The systematic significance of testa anatomy in the Leguminosae — an illustrated survey

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Seed from all three subfamilies of the Leguminosae was surveyed for anatomical features of the testa which could be used in the systematics of the family. An atlas of testa anatomy is presented, and the possible adaptive significance of certain seed structures is discussed. Seed of the Mimosoideae and Caesalpinioideae remain incompletely separated, but the shape of the micropyle constitutes a useful accessory character. In addition certain genera in these subfamilies have features which are anomalous in the family. Features of the micropyle, cuticle and light line typically characterize the papilionoid seed, but the only characters invariably restricted to this subfamily are hilar features traditionally recognized as such. However, testa anatomy is very useful within the Papilionoideae and certain tribes or groups of phylogenetically related tribes can be recognized by various features of the testa, particularly cuticle sculpturing and micropyle shape. Similarities between mimosoid and caesalpinioid seeds are plesiomorphous, and cannot necessarily imply greater phylogenetic relationship. The occurrence of a direct relationship between epidermal and hypodermal thickness in papilionoid seed suggests an early stabilization of this adaptive structure.

Saad van al drie subfamilies van die Leguminosae is vir anatomiese kenmerke van die saadhuid ondersoek vir moontlike gebruik in die sistematiek van die familie. 'n Atlas van saadhuid-anatomie word aangebied en die moontlike beduidenis van aanpassing van sekere strukture word bespreek. Saad van die Mimosoideae en Caesalpinioideae is nie geredelik onderskeibaar nie. Die vorm van die mikropiel is egter 'n waardevolle kriterium. Daar is ook gevind dat sekere genera in hierdie subfamilies eienskappe besit wat afwyk van familiekenmerke. Eienskappe van die mirkopiel, kutikula en liglyn karaktriseer die papilionoiede-saad, maar die enigste kenmerke wat sonder uitsondering tot hierdie subfamilie beperk is, is daardie eienskappe van die hilum wat reeds bekend is. Saadhuid-anatomie is baie bruikbaar ten opsigte van die Papilionoideae en sekere tribusse of groepe van filogeneties-verwante tribusse kan herken word aan sekere saadhuid-kenmerke, veral die patroon van die kutikula en die mikropiel. Ooreenkomste tussen mimosoïede- en caesalpinioïede-sade is plesiomorfies en dui nie noodsaaklik 'n groter filogenetiese verwantskap aan nie. Die aanwesigheid van 'n direkte verwantskap tussen die dikte van die epidermale en hipodermale lae van die papilionoïede-saad dui op 'n vroeë stabilisering van hierdie aanpassingstruktuur.

Keywords: Anatomy, Leguminosae, seed, systematics, testa

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Introduction

Characters of the seed and embryo have figured prominently in the subdivision of the family Leguminosae since the early endeavour in this regard by De Candolle (1825). Seed anatomy has consistently been most successful in distinguishing two groups comprising the Caesalpinioideae – Mimosoideae and the Papilionoideae: in particular the orientation of the embryo and consequently seed symmetry, the nature of the hilum, and the extent of the testal vascularization (Corner 1951; Isely 1955; Kopooshian & Isely 1966; Gunn 1981). Seeds of the Mimosoideae and Caesalpinioideae cannot be separated save by the presence of an open, hippocrepiform fissure, the pleurogram, on the seed of many mimosoid genera; this is not invariable, however, and a closed pleurogram occurs in some Caesalpinioideae (Corner 1976; Gunn 1981). At lower taxonomic levels, however, numerous features of the seed have been cited as of systematic or diagnostic import.

These studies are largely restricted in extent; very few are concerned with taxa in the Caesalpinioideae and Mimosoideae; few provide direct evidence of the utility of testal characters at generic or higher levels; and none provide accessory characters aiding in the separation of the subfamilies. This study is a survey of testa morphology throughout the family in an attempt to reveal further seed characters which are important in the evolution of the subfamilies and which can be used to distinguish them; to check the taxonomic distribution of some; and to define those characters which are

likely to be of most use in the systematics of the family at all levels of the taxonomic hierarchy. It also constitutes an atlas of the seed structure of many African species hitherto uninvestigated.

Materials and Methods

Mature seeds were collected from plants in the field, or obtained from the Kirstenbosch and Durban Botanic Gardens. Species that produce neotenous or overgrown seeds were not considered: such seeds have an undifferentiated testa of structure that is anomalous within the family. Seeds were frozen in liquid nitrogen, and fractured with a sharp blade. Fractured seed segments were mounted on brass stubs with silver or graphite colloidal paste, sputter-coated with gold-palladium and viewed in a Jeol T200 scanning electron microscope. At least five seeds of each species were examined, but little variation was encountered within a collection.

The surface of the testa was examined in the circumhilar region where it attains maximum development: away from the hilum the pattern becomes attenuated and obliterated, most noticeably in seeds of the Papilionoideae. Terminology used for hilum shape is that of Lersten & Gunn (1982), and for testal sculpturing that of Lersten (1981). A list of all species that were examined, together with their character states and a list of the characters that were codified are included as Appendices.
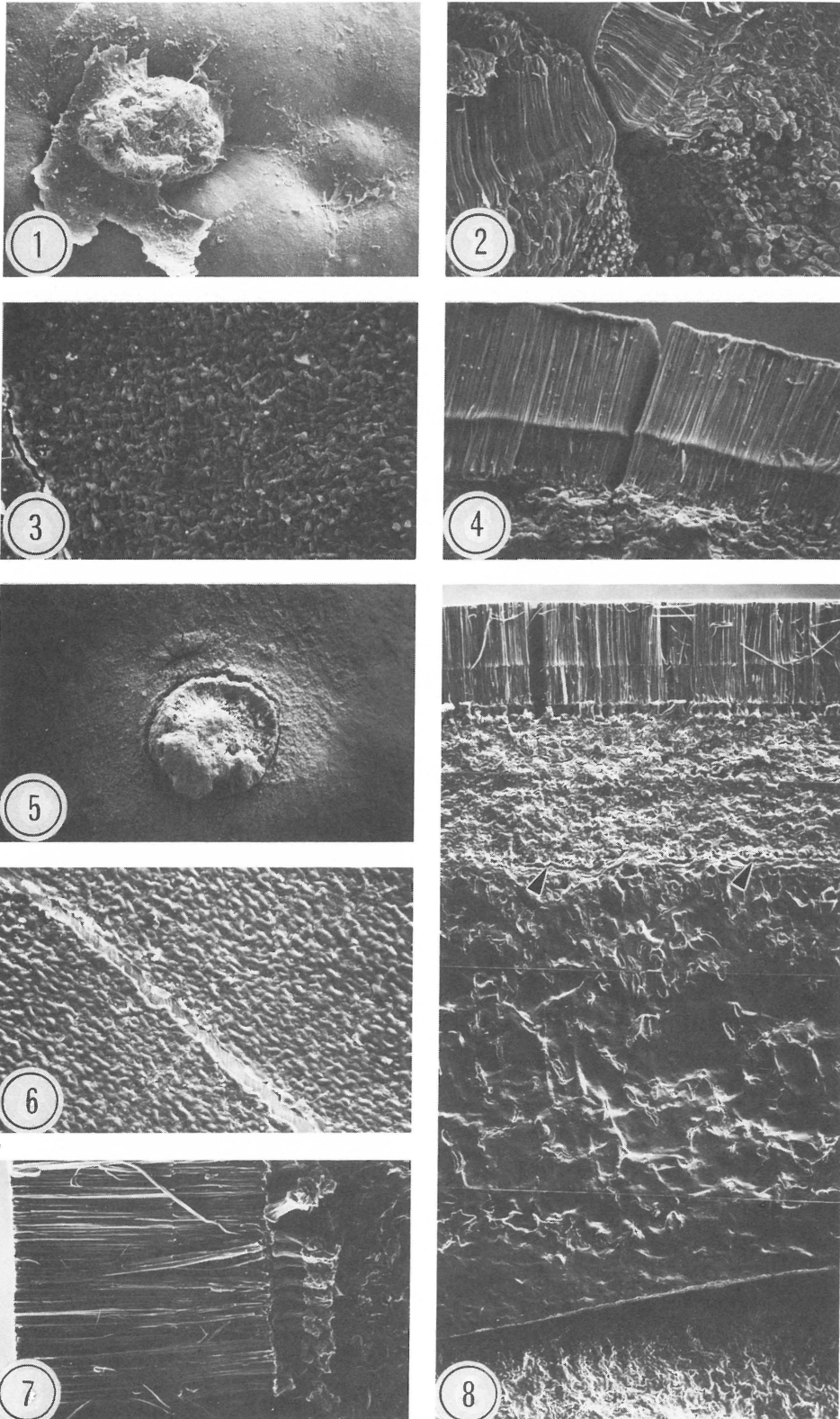
Results

Caesalpinioideae

Genera examined

Caesalpinia, Cassia, Delonix, Parkinsonia, Peltophorum, Schotia, Tamarindus.

Characters examined

1. *Pleurogram*: present in *Tamarindus* only, closed with ovoid areole;

2. *Fracture lines*: present in all species examined. The fracture lines penetrate the epidermis completely in most genera

Figures 1 – 4 *Caesalpinea decapetala*. **1.** Hilum and lens, ×40; **2.** L/S micropyle, ×120; **3.** Testa surface, ×500; **4.** Testa with fracture line, ×200. **Figures 5 – 8** *Delonix regia*. **5.** Hilum and micropyle, ×250; Testa surface with fracture line, ×250; **7.** Testa, ×200; **8.** Testa and endosperm: inner hourglass cells arrowed, ×80.

(Figures 4, 8, 16 & 20), but reach only to the light line or a little beyond in *Parkinsonia* and *Schotia*;

3. *Hilum*: usually circular (Figures 1, 5, 9, 13, 17 & 21) but oval in *Schotia brachypetala* (Figure 25), and of simple structure. The hilum is invariably larger than the micropyle. The funicle does not abscise cleanly from the seed in any of the species examined, and the hilar surface is consequently jagged;

4. *Micropyle*: immediately adjacent to the hilum and invisible in *Caesalpinia* (Figures 1 & 2) and *Schotia* (Figures 21 & 25), but in other genera near the hilum and visible. In the latter instances, at least, the micropyle is bordered with a striated rim although not obvious in *Cassia* (Figure 18). The micropyle is punctate in *Cassia* (Figure 18) and probably *Schotia*, a short transverse slit in *Caesalpinia* (Figure 2), *Delonix* (Figure 5) and *Parkinsonia* (Figure 9) and ypsiloid in *Peltophorum* (Figure 13);

5. *Cuticular sculpturing*: usually rugose (Figures 3, 10, 15 &

22) but modified in the following instances: in *Tamarindus* (Figure 29) the pattern appears multi-reticulate; in *Schotia brachypetala* (Figure 26) the cuticle is papillate; and in *Cassia* (Figure 19) the cuticle is near laevigate. The cuticle ranges from 1 – 5 μm in thickness;

6. *Epidermis*: consists of palisade sclereids (Figures 4, 7, 11, 16, 20, 23, 27 & 28). Epidermal thickness ranges from 43 μm in *Cassia* to 235 μm in *Schotia afra*. The tips of the epidermal cells are less rigid [the 'mucilage stratum' of Corner (1951)] in *Cassia floribunda*, a species with a relatively thick cuticle (Figure 20);

7. *Light line*: present in all species examined and situated near medially in the epidermis;

8. *Hypodermis*: differentiated from the underlying parenchyma into hourglass cells in all taxa (Figures 7, 11, 16, 20, 24, 27 & 28) except *Caesalpinia* (Figure 4). *Schotia* is unusual in possessing markedly tuberculate hypodermal and outer parenchyma cells, particularly near the hilum (Figures 24 &
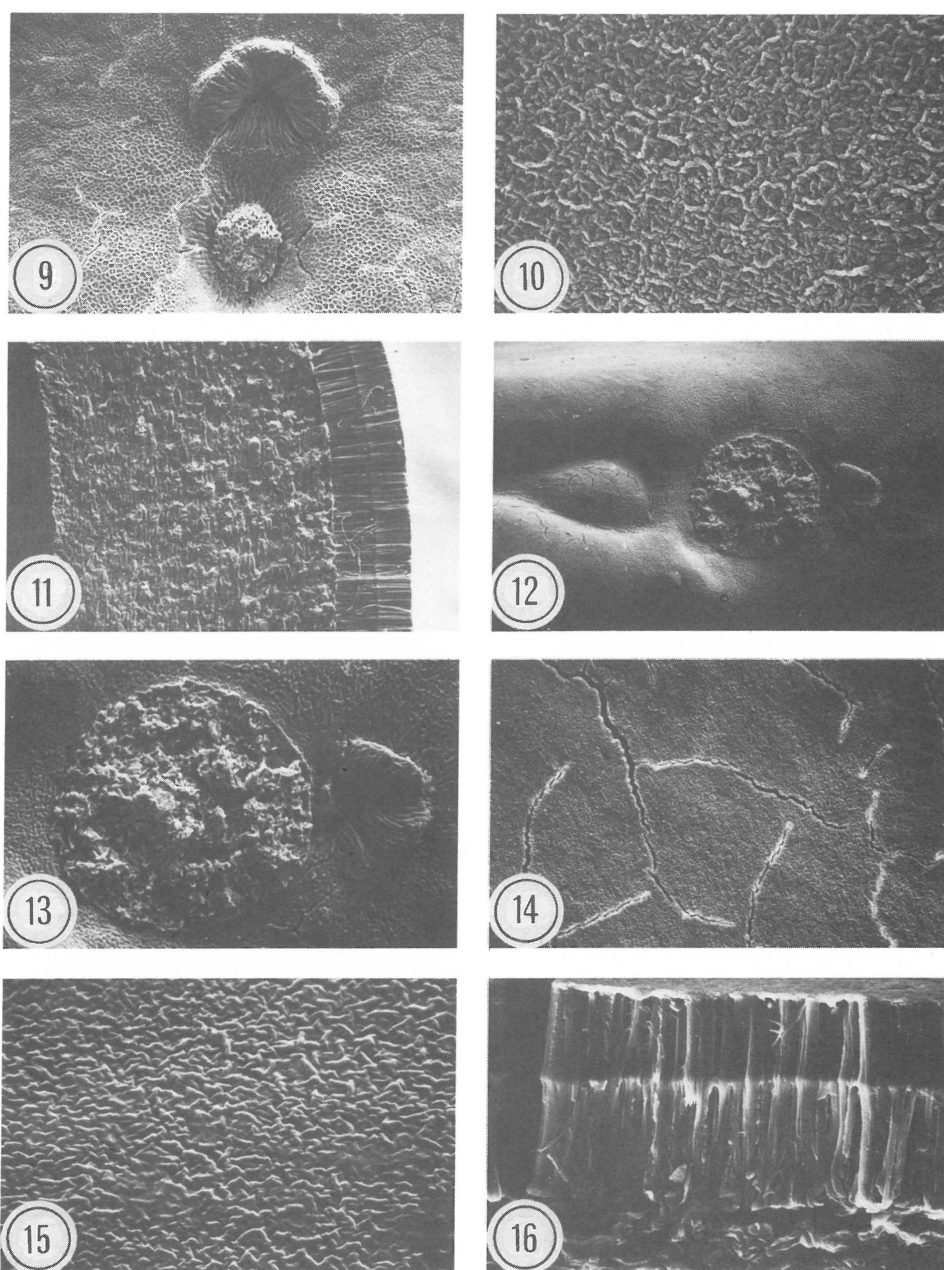
Figures 9 – 11 *Parkinsonia aculeata*. **9.** Hilum and micropyle, ×90; **10.** Testa surface, ×600; **11.** Testa, ×100. **Figures 12 – 16** *Peltophorum africanum*. **12.** Lens, hilum and micropyle, ×60; **13.** Hilum and micropyle, ×100; **14.** Testa surface with fracture lines, ×200; **15.** Testa surface, ×600; **16.** Testa, ×600.

27). Hypodermal cells range in length from 8 μm in *Cassia* to 35 μm in *Delonix* and *Schotia brachypetala*. The thickness of hypodermal and epidermal layers is not related directly, and there is a rapid increase in epidermal thickness in relation to increasing hypodermal thickness (Figure 169A).

9. *Parenchyma*: number of cell layers highly variable. There are few layers of parenchyma in *Tamarindus* (Figure 28), but very many in *Delonix* (Figure 8) and *Parkinsonia* (Figure 11);

10. *Inner hourglass cells*: present in *Delonix* (Figure 8) and *Schotia* (Figure 27). In *Schotia* the cells are well-developed and tuberculate like the hypodermis;

11. *Lens*: present in all species examined. The lens is obvious in *Caesalpinia* (Figure 1) and *Peltophorum* (Figure 12), but insignificant in *Schotia* (Figure 25). The lens is typically a small ovoid protruberance covered with a cuticle which is distinctly sculptured in a regular, substrate pattern. In *Cassia* (Figure 17) the hilum and lens are located in a panduriform depression.

Mimosoideae

Genera examined

Acacia, Albizia, Calliandra, Dichrostachys, Entada.

Characters examined

1. *Pleurogram*: present in all genera examined except *Albizia*. The pleurogram, when present, is open and extends to the hilum, penetrating the epidermis completely (Figures 33, 40, 43, 44, 49 & 53).

2. *Fracture lines*: present in all species examined. Fracture lines may penetrate only the cuticle, especially in those species with a thick cuticle: *Acacia cyclops* (Figure 44), *A. longifolia* (Figure 40) and *Entada spicata* (Figure 36); or they may penetrate partly through the epidermis, often to the light line: *Calliandra surinamense* (Figure 53), *Acacia farnesiana* (Figure 47) and *Albizia adianthifolia* (Figure 50); or in the latter two genera also weakly entirely through the epidermis;
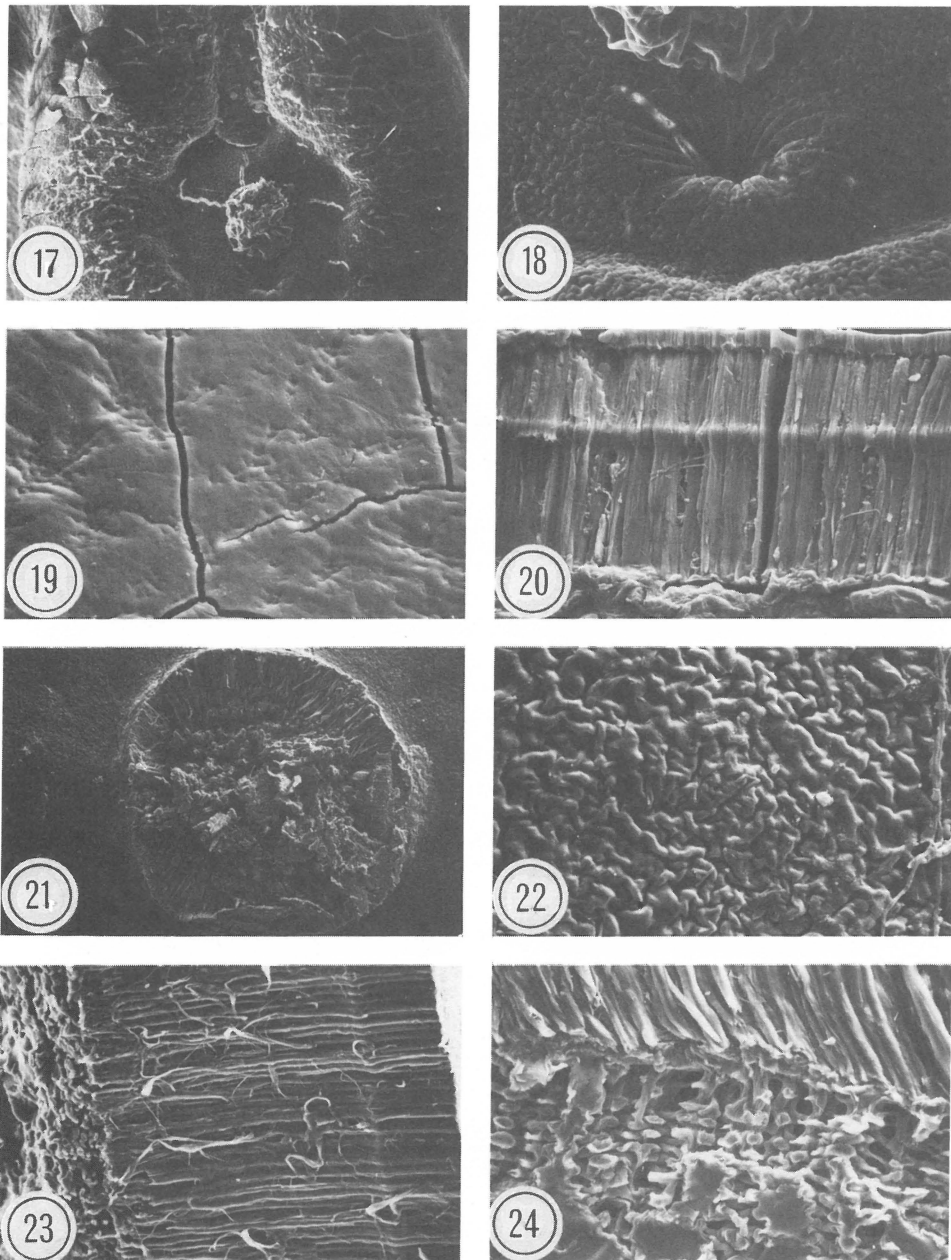
Figures 17–20 *Cassia floribunda*. **17.** Lens, hilum and micropyle, ×100; **18.** Micropyle, ×250; **19.** Testa surface with fracture lines, ×400; **20.** Testa with fracture line, ×600. **Figures 21–23** *Schotia afra*. **21.** Hilum, ×40; **22.** Testa surface, ×100; **23.** Testa, ×200. **Figure 24** *Schotia brachypetala*. **24.** Hypodermis, ×250.

3. *Hilum*: circular (Figures 30, 37 & 45) or oval (Figures 35, 41, 48 & 51), and of simple structure. The size of the hilum relative to that of the micropyle varies: in *Acacia cyclops* (Figure 41), *A. longifolia* (Figure 37) and *Calliandra* (Figure 51) the hilum is far larger than the micropyle, while in *A. farnesiana* (Figure 45), *Albizia* (Figure 48), *Dichrostachys* (Figure 30) and *Entada* (Figure 35) it is not substantially so. In most species the funicle is irregularly broken at the seed, leaving a jagged hilar stub, but in *Acacia cyclops* (Figure 37) and *A. longifolia* (Figure 41) the abscission is more regular;

4. *Micropyle*: abutting against the hilum. The micropyle is almost invariably slit-like and bordered with a striated rim. In nearly all species examined the slit runs along the anti-raphe (Figures 30, 35, 37, 48 & 51), but in *Acacia farnesiana* (Figure 45) it is crescentic about the hilum. This condition occurs also in the caesalpinioid genus *Delonix* (Figure 5);

5. *Cuticular sculpturing*: rugose in all species with a cuticle up to 2,5 µm thick (Figures 31, 46 & 52) but laevigate in species with a cuticle 12 µm thick or thicker (Figures 35, 39, 43 & 49). There is great interspecific variation in the thickness of the cuticle: it is thin (1 – 2,5 µm) in *Dichrostachys* (Figure 32), *Calliandra* (Figure 53) and *Acacia farnesiana* (Figure 47),

but very thick (12 – 40 µm) in *A. cyclops* (Figure 44), *A. longifolia* (Figure 40), *Entada* (Figure 36) and *Albizia* (Figure 50). No stratification of the cuticle is visible;

6. *Epidermis*: consists of palisade sclereids (Figures 32, 36, 40, 44, 47, 50 & 53). Epidermal thickness ranges from 25 µm in *Acacia cyclops* to 192 µm in *A. farnesiana*. The species with a cuticle greater than 10 µm thick (*Albizia adianthifolia*, *Acacia cyclops*, *A. longifolia* and *Entada spicata*) have an epidermis which is amongst the thinnest (*c.* 60 µm) in the family. In these species the epidermal cells protrude as cones a little into the cuticle and the tips are less rigid;

7. *Light line*: present in all species examined and situated near medially in the epidermis of all species except *A. cyclops* and *A. longifolia* in which it occurs in the apical third of the epidermal cells (Figures 32, 36, 40, 44, 47, 50 & 53);

8. *Hypodermis*: differentiated from the underlying parenchyma into hourglass cells in all species (Figures 32, 36, 40, 44 & 53) except *Acacia farnesiana* (Figure 47). Hypodermal cells are commonly 10 – 20 µm long, but up to 26 µm long in *Entada*. The thickness of hypodermal and epidermal layers is not directly related (Figure 169A);

9. *Parenchyma*: Number of cell layers usually few, but many
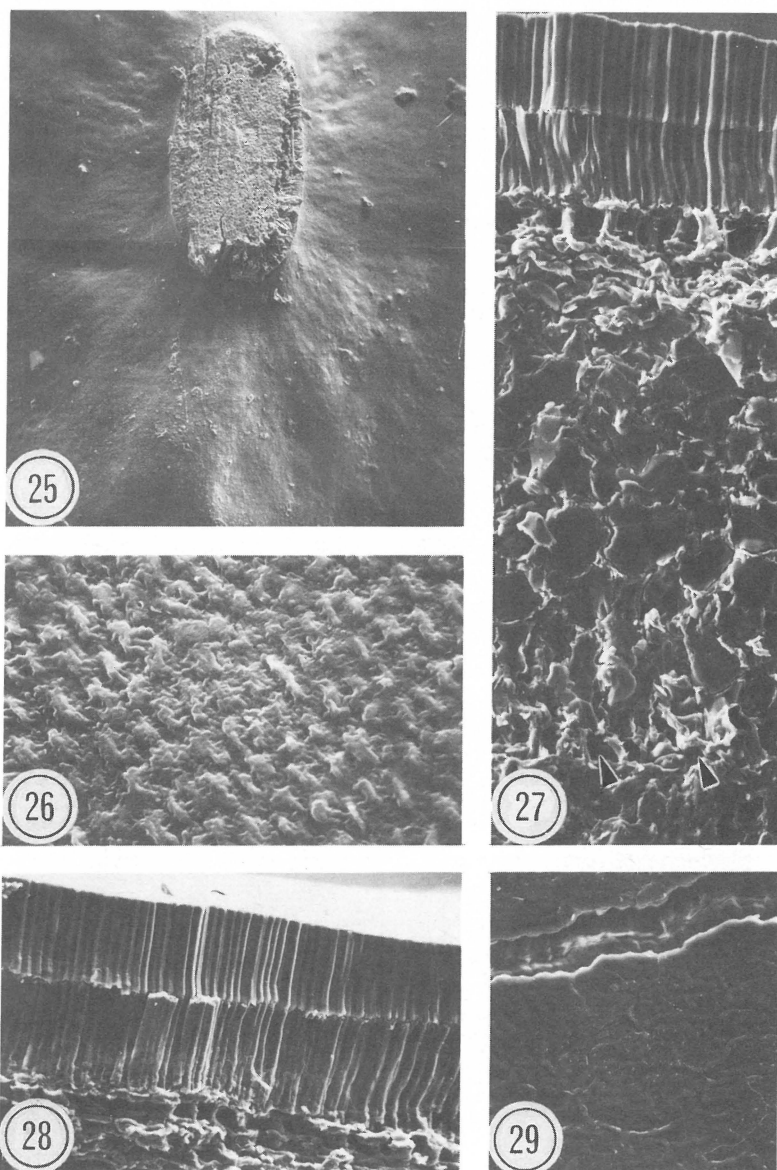
Figures 25 – 27 *Schotia brachypetala*. **25.** Hilum and lens, ×30; **26.** Testa surface, ×600; **27.** Testa: inner hourglass cells arrowed, ×200.
Figures 28 – 29 *Tamarindus indica*. **28.** Testa, ×600; **29.** Testa surface with fracture line, ×400.

in *Acacia farnesiana*;

10. *Inner hourglass cells*: present only in *Entada* (Figure 36);

11. *Lens*: present in all species examined. The lens is insignificant in *Acacia cyclops* (Figure 41) and *A. longifolia* (Figure 37), visible in *Dichrostachys* (Figure 34) and *Entada* (Figure 35) and very obvious in *Calliandra* (Figure 51). The lens is typically a small ovoid protruberance but it is flattened in *Entada*, and in *Calliandra* is surrounded by a tuberculate rim. In all species the lens is covered with a thin cuticle that is distinctly sculptured in a regular, substriate pattern.

Papilionoideae

Genera examined

Abrus, Argyrolobium, Calpurnia, Crotalaria, Dalbergia, Desmodium, Dipogon, Erythrina, Glycine, Indigofera, Lablab, Liparia, Medicago, Milletia, Mundulea, Podalyria, Psoralea, Sophora, Sesbania, Sutherlandia, Virgilia.

Characters examined

1. *Pleurogram*: absent;

2. *Fracture lines*: absent;

3. *Hilum*: variable in shape from almost circular in *Medicago* (Figure 136) to linear in *Lablab* (Figure 113), usually ovate to oblong (Figures 54, 65, 71, 78, 84, 90, 102, 108, 118, 124, 130, 148, 154 & 163). The hilum is characterized by a clean abscission surface more or less flush with the seed and which is penetrated medially by a hilar fissure. Abscission of the seed occurs at the tip of the funicle such that a single layer of funicular cells remains adnate to the hilar palisade as the counter-palisade. A counter palisade is absent only in *Erythrina* (Figure 128). The surface of the hilum is obscured by funicular remains constituting an epihilum in *Dipogon* (Figure 108) and *Lablab* (Figure 113) (tribe Phaseoleae:Phaseolineae). Other funicular remnants are present as a rim-aril. This is well-developed in *Milletia* (Figures 78 & 80), *Liparia* and *Podalyria* (Figure 148), present in most other genera in a less-developed state (Figures 54, 65, 84, 102, 108, 113, 118, 124, 130, 136, 154 & 163), as a rudiment in *Indigofera* (Figure 96) and *Sesbania* (Figure 90) and absent in *Abrus* (Figure 71) and *Sophora* (Figure 62). A hilar tongue or flap is present in *Dipogon, Erythrina, Glycine* (tribe Phaseoleae) and *Argyrolobium* (tribe Crotalarieae);

4. *Micropyle*: always minute in relation to the hilum and of three basic forms: an ypsiloid fissure with the fork directed towards the hilum and the stem along the antiraphe; a more or less deltoid fissure; and a punctate aperture. The micropyle is never bordered by a cuticular rim. The ypsiloid micropyle is invariably separate from the hilum and distanced from it;
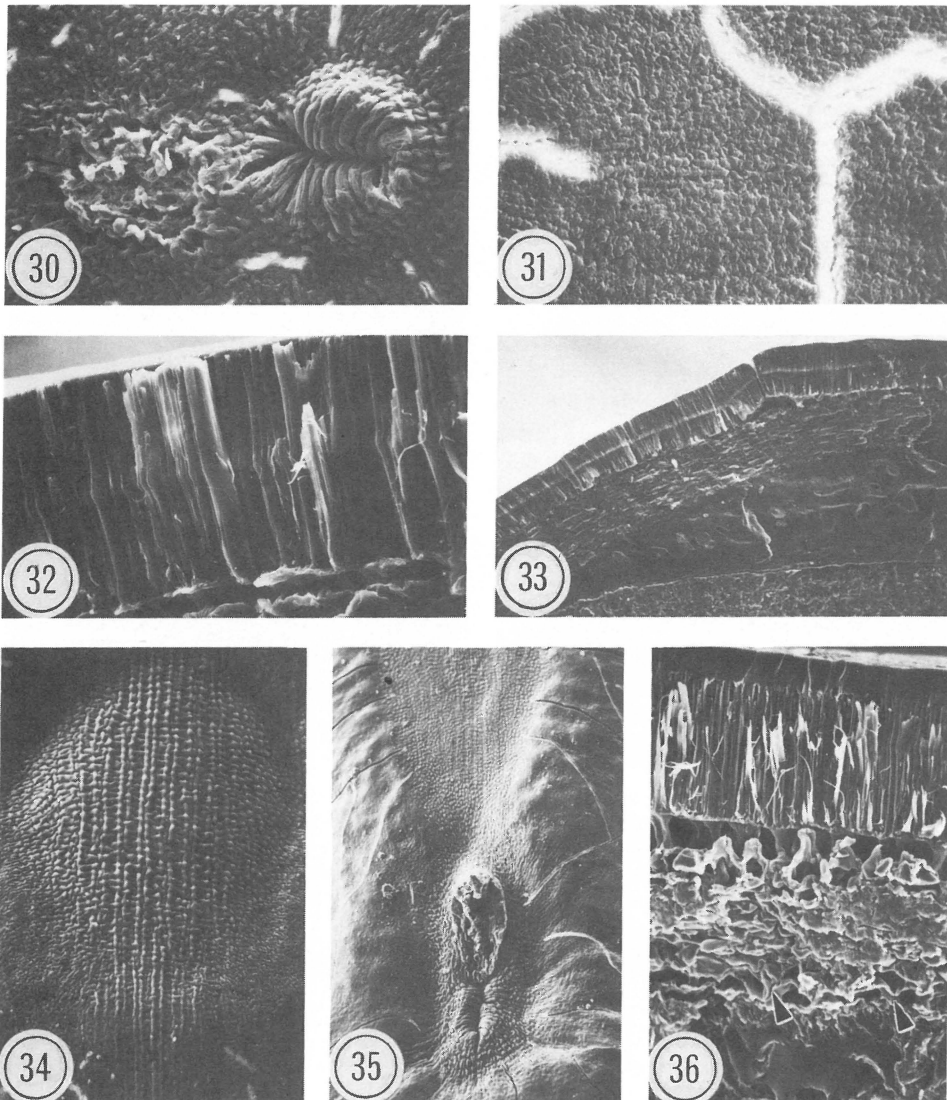
Figures 30 – 34 *Dichrostachys cinerea*. **30.** Hilum and micropyle, ×250; **31.** Testa surface with fracture lines, ×900. **32.** Testa, ×400; **33.** Testa at pleurogram, ×90; **34.** Lens, ×200. **Figures 35 – 36** *Entada spicata*. **35.** Lens, hilum and micropyle, ×100; **36.** Testa, ×250.

the deltoid micropyle is situated on the margin of the hilum; and the punctate micropyle is usually enclosed by the hilum. An intermediate state occurs in *Medicago* (tribe Trifolieae) (Figure 144) and *Sutherlandia* (tribe Galegeae) (Figure 136) in which a punctate micropyle is not quite enclosed by hilar tissue.

An ypsiloid micropyle is present in the tribes Sophoreae: *Sophora* (Figure 60); Robinieae: *Sesbania* (Figure 90); Psoraleeae: *Psoralea* (Figure 131); Abreae: *Abrus* (Figure 72); Desmodieae: *Desmodium* (Figure 103); Tephrosieae: *Milletia* (Figure 79) and *Mundulea* (Figure 85); Dalbergieae: *Dalbergia* (Figure 66) and Phaseoleae: *Dipogon* (Figure 109), *Erythrina* (Figure 125), *Glycine* (Figure 119) and *Lablab* (Figure 114). A punctate micropyle is present in the tribes Sophoreae: *Calpurnia* (Figure 55); Galegeae: *Sutherlandia* (Figure 136); Trifolieae: *Medicago* (Figure 144); Podalyrieae: *Podalyria* (Figure 149) and *Virgilia* (Figure 155); Liparieae: *Liparia* and Crotalarieae *Argyrolobium* (Figure 164) and *Crotalaria*. In the Podalyrieae, Liparieae and Crotalarieae the micropyle is situated in a characteristic patch of tissue external to the rim aril. In *Abrus* (Abreae) and *Milletia* (Tephrosieae) the ypsiloid micropyle is modified, and the stem is unusually long and accompanied distally by infolding of the testa. The micropyle in *Mundulea* (Tephrosieae) has a similarly long stem, but with only slight folds;

5. *Cuticular sculpturing*: a near laevigate cuticle occurs only in *Crotalaria grantiana* which, in addition to a cuticle that is thicker than usual within the subfamily, has a very uniform and smooth epidermal surface (Figure 160). In all other species examined the cuticle is sculptured, most usually in a rugose (Figures 58, 63, 68, 91, 98 & 115) or reticulate (Figures 81, 86, 104, 150, 156 & 165) pattern, less commonly in a foveolate (Figures 137, 138, 142 & 145) or papillose (Figures 73, 126, 110, 144 & 133) pattern. Unusual patterns occur in *Dipogon* (Figure 110) which has a papillose cuticle overlain with a fine reticulum; and in *Argyrolobium* (Figure 165),
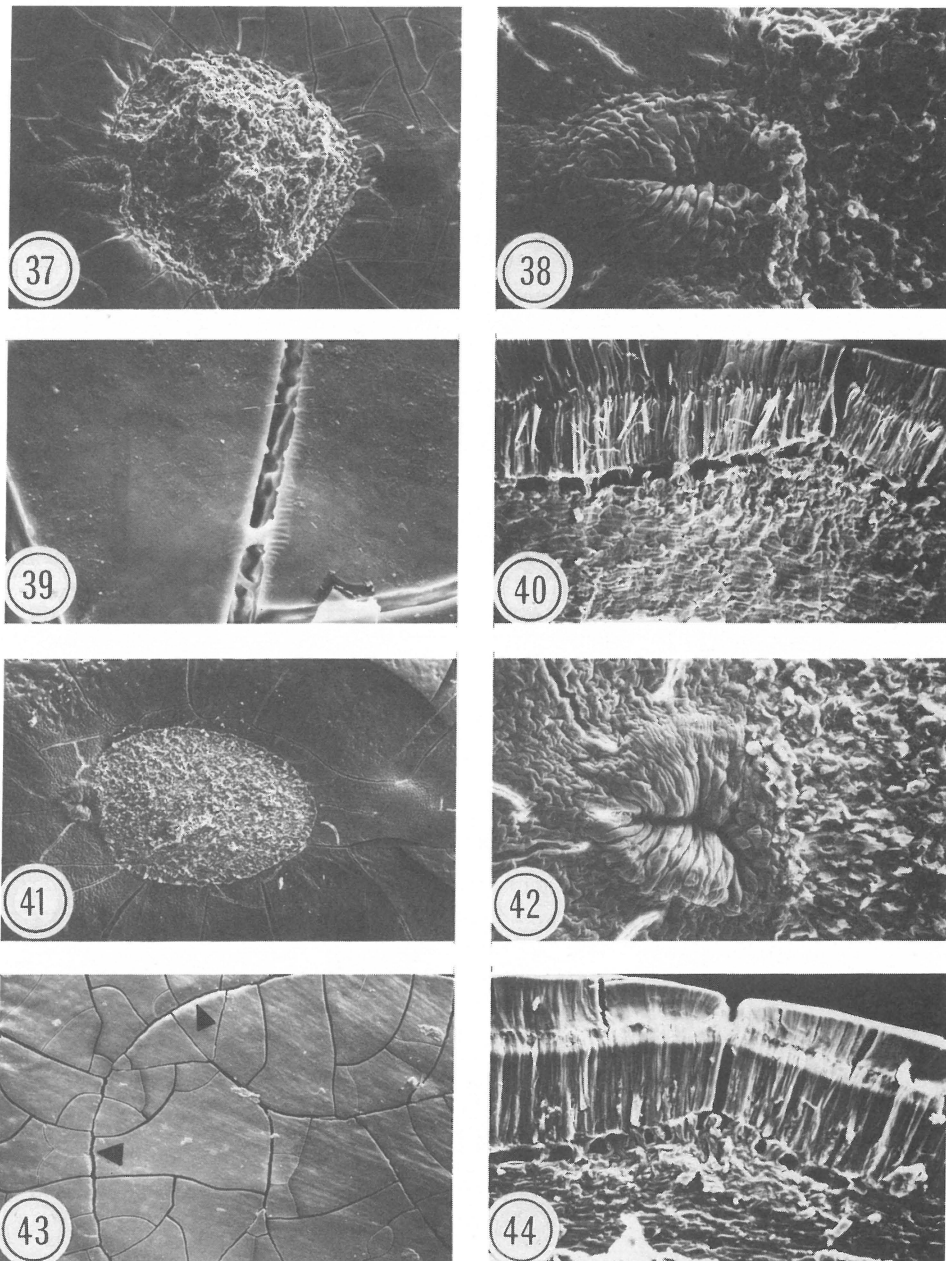
Figures 37 – 40 *Acacia longifolia*. **37.** Lens, hilum and micropyle, ×90; **38.** Micropyle, ×260; **39.** Testa with fracture lines, ×600; **40.** Testa at pleurogram, ×260. **Figures 41 – 44** *Acacia cyclops*. **41.** Lens, hilum and micropyle, ×60; **42.** Micropyle, ×260; **43.** Testa surface with pleurogram (arrowed) and fracture lines, ×60; **44.** Testa at pleurogram, ×200.

Desmodium (Figure 104) and *Glycine* (Figure 120) which have a cuticle with a very rectangular multi-reticulum. The cuticle is usually 0,25 – 3 μm thick, rarely up to 4 μm in *Crotalaria, Glycine* and *Lablab*;

6. *Epidermis*: consists of palisade sclereids (Figures 56, 61, 67, 82, 87, 93, 100, 105, 121, 128, 132, 139, 146, 151, 157, 161 & 167). The epidermis is commonly 50 – 120 μm thick, but ranges in thickness from 31 μm in *Medicago* to 205 μm in *Erythrina*. The outer tangential faces of the cells may be flattened and closely appressed, as in *Crotalaria* (Figure 160), but in *Medicago* (Figure 144), *Sutherlandia* (Figure 138) and *Lessertia* (Figure 142) there is apparently an alteration in wall chemistry and the outer ends of the cells are distorted and separate. A foveolate/papillose testal pattern is the result. The chemical changes associated with a foveolate testa appear to render the cell walls less rigid, resulting in an apparent 'mucilage-stratum'. Consequently this feature is present only in *Medicago, Sutherlandia* and, weakly so, in *Lessertia*. In
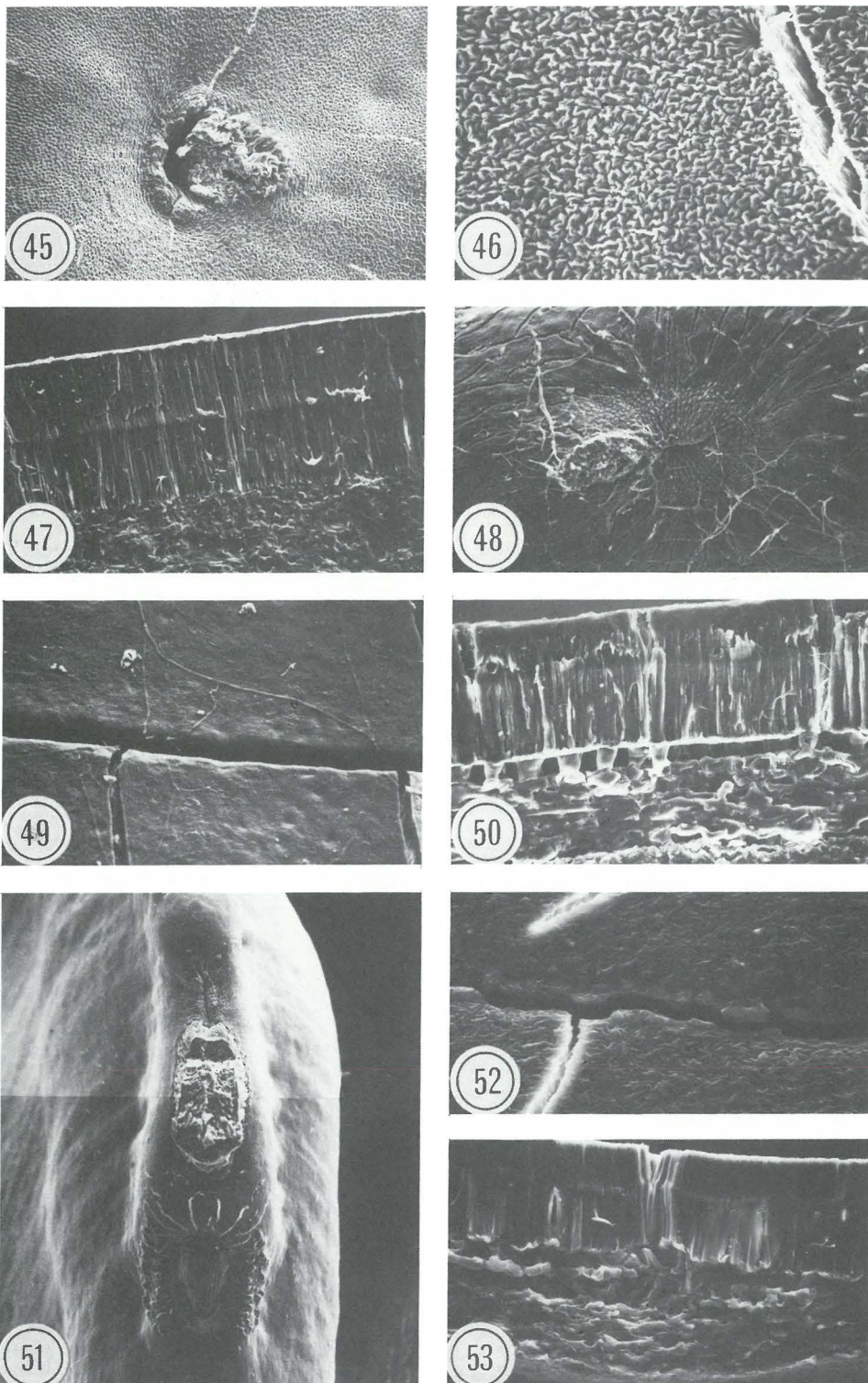

Figure 45 – 47 *Acacia farnesiana*. **45.** Hilum and micropyle, ×100; **46.** Testa surface with fracture line, ×600; **47.** Testa, ×120. **Figures 48 – 50** *Albizia adianthifolia*. **48.** Hilum and micropyle, ×120; **49.** Testa surface with fracture lines, ×250; **50.** Testa at fracture lines, ×260; **Figures 51 – 53** *Calliandra surinamense*. **51.** Lens, hilum and micropyle, ×55; **52.** Testa surface with pleurogram and fracture lines, ×800; **53.** Testa at pleurogram, ×400.

Sutherlandia abrupt changes in the length of the epidermal cells are responsible for the undulate testa;

7. *Light line*: not visible in most species, but when visible occurring in the apical fourth of the epidermal cells immediately beneath the cuticle;

8. *Hypodermis*: differentiated from the underlying parenchyma into hourglass cells in all species. The length of the hypodermal cells increases in the circumhilar region, sometimes markedly so. The hypodermal cells are papillate in *Abrus* (tribe Abreae) (Figure 75) and *Millettia* (tribe Tephrosieae) (Figure 82), especially near the hilum where the cells are exceptionally slender and elongate. Hypodermal cells range in length from 10 – 40 μm (rarely to 63 μm in *Sesbania*), but may be as long as 90 μm at the hilum. The thickness of the epidermis is related directly to that of the hypodermis through the function $y = 3,5x + 15,4$; $r = 0,8$; $p = 0,00022$ (Figure 169B) where y = thickness of the epidermis and x = thickness of the hypodermis.

9. *Parenchyma*: layers few and much compressed in all species, but somewhat less so in *Dalbergia* (Figure 67), *Desmodium* (Figure 105) and *Erythrina* (Figure 128);

10. *Inner hourglass cells*: absent;

11. *Lens*: present in all species;

12. *Hilar aerenchyma*: present as a ring surrounding the tracheid bar. This zone of tissue may be well-developed, as in *Abrus* (Figure 74) and *Dalbergia* (Figure 69), or much reduced, as in *Glycine* (Figure 122). One or more rows of aerenchyma immediately beneath the hypodermis may become similarly differentiated into hourglass cells resembling those of the hypodermis. The following categories can be recognized: hypodermis weakly differentiated from the underlying parenchyma at the hilum, in *Abrus* (Figure 74) and *Mundulea* (Figure 88); hypodermis differentiated at the hilum, in most species (Figures 57, 62, 69, 80, 88, 92, 106, 122, 140, 153 & 159); hypodermis differentiated with an additional row of hourglass cells derived from the aerenchyma, in *Indigofera*
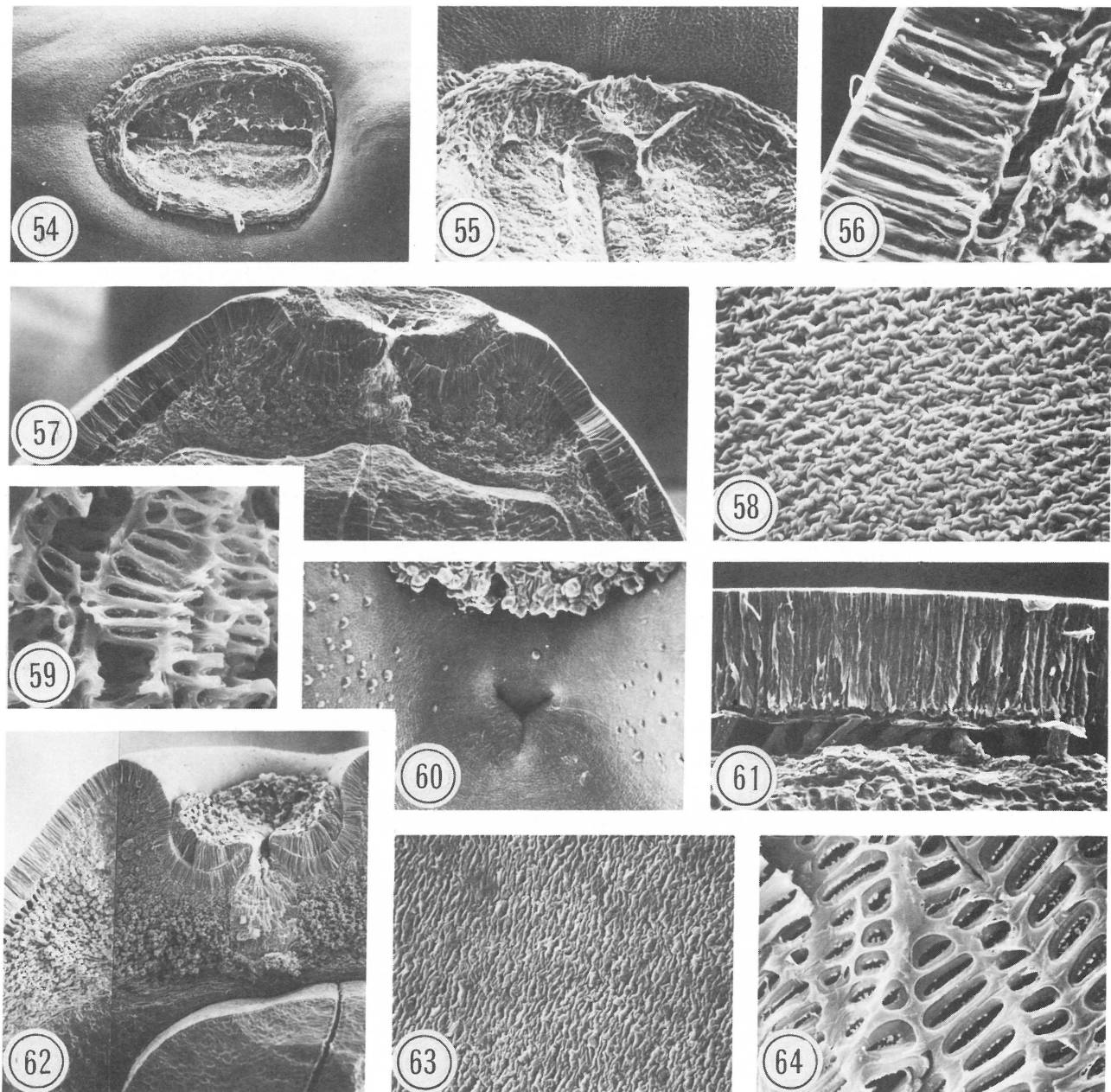
Figures 54 – 59 *Calpurnia aurea*. **54.** Hilum and micropyle, ×40; **55.** Micropyle, ×100; **56.** Testa, ×260; **57.** Hilar region, ×50; **58.** Testa surface, ×600; **59.** Tracheoid pits, ×1000. **Figures 60 – 64** *Sophora japonica*. **60.** Micropyle, ×75; **61.** Testa, ×100; **62.** Hilar region, ×26; **63.** Testa surface, ×500; **64.** Tracheoid pits, ×1500.

(Figure 99) and *Psoralea* (Figure 134); hypodermis differentiated with more than one row of hourglass cells derived from the aerenchyma, in *Dipogon* (Figure 111), *Erythrina* (Figure 128), *Lablab* (Figure 116) (tribe Phaseoleae) and *Argyrolobium* (Figure 166) (tribe Crotalarieae). Multiple layers of circum-hilar hourglass cells are thus largely characteristic of genera in the Phaseoleae;

13. *Tracheid bar*: present in all species. The tracheoids are anticlinally oriented;

14. *Tracheoid pits*: commonly ovoid in shape, but elongate in *Dalbergia* (Figure 70), *Sutherlandia* (Figure 141) and *Lessertia* (Figure 143). In the latter two genera the secondary wall is not deposited uniformly about the pits but in more or less irregular, rather unoriented strips. This unusual conformation seems restricted to genera in the Galegeae. The pits may be regularly arranged in opposite rows, as in *Dipogon*
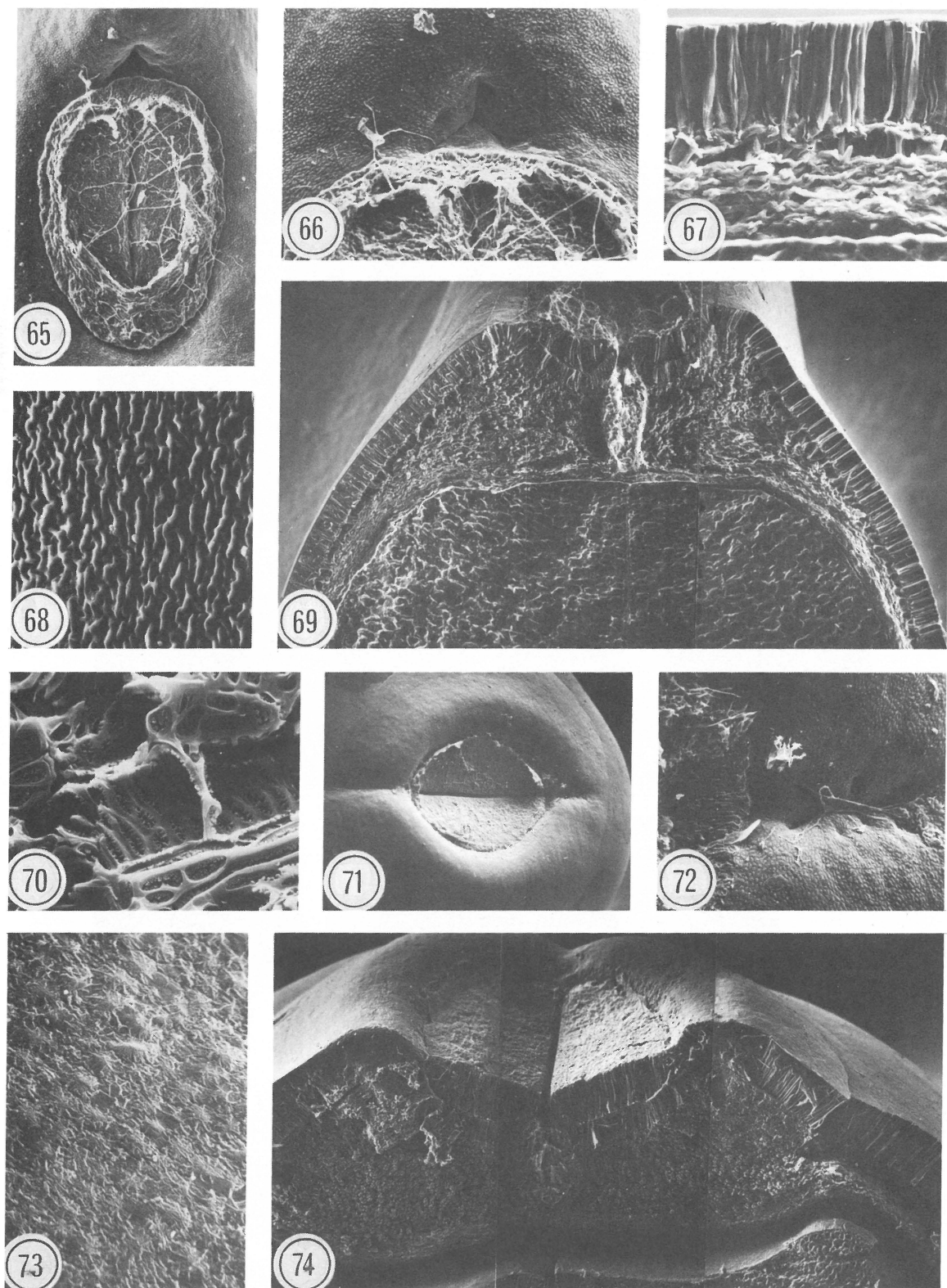

Figures 65 – 70 *Dalbergia obovata*. 65. Hilum and micropyle, ×60; 66. Micropyle, ×120; 67. Testa, ×250; 68. Testa surface, ×500; 69. Hilar region, ×50; 70. Tracheoid pits, ×1200. Figures 71 – 74 *Abrus precatorius*. Hilum and micropyle, ×20; 72. Micropyle, ×100; 73. Testa surface, ×500; 74. Hilar region, ×40.

(Figure 112), or they may be more or less alternately or irregularly disposed, as in *Lablab* (Figure 117) and *Psoralea* (Figure 135).

The primary pit wall may persist as a lacy membrane (Figure 77), or it may be torn or almost entirely absent (Figures 94 & 95). The secondary wall at the pit margin may be smooth (Figure 112), but in most instances all or some of the pits in a tracheoid exhibit, to a greater or less degree, elaboration of the secondary wall in the form of vestures. The vestures may be simple and warty (Figures 94 & 95), but are usually more extensively developed and branched (Figures 70 & 101), sometimes to the extent that they occlude the pit aperture (Figure 83). There may be variation in pit state within a species, individual or even a single tracheoid (Figures 94, 95 & 127). Tracheoid pits with well-developed vestures occur in the tribes Sophoreae (Figure 64), Tephrosieae (Figures 83 & 89), Dalbergieae (Figure 70), Crotalarieae (Figures 162 & 168), Indigofereae (Figure 101) and part of the Phaseoleae: *Erythrina* (Figure 127) and *Glycine* (Figure 117). Unvestured pits with the primary wall persisting as a lacy membrane occur in *Calpurnia* (tribe Sophoreae) (Figure 59) and *Abrus* (tribe Abreae) (Figure 77). Unvestured pits with the primary wall absent occur in the phylogenetically advanced tribes Trifolieae (Figure 147), Robinieae (Figure 94), Desmodieae (Figure 107), Liparieae, Podalyrieae (Figures 152 & 158) and the subtribe Phaseolineae of the Phaseoleae (Figures 112 & 117).
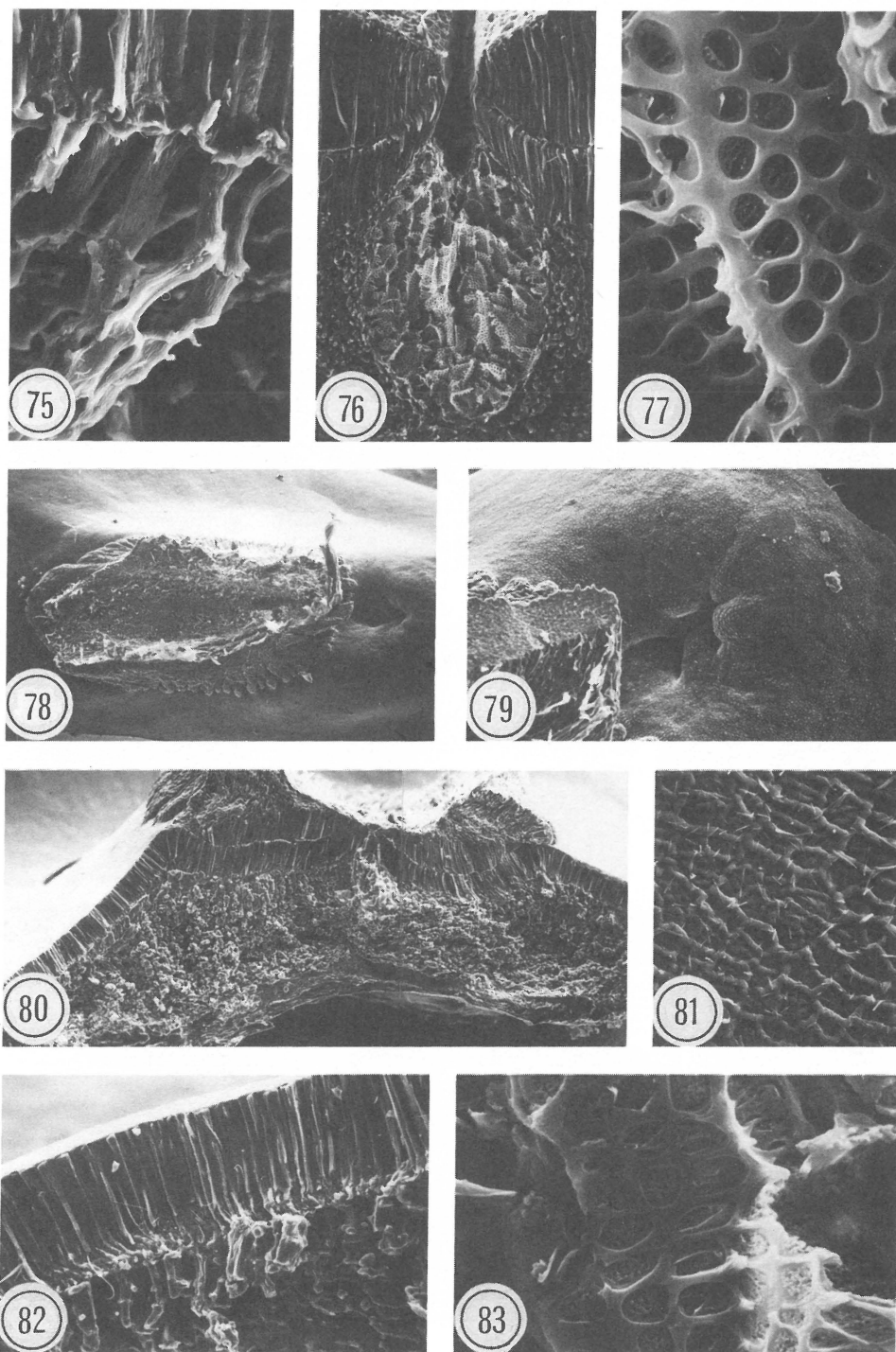
Figures 75 – 77 *Abrus precatorius.* **75.** Hypodermis near hilum, ×600; **76.** Tracheid bar, ×120; **77.** Tracheoid pits, ×2000. **Figures 78 – 83** *Millettia dura.* **78.** Hilum and micropyle, ×20; **79.** Micropyle, ×60; **80.** Hilum, ×40; **81.** Testa surface, ×400; **82.** Testa, ×200; **83.** Tracheoid pits, ×2000.

Discussion

The structure of the leguminous seed coat is remarkably consistent, and the following features of the mature testa characterize the family: an outermost epidermal palisade layer, usually with a light line; and a hypodermis differentiated, with few exceptions, into a layer of osteosclereids, and surmounting a zone of parenchyma which may be well-developed or reduced. The derivation of the testa from the outer integument alone of a bitegmic ovule is also invariable (Manning & Van Staden 1985, 1986). In certain species, however, there is a marked deviation from the typical. This is particularly obvious in those species with neotenous seeds in which the testa is quite undifferentiated (see Corner 1951), but certain caesalpinioid and mimosoid species have seeds in which the hypodermis is undifferentiated or the cuticle developed to an unusual degree. No fundamental differences exist between the seeds of the Caesalpinioideae and Mimosoideae, and they are similar in gross morphology, anatomy, and in the orientation of the embryo axis. However, a number of features of the seed separate these two subfamilies from the Papilionoideae, and structural and anatomical features of the seed of all three subfamilies are summarized in Table 1. The following features may with few exceptions be held to be primitive or plesiomorphous: anatropous ovule and straight embryo axis,
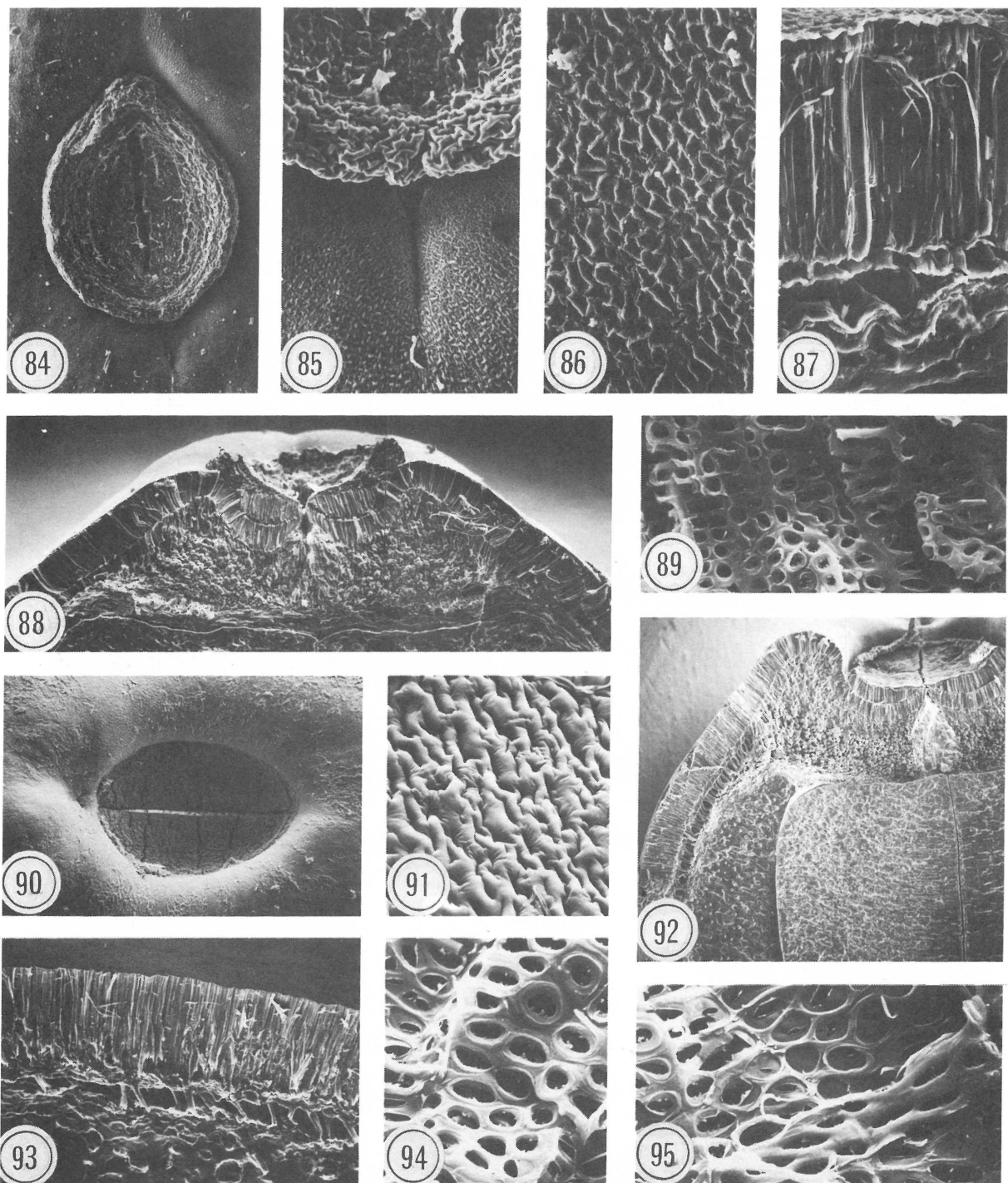
Figures 84 – 89 *Mundulea sericea*. **84.** Hilum and micropyle, ×50; **85.** Micropyle, ×200; **86.** Testa surface, ×500; **87.** Testa, ×400; **88.** Hilar region, ×50; **89.** Tracheoid pits, ×1000. **Figures 90 – 95** *Sesbania punicea*. **90.** Hilum and micropyle, ×30; **91.** Testa surface, ×500; **92.** Hilar region, ×30; **93.** Testa, ×100; **94.** Tracheoid pits, ×1000; **95.** Tracheoid pits, ×1000.

unbranched vascular trace extending almost completely around the seed and simple hilum (Isely 1955; Kopooshian & Isely 1966).

The presence of an open pleurogram in mimosoid seed and of a closed pleurogram in caesalpinioid seed is not invariable, and although useful, is not an absolute distinction between the subfamilies. The shape of the micropyle also is useful as a guide. Fracture lines occur in the testa of all mimosoid and caesalpinioid seeds and are apparently functional in seed dehydration (Trivedi *et al*. 1979). In the Mimosoideae the fracture lines penetrate usually only to the light line, but in the Caesalpinioideae complete penetration is usual. This apparent difference may relate to the more general occurrence of a pleurogram which penetrates completely through the
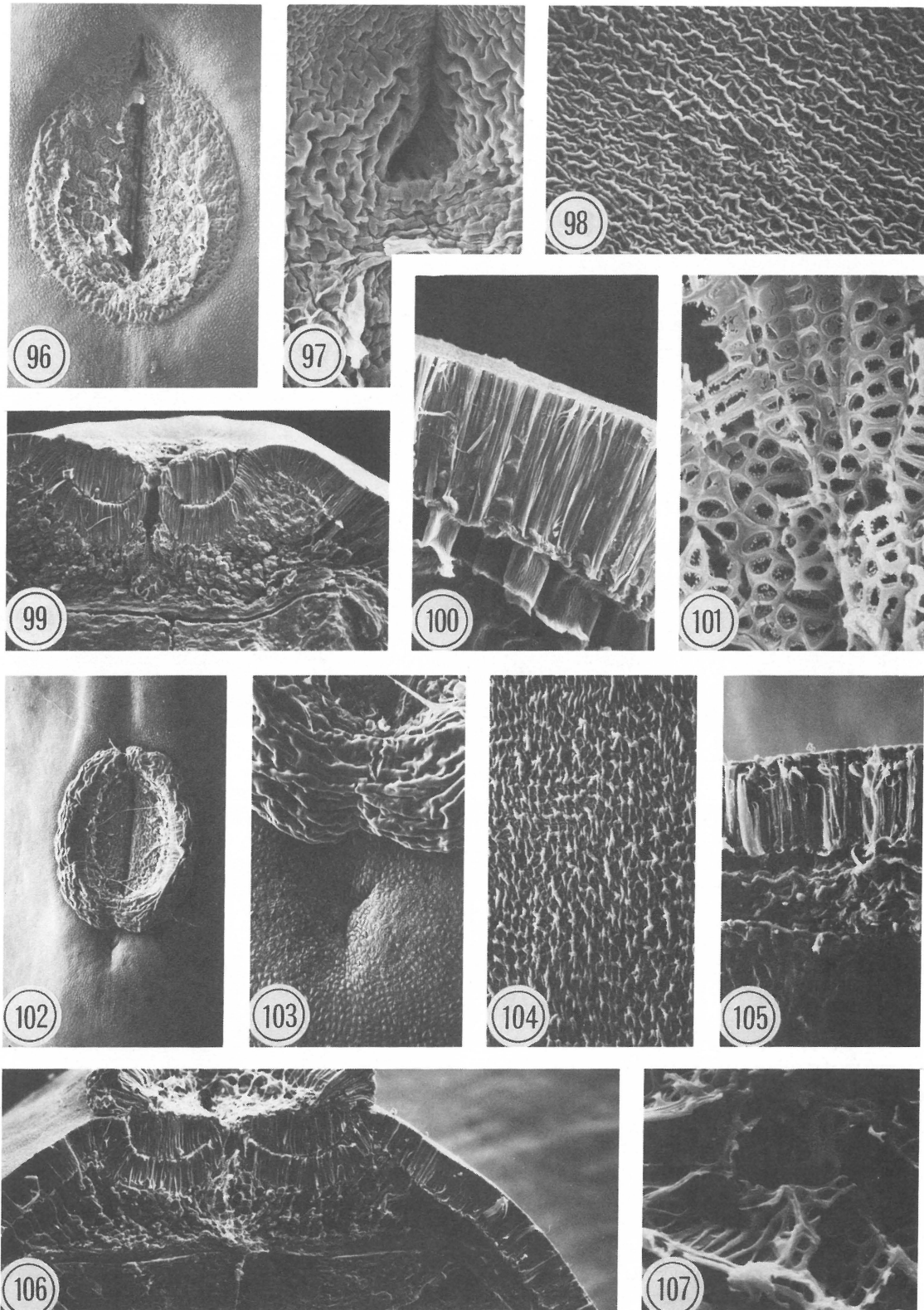
Figures 96 – 101 *Indigofera arrecta*. **96.** Hilum and micropyle, ×100; **97.** Micropyle, ×400; **98.** Testa surface, ×1000; **99.** Hilar region, ×100; **100.** Testa, ×400; **101.** Tracheoid pits, ×100. **Figures 102 – 107** *Desmodium canum*. **102.** Hilum and micropyle, ×50; **103.** Micropyle, ×200; **104.** Testa surface, ×500; **105.** Testa, ×250; **106.** Hilar region, ×100; **107.** Tracheoid pits, ×1000.

epidermis in the Mimosoideae, and which is also functional in seed dehydration.

Caesalpinioid seeds tend to have a thicker epidermis than is customary in the other subfamilies, but this is not invariable. In both mimosoid and caesalpinioid seed the light line is placed more or less medially in the epidermal cells. In *Acacia* subgenus *Vulgaris* the light line, medially placed elsewhere, occurs near the tip of the epidermal cells at the raphe-antiraphe and over most of the areole (Robbertse 1973). Certain mimosoid species are unusual in having seed with an exceptionally thick cuticle (up to 40 µm). The thickness of the cuticle in caesalpinioid and papilionoid seeds rarely exceeds 5 µm, and is consistently less than this in the latter. Bragg & Bridges (1984) report the occurrence of a double layer of palisade in seed of *Cassia*, but it is clear that the outer layer is nothing more than a very thick cuticle. The cuticle is smooth in seeds in which it is more than 10 µm thick, and near laevigate in

Cassia which has a cuticle 5 µm thick. In such mimosoid seeds the cuticle is thinner over the lens and here alone is sculptured. This suggests that the expression of cuticular sculpturing is related to the proximity of the underlying epidermal cells, the influence of which is attenuated when exerted over distances greater than 10 µm. The presence of a 'mucilage-stratum' (Corner 1951) seems correlated with the presence of a thick cuticle in the Mimosoideae, and in the Caesalpinioideae a weakly developed 'mucilage-stratum' occurs only in *Cassia*, which has a relatively thick cuticle. Cuticular sculpturing in the Mimosoideae and Caesalpinioideae is rather conservative in diversity, and is usually rugose, rarely with the rugae overlain with a reticulum. Other studies have reported only these three patterns in the Mimosoideae (Triveda *et al*. 1979) but a somewhat greater diversity in the Caesalpinioideae (Bragg & Bridges 1984).

Certain caesalpinioid and mimosoid species have seed
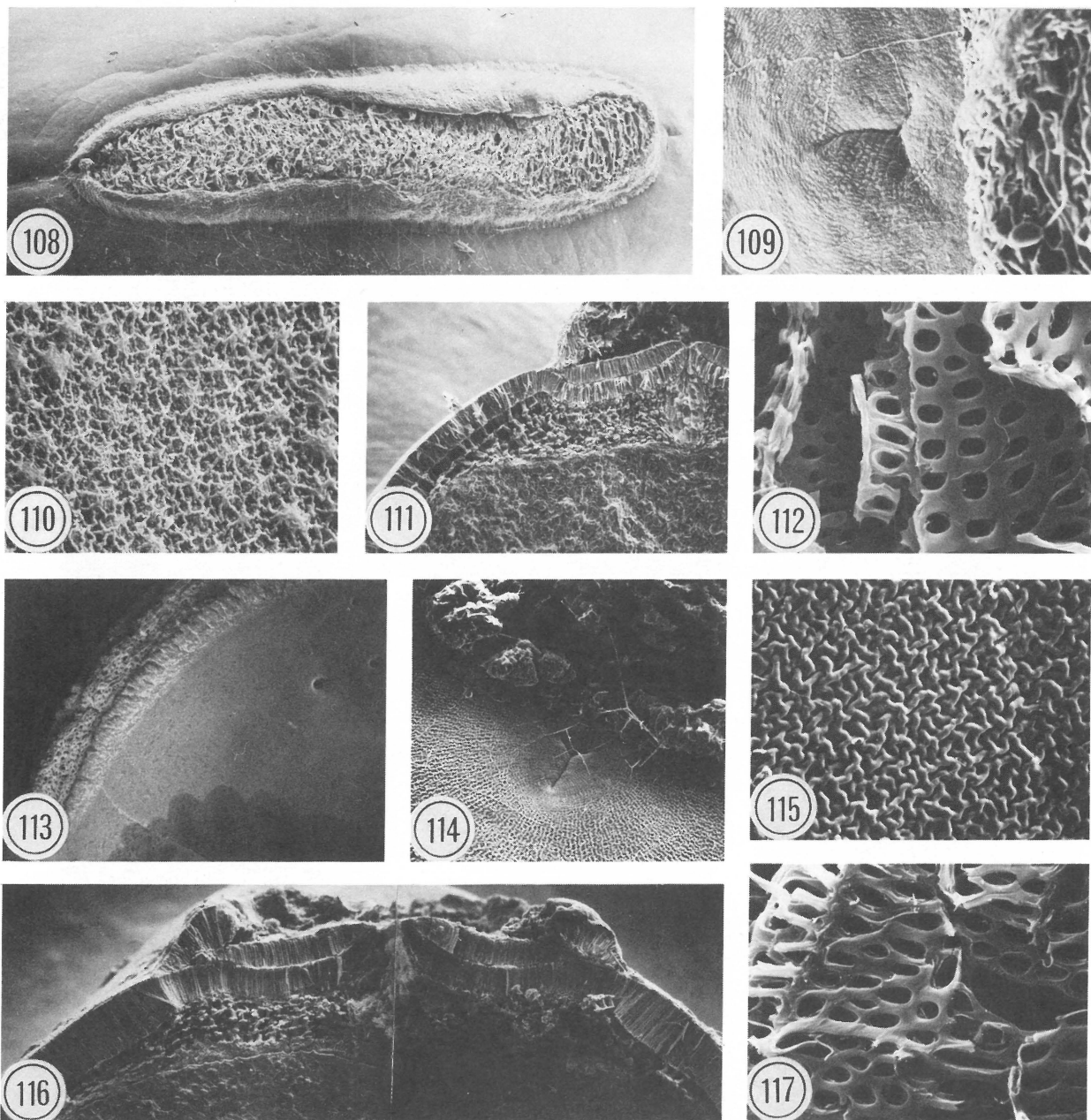
Figures 108 – 112 *Dipogon lignosus*. **108.** Hilum and micropyle, ×26; **109.** Micropyle, ×200; **110.** Testa surface, ×100; **111.** Hilar region, ×40; **112.** Tracheoid pits, ×1200. **Figures 113 – 117** *Lablab purpurea*. **113.** Part of hilum, ×15; **114.** Micropyle, ×50; **115.** Testa surface, ×200; **116.** Hilar region, ×40; **117.** Tracheoid pits, ×1200.

features which are anomalous in the family. Seed of *Acacia farnesiana* and *Caesalpinia decaptetala* lack the usual differentiated hypodermis. Within *Acacia*, at least, this is not altogether unusual, and the occurrence of an undifferentiated hypodermis is associated to some degree with infrageneric taxa (Robbertse 1973). This feature, in *Acacia* at least, is probably apomorphic and not primitive. Details of testa anatomy are rather variable within the genus *Acacia* and probably in similar
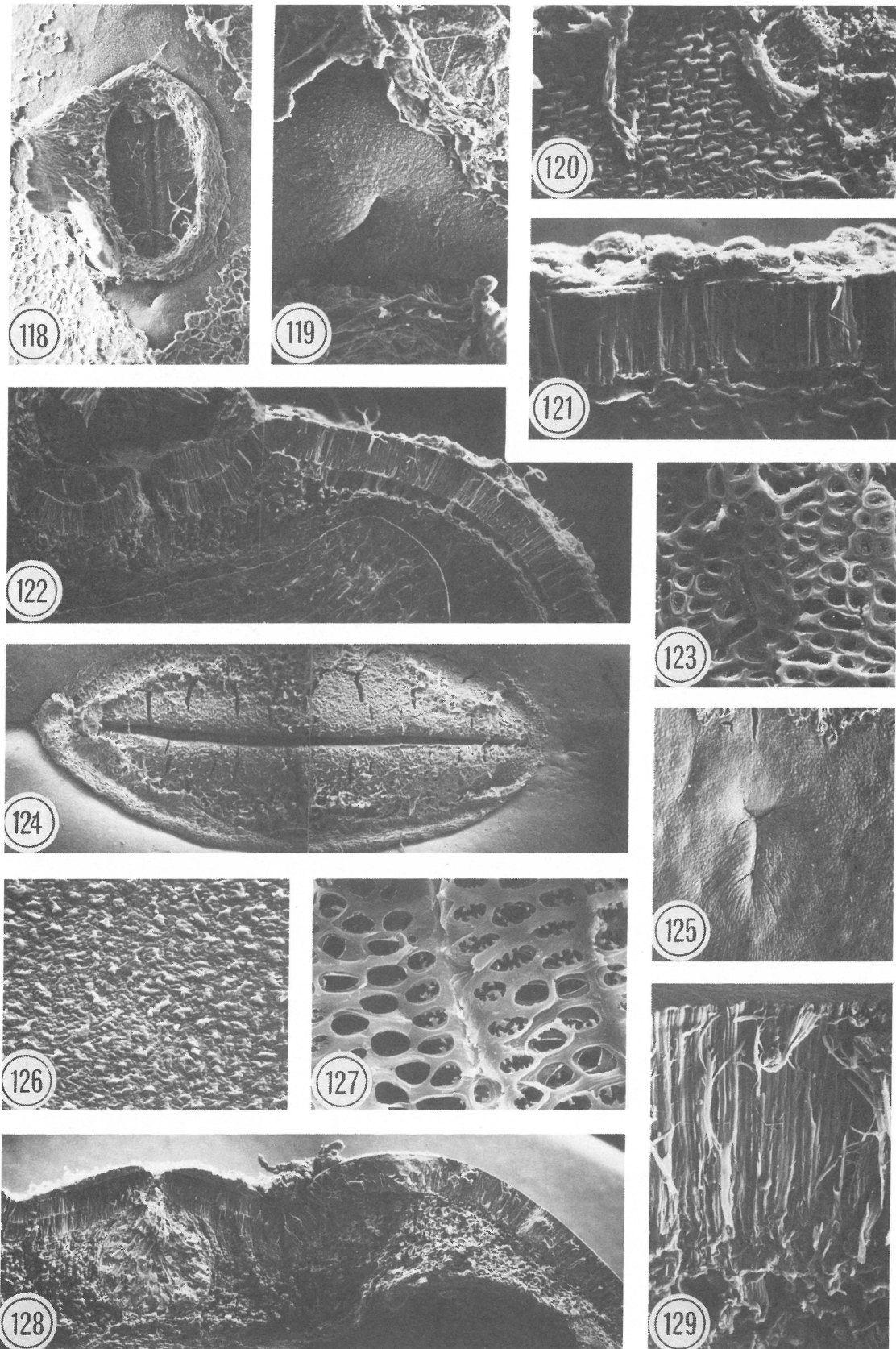
Figures 118 – 123 *Glycine wightii*. **118.** Hilum and micropyle, ×50; **119.** Micropyle, ×200; **120.** Testa surface: partly obscured by epitesta, ×400; **121.** Testa and epitesta, ×250; **122.** Hilar region, ×100; **123.** Tracheoid pits, ×1200. **Figures 124 – 129** *Erythrina humeana*. **124.** Hilum and micropyle, ×20; **125.** Micropyle, ×100; **126.** Testa surface, ×400; **127.** Tracheoid pits, ×1000; **128.** Hilar region, ×30; **129.** Testa, ×200.

large and diverse genera. In the genera *Entada* (Mimosoideae), *Delonix* and *Schotia* (Caesalpinioideae) the seeds have an inner layer of hourglass cells, differentiated from the inner epidermis of the outer integument. These rather exaggerated variations in the basic seed structure suggest phylogenetic radiation from a relatively unstable stock, and are not encountered in the Papilionoideae.

Seeds of the Papilionoideae are readily distinguished from caesalpinioid – mimosoid seed by the complex hilum with hilar fissure, counter palisade, aerenchyma and, especially, tracheid bar. In addition, the seed generally abscises cleanly from the funicle, and the hilum is often surrounded by hilar tissue.
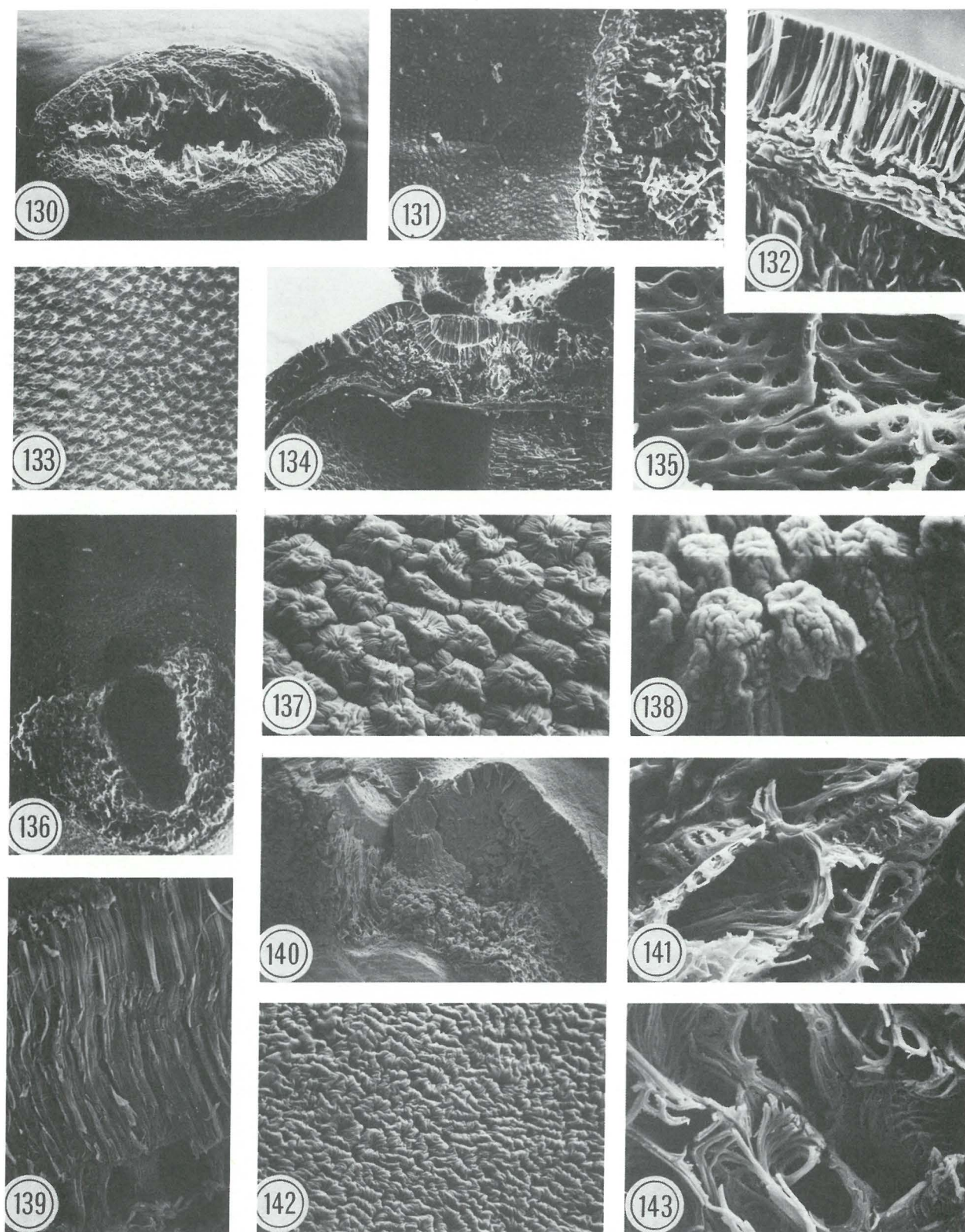
Figures 130 – 135 *Psoralea pinnata.* **130.** Hilum with rim aril, ×40; **131.** Micropyle, ×200; **132.** Testa, ×250; **133.** Testa surface, ×400; **134.** Hilar region, ×50; **135.** Tracheoid pits, ×1000. **Figures 136 – 141** *Sutherlandia frutescens.* **136.** Hilum and micropyle, ×120; **137.** Testa surface, ×1000; **138.** Tips of epidermal cells, ×2000; **139.** Testa, ×500; **140.** Hilar region, ×80; **141.** Tracheoid pits, ×1000. **Figures 142 – 143** *Lessertia perennans.* **142.** Testa surface, ×1000; **143.** Tracheoid pits, ×1200.

Papilionoid seeds lack a pleurogram and fracture lines, and moisture is lost through the hilar fissure instead. The papilionoid cuticle is invariably thin and rarely laevigate.

The range of patterns of cuticular sculpturing encountered in papilionoid seeds greatly exceeds that in the other sub-families. Lersten (1981) concluded that although testa surface patterns are significant within and between adjacent tribes, they will not reveal broader evolutionary trends. The Vicieae, for instance, were characterized by a distinctive and conspicuous papillose pattern caused by protrusion of the tips of the palisade cells (Lersten 1979; Lersten & Gunn 1982), and this pattern was not located in 150 other genera examined (Lersten 1981). However, this study reveals that a form of papillose sculpturing is present in *Abrus* (Abreae), *Medicago* (Trifolieae) and *Erythrina* (Phaseoleae:Erythrinineae). The Trifolieae is closely related to the Vicieae, and *Abrus* has been included in this tribe in the past (Lersten & Gunn 1982). In addition *Dipogon* (Phaseoleae: Phaseolineae) has a distinctly papillose testa overlain with a

reticulum, and a similar pattern is reported also in *Canavalia ensiformis* (Phaseoleae:Dioclineae) (Lersten 1981). The present study suggests that the closely allied tribes Podalyrieae, Liparieae and Crotalarieae are linked by a predominantly multireticulate sculpturing, while a foveolate pattern occurs in the Galegeae and related Trifolieae (here sub-papillose). Clearly cuticular patterns may be useful in assessing phylogenetic relationships between related tribes, but until the pathways of derivation of the patterns are elucidated, their value in assessing broader phylogenetic trends is limited. Although information is too scant to justify further speculation on the systematic significance of testa sculpturing, it is probable that the rugose pattern is plesiomorphic within the family. It occurs in many mimosoid and caesalpinioid genera and is widespread in the Papilionoideae, including the primitive genus *Sophora* (Sophoreae), and is the only pattern common to all three sub-families.

The papilionoid micropyle is ypsiloid, deltoid or punctate
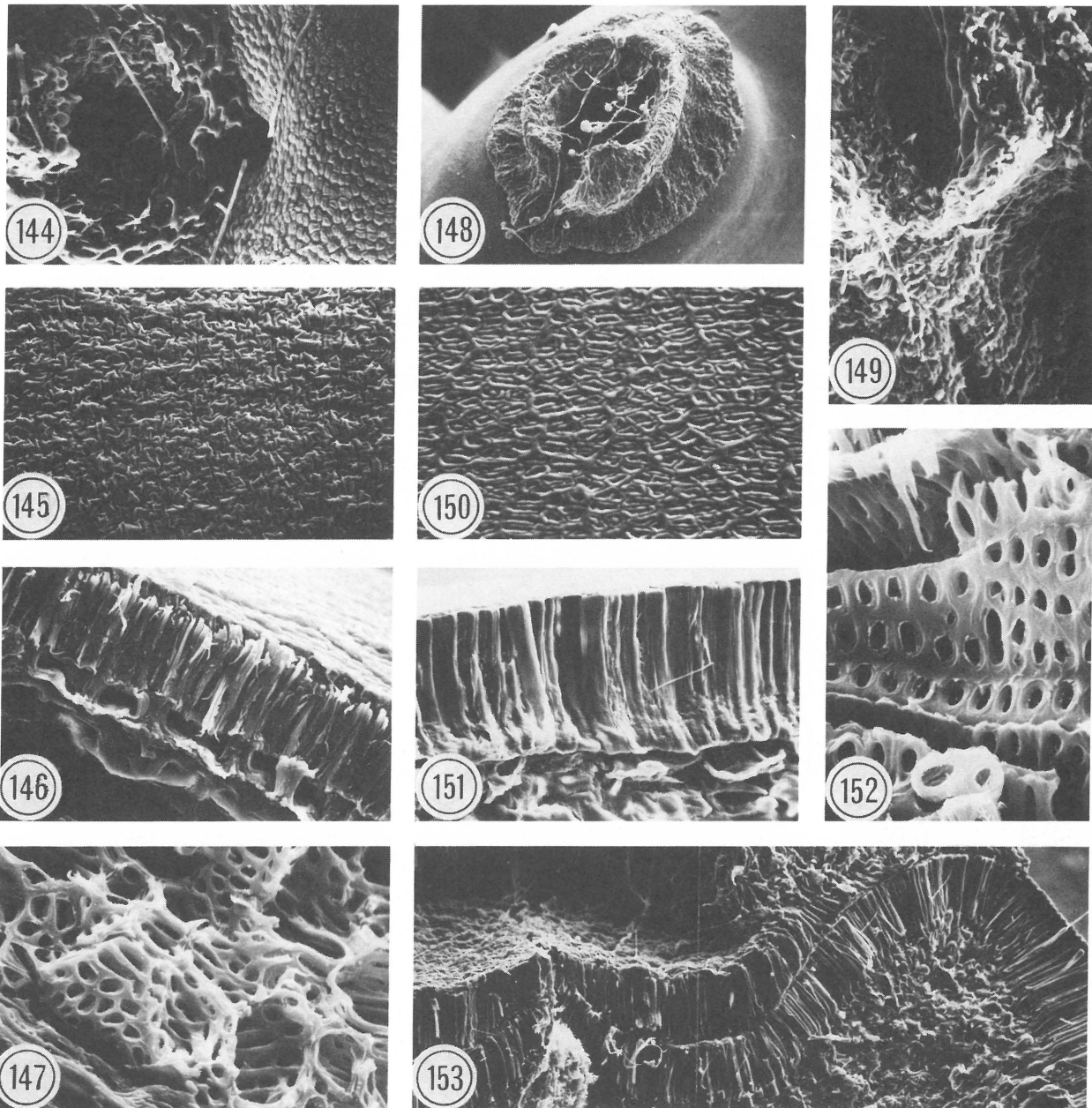
Figures 144 – 147 *Medicago polymorpha*. 144. Hilum and micropyle, ×260; 145. Testa surface, ×500; 146. Testa, ×500; 147. Tracheoid pits, ×1200. Figures 148 – 153 *Podalyria sericea*. 148. Hilum, ×20; 149. Micropyle, ×200; 150. Testa surface, ×250; 151. Testa, ×250; 152. Tracheoid pits, ×1000; 153. Hilar region, ×120.

and lacks the rim usually present in the other subfamilies. The shape and position of the micropyle in the Papilionoideae seems to be phylogenetically significant. The Abreae and some related Tephrosieae have a curiously modified ypsiloid micropyle; otherwise ypsiloid micropyles occur in diverse, usually phylogenetically less advanced taxa and punctate micropyles in a few, usually advanced tribes (the Sophoreae, Galegeae, Trifolieae, Podalyrieae, Liparieae and Crotalarieae). In particular, seed of the closely allied tribes Podalyrieae, Liparieae and Crotalarieae, considered to represent a single phylogenetic branch (Polhill 1981a), are characterized by a punctate micropyle completely enclosed by funicular remains and forming part of the hilum. The unusual conformation of a punctate hilum not completely enclosed by the hilum
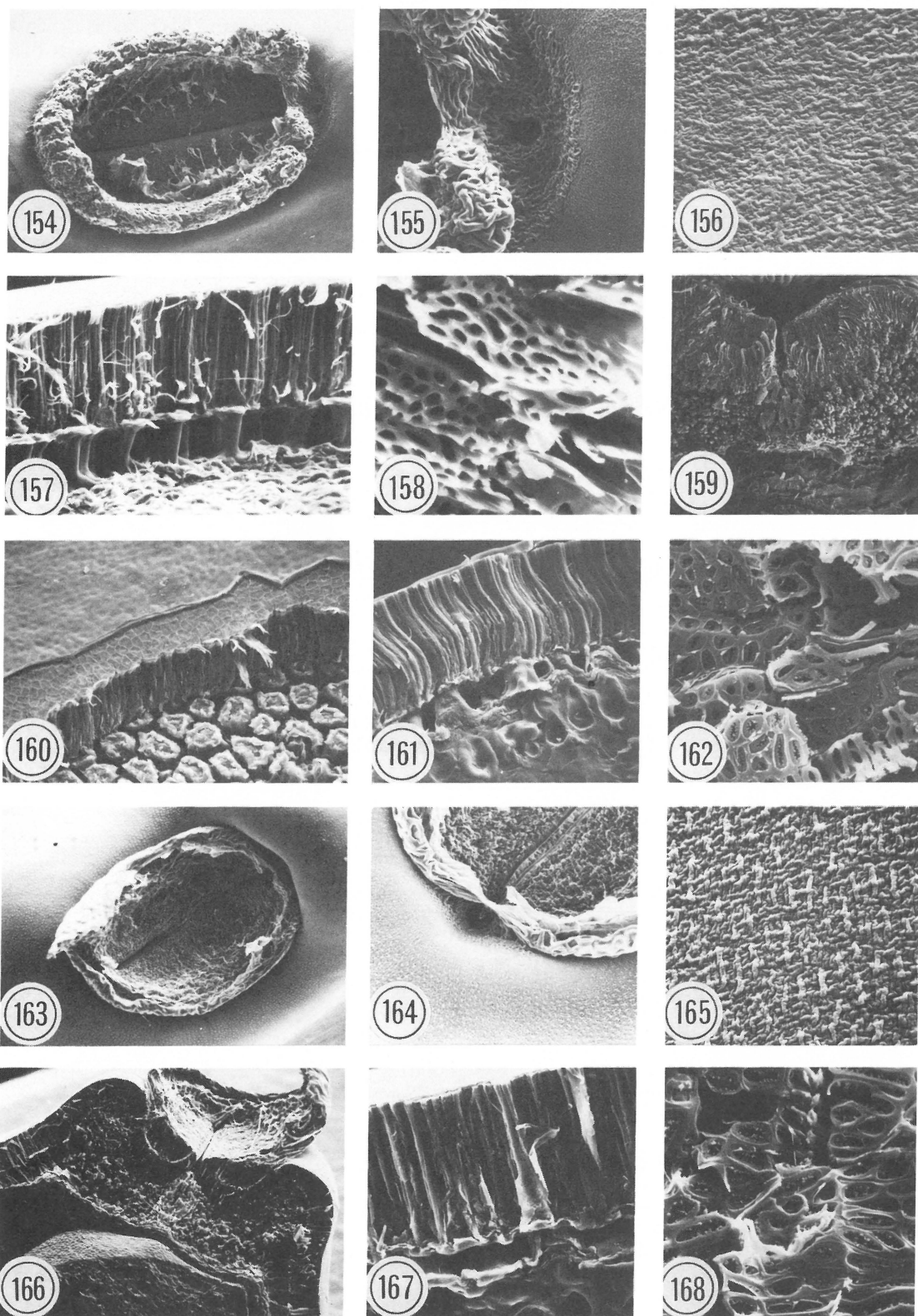
Figures 154 – 158 *Virgilia divaricata.* **154.** Hilum and micropyle, ×25; **155.** Micropyle, ×100; **156.** Testa surface, ×600; **157.** Testa, ×400; **158.** Tracheoid pits, ×800. **Figures 159 – 162** *Crotalaria grantiana.* **159.** Hilar region, ×80; **160.** Cuticle, epidermis and hypodermis, ×250; **161.** Testa, ×250; **162.** Tracheoid pits, ×1000. **Figures 163 – 168** *Argyrolobium tomentosum.* **163.** Hilum, ×60; **164.** Micropyle, ×120; **165.** Testa surface, ×600; **166.** Hilar region, ×60; **167.** Testa, ×400; **168.** Tracheoid pits, ×1200.

occurs in the Trifolieae and related Galegeae and a deltoid, enclosed hilum occurs in the Indigofereae and is reported from the related Vicieae (Lersten & Gunn 1982). The close association between micropyle and hilum may be functional in facilitating fertilization of the ovule, and will thus be prone to independent origin in unrelated evolutionary lines. The distribution of the various forms of micropyle within the family also seems to help in interpreting the phylogenetic relationships between the subfamilies. The Caesalpinioideae alone has micropyles of the shapes found in both other subfamilies. The Mimosoideae is characterized by seed with a slit-like micropyle surrounded by a cuticular rim, and similar

forms occur in the Caesalpinioideae along with other forms, including an ypsiloid micropyle in *Peltophorum*. The punctate micropyle enclosed in hilar tissue appears to be unique to the Papilionoideae, although an approach is found in *Cassia* where a punctate micropyle, lacking a rim, is placed distant from the hilum. This indicates an independent derivation of the Mimosoideae and Papilionoideae from ancestral stocks closely related to the Caesalpinioideae, the Papilionoideae probably from a more restricted or specialized group.

The hypodermis of the papilionoid seed is always differentiated into an osteosclereid layer, and is usually thicker than that of the mimosoid – caesalpinioid seeds. This may be
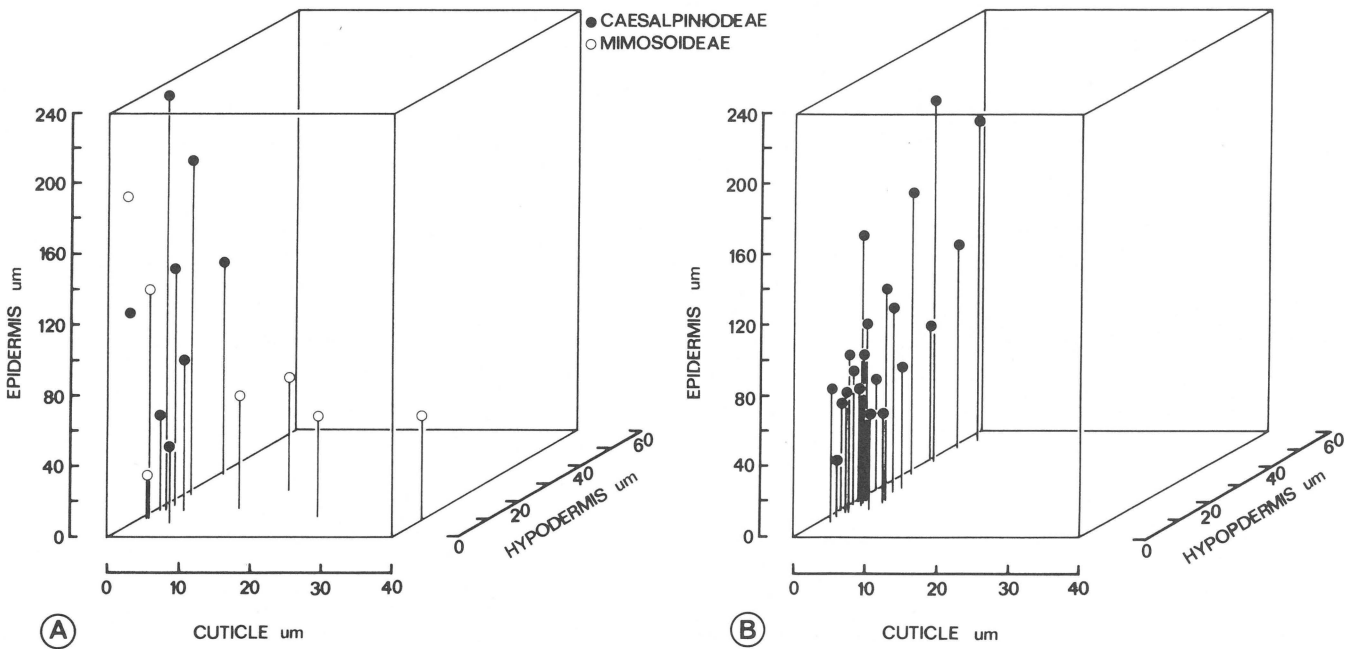
Figure 169 Three-dimensional relationship between cuticular, epidermal and hypodermal thickness in seeds of the Leguminosae. A. Caesalpinioideae and Mimosoideae; B. Papilionoideae. Correlation co-efficients between epidermal and hypodermal thickness are: Caesalpinioideae $r = 0,42$, $p = 0,18$; Mimosoideae $r = -0,11$, $p = 0,42$; Papilionoideae $r = 0,8$, $p = 0,0022$ for $y = 3,5x + 15,4$.

Table 1 Summary of seed features in the subfamilies of the Leguminosae

Character	Character State		
	Mimosoideae	Caesalpinioideae	Papilionoideae
1. pleurogram	usually present; open	usually absent; closed	absent
2. Fracture lines	present; penetrate usually to light line	present; penetrate usually to hypodermis	absent
3. Cuticle	thin – very thick (1 – 40 μm) $\bar{x}$ 13,7 ± 13,4	thin – thick (0,75 – 5 μm) $\bar{x}$ 2,3 ± 1,4	thin (0,5 – 4 μm); $\bar{x}$ 1,8 ± 1,3
4. Cuticular sculpturing	laevigate or rugose (rarely reticulate)	rugose or reticulate (rarely laevigate)	various, never laevigate
5. Epidermis	(25 – 130 μm) $\bar{x}$ 85 ± 53	(43 – 235 μm) $\bar{x}$ 129 ± 63	(31 – 205 μm) $\bar{x}$ 93 ± 46
6. Light line	present; near median	present; near median	often absent; apical
7. Hypodermis	(10 – 26 μm) $\bar{x}$ 15 ± 6; rarely undifferentiated	(8 – 25 μm) $\bar{x}$ 21 ± 11; rarely undifferentiated	(10 – 50 μm) $\bar{x}$ 22 ± 14
8. Hilar fissure	absent	absent	present
9. Counter palisade	absent	absent	present (absent in *Erythrina*)
10. Tracheid bar	absent	absent	present
11. Micropyle	slit along antiraphe; border present, raised	punctate, rarely ypsiloid or transverse slit; border usually raised	punctate, deltoid or ypsiloid
12. Inner hourglass cells	rarely present	rarely present	absent

associated with its role in papilionoid seeds of facilitating movement of water vapour to the tracheid bar from throughout the seed; in the Caesalpinioideae – Mimosoideae moisture is lost through pleurogram and fracture lines and movement over any distance is unnecessary. Papillate hypodermal cells occur in *Abrus* (Abreae) and *Milletia* (Tephrosieae), but not in *Mundulea* (Tephrosieae). *Milletia* resembles *Abrus* in a number of respects: modified micropyle, papillate hypodermis and double row of hourglass-shaped aerenchyma in the hilar region. The similarity between *Abrus* and *Milletia* (particularly the Madagascan species) in plant morphology, although possibly convergent, has been indicated by Polhill (1981b). The present information on seed structure supports ideas on their close relationship and, constituting features from a different adaptive mode, begs a re-examination of the supposed convergence of their similarity.

Multiple layers of hourglass cells in the circumhilar region occur in various genera of the Phaseoleae, and elsewhere only in *Argyrolobium* (Crotalarieae). A counter palisade is present in seed of all papilionoid genera except in at least some species of *Erythrina* (*E. humeana, E. latissima* and *E. lysistemon*) from Africa, and is also absent in the Asiatic *E. subumbrans* Merr. (Corner 1976). The relationship between this genus and the remainder of the Papilionoideae is obscure (Lackey 1981), and this feature of the seed furnishes further evidence of its phylogenetic distance from other groups.

Other unusual structures of restricted distribution within the Papilionoideae include the epitesta (*Glycine*) and the hilar tongue (present in *Argyrolobium*: Crotalarieae and all genera in the Phaseoleae). The subtribe Phaseolineae in particular exhibits a rather consistent suite of characters (epitesta, epihilum, smooth tracheoid pits, and multiple layers of hourglass cells in the hilar region), suggesting a particularly close phyletic cohesion.

Although there are a number of features of the testa which typically characterize the papilionoid seed, it appears that the only characters which are invariably restricted to this subfamily are those hilar features traditionally recognized in distinguishing the papilionoid seed. Furthermore, the similarities between the Caesalpinioideae and Mimosoideae are largely plesiomorphous and cannot be taken to imply a greater phylogenetic relationship. In neither of these subfamilies is there an established relationship between hypodermal and epidermal thickness, although this is marked in the Papilionoideae. This suggests that at the stage of phylogenetic progression attained by papilionoid seeds, the ratio between epidermal and hypodermal thickness has been stabilized at 3,5 in the interest of structural efficiency. The correlation of such a relationship with apomorphous features free of major deviation suggests that papilionoid seeds became stabilized at an early stage in a structure that represents a very efficient structural – functional unit of great phylogenetic reliability.

Acknowledgements

References

BRAGG, L.H. & BRIDGES, T.L. 1984. Testa characterization of selected Caesalpinioideae (Leguminosae) genera. *Scanning Electron Microsc.* 4: 1751 – 1758.

CORNER, E.J.H. 1951. The leguminous seed. *Phytomorphology* 1: 117 – 150.

CORNER, E.J.H. 1976. The seeds of dicotyledons, Vols. I and II, Cambridge University Press, Cambridge.

DE CANDOLLE, A.P. 1825. Mémoires sur la Famille des Légumineuses, A. Belin, Paris.

GUNN, C.R. 1981. Seed topography in the Fabaceae. *Seed Sci. & Technol.* 737 – 757.

ISELY, D. 1955. Observations on seeds of the Leguminosae: Mimosoideae and Caesalpinioideae. *Proc. Iowa Acad. Sci.* 62: 142 – 145.

KOPOOSHIAN, H. & ISELY, D. 1966. Seed character relationships in the Leguminosae. *Proc. Iowa Acad. Sci.* 73: 59 – 67.

LACKEY, J.A. 1981. Phaseoleae DC. (1825). In: Advances in legume systematics, ed. Polhill, R.M. & Raven, P.H. Part 1, pp. 301 – 327, Royal Botanic Gardens, Kew.

LERSTEN, N.R. 1979. A distinctive seed coat pattern in the Vicieae (Papilionoideae; Leguminosae). *Proc. Iowa Acad. Sci.* 86: 102 – 104.

LERSTEN, N.R. 1981. Testa topography in Leguminosae, subfamily Papilionoideae. *Proc. Iowa Acad. Sci.* 88: 180 – 191.

LERSTEN, N.R. & GUNN, C.R. 1982. Testa characters in tribe Vicieae, with notes about tribes Abreae, Cicereae, and Trifolieae (Fabaceae). Agricultural Research Service Technical Bulletin Number 1667, United States Department of Agriculture.

MANNING, J.C. & VAN STADEN, J. 1985. The development and ultra-structure of the testa and tracheid bar in *Erythrina lysistemon* Hutch. (Leguminosae:Papilionoideae). *Protoplasma* 129: 157 – 167.

MANNING, J.C. & VAN STADEN, J. 1986. The functional ontogeny of the testa in *Indigofera parviflora*. *Bot. Gaz.* in press.

POLHILL, R.M. 1981a. Papilionideae. In: Advances in legume systematics ed. Polhill, R.M. & Raven, P.H. Part 1, pp. 191 – 208, Royal Botanic Gardens, Kew.

POLHILL, R.M. 1981b. Tribe 5. Abreae (Wight & Arn.) Hutch. (1964). In: Advances in legume systematics, ed. Polhill, R.M. & Raven, P.H. Part 1, pp. 243 – 244, Royal Botanic Gardens, Kew.

ROBBERTSE, P.J. 1973. Die genus *Acacia* in Suid-Afrika — 3 (met spesiale verwysing na die morfologie van die saad). *Tydskr. vir Natuurwetenskappe* 13: 72 – 95.

TRIVEDI, B.S., BAGCHI, G.D. & BAJPAL, V. 1979. Scanning electron microscopic studies on the sporoderm of some Mimosoideae (Leguminosae). *Phytomorphology* 29: 211 – 218.

Appendix 1 List of characters and character states

Characters	Character states
1. Epitesta	1 absent 2 present
2. Testa surface	1 smooth 2 wrinkled
3. Surface sculpturing	1 laevigate 2 rugose 3 substriate 4 simple-reticulate 5 multi-reticulate 6 simple-foveolate 7 multi-foveolate 8 lophate 9 papillose
4. Pleurogram	1 absent 2 present
5. Pleurogram form	1 open 2 closed
6. Fracture lines	1 absent 2 present
7. Hilum shape	1 round 2 oval 3 wedge 4 oblong 5 linear 6 circumlinear
8. Hilar fissure	1 absent 2 present
9. Epihilum	1 absent 2 present
10. Micropyle position	1 distant 2 proximate 3 included
11. Micropyle shape	1 antiraphal slit 2 transverse slit 3 ypsiloid 4 deltoid 5 punctate
12. Tracheid bar	1 absent 2 present

Appendix 1 Continued

13. Tracheoid pits — 1 lacy   2 warty   3 vestured   4 smooth
14. Counter palisade — 1 present   2 absent
15. Cuticle thickness (μm)
16. Epidermal thickness (μm)
17. Light line — 1 near median   2 in apical third   3 not visible
18. Hypodermal thickness (μm)

Appendix 1 Continued

19. Hypodermal thickness near hilum (μm)
20. Hourglass cells — 1 absent   2 smooth   3 papillate
21. Hourglass cells at hilum — 1 none   2 one row   3 two rows   4 three or more rows
22. Inner hourglass cells — 1 absent   2 present
23. Rim aril — 1 absent   2 present   3 strongly developed

Appendix 2 List of species examined and their character states

Tribe	Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Caesalpinioideae																								
Caesalpineae	*Caesalpinia decapetala* (Roth.) Alston	1	1	2	1	NA	2	1	1	NA	2	2	1	NA	NA	3	127	1	NA	NA	1	NA	1	1
	Delonix regia (Hook.) Raf.	1	1	2	1	NA	2	1	1	NA	1	2	1	NA	NA	0,75	188	1	35	NA	2	NA	2	1
	Parkinsonia aculeata L.	1	1	5	1	NA	2	1	1	NA	1	2	1	NA	NA	4	85	1	15	NA	2	NA	1	1
	Peltophorum africanum Sond.	1	1	2	1	NA	2	1	1	NA	1	3	1	NA	NA	1	54	1	14,2	NA	2	NA	1	1
Cassieae	*Cassia floribunda* Cav.	1	1	1/2	1	NA	2	1	1	NA	1	5	1	NA	NA	5	43	1	8	NA	2	NA	1	1
Detarieae	*Schotia afra* (L.) Thunb.	1	1	2	1	NA	2	1	1	NA	2	2	1	NA	NA	1,5	235	1	15	NA	3	NA	?	1
	Schotia brachypetala Sond.	1	1	2/9	1	NA	2	2	1	NA	2	2	1	NA	NA	1,9	120	1	35	NA	3	NA	2	1
Amherstieae	*Tamarindus indica* L.	1	1	5	2	2	2	–	1	NA	–	–	1	NA	NA	2,8	135	1	17	NA	2	NA	1	1
Mimosoideae																								
Mimoseae	*Dichrostachys cinerea* (L.) Wight & Arn.	1	1	2	2	1	2	1	1	NA	2	1	1	NA	NA	1,2	130	1	10	NA	2	NA	1	1
	Entada spicata (E.Mey.) Druce	1	1	1/2	2	1	2	2	1	NA	2	1	1	NA	NA	14	64	1	26	NA	2	NA	2	1
Acacieae	*Acacia cyclops* A. Cunn ex G. Don.	1	1	1	2	1	2	1	1	NA	2	1	1	NA	NA	25	58	1/2	10	NA	2	NA	1	1
	Acacia longifolia (Andr.) Willd.	1	1	1	2	1	2	1	1	NA	2	1	1	NA	NA	40	58	2	18	NA	2	NA	1	1
	Acacia farnesiana (L.) Willd.	1	1	2	2	1	2	1	1	NA	2	2	1	NA	NA	2,5	192	1	NA	NA	1	NA	1	1
Ingeae	*Albizia adiantifolia* (Schumach.) W.F. Wight	1	1	1	1	NA	2	2	1	NA	2	1	1	NA	NA	12	65	2/1	14,5	NA	2	NA	1	1
	Calliandra surinamense	1	1	2	2	1	2	4	1	NA	2	1	1	NA	NA	1	25	1	10	NA	2	NA	1	1
Papilionoideae																								
Sophoreae	*Calpurnia aurea* Benth.	1	1	2	1	NA	1	2	2	1	3	5	2	1	1	3	104	3	25	58	2	2	1	2
	Sophora japonica L.	1	1	2	1	NA	1	2	2	1	1	3	2	2/3	1	3	180	2	55	130	2	2	1	1
Dalbergieae	*Dalbergia obovata* E. Mey.	1	1	2	1	NA	1	2	2	1	1	3	2	3	1	0,8	65	3	19	35	2	2	1	2
Abreae	*Abrus precatorius* L.	1	1	9	1	NA	1	2	2	1	1	3	2	1	1	1	152	3	20	90	2/3	1	1	1
Tephrosieae	*Millettia dura* Dunn	1	1	5	1	NA	1	4	2	1	1	3	2	3	1	2,3	68	3	27	50	2/3	2	1	3
	Mundulea sericea (Willd.) A. Chev.	1	1	?4	1	NA	1	2	2	1	1	3	2	2	1	2	90	2	16	30	2	1	1	2
Robinieae	*Sesbania punicea* (Car.) Benth.	1	1	2	1	NA	1	2	2	1	1	3	2	4	1	0,75	160	3	35	90	2	1	1	1
Indigofereae	*Indigofera arrecta* A. Rich.	1	1	2	1	NA	1	2	2	1	3	4	2	2	1	0,6	63	3	25	39	2	3	1	2
Desmodieae	*Desmodium canum* (J.F. Gmel.) Schinz & Thell.	1	1	5	1	NA	1	2	2	1	1	3	2	4	1	1,5	58	3	13,5	47	2	1	1	2
Phaseoleae	*Erythrina humeana* Spreng.	1	1	9	1	NA	1	4	2	1	1	3	2	3	2	1	205	2	42	45	2	4	1	2
	Glycine wightii (Wright & Arn.) Verdc.	2	1	5	1	NA	1	2	2	1	1	3	2	3	1	4	54	3	15	30	2	2	1	2
	Lablab purpureus (L.) Sweet	1	1	2	1	NA	1	5	2	2	1	3	2	4	1	4	120	3	20	30	2	4	1	2
	Dipogon lignosus (L.) Verdc.	1	1	9	1	NA	1	4	2	2	1	3	2	4	1	0,5	77,5	2	42,5	62,5	2	4	1	2
Psoraleae	*Psoralea pinnata* L.	1	1	9	1	NA	1	2	2	1	1	3	2	4/2	1	1,5	67	3	13,5	35	2	3	1	2
Galegeae	*Sutherlandia frutescens* R. Br.	1	2	7	1	NA	1	1	2	1	2	5	2	4/2	1	1,3	100	2	20	23	2	2	1	1
Trifolieae	*Medicago polymorpha* L.	1	1	6/9	1	NA	1	1	2	1	2	5	2	4	1	1,2	31	2	11	–	2	2	1	2
Podalyrieae	*Podalyria sericea* R. Br.	1	1	5	1	NA	1	2	2	1	3	5	2	4	1	3	85	2	17	35	2	2	1	3
	Virgilia divaricata Adamson	1	1	5	1	NA	1	2	2	1	3	5	2	4	1	0,5	115	3	50	110	2	–	1	2
Liparieae	*Liparia sphaerica* L.	1	1	5	1	NA	1	2	2	1	3	5	2	4	1	2	75	3	8	60	2	2	1	3
Crotalarieae	*Crotalaria grantiana* Harv.	1	1	1	1	NA	1	2	2	1	3	5	2	2	1	4	50	2	19	20	2	2	1	1
	Argyrolobium tomentosum (Andr.) Druce	1	1	5	1	NA	1	2	2	1	3	5	2	2/3	1	0,25	61	3	14	62	2	4	1	2