderson-Clayton Oil Mill, Paraguaçú Paulista, São Paulo, Brazil. Sandy and red soil. Taken at random from different portions of the mill process.
565	262059	Colorado y violáceo. Anderson-Clayton Oil Mill, Paraguaçú Paulista, São Paulo, Brazil. Fruits very large. From red and sandy soil. Taken at random from different portions of the mill process.
566	262060	Colorado. Anderson-Clayton Oil Mill, Paraguaçú Paulista, São Paulo, Brazil. Fruits larger than RCM 565. From sand and red soil. Taken at random from different portions of the mill process.
567	262061	Violáceo. Anderson-Clayton Oil Mill, Paraguaçú Paulista, São Paulo, Brazil. (chosen large seeds) Taken at random from different portions of the mill process.
568	262062	Colorado. Tatu. P. Prudente, São Paulo, Brazil. Large fruits. From sandy soil. Taken at random from a storage in P. Prudente.
569	262063	″
570	262064	Colorado. Tatu. P. Prudente, São Paulo, Brazil. Medium size fruits. From sandy soil. Taken at random from storage.
571	262065	″
572	262066	Colorado. Tatu. P. Prudente, São Paulo, Brazil. Medium size fruits. From red soil. Taken at random from storage.
573	262067	″
574	262068	Pálido. P. Prudente, São Paulo, Brazil. Small fruits. From sandy soil. Chosen from sacks in storage.
575	262069	Pálido. P. Prudente, São Paulo, Brazil. Large fruits. From sandy soil. Chosen from sacks in storage.
576	262070	Pálido. P. Prudente, São Paulo, Brazil, Large fruits. From red soil. Chosen from sacks in storage.
577	262071	Violáceo. P. Prudente, São Paulo, Brazil. Large fruits. From sandy soil. Chosen from sacks in storage.
578	262072	Colorado. P. Prudente, São Paulo, Brazil. Medium to large fruits from sandy soil. Chosen from sacks in storage.
579	262073	Colorado. P. Prudente, São Paulo, Brazil. Fruits of various sizes. From sandy soil. Chosen from sacks in storage.
580	262074	Colorado. Miguel Antonio's drugstore, Xavantina, Mato Grosso, Brazil. Fruits of various sizes.
581	262075	Blanco Amarillento. Banks of Río Pardo, Mato Grosso, Brazil. Fruits of various sizes. From a store from local Fazendas.
582	262076	Pálido. Banks of Río Pardo, Mato Grosso, Brazil. Fruits of various sizes. From a store from local Fazendas.
583	262077	Violáceo. Banks of Río Pardo, Mato Grosso, Brazil. Fruits of various sizes. From a store from local Fazendas.

Guaraní region (cont.)

Manfredi RCM No.	P.I. No.	Locality
584	262078	Colorado. Banks of Río Pardo, Mato Grosso, Brazil. Fruits of various sizes. From a store from local Fazendas.
585	262079	Colorado. Jatoba at 42 kms from Campo Grande, road to Cuiabá, Mato Grosso, Brazil. Fruits of medium size.
586	262080	Colorado. Congonha at 100 kms from Campo Grande, road to Cuiabá, Mato Grosso, Brazil. Medium size fruits.
587	262081	Blanco amarillento (Amarelo). Congonha at 100 kms from Campo Grande, road to Cuiabá, Mato Grosso, Brazil. Medium size fruits.
588	262082	Colorado. Río Verde at 240 kms from Campo Grande, Mato Grosso, Brazil. Bought at a hotel. Medium size fruits.
589	262083	Colorado. Bought at a store in Coxim, Mato Grosso, Brazil. Medium size fruits.
590	262084	Colorado. Bought at a store in Cuiabá, Mato Grosso, Brazil. Medium size fruits.
591	262085	Violáceo. Fazenda de Luis Bata, Anhuma, Mato Grosso, Brazil. (Between Cuiabá and Birro.) Medium size fruits.
592	262086	Colorado. Bought at a store in Rosario Oeste, Mato Grosso, Brazil. Medium to large fruits.
593	262087	Colorado. Bought at a store in Cerro de Saudades, Mato Grosso, Brazil. Medium size fruits. Sample of the culture of the area.
595	262089	Colorado. Bought at a store in Corumbá, Mato Grosso, Brazil. Large fruits.

Goiás and Minas Gerais region

(Walton C. Gregory, Antonio Krapovickas, and José Pietrarelli, 1959)

P.I. No.	Locality
262088	Itumbiara, Goiás, Brazil.
275687	Ituiutaba, Minas Gerais, Brazil.
275688	"
275689	Piracanjuba, Goiás, Brazil.
275690	Between Morrinhos and the Rio Piracanjuba, Goiás, Brazil.
275691	Piracanjuba, Goiás, Brazil.
275692	Corumbá, Goiás, Brazil.
275693	Trairas, Goiás, Brazil.
275694	"
275695	Rio Maranhao, Goiás, Brazil.
275696	Anapolis, Goiás, Brazil.
275697	"
275698	40 km N of Ceres, Goiás, Brazil
275699	162 km N of Brasilia on the Brasilia-Belem road near Ceres, Goiás, Brazil.
275700	Near Ceres, 151 km N of Brasilia on Brasilia-Belem road, Goiás, Brazil.

Goiás and Minas Gerais region (cont.)

P.I. No.	Locality
275701	174 km out on Brasilia-Belem road, Goiás, Brazil.
275702	"
275703	"
275704	40 km N of Ceres, Goiás, Brazil.
275705	"
275706	"
275707	"
275708	"
275709	"
275710	"
275711	"
275712	147 km out on Brasilia-Belem road, Ceres, Goiás, Brazil.
275713	"
275714	Rio das Almas, Minas Gerais, Brazil.
275715	On the road to Patos south from highway Belo Horizonte-Brasilia, Minas Gerais, Brazil.
275716	Patos de Minas, Minas Gerais, Brazil.
275717	Varjou on road to Patos, Minas Gerais, Brazil.
275718	Valle Grande near Curvelo, Minas Gerais, Brazil.
275719	Mendanha, 27 km N of Diamantina, Minas Gerais, Brazil.
275720	Corrego do Crimen between Gouveo and Curvelo, Minas Gerais, Brazil.
275721	Sete Lagoas, Minas Gerais, Brazil, Experiment Station.
275722	"
275723	"
275724	"
275725	"
275726	"
275727	"
275728	"
275729	"
275730	"
275731	"
275732	"
275733	"
275734	"
275735	"
275736	"
275737	"
275738	"
275739	"

Goiás and Minas Gerais region (cont.)

P.I. No.	Locality
275740	Sete Lagoas, Minas Gerais, Brazil, Experiment Station.
275741	"
275742	"
275743	"
275744	"

Bolivian region

(Antonio Krapovickas, 1958)

Manfredi RCM No.	P.I. No.	Locality
422	261891	"Overo." Large seeded, bought in a store in San José de Chiquitos in Bolivia.
423	261892	Overo. Large seeded, bought in the market in Santa Cruz de la Sierra, Bolivia.
424	261893	Overo. Bought at a store in Cochabamba, Bolivia.
425	261894	Overo. Seed from Santa Cruz, Bolivia.
426	261895	"
427	261896	Colorado. From a market in Santa Cruz, Bolivia.
428	261897	
429	261898	Colorado. From Cochabamba, Bolivia.
430	261899	"Rosario Salmon." Cochabamba, Bolivia.
431	261900	Colorado. From Cochabamba, Bolivia.
432	261901	Pale rose to deep rose. Cultivated by "Yuras" Indians. Collected at Villa Tunari, Río Chapare, Bolivia.
433	261902	Mixture of various types. Cochabamba, Bolivia.
436	261903	Deep red. Collected at Villa Tunari, Río Chapare, Bolivia.
437	261904	Rose to claret red. From Samaipata, Bolivia.
438	261905	Rose salmon color seed. From Villa Tunari, Bolivia.
439	261906	Overo. Collected at Samaipata, Bolivia.
440	261907	Samaipata, Bolivia.
441	261908	Dark red. From Samaipata, Bolivia.
442	261909	Samaipata, Bolivia.
443	261910	"
444	261911	"
445	261912	"

(Walton C. Gregory, Antonio Krapovickas, and José Pietrarelli, 1959)

Manfredi RCM No.	P.I. No.	Locality
596-1	262090	Overo (Blanco y Colorado). Plant harvested from the farm of a settler. 4 kms from Roboré, Bolivia.
596-2	262091	"

Bolivian region (cont.)

Manfredi RCM No.	P.I. No.	Locality
597-1	262092	Colorado. Warnes, 30 kms from Santa Cruz, Bolivia. Shells medium size. From a Valencia type culture. Plants with and without bristles in addition to variation on the central axis.
597-2	262093	Colorado. Warnes, 30 kms from Santa Cruz de Sierra, Bolivia. Shells medium size.
597-3	262094	"
597-4	262095	"
597-5	262096	"
597-6	262097	"
597-7	262098	Colorado. Warnes, 30 kms from Santa Cruz de Sierra, Bolivia. Shells more or less large.
597-8	262099	Colorado. Warnes, 30 kms from Santa Cruz de Sierra, Bolivia. Medium size shells.
597-9	262100	"
597-10	262101	"
597-11	262102	"
597-12	262103	Colorado. Warnes, 30 kms from Santa Cruz de Sierra, Bolivia. Small to medium shells.
597-13	262104	Colorado. Warnes, 30 kms from Santa Cruz de Sierra, Bolivia. Medium size shells.
598	262105	Colorado. Warnes, Bolivia. Medium to large size fruits. From a culture already harvested.
599	262106	Overo. Seed bought at a market. Santa Cruz, Bolivia.
600	262107	Pálido y Colorado suave. Santa Cruz, Bolivia. Seeds very large. Purchased in the market.
701	262108	"Rosado salmón." Santa Cruz, Bolivia. Large seeds. Bought in the market.
702	262109	"
703	262110	Colorado. Santa Cruz, Bolivia. Small seeds. Bought in the market.
704	262111	"Colorado San Simón." Collected at the Experiment Station de Los Llanos, Santa Cruz, Bolivia. Original source: Tarija.
705	262112	"Criollo." Collected at the Experiment Station de Los Llanos, Santa Cruz, Bolivia. Original source?
706	262113	"Overo erquis." Collected at the Experiment Station de Los Llanos, Santa Cruz, Bolivia. Original source: Tarija.
707	262114	"Overo San Simón." Collected at the Experiment Station de Los Llanos, Santa Cruz, Bolivia.
708	262115	"Overo Criollo." Collected at the Experiment Station de Los Llanos, Santa Cruz, Bolivia. Original source: Tarija.
709	262116	Overo. Collected at the Experiment Station de Los Llanos, Santa Cruz, Bolivia. Original source: Samaipata.
710	262117	"Erquis." Collected at the Experiment Station de Los Llanos, Santa Cruz, Bolivia. Original source: Tarija.
711	262118	"Perla de Saavedra." Collected at the Experiment Station de Los Llanos, Santa Cruz, Bolivia. Received as Muyurina (Muy rendidora).
712	262119	"Tennessee Red." Collected at the Experiment Station de Los Llanos, Santa Cruz, Bolivia. Variety introduced through Point 4 (distributed among the farmers).

Peruvian region

(Walton C. Gregory, 1959)

P.I. No.	Locality
262121	Bought in a Lima market. Came from Cuzco, Peru.
262122	Bought in a La Molina market. Came from Cuzco, Peru.
262123	Bought in a Lima market. Peru.
262124	"
262125	Bought in a Lima market. Came from Chanchamayo, Peru.
262126	Bought in a Lima market. Came from Cuzco, Peru.
262127	Bought in a Lima market. Came from Montagne (Peru).
262128	Bought in a Lima market. Came from Trujillo, Peru.
262129	Came from Tingo María, Peru.
	(Walton C. Gregory, 1961)
275745	Iquitos, Peru.
275746	"
275747	Locality unknown (Peru).
275748	Iquitos area, Peru.
275749	Tropical Peru.
275750	Tournavista, near Pucallpa, Peru.
275751	Puerta Azul, 3 days up the Ucayali River from Pucallpa, Peru.

The Peanut and Its Relatives

The plants of the genus *Arachis,* of which the cultivated peanut *A. hypogaea* L. is the best known, may be grouped at present into 30-50 different species. Or, one might say that the selecting environments of South America have devised 30-50 distinctly different ways to make a peanut. The different ways in which this tremendous task has been accomplished over thousands of years provide mankind with some of his most important materials with which to correct major defects in his cultivated species. Despite a long history of cultivation, broad sub-specific variability and wide geographic distribution of the cultivated peanut, defects in its genetic composition with respect to the requirements of man are widespread and for many of these, no remedial genetic resources are known to exist among its varietal forms. Aside from the remote chance that these remedial genetic components can be induced by mutagenic agents, the wild relatives of the peanut present the only resource to which the breeder can turn.

Among the economically important characteristics which have been discovered in wild *Arachis* species are near immunity or very high resistance to:

1. Cercospora leafspot diseases (Frezzi, 1960; Abdou, Y., unpublished thesis; Gibbons and Bailey, 1967).
2. Peanut rust (Wallace Bailey, personal communication).
3. Virus diseases including stunt (Hebert, unpublished annual reports) and virus and rosette disease (R. Gibbons, personal communication).

Moderate to high resistance to:

4. Northern rootknot nematode (Banks, personal communication).

The degree to which the different species have succeeded in becoming differentiated is a measure of the difficulty of recovering genetic information from them and incorporating it into the peanut genome. Therefore, the task of exploiting these resources will be long and sometimes tedious. For these reasons, the rapid expansion of man's cultural activities in the native areas of the wild species of *Arachis* may destroy the species before their resources are established in breeding stocks. It is therefore imperative that continued effort be directed toward this end; but much needs to be done, especially in establishing accepted procedures, names and numbers which will guarantee to the peanut breeders of the world that when they mention a name, number, or procedure, the rest of their colleagues will not only know what they are talking about but have a measure of confidence that the material described is in fact what the labels designate.

In these species with their underground fruits and wide-ranging runners which can peg down in adjacent plots, the possibility of confusion is extraordinarily high. This fact, coupled with the history of taxonomic uncertainty and involved synonymy, renders the problem far more acute than in plants whose distinguishing characteristics are less esoteric. When one adds to these conditions the fact that the culture and care of wild species of *Arachis* are demanding and time-consuming, the problem of the preservation of exotic germ plasm resources becomes formidable.

To these ends, the authors have devoted their efforts toward a clarification of the taxonomic organization of the genus *Arachis* through collecting expeditions into the native habitats of peanuts and their wild relatives, through species cross-compatibility studies, chemotaxonomic studies, ethnic associations, and other commonly accepted lines of investigation. The need to prepare the present thesis has caught these investigations in the process of presentation and necessitates the citing of unpublished works to support many of the generalizations brought forward. While such a situation is unfortunate with respect to chronology, it is to be hoped that subsequent revisions of the present work will allow citation to the completed works. Meantime, what we have learned begs to be presented in such a work as the present volume.

In this chapter we have concentrated our description of morphology on the common peanut, type species of the genus, and long known to the botanical world before a single species of wild *Arachis* was seen by Europeans. We have presented the material on the taxonomic framework of the genus and have eventually supplied a list of all of the wild species of *Arachis* which we have collected either jointly or independently or, if collected by other men, seen alive by at least one of the authors.

The numbers under which the collections have been made or catalogued by different people and agencies have been collated to create a comprehensive and intelligible listing of *Arachis* available to peanut investigators over the world. Our procedure in making collections in the field has been to visit the type localities of wild species of peanuts, and to collect cultivated peanuts in the linguistic regions and cultural centers of native pre-Colombian civilizations. These decisions have indeed been rewarding, giving rise to a satisfying subordination of cultivated peanuts according to regions where grown in South America and to an equally satisfying grouping of the wild species into sections and series of the genus *Arachis,* bringing, for the first time, some semblance of order and understanding to this genus of plants.

The significant findings on the cultivated peanuts have been published by Krapovickas and Rigoni (1960), Krapovickas (1960), and Krapovickas (1968). The monographic treatment of the entire genus by Krapovickas and Gregory remains to be published. The outline treatment of the taxonomic problem in the present chapter is a synopsis drawn from the unpublished work of these two authors. The working prospectus thus adopted will, of course, present shortcomings and errors which time and further study will erase. Meantime, the study is presented, without apology, for its obvious utility to peanut species breeding enterprises throughout the world.

The genus *Arachis* was introduced to modern botany through its most important species *A. hypogaea* L. (Linnaeus 1737, 1753). Bentham (1841) associated *Arachis* with *Stylosanthes* and *Chapmannia* in the tribe Hedysareae. Taubert (1894) assigned the genera of the tribe Hedysareae to six subtribes, one of which, Stylosanthineae, contained the peanut and its relatives. The basic features which presently tie the peanut and its relatives — *Stylosanthes, Chapmannia,* and *Pachecoa* — into the subtribe were given by Taubert as follows: "Stamens all united into a tube, anthers alternately basally and dorsally attached;" (adnate introrse in *Arachis)* "flowers in terminal or axillary spikes or small heads, seldom somewhat raceme-like; leaves pinnate, mostly with few leaflets, without stipels." The detailed morphological description of *A. hypogaea* L. given above further characterizes the genus *Arachis* which is distinguished from the remaining genera of the Stylosanthineae by the unique fruiting structure of *Arachis,* the peg, and its subterranean fruiting habit (Taubert, 1894; Burkart, 1940; Hoehne, 1940; Smith, 1950; Gregory *et al.,* 1951; Krapovickas and Rigoni, 1957).

The genus *Arachis* prior to 1839 consisted only of the cultivated peanut. However, Bentham (1841) briefly described five additional but wild species of *Arachis* — *A. glabrata, A. pusilla, A. prostrata, A. villosa,* and *A. tuberosa.* Bentham went on to say, "Amongst the above species I have seen the fruit of *A. hypogaea* only. It is probable that when the legumes are known, better distinctive characters may be found, or possibly, that some of the above may be mere varieties of each other, but as far as my specimens go, they appear perfectly distinct." How right he was. He had just described five species, one each of five out of the seven distinct sections of the genus *Arachis* as described by Krapovickas and Gregory (unpublished):

A. glabrata—Rhizomatosae	Riedel, Río Pardo, Mato Grosso, Brazil.
A. pusilla—Triseminalae	Blanchet No. 2669; Serra do Jacobina, Bahía, Brazil.
A. prostrata—Extranervosae	Pohl, Trairas, Goiás, Brazil.
A. villosa—Axonomorphae	Tweedie, Río Grande, southern Brazil.
A. tuberosa—Erectoides	Riedel, Río Pardo, Mato Grosso, Brazil.

Following the work of Bentham, Gardner (1842) described *Arachis marginata* [Section Extranervosae (Krapovickas and Gregory, unpublished)], Gardner No. 3103, Misión Duro, Goiás, Brazil.

Other described species recognized as distinct by Krapovickas and Gregory, along with their sectional subordination, are:

A. hagenbeckii Harms, in O. Kuntze (1898) [section Rhizomatosae],
Hagenbeck 2255, type Caapucú, Paraguay.

A. paraguariensis Chod. *et* Hassl. (1904) [section Erectoides],
Hassler 6358, type Tobatí, Paraguay.

A. guaranitica Chod. *et* Hassl. (1904) [section Erectoides],
Hassler 4975, type Ipe Yhu, Sierra Maracayú, Paraguay.

A. diogoi Hoehne (1919) [section unknown], Diogo, type Gahyba Bay,
Mato Grosso, Brazil.

A. villosulicarpa Hoehne (1944) [section Extranervosae], Telles, Inst. Bot. São Paulo No. 47535, type cult. from seed brought from the indigenes of Juruena and Diamantino, Mato Grosso, Brazil.

A. burkartii Handro (1958) [section Rhizomatosae], Archer 4439 (S.P. 45487), type Sant' Anna, Río Grande do Sul, Brazil.

A. benthamii Handro (1958) [section Erectoides], Handro 682 cult. in São Paulo (S.P. 55525 type), Campo Grande, Mato Grosso, Brazil.

A. martii Handro (1958) [section Erectoides], Otero 174 (S.P. 30158 type), Campo Grande, Mato Grosso, Brazil.

A. repens Handro (1958) [section Caulorhizae], Otero 2999 (S.P. 46152 type), cult. Deodora, Distrito Federal; proc. Estacáo Engenheiro Dolabela, margin of Río Jequitahy (branch of the Jequitinhonha, Minas Gerais, Brazil.

A. monticola Krap. *et* Rig. (1957) [section Axonomorphae], Krapovickas 8012, Holotype, Yala, Jujuy, Argentina.

A. helodes (Martius) Krap. *et* Rig. (1957) [section Axonomorphae], Manso Martius Herb. Florae Brazil 588 (1839), Holotype, Cuiabá, Mato Grosso, Brazil.

A. lutescens Krap. *et* Rig. (1957) [section Extranervosae], Stephens SH255 (LIL 397456), Holotype, Cuiabá, Mato Grosso, Brazil.

A. rigonii Krap. *et* Greg. (1960), [section Erectoides], Krapovickas 9459 Holotype, Santa Cruz de la Sierra, Bolivia.

We have seen the *Arachis* materials growing in the type localities of all of these species except *A. diogoi* Hoehne and *A. repens* Handro. In the latter case, we have visited in person Dr. Thomas A. Dalton who collected in the type locality and whose collection we have seen growing on the Experimental Station, Instituto Agronómico de Oeste, Sete Lagoas, Minas Gerais, Brazil. The species *A. diogoi* Hoehne, though recognized by Krapovickas and Gregory, still presents a problem as to its affinities. The resolution of this problem will not be in hand until living material from the type locality is studied by a qualified investigator.

Other specific names ascribed to the above species and the reference of other specimens to the above names coupled with adventurous use of fragmentary herbarium specimens and their inherent special difficulty in the case of *Arachis* have led to a complicated synonymy and ill-advised speciment reference of species described and undescribed. The present chapter is not the proper medium for the extended taxonomic treatise required to clarify the situation in *Arachis*. The selected illustrations of taxonomic confusion will assist the reader in the exercise of caution until a taxonomic monograph is available. Until that time, investigators should report their results in terms of collection numbers and names of collectors along with the geographic location of original source where available.

Failure to understand the sectional assignments and species relationships of *Arachis* is not confined to other botanists of the 19th and 20th centuries. Krapovickas and Gregory (1960) associated *A. rigonii* with the Axonomorphae but subsequent work has shown that it is in reality a member of the section Erectoides. Krapovickas and Rigoni (1957) confused the annual *Arachis* species of northern Argentina, the perennial species of Bolivia (Axonomorphae), and the annual and perennial species of Ceará, Piauhy, and Pernambuco (Pseudoaxonomorphae) with *A. pusilla* (Triseminalae). The name *A. prostrata* Benth. (Extranervosae) has been assigned to many different decumbent species, in fact, to every other section of the genus:

A. glabrata (Rhizomatosae)	Chevalier (1933), Hermann (1954), and Bentham (1859)
A. prostrata var. *hagenbeckii* (Rhizomatosae)	Hoehne (1940)
A. spp. (Rhizomatosae, Erectoides)	Chodat *et* Hassler (1904) and Hermann (1954)
A. pusilla (Triseminalae)	Chevalier (1933)
A. spp. Gard. 3104 (Pseudo-axonomorphae	Bentham (1859)
A. hypogaea (Axonomorphae)	Hoehne (1940)
A. helodes (Axonomorphae)	Bentham (1859)
A. spp. *(lignosa)* (section unknown)	Chodat *et* Hassler (1904)
A. repens (Caulorhizae)	Hoehne (1940)

et alias.

A similar story may be told for the species name, *A. marginata* Gard.: (Extranervosae)

A. prostrata var. *lignosa* (section unknown)	Hermann (1954)
A. prostrata var. *genuina* (Rhizomatosae)	Chevalier (1933)
A. prostrata var. *pseudovillosa* (Rhizomatosae)	Chevalier (1933)
A. prostrata var. *intermedia* (Rhizomatosae)	Chevalier (1933)
A. burkartii (Rhizomatosae)	Hermann (1954)
A. burkartii (Rhizomatosae)	Hoehne (1940)
A. spp. (Erectoides)	Hoehne (1940)

et alias.

Other isolated examples are:

A. diogoi Hoehne (section unknown) = *A. glabrata* Benth. (Rhizomatosae) (Hermann, 1954)

A. glabrata Benth. (Rhizomatosae) = *A. helodes* Mart. (Axonomorphae) (Chevalier, 1933)

A. pusilla Benth. (Triseminalae) = *A. sylvestris* Chev. = *A. hypogaea* (Axonomorphae) (Chevalier, 1929b, 1933)

The distribution of known collections to sections and series of the genus by plant morphology, geographic area, and cross-compatibility between species has been attempted in Krapovickas and Gregory (unpublished). These sectional names have already been alluded to in the literature by Smartt and Gregory (1967) and by Gregory and Gregory (1967). However, the treatment given here is the first comprehensive English language presentation of excerpts from the formal treatise under preparation by Krapovickas and Gregory. Like all other such treatments, it requires only an additional fundamental geographic area, morphological feature, or new cross-compatibility discovery to alter the scheme below. Nevertheless, we make this premature presentation in the spirit that it is unlikely of basic alteration and it is badly needed by those working with the materials for the improvement of peanuts.

Key to sections of the genus Arachis L.[5]
(after Krapovickas and Gregory, unpublished)

A. Plants with rhizomes.

Sect. *Rhizomatosae*

a. Plants delicate, few leaved, leaflets small coriaceous, with heavy marginal vein. Flowers large, standard (circa 20 mm wide, 18 mm high), deep orange, not fading when dry. Wings usually widely flared open at lower margin, red veins more or less conspicuous on both faces of the standard; diploid.

Ser. *Prorhizomatosae*

aa. Plants usually robust, sometimes small and delicate; in some species leaves adpressed to the soil; occasional specimens very similar to preceding in stem and leaf; flowers large, standard (22-25 mm wide, 18-22 mm high), yellow, soft orange to brilliant orange, no red veins on back of standard, wings usually not flared; tetraploid.

Ser. *Eurhizomatosae*

AA. Plants without rhizomes.

B. Plants tap-rooted.

b. Pegs vertical or nearly so.

c. Plants rooting at the nodes, standard yellow.

Sect. *Caulorhizae*

cc. Plants not rooting at the nodes; standard yellow or orange.

d. Flowers very small, standard (6-8 mm wide, 5-6 mm high), yellow, red veined on back and front.

Sect. *Pseudoaxonomorphae*

dd. Flowers small to medium or large, standard yellow or orange; no red veins on back of standard (pink blush in case of *A. batizocae*).

Sect. *Axonomorphae*

e. Flowers small to medium, standard (9-14 mm wide, 7-12 mm high), yellow or orange; annual or nearly so.

Ser. *Annuae*

ee. Flowers medium to large, standard (14-22 mm wide, 12-18 mm high), orange or yellow; perennial.

Ser. *Perennes*

eee. *A. hypogaea* and *A. monticola.* Flowers small, medium, or large, standard (10-21 mm wide, 8-14 mm high).

Ser. *Amphiploides*

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[5] Flower size of greenhouse plants. The absolute measurements may be greater out of doors.

bb. Pegs horizontal or nearly so.

f. Flowers small, standard (10-12 mm wide, 8-10 mm high), orange with conspicuous purple mark on inside of standard; fruits often 3-segmented.
Sect. *Triseminalae*

ff. Flowers medium to large, standard (16-24 mm wide, 12-20 mm high), no conspicuous marking; fruits usually 2-segmented.
Sect. *Erectoides*

g. Standards yellow, plants prostrate.
Ser. *Procumbensae*

gg. Standards orange, plants erect or prostrate.
Ser. *Tetrafoliolatae*

BB. Plants with thickened lomentiform tuberoid roots or with tuberiform hypocotyl.

h. Pegs horizontal or nearly so; flowers large.
Sect. *Erectoides*

i. Hypocotyl tuberiform, 3-foliolate.
Ser. *Trifoliolatae*

ii. Hypocotyl not tuberiform, 4-foliolate.
Ser. *Tetrafoliolatae*

hh. Pegs vertical or nearly so, frequently with adventitious roots; flowers small to medium, standard orange or yellow with red veins on back.
Sect. *Extranervosae*

SUBORDINATION OF SPECIES OF *ARACHIS* L. (n = 10)

(Specimens seen alive by the authors)

Excerpted from Krapovickas and Gregory (unpublished)

SECTION I. AXONOMORPHAE		
	SERIES 1. ANNUAE	2n
	SERIES 2. PERENNES	2n
	SERIES 3. AMPHIPLOIDES	4n
SECTION II. ERECTOIDES		
	SERIES 1. TRIFOLIOLATAE	2n
	SERIES 2. TETRAFOLIOLATAE	2n
	SERIES 3. PROCUMBENSAE	2n
SECTION III. CAULORHIZAE		2n
SECTION IV. RHIZOMATOSAE		
	SERIES 1. PRORHIZOMATOSAE	2n
	SERIES 2. EURHIZOMATOSAE	4n
SECTION V. EXTRANERVOSAE		2n
SECTION VI. PSEUDOAXONOMORPHAE		2n
SECTION VII. TRISEMINALAE		2n

Figure 18. The rivers of South America important in the distribution of the subgeneric sections of *Arachis.*

Figure 19. *AXONOMORPHAE.* Closest relatives of the cultivated peanut. Except for migration around the La Plata coast of Uraguay and up the Atlantic Seaboard, they lie generally to the west of the 57th parallel. The Axonomorphae may be the most youthful of all sections of the genus.

SUBORDINATION OF THE SPECIES OF *ARACHIS* L. (only specimens seen alive by the authors)

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality[6]
SECTION 1. AXONOMORPHAE					
SERIES 1. ANNUAE					
178 (10038)	HL (GKP)	331189	1968	*A.* sp.	Cult. Manfredi, Argentina.
207 (9484)	HLP (K)	338312		*A. batizocae* Krap. *et* Greg. (unpub.)	Cult. Corrientes, Argentina.
7988	K	219823	5-29-53	*A. duranensis* Krap. *et* Greg. (unpub.)	On road to oil wells, Dep. Campo Durán, Prov. San Martín, Salta, Argentina; 22°19′, 63°43′, 500m.
9484 (207)	K (HLP)	298639 (338312)	2-24-58	*A. batizocae* Krap. *et* Greg. (unpub.)	Near railway station on the r.r. S. Cruz de la Sierra to Yacuiba, Parapetí, Dep. Santa Cruz, Prov. Cordillera, Bolivia; 20°5′, 63°14′, 700m.
10038	GKP	263133 262133	4-7-59	*A.* sp.	Along edge of stream (Río Arenates), 12 km SW of Salta, Argentina; 24°47′, 65°32′, 1250m.
SERIES 2. PERENNES					
8	HLP	338321	4-26-68	*A. villosa* Benth.	67 m from the bank of Río de la Plata, Playa Artilleros, 9 km NW Colonia, Uruguay; 34°24′, 57°51′, 0+m.
9	HLP	330650	4-26-68	*A. villosa* Benth.	67 m from the bank of Río de la Plata, Playa Artilleros, 9 km NW Colonia, Uruguay; 34°24′, 57°51′, 0+m.
10	HLP	338322	4-26-68	*A. villosa* Benth.	Sand dunes, 200 m from Río de la Plata, 7 km NW of Colonia, Uruguay; 34°24′, 57°51′, 0+m.
11	HLP	330651	4-26-68	*A. villosa* Benth.	Sand dunes, 200 m from Río de la Plata, 7 km NW Colonia, Uruguay; 34°24′, 57°51′, 0+m.
12	HLP	338323	4-26-68	*A. villosa* Benth.	125 m from Río de la Plata, 14 km E of Colonia, Uruguay; 34°27′, 57°40′, 0+m.
13	HLP	330652	4-26-68	*A. villosa* Benth.	125 m from Río de la Plata, 14 km E of Colonia, Uruguay; 34°27′, 57°40′, 0+m.
14	HLP	338324	4-26-68	*A. villosa* Benth.	40 m from Río de la Plata, 7 km E of Colonia, Uruguay; 34°27′, 57°40′, 0+m.
15	HLP	330653	4-26-68	*A. villosa* Benth.	40 m from Río de la Plata in sand dunes, 7 km E of Colonia, Uruguay; 34°27′, 57°40′, 0+m.

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[6] Latitude in degrees and minutes south and longitude in degrees and minutes west. These data and the elevation obtained from maps of scale 1:1,000,000.

Coll. No.	Collec-tor	P.I. No.	Mo/day/yr	Name	Locality
SECTION 1. AXONOMORPHAE — SERIES 2. PERENNES (cont.)					
77 (12404)	HL (KCPa)	331198	1868	*A.* sp.	Cult. Manfredi, Argentina.
173 (7830)	HL (K)	331191	1968	*A. correntina* (Burk.) Krap. *et* Greg. (unpub.)	Cult. Manfredi, Argentina.
174 (7897)	HL (K)	331192	1968	*A. correntina*	Cult. Manfredi, Argentina.
175 (9530) (9531)	HL (GKP) (GKP)	331193	1968	*A. correntina*	Cult. Manfredi, Argentina.
176 (9548)	HL (GKP)	331194	1968	*A. correntina*	Cult. Manfredi, Argentina.
177 (22585)	HLP (B)	331196 (298636)	1968	*A. villosa* Benth.	Cult. Manfredi, Argentina, proc. Prov. Entre Ríos, Dep. Santa Ana, Federación, Argentina; 30°56′, 57°57′, 35m.
179	HL	331197	1968	*A.* sp. (listed by Hammons as *A. villosa)*	Cult. Manfredi, Argentina.
183 (10602)	HL (GKP)	331200	1968	*A. chacoense* Krap. *et* Greg. (unpub.)	Cult. Manfredi, Argentina.
186 (12593)	HL (KCPa)	331195	1968	*A.* sp.	Cult. Manfredi, Argentina.
206	HLKP	338310	1968	*A. correntina*	Río Riachuelo, Corrientes, Argentina.
322 (12593)	HL (KCPa)	338313	1968	*A.* sp.	Cult. Corrientes, Argentina.
332	HLO	338311	1968	*A.* sp.	9 km SE of San Luis de Palmar, Route 5, Corrientes, Argentina; 27°36′, 58°35′, 58m.
357	HLKO	338309	5-19-68	*A.* sp.	Paso de los Libres, 500 m S of International Bridge, Corrientes, Argentina; 29°44′, 57°7′, 63m.
408 (409)	HLK (HLK)	338279 (337308)	5-28-68 (5-28-68)	*A.* sp.	Ponta de Pita, 1 km SW of Port Administration Office, near sea coast, 6 km from center of Antonina, Paraná, Brazil; 25°24′, 48°44′, 3m.
410 (411)	HLK (HLK)	338280 (337309)	5-28-68 (5-28-68)	*A.* sp.	Near railway, 200 m from sea coast, Porto Dom Pedro II (Vila dos Portuarios, Paranaguá, Paraná, Brazil; 25°31′, 48°31′, 3m.
7830	K	262137 298634	3-3-53	*A. correntina* (Burk.) Krap. *et* Greg. (unpub.)	Arroyo Riachuelo, Ruta 12, 15 km S of Corrientes city on the road to Empedrado, Corrientes, Argentina; 27°33′, 58°46′, 50m.
7897	K	262134 298635	3-5-53	*A. correntina* (Burk.) Krap. *et* Greg. (unpub.)	Ituzaingó, Dep. Ituzaingó, Corrientes, Argentina.

Coll. No.	Collector	P.I. No.	Mo/day/yr.	Name	Locality
SECTION 1. AXONOMORPHAE — SERIES 2. PERENNES (cont.)					
9530	GKP	262808	1-23-59	*A. correntina* (Burk.) Krap. *et* Greg. (unpub.)	Arroyo Riachuelo, Ruta 12, 15 km S of Corrientes city on the road to Empedrado, Corrientes, Argentina; 27°33′, 58°46′, 50m.
9531	GKP	262880 262809	1-23-59	*A. correntina* (Burk.) Krap. *et* Greg. (unpub.)	Arroyo Riachuelo, Ruta 12, 15 km S of Corrientes city on the road to Empedrado, Corrientes, Argentina; 27°33′, 58°46′, 50m.
9901	GKP	262270 262290	3-9-59	*A.* sp.	By the side of the road, 176 km N of São Lourenço, 70 km ± E of Cuiabá, Mato Grosso, Brazil; 15°43′, 55°48′, 130m.
9926	GKP	262275 262300	3-13-59	*A. helodes* (Mart.) Krap. *et* Rig.	At end of bridge over a small river at the NW edge of the city of Cuiabá, Mato Grosso, Brazil; 15°36′, 56°6′, 170m.
10017	GKP	262141	3-31-59	*A. cardenasii* Krap. *et* Greg. (unpub.)	Roboré, Bolivia; 18°20′, 59°46′, 200m.
10026	GKP		4-1-59	*A. cardenasii* Krap. *et* Greg. (unpub.)	2 km SW Roboré, Bolivia; 18°20′, 59°46′, 200m.
10602	GKP	276235	5-19-61	*A. chacoense* Krap. *et* Greg. (unpub.)	In 2 football fields & along the r.r. in Puerto Casado, Paraguay; 22°17′, 57°59′, <100m.
12404	KCPa		2-4-66	*A.* sp.	Bank of Río Tebicuary, Frente a Florida, Paraguay; 26°22′, 57°5′, 65m.
12593	KCPa		2-10-66	*A.* sp.	Cerró Peró, between Ipacaray and Pirayu, Paraguay; 25°26′, 57°15′, 175m. (cult. Corrientes, Argentina—HLK).
(186)	(HLK)	(331195)	(1968)		
(322)	(HLK)	(338313)	(1968)		
(328)	(HLK)	(337360)	(1968)		
SERIES 3. AMPHIPLOIDES					
7264	K	219824 263393 298364 298365	5-23-50	*A. monticola* Krap. *et* Rig.	Border of road near r.r. station, Yala, Jujuy, Argentina; 24°7′, 65°24′, 1445m. (cult. Manfredi, Argentina—HLP).
(104)	(HLP)	(331338)	(1968)		
(105)	(HLP)	(331339)	(1968)		
For P.I. No's., see: pp. 51-67 of this chapter & *Catalogue of Seed,* Section A. *Arachis* spp. *Southern Regional Plant Introduction Station,* Experiment, Georgia 30212.				*A. hypogaea* L.	Cultivated: Pre-Columbian; Mexico, Antilles, and South America—Post-Columbian; throughout warm temperate and tropical world.

Figure 20. *ERECTOIDES.* Except for the Procumbensae, the Erectoides are limited to the Paraguay-Paraná basin. They are sympatric with the Rhizomatosae with which they intercross freely in artificial culture. They appear to have made the most profound biological commitment to geocarpy of all species of peanuts.

SECTION II. ERECTOIDES

SERIES 1. TRIFOLIOLATAE

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
9665	GKP	262799	2-17-59	*A. guaranitica* Chod. *et* Hassl.	1 km to Río Amambay on the road to Amambay from Ponta Porá, Mato Grosso, Brazil; 22°57′, 55°13′, 400m.
9680	GKP	262868	2-18-59	*A. guaranitica* Chod. *et* Hassl.	1 km from Capitán-Bado on the Capitán-Bado to Ipe Yhu road, Mato Grosso, Brazil; 23°16′, 55°33′, 500m.
9701	GKP	262869	2-19-59	*A. guaranitica* Chod. *et* Hassl.	5 km from Amambay on the Amambay-Ponta Porá road, Mato Grosso, Brazil; 23°3′, 55°15′, 500m.
9818	GKP		2-25-59	*A. tuberosa* Benth.	15 km SE Campo Grande on Fazenda Imbírussú, Mato Grosso, Brazil; 20°34′, 54°30′, 550m.
9837	GKP	262277	3-5-59	*A. tuberosa* Benth.	54 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 20°1′, 54°24′, 570m.
9942	GKP	262302	3-16-59	*A. tuberosa* Benth.	10 km NW of Jatai, Goiás, Brazil; 17°56′, 51°47′, 650m.
10568 (574)	GK (HLKHe)	276194 (338269)	5-14-61 (6-13-68)	*A. guaranitica* Chod. *et* Hassl.	1 km N of Río Amambay on road from Ponta Porá to Amambay, Mato Grosso, Brazil; 22°57′, 55°13′, 400m.

SERIES 2. TETRAFOLIOLATAE

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
78 (11462)	HL (KCF)		1968	*A. paraguariensis* Chod. *et* Hassl.	Cult. Manfredi, Argentina.
180 (9812)	HL (GKP)	331199	1968	*A.* sp.	Cult. Manfredi, Argentina.
181 (9835)	HL (GKP)	331184	1968	*A.* sp.	Cult. Manfredi, Argentina.
182 (9841)	HL (GKP)	331185	1968	*A.* sp.	Cult. Manfredi, Argentina.
185 (9993)	HL (GKP)	331201	1968	*A.* sp.	Cult. Manfredi, Argentina.
187 (11488)	HL (KC)	331187	1968	*A. paraguariensis* Chod. *et* Hassl.	Cult. Manfredi, Argentina.
188 (11462)	HL (KCF)	331188	1968	*A. paraguariensis* Chod. *et* Hassl.	Cult. Manfredi, Argentina.
208 (11462)	HL (KCF)	338306	1968	*A. paraguariensis* Chod. *et* Hassl.	Cult. Corrientes, Argentina.
324 (11488)	HL (KC)	338307	1968	*A. paraguariensis* Chod. *et* Hassl.	Cult. Corrientes, Argentina.
325 (11462)	HL (KCF)	338308	1968	*A. paraguariensis* Chod. *et* Hassl.	Cult. Corrientes, Argentina.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION II. ERECTOIDES — SERIES 2. TETRAFOLIOLATAE (cont.)					
330 (11488)	HL (KC)	336899	1968	*A. paraguariensis* Chod. *et* Hassl.	Cult. Corrientes, Argentina.
499	HLKHe	338252	6-5-68	*A. benthamii* Handro.	Cult. Matáo, São Paulo, Brazil. (Gullöve No. 1482, 7-18-62)
520 (578)	HLKHe (HLKHe)	338253 (336901)	6-7-68 (6-13-68)	*A. benthamii* Handro.	42 km W of bridge, Porto 15 de Noviembre, Mato Grosso, Brazil; 21°45′, 52°36′, 275m.
521 (579)	HLKHe (HLKHe)	338285 (336907)	6-7-68 (6-13-68)	*A. oteroi* Krap. *et* Greg. (unpub.)	42 km W of bridge, Porto 15 de Noviembre, Mato Grosso, Brazil; 21°45′, 52°36′, 275m.
522 (10545)	HLKHe (GK)	338286	6-7-68	*A. oteroi* Krap. *et* Greg. (unpub.)	230 km W of Mato Grosso, São Paulo border at P. 15 de Noviembre highway, BR 267, Brazil; 21°40′, 54°1′, 400m.
523	HLKHe	338287	6-7-68	*A. oteroi* Krap. *et* Greg. (unpub.)	5 km N of entrocamento, Campo Grande, Río Brillante highway, Mato Grosso, Brazil; 21°25′, 54°20′, 400m.
524	HLKHe	338288	6-8-68	*A. oteroi* Krap. *et* Greg. (unpub.)	10 km S of Campo Grande on road S to Faz. Imbirussú, Mato Grosso, Brazil; 20°34′, 54°35′, 500m.
526 (525)	HLKHe (HLKHe)	338270	6-8-68 (6-8-68)	*A. martii* Handro.	Praça de Esportes de Colegio Batista Matogrossense, 15 km SE of Campo Grande, Imbirussú, Mato Grosso, Brazil; 20°34′, 54°30′, 550m.
457 547	HLKHe	338268	6-9-68	*A.* sp.	Airport Campo Grande, Mato Grosso, Brazil; 20°29′, 54°40′, 543m.
548	HLKHe	338289	6-9-68	*A.* sp.	Airport near highway Campo Grande, Mato Grosso, Brazil; 20°29′, 54°40′, 543m.
550	HLKHe	338200	6-9-68	*A.* sp.	Mun. Terenos, 4 km E of Murtinho, 70 km W of Campo Grande, Mato Grosso, Brazil; 20°26′, 55°10′, 300m.
551	HLKHe	338291	6-9-68	*A.* sp.	Mun. Terenos, 70 km W. of Campo Grande, Mato Grosso, Brazil; 20°26′, 55°10′, 300m.
554	HLKHe	338292	6-9-68	*A.* sp.	2 km W of Palmeira and bridge across Aquidauana, Mun. Anastácio, Mato Grosso, Brazil; 20°26′, 55°23′, 225m.
555	HLKHe	338293	6-9-68	*A.* sp.	2 km E of Piraputanga, 28 km E of Aquidauana, Mun. Anastácio, Mato Grosso, Brazil; 20°25′, 55°31′, 200m.
559	HLKHe	338294	6-10-68	*A.* sp.	On road to Nioaque, 40 km S of Aquidauana, Mato Grosso, Brazil; 20°50′, 55°53′, 250m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION II. ERECTOIDES — SERIES 2. TETRAFOLIOLATAE (cont.)					
562	HLKHe	338295	6-10-68	*A.* sp.	8 km W of Jardim on road to Porto Murtinho, Mato Grosso, Brazil; 21°29′, 56°13′, 300m.
570	HLKHe	338271	6-12-68	*A. paraguariensis* Chod. *et* Hassl.	64 km E Porto Murtinho highway BR-34, Mato Grosso, Brazil; 21°39′, 57°19′, 200m.
572	HLKHe	338302	6-12-68	*A.* sp.	87 km E of Porto Murtinho highway BR-34, Mato Grosso, Brazil; 21°34′, 57°10′, 250m.
573	HLKHe	338272	6-12-68	*A. paraguariensis* Chod. *et* Hassl.	108 km E of Porto Murtinho, BR-34, Mato Grosso, Brazil; 21°31′, 56°58′, 300m.
9632	GKP		2-12-59	*A.* sp.	Valley in the Sierra Amambay, 30 km W of Ponta Porá on the road to Concepcion, Paraguay; 22°39′, 56°0′, 350m.
9646	GKP	262842 262874	2-14-59	*A. paraguariensis* Chod. *et* Hassl.	Bela Vista, Mato Grosso, Brazil; 22°7′, 56°32′, 200m.
9648	GKP		2-14-59	*A. paraguariensis* Chod. *et* Hassl.	7 km from Bela Vista on road from Bela Vista to Ponta Porá, Paraguay-Brazilian frontier, 3-4 km S of Arroyo Estrella; 22°4′, 56°29′, 250m.
9651	GKP		2-14-59	*A.* sp.	20-25 km from Bela Vista on road from Bela Vista to Ponta Porá, Paraguay-Brazilian frontier; 22°5′, 56°18′, 300m.
9652	GKP	262846	2-14-59	*A.* sp.	About 10 km before reaching Penso on the road Bela Vista-Ponta Porá, Paraguay-Brazilian frontier; 22°13′, 55°58′, 650m.
9735	GKP		2-22-59	*A. oteroi* Krap. *et* Greg. (unpub.)	Airport, Campo Grande, Mato Grosso, Brazil; 20°29′, 54°40′, 543m.
9736	GKP		2-22-59	*A.* sp.	Airport, Campo Grande, Mato Grosso, Brazil; 20°29′, 54°40′, 543m.
9747	GKP	262856	2-26-59	*A. oteroi* Krap. *et* Greg. (unpub.)	3 km from Bataguaçú on the road to Xavantina, Mato Grosso, Brazil; 21°40′, 52°22′, 250m.
9753	GKP	262857 262876	2-26-59	*A. benthamii* Handro	12 km from Bataguaçú on the road to Xavantina, Mato Grosso, Brazil; 21°41′, 52°28′, 250m.
9761	GKP	262858	2-26-59	*A. benthamii* Handro	5-7 km from ferry across the Río Pardo on road from Bataguaçú to Xavantina, Mato Grosso, Brazil; 21°38′, 52°31′, 250m.
9763	GKP		2-26-59	*A. oteroi* Krap. *et* Greg. (unpub.)	Fazenda Tres Barros, between Xavantina and Porto Ueve (ferry), Mato Grosso, Brazil; 21°34′, 52°34′, 300m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION II. ERECTOIDES — SERIES 2. TETRAFOLIOLATAE (cont.)					
9764	GKP	262859	2-26-59	*A. benthamii* Handro	30 km SE of Xavantina on the road from Bataguaçú, on Fazenda Pozo Alto, Mato Grosso, Brazil; 21°28′, 52°37′, 350m.
9765	GKP	262877 262860	2-26-59	*A. oteroi* Krap. *et* Greg. (unpub.)	30 km SE of Xavantina on road from Bataguaçú, on Fazenda Pozo Alto, Mato Grosso, Brazil; 21°28′, 52°37′, 350m.
9766	GKP	262861 262878	2-27-59	*A. oteroi* Krap. *et* Greg. (unpub.)	3-4 km NW of Fazenda Pozo Alto on road from Bataguaçú to Xavantina, Mato Grosso, Brazil; 21°27′, 52°39′, 350m.
9769	GKP	262862	2-27-59	*A. benthamii* Handro	Between Fazenda Pozo Alto and Xavantina on road from Bataguaçú, Mato Grosso, Brazil; 21°24′, 52°44′, 350m.
9770	GKP		2-27-59	*A.* sp.	Between Fazenda Pozo Alto and Xavantina on road from Bataguaçú, Mato Grosso, Brazil; 21°24′, 52°44′, 350m.
9771	GKP	263103	2-27-59	*A.* sp.	Near Xavantina, Mato Grosso, Brazil; 21°20′, 52°45′, 400m.
9772	GKP	263096	2-27-59	*A.* sp.	Near Xavantina, Mato Grosso, Brazil; 21°20′, 52°45′, 400m.
9774	GKP		2-27-59	*A.* sp.	Near Xavantina, Mato Grosso, Brazil; 21°20′, 52°45′, 400m.
9775	GKP		2-28-59	*A.* sp.	25 km W of Bataguaçú on road to Campo Grande, Mato Grosso, Brazil; 21°45′, 52°36′, 275m.
9776	GKP		2-28-59	*A.* sp.	25 km W of Bataguaçú on road to Campo Grande, Mato Grosso, Brazil; 21°45′, 52°36′, 275m.
9784	GKP		2-28-59	*A. benthamii* Handro	Bataguaçú, Mato Grosso, Brazil; 21°43′, 52°25′, 275m.
9786	GKP		2-28-59	*A. oteroi* Krap. *et* Greg. (unpub.)	Bataguaçú, Mato Grosso, Brazil; 21°43′, 52°25′, 275m.
9788	GKP	262790	2-28-59	*A.* sp.	Fazenda San Jorge, 80 km W of Bataguaçú on road to Campo Grande, Mato Grosso, Brazil; 21°37′, 53°6′, 275m.
9790	GKP	262805 262870	2-28-59	*A. oteroi* Krap. *et* Greg. (unpub.)	135 km W of Bataguaçú on road to Campo Grande, Mato Grosso, Brazil; 21°36′, 53°36′, 300 m.
9792	GKP		2-28-59	*A. oteroi* Krap. *et* Greg. (unpub.)	150 km W of Bataguaçú, Mato Grosso, Brazil; 21°37′, 53°45′, 400m.
9793	GKP		3-1-59	*A. oteroi* Krap. *et* Greg. (unpub.)	10 km E of intersection of roads from Bataguaçú to Campo Grande and Campo Grande to Río Brillante, Mato Grosso, Brazil; 21°30′, 54°16′, 400m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION II. ERECTOIDES — SERIES 2. TETRAFOLIOLATAE (cont.)					
9795	GKP	262863	3-1-59	*A.* sp.	10 km E of intersection of roads from Bataguaçú to Campo Grande and Campo Grande to Río Brillante, Mato Grosso, Brazil; 21°30′, 54°16′, 400m.
9799	GKP		3-1-59	*A.* sp.	10 km E of intersection of roads from Bataguaçú to Campo Grande and Campo Grande to Río Brillante, Mato Grosso, Brazil; 21°30′, 54°16′, 400m.
9800	GKP	263104 262879	3-1-59	*A.* sp.	10 km E of intersection of roads from Bataguaçú to Campo Grande and Campo Grande to Río Brillante, Mato Grosso, Brazil; 21°30′, 54°16′, 400m.
9803	GKP		3-1-59	*A. benthamii* Handro	Road intersection Campo Grande, Río Brillante, Mato Grosso, Brazil; 21°29′, 54°20′, 400m.
9805	GKP	262866	3-1-59	*A.* sp.	70 km S of Campo Grande on road to Río Brillante, Mato Grosso, Brazil; 21°5′, 54°30′, 400m.
9810 (180)	GKP (HL)	(331199)	3-1-59 (1968)	*A. oteroi* Krap. *et* Greg. (unpub.)	16 km toward Campo Grande, beyond intersection of roads Campo Grande, Río Brillante & Bataguaçú, Mato Grosso, Brazil; 21°20′, 54°20′, 400m.
9811	GKP		2-23-59	*A.* sp.	7 km S of Campo Grande, Mato Grosso, Brazil; 20°32′, 54°36′, 500m.
9812	GKP		2-23-59	*A.* sp.	7 km S of Campo Grande, Mato Grosso, Brazil; 20°32′, 54°36′, 500m.
9814	GKP	262867	2-24-59	*A.* sp.	Criaçáo Expt. Sta., 30 km S of Campo Grande, Mato Grosso, Brazil; 20°43′, 54°33′, 450m.
9816	GKP		2-24-59	*A.* sp.	Criaçáo Expt. Sta., 30 km S of Campo Grande, Mato Grosso, Brazil; 20°43′, 54°33′, 450m.
9817	GKP		2-24-59	*A.* sp.	Indubrazil 18 km W of Campo Grande, Mato Grosso, Brazil; 20°29′, 54°43′, 500m.
9819	GKP	262806	2-25-59	*A. oteroi* Krap. *et* Greg. (unpub.)	Fazenda Imbirussú, 15 km SE of Campo Grande, Mato Grosso, Brazil; 20°34′, 54°30′, 550m.
9820	GKP	262791	2-25-59	*A.* sp.	Fazenda Imbirussú, 15 km SE of Campo Grande, Mato Grosso, Brazil; 20°34′, 54°30′, 550m.
9821	GKP		3-3-59	*A.* sp.	Fazenda Imbirussú, 15 km SE of Campo Grande, Mato Grosso, Brazil; 20°34′, 54°30′, 550m.

SECTION II. ERECTOIDES — SERIES 2. TETRAFOLIOLATAE (cont.)

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
9824	GKP		2-27-59	*A.* sp.	Aquidauana, Mato Grosso, Brazil; 20°28′, 55°46′, 200m.
9825	GKP	263105	2-27-59	*A.* sp.	Aquidauana, Mato Grosso, Brazil; 20°28′, 55°46′, 200m.
9826	GKP	262865	2-27-59	*A.* sp.	Airfield, Aquidauana, Mato Grosso, Brazil; 20°28′, 55°46′, 200m.
9828	GKP		3-3-59	*A. oteroi* Krap. *et* Greg. (unpub.)	Río Pardo, Mato Grosso, Brazil (on the west side of the river); 20°27′, 53°43′, 365m.
9829	GKP		3-3-59	*A.* sp.	Río Pardo, Mato Grosso, Brazil (on the west side of the river); 20°27′, 53°43′, 365m.
9831	GKP		3-5-59	*A.* sp.	21 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 20°20′, 54°31′, 500m.
9832	GKP		3-5-59	*A. oteroi* Krap. *et* Greg. (unpub.)	37 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 20°12′, 54°27′, 500m.
9835	GKP	262308	3-5-59	*A.* sp.	48 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 20°5′, 54°24′, 570m.
9839	GKP	262267 262283	3-5-59	*A.* sp.	54 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 20°1′, 54°24′, 570m.
9841 (326)	GKP (HLK)	262278 (337359)	3-5-59 (1968)	*A.* sp.	54 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 20°1′, 54°24′, 570m. (cult. Corrientes, Argentina—HLK)
9843	GKP	262279	3-5-59	*A.* sp.	54 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 20°1′, 54°24′, 570m.
9848	GKP	262280	3-6-59	*A.* sp.	100 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil, ±25 km N of Bandeirante; 19°41′, 54°19′, 500m.
9853	GKP		3-6-59	*A.* sp.	±103 km N of Campo Grande on road to Cuiabá, Congonha, Mato Grosso, Brazil; 19°40′, 54°20′, 500m.
9855	GKP		3-6-59	*A. oteroi* Krap. *et* Greg. (unpub.)	135 km N of Campo Grande on the road to Cuiabá, Mato Grosso, Brazil; 19°33′, 54°26′, 500m.
9858	GKP	262281	3-6-59	*A. oteroi* Krap. *et* Greg. (unpub.)	163 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 19°24′, 54°38′, 400m.
9863	GKP	262282	3-6-59	*A. oteroi* Krap. *et* Greg. (unpub.)	190 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 19°13′, 54°45′, 500m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION II. ERECTOIDES — SERIES 2. TETRAFOLIOLATAE (cont.)					
9864	GKP		3-6-59	*A.* sp.	190 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 19°13′, 54°45′, 500m.
9865	GKP		3-6-59	*A.* sp.	195 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 19°10,′ 54°45,′ 500m.
9869	GKP	262268 262284	3-6-59	*A.* sp.	221 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 19°0′, 54°50′, 400m.
9875	GKP	262285	3-7-59	*A.* sp.	11 km N of Río Verde, Mato Grosso, Brazil; 18°50′, 54°49′, 290m.
9880	GKP		3-7-59	*A.* sp.	32 km N of Río Verde on road to Cuiabá, Mato Grosso, Brazil; 18°39′, 54°45′, 270m.
9883	GKP		3-7-59	*A.* sp.	52 km N of Río Verde, Mato Grosso, Brazil; 18°28′, 54°46′, 247m.
9889	GKP		3-8-59	*A.* sp.	108 km N of Gaucho, Mato Grosso, Brazil; 17°4′, 54°48′, 300m.
9990	GKP	261877	3-27-59	*A.* sp.	Airport, Corumbá, Mato Grosso, Brazil; 19°2,′ 57°41′, 200m.
9993	GKP	261878	3-28-59	*A.* sp.	At base of hill on road to Urucum, outskirts of Corumbá, Mato Grosso, Brazil; 19°0′, 57°40′, 166m.
10000	GKP		3-29-59	*A.* sp.	Road to Urucum on outskirts of Corumbá, Mato Grosso, Brazil; 19°0′, 57°40′, 166m.
10002	GKP		3-29-59	*A.* sp.	3 km from Corumbá on road to Urucum, Mato Grosso, Brazil; 19°1′, 57°39′, 166m.
10138	GKP	276204	4-5-61	*A.* sp.	Near Itumbiara, across the river into Goiás, Brazil; 18°25′, 49°11′, 450m.
10541	GK	276208	5-11-61	*A. oteroi* Krap. *et* Greg. (unpub.)	10 km W of Douradinha, Mato Grosso, Brazil; 21°36′, 53°20′, 300m.
10543	GK	276209	5-11-61	*A.* sp.	45 km W of Douradinha, Mato Grosso, Brazil; 21°37′, 53°41′, 400m.
10545	GK	276210	5-11-61	*A. oteroi* Krap. *et* Greg. (unpub.)	40 km E of entrocamento of roads from Porto 15 de Noviembre to Río Brillante & Compo Grande, Mato Grosso, Brazil; 21°40′, 54°1′, 400m.
10547	GK		5-11-61	*A. Benthamii* Handro	9 km E of entrocamento road Porto 15 de Noviembre to Río Brillante, Mato Grosso, Brazil.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION II. ERECTOIDES — SERIES 2. TETRAFOLIOLATAE (cont.)					
10548	GK		5-11-61	*A. Benthamii* Handro	5 km E of entrocamento road Porto 15 de Noviembre to Río Brillante, Mato Grosso, Brazil.
10549	GK	276211	5-11-61	*A.* sp.	9 km E of entrocamento of roads from Porto 15 de Noviembre to Río Brillante and Campo Grande, Mato Grosso, Brazil; 21°30′, 54°17′, 400m.
10551	GK		5-11-61	*A.* sp.	5 km E of entrocamento of roads from Porto 15 de Noviembre to Río Brillante and Campo Grande, Mato Grosso, Brazil.
10554	GK	276212	5-12-61	*A.* sp.	5 km S of Río Brillante on road to Dourados, Mato Grosso, Brazil; 21°51′, 54°32′, 400m.
10556	GK	276214	5-12-61	*A.* sp.	5 km NE of Dourados on road from Río Brillante, Mato Grosso, Brazil; 22°14′, 54°46′, 400m.
10557	GK	276215	5-12-61	*A.* sp.	28 km SW of Dourados on road to Ponta Porá, Mato Grosso, Brazil; 22°19′, 55°2′, 400m.
10562	GK	276220	5-13-61	*A.* sp.	Near Estancia San Luis, ±40 km NW of Ponta Porá, Paraguay; 22°28′, 55°57′, 600m.
10573	GK	276225	5-16-61	*A.* sp.	48 km W of Ponta Porá on road to Concepción, Paraguay; 22°40′, 56°7′, 300m.
10575	GK	276227	5-16-61	*A.* sp.	54 km W of Ponta Porá on road to Concepción, Paraguay; 22°42′, 56°11′, 300m.
10576	GK	276228	5-16-61	*A.* sp.	62 km W of Ponta Porá on road to Concepción, Paraguay; 22°43′, 56°15′, 300m.
10580	GK	276229	5-16-61	*A.* sp.	70 km W of Ponta Porá on road to Concepción, Paraguay; 22°45′, 56°19′, 250m.
10582	GK	276230	5-16-61	*A.* sp.	2 km W of Nu Porá, ±100 km W of Ponta Porá on road to Concepción, Paraguay; 22°51′, 56°26′, 200m.
10585	GK	276231	5-16-61	*A. paraguariensis* Chod. *et* Hassl.	Ñu Porá, 100 km W of Ponta Porá on road to Concepción, Paraguay; 22°52′, 56°29′, 200m.
10588	GK	276232	5-16-61	*A.* sp.	Ñu Porá, 100 km W of Ponta Porá, Paraguay; 22°52′, 56°29′, 200m.
11462 (331)	KCF (HLK)	(33735~~0~~8)	5-24-64 (1968)	*A. paraguariensis* Chod. *et* Hassl.	Tobatí, Dep. Cordillera, Paraguay; 25°15′, 57°4′, 125m. (cult. Corrientes, Argentina—HLK).

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION II. ERECTOIDES — SERIES 2. TETRAFOLIOLATAE (cont.)					
11488	KC		5-26-64	*A. paraguariensis* Chod. *et* Hassl.	Ipacaray, Camino San Bernardino, 2 km de la Ruta II, Paraguay; 25°23′, 57°16′, 175m.
12456	KCPa		2-6-66	*A. paraguariensis* Chod. *et* Hassl.	17 km from Paraguarí on road to Peribebuy, Dep. Cordillera, Paraguay.
14389	KHe		6-7-68	*A.* sp.	42 km W of Porto 15 de Noviembre, Mato Grosso, Brazil.
14424	KHe		6-10-68	*A.* sp.	5 km S of Nioaque, Mato Grosso, Brazil.
14442	KHe		6-12-68	*A.* sp.	90 km E of Porto Murtinho, Mato Grosso, Brazil.
14444	KHe	338320	6-14-68	*A.* sp.	Cerró Corá, Dep. Amambay, Paraguay, 45 km W of Ponta Porá; 22°40′, 56°9′, 300m.
14447	KHe		6-9-68	*A.* sp.	4 km E of Murtinho, Terenos, Mato Grosso, Brazil.
SERIES 3. PROCUMBENSAE					
10034 (184)	GKP (HLP)	262142 (331190)	4-5-59 (1968)	*A. rigonii* Krap. *et* Greg.	Outskirts of Santa Cruz de Sierra, Bolivia, on road to Warnes; 17°50′, 63°10′, 400m. (cult. Manfredi, Argentina—HLP).
SECTION III. RHIZOMATOSAE					
SERIES 1. PRORHIZOMATOSAE					
16	HLP	338325	4-28-68	*A. burkartii* Handro	Mirador Las Lavanderas at Salto, 50 m from Río Uruguay, Uruguay; 31°24′, 57°58′, 48m.
17	HLP	338326	4-28-68	*A. burkartii* Handro	4 km S of Salto on bank of Río Uruguay, Uruguay; 31°25′, 57°59′, 48m.
23	HLP	338327	4-29-68	*A. burkartii* Handro	Route 5, 30 km NE Tacuarembó, Uruguay; 31°37′, 55°45′, 178m.
24	HLP	338328	4-29-68	*A. burkartii* Handro	Route 5, 74 km N of Tacuarembó, 46 km S of Rivera, Uruguay; 31°17′, 55°38′, 200m.
27	HLP	338329	4-30-68	*A. burkartii* Handro	8 km W of Route 5 on Route 30, 6 km E of Tranqueras, Uruguay; 31°14′, 55°42′, 200m.
354	HLKO	338319	5-19-68	*A. burkartii* Handro	Route 23, toward Paso de los Libres, 16 km SE of Mercedes, Corrientes, Argentina; 29°17′, 57°57′, 100m.
355	HLKO		5-19-68	*A. burkartii* Handro	38 km SE of Mercedes, Corrientes, Argentina; 29°23′, 57°46′, 90m.
362	HLK	338254	5-21-68	*A. burkartii* Handro	14 km E of Uruguaiana on road to Alegrete, Río Grande do Sul, Brazil; 29°50′, 56°56′, 100m.

Figure 21. *RHIZOMATOSAE.* Widespread in the Paraguay-Paraná basin, in the upper waters of southern branches of the Amazon to the north and the Uruguay to the south, the Rhizomatosae appear to be a recent and aggressive addition to *Arachis* paralleling in many ways the development of the Axonomorphae.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION III. RHIZOMATOSAE — SERIES 1. PRORHIZOMATOSAE (cont.)					
364	HLK	338255	5-21-68	*A. burkartii* Handro	10 km SE of Alegrete, Río Grande do Sul, Brazil; 29°49′, 55°42′, 100m.
9974	GKP	262307	3-23-59	*A. burkartii* Handro	Cultivated Instituto Botanico São Paulo, Brazil; Proc. Río Grande do Sul, Brazil.
SERIES 2. EURHIZOMATOSAE					
2 (v. 799)	HL	338256	1968	*A.* sp.	Cult. Campinas, São Paulo, Brazil.
333	HLO	338316	5-16-68	*A.* sp.	Paso Florentín, Route 5, Corrientes, Argentina.
334	HLO	338304	5-16-68	*A.* sp.	10 km W of Gen. Páz, between Paso Florentín & Gen. Páz, Corrientes, Argentina; 27°45′, 57°44′, 60m.
335	HLO	338317	5-16-68	*A.* sp.	10 km N of General Páz, Corrientes, Argentina; 27°41′, 57°36′, 60m.
346	HLKO	338318	1968	*A.* sp.	Ruta 12 at Río Empedrado, Corrientes, Argentina; 27°52′, 58°47′, 50m.
349	HLKO	338305	5-68	*A.* sp.	400 m SE of r.r. crossing on Route 17, Saladas, Corrientes, Argentina; 28°15′, 58°40′, 70m.
486 (v. 361)	HL	338267	1968	*A.* sp.	Cult. Campinas, São Paulo, Brazil.
489 (10550)	HL (GK)	338257	1968	*A.* sp.	Cult. Campinas, São Paulo, Brazil.
492 (10105) (v. 774)	HL (GKP)	338284	1968	*A.* sp.	Cult. Campinas, São Paulo, Brazil.
552	HLKHe	338261	6-9-68	*A.* sp.	Where the Río Cachoetrinha empties into the Aquidauana, Palmeira, Mato Grosso, Brazil; 20°26′, 55°22′, 225m.
553	HLKHe	338262	6-9-68	*A.* sp.	2 km W of Palmeira, Mun. Anastácio, Mato Grosso, Brazil; 20°26′, 55°23′, 225m.
560	HLKHe	338263	6-10-68	*A.* sp.	40 km S of Aquidauana, Mato Grosso, Brazil; 20°50′, 55°53′, 250m.
563	HLKHe	338264	6-10-68	*A.* sp.	8 km W of Jardim toward Porto Murtinho, Mato Grosso, Brazil; 21°29′, 56°13′, 300m.
564	HLKHe	338296	6-10-68	*A.* sp.	63 km W of Jardim toward Porto Murtinho, Mato Grosso, Brazil; 21°33′, 56°39′, 300m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION III. RHIZOMATOSAE — SERIES 2. EURHIZOMATOSAE (cont.)					
567	HLKHe	338299	6-12-68	*A.* sp.	51 km E of Porto Murtinho, Mato Grosso, Brazil; 21°43′, 57°26′, 200m.
568	HLKHe	338300	6-12-68	*A.* sp.	51 km E of Porto Murtinho, Mato Grosso, Brazil; 21°43′, 57°26′, 200m.
569	HLKHe	338301	6-12-68	*A.* sp.	51 km E of Porto Murtinho, Mato Grosso, Brazil; 21°43′, 57°26′, 200m.
571	HLKHe	338265	6-12-68	*A.* sp.	64 km E of Porto Murtinho, Mato Grosso, Brazil; 21°39′, 57°19′, 200m.
575	HLKHe	338273	6-13-68	*A.* sp.	Río Amambay, S of Ponta Porá, Mato Grosso, Brazil; 22°58′, 55°13′, 375m.
576	HLKHe	338266	6-13-68	*A.* sp.	At Río Amambay S of Ponta Porá, Mato Grosso, Brazil; 22°58′, 55°13′, 375m.
577	HLKHe	338303	6-13-68	*A.* sp.	At Río Amambay bridge, S of Ponta Porá, Mato Grosso, Brazil; 22°58′, 58°13′, 375m.
7847	K	261866	3-4-53	*A.* sp.	Mburucuyá, Corrientes, Argentina.
7864	K	261851	3-4-53	*A.* sp.	Road to Itá Ibaté, Gen. Páz, Corrientes, Argentina.
7870	K	261862	3-4-53	*A.* sp.	10 km S of Itá Ibaté, Corrientes, Argentina.
7910	K	261865 298637	3-7-53	*A.* sp.	In the street of San Ignacio, Misiones, Argentina.
7934	K	261856 298638	3-53	*A.* sp.	Arroyo Pindapoy, Route 10, Misiones, Argentina.
9553	GKP	262801	1-25-59	*A.* sp.	Road to Loreto ±10 km S of Ruta 12 roadside, Corrientes, Argentina; 27°38′, 57°4′, 75m.
9564	GKP	262811	1-28-59	*A.* sp.	3 km NE of Encarnación on the road to Trinidad, Arroyo Santa María, Paraguay; 27°18′, 55°50′, 80m.
9566	GKP	262812 262871 262813	1-28-59	*A.* sp.	7-8 km NE Encarnación on road to Trinidad, Arroyo Porá Paraguay; 27°17′, 55°46′, 80m.
9567	GKP	262814	1-28-59	*A.* sp.	7-8 km NE Encarnación on road to Trinidad, Arroyo Porá, Paraguay; 27°17′, 55°46′, 80m.
9568	GKP	262815	1-29-59	*A.* sp.	*Ca.* 1 mile from Trinidad near an old Jesuit ruin, 1 mile above Arroyo Capiibary, Paraguay; 27°10′, 55°40′, 60m.
9569	GKP	262816	1-29-59	*A.* sp.	Top of hill near old Jesuit ruin, 1 mile from Trinidad, Paraguay; 27°10′, 55°40′, 80m.

Coll. No.	Collec- tor	P.I. No.	Mo/day/yr	Name	Locality
SECTION III. RHIZOMATOSAE — SERIES 2. EURHIZOMATOSAE (cont.)					
9570	GKP	262817	1-29-59	*A. sp.*	Top of hill near old Jesuit ruin, 1 mile from Trinidad, Paraguay; 27°10′, 55°40′, 80m.
9571	GKP	262818	1-29-59	*A. sp.*	Near Trinidad & old Jesuit ruin, Paraguay; 27°10′, 55°40′, 70m.
9572	GKP	262819	1-29-59	*A. sp.*	At N end of bridge across Arroyo Capiibary Hohenau, near Trinidad, Paraguay; 27°8′, 55°37′, 50m.
9574	GKP	262820	1-31-59	*A. sp.*	Between San Luis & Santa Rosa, near km 273 on road from Encarnación to Asunción, Paraguay; 27°5′, 56°30′, 75m.
9575	GKP	262821	1-31-59	*A. sp.*	San Ignacio, in yard of highway machine storage & shops on the W edge of the village between Encarnación & Asunción, Paraguay; 26°52′, 57°0′, 75m.
9576	GKP	262822	1-31-59	*A. sp.*	Caapucú, km 139 on road from Encarnación to Asunción, Paraguay; 26°13′, 57°10′, 90m.
9577	GKP	262823	2-1-59	*A. sp.*	Jardim Botanico, Asunción, Paraguay; 25°16′, 57°42′, 75m.
9578	GKP	262824	2-1-59	*A. sp.*	Jardim Botanico, Asunción, Paraguay; 25°16′, 57°42′, 75m.
9580	GKP	262825	2-3-59	*A. sp.*	Outskirts of Eusebio Ayala on Ruta 2, km 73 Asunción to Hernandarias, Paraguay; 25°25′, 56°58′, 220m.
9587	GKP	262826	2-3-59	*A. sp.*	km 80 Ruta 2, Paraguay; 25°26′, 56°55′, 220m.
9591	GKP	262827	2-3-59	*A. sp.*	Ruta 2, km 116, Asunción to Hernandarias, Paraguay; 25°29′, 56°35′, 220m.
9592	GKP	262828	2-3-59	*A. sp.*	Ruta 2, km 116, Asunción to Hernandarias, Paraguay; 25°29′, 56°35′, 220m.
9596	GKP	262829	2-5-59	*A. sp.*	3-5 km E of Caaguaçú, Ruta 2, Paraguay; 25°27′, 55°59′, 375m.
9606	GKP	262830 298642	2-5-59	*A. sp.*	Pastoreo, S of Ruta 2, Paraguay; 25°47′, 55°53′, 375m.
9610	GKP	262831 262832	2-5-59	*A. sp.*	Pastoreo Village, S of Ruta 2, Paraguay; 25°47′, 55°53′, 375m.
9618	GKP		2-7-59	*A. sp.*	Arroyos y Esteros, 1 mile S of Río Peribebuy, Itobatí, Paraguay; 25°12′, 57°5′, 80m.
9625	GKP	262872	2-11-59	*A. sp.*	7 km from Ponta Porá on road to Bela Vista on the Paraguay-Brazilian frontier; 22°29′, 55°44′, 650m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION III. RHIZOMATOSAE — SERIES 2. EURHIZOMATOSAE (cont.)					
9626	GKP		2-11-59	*A. sp.*	7 km from Ponta Porá on the road to Bela Vista, Paraguay-Brazilian frontier; 22°29′, 55°44′, 650m.
9627	GKP		2-11-59	*A. sp.*	8-9 km from Ponta Porá off to the left of the road from Ponta Porá to Bela Vista, Paraguay-Brazilian frontier; 22°28′, 55°44′, 650m.
9628	GKP	263098	2-11-59	*A. sp.*	8-9 km from Ponta Porá off to the left of the road from Ponta Porá to Bela Vista, Paraguay-Brazilian frontier; 22°28′, 55°44′, 650m.
9629	GKP	262834	2-11-59	*A. sp.*	9-10 km from Ponta Porá off to left of road from Ponta Porá to Bela Vista, Paraguay-Brazilian frontier; 22°27′, 55°44′, 600m.
9630	GKP	262835	2-11-59	*A. sp.*	10-11 km from Ponta Porá off to left of road from Ponta Porá to Bela Vista, Paraguay-Brazilian frontier; 22°26′, 55°44′, 600m.
9634	GKP	262836	2-13-59	*A. sp.*	40± km from Ponta Porá on road from Ponta Porá to Bela Vista before reaching Colonio Penso, Paraguay-Brazilian frontier; 22°13′, 55°53′, 700m.
9635	GKP	263099	2-13-59	*A. sp.*	40± km on road from Posta Porá to Colonio Penso & Bela Vista, Paraguay-Brazilian frontier; 22°13′, 55°53′, 700m.
9637	GKP	262838 298641	2-13-59	*A. sp.*	10 km from Penso to Bela Vista on road from Ponta Porá to Bela Vista, Paraguay-Brazilian frontier; 22°13′, 55°58′, 650m.
9640	GKP	263100	2-13-59	*A.* sp.	11-12 km from Penso to Bela Vista on road from Ponta Porá to Bela Vista, Paraguay-Brazilian frontier; 22°13′, 56°0′, 600m.
9642	GKP	262839 262873	2-13-59	*A.* sp.	8 km from Arroyo Mongaba, 30 km to Bela Vista on road from Ponta Porá to Bela Vista, Paraguay-Brazilian frontier; 22°8′, 56°16′, 300m.
9643	GKP		2-14-59	*A.* sp.	Bella Vista, Paraguay, across the Río Apa from Bela Vista, Brazil; 22°7′, 56°31′, 200m.
9644	GKP	262840	2-14-59	*A.* sp.	Bela Vista, Brazil; 22°7′, 56°32′, 200m.
9645	GKP	262841	2-14-59	*A.* sp.	Bela Vista, Brazil; 22°7′, 56°32′, 200m.
9647	GKP	262843	2-14-59	*A.* sp.	2 km from Bela Vista on road from Bela Vista to Ponta Porá, Paraguay-Brazilian frontier; 22°5′, 56°31′, 200m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION III. RHIZOMATOSAE — SERIES 2. EURHIZOMATOSAE (cont.)					
9649	GKP	262844	2-14-59	*A.* sp.	7 km from Bela Vista on road from Bela Vista to Ponta Porá, Paraguay-Brazilian frontier; 22°4′, 56°29′, 250m.
9650	GKP	262845 298640	2-14-59	*A.* sp.	20-25 km from Bela Vista on road from Bela Vista to Ponta Porá, Paraguay-Brazilian frontier; 22°5′, 56°18′, 300m.
9664	GKP	262847	2-17-59	*A.* sp.	1 km from Río Amambay on road to Amambay from Ponta Porá, Mato Grosso, Brazil; 22°57′, 55°13′, 400m.
9667	GKP	262848	2-17-59	*A.* sp.	1 km from Río Amambay on road to Amambay from Ponta Porá, Mato Grosso, Brazil; 22°57′, 55°13′, 400m.
9672	GKP	262849	2-17-59	*A.* sp.	±20 km S of Amambay on Amambay-Capitán-Bado road, Mato Grosso, Brazil; 23°10′, 55°16′, 500m.
9674	GKP	262850	2-17-59	*A.* sp.	±25 km from Amambay on Amambay-Capitán-Bado road, Mato Grosso, Brazil; 23°12′, 55°16′, 500m.
9678	GKP	262851	2-17-59	*A.* sp.	1 km from Capitán-Bado on Amambay-Capitán-Bado road, Mato Grosso, Brazil; 23°14′, 55°31′, 500m.
9679	GKP	263101	2-18-59	*A.* sp.	1 km from Capitán-Bado on road to Ipe Yhu, Mato Grosso, Brazil; 23°16′, 55°33′, 500m.
9681	GKP	262852	2-18-59	*A.* sp.	1 km from Capitán-Bado on Capitán-Bado-Ipe Yhu road, Mato Grosso, Brazil; 23°16′, 55°33′, 500m.
9688	GKP	263102	2-19-59	*A.* sp.	5 km from Amambay on Amambay-Ponta Porá road, Mato Grosso, Brazil; 23°3′, 55°15′, 500m.
9696	GKP	262853	2-19-59	*A.* sp.	5 km from Amambay on Amambay-Ponta Porá road, Mato Grosso, Brazil; 23°3′, 55°15′, 500m.
9703	GKP	262854	2-19-59	*A.* sp.	5 km from Amambay on Amambay-Ponta Porá road, Mato Grosso, Brazil; 23°3′, 55°15′, 500m.
9706	GKP	262855	2-19-59	*A.* sp.	5 km from Amambay on Amambay-Ponta Porá road, Mato Grosso, Brazil; 23°3′, 55°15′, 500m.
9797	GKP	262807	3-1-59	*A.* sp.	10 km E of intersection of roads Bataguaçú to Campo Grande & Campo Grande to Río Brillante, Mato Grosso, Brazil; 21°30′, 54°16′, 400m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION III. RHIZOMATOSAE — SERIES 2. EURHIZOMATOSAE (cont.)					
9801	GKP	262864	3-1-59	*A.* sp.	10 km E of junction of roads from Bataguaçú to Campo Grande & Campo Grande to Río Brillante, Mato Grosso, Brazil; 21°30′, 54°16′, 400m.
9806	GKP	262792	3-1-59	*A.* sp.	70 km S of Campo Grande on road to Río Brillante, Mato Grosso, Brazil; 21°5′, 54°30′, 400m.
9813	GKP	262793	2-24-59	*A.* sp.	Criaçao Expt. Sta., 30 km S of Campo Grande, Mato Grosso, Brazil; 20°43′, 54°33′, 450m.
9815	GKP	262794	2-24-59	*A.* sp.	Criaçao Expt. Sta., 30 km S of Campo Grande, Mato Grosso, Brazil; 20°43′, 54°33′, 450m.
9822	GKP	262795	2-25-59	*A.* sp.	Fazenda Imbirussú, 15 km SE of Campo Grande, Mato Grosso, Brazil; 20°34′, 54°30′, 550m.
9823	GKP		2-25-59	*A.* sp.	Fazenda Imbirussú, 15 km SE of Campo Grande, Mato Grosso, Brazil; 20°34′, 54°30′, 550m.
9827	GKP	262796	3-3-59	*A. glabrata* Benth.	Río Pardo, Mato Grosso, Brazil, in the streets of the city; 20°27′, 53°45′, 365m.
9830	GKP	262797	3-3-59	*A. glabrata* Benth.	Río Pardo, Mato Grosso, Brazil, on the W side of river; 20°27′, 53°43′, 365m.
9834	GKP	262798	3-5-59	*A.* sp.	48 km N of Campo Grande on road to Cuiabá, Mato Grosso, Brazil; 20°5′, 54°24′, 570m.
9882	GKP	262286	3-7-59	*A.* sp.	52 km N of Río Verde on road to Cuiabá, Mato Grosso, Brazil; 18°28′, 54°46′, 247m.
9893	GKP	262287	3-8-59	*A.* sp.	176 km N of Gaucho on road to Cuiabá, Rondonopolis, Mato Grosso, Brazil; 16°32′, 54°37′, 400m.
9894	GKP	262288	3-8-59	*A.* sp.	10 km W of Rondonopolis, Mato Grosso, Brazil; 16°33′, 54°43′, 300m.
9918	GKP	262294	3-11-59	*A.* sp.	70 km N of Cuiabá on road to Rosario Oeste, Mato Grosso, Brazil; 15°13′, 56°19′, 150m.
9921	GKP	262296	3-12-59	*A.* sp.	17 km NE of Rosario Oeste on road to Estevado, Mato Grosso, Brazil; 14°42′, 56°19′, 183m.
9922	GKP	262297	3-12-59	*A.* sp.	17 km NE of Rosario Oeste on road to Estevado, Mato Grosso, Brazil; 14°42′, 56°19′, 183m.

SECTION III. RHIZOMATOSAE — SERIES 2. EURHIZOMATOSAE (cont.)

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
9925	GKP	262299	3-12-59	*A.* sp.	34 km NE of Rosario Oeste on road to Estevado, Mato Grosso, Brazil; 14°35′, 56°13′, 350m.
9935	GKP	262301	3-14-59	*A.* sp.	20 km E of Birro which is 155 km NW of Alto Garças on road from Rondonopolis to Alto Araguaria, Mato Grosso, Brazil; 17°2′, 54°31′, 500m.
9944	GKP		3-16-59	*A.* sp.	Banks of the Río Claro, Goiás, Brazil; 17°56′, 51°45′, 600m.
9947	GKP		3-17-59	*A.* sp.	Río Verde, Goiás, Brazil; 17°48′, 50°57′, 675m.
9948	GKP	262303 262276	3-17-59	*A.* sp.	35 km SE of Río Verde on road to Itumbiara, Goiás, Brazil; 17°59′, 50°42′, 600m.
9949	GKP		3-17-59	*A.* sp.	35 km SE of Río Verde, Goiás, Brazil; 17°59′, 50°42′, 600m.
9951	GKP		3-18-59	*A.* sp.	53 km E of Bom Jesus on road to Itumbiara, Goiás, Brazil; 18°22′, 49°21′, 550m.
9954	GKP	262304	3-18-59	*A.* sp.	Near bridge across river, Itumbiara, Goiás, Brazil; 18°25′, 49°11′, 450m.
9958	GKP		3-18-59	*A.* sp.	24 km W of intersection of road to Ituiutaba from Avantiguara, Goiás, Brazil; 18°53′, 49°20′, 600m.
9960	GKP		3-18-59	*A.* sp.	5 km E of Ituiutaba, Goiás, Brazil; 18°56′, 49°26′, 500m.
9964	GKP	262305	3-19-59	*A.* sp.	100 km NW of Frutal, 55 km S of Bela Vista on route from Ituiutaba to Frutal, Triangulo Mineiros, Minas Gerais, Brazil; 19°26′, 49°34′, 500m.
9966	GKP	262306	3-19-59	*A.* sp.	10 km S of Frutal, Triangulo Mineiros, Minas Gerais, Brazil; 20°4′, 48°52′, 500m.
10105	GKP	276200	4-2-61	*A.* sp.	Planura, just across Río Grande into Triangulo Mineiros, Minas Gerais, Brazil; 20°9′, 48°42′, 450m.
10120 (493) (v. 775)	GKP (HL)	276202	4-4-61 (1968)	*A.* sp.	Capinopolis, about 40 km NNW of Ituiutaba, Minas Gerais, Brazil; 18°41′, 49°35′, 500m. (cult. Campinas, São Paulo, Brazil—HL).
10139	GKP		4-5-61	*A.* sp.	Edge of road to Goiania, Goiatuba, Goiás, Brazil.
10550 (489)	GK (HL)	(338257)	5-11-61 (1968)	*A.* sp.	5 km of entrocamento road Porto 15 de Noviembre to Río Brillante, Mato Grosso, Brazil.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION III. RHIZOMATOSAE — SERIES 2. EURHIZOMATOSAE (cont.)					
10555	GK	276213	5-12-61	*A.* sp.	5 km SW of Río Brillante on road to Dourados, Mato Grosso, Brazil; 21°51′, 54°32′, 400m.
10558	GK	276216	5-12-61	*A.* sp.	28 km SW of Dourados on road to Ponta Porá, Mato Grosso, Brazil; 22°19′, 55°2′, 400m.
10559	GK	276217	5-13-61	*A.* sp.	Finca Elvira, 43 km by the road & ±20 km as the crow flies, NW of Ponta Porá, Mato Grosso, Brazil; 22°28′, 55°57′, 600m.
10560	GK	276218	5-13-61	*A.* sp.	Estancia San Luis, ±40 km NW Ponta Porá, ±20 km as the crow flies, Mato Grosso, Brazil; 22°28′, 55°57′, 600m.
10561	GK	276219	5-13-61	*A.* sp.	Estancia San Luis, ±40 km NW Ponta Porá, ±20 km as the crow flies, Mato Grosso, Brazil; 22°28′, 55°57′, 600m.
10563	GK	276221	5-13-61	*A.* sp.	Near Estancia, San Luis, ±40 km NW of Ponta Porá, Mato Grosso, Brazil; 22°28′, 55°57′, 600m.
10565	GK	276222	5-14-61	*A.* sp.	1 km N of Río Amambay on road from Ponta Porá to Amambay, Mato Grosso, Brazil; 22°57′, 55°13′, 400m.
10566	GK	276223	5-14-61	*A.* sp.	1 km N of Río Amambay on road from Ponta Porá to Amambay, Mato Grosso, Brazil; 22°57′, 55°13′, 400m.
10567	GK	276224	5-14-61	*A.* sp.	1 km N of Río Amambay on road from Ponta Porá to Amambay, Mato Grosso, Brazil; 22°57′, 55°13′, 400m.
10574 (485) (v. 793)	GK (HL)	276226 (338281)	5-16-61 (1968)	*A.* sp.	48 km W of Ponta Porá on road to Concepción, Paraguay; 22°40′, 56°7′, 300m.
10596	GK	276233	5-17-61	*A.* sp.	10 km W of Horqueta on road from Ponta Porá to Concepción, Paraguay; 23°25′, 57°5′, 100m.
12142	KCPa		1-29-66	*A.* sp.	Ita, Granja Isapy, bank of Arroyo Lazarill, Dep. Central, Paraguay; 25°30′, 57°22′, 150m.
12290	KCPa		2-1-66	*A.* sp.	Yaguaron, bank of Arroyo Yaguaron, Dep. Central, Paraguay; 25°33′, 57°17′, 173m.
12363	KCPa		2-3-66	*A.* sp.	Paraguarí, .5 km S bank of Arroyo, Dep. Paraguarí, Paraguay; 25°39′, 57°9′, 150m.
12450	KCPa		2-6-66	*A.* sp.	17 km from Paraguarí on road to Peribebuy, Dep. Cordillera, Paraguay; 25°29′, 57°4′, 250m.

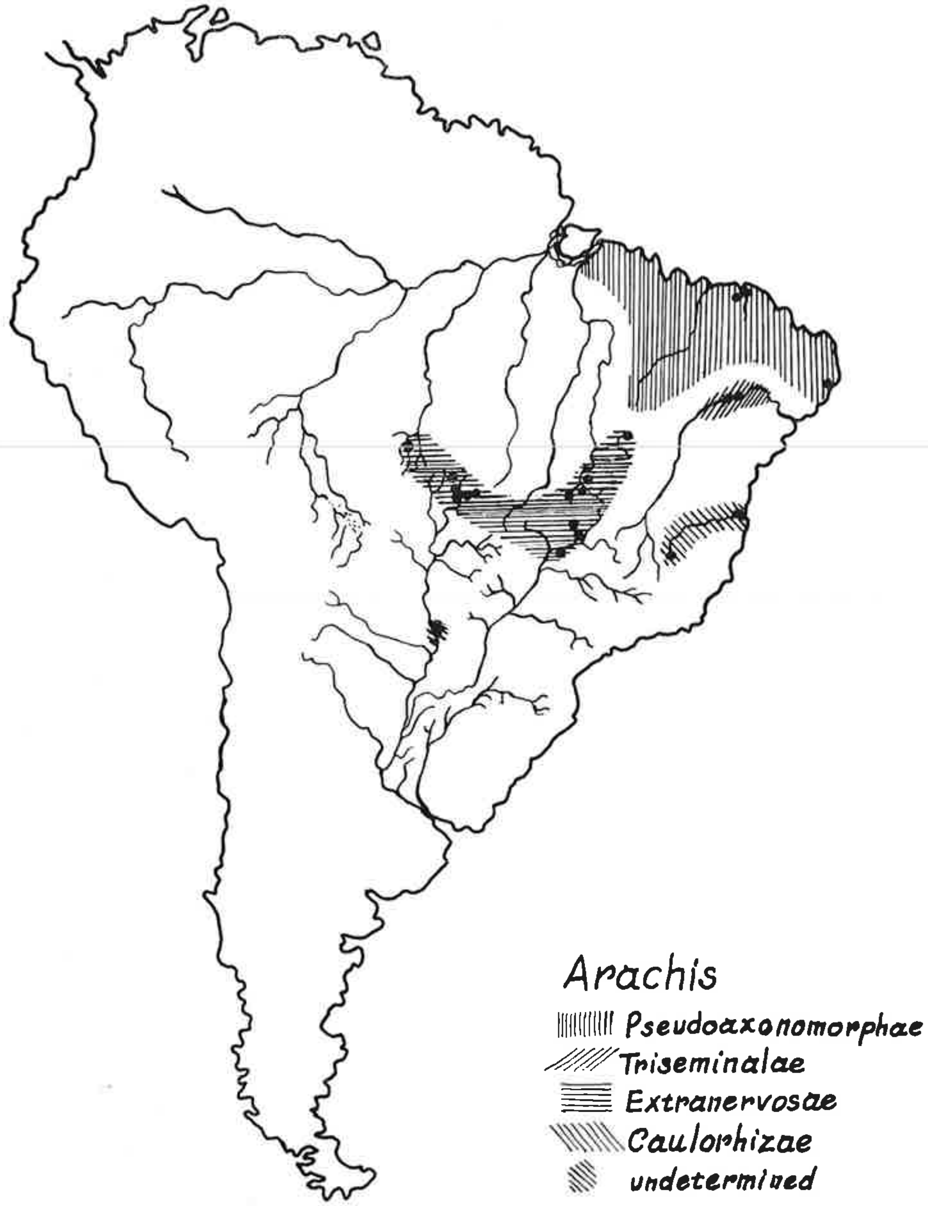

Figure 22. *EXTRANERVOSAE.* This old and conservative section of *Arachis* occupies the epicenter of dispersal of the genus and perhaps its center of origin in the uppermost reaches of the Paraguay-Paraná and southern branches of the Amazon River basins. This section, though sympatric in part with Rhizomatosae, Axonomorphae, and Erectoides, appears to be completely genetically isolated. Shown also are the geographic areas and drainage basins occupied by the peripheral sections of the genus: *CAULORHIZAE*—valley of the Jequitinhonha, *TRISEMINALAE*—the São Francisco, *PSEUDOAXONOMORPHAE*—coastal drainage north of the São Francisco basin and east of the Tocantins; the range shown includes collections by Gardner and other botanists.

Coll. No.	Collec-tor	P.I. No.	Mo/day/yr	Name	Locality
SECTION III. RHIZOMATOSAE — SERIES 2. EURHIZOMATOSAE (cont.)					
12460	KCPa		2-6-66	*A.* sp.	17 km from Paraguarí on road to Peribebuy, Dep. Cordillera, Paraguay; 25°29′, 57°4′, 250m.
14425	KHe		6-10-68	*A.* sp.	27 km S of Nioaque on road to Jardim, Mato Grosso, Brazil.
14443	KHe		6-12-68	*A.* sp.	95 km E of Porto Murtinho, Mato Grosso, Brazil.
SECTION IV. EXTRANERVOSAE					
484 (14446) (v. 44)	HL (KHe)	263394 263395 263396 273482 336984	6-5-68 (6-5-68)	*A. villosulicarpa* Hoehne	At Juruena & Diamantino, Mato Grosso, Brazil (village of the Nambyquarae, also found growing among the Mama Inde); 12°51′, 58°55′ (cult. Campinas, Brazil).
487 (10234) (v. 780)	HLKHe (GKP)		6-4-68	*A. prostrata* Benth.	Cult. Campinas, São Paulo, Brazil (proc. 10 km from Trairas River, 15 km S. of Niquelandia, Goiás, Brazil).
490 (14445) (v. 862)	HL (KHe)	336985	6-5-68 (6-5-68)	*A. villosulicarpa* Hoehne	At Juruena & Diamantino, Mato Grosso, Brazil (village of the Nambyquarae, also found growing among the Mama Inde); 12°51′, 58°55′ cult. Campinas, Brazil).
9898	GKP	262269 262289	3-9-59	*A. lutescens* Krap. *et* Rig.	144 km NW of São Lourenço, Mato Grosso, Brazil; 15°38′, 55°31′, 400m.
9900	GKP	262131	3-8-59	*A. lutescens* Krap. *et* Rig.	147 km NW of São Lourenço, Mato Grosso, Brazil; 15°40′, 55°32′, 400m.
9903	GKP	262271 262291	3-9-59	*A. lutescens* Krap. *et* Rig.	176 km N of São Lourenço about 70 km SE of Cuiabá, Mato Grosso, Brazil; 15°43′, 55°48′, 130m.
9905	GKP	262292	3-9-59	*A. lutescens* Krap. *et* Rig.	13 km E of Cuiabá, 5 km E of Coxipo da Ponte, Mato Grosso, Brazil; 15°39′, 56°1′, 170m.
9906	GKP	262272 262293	3-11-59	*A. lutescens* Krap. *et* Rig.	10 km NW of Cuiabá on road from the city to Rosario Oeste, Mato Grosso, Brazil; 15°32′, 56°8′, 141m.
9907	GKP		3-11-59	*A. lutescens* Krap. *et* Rig.	Río Mirim, 37-44 km N of Cuiabá, Mato Grosso, Brazil; 15°24′, 56°13′, 148m.
9909	GKP		3-11-59	*A. lutescens* Krap. *et* Rig.	50-54 km N of Cuiabá on road to Rosario Oeste, Mato Grosso, Brazil; 15°22′, 56°13′, 148m.
9920	GKP	262273 262295	3-12-59	*A. lutescens* Krap. *et* Rig.	17 km NE of Rosario Oeste on road to Estevado, Mato Grosso, Brazil; 14°42′, 56°19′, 183m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
SECTION IV. EXTRANERVOSAE (cont.)					
9923	GKP	262274 262298	3-12-59	*A.* sp.	17 km NE of Rosario Oeste on road to Estevado, Mato Grosso, Brazil; 14°42′, 56°19′, 183m.
9927	GKP		3-13-59	*A. lutescens* Krap. *et* Rig.	2 km NE of edge of city of Cuiabá, Mato Grosso, Brazil; 15°36′, 56°6′, 170m.
10127 (491) (v. 776)	GKP (HLKHe)	276203 276309 (338283)	4-4-61 (6-4-68)	*A. macedoi* Krap. *et* Greg. (unpub.)	Fazenda Santa Terezinha, near Capinopolis, Minas Gerais, Brazil; 18°43′, 49°45′, 650m.
10160	GKP	276195	4-6-61	*A.* sp.	Río Piracanjuba, between Morrinhos & Caldes Novas, Goiás, Brazil; 17°45′, 48°51′, 600m.
10174	GKP	276196	4-7-61	*A.* sp.	On the road between Caldes Novas & Piracanjuba, Goiás, Brazil; 17°36′, 48°46′, 650m.
10176	GKP	276197 276307	4-7-61	*A.* sp.	Between the Río Piracanjuba & Piracanjuba on road from Caldes Novas, Goiás, Brazil; 17°19′, 48°58′, 650m.
10234 (487)	GKP (HLKHe)	276205	4-12-61 (6-4-68)	*A. prostrata* Benth.	10 km from the Trairas River, 15 km S of Niquelandia, Goiás, Brazil; 14°38′, 48°36′, 600m.
10240	GKP	276206	4-12-61	*A. prostrata* Benth.	3 km S of the Río Maranhao on road from Niquelandia to Corumbá, Goiás, Brazil; 15°3′, 48°45′, 600m.
10259	GKP	276207 276311	4-16-61	*A.* sp.	15 km S of Ceres, on road to Anapolis, Goiás, Brazil; 15°25′, 49°31′, 600m.
10292	GKP		4-19-61	*A. prostrata* Benth.	86 km NE of Formosa on the Brazilia-Fortaleza road, Goiás Brazil.
10406	GKP	276198	4-22-61	*A. marginata* Gard.	30 km E of Dianopolis (Mision Duro), Goiás, on trail from Barreiras, Bahía, Brazil; 11°38′, 46°31′, 500m.
10449	GKP	276312	4-24-61	*A. prostrata* Benth.	115 km NE of Formosa & 65 km SW of Alvorada, Goiás, Brazil.
SECTION V. PSEUDOAXONOMORPHAE					
12939	GK	338450	4-12-67	*A.* sp.	Fortaleza-Sobral on road 50 km E of Sobral, Ceará, Brazil; 3°35′, 39°56′, 75m.
12941	GK	338451	4-12-67	*A.* sp.	40 km E of Sobral, Ceará, Brazil; 3°35′, 40°0′, 75m.
12943	GK	338452	4-12-67	*A.* sp.	Praça Fernando Mendes, Sobral, Ceará, Brazil; 3°43′, 40°22′, 75m.
12945	GK		4-12-67	*A.* sp.	Praça Fernando Mendes, Sobral, Ceará, Brazil; 3°43′, 40°22′, 75m.
12946	GK	338453	4-15-67	*A.* sp.	Tapera, Pernambuco, Brazil; 8°7′, 35°11′, 100m.

Coll. No.	Collector	P.I. No.	Mo/day/yr	Name	Locality
				SECTION VI. TRISEMINALAE	
12881	GK	338448	4-6-67	*A. pusilla* Benth.	Joazeiro, Est. Exp. do Mandacarú, Bahía, Brazil; 9°24′, 40°27′, 371m.
12922	GK	338449	4-8-67	*A. pusilla* Benth.	15 km SW of Joazeiro, Bahía, Brazil; 9°32′, 40°37′, 400m.
				SECTION VII. CAULORHIZAE	
10538	GKP	276199	5-2-61	*A. repens* Handro	Exp. Sta. Instituto Agronómico de Oeste, Sete Lagoas, Minas Gerais, Brazil. Proc. collection of Dr. Thomas Dalton "in vaso do Río Jequitahy" (a branch of the Jequitinhonha) "cerca de Estaçao Eng. Dolabela, Minas Gerais, Brazil;" 18°10′, 43°26′, 600-700m (other numbers in parentheses were cultivated in various localities but all referable via vegetative propagation to original proc. cited under 10538—GKP).
(3)	(HL)	(338274)	(1968)		
(365)	(HLK)	(338275)	(5-22-68)		
(461)	(HLK)	(338276)	(1968)		
(467)	(HLK)	(338277)	(6-2-68)		
(498)	(HL)	(338278)	(1968)		
(500)	(HLKHe)	(338258)	(6-5-68)		
12787	GK	338447	3-31-67	*A. pintoi* Krap *et* Greg. (unpub.)	IPEAL, Cruz das Almas, Bahía, Brazil (cult.). Proc. Río Jequitinhonha (Sud de Bahía) near the Atlantic coast in a sand bank between the mouth of river & Belmonte City (collected by Geraldo C. P. Pinto in April, 1954); 15°52′, 39°6′, 50m (numbers in parentheses cultivated Facultad de Agronomia Universidad Nacional del Nordeste, Corrientes, Argentina).
(323)	(HL)	(338314)	(1968)		
(329)	(HL)		(1968)		
				OF UNCERTAIN AFFINITY	
488	HL	338282	1968	Hybrid between 10573 GKP & *A. repens*	Cult. Campinas, São Paulo, Brazil.
501	HLKHe	338259	1968	*A.* sp.	Cult. Matao, São Paulo, Brazil.
502	HLKHe	338260	1968	*A.* sp. also hybrid?	Cult. Matao, São Paulo, Brazil.
565-66	HLKHe	338297 338298	6-12-68	*A.* sp.	43 km E of Porto Murtinho, Mato Grosso, Brazil; 21°45′, 57°29′, 200m.
10598	GK	276234	5-18-61	*A. lignosa* (Chod. *et* Hassl.) Krap. *et* Greg. (unpub.)	2 km NE of Concepción in the edge of suburbs of city, Paraguay; 23°25′, 57°26′, 100m (allied to the Caulorhizae & Erectoides, but similar to the Axonomorphae).
(327)	(HL)	(338315)			

ABBREVIATION OF COLLECTORS' NAMES

B = Burkart
HL = Hammons-Langford
HLO = Hammons-Langford-Ojeda
HLKO = Hammons-Langford-Krapovickas-Ojeda
KHe = Krapovickas-Hemsy
HLKHe = Hammons-Langford-Krapovickas-Hemsy
HLP = Hammons-Langford-Pietrarelli

GKP = Gregory-Krapovickas-Pietrarelli
GK = Gregory-Krapovickas
K = Krapovickas
KCPa = Krapovickas-Cristobal-Palacios
KC = Krapovickas-Cristobal
KCF = Krapovickas-Cristobal-Fugarazzo

Figure 23. *Arachis*—Joint geographic distribution of all sections of the genus.

Geographic and Genetic Isolation and the Conservation of the Germ Plasm

It may well be that the present human invasion of the habitats of *Arachis* by means of powered equipment will provide an environmental disturbance of sufficient magnitude to be followed by a burst of new hybrid forms in the genus and a new era of peanut evolution. It may also be true that man's continued presence in their habitats may turn the past success of the species of *Arachis* into biological extinction. Such an extinction with its consequent loss to humanity, of whatever of value this genus holds for the improvement of man's chosen species, *A. hypogaea,* would be a loss of great magnitude. It is the reasonably high probability of the latter event that has motivated the attempts to collect and preserve the wild species germ plasm of peanuts.

Examination of the distribution maps in Figures 18-23 shows that the present sectional and series differentiation of the genus is accompanied by a pattern of geographic isolation dictated by the distinct drainage basins in which the different sections occur. These distribution maps are based upon the collections made by the authors and such additions as were made by the Hammons-Langford expedition of 1968. The maps do not include the information available from the various herbaria of the world. The reason for this limitation is that we wished to convey the precise sectional limits as we know them. Also, to have included the total of collected specimens of *Arachis* would have been too large a task for the present work and little loss of information is incurred by their omission. Peripheral exception to the generalization that sections of the genus are represented only in certain river basins may be noted in the present center of concentration of the genus, the Paraguay-Paraná basin, where it is obvious that some of the species have escaped the confines of their homes and are now growing in the fringes of other river systems. Nevertheless, the limitation of specific sections to certain drainage basins is sufficiently general to suggest that this limitation has been a major factor in the recent evolution of *Arachis.* It also suggests that flowing water may be the prime agent in the distribution of *Arachis* and that geocarpic commitment has been the prime biological characteristic which has brought this about. The temptation is to think back to a time when some aerial-fruited precursor of the genus *Arachis* was not fettered in its distribution by a single preponderant agent, flowing water. Such a group of plants could have, like *Stylosanthes,* easily crossed continental divides of the present drainage pattern of South America. *Stylosanthes,* the most widespread of the aerial-fruited Stylosanthineae may be found all over South America, a small representation on the west coast of Africa, the Galapagos Islands and the United States from Texas to New Jersey. If one assumes that there was a time in the evolutionary life of the genus *Arachis* when subterranean and aerial fruiting both occurred on the same plants, a transitional state that must have been traversed, one can imagine the full continental distribution of the commitment to geocarpy prior to the loss of aerial fruiting. Thus the dependence on drainage pattern for geographic distribution probably occurred after the complete loss of aerial fruiting habit and the freedom to move across drainage barriers which it provided. If this line of imagination follows the line of events, in fact, then it may be said with some reason that the present evolutionary pattern of *Arachis* was attained approximately *in situ;* that is, in the basins of the Paraguay-Paraná, the Uruguay, the Jequitinhonha, the São Francisco, the Parnaiba, and the northeast coast, the south-reaching branches of the Amazon (Tocantins, Araguaia, Xingú, and southeast branches of the Tapajos and the Madeira.

The violations of the above statement at the periphery of the sectional distributions may represent post-geocarpic events in the drainage patterns themselves, such as, for example, various occasions of stream piracy where the headwaters of the Tocantins, São Francisco, and Paraná meet or the headwaters of the Amazon branches meet those of the Paraguay. The Prorhizomatosae, so far as is presently known, are limited to the waters of the Uruguay. The Erectoides, with the exception of the series Procumbensae represented by the single species *A. rigonii* (Krap. *et* Greg.), lie between the Paraná and the Paraguay. The Eurhizomatosae extend from the mouth of the Paraná to the headwaters of the Paraná and Paraguay, largely east of the latter. The Extranervosae occupy the headwaters of the southern branches of the Amazon from the Tocantins in the east to the branches of the Juruena in the west. They might be thought of as denizens of the Amazon rim on the Amazon side were it not for their presence in both the upper branches of the Paraguay near Cuiabá and in the upper Paranaiba-Paraná south into the Triangulo Mineiros region of Minas Gerais. The annual Axonomorphae extend as far north as the Parapetí in Bolivia where the waters of the Río Grande of the Amazon basin mix with those of the Paraguay basin during the rainy season. The same might be said of the waters of the upper Paraguay near Cuiabá. However, the rugged, high, and well dissected headwaters plateau where the Tocantins, Paranaiba, and São Francisco meet offers little else to the alternatives that either the Paranaiba has invaded the Tocantins basin or the species of Extranervosae of the area have invaded the Paraná system. The third possibility, that the Extranervosae cannot migrate from the Amazon rim because of ecological limitations, must be entertained. Until explorations down river into the Amazon basin to the edge of the forests can be arranged, there will be no answer to the question with respect to the north. With respect to the south, it can only be said that we do not know. There seems little reason for these species to remain restricted to the headwaters of the Paraguay and Paranaiba, but that is where they are found. A similar situation is found in the Annuae of the Axonomorphae. This is in contrast to the widely scattered Perennes which extend from Cuiabá, eastern Bolivia, and Paraguay south to Colonia, Uruguay, up the Uruguay to Paso de los Libres and around the coast as far as Paranaguá and perhaps to Río de Janeiro. Surely this peripheral coastal distribution represents extra drainage invasion permitted by the limitless relatively barrier-free coastal strip. This appears to be the case with another coastwise section, the Pseudoaxonomorphae, which appear to have spread over considerable area possibly from the Ilha Marajo at the mouth of the Amazon to Recife, but always north of the divide separating the basin of the São Francisco from the coastal rivers to the north and east and to the east of the Tocantins.

The above interpretation of the correlation between sub-generic differentiation and river basin area in South America suggests that the geocarpic commitment occurred genetically in the presence of a wide genetic base for aerial fruit production in the *Arachis* precursor with the attendant mechanisms for dispersal having already accomplished a pan-continental distribution south of the Amazon and north of the La Plata. We have then supposed that the inevitable consequences of advancing geocarpy at once provided for dependence upon flowing water for dispersal followed by geographic isolation. It was then that the slow adaptive processes fitting these geocarpic plants to their various areas slowly created the morphological differentiation observable today.

In contrast to the idea of a pan-continental aerially-fruited precursor of *Arachis* is the notion (1) that somewhere near the area where the distributions of Extranervosae, Erectoides, Rhizomatosae, and Axonomorphae presently overlap, a primitive *Arachis*-like geocarpic event occurred, possibly in a close relative of the present Extranervosae, and (2) that all *Arachis* slowly found their ways into the isolated river valleys characteristic of the isolated sections of the genus by means of dispersal factors not yet recognized. While the above could have happened, it is hard to accept in the light of the genetic isolation present between species of the same section in the same river valley. It seems more reasonable to suppose that *Arachis,* like other plants, evolved isolating mechanisms under the pressure of selection to preserve the many and particular ways that a given species found of fitting itself into a given ecological situation. If one accepts this idea, then it is likely that many of the sectional differences and interspecific mechanisms of isolation must have been evolving in the precursor population after the commitment to geocarpy but before the ultimate consequences of its restrictions limited the isolated groups to individual drainage basins.

The above concepts are harsh on the notion of a center of origin of *Arachis* as we know it today. The center of origin long ago associated with the aerially-fruited precursor of *Arachis* may have in fact been very different from the center of concentration of species of *Arachis* in the Paraguay-Paraná basin. The old precursor center may have been in this basin, but there are some reasons to suppose that it was to the north and east of the present center of *Arachis.* A third possibility, the pre-Colombian pan-continental distribution of all *Arachis* species subsequently dissected by changes in continental drainage, appears to be ruled out on the grounds of the great antiquity of present river systems in South America. The possibility that a pan-continental distribution was destroyed by the advent of man is even more remote.

Interspecific cross-compatibility studies between and within sections of *Arachis* throw some light on the sectional relationships. Gregory (1946) reported what probably was one of the first efforts at inter-specific hybridization in *Arachis.* He attempted crosses of *A. hypogaea* by two wild species not realizing that each of them belonged to a different section of the genus. No hybrid plants were obtained, but failing hybrid embryos were formed. Johansen and Smith (1956) examined the ovules containing the hybrid embryos. They showed that a typical hybrid failure was occurring in these ovules. The embryos grew only slightly, failed to differentiate and their cells became starved. Similar failure of the endosperm took place and the whole was followed by hyperplastic thickening of the seed coats. Ultimately the entire structure died and turned black. Meantime, the fruits developed almost normally. Krapovickas and Rigoni (1951) hybridized *A. hypogaea* x *A. villosa* var. *correntina* Burk. *(A. correntina* — Krapovickas and Gregory) to make the first inter-specific hybrid of peanuts which survived. The hybrid was triploid and sterile. Kumar *et al.* (1957) remade this hybrid and obtained fertile hexaploids following colchicine treatment. D'Cruz and Chakravarty (1961) reported a similar allo-hexaploid occurring spontaneously. Ramanathan *et al.* (1964) reported a successful hybrid between cultivated peanut and *A. glabrata.* It is probable that the species they used was not *A. glabrata* at all, since this hybrid fails (Gregory, 1946). The probability of mistaken identity of species is supported by the report of Gopinathan Nair *et al.* (1964) that these hybrids were highly fertile and resembled the seed parent *(A. hypogaea).* Smartt and Gregory (1967) reported the first comprehensive trials at species hybridization with *A. hypogaea* and *A. monticola* as female parents. The number of females from each center of variation in South America was as follows: Peruvian (1), Bolivian (5), Guaraní (8) plus 3 African and 1 Maní Pintar derivative from Africa and *A. monticola.* They made from 10-394 pollinations (but mostly more than 100) per cross attempted using the following species as male parents: *A. glabrata, A. hagenbeckii,* 10596 (GKP), of the Rhizomatosae; *A. villosulicarpa,* 10127 (GKP), 9923 (GKP), of the Extranervosae; *A. benthamii,* 9646 (GKP), 9848 (GKP), 9990 (GKP), 10002 (GKP), 10573 (GKP), *A.* sp. (diogoi), *A. guaranitica, A. tuberosa, A. rigonii,* of the Erectoides; *A. villosa, A. correntina, A. helodes,* 10017 (GKP), 10602 (GKP), 9901 (GKP), 10038 (GKP), and *A. duranensis* of the Axonomorphae; *A. repens* of the Caulorhizae and 10598 (GKP) section unknown. All of these crosses failed except those by seven members of the Axonomorphae. The cross with 10038 (GKP) which failed can be made with *A. hypogaea* as a male parent.

Gibbons and Turley (1967) made interspecific cross-pollinations among five members of the Axonomorphae, not including *A. hypogaea.* They also cross-pollinated *A. rigonii* (Erectoides) with all five of the axonomorph species. The number of pollinations made was too small to say a certain combination failed. However, they reported the following successful hybrids and their percentages of pollen stainability:

A. batizocae x *A. villosa*	11 seeds	5.5%	pollen stained
A. batizocae x *A. duranensis*	5 seeds	10.9%	pollen stained
A. batizocae x *A. correntina*	5 seeds	0%	pollen stained
A. sp 10038 (GKP) x *A. duranensis*	2 seeds	50.9%	pollen stained
A. sp. 10038 (GKP) x *A. batizocae*	1 seed	0%	pollen stained
A. villosa x *A. correntina*	1 seed	96.5%	pollen stained

Gregory *et al.* (1965) and Gregory and Gregory (1967) reported the first successful hybrids between species belonging to different sections of the genus *Arachis.* They reported hybrids between the following sections:

Axonomorphae x Erectoides
Erectoides x Rhizomatosae
Erectoides x Caulorhizae
Axonomorphae x Rhizomatosae

Since that time these authors have succeeded in making additional intersectional hybrids. These are (Gregory and Gregory, unpublished):

Erectoides x Pseudoaxonomorphae
Caulorhizae x Erectoides
Caulorhizae x (section undetermined)

The number of possible intersectional combinations among the seven sections of the genus *Arachis* is 42. The number of these attempted by the Gregorys is 40. The number of combinations from which they obtained at least one hybrid is 6.

The Extranervosae lying across the top rims of the Paraguay-Paraná and South Amazon basins, central in the continent and central geographically in the peanut distribution, have never hybridized with species of any other section of the genus. They appear to have achieved complete genetic isolation. The same is true of the Triseminalae along the São Francisco, and almost the same thing may be said of the Pseudoaxonomorphae of the northeast.

The Caulorhizae, Erectoides, Axonomorphae, and the series Eurhizomatosae of the Rhizomatosae, though not exchanging genes freely, at least will make viable hybrids. In terms of centers of origin, it appears that as one moves out of the center of diversity in the Paraguay-Paraná River basins to the north and northeast along the south Amazon rim and down the São Francisco, he encounters what appears to be the oldest, most isolated even relict members of an old genus. Nothing but the fundamental *Arachis* morphology appears to tie these relict forms to the more dynamic members of the genus of the central Paraguay-Paraná axis, Bolivia and northwest Argentina. The temptation is to think of the genus *Arachis* as having arisen somewhere in the vast areas along the Amazon rim and to have preserved a youthful leading edge of migration to the southwest where the youngest, most labile wild species occur today, and where *A. hypogaea* probably originated (Krapovickas, 1968). And yet, such a notion defies the principal that flowing water is probably the most active physical agent in the distribution of *Arachis.* One might reasonably ask how it is that the Annuae of the Axonomorphae migrated up the western branches of the Paraguay to remote streams of northwest Argentina and even the Parapetí which begins and ends in southern Bolivia, without leaving a remnant downstream to suggest the path of movement. The only possible alternative route lies along the low mixing waters of the continental divide which extends in a long sweeping curve from the headwaters of the Paraguay in the region of Cuiabá, Mato Grosso westward, and then sharply southwestward through eastern Bolivia and down into northwest Argentina. The chronology of these events will probably never be known. Their antiquity defies even the imagination. The distribution of the Prorhizomatosae at the lower end of the whole rhizomatous distribution also poses a problem for the thesis that flowing water was the principal agent in the dispersal of these species.

Conservation of the Germ Plasm

As a subject which promotes discussion and frustrates action, the conservation of germ plasm has had few equals. All knowledgeable persons recognize the need for and the irreplaceability of the wild and weed relatives of our cultivated plants as sources for new genetic material. In recent years numbers of national and international programs, especially for the important cereal grains, have been developed. The success of most of these depends on the free interchange of collections made in different areas. The widespread recognition of their value by individual breeders has concentrated efforts to amass collections. The development of modern, highly systematic cold storage and automated recall for preservation and distribution is a recent development in plant breeding on an international scale.

Little of this exists for the genus *Arachis.* The seeds are large, short-lived, and despite its importance, the crop is of secondary interest except in a few places such as Georgia and Nigeria or clusters of counties in other states of the United States and restricted regions of other countries. There is no international program for the preservation and extension of germ plasm resources of peanuts. There are no state programs in the United States and the national program is strictly under-coordinated, under-financed, and its basic problems misunderstood. The problems peculiar to peanut production costs, storage space, longevity and division of labor on an international scale need to be worked out. A plan of action should be substituted for haphazard distribution, subsequent mislabeling and loss of stocks gathered at great pains from areas in South America that are sure to be physically and environmentally transformed in the immediate future. The program in North Carolina in cooperation with the Plant Introduction Section in the U. S. Department of Agriculture and of I.N.T.A. and associated institutions in Argentina consists of sending seeds or plant material to anyone who requests them. Efforts have been made to get the wild species collections established in Malawi and Nigeria in Africa; in Corrientes and Manfredi, Argentina, in South America; and in Georgia, Oklahoma, Texas, and North Carolina in the United States. Crops Research, ARS-USDA does cooperative production in Puerto Rico and furnishes material to the regional center of Plant Introduction at Experiment, Georgia. Cooperation of individuals in these areas can be said to be excellent insofar as their interests and resources permit. Intra-agency collaboration, such as is possible between Crops Research-ARS and Plant Introduction-ARS, is reasonably good. Inter-agency cooperation of wider scope extending to the international level has no administrative framework upon which to build and no central assumption of responsibility for the preservation of peanut germ plasm or even a centrally oriented recognition of the requirement that the job be done. If the problem is raised in the presence of knowledgeable growers, political representatives, or leaders of growers associations in the United States, one and all point to the Plant Introduction Service-ARS-USDA. And yet the Plant Introduction Service is only partially equipped to do the job that needs doing and has no authority or at least no funds to enter international negotiation for a worldwide peanut germ plasm bank. As far as we can ascertain, the limited facilities and the very large number of crops, etc., with which Plant Introduction must contend, makes it virtually impossible for them to take detailed responsibility for growing out collections themselves. The limited contractual arrangements which they can effect do not extend to the complete job required by *Arachis.* The spirit of cooperation exists; only the direction, coordination, and financial commitment are lacking. That the peanut breeders of the world could come up with such a plan, there is hardly a question. They need a medium of communication and a means of joint assistance in the maintenance of the germ plasm of *Arachis.* They need some organization to whom and through whom they can speak and some authority with the responsibility and the means as well as the knowledge to whom they can give the problem and their cooperation in its solution. Perhaps a private agency could take on the organizational and structural problem with previously built-in arrangements for graduated transfer of stated obligations and privilege to national agencies through the United Nations.

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