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CROTALARIA SEED MORPHOLOGY, ANATOMY, AND IDENTIFICATION
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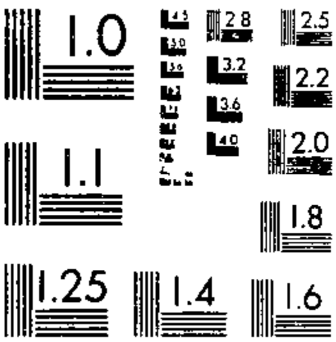

MICROCOPY RESOLUTION TEST CHART
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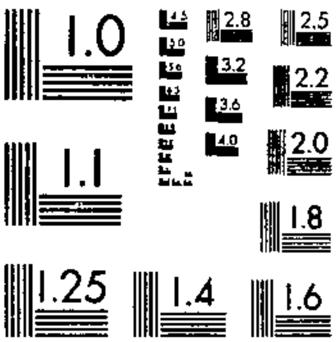

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CROTALARIA SEED MORPHOLOGY, ANATOMY, AND IDENTIFICATION

By
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Crotalaria Seed Morphology, Anatomy, and Identification

INTRODUCTION

The accurate identification of seeds has always been problematical and difficult, but not entirely impossible. Seeds should not be considered entirely featureless, for there are often many reliable differences in their morphology and anatomy. Furthermore, seed characters are highly stable and conservative and therefore have considerable diagnostic value. Many seeds have easily recognizable familial characteristics. The problem of positive identification becomes more acute, however, at the generic and species levels.

The need for accurate seed identification is apposite to many branches and fields of the biological sciences, e.g., agriculture, agronomy, biochemistry, forestry, genetics, pharmacognosy, plant systematics, seed analysis, wildlife biology, and others. The current search by the United States Department of Agriculture for new crops as potential sources of industrial raw materials has further prompted activity in seed research and for the concomitant need for proper identification. Additional impetus has been given to the program in the worldwide search for seed with high protein content.

Crotalaria species have considerable utilitarian value as forage and silage, as a green manure, as a source of fibers, as a cover or "smother" crop in the control of weeds, as a soil binder in erosion control, and as ornamentals. Their economic potential appears to be extending. Recently, the seed constituents have been analyzed and found to contain large amounts of water-soluble gums and mucilages, as well as proteins. A few species are known to be toxic to animals and fowl (discussed under Seed Toxicity).

The relatively large genus *Crotalaria* is a member of the family Leguminosae, subfamily Papilionoideae, and the tribe Genisteae. It contains approximately 400 species distributed throughout the warmer temperate, subtropical, and tropical regions of the world as herbaceous to woody annuals or perennials (table 1). Three-fourths of the species are endemic to Africa (Baker, 1914; Baker, 1926, *pp. 23–59*).[1] The genus derives its name from the Greek *krotalon,* meaning "a rattle" or "castanet," alluding to the rattle

[1] See Literature Cited, page 70.

of the loose seeds in the mature chartaceous legume or pod when shaken. In the vernacular it is known as castanet-plant, crotalaire, klapperhülse, klapperschote, rattlebox, rattle-bush, rattle-pea, rattlepod, rattle-wort, and rammelaar.

TABLE 1.—*Crotalarias of North, Central, and South America*
[Putative synonyms are given in the seed keys]

Species	Investigated herein	Indigenous to—	Annual or perennial	Herbaceous (H), suffruticose (S), or fruticose (F)	Seeds per gram [1]	Grams per 1,000 seed [2]
C. acutiflora Benth.	No	Brazil	P	F	40	24.4
C. alata Hamilt.	Yes	Africa	P	F		
C. anagyroides H. B. K.	Yes	S. America	P	H–F	49	23.5
C. berteriana DC.	No	India	P	F		
C. brachycarpa Benth.	No	Brazil	P ?	F ?		
C. brachystachya Benth.	Yes	Brazil	P	F ?	54	
C. breviflora DC.	Yes	S. America	P	F ?	235	
C. bupleurifolia Cham. & Schlect.	No	Mexico				
C. capensis Jacq.	Yes	Africa	P	F		
C. claussenii Benth.	Yes	Brazil	P	F		
C. depauperata Mart.	No	Brazil	A–P	H–S		
C. divaricata Benth.	No	Brazil	P	F		
C. erecta Pilger	No	Brazil				
C. eriocarpa Benth.	Yes	C. America	P	F	72	14.0
C. falcata Vahl	No	Africa	A–P ?	F		4.9
C. ferruginea Grah.	Yes	India	A	H	207	
C. filifolia Rose	Yes	Mexico	A	H		
C. flavicoma Benth.	Yes	Brazil	P	F ?		
C. foliosa Benth.	Yes	Brazil	P	F		
C. goreensis Guill. & Perr.	Yes	Africa	P	F	146	
C. grantiana Harv.	Yes	Africa	A	H	265	3.6
C. hilariana Benth.	No	Brazil	P	F ?		
C. holosericea Nees & Mart.	No	Brazil	P	F		
C. incana L.	Yes	Pantropical	A–P	H–F	218	7.8
C. intermedia Kotschy	Yes	Africa	A–P	H–F	281	5.0
C. juncea L.	Yes	India	A	H	36	38.0
C. laeta Mart.	No	Brazil	P	F		
C. lanceolata E. Mey.	Yes	Africa	P	S	381	2.8
C. leubnitziana Schinz	Yes	Africa	P	F	226	
C. longirostrata Hook. & Arn.	Yes	C. America	A–P	S	97	1.6
C. lotifolia L.	Yes	West Indies	P	F	77	
C. maritima Chapm.	Yes	So. U.S., Mexico, West Indies.	P	H–S		
C. maypurensis H. B. K.	Yes	C. America	A–P	H		

See footnotes at end of table.

TABLE 1.—*Crotalarias of North, Central, and South America*—(continued)

Species	Investigated herein	Indigenous to—	Annual or perennial	Herbaceous (H), suffruticose (S), or fruticose (F)	Seeds per gram [1]	Grams per 1,000 seed [2]
C. mollicula H. B. K.	Yes	C. America	A–P	H–F	-----	-----
C. mucronata Desv.	Yes	Pantropical	A	H–S	183	5.9
C. mysorensis Roth	Yes	India	A	H	252	-----
C. nitens H. B. K.	Yes	C. America, S. America.	A	H–S	-----	-----
C. ochroleuca G. Don.	Yes	Africa	P	F	285	3.9
C. otoptera Benth.	No	Brazil	A	H	-----	-----
C. paulina Schrank	Yes	Brazil	A	H	66	-----
C. picensis Phil.	No	Chile	P	H	-----	-----
C. pilosa Miller	Yes	C. America	A	S	-----	-----
C. pohliana Benth.	Yes	Brazil	P ?	F	-----	-----
C. pumila Ort.	Yes	So. U.S., West Indies, C. America, S. America.	A–P	S	228	10.7
C. purdiana Senn	No	Colombia, Cuba.	P	F	-----	-----
C. purshii DC.	Yes	So. U.S., Mexico.	A	H	-----	-----
C. quinquefolia L.	Yes	India	A	H	32	30.3
C. ramosissima Roxb.	Yes	India	P	F	95	-----
C. retusa L.	Yes	Pantropical	A	S	61	23.6
C. rhodesiae Baker f.	Yes	Africa	P	S	190	5.7
C. rufipila Benth.	No	Brazil	P	F	-----	-----
C. sagittalis L.	Yes	Pan-Americana	A–P	S	383	5.4
C. saltiana Andr.	Yes	Africa	P	S	188	6.0
C. spectabilis Roth	Yes	India	A	H	62	18.3
C. stipularia Desv.	Yes	S. America, West Indies.	A	H–S	198	-----
C. subdecurrens Mart.	No	Brazil	P	F	-----	-----
C. tetragona Roxb.	Yes	India	P	F	59	-----
C. trifoliastrum Willd.	Yes	India	P	F	344	-----
C. tweediana Benth.	No	Brazil	P	F ?	-----	-----
C. unifoliolata Benth.	Yes	Brazil	A–P	S	58	-----
C. usaramoensis Baker f.	Yes	Africa	A–P	S	293	4.4
C. velutina Benth.	No	Brazil	A	H–S	-----	-----
C. verrucosa L.	Yes	Pantropical	A	H	50	8.2
C. vespertilio Benth.	Yes	Brazil	A–P	H–S	-----	-----
C. vitellina Ker.	Yes	C. America	A–P	S–F	-----	16.0

[1] Samples vary from 1 to 10; seed numbers per gram are approximate.

[2] Samples vary from 1 to 6; seed weights are approximate. Data from Northern Utilization Research and Development Division, Agricultural Research Service, U.S. Department of Agriculture.

The purpose of this investigation was to develop a key, or other means, for the accurate identification of the seeds of *Crotalaria* species occurring in the Americas. There is no general seed taxonomy for this genus. Scattered references to a few species are given by Corner (1951), Martin and Barkley (1961), Musil (1963, *pp. 73–74*), and Pammel (1899). During the course of the study it became apparent that insufficient external morphological characters became a limiting factor when a large number of species were involved. The anatomy of the seed was investigated in order to obtain a clearer understanding of its morphology and the structure of its integument. This investigation revealed certain "unique" tissues that are useful in segregating the seed of *Crotalaria* from that of other genera that are similar in appearance.

Although many investigations have been made on legume seeds in general, few have been concerned with *Crotalaria* per se. An excellent treatment on the general subject of seeds and some of their relationships in 17 families is given by Isley (1947); Kopooshian (1963) has examined seed character relationships among the legumes. Pammel's early investigation (1899) on the anatomical characters of legume seeds is a standard reference. There are relatively extensive bibliographies on the chemical nature and structure of the legume integument in Hayward (1948), Mattirolo and Buscalioni (1892), Netolitsky (1926), Pammel (1899), and Zimmermann (1936). Other treatments on legume seed structure may be found in Capitaine (1912, *pp. 21–30*), Maisel (1909), Pitot (1935), and Tschirch and Oesterle (1900).

Few histological studies on the seed coat components of *Crotalaria* have been made. The inferences as to its structure have been drawn largely from various earlier investigations on the testa of legumes in general. This has resulted in a number of misconceptions and erroneous interpretations. Seed development of *Crotalaria sagittalis* is briefly discussed by Cook (1924), and some aspects of seed anatomy are reported by Brown and Fudge (1960), Pammel (1899), and Wellendorf (1964). The general morphology and anatomy of *C. retusa* seed is given some attention by Corner (1951). Consideration of the internal morphology of *C. spectabilis* seed is given by Martin (1946). Endosperm development in *C. verrucosa* is described by Rau (1951), and the chemical nature of the endosperm of the latter species is considered by Nadelmann (1890). More precise and analytical chemical analyses of the *Crotalaria* endosperm are given by Anderson (1949), Earle and Jones (1962), Jones and Earle (1966), Tookey and Jones (1965), and Tookey et al. (1962, 1963).

The structure of the testa of *Crotalaria* is similar in large part to other taxa of the Leguminosae, and especially to other members of the subfamily Papilionoideae. It may prove to be characteristic of the legume seed in general. While there is considerable variation in the histological structures of seed coats, such variation, nevertheless, is as specific for a genus or species, as are the vegetative characters of the plant themselves. It is unfortunate that the comparative anatomy of seeds has been so largely neglected.

This investigation does not purport to cover all species of *Crotalaria* occurring in the New World. From an examination of several floras and monographs, it is estimated that approximately 65 species may occur in both hemispheres of the Americas. Bentham (1859–62) describes 32 species in Brazil alone, while Senn (1939) recognizes 31 species for the entire New World, including 10 introductions. Table 1 indicates the species which have been investigated in this study and those which have not. Seeds of the latter category were unobtainable, or of insufficient quantity or maturity to study satisfactorily. Thus, the present investigation is concerned with 40 species probably endemic to the New World, 21 species of the Old World, and 4 pantropicals. Synonymies have been arbitrarily deleted (see discussion under Seed Similarities). A total of 47 species, included in the keys, have been investigated anatomically.

MATERIALS AND METHODS

Mature undamaged seeds were obtained from various individual collaborators and herbaria in the Americas (see Acknowledgments). Some material was also obtained from the general seed collection and from germ plasm depositories of the United States Department of Agriculture. For the histological studies, a minimum of 10 samples of each species was used whenever possible; in constructing the keys, 50 random samples representative of each species were chosen as a standard. Desirable quantities of seed were not always available and some species were entirely unobtainable (see table 1). Whenever possible the seeds were authenticated against herbarium voucher material, and some seeds were "grown out" in the greenhouse to further validate their identity.

Soaking seeds (lightly scarified by pricking the hilum) in warm water for several hours usually softened the testa enough to enhance macrosectioning for gross morphological observations, and for testing with various reagents. Anatomical investigations involved microsectioning paraffined material. Since most of the seeds were so small, whole seeds, after scarification, were softened in warm water for 12 to 24 hours until turgid and then aspirated in a warm killing and fixing solution of FAA or modified Navaschin fluid. After 12 to 48 hours in this solution (depending upon seed size), the seeds were dehydrated in a warm ethyl alcohol to xylol series and infiltrated with 56° to 58° C. "Tissuemat." The imbedded material was exposed by trimming and soaked in warm water for 15 minutes immediately prior to sectioning. Sections were cut at 8 to 10 microns and stained with Heidenhain's hematoxylin or safranin and fast green.

To verify the exact configurations of the various cellular components of the testa, scarified seeds were also soaked in a warm solution of equal parts of 10 percent aqueous chromic acid and 10 percent aqueous nitric acid for 12 to 24 hours. After thoroughly washing out the macerating fluid the material was stained with safranin and mounted in glycerine.

Standard reagents, and Johansen's (1940) methods, were used for routine microchemical tests (see Microchemical Tests and Seed Constituent Analyses). Polarized light further enchanced the study of the various tissue and cellular components of the seed. Determination of relative seed coat hardness, gelatinity, and water discoloration, was based upon immersion of 10 undamaged mature seeds of each available species in distilled water at room temperature for a period of 12 hours to 1 week. Seeds requiring a week or longer to soften are arbitrarily considered hard coated (table 2).

Inasmuch as age affects coloration, only mature seeds were utilized in assessing color values. The seed coat colors, as used in the keys, are based upon the Nickerson Color Fan (distributed by the American Horticultural Council). Unfiltered ultraviolet light at 3,650 A.U. was used to determine irradiation effects on seed coat coloration. These colors (and those given as water discolorations in table 4) are not based upon any standards.

Due to the paucity of seed it was more convenient to obtain weights by the number of seeds per gram. Whenever possible the number of grams per 1,000 seeds is also included. Sample numbers per species varied from 1 to 10. In spite of the attempt to utilize only mature seed, enough variation existed that all seed weights given are only indicative of the approximate average per sample (see table 1).

Figures given for overall seed dimensions (table 3) are only relative, not absolute, because of sample variability in—among other factors—development, maturation, and age (this may also

TABLE 2.—*Hardness and gelatinity of* Crotalaria *seed coats*

[Based upon undamaged and nonscarified seed; NG = not gelatinous]

Species	Immersion time	Soft (S) or hard (H)	Gelatinity
C. alata	1 week +	H	G
C. anagyroides	after 3 days	S	G
C. brachystachya	3 days	S	G
C. breviflora	24–48 hours	S	NG
C. capensis	1 week +	H	G
C. claussenii	after 3 days	S	G
C. eriocarpa	1 week +	H	NG
C. ferruginea	1 week +	H	NG
C. filifolia	3 days–week +	S–H	NG
C. flavicoma	1 week +	H	NG
C. foliosa	12–24 hours	S	NG
C. goreensis	24–48 hours	S	G
C. grantiana	24–48 hours	S	NG
C. incana	1 week +	H	G
C. intermedia	3 days–week	S–H	NG
C. juncea	24–48 hours	S	NG
C. lanceolata	24–48 hours	S	NG
C. leubnitziana	1 week +	H	NG
C. longirostrata	1 week +	H	NG
C. lotifolia	1 week +	H	NG
C. maritima	1 week +	H	NG
C. maypurensis	1 week +	H	
C. mollicula	1 week +	H	NG
C. mucronata	1 week +	H	G
C. mysorensis	1 week +	H	NG
C. nitens	3 days–week +	S	NG
C. ochroleuca	1 week +	H	NG
C. paulina	24–48 hours	S	NG
C. pilosa	24–48 hours	S	NG
C. pohliana	24–48 hours	S	NG
C. pumila	1 week +	H	NG
C. purshii	3 days–week +	S–H	NG
C. quinquefolia	1 week +	H	NG
C. ramosissima	1 week +	H	NG
C. retusa	1 week +	H	G
C. rhodesiae	1 week +	H	NG
C. sagittalis	1 week +	H	NG
C. saltiana	1 week +	H	G
C. spectabilis	1 week +	H	G
C. stipularia	1 week +	H	NG
C. tetragona	1 week +	H	NG
C. trifoliastrum	1 week +	H	NG
C. unifoliolata	1 week +	H	NG
C. usaramoensis	1 week +	H	NG
C. verrucosa	1 week +	H	NG
C. vitellina	1 week +	H	G

TABLE 3.—Crotalaria *seed histomeasurements (in microns)*[1]

Species	Cuticle (thickness)	Epidermal macrosclereids (width × length)	Subepidermal lagenosclereids (length)	Testa (thickness)	Endosperm (thickness)
C. alata	14	10.5 × 94	32	140	900
C. anagyroides	14	9 × 91	42	147	675
C. brachystachya	14	7 × 74	35	123	315
C. breviflora	3.5	7 × 64	21	89	240
C. capensis	7	10.5 × 77	32	116	705
C. claussenii	4	10.5 × 66	35	105	525
C. eriocarpa	3.5	7 × 53	12	69	450
C. ferruginea	7	7 × 77	35	119	405
C. filifolia	2	7 × 53	14	69	465
C. flavicoma	17.5	9 × 74	39	131	675
C. foliosa	11	8 × 63	35	109	900
C. goreensis	8	10.5 × 56	31	95	525
C. grantiana	7	6 × 59	18	84	150
C. incana	7	7 × 49	28	84	165
C. intermedia	4	7 × 53	21	78	150
C. juncea	10.5	10.5 × 60	25	96	405
C. lanceolata	7	7 × 46	18	71	315
C. leubnitziana	6	7 × 68	31	105	355
C. longirostrata	10.5	10.5 × 88	35	134	150
C. lotifolia	3.5	10.5 × 60	38	102	345
C. maritima	4	13 × 39	25	68	150
C. maypurensis	14	14 × 70	51	135	600
C. mollicula	3.5	7 × 56	18	78	390
C. mucronata	17.5	10.5 × 46	21	85	450
C. mysorensis	5.5	7 × 50	35	91	360
C. nitens	7	10 × 63	25	95	300
C. ochroleuca	3.5	7 × 60	17	81	355
C. paulina	7	10 × 56	28	91	345
C. pilosa	4	18 × 56	21	81	400
C. pohliana	5	14 × 70	32	107	525
C. pumila	7	10.5 × 67	21	95	330
C. purshii	4	10.5 × 60	18	82	300
C. quinquefolia	10.5	10.5 × 105	46	162	750
C. ramosissima	10.5	7 × 70	18	99	605
C. retusa	17.5	10.5 × 98	52	168	755
C. rhodesiae	9	10 × 60	30	99	525
C. sagittalis	4	7 × 42	18	64	505
C. saltiana	5	12 × 66	56	127	400
C. spectabilis	14	14 × 109	42	165	105
C. stipularia	8	10.5 × 53	32	93	375
C. tetragona	17.5	13 × 81	42	141	625
C. trifoliastrum	3.5	7 × 35	28	67	405
C. unifoliolata	10.5	10.5 × 63	39	113	390
C. usaramoensis	3.5	10 × 49	21	74	95
C. verrucosa	9	10.5 × 95	39	143	480
C. vespertilio	9	7 × 58	25	92	525
C. vitellina	3.5	10 × 74	24	102	375

[1] Measurements obtained from the midregion of median transections of prepared slide material and from seed soaked to a condition of turgidity.

hold true for the cell measurements). Tissue and cellular component measurements were obtained from longi- and transections of the seed midregion of fresh and paraffined material.

In order to evaluate seed characters and thus, concomitantly, possibly enhance their identification, various approaches were undertaken. The methods employed are morphological, anatomical, physical, and chemical in nature.

Seed was heated in distilled water at 75° to 100° C. at varying time intervals to observe any distinctive morphological modifications. None was found. Unfiltered ultraviolet irradiation, which produced some interesting colorations of the seed coat, can be used for the positive identification of some species, but it is limited as a tool where large numbers are involved. Too many species tend to exhibit similar color irradiations (table 4). Hardness and gelatinity tests of the seed coats yielded information of some value for identification purposes (table 2). Gross microchemical analyses of the various seed tissues revealed that certain constituents are present or absent throughout many species of the genus. While information of this type may have little value at the species level, it would appear to be useful in the overall generic systematics of the legumes. The lack of a fatty cutin in the seed testa, the presence of endosperm in all species examined, and the absence of starch per se, as well as of amyloids, should provide additional definitive values for the modern systematist attempting to derive more "natural" relationships.

The degree of prominence of the funicular remnant also provided a valuable criterion for species differentiation and is utilized in the construction of the keys (see discussion under Anatomy of the Seed Coat, Endosperm, Hilum, and Boss Region). The coloration of the funicular remnant varies from a dull white to brown. It was found to be too variable in any given species to be utilized as a definitive.

The construction of a key to seed identification is hazardous at best. The attempt was made to utilize only stable characters for the subdivisions, but certain artificialities become apparent. A synopsis of the characteristics of each species is provided in the body of the keys. An anatomical key has not been developed because of the relatively few differences in available diagnostic characters. The anatomical illustrations for each species provide their own pertinent information.

All drawings indicating cellular detail were made with the aid of a camera lucida. The photographs were prepared by the photographic laboratory of the United States Department of Agriculture, Beltsville, Md. All seed photographs are enlarged approximately 3.5 to 6 times. For the sake of comparison and to convey an idea of the normal relative size of the seed, an average lifesize silhouette is included with each photograph. The various illustrations were made to enable direct comparisons of the seeds and are of such a nature as to provide essential information without having recourse to lengthy descriptions.

A number of the terminologies encountered in the literature relative to the present investigation are either obsolete, inaccurate, or too ambiguous. Therefore it was felt that a glossary should be included, with the recognition that definition of terms is often controversial.

Specimens of the seed species under consideration have been deposited in the general seed collection of the United States Department of Agriculture, Plant Industry Station, Beltsville Md.

TABLE 4.—Crotalaria *seed coat coloration exhibited under unfiltered ultraviolet irradiation at 3,650 A.U.*

Species	Coloration
C. alata	Gray brown, brown.
C. anagyroides	Rusty brown.
C. brachystachya	Umber, light orange brown, tan.
C. breviflora	Pastels of red brown, ochre, ecru, light orange, tan.
C. capensis	Dark brown.
C. claussenii	Brown, red brown.
C. eriocarpa (viminalis)	Yellow, olive, olive brown, gray brown.
C. ferruginea	Brown, dark brown, some minute yellow fluorescence in hilar region.
C. filifolia	Light gray, gray white.
C. flavicoma	Brown.
C. foliosa	Red brown.
C. goreensis	Rusty.
C. grantiana	Fluorescent yellow, tan, ecru, brown, gray.
C. incana	Light blue, gray, brown, blue gray.
C. intermedia	Pastels of white yellow, red orange, orange, tan, gray, ecru.
C. juncea	Gray, blue gray, gray brown.
C. lanceolata	Pastels of yellow, yellow orange, ecru, tan.
C. leubnitziana	Brown, dark brown; occasional yellow fluorescence.
C. longirostrata	Tan, gray yellow, gray brown, some bright yellow fluorescence around hilum.
C. lotifolia	Rusty.
C. maritima	Red brown, brown.
C. maypurensis	Brown.
C. mollicula	Tan, gray brown, brown, dark brown.

TABLE 4.—*Crotalaria seed coat coloration exhibited under unfiltered ultraviolet irradiation at 3,650 A.U.*—Continued

Species	Coloration
C. mucronata (*striata*)	Striations visible as dark streaks on light gray, gray.
C. mysorensis	Pastels of yellow, yellow orange, ecru, tan, gray yellow, pink yellow.
C. nitens	Red brown.
C. ochroleuca	Pastels of light yellow, yellow orange, orange red.
C. paulina	Olive, olive brown, orange brown.
C. pilosa (*pterocaula*)	Red brown.
C. pohliana	Orange-red brown.
C. pumila	Light gray, gray, tan, brown.
C. purshii	Brown.
C. quinquefolia	Pastels of gray, gray violet, tan, brown.
C. ramosissima	Gray, orange brown, light brown.
C. retusa	Tan, light brown, greenish yellow, gray yellow.
C. rhodesiae	Pastels of pink tan, gray tan, pink orange.
C. sagittalis (*angulata, rotundifolia, tuerckheimii*).	Tan, orange brown, brown.
C. saltiana	Pastels of pink tan, gray tan, pink orange.
C. spectabilis (*retzii, sericea*).	Brown.
C. stipularia	Pastels of ecru, tan, green gray, light brown.
C. tetragona	Red brown, black.
C. trifoliastrum	Rusty, brown rusty.
C. unifoliolata	Red brown, brown, dark brown.
C. usaramoensis	Pastels of pink orange, yellow orange, pale gray yellow.
C. verrucosa	Tan, ecru, light yellow, green yellow.
C. vespertilio	Orange brown.
C. vitellina (*guatemalensis*).	Yellow brown, light red brown, brown.

MICROCHEMICAL TESTS AND SEED CONSTITUENT ANALYSES

Dry untreated seed and seed softened by scarification and water immersion at room temperature were subjected to various microchemical reagents to determine their general chemical nature. Almost all histochemical testing followed principally the procedures and use of reagents as outlined by Johansen (1940). The tests for amyloids in the cell walls were made according to Kooiman (1960), with potassium triiodide without sulfuric acid. No attempt was made to study the cell contents in their entirety of the various tissues comprising the seed (table 5).

TABLE 5.—Crotalaria *seed constituents*[1]

Species	Mucilage (N-free; percent water soluble)	Oil (percent dry basis)	Protein (percent N × 6.25)
C. alata	17.1	2.8	28.2
C. anagyroides	11.6	5.2	34.9
C. capensis		8.0	27.4
C. eriocarpa	10.4	4.4	33.8
C. grantiana	16.5	1.9	30.3
C. incana	17.5	3.3	30.1
C. intermedia	22.8	3.0	32.2
C. juncea	15.0	3.6	35.4
C. lanceolata	18.5	2.5	31.1
C. longirostrata		3.2	32.7
C. mucronata	13.3	2.4	27.5
C. ochroleuca	24.6	2.6	31.0
C. pumila	18.6	3.4	31.2
C. quinquefolia		2.6	24.2
C. retusa	18.0		24.1
C. rhodesiae	21.2	2.2	29.4
C. sagittalis		4.5	33.8
C. saltiana	19.4	2.1	29.0
C. spectabilis	20.1	2.6	26.6
C. usaramoensis	18.4	2.5	31.3
C. verrucosa	18.6	3.0	29.3
C. vitellina		4.3	31.5

[1] Percentages of mucilage, oil, and protein from data of the Northern Utilization Research and Development Division, USDA. Sample numbers vary from 1 to 12.

None of the seeds indicated the presence of either lignin, amyloid, or starch.

Alkaloids.—Appear to be localized principally in the testa. See discussion under Seed Toxicity, and Tookey et al. (1963).

Amyloids.—None present in the cell walls of the seed. (See table 5).

Anthocyanins, carotins, and **xanthophylls.**—No crystals of these pigments were obtained when tests were made for their presence. However, various species (and especially those whose seeds are relatively highly colored) imparted a distinct coloration when immersed at room temperature in 1 to 2 cc. of distilled water for a period of 12 to 24 hours. The various water discolorations obtained, given in table 6, are based upon five trials which proved to be very consistent. Not all highly colored seeds yielded a water discoloration. Pigments in the form of granules are concentrated in the macrosclereid and lagenosclereid layers; plastids are not present. In both the macrosclereids and lagenosclereids, the pigments tend to be located principally in the basal portion of the cells. No pigment was recognizable in the cuticle.

Cellulose.—Omnipresent as the chief component of all cell walls.

Cutin.—In *Crotalaria* species this is a nonfatty substance deposited in variable thicknesses principally as a cuticle on the external walls of the macrosclereids. The cutin appears to be principally hemicellulosic and pectinaceous rather than fatty. It forms the relatively hard and continuous, more or less semihydrophilous layer over the surface of the seed coat, interrupted only at the hilum. No cuticularization per se was evident on any tissue internal to the testa. In a number of species the cuticle is pervious to water and relatively gelatinous (see table 2 and discussion under Mucilages or gums below). The cuticle of the following *Crotalaria* species has an affinity for potassium triiodide: *anagyroides, brachystachya, capensis, claussenii, incana, mucronata, rhodesiae* and *saltiana* (see Mucilages or gums).

TABLE 6.—*Water discolorations of saturated* Crotalaria *seed coats*

[Seed coat color description given in the seed keys]

Species	Pigmentation	Species	Pigmentation
C. alata	Colorless.	*C. mucronata*	Yellow.
C. anagyroides	Yellow.	*C. mysorensis*	Orange.
C. brachystachya	Light yellow.	*C. nitens*	Yellow.
C. breviflora	Orange.	*C. ochroleuca*	Colorless.
C. capensis	Light yellow.	*C. paulina*	Yellow.
C. claussenii	Yellow tinge.	*C. pilosa*	Undetermined.
C. eriocarpa	Yellow.	*C. pohliana*	Light yellow.
C. ferruginea	Colorless.	*C. pumila*	Light yellow.
C. filifolia	Undetermined.	*C. purshii*	Yellow.
C. flavicoma	Undetermined.	*C. quinquefolia*	Yellow tinge.
C. foliosa	Undetermined.	*C. ramosissima*	Colorless.
C. goreensis	Yellow.	*C. retusa*	Yellow tinge.
C. grantiana	Light orange.	*C. rhodesiae*	Colorless.
C. incana	Yellow.	*C. sagittalis*	Colorless.
C. intermedia	Light orange.	*C. saltiana*	Colorless.
C. juncea	Yellow tinge.	*C. spectabilis*	Yellow.
C. lanceolata	Colorless.	*C. stipularia*	Yellow.
C. leubnitziana	Colorless.	*C. tetragona*	Yellow tinge.
C. longirostrata	Colorless.	*C. trifoliastrum*	Yellow.
C. lotifolia	Colorless.	*C. unifoliolata*	Light yellow.
C. maritima	Undetermined.	*C. usaramoensis*	Orange.
C. maypurensis	Undetermined.	*C. verrucosa*	Light yellow.
C. mollicula	Colorless.	*C. vitellina*	Yellow.

Fats or oils.—See table 5. Small amounts were also detected in the cotyledons of *Crotalaria brachystachya, C. foliosa, C. lotifolia, C. purshii*, and *C. trifoliastrum*. A trace was found in the aleurone layer of *C. unifoliolata*. Jones and Earle (1966) report seed oils present from 1.7 to 4.5 percent (see Earle and Jones, 1962).

Lignin.—Only components of the tracheid bar (see The Hilar Region) were found to be lignified. There was no lignification of the macrosclereids or lagenosclereids. (See table 5).

Mucilages or gums.—These appear to be present in small amounts principally in the endosperm, and as part of the cuticle in some species (see Cutin above). The seed coat becomes gelatinous in some species when moistened, but it is not viscid in nature. Gelatinity of the testa appears to be variable. In some species it is filmy and ensheathes the entire seed, except the hilum. In others it appears relatively thick and occurs in "curls," superficially resembling scraped paraffin, usually around the sinus of the hilar region. In some species the gelatinity is indistinctive and present only on the cotyledonary or radicular lobe(s) (see tables 2 and 5). Tookey and Jones (1965) report gums or mucilages of 10 to 26 percent in *Crotalaria* seeds. According to Anderson (1949), the endosperm mucilages of legumes are galactomannans (see Tookey et al., 1962, 1963).

Pectic compounds.—While the different forms were not tested, there appear to be distinctive variable amounts of pectic material throughout the seed tissues. Large amounts occur principally in the testa cuticle and in the walls of the macrosclereids, lagenosclereids, aleurone layer, endosperm, and parenchyma (see Wax below).

Pentosans and "hemicellulose."—No xylose or arabinose pentosans were found, but methyl pentoses appeared in the walls of the macrosclereids and lagenosclereids. Small amounts also appear to be present in the endosperm (see Wax below).

Proteins.—Relatively abundant in the aleurone layers, endosperm, and cotyledons of all species examined. Small amounts present in macrosclereids and lagenosclereids (see table 5). According to Earle and Jones (1962), Jones and Earle (1966), *Crotalaria* seeds may contain 24 to 41 percent protein.

Starch.—None present in the seed (see Amyloids above and table 5).

Suberin.—None present in the testa, hilar tissue, or funicular remnant. The cuticle does not appear to be suberized.

Tannins.—Minute amounts appear to be present in the lower portion of the lagenosclereids and the subtending crushed parenchyma.

Wax.—Not present as such. Verrucose and waxlike deposits on the radicular and cotyledonary lobes of *C. spectabilis* appear to be hemicellulosic and pectinaceous.

GENERAL MORPHOLOGY OF THE SEED

The usual means of subjective identification is to utilize visible characteristics. When a large number of species have similar characters the problem of identification then becomes manifold. While only 47 species of *Crotalaria* seed are investigated here, the problem is nevertheless complex since many of the seeds are practically indistinguishable. To provide a working key to the identification of all known species (estimated at ±400) based upon external characters alone would be redoubtable.

The seeds of *Crotalaria* tend to be oblique or asymmetrical in combination with a cordate, cuneate, orbicular, or reniform shape (see outlines in figs. 1–5, and the seed photographs). These combinations are generally uniform for a given species. They vary from slightly compressed to well rounded, plump (turgid), or rotund. They are usually smooth (and sometimes slippery) but they may be minutely verrucose and even rough in appearance. Some species possess surface irregularities or sculpturings while in others the entire seed appears somewhat distorted. In a number of species a small furrow exists between the radicle and cotyledon configurations. A rounded protuberance, the "boss," which is variable in its prominence (see figs. 1–5, 20, and discussion under The Boss Region), is located slightly above the hilum on the cotyledonary lobe and becomes part of the overall configuration of the seed. The seed of *Crotalaria* develops from a campylotropous-like ovule; a raphe is not present (fig. 6). The seed is also estrophiolate, noncarunculate, and nonarillate (see discussion under The Boss Region.)

The radicular lobe is also variable and contributes greatly to the general shape of the seed. *Crotalaria* seed morphology exhibits distinctive convergencies and divergencies of the radicular lobe in its positional relationships to the hilum. Median sagittal longisections of the seed reveals that all investigated species possess radicular lobes that are actually convergent, but with varying degree (figs. 1–5). External observations of the general seed configuration does not always indicate this condition. The radicular lobe may appear to be widely divergent from, or completely convergent upon, the cotyledonary lobe so as to occlude the sinus of the hilum more or less completely. It is often angular and recurved or somewhat hook shaped, and may have a bulbous tip (figs. 1–5).

The appearance of the hilum also contributes to the general seed configuration (see The Hilar Region). Invariably sunken, it is surrounded by a small rim. The hilar groove or fissure is usually visible only in seeds where the funicular remnant is not predominant or where the hilar sinus is not occluded by the radicular lobe (figs. 1, 21; pl. 1, A). In side view the sinus, or hilar notch ("Nabelspalte"), may be minute or relatively large, wide or open, to U-shaped, or even distinctly occluded. The hilar sinus angle thus formed between the cotyledonary and radicular lobes is very characteristic per species (figs. 1–5; pls. 2–10). Viewed from above, the sinus may be almost circular to narrowly oblong, as well as variously occluded. The micropylar opening in the hilum is not readily discernible because of its sunken position relative to the radicular lobe (fig. 20). While the prominence of the funicular remnant is variable, it is not an attribute to the actual shape of the seed (see fig. 7 and seed photographs; see discussion under The Hilar Region).

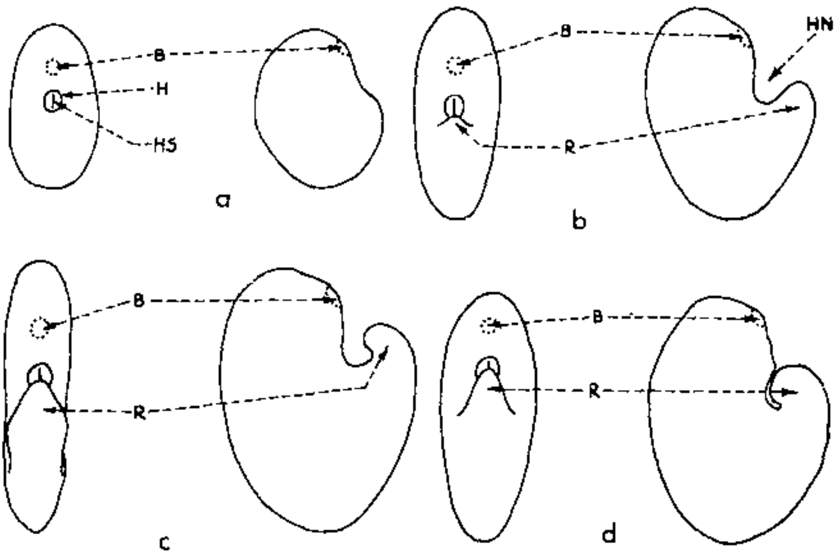


FIGURE 1.—Variation in radicular configurations of *Crotalaria* seed, × 7.5. a, *C. ochroleuca;* b, *C. nitens;* c, *C. flavicoma;* d, *C. retusa.* (B) boss, (H) hilum, (HN) hilar notch, (HS) hilar groove, (R) radicle. See figs. 2–5 for other species.

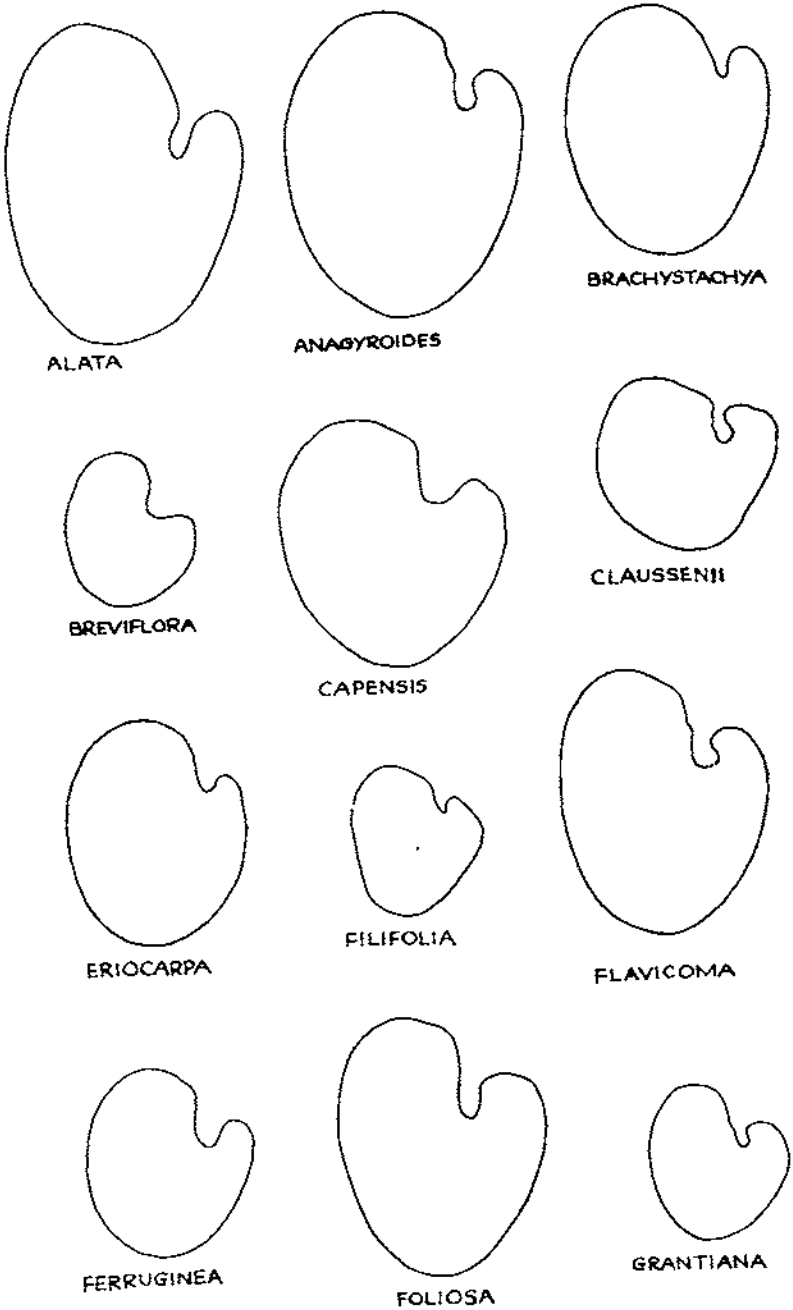


FIGURE 2.—Seed configurations of *Crotalaria* species *alata* through *grantiana*, × 7.5 (see pls. 2–4).

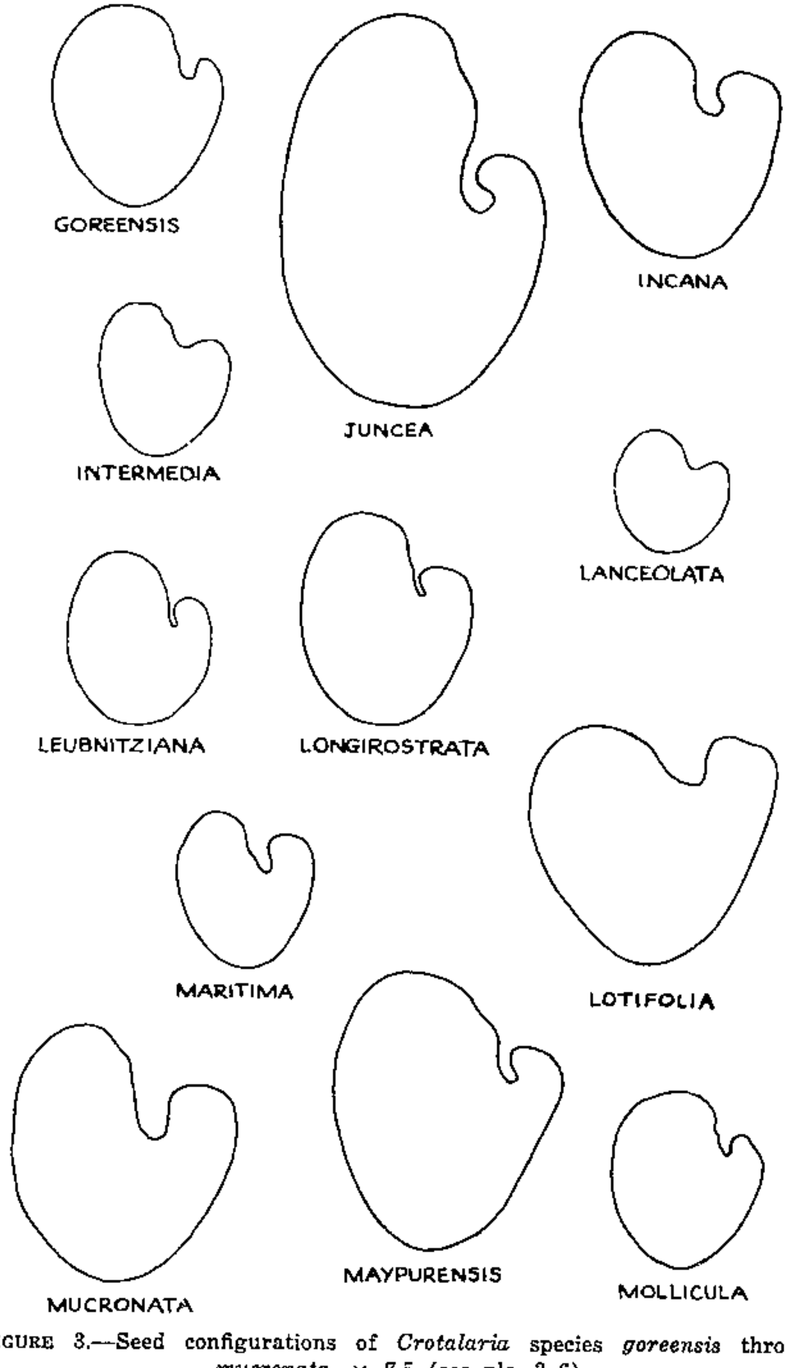


FIGURE 3.—Seed configurations of *Crotalaria* species *goreensis* through *mucronata*, × 7.5 (see pls. 3–6).

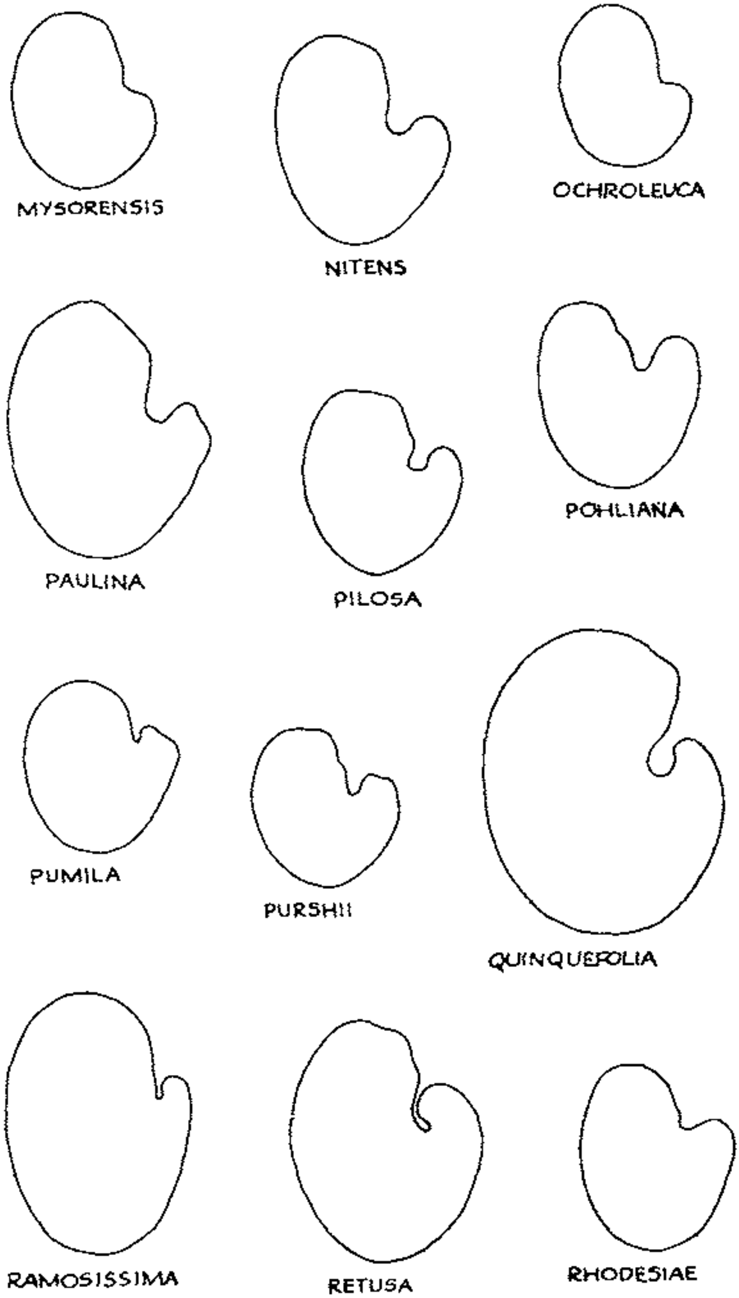


FIGURE 4.—Seed configurations of *Crotalaria* species *mysorensis* through *rhodesiae*, × 7.5 (see pls. 6–8).

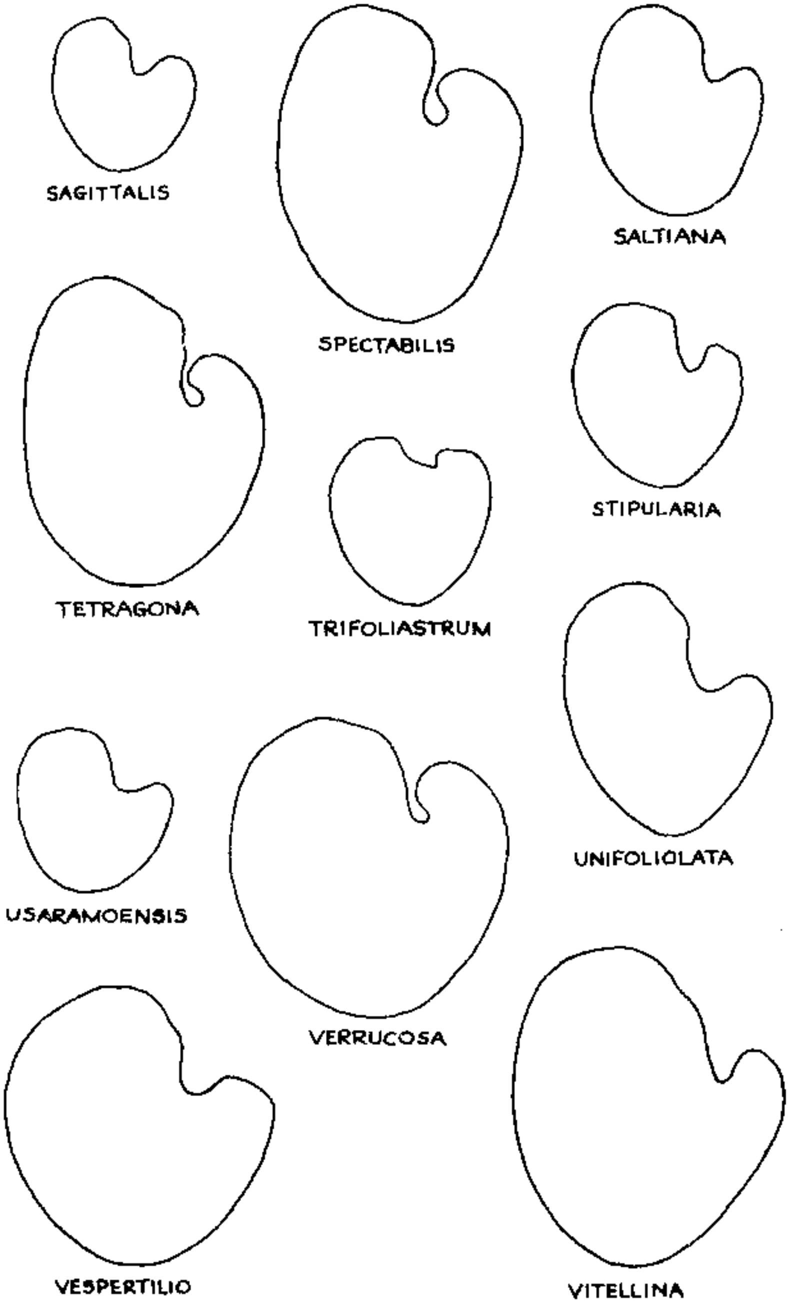


FIGURE 5.—Seed configurations of *Crotalaria* species *sagittalis* through *vitellina*, × 7.5 (see pls. 8–10).

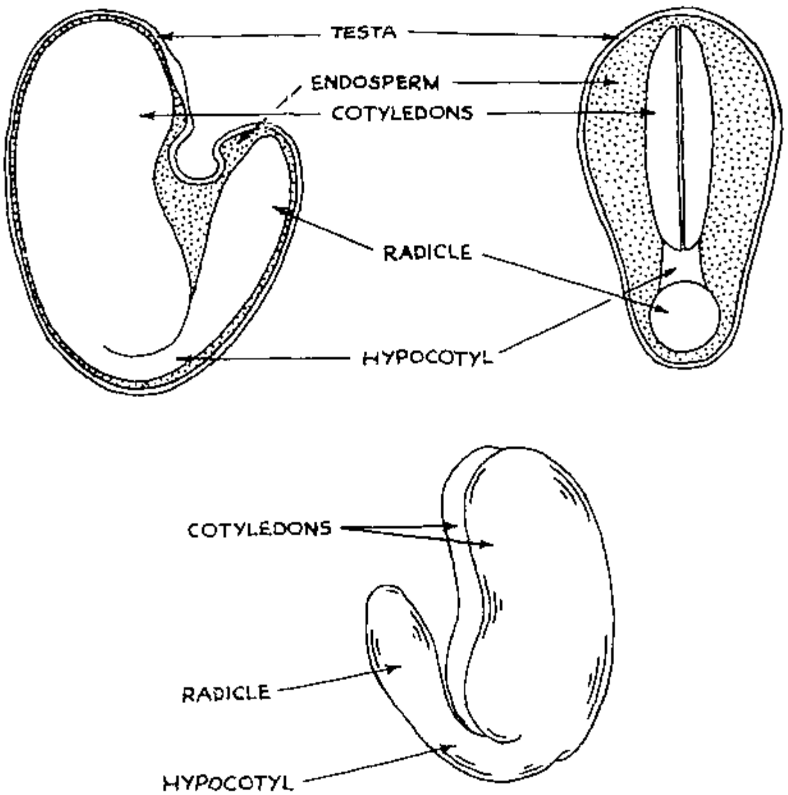


FIGURE 6.—General morphology of the mature embryo and seed in *Crotalaria intermedia* in longi- and transectional views. The embryo with its accumbent cotyledons, as it appears when removed from the seed, is depicted in the lower drawing, × 15.

Although there is a general uniformity to the configuration of the seeds of *Crotalaria,* they vary considerably in size. Relative dimensions for each species are given in the keys. They vary in length from 1.5 to 7 mm. and from 1.5 to 4.75 mm. in width, and are 0.75 to 3 mm. in thickness (see discussion in Materials and Methods).

The color, hue, and markings of the seed coats are also diverse. Colors range from light yellow to blue purple; many species exhibit similar colorations. Certain species possess irregular markings or mottling on their seed coat. Other species have more or less distinctive marginal bands of color around the hilar region. The boss may be pigmented or not. In some species the testa gives the appearance of being covered with a minute stippling.

The surface condition or polish of the various species varies from dull to highly glossy.

The seed of *Crotalaria* comprises a dicotyledonous embryo enclosed by an endosperm (variable in amount) and the distinctive tissues of the testa (described in detail under The Seed Coat). The relatively large accumbent, reniform cotyledons comprise the bulk of the embryo. They are conspicuously larger than the shorter,

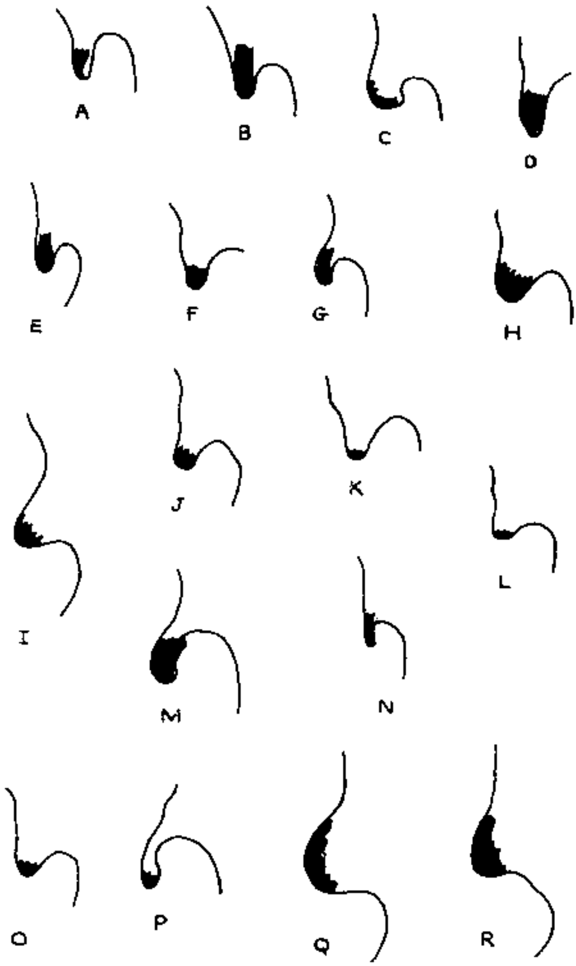


FIGURE 7.—Funicular remnant configurations (solid areas) on various species of *Crotalaria* seed, × 7.5. a, *C. anagyroides;* b, *C. brachystachya;* c, *C. flavicoma;* d, *C. foliosa;* e, *C. goreensis;* f, *C. maritima;* g, *C. maypurensis;* h, *C. nitens;* i, *C. paulina;* j, *C. pilosa;* k, *C. pohliana;* l, *C. purshii;* m, *C. quinquefolia;* n, *C. ramosissima;* o, *C. stipularia;* p, *C. tetragona;* q, *C. unifoliolata;* r, *C. vespertilio.*

more or less clavate, hypocotyl-radicle axis on which they are borne (fig. 6). This axis appears divergent in its relation to the longitudinal axis of the seed. The plumule is not well differentiated and is usually not evident in the dry seed state. These features of the embryo, along with its curvature on its longitudinal axis, contribute largely to the general configuration of the seed.

SEED SIMILARITIES

Among the legumes are a number of genera which have seeds that are superficially similar in appearance to those of *Crotalaria* species. Some that have been mistaken for *Crotalaria* (and there are probably others) are the seeds of species of *Astragalus, Biserrula, Dalea, Galega, Lonchocarpus, Lotononis, Oxytropis,* and *Trigonella.*

The crotalarias themselves have a large number of species with seeds that resemble one another. While all the known species of this genus have not been compared, the following species in the same group closely resemble one another externally: *alata* and *spectabilis; breviflora, grantiana, intermedia, lanceolata, mysorensis, ochroleuca,* and *usaramoensis; falcata, mucronata, rhodesiae,* and *saltiana; anagyroides, brachystachya,* and *verrucosa; pilosa* and *stipularia; nitens* and *pohliana; paulina* and *unifoliolata; eriocarpa* and *vitellina.* (See comparisons in the seed keys.)

In addition to external morphological resemblances, close anatomical investigations reveal that seeds of a number of species of *Crotalaria* are so similar in their internal structure that it is apparently impossible to distinguish one from another. One of the direct results of the present anatomical investigation has been to infer that certain species are really conspecific with others. Thus, from the standpoint of seed identification alone, the species *angulata* and *tuerckheimii* have been considered here the same as *C. sagittalis;* Senn (1939) considers them as distinct species. The species *retzii* and *sericea* are the same as *C. nitens; C. guatemalensis* is the same as *C. mucronata; C. setifera* is similar to *C. incana; C. viminalis* is the same as *C. eriocarpa;* and *C. obtecta* is similar to *C. tetragona.* (See seed keys.)

To determine what corroboration, if any, existed with regard to the validity of the putative conspecificities resulting from the present investigation, a number of floras and monographs were perused: Baker (1914), Bentham (1859-62), Burkart (1952), *pp. 326-329),* Senn (1939), Standley and Steyermark (1946), Wilbur (1963). Considerable accord appears to exist between the present findings and those based wholly upon vegetative morphology.

ANATOMY OF THE SEED COAT, ENDOSPERM, HILUM, AND BOSS REGION

The anatomy of leguminous seed has been described in detail by a number of earlier workers; however, that of *Crotalaria* has received little attention. Although the present investigation was undertaken primarily to aid in the identification of *Crotalaria* seed, it has also presented an opportunity to enhance some of the earlier concepts of legume seed anatomy.

While the external morphology of *Crotalaria* seeds is peculiar to the genus, the basic anatomical features of their integument may well prove to be characteristic of the entire subfamily Papilionoideae, and possibly for the entire family of legumes as well. The outward similarity of many *Crotalaria* species presents difficulty in their identification. The internal structural organization of the seed coat, however, reveals certain tissue variables that can provide an aid to their correct identity. Illustrations of each species are included (figs. 9-18); their histomeasurements are collectively presented in table 3.

For the purpose of the present investigation, the anatomy of *Crotalaria* seed integuments will be considered under four distinct regions of modified tissues, namely, those of the testa itself, the endosperm tissue, the tissues of the hilar region, and the tissues of the so-called "boss" region. The funicular remnant, as an adnate hilar vesture, is considered, in part, as an attribute of the testa.

The Seed Coat

The seed coat has been designated by some earlier investigators as the "spermoderm' (Maisel, 1909; Winton, 1916). According to various workers (Eames and MacDaniels, 1947; Hayward, 1948; Martin and Watt, 1944; Pammel, 1899; Pitot, 1935; Reeves, 1930) the various cellular components of the leguminous seed coat are differentiated from the outer integument of the ovule. The inner integument and nucellar tissue are completely absorbed. Cook (1924), however, reports that the testa of *Crotalaria sagittalis* is derived from an ovule with a single integument. This may be a misinterpretation, for in his illustrations he figures a layer adjoining the nucellus that disintegrates. This layer may be that of the inner integument. No attempt was made during the course of the present investigation to study ovule development in *Crotalaria*.

The seed coat of *Crotalaria* is highly specialized and relatively strongly developed mechanically. It consists of two distinctive outer layers, namely, the epidermis and the hypodermis or subepidermis, and an inner multicellular parenchyma tissue. Among the species examined it varied in thickness from approximately 64 to 168 microns (table 3). Immediately adjacent to the parenchyma is a multicellular endosperm, which is further demarcated outwardly by its relatively distinct aleurone layer (multilayered in the subhilar region).

Cuticle

The cuticle, a well-defined outer pellicle or membrane, a single layer in thickness, is continuous over the seed surface except in the area of the hilum. Among the seeds investigated, it varies in thickness from approximately 2 microns to 17.5 microns (table 3, figs. 9-18). Its appearance and properties are given further consideration under Microchemical Tests and Seed Constituent Analyses. The cuticle is described as the "strati esterno ed interno della membrana rivestimento" by Mattirolo and Buscalioni (1892, p. 437). A stratum of mucilage cells does not subtend the cuticle of *Crotalaria* seeds, although the latter does exhibit gelatinity in some species.

Epidermis

The epidermis, a highly specialized layer of cells, has been variously designated as the columnar layer, Malpighian layer, palisade layer, palisade parenchyma, palisade sclerenchyma, and prism layer. The cells themselves have been referred to as, among other terms, columnar cells, macrosclereids, Malpighian cells, palisade cells, prism cells, and rod cells. In modern usage, "macrosclereids," is the preferable histological term and will accordingly be used here.

The macrosclereids of *Crotalaria* are highly modified, thick walled, and nonlignified. They are variously elongated, rodlike or columnar cells, with their long axis arranged perpendicular to the surface of the seed. In transections they appear polyhedral in shape, usually with five or six sides (fig. 8). Their cellulosic and prismatic secondary walls are variable in thickness, with the radial usually much thicker than the inner tangential wall. Their apices are truncated and their inner tangential walls may be variously shaped. An outer tangential wall is not present, so that the lumen at the cell apex is in direct contact with the overlying contiguous cuticle (fig. 9; pl. 1, B). The tissue formed by these compacted palisade-like cells is devoid of intercellular spaces (see The Boss Region below). In the present study, the cells varied in their dimen-

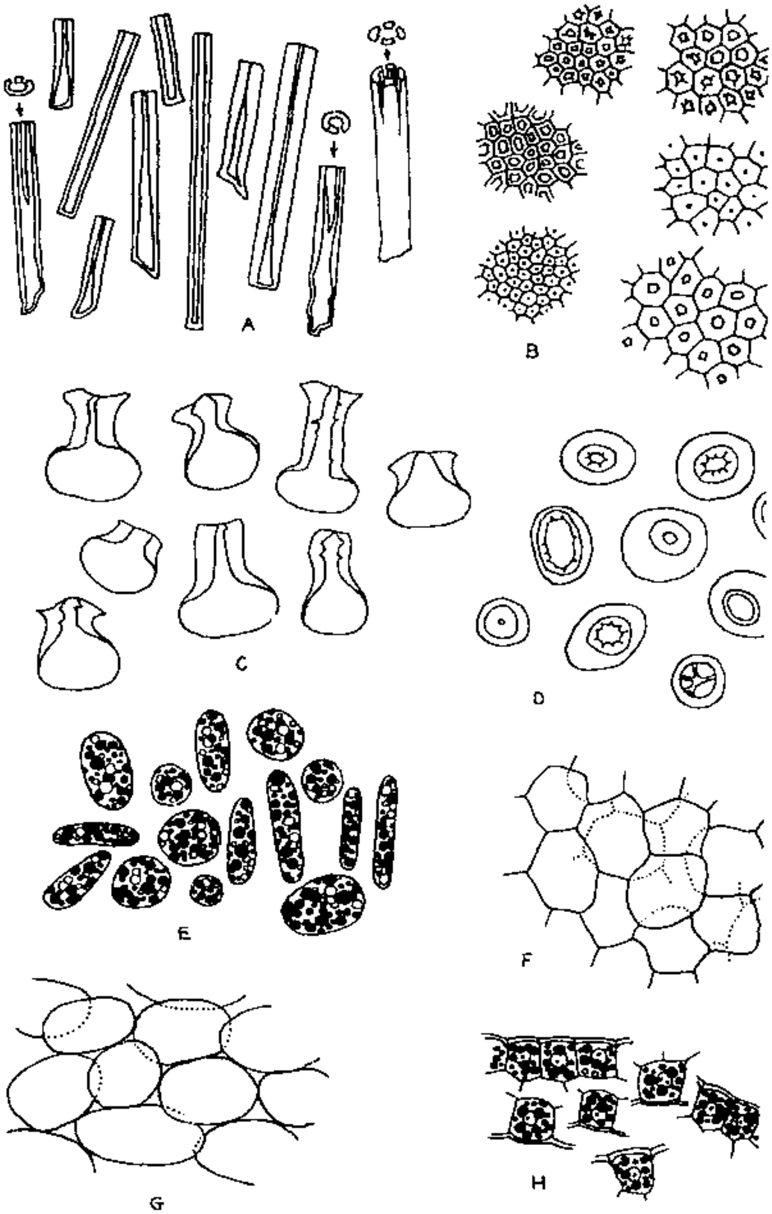


FIGURE 8.—Various cell components of the testa, and some adjoining tissues, of *Crotalaria* species, × 296. a, macrosclereids; b, surface appearance of apical ends of macrosclereid tissue; c, lagenosclereids; d, lagenosclereids viewed from their apical ends; e, cotyledon storage parenchyma containing protein granules and fat globules; f, endosperm parenchyma; g, seed coat parenchyma; h, aleurone cells with nuclei and protein granules. (see fig. 9 for tissue arrangements.)

sions from approximately 6 to 8 microns in width and 35 to 109 microns in length (table 3 and figures). Their length and width also vary depending upon their relative position in various regions of the seed coat, enlarging considerably in the boss region and somewhat less so in the hilar region.

In many species the inner radial walls bear conspicuous fluted or flangelike thickenings at their apical ends; thus, if given only a cursory examination, they impart the impression that the cells are forked or *Y*-shaped (as inaccurately depicted for *Crotalaria juncea* by Brown and Fudge, 1960). These have also been described as "longitudinal pore canals." The actual configurations may best be observed by examining isolated macrosclereids (figs. 8, 19). While all species may occasionally exhibit the condition of fluting, it appears to be more common in certain species than in others. The normal compactness of the contiguous macrosclereids sometimes contributes to an illusion of corrugations, fissurings, or radiating arms in this part of the cell.

The lumen or cell cavity is also variable in shape. This variation is often an attendant feature concommitant with the wall variability of the cell. The width of the lumen may be the same throughout the macrosclereid, or it may be widest at the base and gradually taper toward the top, often appearing more or less bottle shaped. Transections of the cell at various levels reveal that the lumen may be circular or somewhat oval at the bottom, with this appearance remaining the same or gradually diminishing in size until it is only slitlike or even completely occluded at the upper end (see figures). The lumen may also appear stellate when viewed from the apical end. In side view of the macrosclereids with fluted thickenings on their uppermost radial walls, the cell lumen often appears to be convoluted or to have canaliculate or slitlike elongations (fig. 8). A nucleus is often visible in the central region of the lumen. (See also the discussion under Microchemical Tests and Seed Constituent Analyses for cell contents.).

The radial walls of the macrosclereids exhibit a distinctively light-colored band or bright spot of strong birefringence in their apical portions. This so-called "light line" (*ligne lumineuse, ligne luminiere, Lichtlinie, Lichtzone,* or *linea lucida*) appears to be a common phenomenon in the seeds of legumes, and certain other families (e.g. Cucurbitaceae, Labiatae, Malvaceae, et al.). In some taxa a double band is visible, but in *Crotalaria* it occurs only as a single line. In the species studied here (in fresh as well as in stained sections), it always subtends the apex of the cell from 1 to 4 microns below the cuticle, and is approximately 1 to 3.5 microns wide (shown diagrammatically in fig. 9). There are no indications that the radial wall of this region is chemically altered or different from the remainder of the cell. No encrustations are visible and it does not contain a deposit of amyloid, callose, cutin, lignin, starch, suberin, or wax.

Earlier investigators have given various interpretations to the chemistry, structure, and significance of the light line. In *Crotalaria* it appears to be no more than an artifact of light resulting from the differences in refractive indices in this portion of the thick secondary wall, and not a definitive structural entity. A lengthy dissertation on the function of the light line is given by Mattirolo and Buscalioni (1892); see also Frey-Wyssling (1959), Pammel (1899), and Reeve (1946).

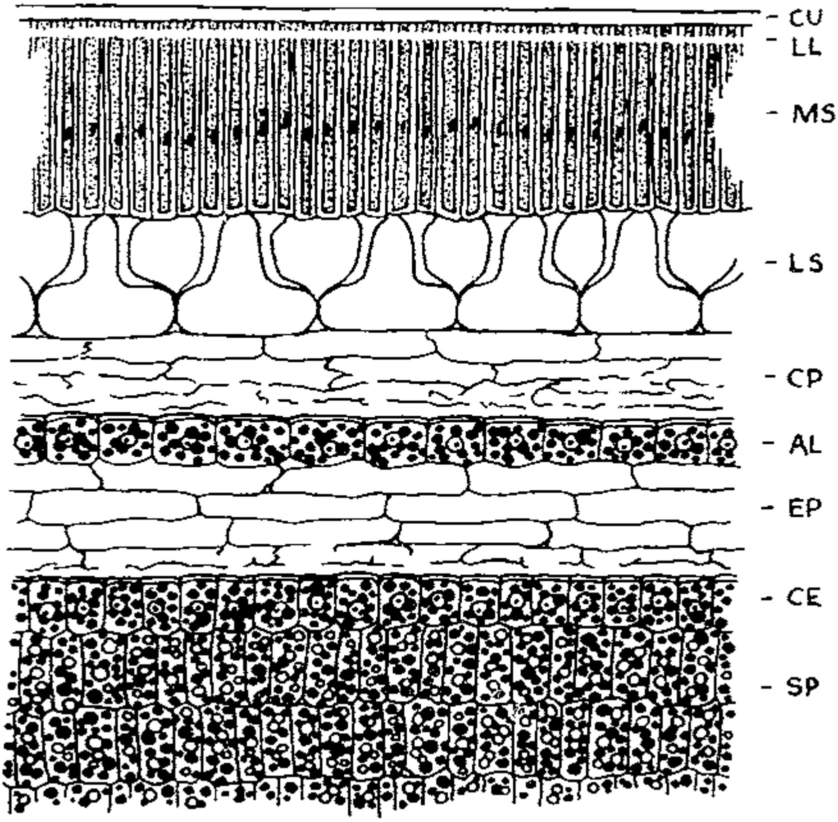


FIGURE 9.—Semidiagrammatic transection of *Crotalaria intermedia* testa, × 430. (AL) aleurone, (CE) cotyledon epidermis, (CP) crushed parenchyma, (CU) cuticle, (EP) endosperm parenchyma, (LL) light line, (LS) lagenosclereids, (MS) macrosclereids, (SP) storage parenchyma. (See figs. 10–18 for illustrations of other species, and pl. 1, B.)

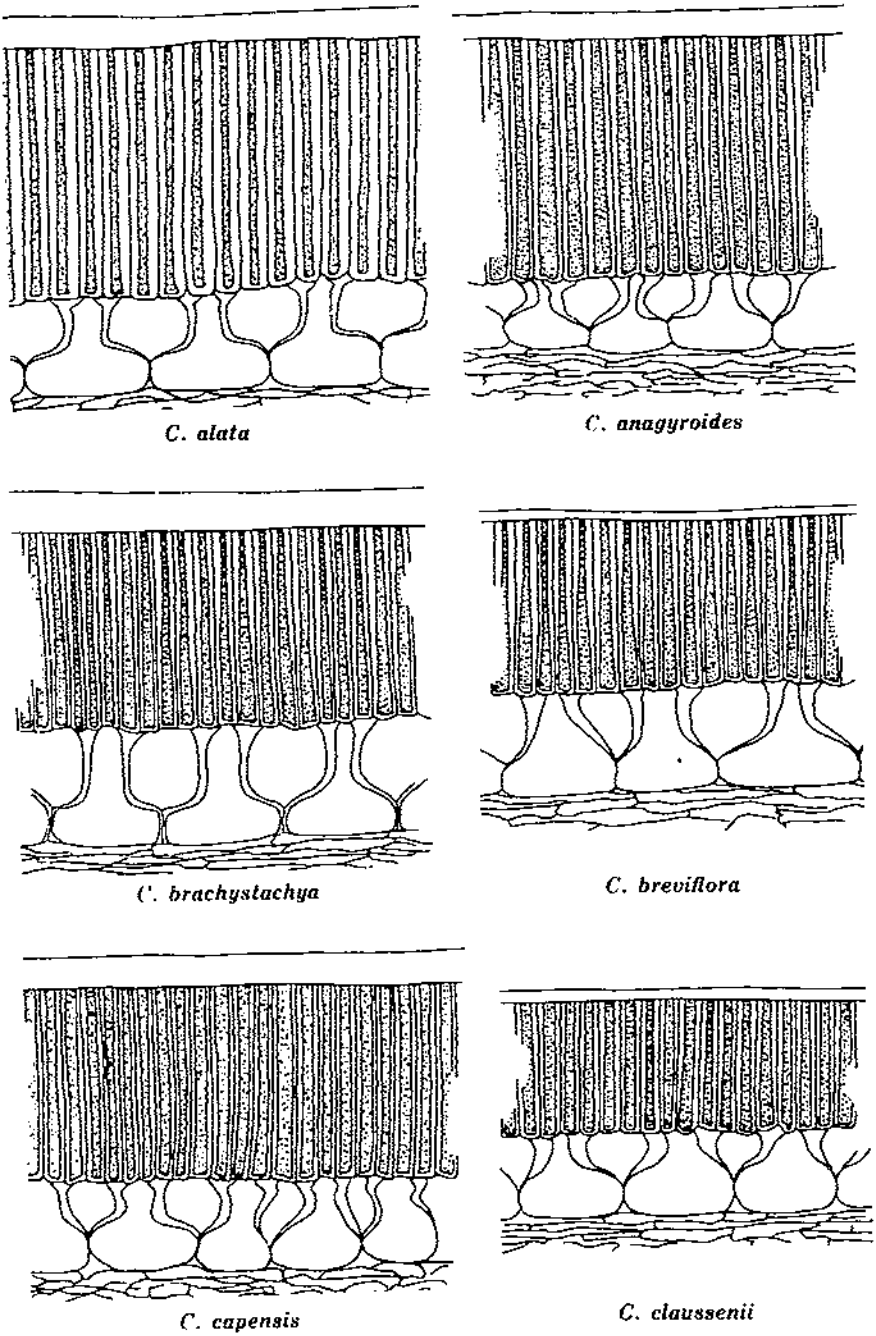


FIGURE 10.—Seed coat transections of *Crotalaria* species *alata* through *claussenii*, × 322 (for tissue nomenclature see fig. 9).

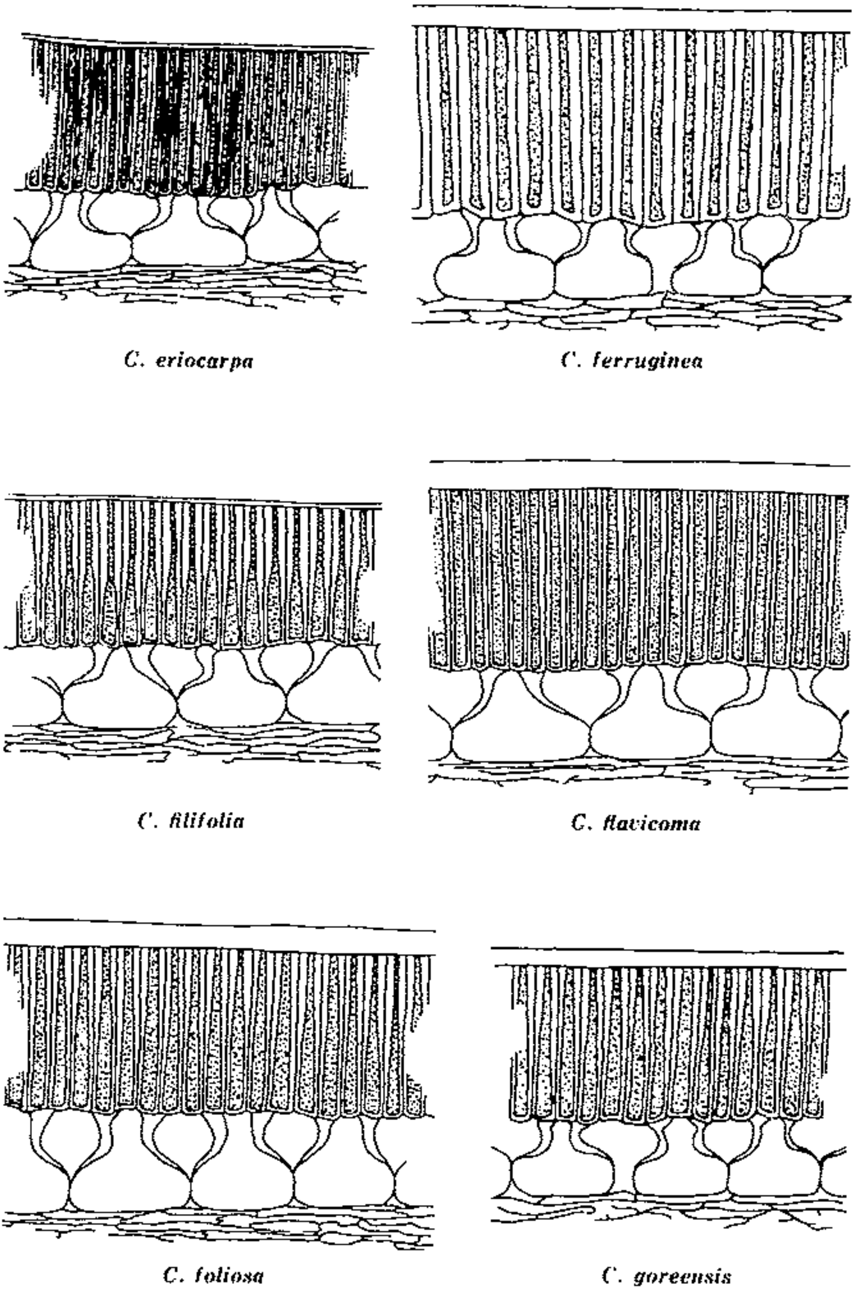


FIGURE 11.—Seed coat transections of *Crotalaria* species *eriocarpa* through *goreensis*, × 322 (for tissue nomenclature see fig. 9).

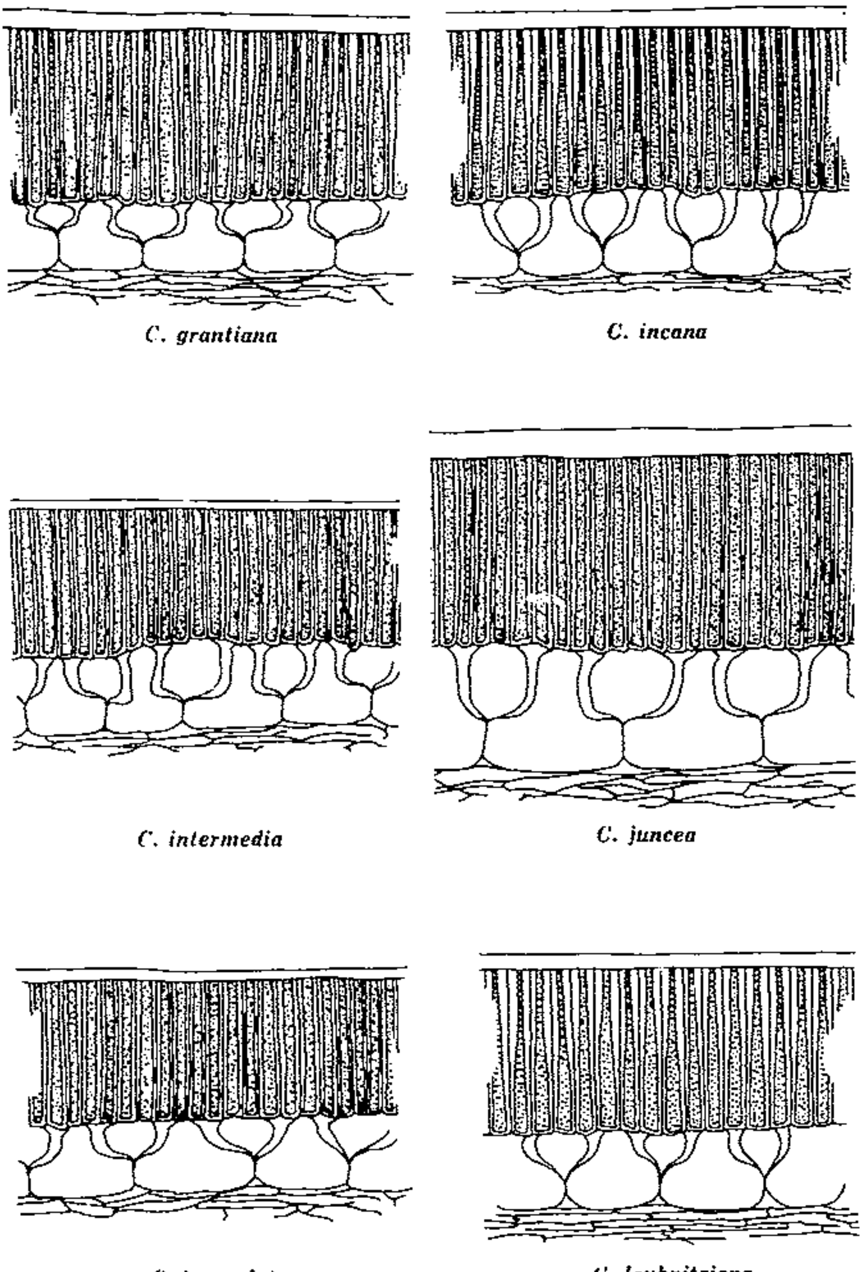


FIGURE 12.—Seed coat transections of *Crotalaria* species *grantiana* through *leubnitziana*, × 322 (for tissue nomenclature see fig. 9).

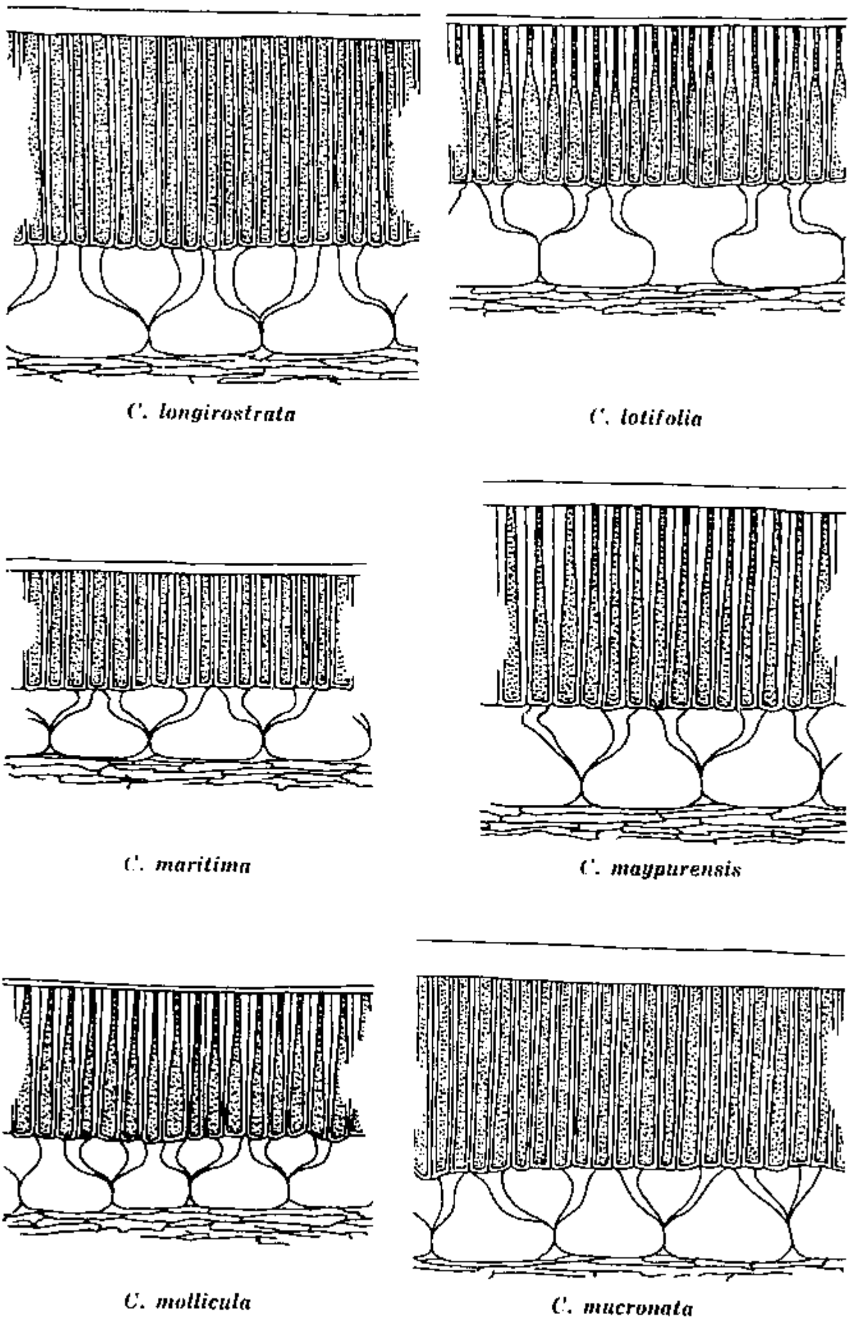


FIGURE 13.—Seed coat transections of *Crotalaria* species *longirostrata* through *mucronata*, × 322 (for tissue nomenclature see fig. 9).

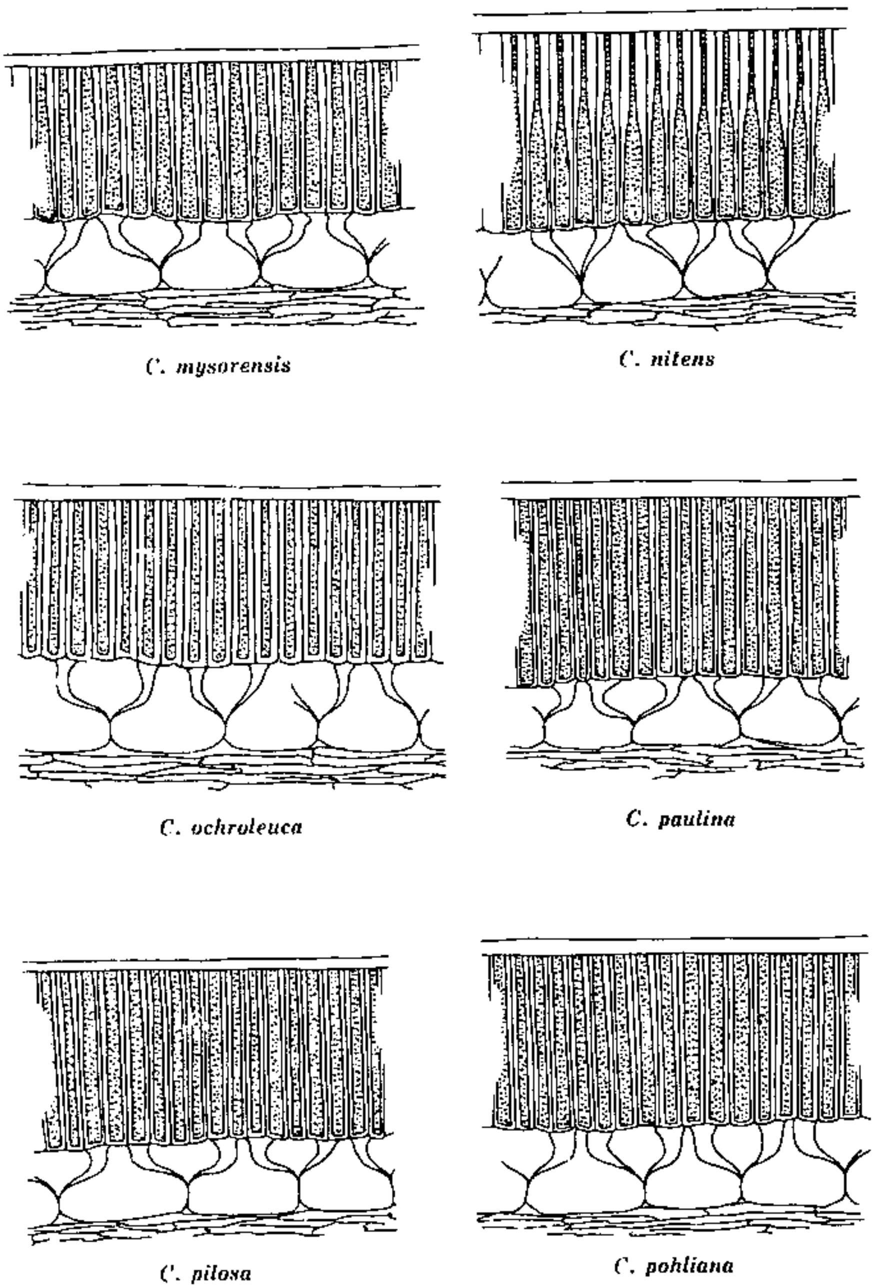


FIGURE 14.—Seed coat transections of *Crotalaria* species *mysorensis* through *pohliana*, × 322 (for tissue nomenclature see fig 9).

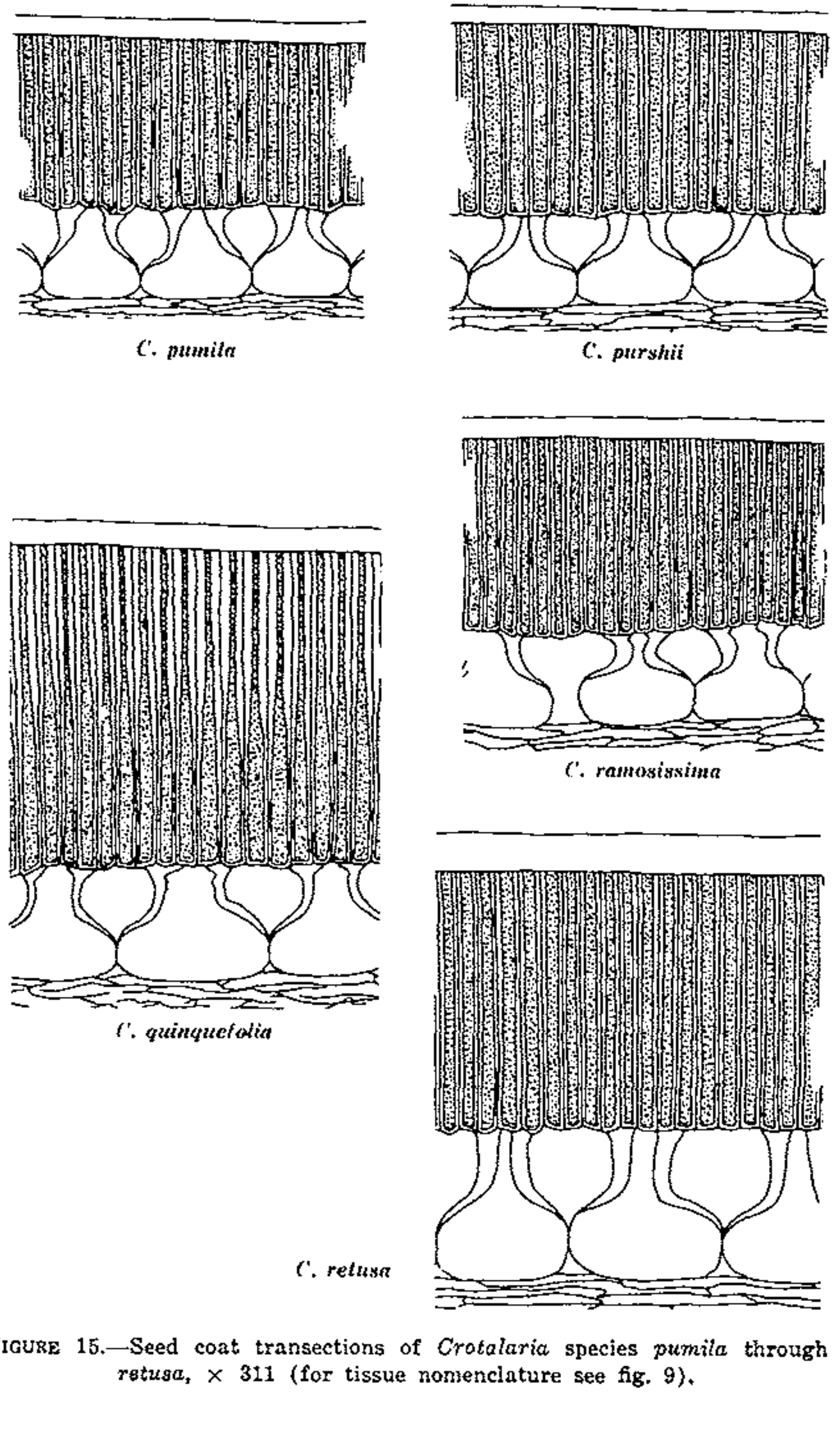
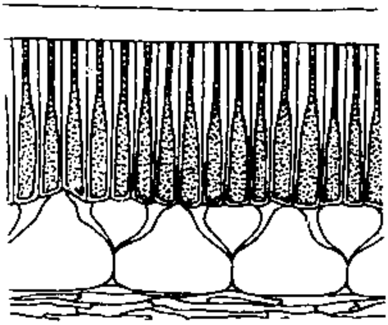
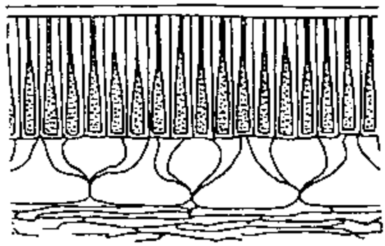


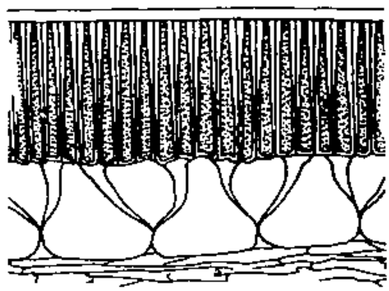
FIGURE 15.—Seed coat transections of *Crotalaria* species *pumila* through *retusa*, × 311 (for tissue nomenclature see fig. 9).



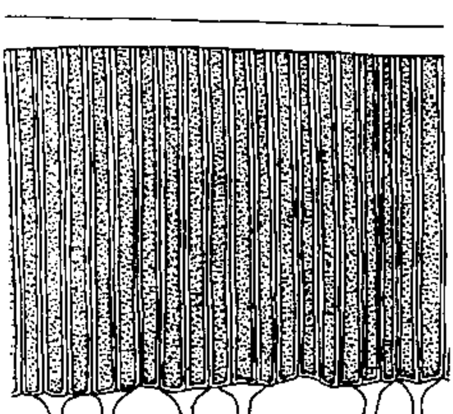
C. rhodesiae



C. sagittalis

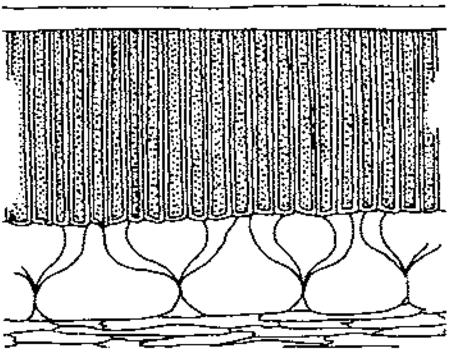


C. saltiana

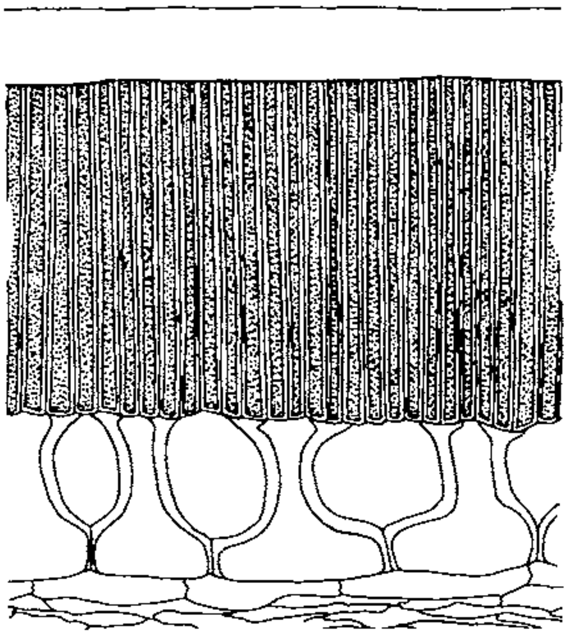


C. spectabilis

FIGURE 16.—Seed coat transections of *Crotalaria* species *rhodesiae* through *spectabilis*, × 311 (for tissue nomenclature see fig. 9).



C. stipularia



C. tetragona

FIGURE 17.—Seed coat transections of *Crotalaria* species *stipularia* and *tetragona*, × 322 (for tissue nomenclature see fig. 9).

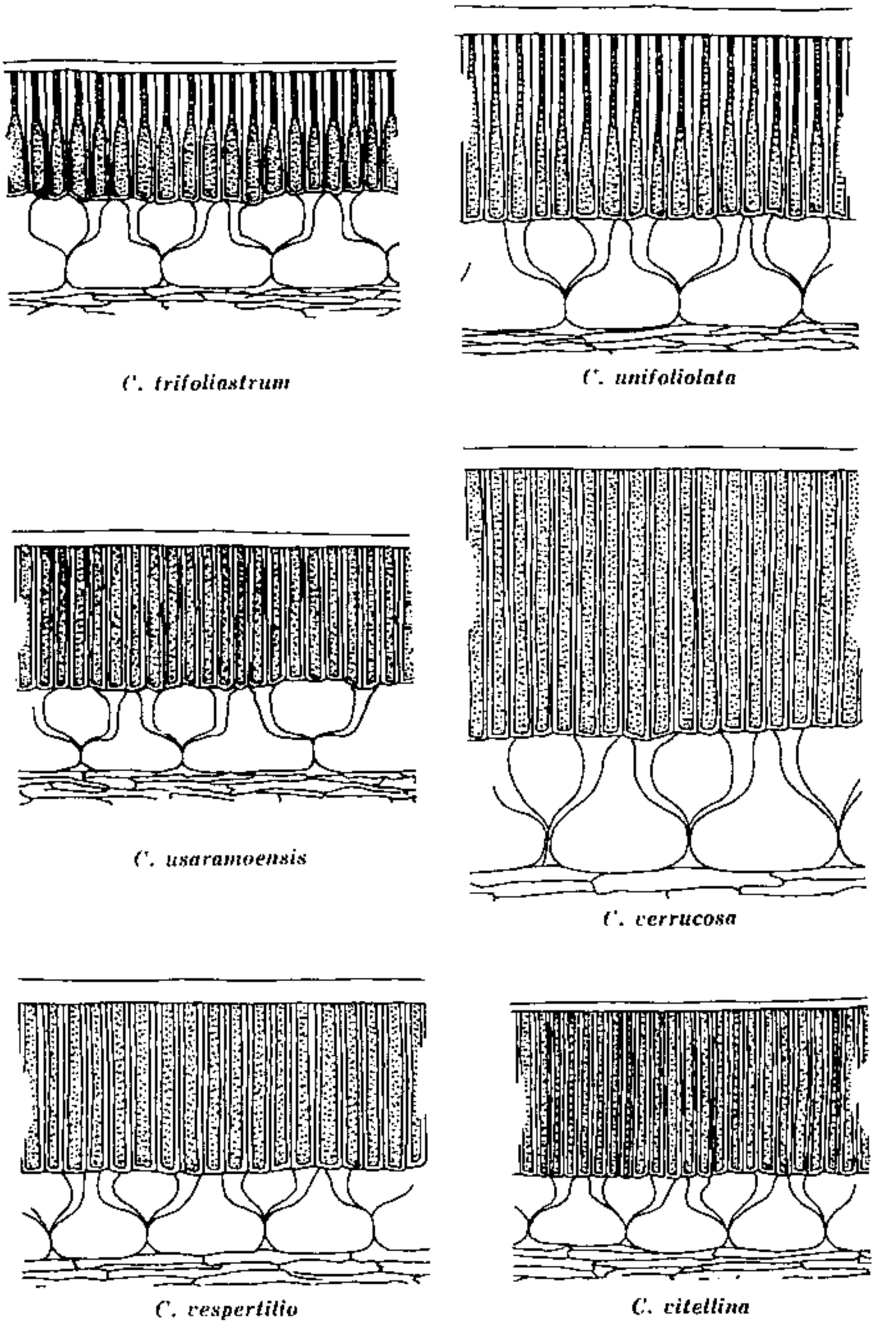


FIGURE 18.—Seed coat transections of *Crotalaria* species *trifoliastrum* through *vitellina*, × 322 (for tissue nomenclature see fig. 9).

Hypodermis

In *Crotalaria* the hypodermis consists of a single layer of cells that form a semimechanical tissue of the testa. They have been variously described, in addition to other terms, as colonne, hourglass cells, I-beam cells, osteosclereids, prop cells, support cells, Tragerzellen, and T-shaped cells. They are reportedly common throughout the Leguminosae, as well as in other families. While the histological term "osteosclereid" is generally used today to designate this type of cell, it is not appropriate for *Crotalaria*. In this genus they are not "bone shaped," as the term implies, but instead resemble a flask. Therefore from a purely descriptive sense they would be more accurately described as "flask shaped." These cells are thin walled and parenchymoid at their basal end and possess thick secondary walls in their upper "necklike" region (see figs. 8, 9; pl. 1, B). Freshly sectioned tissue as well as paraffin-embedded and dissociated material all clearly indicate the actual configuration and structure of these cells. If the testa is not sectioned carefully, however, the basal portion of the cell can easily be mutilated or entirely crushed beyond recognition, leaving only the neck portion. Thus, upon examination, one may gain the erroneous impression that the cell is somewhat columnar and osteosclereid-like in appearance. In many *Crotalaria* species the upper and lower extremities of the neck exhibit serifoid or flangelike expansions (fig. 8, C). When the basal portion of the cell is not evident, one may observe only the upper portion and it will, in effect, appear as an I-beam-shaped cell or an osteosclereid.

In the present investigation the term "osteosclereid" is therefore supplanted by one that is considered to be more congruous namely, the "lagenosclereid." This neoteric term is derived from the Greek *lagenos*, flask, and *skleros*, hard, and is considered to be both appropriately and histologically descriptive for a flask-shaped sclereid. While it is a purely descriptive term, it may nevertheless be considered as histologically valid as the one supplanted. The hypodermal layer of the *Crotalaria* seed coat, then, is characterized by its distinctive lagenosclereids. They are absent from the boss and hilar regions. It would be of interest to determine if this type of cell is unique to this genus alone, or if it actually occurs in other taxa as well.

The lagenosclereids are variable in form in different species. In this study they range from approximately 12 to 56 microns in length, and from 30 to 70 microns in width in their basal portion (see table 3, figs. 8, C, 9–18). In addition to their configurations, as described above, the lagenosclereids also exhibit various modifications in their neck portion. The radial wall of the neck varies from approximately 1.75 to 5.25 microns in thickness. The length of the neck is variable in different regions of the testa. In some species the thick-walled, nonlignified neck region extends downward to the base of the cell, with only the inner tangential surface remaining thin-walled. Corrugations or flutings are often evident on the internal radial walls of the neck (fig. 8, C). Relatively large intercellular spaces commonly occur between the necks of the lagenosclereids, with smaller spaces often occurring between their bases and the contiguous parenchyma below. The cell lumen is widest at the base and usually gradually narrows toward the apex, in some instances being almost occluded by the secondary wall constriction of the neck region.

In apical surface view the lagenosclereid usually appears as a ring within a ring (fig. 8, D). The conspicuously thickened wall of the neck appears much smaller in diameter and is seemingly situated inside the larger and bulbous lower part of the cell. The lumen may appear stellate as a result of the fluted or channeled inner walls of the neck (fig. 8, C, D).

Parenchyma

In *Crotalaria* the three- to five-layered tissue of the parenchyma lies immediately below the lagenosclereids (fig. 9; pl. 1, B). Some earlier investigators have designated it as a "spongy mesophyll," while others have considered it as the "nutrient tissue" or "*Nahrschicht*" (Tschirch and Oesterle, 1900). The cells of this relatively loosely organized tissue with intercellular spaces are thin walled and polyhedral in shape (fig. 8, G). As the seed coat matures, the cells become horizontally compressed. They are eventually crushed and disintegrate. Dissociation and disintegration of these cells create a space which further demarcates the aleurone layer of the adjoining endosperm. Plastids were not evident in the parenchyma of the testa. The parenchyma is also variously modified in the hilar region and will be further discussed under that topic. Neither an inner epidermis nor perisperm is present in the seed of *Crotalaria.*

The Endosperm

While the endosperm is not a part of the seed coat, brief consideration is given to it at this point, since it is in close attendance to the parenchyma of the testa (figs. 9, 20–21). The endosperm differentiates as a nutrient tissue from the embryo and fills the remainder of the seed not occupied by the embryo itself. The embryo has not been considered in the present study. Anderson (1949) examined 10 species of *Crotalaria* seed and estimated that they contained from 8 to 25 percent endosperm.

Earlier investigators considered the seeds of legumes as being entirely "exalbuminous" or devoid of an endosperm. Subsequent investigations have clearly demonstrated that while an endosperm may not be present in all species of the Leguminosae, a large number do contain such a tissue in their seeds. Rau (1951) concludes that in mature *Crotalaria verrucosa* seed the endosperm is completely "consumed," and Cook (1924) says that it "practically disappears" in *C. sagittalis*. In the present investigation it was found that all mature *Crotalaria* seeds contained a distinct endosperm completely enveloping the embyro. While not considered to be copious, it appeared to be fairly abundant and variable in amount depending upon the species. Median transectional measurements taken from the central region of the soaked seed and from prepared slide material, indicate that the endosperm varies in thickness from approximately 95 to 900 microns. Seed size was not correlative with the amount of endosperm present (table 3).

In dry *Crotalaria* seed the endosperm appears opaque, relatively hard, and shrunken. It becomes gelatinoid and increases considerably in volume when moistened. In its dry condition it has been described as being "horny." Around most of the embryo the endosperm tissue consists of three to five layers. The cells are parenchymatous, thin walled, and compact, with apparently no intercellular spaces. They are more or less polyhedral and somewhat rectangularly elongated around most of the embyro; the innermost cells often appear crushed and disintegrated (figs. 8, F, 9). In the region lying between the cotyledons and the radicle the cells are abundant and usually more or less isodiametric in shape. The cells of the aleurone layer are cubical, with their outer tangential wall thicker than the others (figs. 8, H, 9). The aleurone is two- to three-layered in the subhilar region, and is also often several layered in the radicle-tip region. (See Microchemical Tests and Seed Constituent Analyses for endosperm contents.)

The Hilar Region

The tissues comprising the hilar and subhilar regions of the *Crotalaria* seed are uniquely complex. A greater variety of cell types exists here than anywhere else in the testa (figs. 19–21; pl. 1, A). This may be a distinctive feature of the hilar tissues of all

Papilionoideae of the Leguminosae. The gross features of the hilar region are discussed under General Morphology of the Seed, above.

The cuticle which encompasses the seed coat is absent in the hilar region. It terminates on the hilar rim slightly inside of the hilar sinus at the points of attachment of the funicular tissue. No cuticle is present between the macrosclereids of the funicular remnant (see Funicular Remnant, below) and those of the hilum testa. It is also absent over the surface of the hilar groove or fissure (figs. 20–21; pl. 1, A).

The macrosclereids of the hilar region are similar to those elsewhere in the epidermal layer of the testa, with the exception of small modifications. In this region the epidermis folds inwardly toward the hilar sinus and, with the hypodermal tissues, contributes directly to the rim configuration of the sinus. It then curves upward and ends abruptly within the sinus at the upper level of the hilar groove (figs. 20, 21). The radial walls of the macrosclereids frequently appear curved in their accommodation to the general curvatures of the epidermis. The macrosclereids at either side of the groove are smaller than elsewhere in the testa, and may appear considerably shortened at their terminus on the sides of the hilar groove. Lagenosclereids do not occur in the hilar region.

In median transections the micropyle becomes evident in the epidermis as a minute opening in the macrosclereid tissue below the rim of the sinus. This pore occurs on the radicular lobe side of the seed, slightly below the attachment of the funicular remnant (fig. 20). The radial walls of the macrosclereids are slightly curved in appearance around the micropyle.

The parenchyma tissue of the hilar region is highly proliferated and variously modified, with numerous intercellular spaces. In addition to an abundance of cells similar to those subtending the lagenosclereids elsewhere in the testa (see Parenchyma under The Seed Coat, above), the remainder of subhilar parenchyma is relatively unique in its structure and tissue arrangement. The innermost cells of the parenchyma lie adjacent to the two- to three-layered aleurone cells of the subhilar endosperm (see The Endosperm, above; see figs. 20, 21; pl. 1, A). This nonsclerotic parenchyma, with its thin, polyhedral cell walls, differentiates outwardly into a mass of highly modified tissue with conspicuous intercellular spaces. Its cellular components possess several stellate or armlike extensions from its thick, nonlignified, secondary walls and impart a spongelike appearance to the tissue. The "arms" radiate in all directions, with each arm adjoining that of another stellate cell (pl. 1, A, C, D; fig. 19, D, G).

This type of tissue is described by Corner (1951) as "stellate aerenchyma," by Winton (1916) as "porous sclerenchyma," and by Zimmermann (1936) as "Sternparenchyma." In the present study this tissue will be more appropriately designated as "stellate parenchyma." In median transectional view the stellate parenchyma appears as a broad, curved band situated between the brachysclereid tissue (described below) and the lowermost parenchyma (fig. 21; pl. 1, A). In median longisectional view this tissue is bounded centrally above by the cluster of tracheids comprising the "floor" of the hilar groove, and on its outward ends by the transitional parenchyma (described below; see fig. 20).

The cells between the stellate parenchyma and those of the innermost parenchyma are distinctly transitional in their configurations and in the secondary thickening of their walls. In their differentiation they may possess one or more radiating arms, each with various stages of development and nonlignified secondary wall thickenings (pl. 1, A, C, D; and fig. 19, H). The cells in this region may be designated as "transitional parenchyma" to describe best their singular development.

The hilar region of *Crotalaria* seed also contains other sclerenchymatous tissues. The entire floor of the hilar groove comprises a dense mass of short and closely packed tracheids extending downward into the adjacent subhilar tissue for a short distance. They are somewhat variable in size, being slightly longer in the central part of the tissue. The walls bear scalariform-reticulate thickenings (fig. 19, C; pl. 1, A). Intercellular spaces are not present. This region has been referred to as a "tracheid cushion" (Winton, 1916), "tracheid bar" (Corner, 1951), "tracheid island" (Pammel, 1899), "vascular isle" (Hyde, 1954), and "lamina chilariale" (Mattirolo and Buscalioni, 1892). In the present study, Corner's term seems the most appropriate and will be used to designate this tissue. In median longisectional view the tracheid bar appears as an elongated crescent-shaped band or bar bounded above by the brachysclereids and below by the stellate parenchyma (fig. 20). In median transectional view it appears as the U-shaped cluster forming the floor of the hilar groove, enveloped on its sides and below by the transitional parenchyma (fig. 21; pl. 1, A). Actually, the tracheid bar is ensheathed by a two- to three-layered nonstellate parenchyma in this region. This parenchyma, almost invariably crushed in microsectioning, is in turn enveloped by the contiguous transitional form.

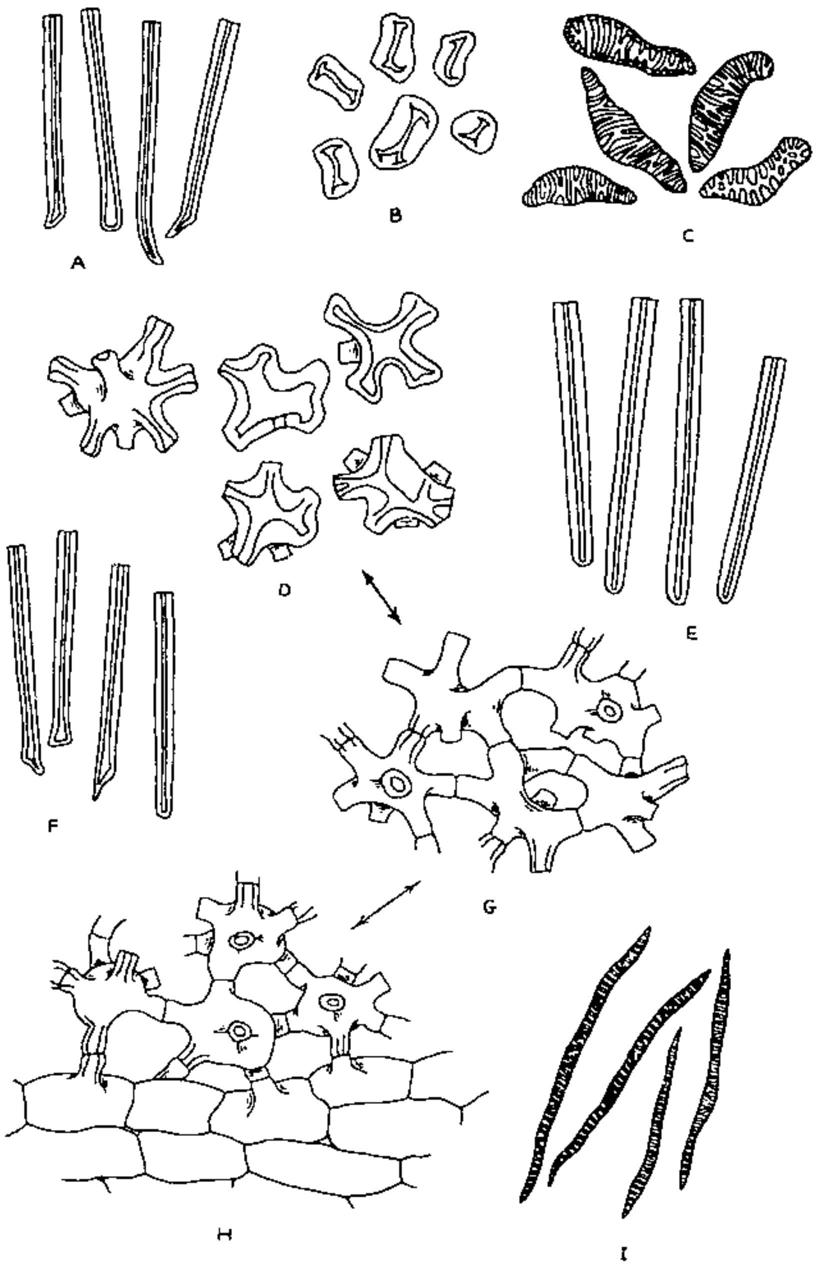


FIGURE 19.—Various cell components of the hilar region of *Crotalaria*, × 307. a, seed coat macrosclereids; b, brachysclereids; c, tracheid bar elements; d and g, stellate parenchyma; e, macrosclereids of the boss region; f, funicular macrosclereids; h, transitional parenchyma; i, tracheids of the vascular trace. (See figs. 20–21; pl. 1, A.)

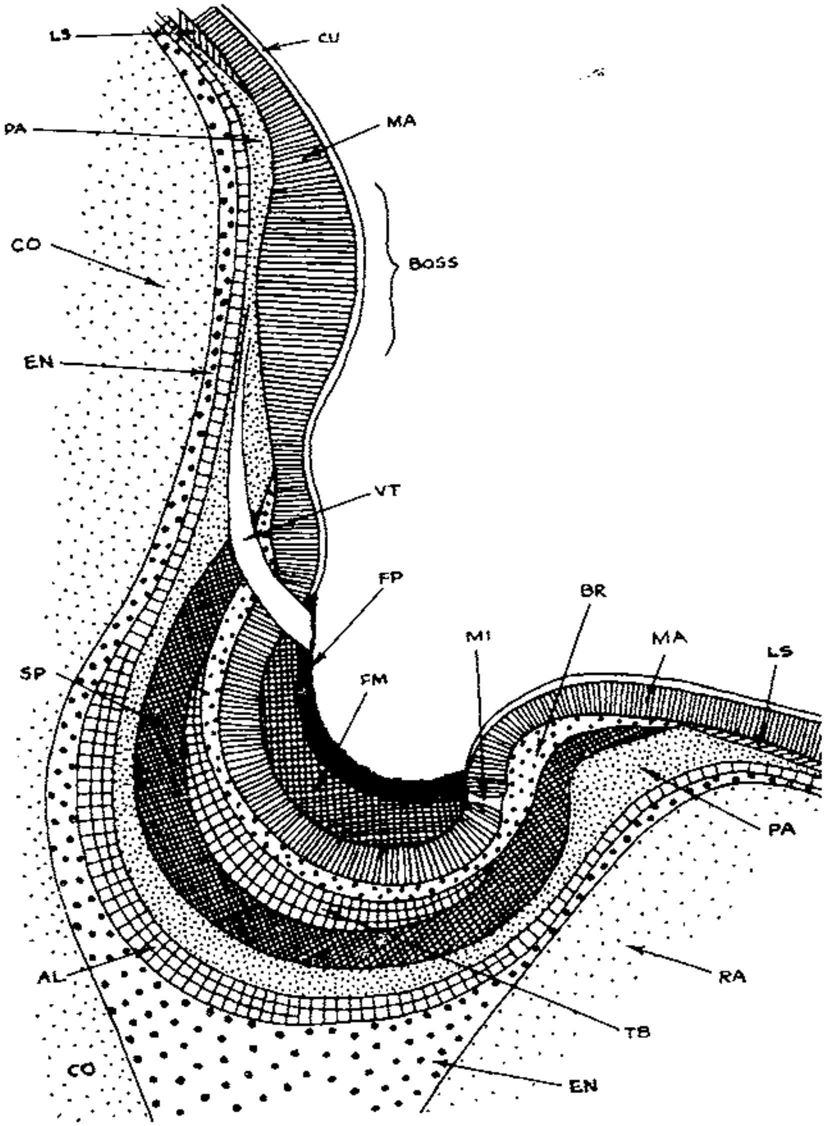


FIGURE 20.—Diagrammatic median longisection of *Crotalaria intermedia* hilar region, × 322. (AL) aleurone, (BR) brachysclereids, (CO) cotyledon, (CU) cuticle, (EN) endosperm, (FM) funicular macrosclereids, (FP) funicular parenchyma, (LS) lagenosclereids, (MA) macrosclereids, (MI) micropyle (PA) parenchyma, (RA) radicle, (SP) stellate parenchyma, (TB) tracheid bar, (VT) vascular trace. (See fig. 19 for illustrations of the various cellular components.)

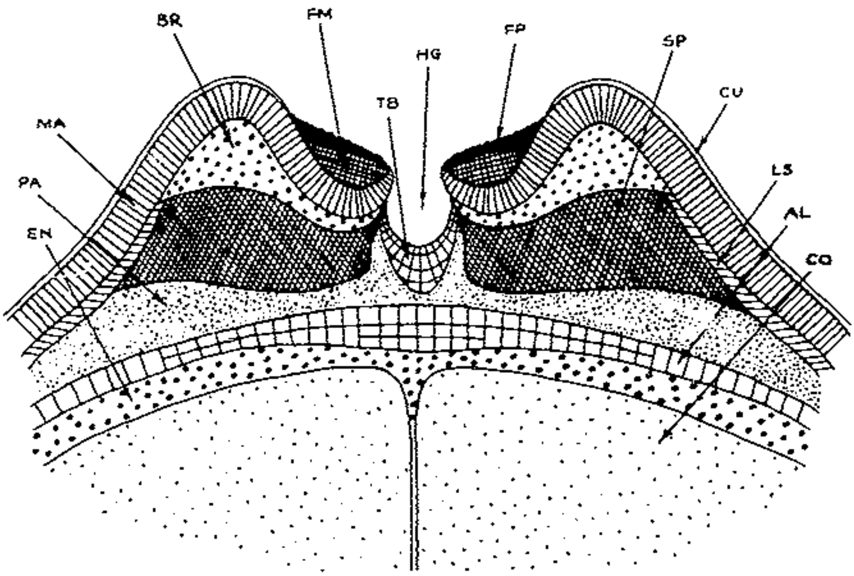


FIGURE 21.—Diagrammatic median transection of *Crotalaria intermedia* hilar region, × 322. (AL) aleurone, (BR) brachysclereids, (CO) cotyledon, (CU) cuticle, (EN) endosperm, (FM) funicular macrosclereids, (FP) funicular parenchyma, (HG) hilar groove, (LS) lagenosclereids, (MA) macrosclereids, (PA) parenchyma, (SP) stellate parenchyma, (TB) tracheid bar. (See fig. 19 for illustrations of the various cellular components, and pl. 1, A).

The cells of the subepidermal region immediately subtending the macrosclereids of the hilar rim are also sclerenchymatous. These form a mechanical tissue consisting entirely of numerous short brachysclereids ("Steinzellen"). They are unevenly thick walled and nonlignified, polymorphic, and possess small lumina (fig. 19, B; pl. 1, A). Simple and ramiform pits are frequently present in the walls. This tissue contains an abundance of intercellular spaces. In median longisectional view the tissue appears as a curved mass subtending the hilar epidermal layer (fig. 20). In median transectional view it appears as subepidermal masses below each side of the hilar rim, bounded above by the distinctively curved epidermal layers and below by the stellate parenchyma (fig. 21; pl. 1, A).

Funicular Remnant

Among *Crotalaria* seeds the funicular remnant may or may not be prominent. Figure 7 indicates the remnant configurations for those species in this study in which a portion of the funiculus remains prominently persistent. Its presence or absence can be used, in part, as a criterion for identification (see seed keys). The present anatomical investigation considers only funicular remnant tissues as they persist upon the hilum. No attempt was made to study the funicular tissues in toto.

Viewed from above the remnant usually appears circular or elliptical in its slightly sunken position immediately below the hilar rim and within the hilar sinus (see seed photographs). When sparingly present it is often collar-like in appearance. It is adnate upon the outer surface of the hilar epidermal layer without an intervening cuticle. The basal cells of the funiculus consist of a single layer of macrosclereids which are contiguous upon the hilar epidermis (the "cellule di rinforzo" of Mattirolo and Buscalioni, 1892). They are similar in general appearance to those comprising the epidermis of the testa. They are not lignified and their radial secondary walls are evenly thickened and without modifications, often appearing slightly curved on their longitudinal axis. No light line is present and they are not birefringent, in contrast to their testa counterparts. The lumen is small and only slightly variable in shape. In the seed literature this tissue is usually referred to as the "counter-palisades." In this study they are designated merely as "funicular macrosclereids" (pl. 1, A; figs. 20-21). Immediately above and contiguous upon the funicular macrosclereids are shriveled and disorganized parenchyma cells. They are here considered as "funicular parenchyma" (figs. 20-21; pl. 1, A).

The vascular connection between the seed and the funiculus remains as a single trace embedded in the tissues of the testa. It enters the seed as a minute vascular bundle below the rim of the hilum, on the cotyledonary lobe side opposite the micropyle. No other vascular traces are present. This trace has no connection with the embryo. It consists entirely of primary xylem and primary phloem elements ensheathed for most of its length in one or two layers of elongated, thin-walled parenchyma cells. Elongated tracheids are predominant with overlapping tapered ends and helical-reticulate, lignified, secondary wall thickenings (fig. 19, I). In *Crotalaria intermedia* the tracheids measure 6 to 7 microns wide and 70 to 77 microns long. The scanty phloem components are sieve-tube elements, whose end walls appear more or less oblique-truncate, and their attendant companion cells. The terminus of the vascular trace consists entirely of tracheids. The trace traverses the epidermis, brachysclereids, and a portion of the stellate parenchyma before terminating within the parenchyma subtending the macrosclereids of the boss region (fig. 20).

The Boss Region

On the cotyledonary lobe, a short distance above the hilar rim, the seed of *Crotalaria* exhibits a rounded integumentary prominence or bulge (figs. 1, 20; see also figs. 2-5, and the seed photographs). Its position, degree of configuration, and coloration is somewhat variable, depending upon the species. This region is the so-called "strophiole" of many investigators and the "lens" of others. Both terms are ambiguous in their connotation. The use of the term "strophiole" (often used synonymously with "caruncle" and "aril") to designate this regional prominence of many legume seeds is incongruous and inexpedient. This term(s) is usually reserved primarily to designate the peculiar hilar excrescences or outgrowths known to occur in certain other taxa (e. g, *Ricinus, Peperomia, Swartzia, Corydalis* et al.). *Crotalaria* seed is estrophiolate, and the tissue under consideration is not hilar in nature and is not functionally analogous to a strophiole. The more appropriately descriptive term "boss" will instead be used in this investigation (derived as a transference of the Latin *bulla,* a boss).

The degree of prominence of the boss results from the progressive elongation of the epidermal macrosclereids in this region (figs. 19, E, and 20). These cells often attain a length twice that of the other cells of the epidermal layer. The cuticularization here is similar as elsewhere on the testa. The lower portion of the radial walls is often curved in this region. The hypodermis consists entirely of thin-walled parenchyma with small intercellular spaces. Lagenosclereids are absent in this region, occurring only on the outer margins (fig. 20). As discussed earlier, the vascular trace from the funiculus terminates in the parenchyma subtending the boss macrosclereids.

In median longisectional view the boss region appears lenticular or doubly convex in its configuration (fig. 20). In face view the central portion in some species appears slightly indented. Occasionally, one or more small clefts or fissures (the median groove or "*Riss*" of Zimmermann, 1936) are observable between some of the centrally located macrosclereids of the boss. In *Crotalaria* these minute cell wall displacements, usually only at the midregions of contiguous cells, result primarily from microsectioning.

The boss region is often devoid of pigmentation, or it may be of a lighter or darker hue than the remainder of the seed coat. Its coloration, as well as prominence, can be utilized in seed identification (see seed keys).

SEED TOXICITY

While there is considerable literature on the intoxicative effects of animals and fowl ingesting *Crotalaria* green forage and hay, there are a relatively small number of species whose seeds have actually been proven to be toxic. There are many diverse imputations of *Crotalaria* poisoning, but few have been definitely substantiated.

Under natural conditions many animals apparently refuse the plants when other forage is available. In the laboratory, chronic and acute intoxications are exhibited principally when the subjects are provided with abnormal dosages, forced feedings, or continuous diets of the suspected seeds (or vegetative parts). The latter conditions are not normally encountered in their natural environments. In a number of instances the toxic effects imputed to crotalarias have been shown to derive from feeding upon plants of (or in conjunction with) other genera instead. Evidence also indicates that not all animals or fowl regularly succumb to ingestion of seed of poisonous crotalarias. It is also possible that direct or indirect variations in climatic and edaphic, as well as genetic, factors contribute to the increase or decrease of the poisonous properties.

The pathological conditions have been variously designated as "crotalism" or "crotalariosis" in addition to several varietal vernaculars dependent upon specific symptoms.

Definitely proven to be toxic are the seeds of the African *Crotalaria burkeana* Benth. to sheep; *C. dura* Wood and Evans to horses and sheep; and the pantropicals *C. retusa* L. and *C. mucronata* Desv. (*C. striata* DC.) to chickens and possibly other fowl. Particularly toxic are the seeds of the East Indian species *C. spectabilis* Roth (*C. retzii* Hitchc., *C. sericea* Retz) to chickens, cattle, dogs, goats, horses, mules, sheep, and swine (see Becker, et al., 1935). Under experimental conditions the Indian species *C. juncea* L. has been shown to be toxic to sheep. There are a few species whose seed is suspect, but there is no definite proof, namely the Australian *C. mitchellii* Benth. to stock animals, and the North American *C. sagittalis* L. (*C. angulata* Mill., *C. tuerckheimii* Senn) to horses.

The alkaloid monocrotaline ($C_{16}H_{23}O_6N$, mp 197–198°, dec.), the monocrotalic acid ester of retronecine, has been shown to be the active toxic principle in the seeds of *C. mucronata*, *C. retusa*, and *C. spectabilis*. It was first isolated by Neal and coworkers (1935). It is suspected to be the active principle in some or all of the other known toxic seeds (or vegetative parts) of *Crotalaria*. According to Adams and Rogers (1939), monocrotaline upon alkaline hydrolysis yields retronecine ($C_8H_{13}O_2N$), monocrotic acid ($C_9H_{12}O_3$, bp 145–146°/18 mm.), and carbon dioxide. Under hydrogenolysis it yields retronecanol ($C_9H_{15}ON$, bp 140°/30 mm., mp 95–96°) and monocrotalic acid ($C_8H_{12}O_5$, mp 182°).

Hydrocyanic acid (HCN) has been reported isolated from the seed of *C. juncea*, but there is no indication that it functions as the primary poisonous principle (Quisumbing, 1947).

Considering the large number of *Crotalaria* species, very few have actually been assayed biochemically. They may harbor many other toxic alkaloids that are presently unknown; there are a number that are known but as yet unnamed. Extensive treatments and references on this subject may be found in Kingsbury (1964 *pp. 314–320*), Steyn (1934), and Watt and Breyer-Brandwijk (1962, *pp. 577–590*).

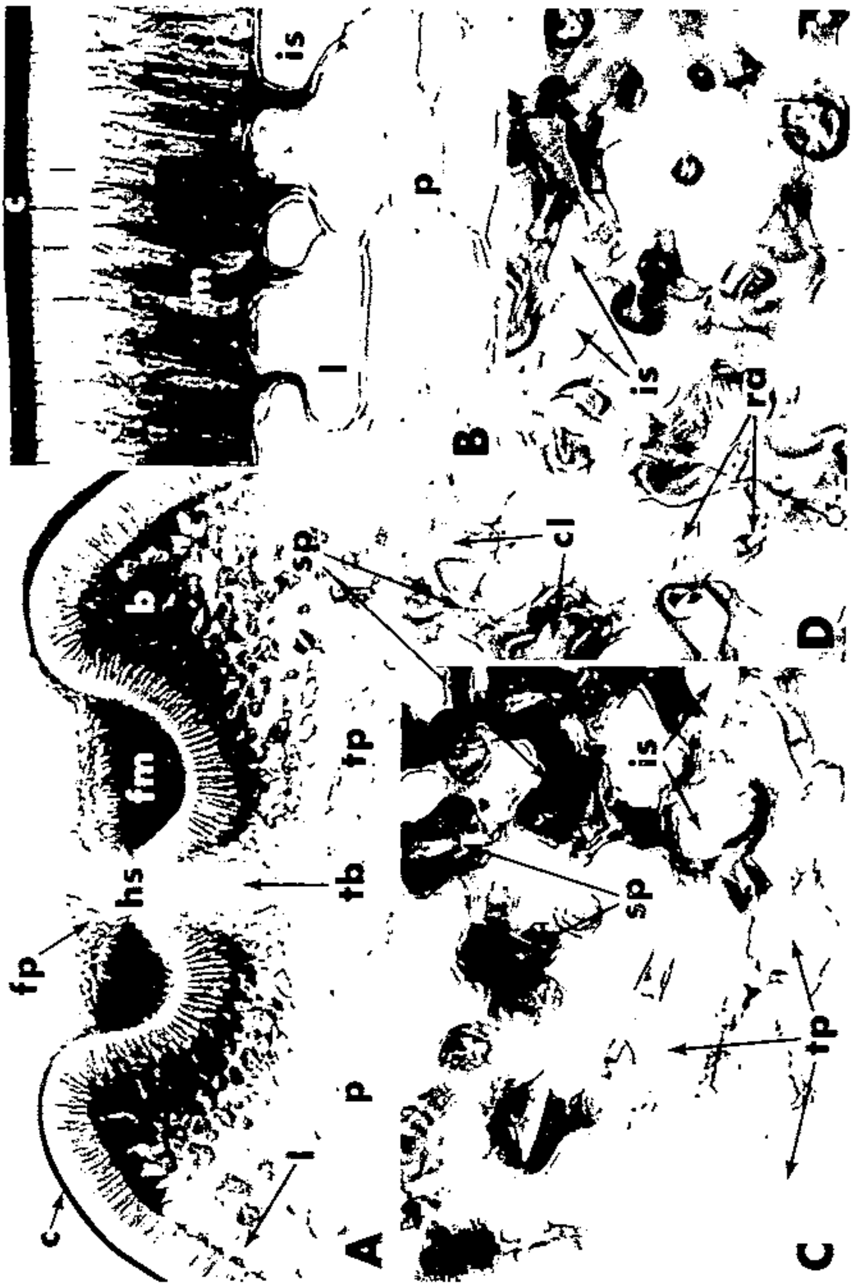
KEY TREATMENT

Many of the seeds of *Crotalaria* species appear very similar to one another, and species variations further augment the identification problem. Moreover, there is a paucity of external morphological seed characters that can be utilized in constructing a key where a large number of *Crotalaria* species are involved. These factors are recognized as inherent problems. Therefore, for the sake of expediency, the seeds have been segregated into two groups. One provides a key to the New World species and the other a key to the Old World species occurring in the Americas. Table 1 includes authorities for species names.

Four *Crotalaria* species, namely, *incana, mucronata, retusa,* and *verrucosa,* are here considered to be pantropical in their geographical distribution. They are included in both keys. All species deemed to be putative synonyms are given in parentheses.

Enlarged photographs of all species, along with their average life-size silhouettes, are presented in plates 2 to 10. Additional comparisons can be made by utilizing text figures 1 to 5. To more accurately distinguish between species of seeds possessing similar morphology requires that a representative sampling of mature seeds of each species be available.

PLATE 1



A, *Crotalaria intermedia* hilar transection, × 115. See fig. 21 for diagrammatic representation. B, Seed coat transection of *C. juncea*, × 522. C, Enlargement indicating transitional and stellate parenchyma in subhilar region of *C. intermedia*, × 499. D, Enlargement of stellate parenchyma in subhilar region of *C. juncea*, × 522. b, brachysclereids; c, cuticle; cl, cell lumina; fm, funicular macrosclereids; fp, funicular parenchyma; hs, hilar sinus; is, intercellular spaces; l, lagenosclereids; m, macrosclereids; p, parenchyma; ra, radiating arms of cells; sp, stellate parenchyma; tb, tracheid bar; tp, transitional parenchyma.

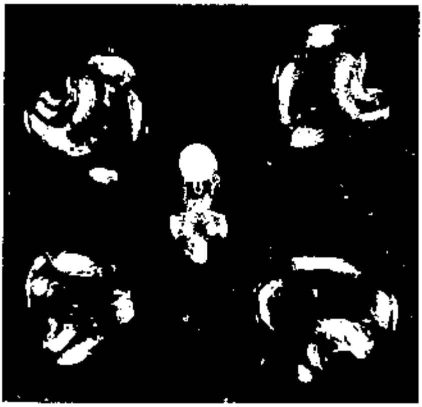
PLATE 2

C. alata

C. anagyroides

C. brachystachya

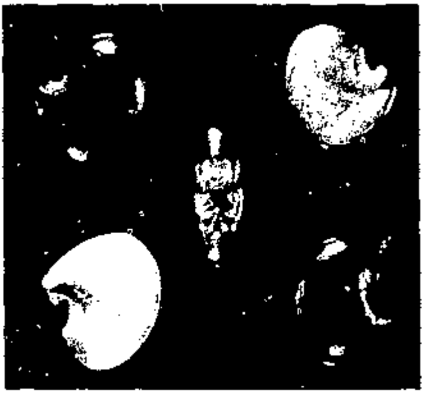
C. breviflora



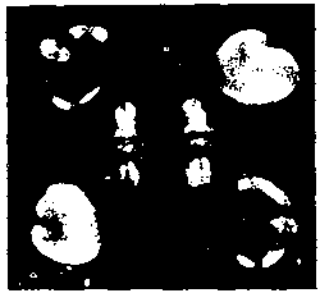
C. capensis

C. claussenii

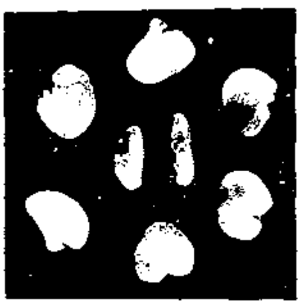
PLATE 3



C. eriocarpa



C. ferruginea



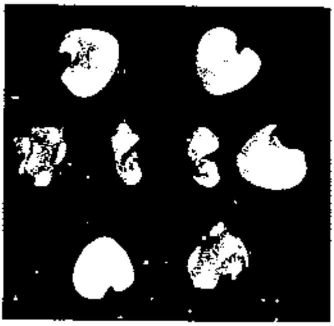
C. filifolia

C. flavicoma

C. foliosa

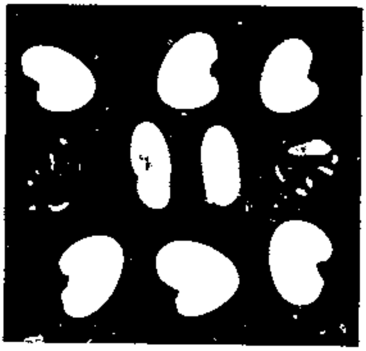
C. goreensis

PLATE 4



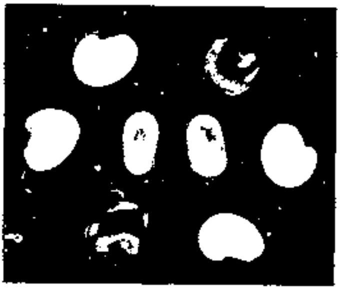
C. grantiana

C. incana



C. intermedia

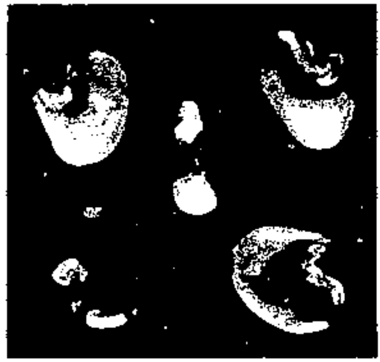
C. juncea



C. lanceolata

PLATE 5

C. leubnitziana

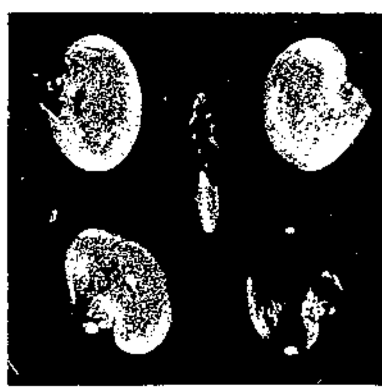


C. longirostrata

C. lotifolia

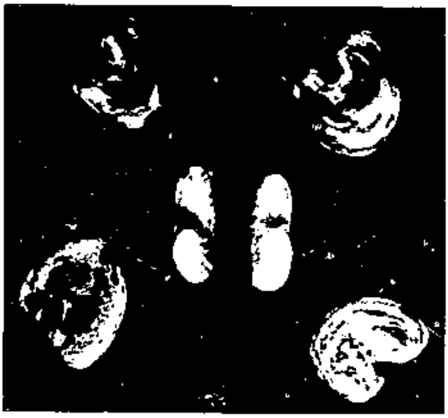
C. maritima

C. mollicula

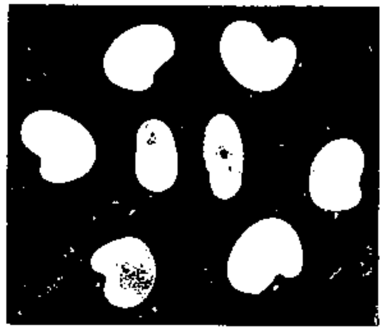


C. maypurensis

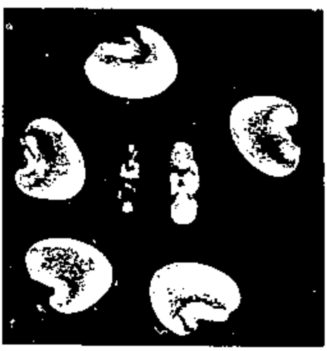
PLATE 6



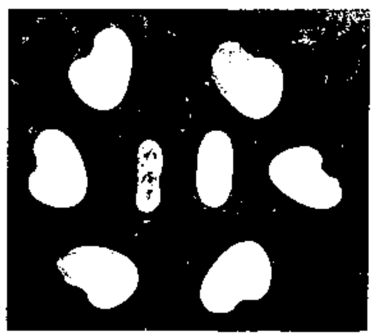
C. mucronata



C. mysorensis



C. nitens



C. ochroleuca

C. paulina

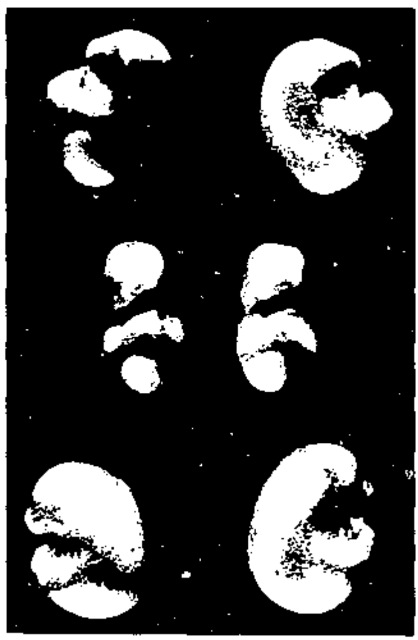
C. pilosa

PLATE 7

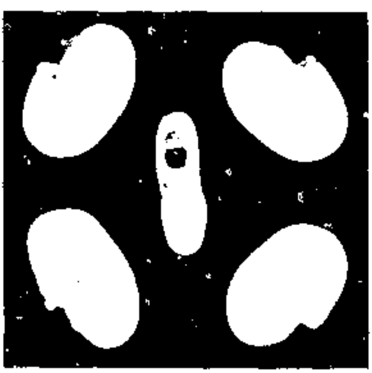
C. *pohliana*

C. *pumila*

C. *purshii*

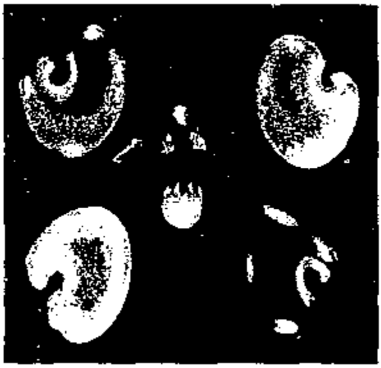


C. *quinquefolia*

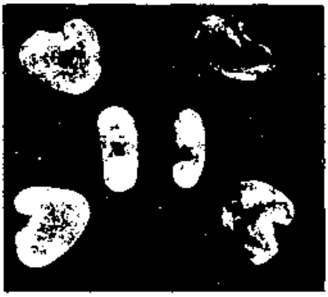


C. *ramosissima*

PLATE 8



C. retusa



C. rhodesiae

C. sagittalis

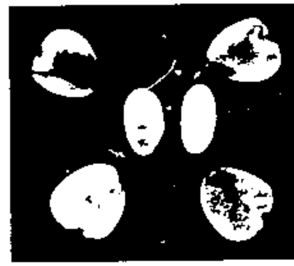
C. saltiana

C. spectabilis

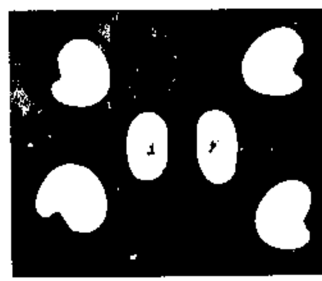
C. stipularia

PLATE 9

C. tetragona



C. trifoliastrum

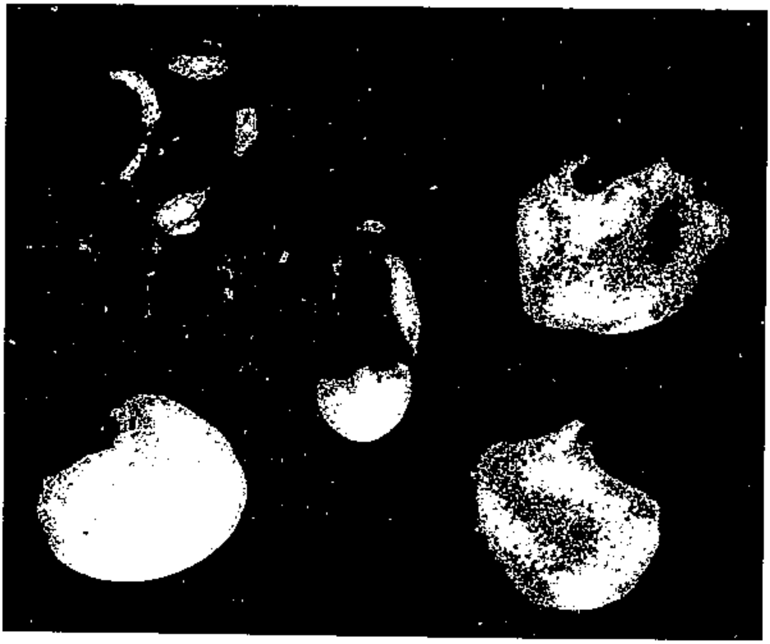


C. usaramoensis

C. unifoliolata

C. vitellina

PLATE 10



C. verrucosa

C. vespertilio

KEY TO THE SEED OF THE NEW WORLD *CROTALARIA* SPECIES

A. Hilum open, not occluded or only slightly so by convergence of radicular lobe.

B. Seed small (1.5–3 mm. long, 1.5–2 mm. wide, 0.75–2 mm. thick).

C. Glossy; funicular remnant collarlike, distinct or nearly so.

D. Boss prominent—(*pilosa* and *stipularia* similar in general morphology).

1. Hilar sinus narrow, slightly occluded; high glossy; deep yellow to light olive brown; 2–3 mm. long, 1.5–2.25 mm. wide, 1.25–1.5 mm. thick; South America and West Indies (pl. 8) .... *C. stipularia*

2. Hilar sinus broader; not highly glossy; light olive to olive brown; 2–2.75 mm. long, 1.75–2.25 mm. wide, 1.25–1.5 mm. thick; Central America (pl. 6) .... *C. pilosa* (*pterocaula*)

DD. Boss not prominent.

E. Funicular remnant distinct—(*nitens* and *pohliana* similar in general morphology).

1. Hilum submarginal banding with distinctively light color; glossy to high glossy; moderate yellow brown to brown, with distinctive black stippling; 2–3 mm. long, 2–2.5 mm. wide, 1–1.25 mm. thick; Central and South America (pl. 6) .... *C. nitens* (*schiedeana*)

2. Hilum submarginal bands indistinctive; dull glossy to glossy; brown to reddish brown; 2.5–2.75 mm. long, 2.25–2.5 mm. wide, 1.25–1.5 mm. thick; Brazil (pl. 7). .... *C. pohliana*

EE. Funicular remnant absent, or only fragmentary. Hilum small; submarginal band indistinctive; moderate olive brown to brown; 1.5–2.25 mm. long, 1.75–2 mm. wide, 1.25–1.5 mm. thick; Pan-Americana (pl. 8). .... *C. sagittalis* (*angulata, tuerckheimii*)

CC. Not glossy; funicular remnant indistinct or nearly so. Dull to lustrous; orange yellow to dark red orange; 2–2.75 mm. long, 1.75–2.25 mm. wide, 1.25–1.5 mm. thick; (closely resembles *usaramoensis*); South America (pl. 2). .... *C. breviflora*

BB. Seed medium (3–5 mm. long, 2–4.75 mm. wide, 1.25–2.25 mm. thick).

C. Glossy; funicular remnant collarlike, distinct or nearly so.

D. Hilum slightly occluded by convergent tip of radicular lobe.

1. Oblique-cordate; distinctly compressed; minute dark stippling distinct; gray brown to red brown; 4–4.5 mm. long, 3–3.75 mm. wide, 1–1.5 mm. thick; Brazil (pl. 3). .... *C. flavicoma*

2. Oblique-reniform; distinctly turgid; minute stippling indistinct; moderate brown to brown; 3.75–4 mm. long, 2.75–3 mm. wide, 1.5–1.75 mm. thick; Brazil (pl. 3). .... *C. foliosa*

DD. Hilum not occluded; radicular lobe appears more or less divergent.

E. Seed surface smooth; finely stippled—(*paulina* and *unifoliolata* similar in general morphology).

1. Hilum submarginal band wide; hilum surface usually light colored; moderate yellow brown to light olive brown; 3–4.75 mm. long, 2.25–3 mm. wide, 1.75–2.25 mm. thick; Brazil (pl. 6). ---------------- *C. paulina*
2. Hilum submarginal band narrow; hilum surface usually distinctly dark colored; moderate yellow brown to gray brown; 3–4 mm. long, 2.5–3.5 mm. wide, 1.75–2 mm. thick; Brazil (pl. 9). *C. unifoliolata*

EE. Seed surface not smooth; not stippled.
Cotyledon lobe margins lustrous; turgid; moderate yellow brown to moderate brown; 4–5 mm. long, 3–3.75 mm. wide, 1.75–2 mm. thick; Brazil (pl. 10). ------------------------------------ *C. vespertilio*

CC. Not glossy; funicular remnant absent.

D. Hilum slightly occluded by convergent tip of radicular lobe. Slightly compressed to turgid, often contorted; light olive green to red brown, occasional markings; 2.75–4 mm. long, 2.5–3.25 mm. wide, 0.75–2 mm. thick; Central America (pl. 9). ------------- *C. vitellina* (*guatemalensis*)

DD. Hilum not occluded; radicular lobe appears more or less divergent.

E. Seed with distinctive irregular marking and/or mottling. Oblique-cordate to oblique-reniform; dull to glossy; orange yellow to olive, moderate reddish brown to gray; 2.5–4 mm. long, 2–3 mm. wide, 1.25–1.75 mm. thick; pantropical (pl. 6). ----- *C. mucronata* (*striata*)

EE. Seed not marked or mottled.
Hilar sinus relatively wide, distinctly U-shaped; light olive brown to moderate brown; 3.25–4 mm. long, 3–3.75 mm. wide, 1–1.5 mm. thick; West Indies (pl. 5). ------------------------------- *C. lotifolia*

AA. Hilum distinctly occluded, partly or completely so by strongly convergent radicular lobe.

B. Seed small (1.5–3 mm. long, 1.5–2 mm. wide, 0.75–2 mm. thick).

C. Glossy; funicular remnant distinct or nearly so.

1. Boss prominent; moderate yellow brown to strong brown; oblique-cordate to oblique-reniform; turgid; dull glossy; 2–2.5 mm. long, 1.75–2.25 mm. wide, 1–1.5 mm. thick; southern United States and Mexico (pl. 7). ------------- *C. purshii*
2. Boss not prominent; oblique-cuneate-cordate; compressed; highly glossy; light olive brown to reddish brown; 2–2.5 mm. long, 1.5–2 mm. wide, 0.75–1 mm. thick; southern United States, Mexico and West Indies (pl. 5). --*C. maritima*

CC. Not glossy, (lustrous to almost glossy in *claussenii* and *incana*); funicular remnant indistinct or absent.

D. Hilum completely occluded by convergent radicular lobe.
Distinctly contorted; hilum very small, indistinct; hilum sinus a minute slit; strong yellow brown to moderate olive brown; 1.5–2 mm. long, 2–2.5 mm. wide, 1–1.25 mm. thick; Mexico (pl. 3) ------------------------- *C. filifolia*

DD. Hilum not completely occluded.

E. Radicular lobe distinctly recurved and hook-shaped.

1. Hilar sinus rounded; oblique-cordate; seed distinctly contorted and minutely warty; boss prominent; dark reddish brown, occasionally light mottled; lustrous to almost glossy; 2–3 mm. long, 1.75–2 mm. wide, 1–1.25 mm. thick; Brazil (pl. 2). --*C. claussenii*
2. Hilar sinus U-shaped; oblique-cordate to oblique-cuneate; minutely rough; compressed and often contorted; lustrous to almost glossy; moderate yellow to brown, blue green to purple, maroon, often with distinctive irregular light or dark markings and mottling; 2.5–3 mm. long, 2–3 mm. wide, 1.25–1.5 mm. thick; pantropical (pl. 4). ---*C. incana* (*setifera*)

EE. Radicle not hook-shaped.

1. Hilar sinus small and somewhat U-shaped; radicular lobe tip distinctly longer than in *pumila*; radicular lobe with a distinctive bulge; boss relatively prominent; moderate olive brown, olive green to green purple, purple; 2–2.75 mm. long, 2.25–2.75 mm. wide, 1.5–1.75 mm. thick; Central America (pl. 5). -- *C. mollicula*
2. Hilar sinus relatively smaller and V-shaped; radicular lobe tip very short; boss not prominent, distinctly light colored; strong yellow brown to dark red purple; 2–2.5 mm. long, 2–2.5 mm. wide, 1.25–1.5 mm. thick; southern United States, West Indies, Central and South America (pl. 7). -------*C. pumila*

BB. Seed medium (3–5 mm. long, 2–4.75 mm. wide, 1.25–2.25 mm. thick).

C. Glossy; boss not prominent.

D. Funicular remnant distinct.

E. Oblique-reniform (seed usually larger than either *brachystachya* or *maypurensis*).

Radicular lobe-tip prominently recurved, bulbous; compressed-turgid; smooth; strong yellow to strong yellow brown, red brown; 5–5.5 mm. long, 3–4 mm. wide, 1.75–2 mm. thick; South America (pl. 2). -- *C. anagyroides*

EE. Oblique-cordate (seed usually smaller than *anagyroides*).

1. Radicular lobe tip distinctly rounded, slightly recurved; compressed-turgid; smooth; deep yellow to light brown; 4–5 mm. long, 3.5–4.75 mm. wide, 1.5–1.75 mm. thick; Brazil (pl. 2).---*C. brachystachya*
2. Radicular lobe tip distinctly angular, hook-shaped; compressed, somewhat irregular; not smooth, minutely rough; light olive to olive brown; 4–4.75 mm. long, 3–3.5 mm. wide, 0.75–1.5 mm. thick; Central America (pl. 5).------------*C. maypurensis*

DD. Funicular remnant absent.

Hilum completely occluded by radicular lobe apparently touching cotyledonary lobe; dark orange yellow to dark red brown; 3.25–3.5 mm. long, 2.75–3 mm. wide, 1.5–2 mm. thick; pantropical (pl. 8). ______________ *C. retusa*

CC. Not glossy (lustrous to almost glossy in *longirostrata*).

D. Hilum completely occluded by convergent radicular lobe.

1. Radicular lobe distinctly angular; oblique-cordate; often contorted; moderate olive to strong yellow brown; 3–3.25 mm. long, 2.25–2.75 mm. wide, 1.25–1.75 mm. thick; Central America (pl. 5). ________ *C. longirostrata*

2. Radicular lobe tip distinctly bulbous, minutely rough; oblique-orbicular to oblique-reniform; strong yellow to moderate reddish brown; 3.25–5 mm. long, 3–4 mm. wide, 2–2.5 mm. thick; pantropical (pl. 10). __ *C. verrucosa*

DD. Hilum not completely occluded; boss prominent.

Oblique-reniform; turgid; olive to dark olive brown, with occasional mottling; 4–4.5 mm. long, 3–3.5 mm. wide, 1.5–1.75 mm. thick; Central America (pl. 3). ______________________________________ *C. eriocarpa (viminalis)*

KEY TO THE SEED OF THE OLD WORLD *CROTALARIA* SPECIES

A. Hilum open, not occluded or only slightly so by convergence of radicular lobe.

B. Seed small (1.5–3 mm. long, 1.5–2 mm. wide, 0.75–2 mm. thick).

C. Hilum slightly occluded, more so than in *ferruginea* or *usaramoensis;* seed coat minutely rough.

Glossy; dark green yellow to light olive, moderate brown, occasionally with irregular gray or brownish markings or mottling; 2–3 mm. long, 2–2.5 mm. wide, 1.25–1.5 mm. thick; (closely resembles *saltiana*); Africa (pl. 8). ________ *C. rhodesiae*

CC. Hilum not occluded; seed coat smooth.

D. Boss prominent.

1. Glossy to high glossy; radicular lobe appears convergent; dark red brown to dark purple brown, occasionally light olive with brown mottling; 2.25–3 mm. long, 2–2.5 mm. wide, 1–1.25 mm. thick; India (pl. 3). ______________________________________ *C. ferruginea*

2. Not glossy to lustrous; radicular lobe appears divergent; moderate orange yellow to moderate yellow orange, orange to red; 2–2.5 mm. long, 1.5–2 mm. wide, 1–2 mm. thick; (closely resembles *breviflora*); Africa (pl. 9). ________________________________ *C. usaramoensis*

DD. Boss not prominent.

E. Hilar sinus angle obtuse.

1. Hilar sinus wide and shallow; radicular lobe strongly divergent from, and approximately same length as, cotyledonary lobe; cuneate; lustrous to glossy; moderate to strong orange, yellow to strong brown, occasionally red orange; 2–2.75 mm. long,

1.5–2 mm. wide, 1–1.5 mm. thick; Africa (pl. 6). ---------------------------------*C. ochroleuca*

2. Hilar sinus much narrower and not shallow; radicular lobe much shorter than, and less divergent from, cotyledonary lobe; rotund, distinctly turgid; lustrous; moderate orange yellow to yellow orange; 2–3 mm. long, 1.5–2 mm. wide, 1–1.5 mm. thick; India (pl. 6). ---------------------- -----*C. mysorensis*

EE. Hilar sinus angle acute—(*intermedia* and *lanceolata* similar in general morphology).

1. Seed larger and much more variable in color than *lanceolata;* 2–2.5 mm. long, 1.75–2 mm. wide, 1.25–1.5 mm. thick; moderate yellow to strong orange yellow, red to strong brown, gray brown to dark gray blue; not glossy to glossy; Africa (pl. 4).----- ---------------------------------------*C. intermedia*

2. Seed smaller than *intermedia;* 1.5–2.25 mm. long, 1.5–1.75 mm. wide, 1–1.25 mm. thick; strong yellow to brown orange, occasionally orange red; lustrous to glossy; Africa (pl. 4). --------------*C. lanceolata*

BB. Seed medium (3–5 mm. long, 2–4.75 mm. wide, 1.25–2.25 mm. thick).

C. Boss prominent; seed much larger than either *mucronata* or *saltiana.*
Slightly compressed to turgid; hilum slightly occluded by convergence of radicular lobe tip; tan to gray brown, dark purple, with occasional light mottling; 3.5–4.25 mm. long, 3.5–4 mm. wide, 1.75–2.25 mm. thick; Africa (pl. 2). *C. capensis*

CC. Boss not prominent; seed much smaller than *capensis*—(*mucronata* and *saltiana* similar in general morphology).

1. Seed often contorted; dark yellow to light olive, brown; grayish or brownish markings and mottling not as distinctive as in *mucronata;* glossy; 2.75–3.5 mm. long, 2.5–2.75 mm. wide, 1.25–1.75 mm. thick; (closely resembles *rhodesiae*); Africa (pl. 8). ------------------------*C. saltiana*

2. Seed usually not contorted; orange yellow to olive, moderate reddish brown to gray; distinctive irregular markings and mottling (gray, brown, purple); dull to glossy; 2.5–4 mm. long, 2–3 mm. wide, 1.25–1.75 mm. thick; pantropical (pl. 6). ------------------------------*C. mucronata* (*striata*)

AA. Hilum distinctly occluded, incompletely or completely so, by strongly convergent radicular lobe.

B. Seed small (1.5–3 mm. long, 1.5–2 mm. wide, 0.75–2 mm. thick).

C. Glossy.
Oblique-cordate; turgid; boss conspicuously colorless; moderate olive to yellow brown, dark purple brown to purple; 1.5–2.75 mm. long, 1.5–2.5 mm. wide, 1–1.5 mm. thick; Africa (pl. 5). ---------------------------------------*C. leubnitziana*

CC. Not glossy.

1. Radicular lobe minute; hilar sinus minute; distinctly oblique-cordate; dull; compressed-turgid; light olive to deep yellow,

dark brown; 2–2.5 mm. long, 1.5–2 mm. wide, 1–1.25 mm. thick; India (pl. 9). .... *C. trifoliastrum*

2. Radicular lobe large; hilar sinus large; oblique-cordate to oblique-cuneate; compressed and contorted; minutely rough; lustrous to almost glossy; moderate yellow to brown, blue green to purple, maroon, often with distinctive irregular light or dark markings and mottling; 2.5–3 mm. long, 2–3 mm. wide, 1.25–1.5 mm. thick; pantropical (pl. 4). .... *C. incana (setifera)*

BB. Seed medium (3–5 mm. long, 2–4.75 mm. wide, 1–1.25 mm. thick); *juncea* seed large (6–7 mm. long, 4–4.75 mm. wide, 2–3 mm. thick).

C. Funicular remnant distinct, or nearly so.

D. Glossy.

E. Radicular lobe distinctly hook-shaped.

1. Dark olive green to brownish black, black; turgid; funicular remnant collarlike; highly glossy; 4–5 mm. long, 3.5–4 mm. wide, 1.25–2 mm. thick; India (pl. 9). .... *C. tetragona (obtecta)*

2. Red orange to orange red; compressed; funicular remnant not collarlike; 2.25–3.25 mm. long, 1.75–2.25 mm. wide, 1–1.5 mm. thick; Africa (pl. 3). .... *C. goreensis*

EE. Radicular lobe not hook-shaped.

Tan to light brown, deep red brown; compressed; distinctly ellipsoidal; boss distinctly dark; 4–4.5 mm. long, 2.5–3 mm. wide, 1.25–1.5 mm. thick; India (pl. 7). .... *C. ramosissima*

DD. Not glossy; minutely rough; funicular remnant more or less fragmentary.

Olive brown to dark brown, dark purple; turgid; lateral surfaces sunken; oblique-reniform; 4.5–5.25 mm. long, 3–4 mm. wide, 2–2.5 mm. thick; India (pl. 7). *C. quinquefolia*

CC. Funicular remnant absent (remnant more or less evident in *juncea*).

D. Glossy.

E. Seed small (1.5–3 mm. long, 1.5–2 mm. wide, 0.75–2 mm. thick).

Oblique-cordate; dull glossy to glossy; deep yellow to strong yellow brown; 1.75–2.5 mm. long, 1.75–2.25 mm. wide, 1–1.5 mm. thick; Africa (pl. 4). *C. grantiana*

EE. Seed medium (3–5 mm. long, 2–4.75 mm. wide, 1.25–2.25 mm. thick).

F. Radicular lobe distinctly white encrusted—(*alata* and *spectabilis* similar in general morphology).

1. Seed generally larger than *spectabilis*, and with a grayish cast;not glossy to glossy; moderate olive brown to gray brown, brown purple to dark purple, occasionally light mottled; 4–6 mm. long, 3–4 mm. wide, 1–2 mm. thick; Africa (pl. 2). .... *C. alata*

2. Seed usually smaller and glossier than *alata;* dull glossy to high glossy; moderate olive brown to blackish brown; 4–5 mm. long, 2.75–3.25 mm. wide, 1–1.75 mm. thick; India (pl. 8). ________________________ ***C. spectabilis*** (*retzii, sericea*)

FF. Radicular lobe not encrusted.
Boss dark, with distinctive dark marking above; dark orange yellow to dark red brown; 3.25–3.5 mm. long, 2.75–3 mm. wide, 1.5–2 mm. thick; pantropical (pl. 8). ____________________***C. retusa***

DD. Not glossy, to lustrous.

E. Seed medium (3–5 mm. long, 2–4.75 mm. wide, 1.25–2.25 mm. thick).
Oblique-orbicular to oblique-reniform; smooth; turgid, occasionally contorted; radicular lobe minutely rough; strong yellow to moderate reddish brown; 3.25–5 mm. long, 3–4 mm. wide, 2–2.5 mm. thick; pantropical (pl. 10). ___________________________________*C. verrucosa*

EE. Seed large (6–7 mm. long, 4–4.75 mm. wide, 2–3 mm. thick).
Compressed, often contorted on one surface; smooth to minutely rough, occasionally pitted; funicular remnant present or absent; boss prominent; cotyledonary lobe distinctly angular; dull to lustrous or dull glossy; grayish olive green to olive gray, light olive brown to bluish purple; India (pl. 4). __***C. juncea***

GLOSSARY

Accumbent.—With cotyledons lying face to face against the radicle.

Albuminous.—With endosperm.

Aleurone layer.—The outermost layer of the endosperm.

Amyloid.—A "hemicellulose" resembling starch.

Boss.—A rounded protuberance varying in position on the cotyledonary lobe above the hilum, often conspicuous by the presence or absence of coloration.

Brachysclereids.—Short, somewhat isodiametric, thick-walled and lignified stonelike cells.

Bulbous.—Bulb-shaped.

Callose.—A polymer of glucose residues (a carbohydrate).

Campylotropous.—An ovule type in which the base and apex approximate one another as a result of its developmental curvature; its axis being at right angles to the funiculus (see fig. 6).

Compressed.—Flattened laterally.

Contorted.—Distorted or twisted.

Convergent.—Approaching or converging.

Cotyledonary lobe.—An apparent projection of the cotyledons in comparison with the radicular lobe.

Counter-palisades.—Funicular remnant macrosclereids.

Cuneate.—Wedge-shaped.

Cuticle.—A cutinous layer covering the entire seed surface except the hilum (see Cutin).

Cutin.—Usually a fatty substance, waxlike in appearance, forming the cuticle. On *Crotalaria* seed it is nonfatty (in nature).

Divergent.—Extending away from or diverging.

Dull.—Not lustrous or glossy.

Ellipsoidal.—Elliptical in outline; oval in form, narrowing to round ends and widest near the middle.

Endemic.—Indigenous or native to.

Endosperm.—The reserve food tissue (albumen) surrounding the embryo.

Estrophiolate.—Without a strophiole.

Exalbuminous.—Without endosperm.

Fruticose.—Shrubby or shrublike and tending to be woody.

Funicular remnant.—A fragment of the funiculus or seed stalk.

Funiculus.—The stalk by which an ovule or seed is attached to the ovary wall or placenta.

Glossy.—Smooth and shiny.

Hardness (of seed coat).—An impermeable or semipermeable condition of the seed coat preventing water imbibition.

Hilar groove.—A very narrow longitudinal furrow or slit extending medianly down the length of the hilum floor.

Hilar sinus.—The recess or space (notch) in the hilar region.

Hilar sinus angle.—The angle of the sinus between the cotyledonary and radicular lobes.

Hilum.—A sunken scar indicating the place of seed attachment to the funiculus.

Intercellular space.—Space between cells or tissues.

Lagenosclereids.—Distinctive flask-shaped sclereids constituting the hypodermal layer of *Crotalaria* seed. The "osteosclereids" and "hour-glass cells" of earlier workers (see fig. 8; pl. 1, B).

Light line.—A light-colored, birefringent, optically illusory "band" in the upper region of the *Crotalaria* macrosclereids near the cuticle.

Lumen.—The central cavity of a cell.

Lustrous.—Having a sheen but not directly shiny or glossy.

Macrosclereids.—Thick-walled, columnar-shaped or rodlike cells, constituting the first or epidermal ("Malpighian" or "palisade") layer of the seed coat in *Crotalaria*, and probably in all papilionaceous seeds.

Micropyle.—A minute pore or orifice on the seed surface indicative of a former opening leading into the nucellus of the ovule.

Nucellus.—Sporogenous and vegetative cells of the ovule containing the embryo sac, and comprising the central body of the ovule.

Oblique.—Assymetrical or unequal-sided.

Occluded.—Closed or obstructed.

Orbicular.—Circular in outline.

Parenchyma.—A tissue of thin-walled, polyhedral-shaped cells variable in form, structure, position, origin, and function.

Perisperm.—Nucellar or integumentary nutritive tissue.

Persistent.—Remaining attached.

Plumule.—The bud or growing point of the embryo.

Radicle.—The embryonic root at the lowest end of the hypocotyl in the seed.

Radicular lobe.—A projection of the radicle.

Reniform.—Kidney-shaped (bean-shaped).

Sagittal.—The median line in a plane of division of bilateral symmetry.

Sclerenchyma.—A complex of thick-walled, often lignified, mechanical cells.

Stellate parenchyma.—Parenchyma tissue composed of cells with armlike or stellate walls more or less separated by an abundance of relatively large intercellular spaces (see figs. 19–20; pl. 1A, C–D).

Stippled.—Microscopic pits appearing as minute spots on the testa of certain *Crotalaria* species.

Striations.—Bands or narrow markings, more or less parallel.

Strophiole.—An integumentary protuberance or outgrowth near the micropyle, not present in *Crotalaria* seed.

Subepidermis or **hypodermis.**—Below or under the epidermis.

Subhilar.—Below the hilum.

Suffruticose.—Somewhat shrubby; woody at the base with herbaceous shoots produced perennially.

Testa.—Seed coat or integument.

Tracheid.—An imperforate, more or less elongated, thick-walled, lignified primary xylem cell.

Tracheid bar.—A band or region of short tracheids in the subhilar region of *Crotalaria* and other leguminous seeds.

Transition parenchyma.—Parenchyma tissue with cells transitional or changing from one form and structure to another (see fig. 19; pl. 1A, C).

Truncate.—Appearing cut off at the end, or straight across with a square end.

-gid.—Swollen or distended.

Vascular trace.—A portion or strand of vascular tissue consisting of xylem and phloem components.

LITERATURE CITED

ADAMS, R., and ROGERS, E. F.
1939. THE STRUCTURE OF MONOCROTALINE, THE ALKALOID IN *Crotalaria spectabilis* AND *Crotalaria retusa*. I. Jour. Amer. Chem. Soc. 61(10): 2815–2819.

ANDERSON, E.
1949. ENDOSPERM MUCILAGES OF LEGUMES. Indus. and Engin. Chem. 41(12): 2887–2890.

BAKER, E. G.
1914. THE AFRICAN SPECIES OF *Crotalaria*. Jour. Linn. Soc. (Botany). 42: 241–425.

———1926. LEGUMINOSAE OF TROPICAL AFRICA. Erasmus Press, Ghent. 215 pp.

BECKER, R. B., NEAL, W. M., ARNOLD, P.T.D., and SHEALY, A. L.
1935. A STUDY OF THE PALATABILITY AND POSSIBLE TOXICITY OF 11 SPECIES OF *Crotalaria*, ESPECIALLY OF *C. spectabilis* ROTH. Jour. Agr. Res. 50(11): 911–922.

BENTHAM, G.
1859–62. LEGUMINOSAE. PART I. PAPILIONACEAE. *In:* Martius. Flora Braziliensis. Apud Fridr. Fleischer in Comm. Lipsiae. Vol. 15(I): Col. 18–32.

BROWN, E. E., and FUDGE, J. F.
1960. DETECTION OF CROTALARIA SEED IN MIXED FEEDS. Tex. Agr. Expt. Sta. Misc. Pub. 474.

BURKART, A.
1952. LAS LEGUMINOSAS ARGENTINAS, SILVESTRES Y CULTIVADAS. Acme Agency. Buenos Aires. 569 pp.

CAPITAINE, M. L.
1912. CONTRIBUTION A L'ETUDE MORPHOLOGIQUE DES GRAINES DE LEGUMINEUSES. Doctoral diss. Paris. 436 pp.

COOK, M. T.
1924. DEVELOPMENT OF SEED OF *Crotalaria sagittalis*. Bot. Gaz. 77: 440–445.

CORNER, E. J. H.
1951. THE LEGUMINOUS SEED. Phytomorphology. 1(1–2) :117–150.

EAMES, A. J., and MACDANIELS, L. H.
1947. AN INTRODUCTION TO PLANT ANATOMY. McGraw-Hill Book Co. New York.

EARLE, F. R., and JONES, Q.
1962. ANALYSES OF SEED SAMPLES FROM 113 PLANT FAMILIES. Econ. Bot. 16(4): 221–250.

FREY-WYSSLING, A.
1959. DIE PFLANZLICHE ZELLWAND. Springer-Verlag. Berlin.

HAYWARD, H. E.
1948. THE STRUCTURE OF ECONOMIC PLANTS. Macmillan Co. New York.

HYDE, E. O. C.
1954. THE FUNCTION OF THE HILUM IN SOME PAPILIONACEAE IN RELATION TO THE RIPENING OF THE SEED AND THE PERMEABILITY OF THE TESTA. Ann. Bot. (n.s.). 18(70): 241–256.

ISLEY, D.
1947. INVESTIGATIONS IN SEED CLASSIFICATION BY FAMILY CHARACTERISTICS. Iowa Agr. Expt. Sta. Res. Bull. 351.

JOHANSEN, D. A.
1940. PLANT MICROTECHNIQUE. McGraw-Hill Book Co. New York.

JONES, Q., and EARLE, F. R.
1966. CHEMICAL ANALYSES OF SEEDS. II. OIL AND PROTEIN CONTENT OF 759 SPECIES. Econ. Bot. 20(2): 127–155.

KINGSBURY, J. M.
1964. POISONOUS PLANTS OF THE UNITED STATES AND CANADA. 626 pp. Prentice-Hall, Inc. Englewood Cliffs, N. J.

KOOIMAN, P.
1960. ON THE OCCURRENCE OF AMYLOIDS IN PLANT SEEDS. Acta Bot. Neerl. 9(2): 208–219.

KOPOOSHIAN, H. A.
1963. SEED CHARACTER RELATIONSHIPS IN THE LEGUMINOSAE. Doctoral diss. Iowa State Univ. Ames, Iowa.

MAISEL, A.
1909. RECHERCHES ANATOMIQUES ET TAXONOMIQUE SUR LE TEGUMENT DE LA GRAINE DES LEGUMINEUSES. Soc. d'Hist. Naturelle d'Autun. Bull. 22, pp. 52–128.

MARTIN, A. C.
1946. THE INTERNAL MORPHOLOGY OF SEEDS. Amer. Midland Nat. 36: 513–660.

——— and BARKLEY, W. D.
1961. SEED IDENTIFICATION MANUAL. 221 pp. Univ. Calif. Press. Berkeley.

MARTIN, J. N., and WATT, J. R.
1944. THE STROPHIOLE AND OTHER SEED STRUCTURES ASSOCIATED WITH HARDNESS IN *Melilotus alba* L. AND *M. officinalis* WILLD. Iowa State Col. Jour. Sci. 18(2): 457–469.

MATTIROLO, O., and BUSCALIONI, L.
1892. RICHERCHE ANATAMO-FISIOLOGICHE SUI TEGUMENTI SEMINALI DELLE PAPILIONACEE. PART I. ANATOMIA. pp. 223–318. PART II. pp. 359–445. STORIA DI SVILUPPO DEL TEGUMENTO SEMINALE. *In*: Memorie della Reale Accademia delle Scienze di Torino. Series 2. Vol. 42.

MUSIL, A. F.
1963. IDENTIFICATION OF CROP AND WEED SEEDS. U.S. Dept. Agr., Agr. Handb. 219. 171 pp.

NADELMANN, H.
1890. UEBER DIE SCHLEIMENENDOSPERME DER LEGUMINOSEN. Prings. Jahrb. Wissen. Bot. 21: 609–691.

NEAL, W. M., RUSOFF, L. L., and AHMANN, C. F.
1935. THE ISOLATION AND SOME PROPERTIES OF AN ALKALOID FROM *Crotalaria spectabilis* Roth. Amer. Chem. Soc. Jour. 57(12): 2560–2561.

NETOLITSKY, F.
1926. ANATOMIE DER ANGIOSPERMEN-SAMEN. *In*: K. Linsbauer, Handbuch der Pflanzenanatomie. Band X. Abt. 2. Teil 2. pp. 161–170.

PAMMEL, L. H.
1899. ANATOMICAL CHARACTERS OF SEEDS OF LEGUMINOSAE. Acad. Sci. St. Louis, Trans. 9: 91–273.

PITOT, A.
1935. LE DEVELOPPEMENT DU TEGUMENT DES GRAINS DE LEGUMINEUSES. Soc. Bot. de France Bul. 82: 307–308; 311–314.

QUISUMBING, E.
1947. VEGETABLE POISONS OF THE PHILIPPINES. Philippine Jour. Forestry 5: 145.

RAU, M. A.
1951. THE ENDOSPERM IN *Crotalaria*. Current Sci. [India] 20(3): 73–74.

REEVE, R. M.
1946. STRUCTURAL COMPOSITION OF THE SCLEREIDS IN THE INTEGUMENT OF *Pisum sativum* L. Amer. Jour. Bot. 33(3) : 191–204.

REEVES, R. G.
1930. DEVELOPMENT OF THE OVULE AND EMBRYO SAC IN ALFALFA. Amer. Jour. Bot. 17: 239–246.

SENN, H. A.
1939. THE NORTH AMERICAN SPECIES OF CROTALARIA. Rhodora. 41: 317–367.

STANDLEY, P. C., and STEYERMARK, J. A.
1946. FLORA OF GUATEMALA. *In*: Fieldiana (Botany). Vol. 24. Part V, pp. 193–201.

STEYN, D. G.
1934. THE TOXICOLOGY OF PLANTS IN SOUTH AFRICA. So. Afr. Agr. Ser. Vol. XIII. Central News Agency, Ltd. Johannesburg.

TOOKEY, H. L., LOHMAR, R. L., WOLFF, I. A., and JONES, Q.
1962. NEW SOURCES OF SEED MUCILAGES. Agr. Food Chem. 10(2): 131–133.

——— PFEIFER, V. F., and MARTIN, C. R.
1963. GUMS SEPARATED FROM *Crotalaria intermedia* AND OTHER LEGUMINOUS SEEDS BY DRY MILLING. Agr. Food Chem. 11(4): 317–321.

——— and JONES, Q.
1965. NEW SOURCES OF WATER-SOLUBLE GUMS. Econ. Bot. 19(2): 165–174.

TSCHIRCH, A., and OESTERLE, O.
1900. ANATOMISCHER ATLAS DER PHARMAKOGNOSIE UND NAHRUNGSMITTELKUNDE. Herm. Tauchnitz. Leipzig.

WATT, J. M., and BREYER-BRANDWIJK, M. G.
1962. MEDICINAL AND POISONOUS PLANTS OF SOUTHERN AND EASTERN AFRICA. E. S. Livingstone, Ltd., Edinburgh. 1457 pp.

WELLENDORF, M.
1964. MORPHOLOGY AND ANATOMY OF CROTALARIA SEEDS. Lloydia. 27(3): 251–253.

WILBUR, R. L.
1963. THE LEGUMINOUS PLANTS OF NORTH CAROLINA. N. C. Agr. Expt. Sta. Tech. Bul. 151.

WINTON, A. L.
1916. THE MICROSCOPY OF VEGETABLE FOODS. John Wiley & Sons. New York.

ZIMMERMANN, K.
1936. ZUR PHYSIOLOGISCHEN ANATOMIE DER LEGUMINOSENTESTA. Landwirts. Versuchs-Stat. Vol. 127(1): 1–56.

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