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Seed-Coat Structure and Anatomy of Some Nigerian Pulses

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Here we report the seed morphology and anatomy of some Nigerian pulses, an investigation that revealed a wide diversity of characteristics in a small collection of seeds. Although these genera share common features, their anatomical differences make it possible to generate a key for identification and classification. Sizes ranged from 5 to 7 × 5 × 3 mm for *Cajanus cajan* up to 25 to 30 × 18 × 19 mm for *Canavalia ensiformis*. Seed colors were monochromatic black/brown to dichromatic eye/mottled (streaked), and surfaces were either smooth-glossy or puckered. Forms varied from ellipsoid or oblong-ellipsoid to spheroid or reniform, and halos (hilar rims) were either complete or incomplete. Lens shapes were spot, linear, broadly linear, or deltoid. The hila were elliptic to linear (or in-between), with sizes ranging from 0.5 to 1.0 mm (*Mucuna pruriens*) up to 1.5 to 3.0 mm (*Phaseolus vulgaris*). Their positions could be completely covered, as in *P. vulgaris*, partially covered and raised above the seed surface (*Vigna subterranea*), or naked (without any funicular residue) and level with the surface, as in *C. ensiformis* (Tce1). The aril caps were collar-like in *Lablab purpureus* or cushion-like, as in *M. pruriens*. Palisade cell sizes ranged from 80.7 μm in *Glycine max* to 173.3 μm in *C. ensiformis* (Tce1), and their shapes varied from a uniformly wall-thickened type (T_1), to a bulbous-end type (T_2), to one with a corrugated structure on the inner wall (T_3). Although these anatomical variations exist, they may not warrant demarcation into sub-familiar or generic classifications. However, we do propose that specific and sub-specific alterations are necessary.

Keywords: aril cap, cotyledon, hilum, lens, palisade cell, radicle, seed color, seed size, taxonomic classification

It is becoming increasingly important when practicing modern scientific agriculture to be able to distinguish individual species by their seeds. Without this skill, it is of little use to attempt to perfect methods for cultivating useful plants. Knowledge of seed anatomy is critical to ensuring commercial quality control of human and animal feeds by detecting possible adulterations and potentially toxic plant materials.

Studying the morphology of leguminous seeds is of great taxonomic value. Early contributions to research on the inherent characteristics of the Fabaceae family have included those by Gunn (1972, 1981, 1982, 1983), Cowan (1974), Corner (1976), Gill et al. (1993), and Idu (1995). Seed coats in this family are simply enlarged ovule walls, which means that they comprise complex, multi-layered tissues. A hard, protective layer is generally formed from all or part of the testa or integuments. Corner (1976) has classified seed coats according to the position of this mechanical layer. For example, in exotestal coats, that layer is formed from the outer epidermis of the outer integument; in endotegmic coats, from the inner epidermis of the inner integument. The mechanical layer may consist of one or more rows of elongated, palisade-like cells, e.g., as seen with the macrosclereids.

Historically, studies of seed anatomy have focused on one of two areas. The first, embryology, emphasizes sequential development, and includes considerable research by Netolitzky (1926) and Zimmerman (1936) on the formation of ovules and integuments, particularly in leguminous seeds. Chowdhury and Buth (1970) have also reported on some pulse seeds, but without providing much anatomical detail of the testa.

The second area of concentration is the economic value of crop seeds. For instance, Coe and Martin (1920) and Martin and Watt (1944) determined the structure and chemical nature of the seed coat in relation to its impermeability in some leguminous forage plants. Ott and Ball (1943) made a similar study with *Phaseolus vulgaris*, and Corner (1951) produced a comprehensive work on the classification of leguminous species, showing that the structures of the coats could be employed as an index for distinguishing their seeds from those of other families. In that research, the emphasis was on the structure of the outer epidermal palisade of the outer integument and its hypodermal layer of hourglass cells, and on characterizing the hilum and its associated tissues in Papilionaceae seeds. Likewise, Hyde (1954) intensively studied the function of the hilum in some

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fodder plants. More recently, the importance of being able to identify isolated seeds for agricultural and commercial purposes has been supported by the publication of a general seed manual by Martin and Barkley (1973), as well as one specifically for crop and weed seeds (Musil, 1963).

Gill et al. (1993) has studied the morphometric and taxonomic characteristics of Nigerian leguminous seeds across three-subfamilies - Caesalpinoideae, Papilionoideae, and Mimosoideae. The latter two groups had previously been surveyed by Gunn (1981), while Lersten (1979) conducted research on the Papilionoideae.

The primary objective of the present study was to describe the morphological and anatomical features of some Nigerian pulses, including 17 species in 10 genera, in order to better understand the systematics of these taxa.

MATERIALS AND METHODS

Seeds of 17 species were obtained from the International Institute of Tropical Agriculture (IITA). Vouchers for the seed samples are held in the Department of Botany, University of Benin, Benin City, Nigeria. These species (and accession numbers) included *Cajanus cajan* (L.) Mill. (CITAI); *Canavalia ensiformis* (L.) DC. (Tce2 and Tce1); *Canavalis gladiata* (L.) DC (Tcg3); *Glycine max* (L.) Merr. (TGM1287); *Lablab purpureus* (L.) Sweet. (Tln1 and Tln2); *Macrotyloma geocarpa* (Harms.) (Tkg8 and Tkg2); *Mucuna pruriens* (L.) DC. (Tmp1); *Phaseolus lunatus* L. (Tpl111a and Tpl84a); *P. vulgaris* L. (Tvu6148); *Physocarpus tetragonolobus* (L.) DC. (Tpt2); *Sphenostylis stenocarpa* Hochst and A. Rich. (TSs1 and TSs9); and *Vigna subterranea* (L.) Verde (TvSu5).

Our morphological study was based on the techniques outlined by Idu (1995), with the following data being recorded: seed color, surface, size, and shape; lens shape; nature of the halo; funicular margin; and cotyledon interface. Measurements were made with a light microscope. The cotyledons were described by first soaking the seeds in cold water for about 24 h, then transferring them to hot water (60°C) for about 30 min. Afterward the seed coats were removed and the cotyledons examined under a light microscope.

For the anatomical study, the seeds were softened in a 1:1 mixture of glycerin and hot water (60°C). This solution was replaced four times daily for 5 d. The softened seeds were then pressed to slip off their coats. A 3-× 3-mm section was sliced approximately 1 mm from the hilum, and another was removed about 2 mm away. These slices were then de-aerated with a vacuum pump; sequentially dehydrated in 50%, 70%, 90%, and 100% ethanol with xylene; then embedded in paraffin wax. Serial sections (10- to 15 µm thick) were cut with a microtome (six per sample), and examined, either stained or unstained, under a light microscope. Palisade-cell measurements were recorded along with observations about the size, position, and shape of the hilum, aril cap, radicular lobe, and ratio of radicle length to cotyledon length.

RESULTS AND DISCUSSION

Comparative seed morphology and anatomy generally are neglected by plant scientists. The ensuing lack of reliable data has hampered identification of isolated seeds and, thus, has reduced their importance when considering the phylogeny of flowering plants (Gill et al., 1993). Consequently, many floral monographs do not include seed characteristics in their descriptions of taxa. Nevertheless, some investigators have overcome this lack of data through their, albeit temporal, accumulation of unrecorded insights into seed identification. For example, Pammel (1899) was the first to describe the seed morphology of Leguminosae, an effort that was later taken up by Corner (1951, 1976), Gunn (1972, 1981, 1982), Cowan (1974), and Newell and Hymozwitze (1978). One can now find in the literature such information as seed size and shape, as well as ornamentation and aril characteristics such as hilum size, shape, and length, all of which are useful when attempting to distinguish various plant genera (see Isely, 1955; Kopooshian, 1963; Polhill, 1976; Gunn and Barnes, 1977).

Morphological Features

In this study, seeds differed widely in their dimensions, even within the same genus, e.g., *P. lunatus* (15 to 21 × 10 × 30 mm) versus *P. vulgaris* (8 to 10 × 9 × 8 mm). Similarly, within the same seed lot, samples of Accession Tce1 of *C. ensiformis* had a size range of 25 to 30 x 18 x 19 mm while Accession Tce2 was 17 to 29 × 16 × 11 mm. For this reason, it was difficult to classify these seeds into generic groups on the basis of size, so one had to rely on significantly more useful traits, such as color, cotyledon interface, and description of radicular lobes. While seed shapes were very similar within the same genus [e.g., *C. ensiformis* and *C. gladiata* (Table 1)], color differed considerably -- monochromatic brown/black or dichromatic eyes in the former compared with the dichromatic mottled and glossy seeds found in the latter. Likewise, in the

Table 1. Morphological features of some Nigerian pulses.

Botanical name	Common name	Accession no.	Seed color: Mono-chrome: Red-orange type	Seed color: Mono-chrome: Brown black type	Seed color: Dichromatic: Red/black/ Orange type	Seed color: Dichromatic: Eye	Seed color: Dichromatic: Mottled (streaked)	Seed surface	Seed size (mm)	Seed shape	Lens shape	Halos	Funicular margin	Cotyledon Interface
Canavalia ensiformis (L.) DC.	Jack bean	Tce2	–	–	–	+	–	Smooth	17-19×12×6	Ellipsoid	Spot	Complete	Thin	Smooth
Canavalia ensiformis (L) DC.	Jack bean	Tce1		+	–	–	–	Smooth	2.5-3.0×18×9	Oblong to ellipsoid	Linear	Complete	Thin	Smooth
Canavalia gladiata (L.) DC.	Sword bean	Tcg3	–	–	–	–	+	Smooth	17-29×16×11	Ellipsoid	Spot	Complete	Thick	Smooth
Cajanus cajan (L.) Mill sp.	Pigeon pea	CITA1	–	+	–	–	–	Smooth and glossy	5-7×5×3	Ellipsoid	Deltoid	Incomplete	Thin	Smooth
Glycine max (L.) Merr.	Soybean	TGM1287	–	–	–	+	–	Smooth	7-8×6×5	Ellipsoid	Spot	Incomplete	Thin	Smooth
Lablab purpureus (L.) Sweet	Lablab bean	Tln1	–	+	–	–	–	Smooth	9-12×8×6	Ellipsoid	Deltoid	Complete	Thin	Flap
Lablab purpureus (L.) Sweet	Lablab bean	Tln2	–	+	–	–	–	Smooth	9-13×8×4	Ellipsoid	Spot	Complete	Thin	Smooth
Macrotyloma geocarpa Harms.	Kersting's groundnut	Tkg8	–	+	–	–	–	Smooth and glossy	9-12×6×2	Reniform	Linear	Incomplete	Thin	Smooth
Macrotyloma geocarpa Harms.	Kersting's groundnut	Tkg2	–	–	–	–	+	Puckered	8-11×7×4	Reniform	Broadly linear	Complete	Thin	Smooth
Mucuna pruriens (L.) DC.	Mucuna	Tmp1	–	+	–	–	–	Smooth and glossy	14-17×12×8	Ellipsoid	Deltoid	Complete	Thick	Smooth
Phaseolus lunatus L.	Lima bean	Tpl111a	–	–	–	–	+	Puckered	15-21×10×13	Reniform	Deltoid	Incomplete	Thick	Smooth
Phaseolus lunatus L.	Lima bean	Tpl 84a	–	+	–	–	–	Smooth and glossy	12-13×9×6	Ellipsoid	Deltoid	Incomplete	Thin	Smooth
Phaseolus vulgaris L.	Cowpea	Tvu6148	–	–	–	+	–	Smooth	8-10×9×8	Reniform	Linear	Complete	Thick	Smooth
Physocarpus tetragonolobus (L.) DC.	Winged bean	Tpt2	–	+	–	–	–	Smooth and glossy	7-10×8×4-6	Ellipsoid	Deltoid	Complete	Thick	Flap
Sphenostylis stenocarpa Hochst and A. Rich.	African yam bean	TSs1	–	+	–	–	–	Smooth and glossy	6-8×5×3	Ellipsoid to spheroid	Deltoid	Complete	Thin	Flap
Sphenostylis stenocarpa Hochst and A. Rich.	African yam bean	TSs9	–	+	–	–	–	Smooth and glossy	7-10×5×3	Ellipsoid to oblong	Deltoid	Complete	Thick	Flap
Vigna subterranea (L.) Verde.	Bambara groundnut	TvSu5	–	+	–	–	–	Smooth	10-12×9×10	Spheroid	Linear	Complete	Thin	Smooth

genus *Phaseolus*, seeds of *P. lunatus* were monochrome brown/black while those of *P. vulgaris* were black-eyed. Fortunately in this study, within-lot color variation was apparent only for *C. ensiformis* and *Macrotyloma geocarpa*. Hence, we were able to categorize the different species into only two color groups: 1) multicolored (dichromatic) e.g. *G. max*, *P. lunatus*, *P. vulgaris*, *M. geocarpa*, *C. ensiformis*, and *C. gladiata*; and 2) those remaining species with uniform (monochrome) coloration, i.e., black, brown, or white.

The seed-coat surfaces for most of our species had somewhat similar textures, an observation consistent with those of Chowdhury and Buth (1970). Seeds of *Canavalia* and *Lablab* were smooth, and those of *Sphenostylis* and *Macrotyloma* were also glossy. However, samples of *P. lunatus* had undulating (puckered) surfaces. We note here that some seeds often develop wrinkled textures when the testa shrink as a result of drying. Therefore, it is of utmost importance that such samples not be confused with species that normally have puckered surfaces e.g., *S. stenocarpa*.

Great similarities were found with the cotyledonal interfaces and radicular lobes of seeds from the same genus or lot. However, whereas *P. lunatus*, *P. vulgaris*, *C. ensiformis*, and *C. gladiata* all presented smooth interfaces, seeds of *Sphenostylis* had a flap interface. No distinct differences were seen among any of the various radicular lobes.

Hilum

We observed wide variations in sizes and shapes of the hila, with the largest being recorded in *P. lunatus* and *P. vulgaris*; the smallest, in *C. ensiformis*, *C. cajan*, and *M. geocarpa* (Table 2). Shapes ranged from linear in *M. geocarpa*, *P. lunatus* and *P. vulgaris*, *S. stenocarpa*, and *V. subterranea* to linear-elliptic in the other taxa. The hila were often obscured with what has been described by Musil (1963) as a corky material; only *C. ensiformis* (Tcel), *C. gladiata*, *C. cajan*, *G. max*, and *M. geocarpa* (Tkg8 and Tkg2) showed no such growth. All the other species had some sort of whitish tissue that either partially or completely obscured the hilum. In most cases, the covered hilum was below the seed surface, while in *Phaseolus lunatus*, it was surrounded by a pouch.

Cuticle

The cuticle is the outermost layer of the seed coat, and is best viewed in the longitudinal section (Chowdhury and Buth, 1970). In this study, *C. cajan* had a very thin cuticle, while the other species had fairy thick tissues (Table 2). Although there were slight variations in

Table 2. Anatomical features of some Nigerian pulses*.

Botanical name	Common name	Accession no.	1 No. of seed	2 (mm)	3 (mm)	4	5	6	7	8 (mm)	Hilum position	Palisade cell: Shape	Palisade cell: Size (μm)	Cuticle
											9	10	11	12
Canavalia ensiformis (L.) DC.	Jack bean	Tce2	5	17.5-20	2-17.1	c	e	–	–	0.5-1	Completely covered with whitish hard tissue	T_1	134	Rough
Canavalia ensiformis (L) DC.	Jack bean	Tce1	5	25.5-30	3.2-25	c	e-l	–	–	1.4-2	Level with seed surface, whitish tissue absent	T_1	173.3	Rough
Canavalia gladiata (L.) DC.	Sword bean	Tcg3	6	25.5-30	7.1-20.5	c	e	–	–	1.5-2	Almost level with seed surface, whitish hard tissue absent	T_1	167.4	Smooth
Cajanus cajan (L.) Mill sp.	Pigeon pea	CITA1	5	5.5-7	2.1-5.4	c	e-l	–	–	0.5-1	Almost level with seed surface, whitish tissue absent	T_2	87.1	Smooth
Glycine max (L.) Merr.	Soybean	TGM1287	5	7.5-9	2.0-5.3	c	e-l	+	–	1.1-2	Almost level with seed surface, whitish hard tissue absent	T_2	80.7	Smooth
Lablab purpureus (L.) Sweet.	Lablab bean	Tln1	5	11.5-14	3.3-9.2	t	e	–	Col +	1.5-2	Completely covered with whitish hard tissue raised above the level of seed surface	T_1	147.4	Smooth
Lablab purpureus (L.) Sweet	Lablab bean	Tln2	6	11.5-13	3.1-10.2	t	e-l	–	Col +	1.5-2	Completely covered with whitish hard tissue raised above the level of seed surface	T_2	131.3	Smooth
Macrotyloma geocarpa (Harms)	Kersting's groundnut	Tkg8	5	10.5-13	3.4-10.3	c	e	–	–	0.5-1	Almost level with seed surface, whitish hard tissue absent	T_1	141.8	Smooth
Macrotyloma geocarpa (Harms)	Kersting's groundnut	Tkg2	6	8.5-10	3.2-6.7	c	l	–	–	1.1-1	Almost level with seed surface, whitish hard tissue absent	T_1	127.3	Smooth
Mucuna pruriens (L.) DC.	Mucuna	Tmp1	5	16.5-18	3-11.2	c	e	–	Cus +	0.5-1	Partially covered with whitish hard tissue raised above the level of seed surface	T_1	160.8	Rough
Phaseolus lunatus L.	Lima bean	Tpl111a	5	20.5-22	2.5-20.1	c	l	–	–	1.5-2	Below the level of seed surface, partially covered with whitish tissue	T_2	100.4	Slightly rough
Phaseolus lunatus L.	Lima bean	Tpl84a	5	9.5-10	3.1-6.0	c	e-l	–	–	1.5-3	Completely covered with whitish hard tissue	T_2	93.8	Slightly rough
Phaseolus vulgaris L.	Cowpea	Tvu6148	4	9.5-11	3.3-6.4	c	l	–	–	1.5-3	Completely covered whitish hard tissue	T_1	134.0	Slightly rough
Physocarpus tetragonolobus (L.) DC.	Winged bean	Tpt2	7	10.5-12	1.0	c	e-l	+	–	1.5-1.7	Partially covered, raised above the level of seed surface	T_2	167.5	Slightly rough
Sphenostylis stenocarpa Hochst and A. Rich.	African yam bean	TSs1	6	8.5-10	3.2-10	c	e	–	–	1-1.3	Completely covered with whitish hard tissue	T_2	100	Smooth
Sphenostylis stenocarpa Hochst and A. Rich.	African yam bean	TSs9	6	8.5-10	1.4-7.2	c	l	–	–	0.5-1	Almost level with seed surface, whitish hard tissue absent	T_2	113.1	Slightly rough
Vigna subterranea (L.) Verde.	Bambara groundnut	TvSu5	6	7.5-10	2.8-6.9	c	l	+	–	1-1.1	Partially covered, raised above the level of seed surface	T_3	140.7	Rough

Column 1. Number of seeds measured and dissected (qualitative features observed in wider range).
Column 2. Length of seed.
Column 3. Ratio of radicle length to cotyledon length.
Column 4. Cotyledon axis: c = coaxial with the hilum, t = transverse.
Column 5. Hilum shape: l = Linear, e = elliptic or elliptic-oblong.
Column 6. Radicular Lobe: + = prominent, - = indistinct.
Column 7. Aril cap: Col = collar-like, Cus = cushion-like, + = prolonged on the side of the lens, - = rim-aril inconspicuous.
Column 8. Hilum size.
Column 9. Position of hilum.
Column 10. Palisade cell shape: T_1 = Uniform wall thickness, T_2 = Bulbous at end of palisade cell, T_3 = distinctly corrugated structure on inner wall at lower end of cell.
Column 11. Palisade cell size.
Column 12. Cuticle surface texture.

thickness among the samples, these sporadic differences were not significant enough to allow us to classify the species into subgroups. Cuticle surfaces were either rough or smooth, with the latter group including *C. gladiata*, *C. cajan*, *G. max*, *L. purpureus*, *M. geocarpa*, and *Sphenostylis stenocarpa*. Although two species, *M. pruriens* and *V. subterranea*, had rough cuticles, theirs were part of a delicate structure. In a third variation, the cuticles of *P. lunatus* seeds showed papillae or papilla-like outgrowths with attached bulbous bases (Table 2).

Palisade Cells

The palisade cells occur next to the seed coat, and are derived from the outer epidermis of the outer integument. They are adjacent to the hilum in two layers -- palisade and counter-palisade -- and are bordered with hourglass cells. These palisade and hourglass cells are equidistant from the counter-palisade. Differential thickening of the palisade walls means that these cell types can be divided into three groups (Chowdhury and Buth, 1970). In this study, our species were separated into: 1) Type 1 – cells of uniform thickness: *C. ensiformis*, *C. gladiata*, *M. geocarpa* (Tkg8 and Tkg2), *M. pruriens*, *P. lunatus* (Tpl111a and Tpl84a) and *P. vulgaris*, and *S. stenocarpa* (TSs1 and TSs9); 2) Type 2 -- ends of the palisade cells away from the cuticle being bulbous: *C. cajan*, *G. max*, *L. purpureus* (Thn1 and Thn2), and *P. tetragonolobus*; and 3) Type 3 -- inner walls showing distinctly corrugated structures at the lower ends of the cells: *V. subterranea* (Table 2).

Epidermal Cells

Epidermal cells (i.e., testa) are the primary insulating layer of the seed. Ripening causes shrinkage and closure of the lumen because of wall-thickening. Under a light microscope, cells in glycerin can be viewed in the expanded state, with their lumens open. In this study, thickening patterns varied considerably among species, being either uniform and regular or convoluted and irregular (Table 2). When this thickening was moderately convoluted, it was possible to distinguish individual cells, as seen in *C. ensiformis* (Tce1, Tce2), *C. cajan*, *G. max*, *M. pruriens*, and *V. subterranea*. In contrast, convolutions and inter-digitations caused clumping in *C. gladiata*, *L. purpureus* (Thn1 and Thn2), *M. geocarpa* (Tkg2 and Tkg8), and *P. lunatus*. Likewise, these convolutions were inter-digitate such that the limits of individual cells were often obscured, as seen in *P. tetragonolobus*, *S. stenocarpa* (TSs1 and TSs9), and *P. vulgaris*.

Although the external morphology of seeds is quite reliable for identifications at the species level, it is of limited use at the genus level. In that case, chemical analysis must be implemented in order to separate genera. Gunn (1970) has reviewed seeds of the tribe Viceae and has proposed four reliable characteristics for generic demarcation and identification – hilum shape, position, distance between lens and hilum, and seed coat morphology. Previously, researchers had consistently overlooked a taxonomically useful set of characters associated with the cuticle and palisade cells, as well as the hilum and its surrounding collar. Here, we were able to exploit these observations in presenting such inter-specific differences.

Characteristics observed in our study were consistent with those found in the sub family Papilionoideae. The majority of the seeds had hard, smooth surfaces and were bean-shaped, with linear to elliptic hila (a few having rim arils) and double palisade layers. Endosperms were absent whereas the hilar rims (i.e., halos) were typically conspicuous. Seed outlines were generally regular, although, in some cases, they were asymmetrical, possibly as a result of pressure from the neighboring seeds in the pod. As at the family and sub family levels, it was impossible to distinguish individual genera for our pulse seeds. However, at the inter-specific level, circumscription was possible because the seed characteristics observed under a dissecting or light microscope are considered of "primary importance diagnostically" (Aston, 1969). In those instances, the emphasis would have been on either a group of related species or those with unclear relationships (Chuang and Ornduff, 1992). For example, in our study, seed shapes differed between Accessions Tpl111a and Tpl84a of *P. lunatus*. Likewise, their seed-coat surfaces also varied, with the former having a puckered texture that contrasted with the smooth, glossy surfaces found with the latter. Seed surfaces of *M. geocarpa* also differed between accessions, being smooth and glossy in Thn2 and puckered in Thn8. Their halos also were dissimilar.

A Key for Identifying Some Nigerian Pulses According to Their Seed Structure and Anatomy

1. Maximum axial length of seed >17.0 mm.
   2. Height of hilum 0.5 to 1.0 mm, completely covered with corky tissue; Palisade cell >134.0 µm; Cuticle rough; Lens spot. *C. ensiformis* (Tce2).
   2. Height of hilum 1.4 to 2.0 mm, naked; Palisade cell >173.3 µm; Cuticle rough; Lens linear. *C. ensiformis* (Tce1).
   2. Height of hilum 1.5 to 2.0 mm, naked; Palisade cell >167.5 µm; Cuticle smooth; Lens spot. *C. gladiata* (Tcg3).
2. Maximum axial length of seed <21.0 mm.
   3. Maximum axial length of seed <21.0 mm but >14.0 mm.
      4. Height of hilum 0.5 to 1.0 mm, partially covered with corky tissue and raised above seed surface; Palisade cell >160.8 µm; Cuticle deltoid; Lens deltoid; Aril cap cushion-like. *M. pruriens* (Tmp1).
      5. Height of hilum 1.5 to 2.0 mm, below seed

surface; Palisade cell >100.4 µm; Cuticle slightly rough. *P. lunatus* (Tpl111a).

3. Maximum axial length of seed <14 mm.
   6. Maximum axial length of seed <14 mm but >9 mm.
      7. Height of hilum 1.5 to 2.0 mm, completely covered with corky tissue and raised above seed surface; Palisade cell >131.3 µm; Aril cap collar-like. *L. purpureus* (Tln2).
         8. Palisade cell >147.4 µm, shape uniformly thickened. *L. purpureus* (Tln1).
      9. Height of hilum 1.0 to 1.1 mm, naked and almost level with seed surface; Palisade cell 127.3 µm. *M. geocarpa* (Tkg2).
         9. Height of hilum 0.5 to 1.0 mm; Palisade cell >141.8 µm. *M. geocarpa* (Tkg8).
      10. Height of hilum 1.5 to 3.0 mm, completely covered with corky tissue; Palisade cell 93.8 µm; Cuticle slightly rough. *P. lunatus* (Tpl84a).
      11. Height of hilum 1.5 to 1.7 mm, partially covered with corky tissue and raised above seed surface; Palisade cell >167.5 µm. *P. tetragonolobus* (Tpt2).
      11. Height of hilum 0.5 to 1.0 mm, almost level with seed surface; Palisade cell >113.1 µm. *S. stenocarpa* (TSs9).
      11. Height of hilum 1.0 to 1.1 mm, partially covered with corky tissue and raised above seed surface. Palisade cell 140.7 µm; Cuticle rough. *V. subterranea* (TvSu5).
      11. Height of hilum 1.5 to 3.0 mm, completely covered with corky tissue; Palisade cell >134.0 µm; Cuticle slightly rough. *P. vulgaris* (Tvu6148).
4. Maximum axial length of seed <9 mm.
   12. Maximum axial length of seed <9 mm but >5 mm.
      13. Height of hilum 1.1 to 2.0 mm, almost level with seed surface; Palisade cell >80.7 µm; Cuticle smooth. *G. max* (TGM1287).
      13. Height of hilum 0.5 to 1.0 mm; Palisade cell >87.1 µm. *C. cajan* (CITA1).
      13. Height of hilum 1.0 to 1.3 mm, completely covered with corky tissue; Palisade cell 100 µm. *S. stenocarpa* (TSs1).

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