Proceedings of the Iowa Academy of Science

Volume 88 | Number Article 10

1981

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Proc. Iowa Acad. Sci. 88 (4): 180-191. 1981

Testa Topography in Leguminosae, Subfamily Papilionoideae

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Seeds of 340 species of 150 genera from 30 of the 32 tribes of Papilionideae were examined by SEM. Nine categories of testa patterns were established: levigate (smooth), rugulate (irregularly roughened), substriate (short parallel ridges), simple-reticulate (meshwork of ridges enclosing single cells), multi-reticulate (primary plus secondary ridges), simple-foveolate (single cell ends isolated by grooves), multi-foveolate (unit of several cells surrounded by grooves), lophate (short ridges with irregular sides), and papillose (single protruding epidermal cells). Patterns in about 85% of species are most conspicuous near the hilum, becoming attenuated or disappearing toward midseed. Vicieae, Trifolieae, and Cicereae, however, typically retain the pattern all over. Some tribes showed a variety of patterns, others had dominant patterns (Robineae and Phaseoleae-rugulate, Psoraleeae and Amorpheae-lophate, Vicieae and Trifolieae-papillose, Loteae and Coronilleae-reticulate). Cicereae has large multicelluar plates which bulge or protrude conically or as long spines. Mirbelieae has an extremely thick rugulate cuticle underlain by an amorphous substance. Testa patterns seem taxonomically significant within or between certain tribes, but they do not identify broad evolutionary trends.

INDEX DESCRIPTORS: legumes, Leguminosae, Papilionoideae, scanning electron microscopy, seeds, seed coat anatomy, taxonomy, testa topography.

The most recent review of the morphology and taxonomic significance of legume seeds was by Gunn (1981). He clarified the definitions of certain features which had become confused. He also discussed the actual and potential taxonomic significance of some seed characters, including surface topography.

In the legume subfamily Papilionoideae, with 440 genera and about 12,000 species in 32 tribes (Polhill, 1981), seeds of many cultivated and common north temperate species have been studied (Mattirolo and Buscalioni, 1892; Pammel, 1899; Kopooshian and Isely, 1966; Corner, 1951, 1976). These light microscope studies, with rare exceptions, have described the testa as smooth and featureless.

In the last decade, topographic studies of papilionoid seeds have appeared using SEM (Brisson and Peterson, 1977 for incidential earlier references; Nwanze, Horber, and Pitts, 1975; Sharma *et al.*, 1977; Gunn and La Sota, 1978; Newell and Hymowitz, 1978; Saint-Martin, 1978; Trevidi, Bagchi, and Bajpai, 1978; Fajendre, Mujeeb, and Bates, 1979). These investigators have described the surface patterns on mature seeds of approximately 100 species of 30 genera in eight tribes. Unfortunately, various vague or cumbersome terms have been used and no standard terminology has been proposed or accepted. Workers evidently assume a uniform pattern, since they rarely indicate where on a seed SEM observations were made.

I have surveyed seeds representing 30 papilionoid tribes using SEM. My purposes were to determine the range of testa patterns, to attempt to describe patterns more precisely than previous workers, and to see if the distribution of testa patterns provides useful taxonomic characters, particularly as related to the delimitation of tribes as proposed recently by Polhill (1981).

MATERIALS AND METHODS

Most seeds were obtained from Dr. C. R. Gunn, Curator of the Seed Herbarium, U.S. Dept. of Agriculture, Beltsville, Maryland. Most seeds did not have voucher sheets but, while some species identifications might be questioned, error at the critical generic level can be disregarded. Additional seeds were made available by the Plant Introduction Station, Ames, Iowa. A minimum of 4 seeds per species were examined, if available. Whole seeds or selected portions of large seeds were dipped in absoulute ethanol, air-dried, then mounted on brass disks and coated with carbon and about 15 nm of gold in a Varian vacuum evaporator or with about 15nm of gold-palladium in a Polaron sputter coater. Observations were made at 15 or 20 Kv with a JEOL JSM-35 SEM.

OBSERVATIONS

Hilum and Micropyle

The hilum is usually circular or slightly oval (Fig. 2-6), but it is elongate in scattered genera of several tribes. Figure 1, for example, shows about half of the somewhat rectangular elongated hilum of *Abrus*. In most seeds a hilar groove traverses the hilum (Fig. 1-6); beneath it is the tracheid bar (described elsewhere in detail by Lersten, 1982). The rim-aril, a remnant of the funiculus, is usually conspicuous (Fig. 1, 3-6). In a few taxa it is reduced or absent (Fig. 2); only in Vicieae is it consistently lacking or almost so (Lersten and Gunn, 1981a).

Except where covered by a massive hilar rim or rim-aril, the micropyle is usually visible as a circular (Fig. 2) or deltoid (Fig. 1, 3, 4) depression. In many seeds, growth of the radicle causes a hump in the testa which often covers the micropyle (Fig. 5, 6). Close examination of the interior of the micropyle of mature seeds by SEM always revealed an unbroken cuticular surface.

I observed that seeds in the more primitive tribes (Swartzieae through Robinieae in Polhill, 1981) tend to have the micropyle separated from the hilum, as in Fig. 1, or even further removed. In tribes considered more advanced than Robinieae the micropyle is adjacent to, or in contact with (Fig. 2-6), the hilum, often appearing to extend into it (Lersten, 1979; Lersten and Gunn, 1981a).

Testa Surface at Low Magnification

Seeds of the vast majority of taxa appear smooth when seen with the naked eye or dissecting microscope. *Cicer* is one striking exception because many of its species have conspicuous outgrowths of the testa surface (Fig. 29; Lersten and Gunn, 1981b). Inconspicuous mounds occur in taxa of several tribes; such outgrowths are common in Trifolieae (Fig. 31, 32; Lersten and Gunn, 1981a), perhaps a result of more sampling in this tribe than in others. The lens is a small domelike bump, in line with the hilum but on the side opposite the micropyle. Only rarely, as in *Cicer* (Fig. 29, arrow), does it appear larger or more elaborate.

Pits in the testa surface occur in species of several tribes (Fig. 33; Table 1). These depressions are lined with an unbroken cuticle, and their surface appears identical to the rest of the testa.

Figures 1-6 show different testa patterns around the hilum at from 100-260×, the range of magnification in which patterns generally can be first detected in various legume seeds. These figures provide orientation for detailed views shown at a standard magnification of 1000.

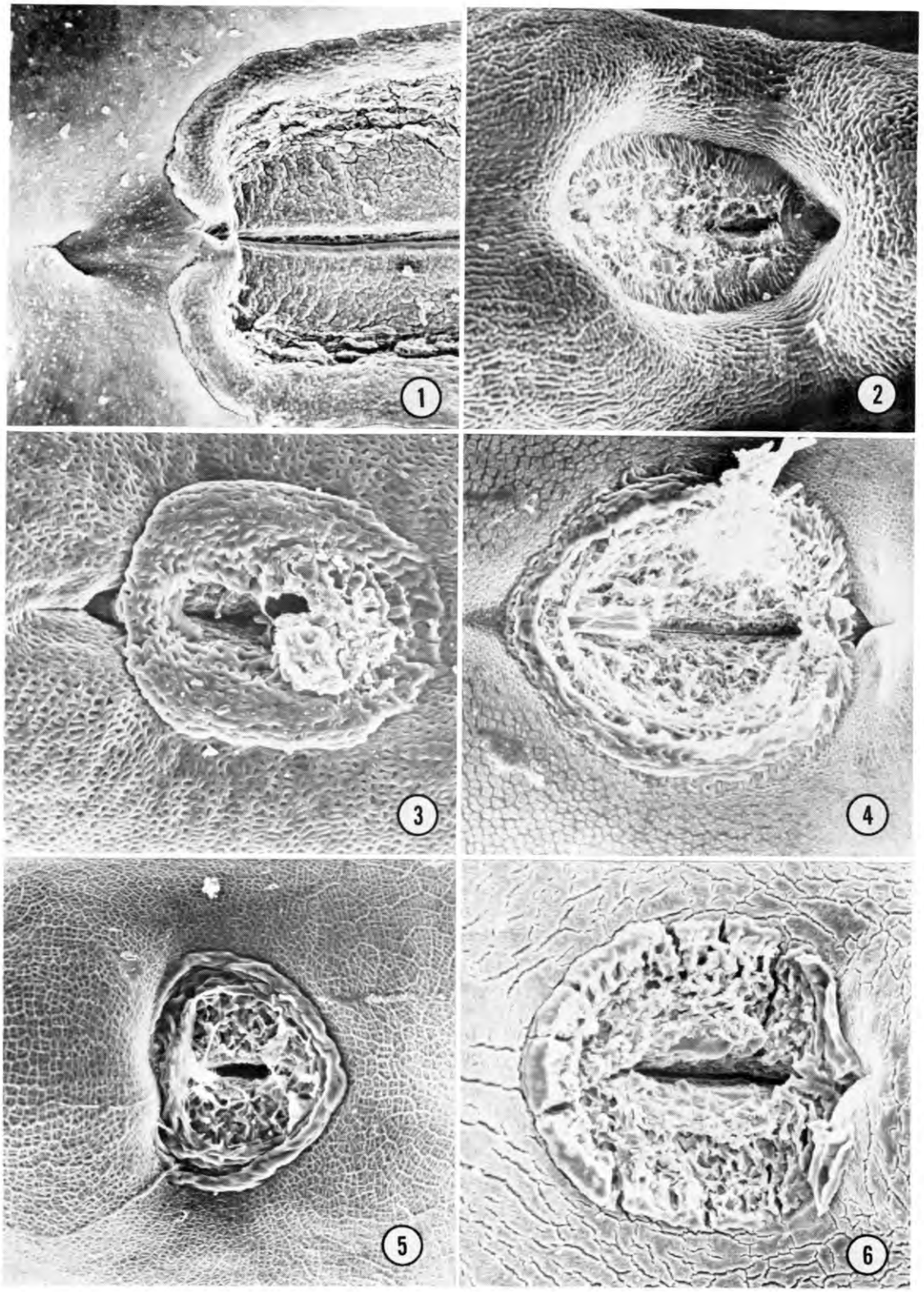


Fig. 1-6. *Overview of representative testa patterns. 1.* Abrus precatorius *(Abreae). Slightly rugulate. Note micropyle distant from hilum at far left ×100. 2.* Aotus ericoides *(Mirbelieae). Conspicuously rugulate. ×100. 3.* Coronilla varia *(Coronilleae). Simple-foveolate. ×200. 4.* Onobrychis antasiatica *(Coronilleae). Simple-foveolate. ×120. 5.* Notospartium carmichaeliana *(Carmichaelieae). Multi-reticulate. ×200. 6.* Swainsona salsula *(Galegeae). Thick, fissured cuticle ×150.*

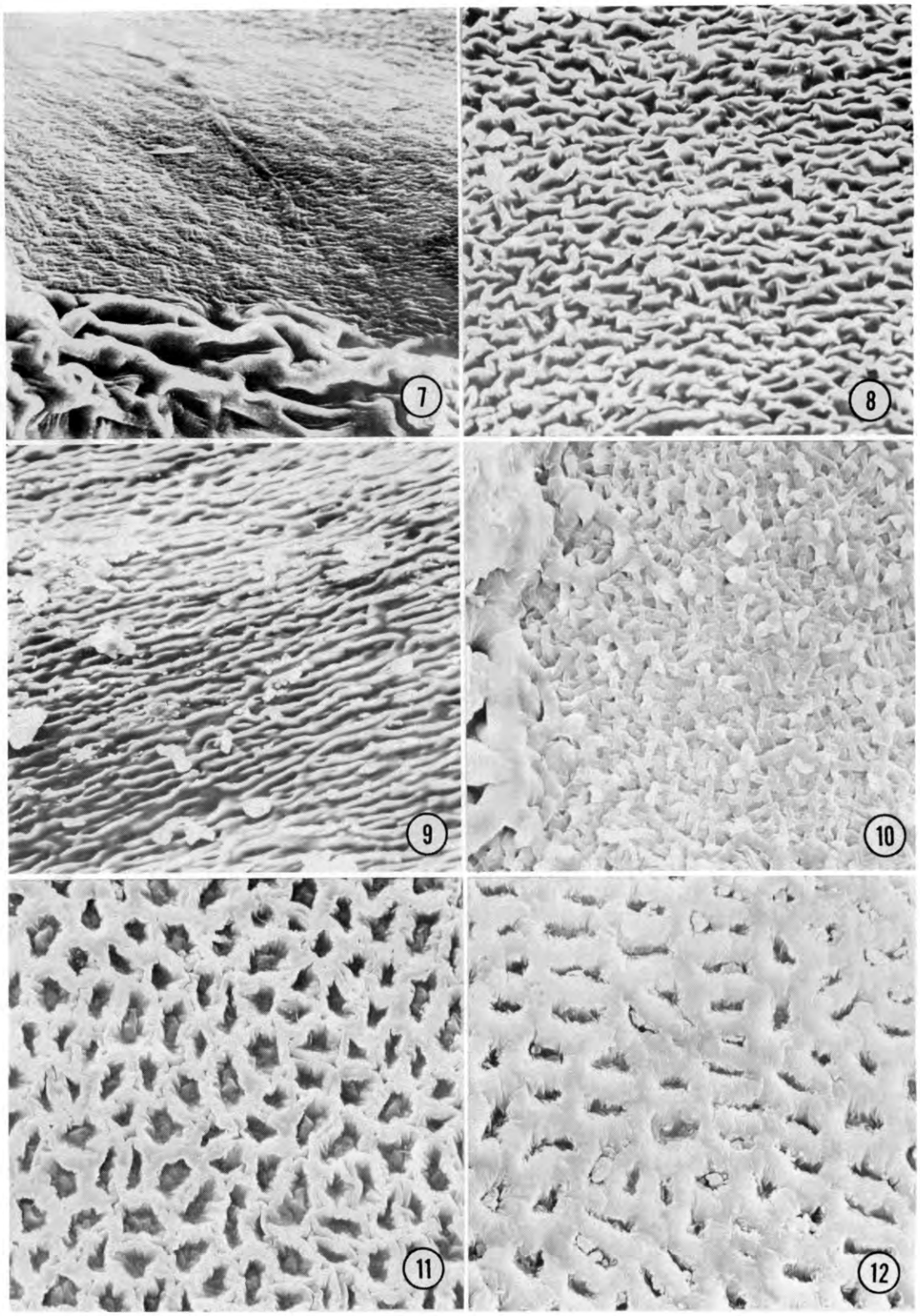


Fig. 7-12. *Detailed view of 4 near-hilar patterns, all at ×1000. 7.* Dalea leporina *(Amorpheae). Levigate. 8.* Robinia pseudoacacia *(Robinieae). Rugulate. 9.* Maackia amurensis *(Sophoreae). Substriate. 10.* Cratylia mollis *(Phaseoleae-Dioclinae). Rugulate. 11.* Poissonia hypoleuca *(Robinieae). Simple-reticulate. 12.* Lotus crassifolia *(Loteae). Simple-reticulate with heavy ridges.*

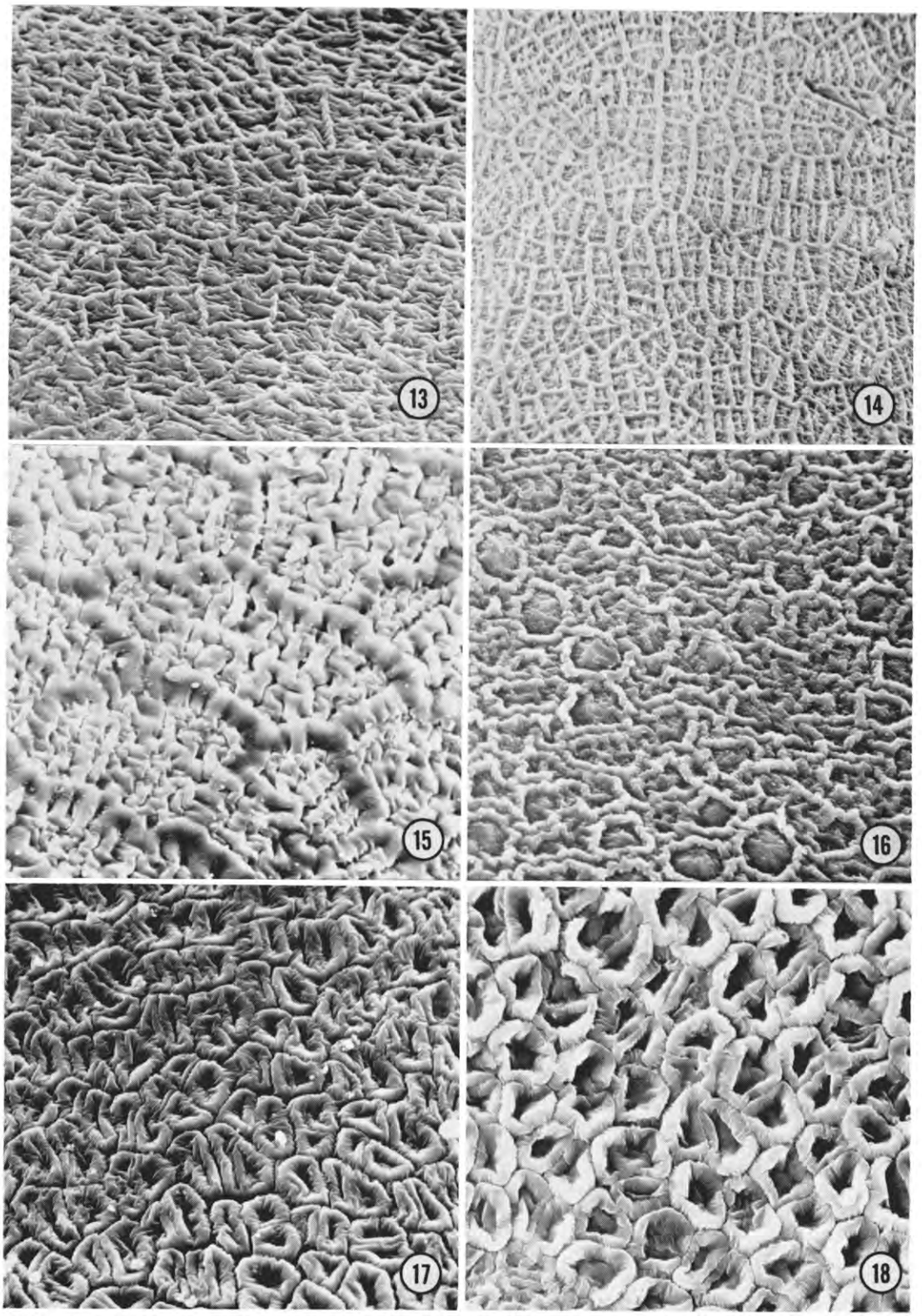


Fig. 13-18. *Detailed view of 2 near-hilar patterns, all at ×1000. 13.* Carmichaelia arborea *(Carmichaelieae). Multi-reticulate. 14.* Lotononis heterophylla *(Crotalarieae). A rather regular multi-reticulate pattern. 15.* Brachysema lanceolata *(Mirbelieae). Multi-reticulate with heavy ridges. 16.* Decorsea schlechteri *(Phaseoleae-Phaseolinae). Unusual multi-reticulate pattern. 17.* Colutea cilicica *(Galegeae). Simple-foveolate. 18.* Canavalia ensiformis *(Phaseoleae-Dioclinae). Simple-foveolate with exaggerated cell walls.*

Figure 1 shows a seemingly smooth testa; much higher magnification is needed to see the inconspicuous rugulate pattern (e.g. Fig. 7). A conspicuously rugulate surface (Fig. 2) was rarely seen. Most rugulate patterns were somewhere between those of Fig. 1 and 2.

A simple-reticulate pattern is shown in Fig. 3, and in Fig. 4 the opposite condition, simple-foveolate. Figure 5 illustrates a multi-reticulate pattern. In Fig. 6, "fracture lines" are evident, a rare pattern in Papilionoideae (Gunn, 1981) in which the thick cuticle becomes cracked during seed maturation.

In most seeds examined (about 85%), a discernible pattern occurred only around the hilum. At a certain distance the pattern either became attentuated, obliterated completely or, occasionally (about 5% of the species), an entirely different pattern was seen. In some seeds (about 10%), however, the pattern remained uniform all over. All seeds in a sample of a species always showed a similar pattern.

Stomata have been described from seeds of some *Bauhinia* (Leguminosae: Caesalpinioideae) species (Rugenstein and Lersten, 1981), but none were seen in any papilionoid seed examined.

Description of Testa Patterns

Nine categories accommodate the topographical variation. These patterns, based on their strongest manifestation near the hilum as seen at a standard magnification of 1000 (Fig. 7-28), are included in Table 1.

Levigate seeds appear smooth or almost so even when magnified 1000× (Fig. 7). This pattern merges imperceptibly in various taxa into the more conspicuous irregularly roughened, or rugulate, pattern. Two examples of the latter are shown in Fig. 8, 10. In some seeds, ridges of various lengths occur more or less parallel to each other, forming the substriate pattern (Fig. 9).

The reticulate pattern consists of a mesh of interlacing ridges. If only single cells are enclosed, the pattern was termed simple-reticulate (Fig. 11, 12). If the ridges enclosed a multi-cellular area, I called the pattern multi-reticulate; Fig. 13-16 show some variations.

A pattern opposite to reticulate is foveolate, in which separation is by grooves instead of ridges. In simple-foveolate, the grooves isolate single epidermal cells (Fig. 17, 18). The multi-foveolate pattern results when grooves surround more than 1 cell. Much variation was found in this category (Fig. 19-22) but no logical subdivision could be made.

The lophate pattern consists of short ridges with irregular sides. In some seeds these tended to merge with adjacent ridges (Fig. 23); in others they were mostly (Fig. 24) or completely (Fig. 25) distinct. Seeds of *Pseudoeriosema borianii* (Fig. 21) have a unique combination of a multi-foveolate pattern with a superimposed lophate pattern.

A papillose pattern results from the protrusion of individual epidermal (malpighian) cells. This pattern was seen rarely except in Vicieae (Fig. 27) and related Trifolieae (Fig. 32). The few other examples recorded were mostly irregularly papillose (Fig. 26) or, in the isolated example of *Dunbaria* (Phaseoleae), low papillae covered by a delicate cuticular reticulum (Fig. 28).

Cuticular blisters were noted in a dozen genera from distantly related tribes, mostly restricted to the vicinity of the hilum. Under the electron beam the blisters swelled and often burst (Fig. 34). I do not regard them as artifacts, but it is clear that they are affected by the electron beam. In the intact seed they may be tiny air spaces between epidermal cell wall and cuticle.

Two types of seed incrustation were encountered which are evidently contributed by the inner pod layer (endocarp). The seeds of 2 genera *(Barbieria (=Clitoria)* and *Nissolia)* had a testa covered by a smooth acellular substance to which many fibers adhered. The second type of covering shows cell outlines and appears to be a cellular remnant of the endocarp layer (Fig. 35, 36). This epitesta (perisperm and texture layer of others) was found only in some Phaseoleae and in *Bituminaria bituminosa* (Table 1).

Distribution of Testa Patterns Among Tribes

Table 1 contains observations on 340 species of 150 genera from 30 of the 32 tribes recognized by Polhill (1981). Seeds of Dipteryxeae and the monotypic Euchrestieae were not available. The following summary of individual descriptions, organized by tribes as listed in Table 1, concerns patterns near the hilum.

Swartzieae through Tephrosieae showed no trends except that seeds of these tribes mostly tended toward irregular patterns. In Galegeae, *Swainsona* stands apart with its thick, fissured cuticle (Fig. 6). Genera of Robinieae sampled had a singularly featureless testa with the exception of *Cracca* and *Poissonia*. Indigoferae had mostly rugulate seeds with mounds.

The large tribe Phaseoleae was well sampled (36 of 90 genera from all subtribes). The levigate to rugulate condition prevails, but other patterns occur including 5 scattered genera with the rather uncommon foveolate patterns. *Dunbaria*, with a papillose testa (Fig. 28), was distinctive within subtribe Cajaninae. The epitesta was restricted to Phaseoleae, except for *Bituminaria* (Psoraleeae), but seemed to occur only sporadically among its members (Table 1).

Psoraleeae, Amorpheae, and Aeschynomenae mostly had quite similar lophate seeds (Fig. 23, 25), whereas Adesmieae exhibited rugulate seeds. The well-sampled Galegeae was dominated by reticulate and foveolate patterns, and these were also mostly the patterns in Carmichaelieae.

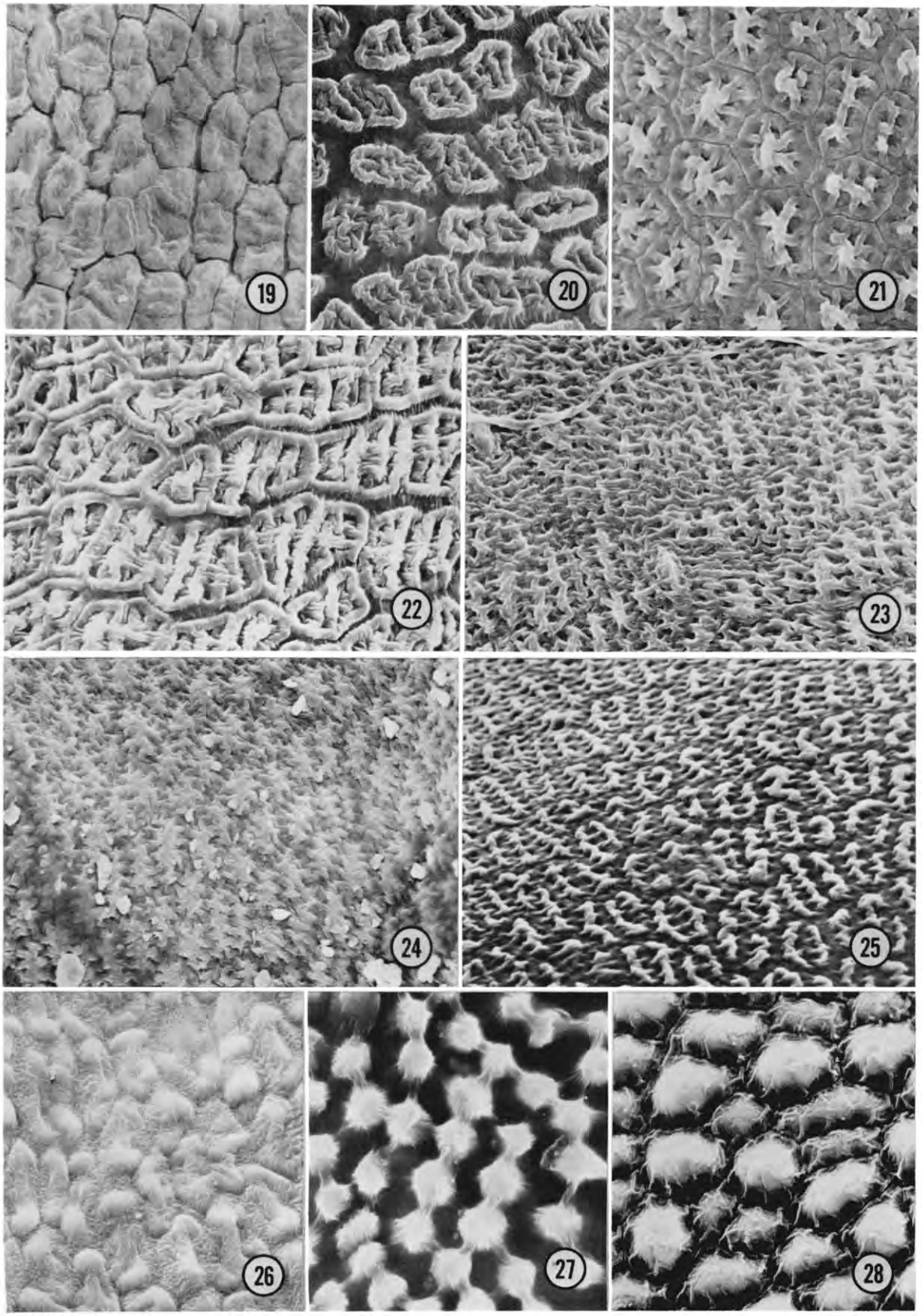
The Loteae and Coronilleae had quite similar mostly simple-reticulate seeds. In Hedysareae, multi-reticulate and foveolate patterns prevailed. The small samples of Bossiaeeae, Podalyrieae, and Liparieae show diversity among these tribes, but no trends. In Crotalarieae, however, *Crotalaria* and *Lebeckia* consistently showed a substriate pattern quite different from the distinctive multi-reticulate patterns of all 4 *Lotononis* species examined.

Because seeds of Vicieae sampled early in the survey were so obviously different from other legumes, this tribe was studied comprehensively and the results published elsewhere (Lersten, 1979; Lersten and Gunn, 1981a). Four seed characters occur consistently in Vicieae; papillose testa surface (e.g., Fig. 27), elongate hilum, virtual absence of a hilar rim, and a linear micropyle adnate to the hilum.

Trifolieae was also well sampled; it showed a progressive shift from elongate to circular hilum, from papillose with mounds (e.g., Fig. 31, 32) to loss of mounds and papillae. All Trifolieae examined had a conspicuous hilar rim. *Ononis, Trigonella, Factorovskya, Melilotus, Trifolium,* and *Parochetus* sequentially showed fewer testa characters in common with Vicieae (Lersten and Gunn, 1981a).

The monotypic Cicereae (Kupicha, 1977) had seeds so different from other legumes (Fig. 29) that a special effort was made to survey it. The results warranted a separate, expanded treatment (Lersten and

Fig. 19-28. *Detailed view of 3 near-hilar patterns, all at ×1000. 19.* Hypocalyptus subcordatus *(Liparieae). Multi-foveolate. 20.* Onobrychis cyri *(Coronilleae). Multi-foveolate with wide grooves. 21.* Pseudoeriosema borianii *(Phaseoleae-Glycininae). Multi-foveolate with lophate pattern superimposed. 22.* Onobrychis arenaris *(Coronilleae). Complex multi-reticulate. 23.* Eysenhardtia texana *(Amorpheae). Lophate, with anastomosing units. 24.* Biserulla pelecinus *(Galegeae). Lophate. 25.* Amorpha fruticosa *(Amorpheae). Lophate with mostly isolated units. 26.* Amphimas pterocarpoides *(Sophoreae). Irregularly papillose. 27.* Lathyrus hirsutus *(Vicieae). Regular, sharply papillose pattern. 28.* Dunbaria rotundifolia *(Phaseoleae-Cajaninae). Low papillose with overlying cuticular reticulum.*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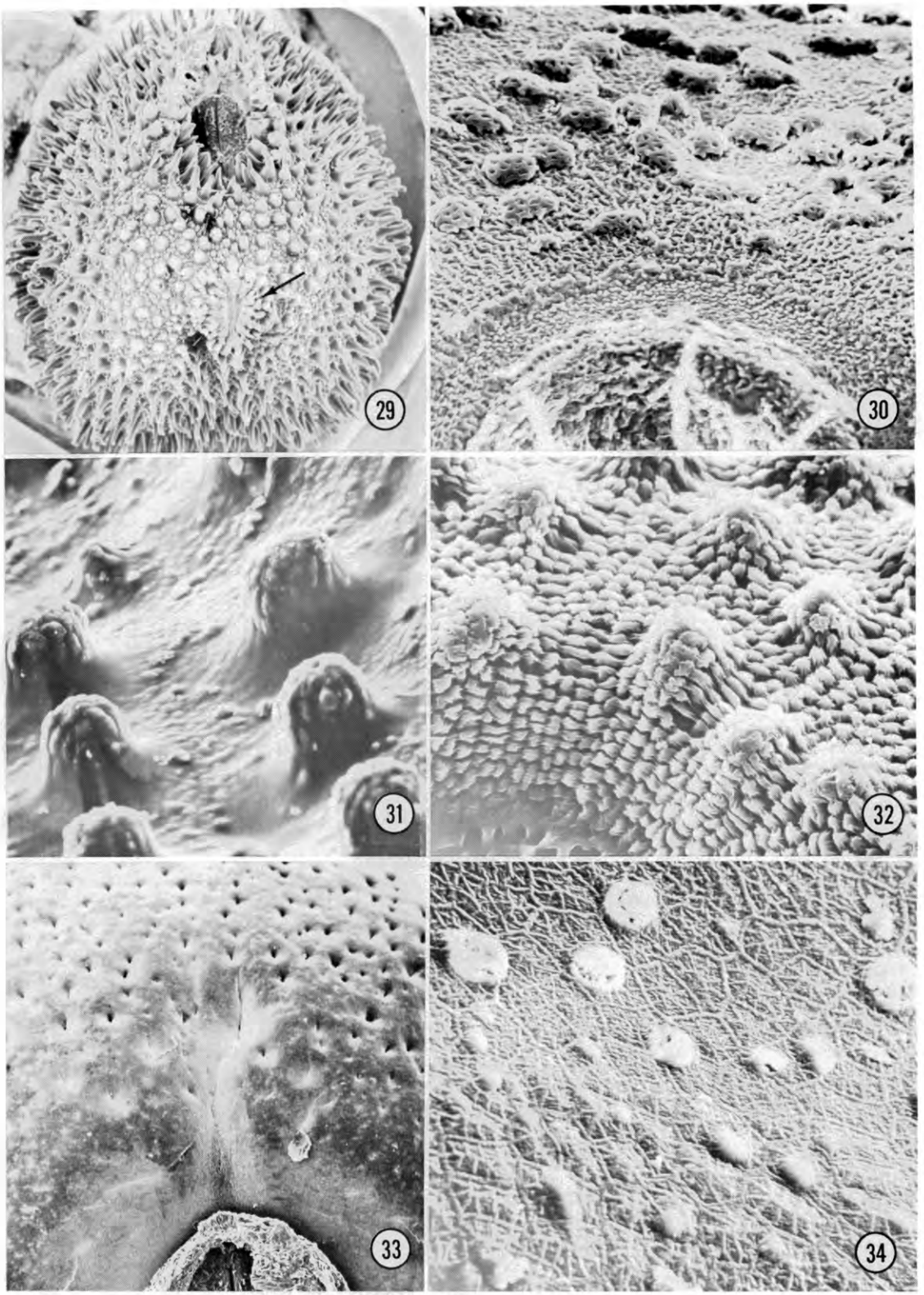

Fig. 29-34. *Additional testa features. 29.* Cicer bijugum *(Cicereae). Testa plates modified into spines. Arrow indicates lens. ×10. 30.* Cracca edwardsii *(Robinieae). One type of mound. ×200. 31.* Ononis mitissima *(Trifolieae). Another type of mound. ×400. 32.* Trigonella arabica *(Trifolieae). Papillose pattern and mounds. ×600. 33.* Cajanus cajan *(Phaseoleae-Cajaninae). Pitted testa. ×40. 34.* Ulex europaeus *(Genisteae). Testa with cuticular blisters. ×1000.*

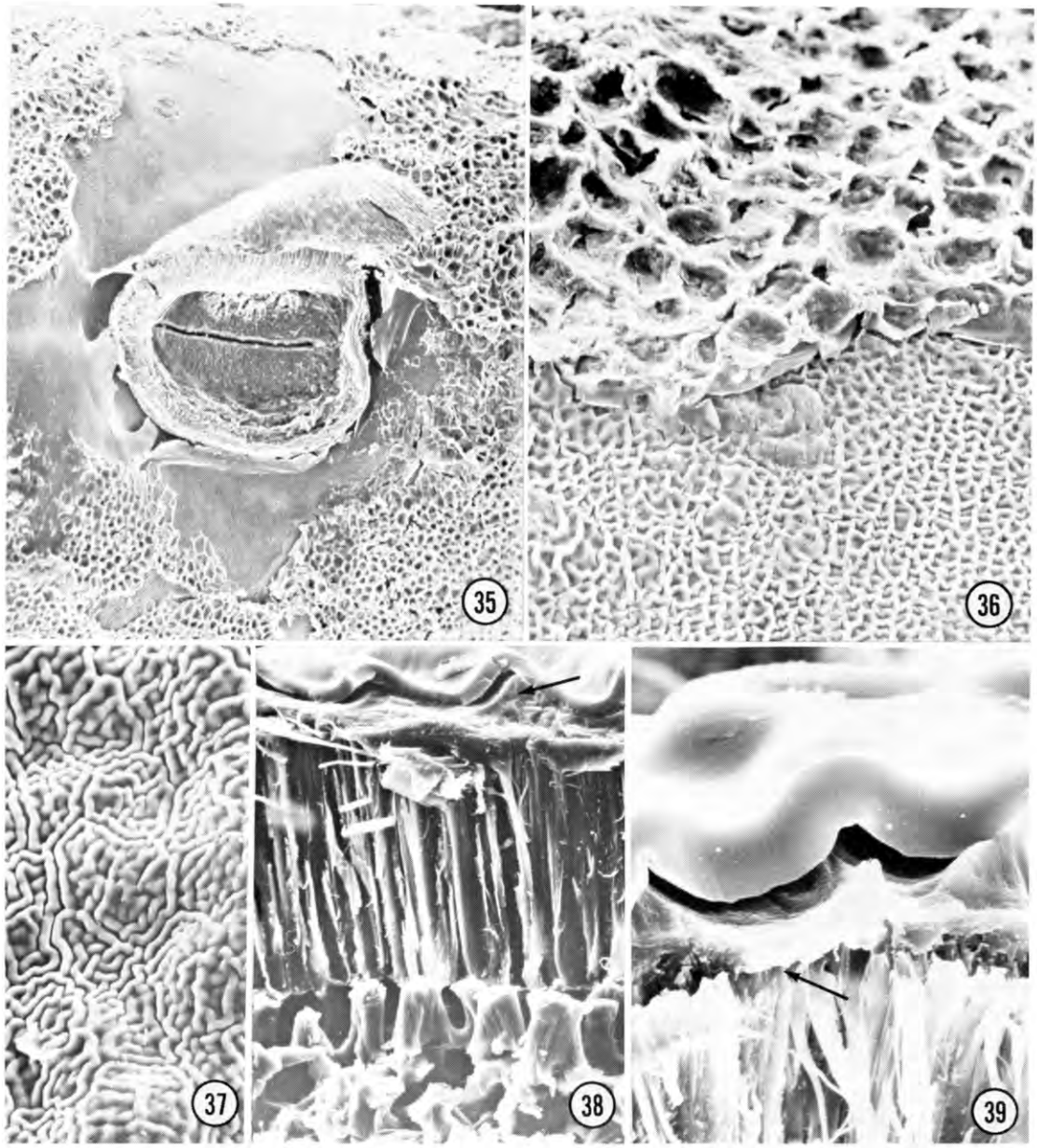

Fig. 35-39. *Unusual testa and associated features. 35.* Pseudeminia comosa *(Phaseoleae-Glycininae). Testa with patchy epitesta. ×30. 36. Enlarged portion of Fig. 35 to show epitesta top portion, true seed coat lower portion. ×200. 37.* Aotus ericoides *(Mirbelieae). Cuticular rugulate pattern. ×200. 38.* Brachysema uniflorum *(Mirbelieae). Transection of cuticular rugulate seed coat of type shown in Fig. 37. Arrow indicates non-cellular material between thick cuticle and underlying epidermal layer. ×360. 39.* Aotus subglauca *(Mirbelieae). Enlarged view of a testa such as in Fig. 38, showing unusually thick cuticle underlain by non-cellular material. Arrow indicates tip of epidermal cell layer. ×39.*

Gunn, 1981b). The basic testa unit is a large, multicellular plate of many cells, separated from other plates by a conspicuous fissure. It could be interpreted as a multifoveolate pattern, but on a far larger scale than seen elsewhere. Individual plates are flat in some species, bulging in some, conspicuously conical in others, and expanded into larger spinose protuberances in still other species (Fig. 29). In addition, the lens is far more elaborate than seen elsewhere (Fig. 29, arrow). Two species, however, *C. microphyllum* and *C. montbretii,* had seed shape and hilum similar to other *Cicer* species, but an inconspicuous lens and a papillose surface identical to Vicieae (Lersten and Gunn, 1981b).

The 3 genera sampled from Polhill's segregate tribe Mirbelieae all exhibited (except for one species of *Brachysema)* a feature not seen elsewhere, a massive rugulate pattern (Fig. 2, 3) formed entirely by the extremely thick cuticle. Epidermal cells appeared uniformly elongated

Table 1. *Testa topography in Papilionoideae. Taxa arranged as per Polhill (1981). Numbers correspond to taxa named in Appendix.*

Taxa (genera sampled / total genera)	Pattern near hilum	Fig. most similar
SWARTZIEAE (1/11)		
1.2a, 1.2b	rugulate	8
SOPHOREAE (18/48)		
2.19	levigate & pitted	8
2.18, 2.15, 2.23, 2.41, 2.45, 2.20a, 2.20b, 2.22, 2.47	rugulate	8, 10
2.26	rugulate & pitted	33
2.32, 2.44	substriate	9
2.43,	simple-foveolate	17
2.48, 2.2	multi-reticulate	13
2.7, 2.34	lophate	24
2.1	papillose (irregular)	26
DIPTERYXEAE (0/3)		
DALBERGIEAE (4/19)		
4.7	parenchymatous[a]	–
4.8, 4.10	rugulate	8
4.6	lophate	23
ABREAE (1/1)		
5.1c	levigate	7
5.1a, 5.1b, 5.1d	lophate	23
TEPHROSIEAE (10/50)		
6.4, 6.43a, 6.43b	levigate	7
6.39	levigate & pitted	23
6.30, 6.44	rugulate	10
6.21, 6.34	substriate	9
6.40	simple-reticulate	12
6.23	multi-reticulate	15
6.14	lophate	25
ROBINIEAE (11/21)		
7.6, 7.1	levigate	7
7.5, 7.14	levigate & pitted	7, 33
7.19, 7.9, 7.4, 7.21, 7.20a	rugulate	10
7.20b	substriate	9
7.8	simple reticulate	11
7.7	simple reticulate & mounds	30
INDIGOFERAE (2/4)		
8.2a, 8.4	levigate & mounds	7, 32
8.2b	rugulate & mounds[f]	8, 34
8.2c	simple-reticulate	12
DESMODIEAE (3/27)		
9.19, 9.9a	rugulate	8
9.9b	multi-foveolate	21
9.14	papillose (irregular)	26
PHASEOLEAE		
Erythrininae (4/9)		
10.6	levigate	7
10.3a	rugulate	10
10.1b	substriate	9
10.1a	simple-foveolate	17
10.3b	multi-foveolate	19
10.9	papillose (irregular)	26
Dioclinae (5/13)		
10.18, 10.10, 10.20 10.14, 10.13	rugulate	8
	simple-foveolate[g]	18
Glycininae (8/16)		
10.29, 10.34[g]	levigate	7
10.28, 10.37, 10.23,[g] 10.24,[g] 10.26a, 10.26b	rugulate	8, 10
10.36	simple-reticulate	11
Ophrestinae (1/3)		
10.40	multi-foveolate	21
Kennediinae (1/3)		
10.42	multi-foveolate	21
Clitoriinae (2/4)		
10.45, 10.47b	rugulate	10
10.47a	papillose (irregular)[c]	
Phaseolinae (9/23)		
10.69	levigate[g]	7
10.53, 10.60, 10.64, 10.59[g], 10.71, 10.50, 10.65a	rugulate	8, 10
10.65b, 10.70	lophate	23
Cajaninae (5/14)		
10.82, 10.78	levigate	7
10.81	rugulate	10
10.72	rugulate & pitted	10, 23
10.74	papillose	28
PSORALEEAE (3/6)		
11.5	rugulate	8
11.1a, 11.1b, 11.6	lophate	24, 25
AMORPHEAE (5/8)		
12.8b	levigate	7
12.2a	substriate	9
12.4, 12.8, 12.8c, 12.2b, 12.3	lophate	23
AESCHYNOMENAE (4/25)		
14.2	rugulate	8
14.8, 14.24	lophate	23
14.7	lophate[b]	23
ADESMIEAE (1/1)		
15.1a, 15.1b	rugulate	8
GALEGEAE (14/20)		
16.20, 16.10	levigate	7
16.11, 16.19	rugulate	8
16.14b, 16.14c, 16.9	simple-reticulate	11
16.14d, 16.15, 16.7, 16.18	multi-reticulate	13, 14
16.16	multi-reticulate and lophate[c]	14, 24
16.1, 16.5a, b, c, 16.4		
16.8, 16.3	simple-foveolate	17, 18
16.14a	lophate	24
16.2	thick cuticle[d]	6
CARMICHAELIEAE (2/5)		
17.5b	rugulate	8
17.5a	simple-reticulate	11
17.2	multi-reticulate	13
HEDYSAREAE (2/7)		
18.2	substriate	9
18.6e,f,g	multi-reticulate & pitted	13, 33
18.6a,d,h,i,j	simple-foveolate	17
18.6b,c	multi-foveolate	20
LOTEAE (3/4)		
19.4e, 19.3	rugulate	10
19.4a-d, f-j	simple-reticulate	12
19.2a,b	simple-reticulate & mounds	11, 30
CORONILLEAE (3/6)		
20.1a-d, 20.4	simple-reticulate	11
20.3a,b	simple-reticulate & mounds	12
VICIEAE (5/5)		
see Lersten and Gunn (1981a)	papillose, often with mounds	27
CICEREAE (1/1)		
see Lersten and Gunn (1981b)	large plates, spines	29
TRIFOLIEAE (7/7)		
see Lersten and Gunn (1981a)	papillose to rugulate, often with mounds	32
BRONGNIARTIEAE (2/2)		
24.2	multi-reticulate & pitted	14, 33
24.1a,b	lophate	23
MIRBELIEAE (4/23)		
25.17a,b, 25.1b,c, 25.19	rugulate cuticle	2, 37
25.1a, 25.20	multi-reticulate	13, 15

BOSSIEEAE (1/10)		
26.3	rugulate	8
PODALYRIEAE (2/3)		
27.1	levigate	7
27.3	simple-reticulate	12
LIPARIEAE (2/5)		
28.3	rugulate	10
28.1	multi-foveolate	19
CROTALARIEAE (4/16)		
29.6a-c, 29.1	substriate	9
29.8a-d,	multi-reticulate	13-15
29.4	multi-foveolate	21
29.6d	papillose (irregular)	26
THERMOPSIDEAE (2/6)		
31.5, 31.4	rugulate	8
GENISTEAE (6/20)		
32.17, 32.4, 32.1, 32.14	rugulate	8
32.1a,b, 32.20a,b	multi-reticulate	14,34

[a] seed circular, flat, lacking malpighian and sclereid layers; surface shows large polygonal shapes of parenchymatous epidermis

[b] seed away from hilum covered with smooth varnish-like coating in which many fibrous strands are embedded

[c] multi-reticulate on seed lobes, lophate elsewhere around hilum

[d] exceedingly thick cuticle obscures epidermal pattern

[e] retiuclum heavy on mounds, much less so between them

[f] mounds small and numerous all over; not clear if all are cuticular

[g] seed surface away from hilar area mostly covered by epitesta

but a homogeneous, non-cellular material occurred between epidermal cells and cuticle and conformed to the cuticular folds (Fig. 38, 39).

The 2 Thermopsideae genera examined both had rugulate seeds. In Genisteae, *Genista* and *Spartium* both showed a rugulate surface, and *Cytisus* and *Ulex* had a multireticulate pattern.

DISCUSSION

Papilionoideae has varied testa topography, but the patterns are revealed only at higher magnifications than are commonly needed in seed studies of other families. The pattern on a mature seed reflects epidermal configuration and cuticular deposition as influenced by seed expansion. LaSota *et al.* (1979) showed that in *Ononis* the pattern develops first on the side of the seed opposite the hilum instead of simultaneously all over; such differential maturation undoubtedly contributes to the differences so commonly seen in this study between patterns near the hilum and at midseed.

Simple patterns involving 1 cell (simple-reticulate, simple-foveolate, papillose) have been shown in transectional seed view to conform to underlying cell patterns. In contrast, some rugulate patterns are entirely of cuticular origin (Fig. 37-39). The patterns I have defined are based on mature, dry seeds and do not take into account development or relative contributions of underlying cells and cuticle. However, after having examined many seeds it seems reasonable to speculate that levigate, rugulate, substriate, and lophate patterns could be regarded as variations on one basic pattern as affected by growth of the seed, whereas reticulate, foveolate, and papillose patterns are fundamentally different.

I have shown in other papers arising from this survey that Vicieae, Trifolieae, and Cicerae are distinct based on seed characters (Lersten and Gunn, 1981a,b), but that seeds of intermediate morphology appear to link them. This supports Polhill's close association of these tribes (Polhill, 1981). Several investigations have shown that members of Vicieae and Trifolieae have a suberized "cap" or "adcrustation" at the external tip of each epidermal cell (Spurny, 1972). This wall specialization may be correlated with the papillose testa pattern. Other tribes should be surveyed for this feature using histochemical techniques.

Psoraleeae and Amorpheae are placed side by side by Polhill (1981), but Barneby (1977) did not regard them as closely related. The dominant lophate pattern in the taxa sampled in both tribes, however, suggests an affinity.

The Phaseoleae, with few exceptions, appears to have an undistinguished rugulate testa. Miège *et al.* (1978) also showed a rugulate surface in *Psophocarpus*, as did Gunn and LaSota (1978) in *Pueraria*, and Rajendra *et al.* (1975) in *Vigna*.

The Robinieae also has mostly levigate to rugulate testa patterns. Gunn and LaSota (1978) have shown a rugulate pattern in *Olneya tesota*, a member of this tribe.

Loteae and Coronilleae seem closely related based on their mostly reticulate testa patterns, thus supporting their contiguous placement by Polhill (1981). Saint-Martin (1978) also reported a simple-reticulate pattern in 12 of 15 species in 5 genera of Loteae that she studied (*Anthyllis, Dorycnium, Lotus, Securigera, Tetragonolobus*). The other 3 species were rugulate. Saint-Martin thus supports my observations in Loteae. In Hedysareae, *Onobrychis* deserves further study to see if the reticulate-seeded species and foveolate seeded species form two natural groups when correlated with other characters.

The Mirbelieae of Polhill (1981) appears from my sample to have unique seeds; more taxa need to be examined to see if seed characters help to define and delimit this tribe.

The SEM observations of Polhill (1976) are from fragmentary pieces of seed coat, but the patterns he showed were all rugulate: *Templetonia hookeri* (Bossieeae), *Coelidium roseum* and *Priestleya thunbergii* (Liparieae), and *Anagyris foetida* (Thermopsideae). These patterns are similar to those I found in other respresentatives of these 3 tribes (Table 1).

Saint-Martin (1978) included 12 species of 8 genera of *Genisteae (Adenocarpus, Chamaespartium, Cytisus, Genista, Goodia, Lupinus, Spartium, Ulex)*. All were rugulate except *Lupinus augustifolius*, which she reported as "cratered." We differ on *Cytisus* and *Ulex*, which I reported as multi-reticulate in 2 species of each genus (Table 1). Heyn and Hermstadt (1977) support Saint-Martin's report that *Lupinus* differs from the rest of the tribe. They showed that a multi-foveolate pattern (rather similar to that in Fig. 21) is dominant in the old world (*L. albus*, however, has a curious pattern much like that in Fig. 16) but that levigate to rugulate patterns occur in new world species. Midseed observations, however, appear to be the only basis for comparison. I also found a rugulate pattern in the new world *Lupinus caudatus*. The Genisteae displays a striking range of surface patterns among the taxa.

The major purpose of my survey was to see if tribal limits as postulated by Polhill (1981) could be supported by evidence from seed coat anatomy. The lack of available seeds for so many genera limited the sample in some tribes. In other tribes the variety of patterns seen do not support any conclusion at present. I have probably delimited the range of variation in general for the subfamily and established defined patterns that can be used by others. I have also demonstrated that, for seeds of most species, the surface pattern is pristine near the hilum, but attenuated toward the midseed. Testa surface patterns are significant within and between certain adjacent tribes but they will not, in my opinion, reveal broader evolutionary trends.

ACKNOWLEDGEMENTS

This work was supported by National Science Foundation grant DEB 78-04296. I thank Dr. C. R. Gunn, Curator of the Seed Herbarium, U.S. Dept. of Agriculture, for seeds and advice, and Seanna Rugenstein and Larry Hufford for technical assistance. Microscopy and ancillary procedures were carried out in the Bessey Microscopy Facility, Department of Botany, Iowa State University.

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APPENDIX

List of all taxa studied. Tribes and genera numbered as in tribal treatments in Polhill (1981). Letters designate species of genera in which more than one species was studied.

SWARTZIEAE: *Swartzia brachyrachis* (1.2a), *S. madagascarensis* (1.2b)

SOPHOREAE: *Acosmium nitens* (2.2), *Ammodendron connollyii* (.48), *Amphimas pterocarpoides* (2.1), *Ateleia herbertsmithii* (2.15), *Baphia massaiensis* (2.23), *Bolusanthus speciosus* (2.41), *Bowdichia virgilioides* (2.34), *Bowringia callicarpa* (2.26), *Cadia purpurea* (2.7), *Calpurnia aurea* (2.43), *Camoensia maxima* (2.19), *Cladrastis lutea* (2.45), *Clathrotropis nitida* (2.32), *Maackia amurensis* (2.44), *Ormosia calavensis* (2.20a), *O. krugii* (2.20b), *Pericopsis mooniana* (2.22), *Sophora davidii* (2.47), *Xanthocercis zambesiaca* (2.18)

DIPTERYXEAE: none

DALBERGIEAE: *Centrolobium robustum* (4.8), *Dalbergia obovata* (4.6), *Platymiscium praecox* (4.7), *Pterocarpus santalinus* (4.10)

ABREAE: *Abrus canescens* (5.1a), *A. laevigatus* (5.1b), *A precatorius* (5.1c), *A. pulchellus* (5.1d)

TEPHROSIEAE: (genera merely listed alphabetically in Geesink, 1981; I have added numbers) *Apurimacia dolichocarpa* (6.4), *Derris scandens* (6.14), *Lonchocarpus margaritensis* (6.21), *Milletia ovalifolia* (6.23), *Piscidia piscipula* (6.30), *Pongamia pinnata* (6.34), *Schefflerodendron gazense* (6.39), *Tephrosia candida* (6.40), *Wisteria floribunda* (6.43)

ROBINIEAE: *Coursetia microphylla* (7.6), *Cracca edwardsii* (7.7), *Diphysa robinioides* (7.19), *Gliriciridia sepium* (7.1), *Glottidium vescarium* (7.21), *Neocracca heteranthera* (7.9), *Olneya tesota* (7.5), *Poissonia hypoleuca* (7.8), *Robinia pseudoacacia* (7.4), *Sabinea carinalis* (7.14), *Sesbania bispinosa* (7.20a), *S. grandiflora* (7.20b)

INDIGOFERAE: *Cyamopsis tetragonoloba* (8.4), *Indigofera cordifolia* (8.2a), *I. pseudotinctoria* (8.2b), *I. subulata* (8.2c)

DESMODIEAE: *Alysicarpus vaginalis* (9.19), *Desmodium canum* (9.9a), *D. cuneatum* (9.9b), *Droogmansia wheptei* (9.14)

PHASEOLEAE—Erythrininae: *Apios americana* (10.6), *Erythrina macrophylla* (10.1a), *E. peoppingiana* (10.1b), *Mucuna deeringianum* (10.3a), *M. horrida* (10.3b), *Neorudolphia volubilis* (10.9)

PHASEOLEAE—Dioclinae: *Canavalia ensiformis* (10.13), *Cratylia mollis* (10.18), *Dioclea multiflora* (10.10), *Galactia volubilis* (10,20), *Pachyrhizus erosus* (10.14)

PHASEOLEAE—Glycininae: *Amphicarpa comosa* (10.38), *Cologania affinis* (10.37), *Dumasia truncata* (10.36), *Eminia antennulifera* (10.23), *Glycine max* (10.29), *Neonotonia wightii* (10.34), *Pseudeminia comosa* (10.24), *Pueraria lobata* (10.26a), *P. phaseoloides* (10.26b)

PHASEOLEAE—Ophrestiinae: *Pseudoeriosema borianii* (10.40)

PHASEOLEAE—Kennediinae: *Kennedia rubicunda* (10.42)

PHASEOLEAE—Clitoriinae: *Centrosema paseuouem* (10.45), *Clitoria terneata* (10.47a), *C.* (= Barbieria) *pinnata* (10.47b)

PHASEOLEAE—Phaseolinae: *Decorsea schlecteri* (10.53), *Lablab purpureus* (10.60), *Macroptilium lathroides* (10.70), *Marcotyloma uniflorum* (10.64), *Neorautenenia brachypus* (10.59), *Phaseolus vulgaris* (10.71), *Psophocarpus tetragonolobus* (10.50), *Strophostyles helvola* (10.69), *Vigna sinensis* (10.65a), *V.* (= Voandzeia) *subteranea* (10.65b)

PHASEOLEAE—Cajaninae: *Cajanus cajan* (10.72), *Dunbaria rotundifolia* (10.74), *Eriosema floribundum* (10.82), *Flemingia floribundum* (10.78), *Rhynchosia minima* (10.81).

PSORALEEAE: *Bituminaria bituminosa* (11.5), *Orbexillum bituminosa* (11.6), *Psoralea aphylla* (11.1a), *P. candicans* (11.1b)

AMORPHEAE: *Amorpha fruticosa* (12.4), *Dalea* (= Petalostemon) *gracilis* 12.8a) *D. leporina* (12.8b), *D. vernica* (12.8c), *Eysenhardtia orthocarpa* (12.2a), *E. texana* (12.2b), *Parryella filifolia* (12.3)

SESBANIEAE: included in Robinieae

AESCHYNOMENAE: *Aeschynomene indica* (14.8), *Nissolia schottii* (14.7), *Stylosanthes mucronata* (14.24), *Zornia diphylla* (14.2)

ADESMIEAE: *Adesmia incana* (14.1a), *A. smithiae* (14.1b)

GALEGEAE: *Alhagi persarum* (16.18), *Astragalus asper* (16.14a), *A. cicer* (16.14b), *A. contortuplicatus* (16.14c), *A. melilotoides* (16.14d), *Biserrula pelecinus* (16.16), *Caragana arborescens* (16.11), *Clianthus puniceus* (16.1), *Colutea cilicica* (16.5a), *C. melanocalyx* (16.5b), *C. orientalis* (16.5c), *Eremosparton flaccidum* (16.9), *Galega officinalis* (16.19), *Glycyrrhiza glandulifera* (16.20), *Halimodendron halodendron* (16.10), *Lessertia stricta* (16.4), *Oxytropis hirta* (16.15), *Smirnowia turkestana* (16.8), *Sphaerophysa salsula* (16.7), *Sutherlandia frutescens* (16.3), *Swainsona salsula* (16.2)

CARMICHAELIEAE: *Carmichaelia arborea* (17.5a), *C. flagelliformis* (17.5b), *Notospartium carmichaeliana* (17.2)

HEDYSAREAE: *Hedysarum alpinum* (18.2), *Onobrychis antasiatica* (18.6a) *O. arenaris* (18.6b), *O. cyri* (18.6c), *O. gaubae* (18.6d), O. gracilis (28.6e), *O. grandis* (18.6f), *O. melanotricha* (18.6g), *O. palasii* (18.6h), *O. stenorrhyza* (18.6i), *O. transcaucasica* (18.6j)

LOTEAE: *Anthyllis cornycina* (19.2a), *A. tetraphylla* (19.2b), *Hymenocarpos circinnatus* (19.3), *Lotus angustissimus* (19.4a), *L. arenarius* (19.4b), *L. corniculatus* (19.4c), *L. crassifolia* (1.4d), *L.* (= Dorycnium) hirsutum (19.4e), *L. ornithopodioides* (19.4f), *L.* (= Tetragonolobus) *purpureus* (19.4g), *L. purshianus* (19.4h), *L.* (= Dorycnium) *rectum* (19.4i), *L. tigerensis* (19.4j), *L. uliginosus* (19.4k)

CORONILLEAE: *Coronilla scorpioides* (20.1a), *C. valentina* (20,1b), *C. varia* (20.1c), *C. viminalis* (20.1d), *Ornithopus sativus* (20.4), *Scorpiurus muricatus* (20.3a), *S. sulcata* (20.3b)

VICIEAE: (5 genera, 88 species studied; results in Lersten and Gunn, 1981a)

CICEREAE: (11 species studied; results in Lersten and Gunn, 1981b)

TRIFOLIEAE: (7 genera, 27 species studied; results in Lersten and Gunn, 1981a)

BRONGNIARTIEAE: *Brongniartia canescens* (24.1a), *B. lupinoides* (24.1b), *Harpalyce loesneriana* (24.2)

MIRBELIEAE: *Aotus ericoides* (25.17a), *A. subglauca* (25.17b), *Brachysema lanceolatum* (25.1a), *B. subcordatum* (25.1b), *B. uniflorum* (25.1c), *Gastrolobium spinosum* (25.19), *Pultenaea daphnoides* (25.20)

BOSSIAEEAE: *Templetonia retusa* (26.3)

PODALYRIEAE: *Podalyria sericea* (27.3), *Virgilia divaricata* (27.1)

LIPARIEAE: *Hypocalyptus subcordatus* (28.1), *Priestleya hirsuta* (28.13)

CROTALARIEAE: *Crotalaria mucronata* (29.6a), *C. recta* (29.6b), *C. spectabilis* (29.6c), *C. usaramoensis* (29.6d), *Lebeckia multiflora* (29.1), *Lotononis argolensis* (29.8a), *L. bainesii* (29.8b), *L. divaricata* (29.8c), *L. heterophylla* (29.8d)

THERMOSIDEAE: *Baptisia leucophaea* (31.5), *Thermopsis montana* (31.4)

GENISTEAE: *Cytisus maderensis* (32.11a), *C. scoparius* (32.11b), *Genista raetan* (32.17), *Laburnum anagyroides* (32.4), *Lupinus caudatus* (32.1), *Spartium junceum* (32.14), *Ulex europaeus* (32.20a), *U. nanus* (32.30b)