

POLLEN MORPHOLOGY OF THE TRIBE DESMODIEAE (LEGUMINOSAE) IN TAIWAN⁽²⁾

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Abstract: The pollen morphology of 12 genera and 34 species belonging to the Desmodieae in Taiwan was studied by light microscope, scanning electron microscope and transmission electron microscope. The great variation in pollen characteristics among these plants was examined.

According to pollen morphology and exine stratification, the pollen grains can be divided into six types. (I) The tectum is coarsely reticulate and distinctly marginate on colpial margins. It has operculum-like structure. The simple columellae have no granular interstitium. (II) This type is divided into two subtypes. (a) The tectum is finely reticulate, marginate and microperforated; the colpus membrane is finely granulate; and the foot layer is reduced. (b) The tectum is reticulate, and it has no microchannel and granular interstitium. The endexine is thicker than the tectum. (III) The tectum is coarsely verrucate or weakly rugulate. Only the pollen of *Alysicarpus* sp. has mesocolpial pouches partially covering the endoapertures. (IV) The tectum is microperforated or weakly rugulate; and the foot layer is discontinuous and reduced. (V) The tectum is finely reticulate; the foot layer is thin and discontinuous. (VI) The tectum is microperforated; the columellae are replaced by granular interstitium; and there is no foot layer.

INTRODUCTION

The majority of Desmodieae are distributed in subtropic areas (Ohashi, 1973). The Desmodieae are taxonomically recognized as three subtribes, only two in Taiwan, i.e. Desmodiinae and Lespedezinae. These two subtribes consist of 12 genera and 45 species. These plants of Desmodieae have herbs, shrub or small trees. The taxonomists formerly emphasized the morphological studies of these plants. These species are localized widely in Taiwan. Huang & Huang (1987) classified the Papilionoideae of Taiwan based on external features. They had not examined pollen wall sculpture and exine stratification. Ohashi (1971, 1973) has studied the pollen morphology of Desmodieae by light microscopy. Ferguson (1984), Ferguson & Skvarla (1979) and Ohashi (1971) have described the pollen morphology of two genera (*Brya* and *Cranocarpus*) of Desmodieae as polyporous. This feature of their pollen differs from that of the other genera. It is suggestible to put these two genera in one subtribe. Hoshi and Ohashi (1987) have described the new species *Maackia taiwanensis* Hoshi and Ohashi by SEM and TEM.

Ferguson and Skvarla (1983) have reported that the pollen grains of Papilionoideae have a wide range of transitional forms of granular interstitia. They have divided the pollen of Papilionoideae into three types: (1) with large, widely spaced irregular granules; (2) with densely packed groups of columellae and granules; and (3) with a mass of more or less disorganized granules. They have proposed that the pollen of Desmodieae and the other five tribes have granular structures; however, these six tribes have more advanced external characteristics. They have concluded that the granular interstitium is a derived structure in Papilionoideae.

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Lately light microscopy and electron microscopy are used to examine the pollen morphology(shape, sculpture, and exine stratification) to distinguish plants in the Desmodieae. These plants have different taxonomic characters and considerable variation in pollen sculptures. We still found some similarities among exine patterns and wall stratification of these plants. It was proposed that the evolutionary patterns of Desmodieae were gradually divergent. We hope to provide more comprehensive and detailed informations of pollen of Desmodieae to help taxonomists interpret relationships among these genera of Desmodieae and their evolutionary pathway.

MATERIALS AND METHODS

Pollen grains of 12 genera and 34 species of Desmodieae were mostly collected from the field in Taiwan, though some were obtained from the TAI Herbarium specimens(Table 1). Materials for light microscope were prepared by the acetolysis method(Erdtman, 1952). The pollen grains were mounted in glycerol jelly, observed and measured with Nikon Optiphot LM. The samples for SEM were dehydrated in the ethyl-alcohol series, by critical point drying, placed on specimen stubs, sputter coated with gold and examined with HITACHI S-520 SEM. The fresh materials for TEM were prefixed in 0.2% glutaraldehyde immediately after collection, transferred to 2.5% glutaraldehyde for 12-14 hours, postfixed in 1% osmium tetroxide for 1-2 hours, rinsed in phosphate buffer half hour, dehydrated in a graded ethanol series, transferred to 100% acetone, embedded in Spurr's resin(Spurr, 1969), and sectioned in 600-750nm thickness. The sections were pre-stained with 5% uranyl acetate and post-stained with lead citrate, then examined and photographed with HITACHI 600 TEM.

The terminology follows Erdtman (1969), Faegri & Iversen(1975), Guinet(1981), Hideux & Ferguson (1976), Huang (1972).

RESULTS

General pollen morphology

The pollen of the Desmodieae is tricolporate and spheroidal, prolate to oblate in equatorial view. The amb types are circular to semiangular, and a few are subangular. The pollen is small to middle in size, ranging from 17 μm to 60 μm in P axes and 17 μm to 65 μm in E axes. The endoapertures are round or elliptic (lalongate or lolongate). The length of endoapertures are about a quarter of colpi in these pollen grains; and the length of colpi is about 3/4 to 4/5 of P axes. The colpial margins are well differentiated in the majority of these genera. The colpus membrane is granulate, with the exception of some species of *Desmodium*. Most of the pollen grains have reticulate or verrucate tectum, but three genera (*Codariocalyx*, *Pycnospora* and *Uraria*) do not. The interstitia are usually columellae, or gradually substituted by granular interstitia. The foot layer of some species is absent. The endexine is well developed and thick. The mesocolpial pouches are obvious in some genera.

Alysicarpus -- Fig.1, A-F; Fig.9, A-B. A genus of four species of herbs in Taiwan. They were examined in our study. The pollen grains of *A. bupleurifolius*, *A. ovalifolius* and *A. vaginalis* have more obvious exine sculpture and endoaperture than that of *A. rugosus*. The former three species have larger subcircular to lalongate endoapertures. The length of endoapertures is about 1/2 to 2/3 of the colpi. The length of colpi is near 3/4 of P axes. After acetolysis, the mesocolpial pouches often open out or collapse; the colpus membrane is densely granulated with coarse granules; the tectum is scabrate to verrucate, weakly perforated; the colpus margins are differentiated. The pollen of *A. rugosus* is dissimilar from that of the other species; it is smaller in size and with thinner exine (Table 1); the shape is oblate

Table 1. List of specimens of Desmodieae examined in this study

species	Collection	p (μm)	E (μm)	P/E	Exine Thickness	
<i>Alysicarpus</i>						
<i>bupleurifolius</i> (L.) DC.	S. F. Huang	3244	41-58	43-60	0.90-1.12	3-4.2
<i>ovalifolius</i>	S. J. Chen	45	19-22	18-23	0.96-1.05	1.5-2
<i>rugosus</i> (Willd) DC.	S. F. Huang	967	33-37	39-43	0.73-0.87	1.5-2.5
<i>vaginalis</i> (Willd) DC.	T. C. Huang	14448	40-60	40-65	0.84-1.2	2.5-3.5
<i>Campylotropis</i>						
<i>giraldii</i> (S.) Schindle	"	13351	23-30	20-29	0.97-1.36	1.2-2.0
<i>Christia</i>						
<i>obcordata</i> (Poir.) Bakh. f. ex van Meeuwen	"	12997	27-44	25-37	0.97-1.5	1.5-2.5
<i>Codariocalyx</i>						
<i>motorius</i> (Houtt.) Ohashi	T. C. Huang	14446	30-51	30-41	1-1.67	1.5-2.5
<i>Dendrolobium</i>						
<i>dispermum</i> (Hay.) Schindle	"	13773	26-33	22-30	1.02-1.51	1-1.5
<i>triangulare</i> (Retz.) Schindle	"	13777	21-28	17-21	1.07-1.65	1-1.5
<i>umbellatum</i> (L.) Benth	K. C. Yang	s.n.	27-34	20-28	1.2-1.6	1.5-2
<i>Desmodium</i>						
<i>caudatum</i> (Thunb.) DC.	"	"	22-28	17-22	1.02-1.37	1.5-2.5
<i>gangeticum</i> (L.) DC.	"	"	26-31	18-22	1.31-1.56	1-1.5
<i>heterocarpon</i> var. <i>heterocarpon</i> (L.) DC.	T. C. Huang	13790	25-35	31-47	0.84-0.90	1.5-2.5
<i>heterocarpon</i> var. <i>strigosum</i> van Meeuwen	S. F. Huang	s.n.	24-29	30-35	0.77-0.85	1.5-2
<i>heterophyllum</i> (Willd.) DC.	T. C. Huang	13775	37-50	44-55	0.82-1	2-3.2
<i>intortum</i> (DC.) Urb.	T. S. Hsieh	554	27-35	32-39	0.75-0.93	2.5-4
<i>laxiflorum</i> subsp. <i>parvifolium</i> <i>parvifolium</i> Ohashi & Chen	T. C. Huang	14402	26-34	29-34	0.92-1.31	1.5-2.5
<i>laxum</i> subsp. <i>laterale</i> (Schindl.) Ohashi	T. C. Huang	13765	25-29	24-27	0.93-1.01	1.5-2.5
<i>laxum</i> subsp. <i>leptopus</i> (A. Gray ex Benth) Ohashi	K. C. Yang	1613	32-40	24-30	1.13-1.42	2-3.5
<i>microphyllum</i> (Thunb.) DC.	T. C. Huang	13912	28-37	30-40	0.99-1.16	2-3
<i>multiflorum</i> DC.	"	14456	27-31	20-28	1.07-1.4	1.5-2.5
<i>scorpiurus</i> (Swartz) Desvaux	"	13967	24-30	24-29	0.96-1.12	1.5-2
<i>sequax</i> Wall	"	13350	24-31	19-24	1.09-1.53	1-1.5
<i>triflorum</i> (L.) DC.	"	13790	33-42	29-38	0.93-1.39	2-3
<i>velutinum</i> (Willd) DC.	K. C. Yang	s.n.	23-28	18-24	1.04-1.39	1-1.5
<i>Kummerowia</i>						
<i>striata</i> (Thunb.) Schindle	S. F. Huang	3800	22.5-26.5	17-24	0.96-1.41	1.5-2.5
<i>Lespedeza</i>						
<i>chinensis</i> (G.) Don	T. C. Huang	13356	21-28	17-25	1-1.3	2-3
<i>cuneata</i> (Dumont d. Coours.) G. Don	S. J. Chen	132	20-26	17-25	0.96-1.47	1.5-2
<i>pubescens</i> Hay.	T. C. Huang	13903	23-29	17-22	1-1.42	1-2.5
<i>virgata</i> (Thunb.) DC.	S. F. Huang	1825	17-21	17-21	1-1.2	1.5-2
<i>Phyllodium</i>						
<i>pulchellum</i> (L.) Desvaux	T. C. Huang	13760	29-37	26-34	1.03-1.55	1.5-2.5
<i>Pycnospora</i>						
<i>lutescens</i> (Poir.) Schindle	"	14410	28-40	23-35	1-1.41	1.5-2.5
<i>Tadehagi</i>						
<i>triquetrum</i> subsp. <i>pseudotriquetrum</i> (DC.) Ohashi	"	13778	19.5-27.5	20-26	0.80-1.3	1.5-2
<i>Uraria</i>						
<i>crinita</i> (L.) Dext. ex DC.	"	13884	40-55	29-41	1.18-1.52	2-3
<i>lagopodioides</i> (1) (L.) Desv.	K. C. Yang	s.n.	40-54	30-42	1.07-1.38	2-3.5
<i>lagopodioides</i> (2)	"	"	35-43	30-35	1-1.33	2-3

(1) The pollen of this type has psilate and microperforated tectum.

(2) The pollen of this type has coarsely granulate to verrucate tectum.

spheroidal to suboblate in equatorial view; there are no mesocolpial pouches; the colpus membrane is sparsely covered by fine granules.

The fractured pollen wall of *A. vaginalis* demonstrates its exine stratification as: the tectum is verrucate; there are many granules between the columellae; the columellae are shorter than the tectum, about 0.25-0.3 μm in length; the foot layer is continuous, thinner than the endexine and about 0.05-0.1 μm ; the endexine is thin, but is as thick as the tectum under the endoapertures.

Campylotropis--- Fig.1,G-I; Fig.9,C-D. This is a monotypic genus of deciduous shrubs in Taiwan. The pollen of *C. giraldii* is circular in polar view and prolate to oblate spheroidal in equatorial view. There are prominent and lalongate endoapertures. In SEM, the mesocolpial pouches are clearly visible. After acetolysis, the coarsely granular colpus membrane often ruptures and the mesocolpial pouches protrude to the endoaperture. The tectum is finely-reticulate with irregular polygonal lumina, but psilate on the colpus margins. The colpi are equal in length to the polar axis and the colpus margins are distinctly undulate.

The tectum is thick, ridged with sparsely microperforation, about 0.33-0.4 μm ; the simple columellae are shorter than the other parts in exine stratification and no granular interstitia; the foot layer is well developed and thinner than the tectum, about 0.05-0.1 μm in thickness; the endexine is as thick as the tectum and twice thicker the mesocolpial regions.

Christia-- Fig.1,J-L; Fig.9, E-F. There are two species of this genus in Taiwan. Both are herbs. The pollen of *Christia obcordata* is examined here. The pollen is semi-angular in polar view and prolate to oblate spheroidal in equatorial view. It has round, lalongate endoapertures, easily observed in LM and SEM. Mesocolpial pouches are present and obvious. In some pollen grains, the pouches partially cover the endoapertures. The colpus membrane is covered by many coarse granules. The tectum is finely striate and weakly rugulate. The lumen are often filled with sexinous remnants.

The tectum is continuous and with sparse microperforation; the columellae are gradually reduced and the granular interstitia are increased toward the aperture; the foot layer is discontinuous and thinner than the tectum; the endexine is as thick as the tectum, but thicker at the colpial regions and not well developed under the endoapertures.

Codariocalyx -- Fig.2,A-C; Fig.9, G-H. This is another monotypic genus of shrubs of Desmodieae in Taiwan. The shape of pollen is subangular in polar view and prolate to prolate spheroidal in equatorial view. The endoapertures are relatively large circular, lalongate and they are easily examined in LM. Mesocolpial pouches are obscure, and the colpus membrane is granulate. The granules are arranged in order on the colpial margins. The tectum is psilate or weakly scabrate.

The tectum is thicker than the endexine, but not equal everywhere in the pollen wall. It is often sparsely microchannelled; the columellae are reduced and shorter than the tectum, 0.1-0.2 μm in length, they gradually disappear near the colpi, but they are not substituted with granular interstitia; the foot layer is not clearly defined and discontinuous; the endexine is gradually thickened near the colpi, about 0.6-0.8 μm in thickness.

Dendrolobium -- Fig.2,D-J; Fig.3,A-C; Fig.9,I-J. There are three species of shrubs and small trees in this genus. The pollen of three species were examined in this study. The shape of *D. dispernum* and *D. umbellatum* is subcircular in polar view, nevertheless, *D. triangulare* is loblate. They are prolate to prolate spheroidal in equatorial view. All of three species have large and obvious endoapertures. The endoapertures of the former two species are lalongate, but the latter is more circular. The mesocolpial pouches are obvious in *D. dispernum* and *D. triangulate*, but in the latter

A: aperture; **CO:** columella; **dT:** discontinuous tectum; **EN:** endexine; **FL:** foot layer; **GI:** granular interstitium; **IN:** intine; **MC:** microchannel; **MP:** microperforation; **OP:** operculum; **rCO:** reduced columellae; **rFL:** reduced foot layer; **T:** tectum; **WL:** white line.

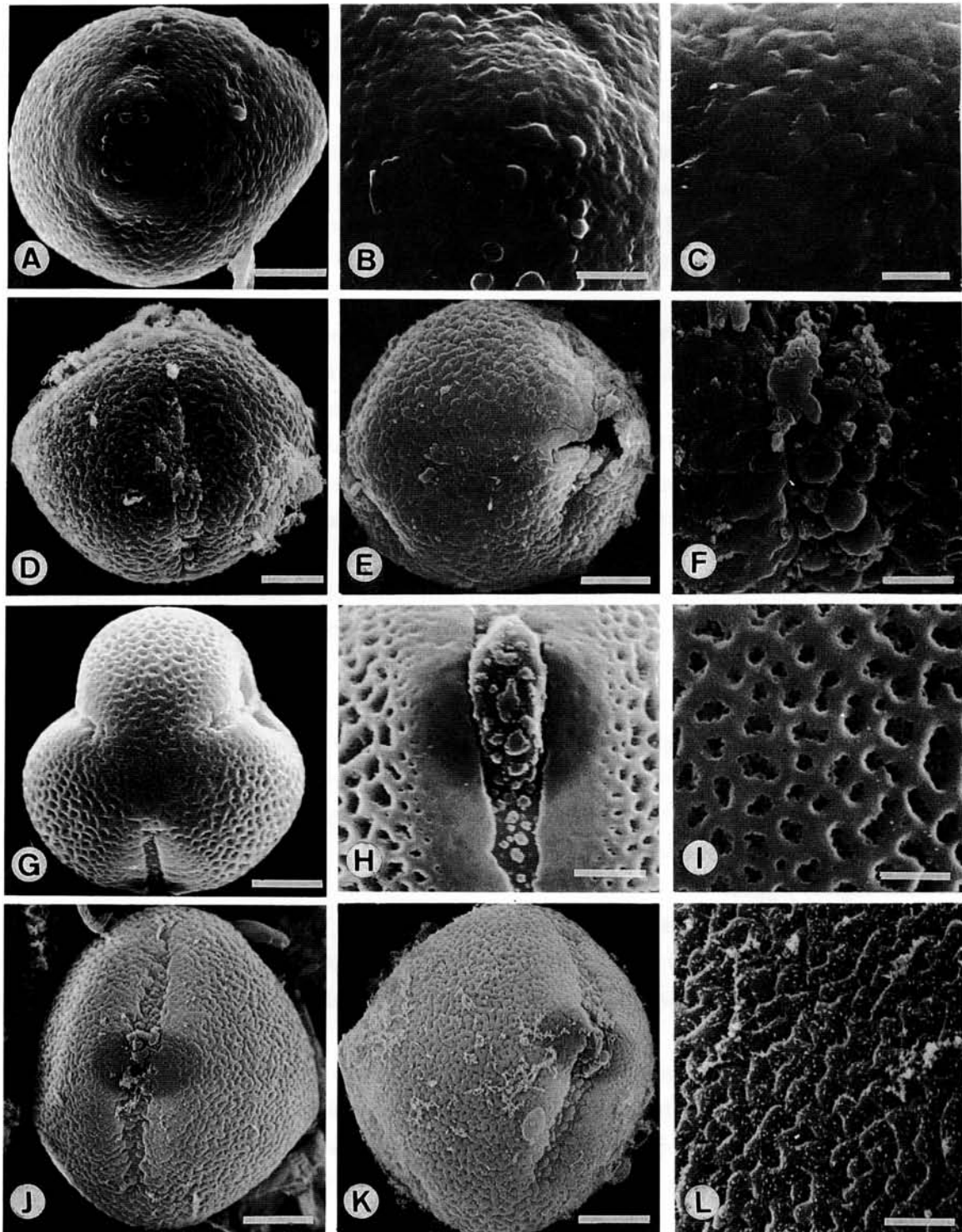


Fig. 1: A-C: *Alysicarpus rugosus*. A. Equatorial view showing short colpus, bar=8.8 μ m; B,C. Detail of sparsely granular colpus membrane and intermesocolpium with verrucate tectum, bar=3 μ m. D-F: *A. vaginalis*. D,E. Equatorial view showing mesocolpus without pouches; intermesocolpium with verrucate tectum, bar=7.5 μ m; F. Detail of densely granular colpus membrane, bar=1.5 μ m. G-I: *Campylotropis girdalii*. G. Polar view showing mesocolpial pouches, bar=4.3 μ m; H,I. Detail of psilate tectum on colpus margins; lalongate endoaperture; and finely-reticulate tectum on intermesocolpium, bar=1.5 μ m. J-L: *Christia obcordata*. J,K. Equatorial view showing lalongate endoaperture and densely granular colpus membrane, bar=3.7 μ m; L. Detail of slightly striate/rugulate tectum with sexinous remnants, bar=1.5 μ m.

does the pouch almost completely cover the endoaperture. The mesocolpial pouches does not appear in *D. umbellatum*. The colpus membrane is sparsely covered by fine granules. The tectum is coarsely reticulate, with irregular or polygonal lumina about 0.5-1 μm in diameter. There are many short rod-like remnants within lumina. The tectum has only a few microperforations at colpus margins.

The tectum is thick and discontinuous; the simple columellae are shorter than the tectum, but as long as the foot layer. The foot layer of *D. dispersum* is thicker than that of the other two species and undulate on the surface. It has no microchannels, and is about 0.15-0.2 μm . The pollen of *D. umbellatum* has a continuous foot layer. The endexine is well developed, about 0.2-0.25 μm in thickness in *D. dispersum* and *D. umbellatum* but thickened endexine is under the endoaperture.

Desmodium -- Fig.3,D-L; Fig.4-5,A-L; Fig.6,A-C; Fig.10,A-F. There are 20 species of herbs of this genus in Taiwan. The pollen of 15 species are examined in this paper and divided into five groups.

Group 1. *D. caudatum* (Fig.3,D-F) is representative of the group. The amb type is circular, and the equatorial view is prolate to prolate spheroidal. The endoapertures are lalongate, about 3.5-5 μm in width. The mesocolpial pouches slightly protrude toward the endoapertures. The colpus membrane is finely granular. The tectum is coarsely reticulate with irregular or rectangular lumina. The colpus margins are less differentiated, jagged and microperforated.

The fractured pollen was examined to study the exine stratification. The thick tectum has microperforations; the columellae are unevenly thick, and there is no granular interstitium; the foot layer is thinner than the endexine; the endexine is well developed, as thick as the tectum about 0.8-1.2 μm .

Group 2. *D. laxiflorum* subsp. *parvifolius*, *D. laxum* (Fig.4,G-I), *D. multiflorum* (Fig.5, A-C) and *D. sequax* (Fig.5,G-I) are representatives of this group. The amb type is circular or semi-angular and the equatorial view is subprolate to suboblate. The endoapertures are lalongate. The mesocolpial pouches are often protruded toward and partially covering the endoapertures. The colpus membrane is covered by coarse granules. The larger granules are arranged near the endoapertures. The tectum is finely reticulate, having small muri. The colpus margins are well differentiated and slightly jagged.

The tetum is thick and microperforated, about 0.6-0.8 μm in thickness. The simple columellae are thinner than the thickness of tectum layer, and narrowly spaced. There is no granular interstitium. The foot layer is thin, distinct and continuous. The endexine of these pollen grains is well developed, as thick as the tectum. They are not thickened under the endoapertures.

Group 3. *D. intortum* (Fig.4,A-C) and *D. scorpiurus* (Fig.5,D-F) are representatives. Both of them came from South America. The pollen grains is subangular in polar view. In equatorial view, is oblate spheroidal to suboblate. The pollen of *D. intortum* is like syncolporate type. Endoapertures are lalongate. The mesocolpial pouches are obscure. The granular colpus membrane is well differentiated. The tectum is verrucate and weakly rugulate. The colpus margins are slightly jagged in *D. scorpiurus*. There are microperforations at the colpus margins. In *D. intortum* the tectum forms obvious smooth colpus margins.

Group 4. *D. heterophyllum*, *D. microphyllum* (Fig.4,J-L; Fig.10,E-F), and *D. triflorum* (Fig.5,J-L) are representatives.

The pollen of these species is semi-angular in polar view and spheroidal to suboblate in equatoial view. The endoapertures of *D. heterophyllum* and *D. microphyllum* are lalongate, but in *D. triflorum* are lolongate. All of their mesocolpial pouches are obscure, the colpus membrane is covered by fine granules, and the colpus margins are well differentiated and microperforated in *D. triflorum*. The pollen of *D. microphyllum* has undifferentiated colpus margins. The tectum is finely reticulate and weakly rugulate.

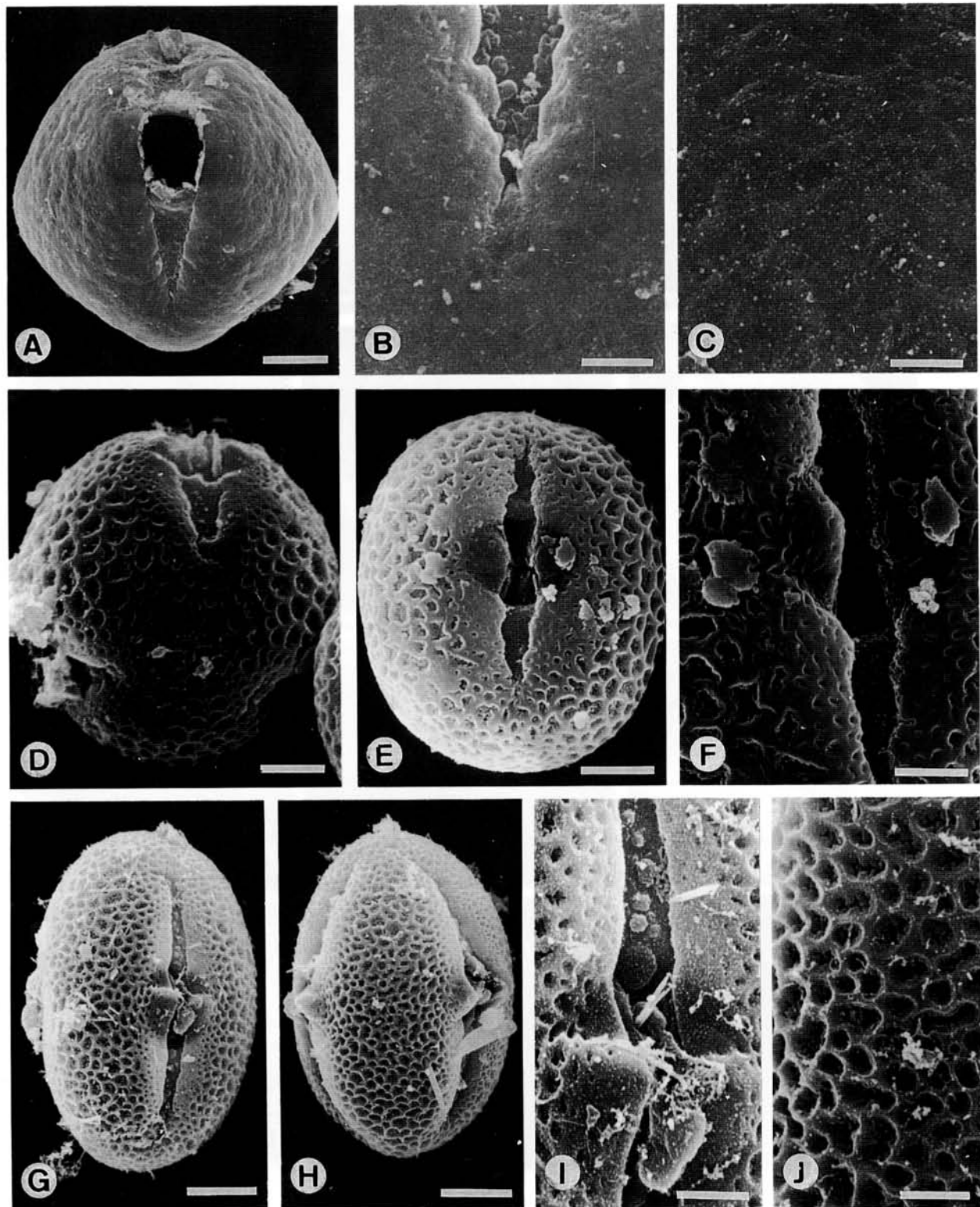


Fig. 2: A-C: *Codariocalyx motorius*. A. Equatorial view showing mesocolpus without obvious pouches, bar=6 μ m; B,C. Detail of colpus margins with orderly arranged granules and psilate/weakly scabrate tectum, bar=1.5 μ m. D-F: *Dendrolobium dispersum*. D. Polar view showing coarsely reticulate tectum, bar=3 μ m; E. Equatorial view showing longitudinal endoaperture, bar=3 μ m; F. Detail of undifferentiated mesocolpial margin, bar=1.5 μ m; G-J: *D. triangulare*. G,H. Equatorial view showing mesocolpial pouches and round endoaperture, bar=5 μ m; I,J. Detail of sparsely granular colpus membrane and finely reticulate tectum, bar=1.5 μ m.

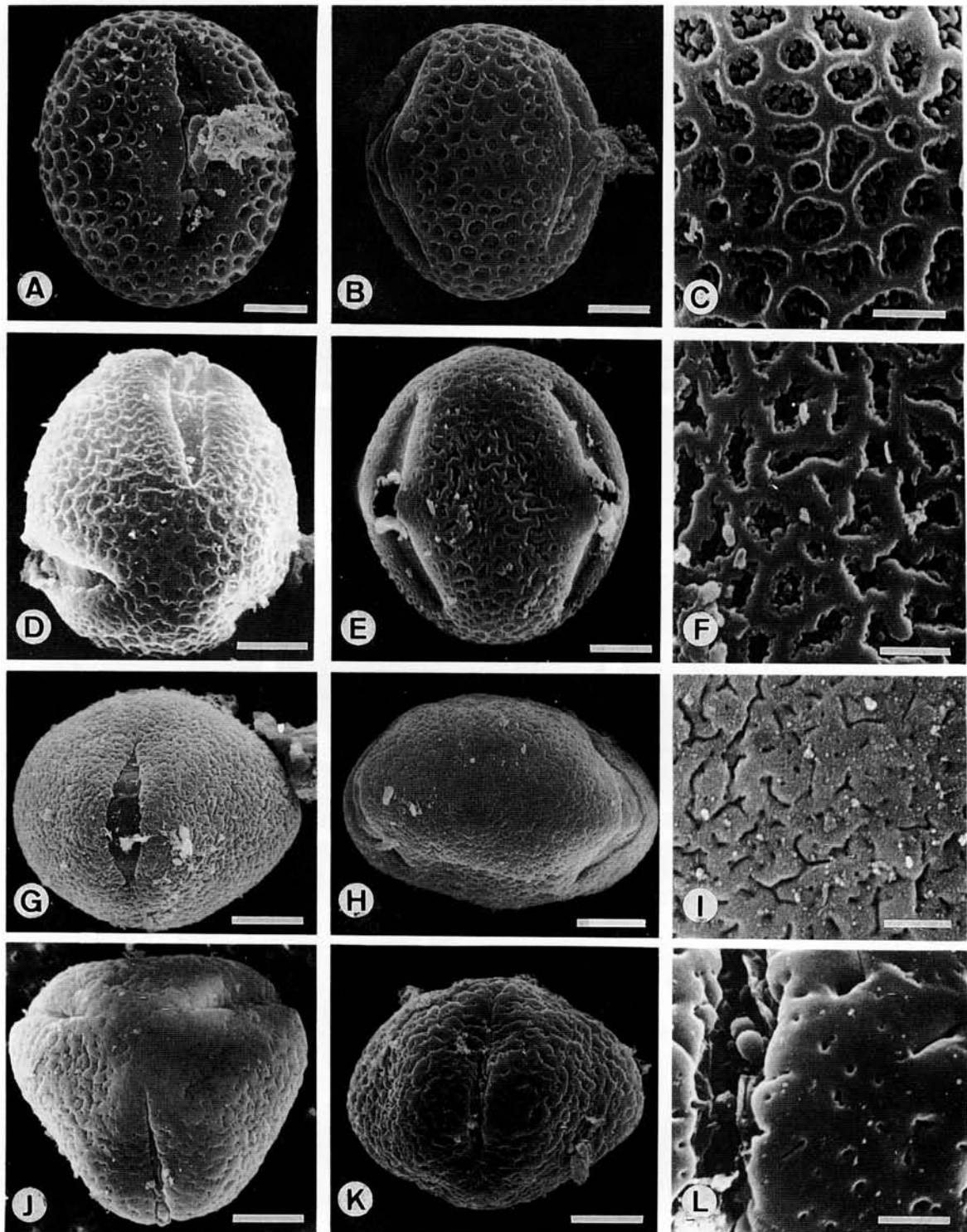


Fig. 3: A-C: *Dendrolobium umbellatum*. A,B. Equatorial view showing colpous margins with undifferentiated tectum and intermescolpium with coarsely reticulate tectum, bar=5 μ m; C. Detail of lumina with short rod-like remnants, bar=1.5 μ m. D-F: *Desmodium caudatum*. D. Polar view showing slightly mesocolpial pouches, bar=3.7 μ m; E. Equatorial view showing intermesocolpium, bar=3.7 μ m; F. Detail of tectum with irregularly rectangular lumina, bar=1.5 μ m. G-H: *D. heterocarpon* var. *heterocarpon*. G,H. Equatorial view showing colpus and intercolpium with finely reticulate tectum, bar=7.5 μ m; I. Detail of markedly rugulate tectum, bar=1.5 μ m. J-L. *D. heterocarpon* var. *strigosum*. J. Polar view showing semiangular pollen, bar=7.5 μ m; K. Equatorial view showing well developed coplus margins, bar=7.5 μ m; L. Detail of colpus membrane with finely granules, bar=1.5 μ m.

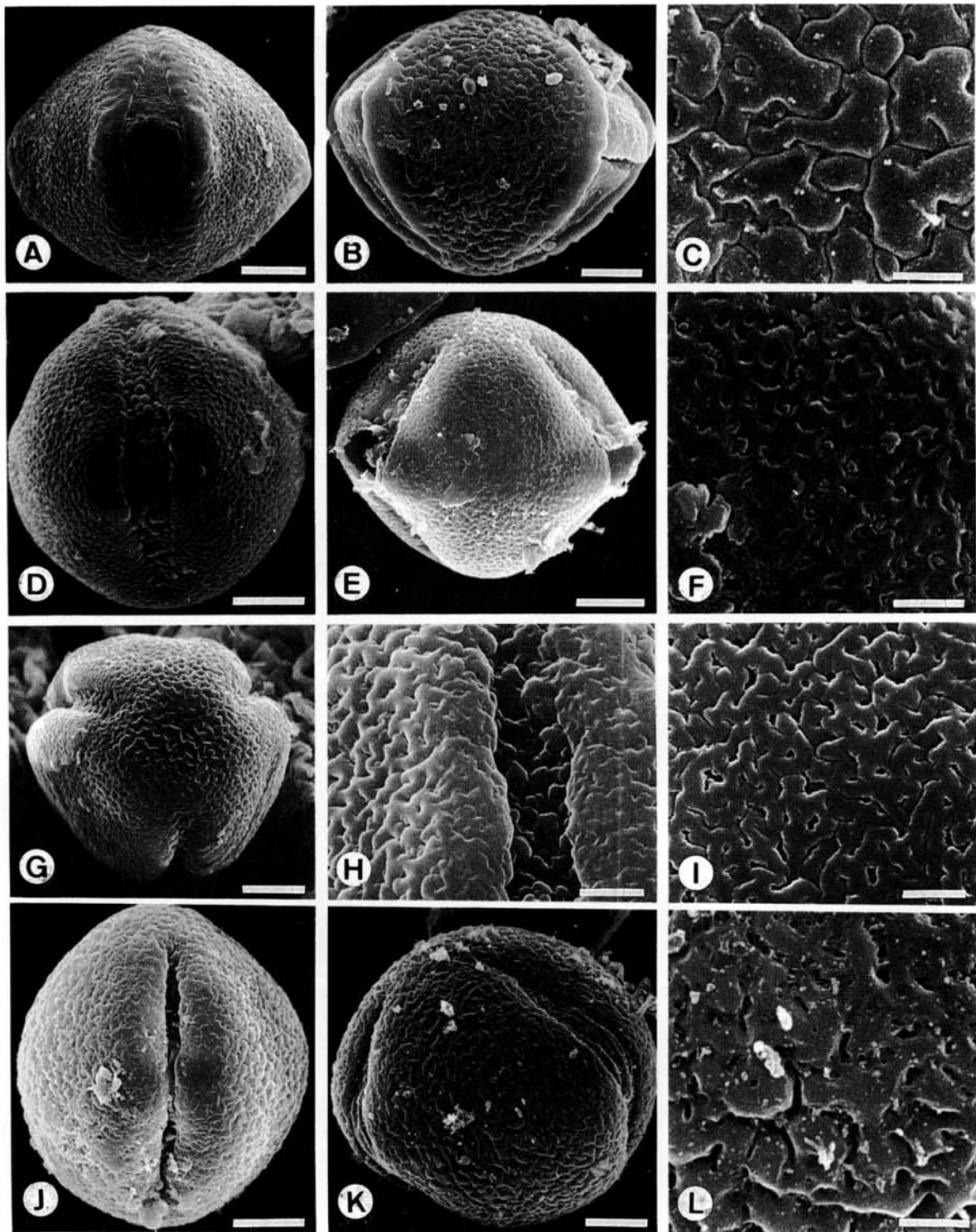


Fig. 4: A-C: *Desmodium intortum*. A,B. Equatorial view showing colpus margins without well developed tectum sculpture and intermesocolpium with verrucate and weakly rugulate tectum, bar=6.8 μ m; C. Detail of verrucate tectum, bar=3 μ m. D-F: *D. laxiflorum* subsp. *parvifolium*. D,E. Equatorial view showing lalongate endoaperture and densely granular colpus membrane, bar=5 μ m; F. Detail of finely reticulate tectum, bar=1.5 μ m. G-I: *D. laxum leptopus*. G. Polar view showing no mesocolpial pouches, bar=6 μ m; H,I. Detail of densely granular colpus membrane and finely reticulate tectum, bar=2.1 μ m. J-L: *D. microphyllum*. J,K. Equatorial view showing obscure mesocolpial pouches and sparsely granular colpus membrane, bar=5 μ m; L. Detail of finely reticulate and weakly rugulate tectum, bar=1.5 μ m.

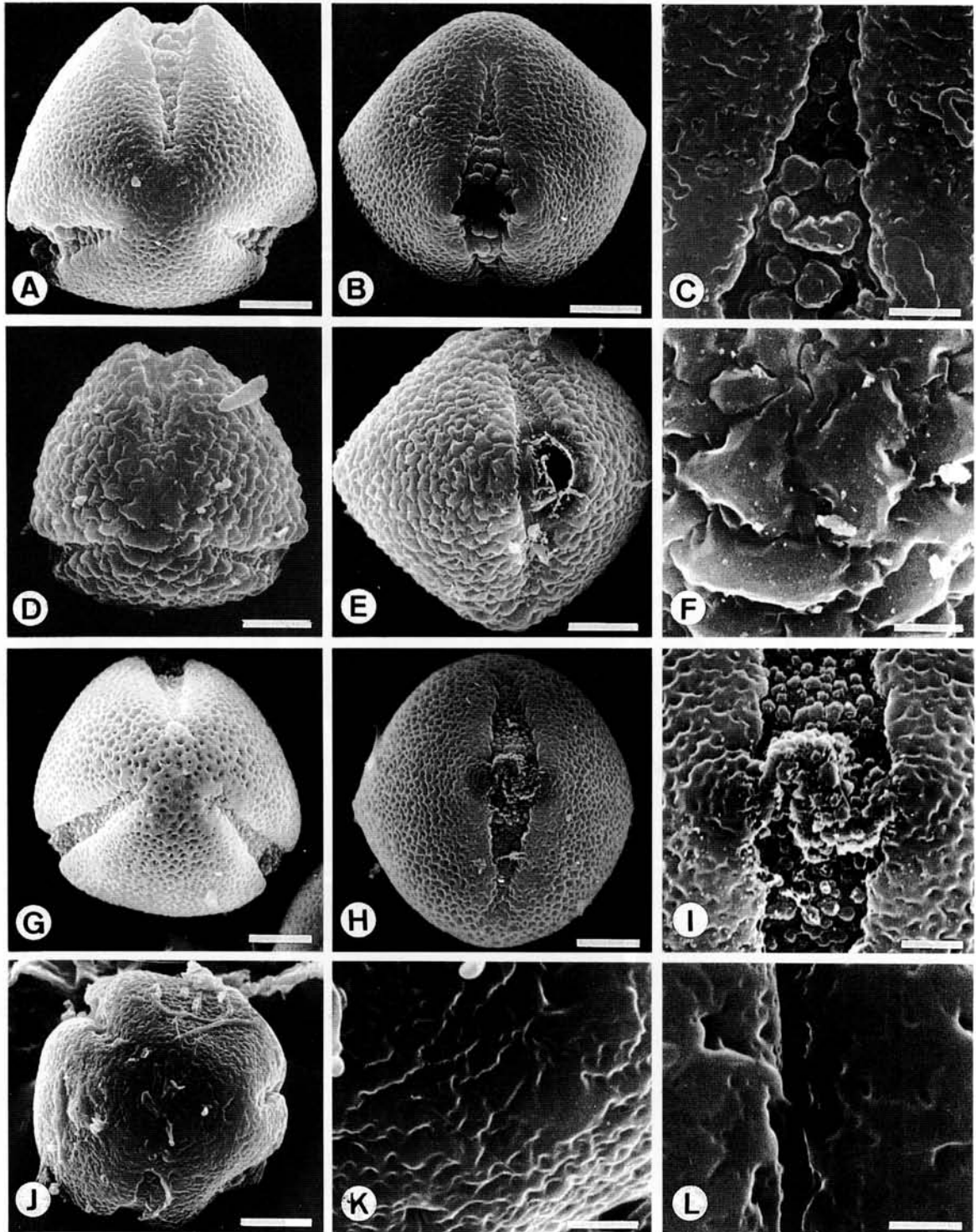


Fig. 5: A-C: *Desmodium multiflorum*. A, B. The pollen showing finely reticulate tectum and densely granular colpus membrane, bar=5 μ m; C. Detail of coplus membrane, bar=1.5 μ m. D-F. *D. scorpiurus*. D, E. The pollen showing finely granular coplus membrane and well differentiated tectum at colpus margins, bar=5 μ m; F. Detail of verrucate and weakly rugulate tectum, bar=1.5 μ m. G-I. *D. sequax*. G, H. The pollen showing slightly mesocolpial pouches and lalongate endoaperture, bar=4.3 μ m; I. Detail of densely granular coplus membrane and well differentiated colpus margins, bar=1.5 μ m. J-L. *D. triflorum*. J. Polar view showing tricolporate pollen with densely granular coplus membrane, bar=6 μ m; K, L. Detail of intermesocolpium and coplus, showing microperforation and weakly rugulate tectum, bar=1.5 μ m.

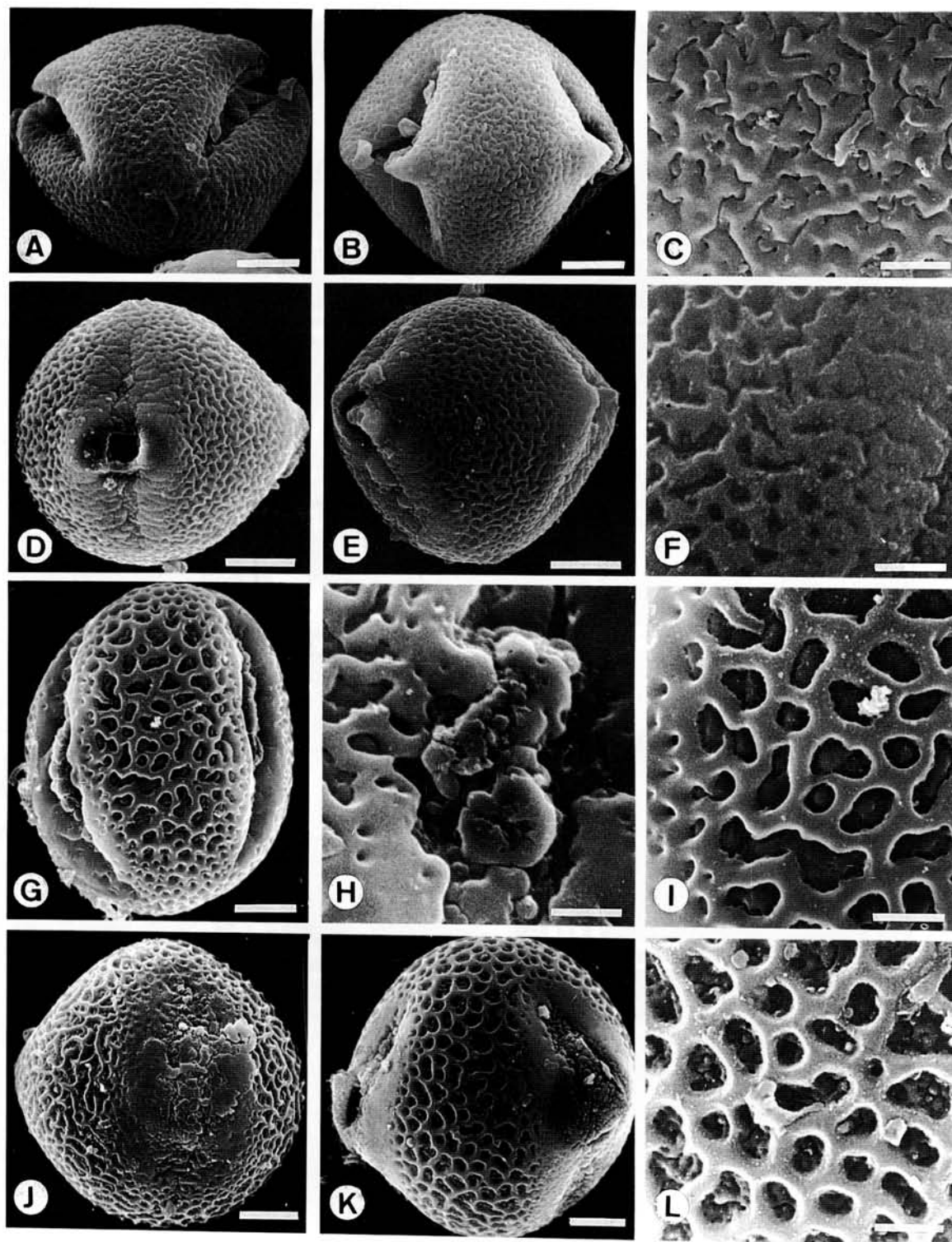


Fig. 6: A-C: *Desmodium velutinum*. A,B. The pollen showing obvious mesocolpial pouches, bar=5 μ m; C. Detail of finely reticulate tectum, bar=1.5 μ m. D-F. *Kummerowia striata*. D. Equatorial view showing granular colpus membrane, longitudinal endoapertures and mesocolpial pouches, bar=5 μ m; F. Detail of reticulate tectum, with irregular lumina, bar=1.5 μ m. G-I. *Lespedeza chinensis*. G. Equatorial view showing undifferentiated coplus margins, bar=3.7 μ m; H-I. Detail of mesocolpus and intercolpium, showing operculum-like structure on endoaperture and coarsely reticulate tectum, bar=1.5 μ m. J-L. *L. cuneata*. J, K. Equatorial view showing not well differentiated colpus margins, slightly longitudinal endoaperture and densely granular colpus membrane, bar=3.7 μ m; L. Detail of coarsely reticulate tectum, bar=1.5 μ m.

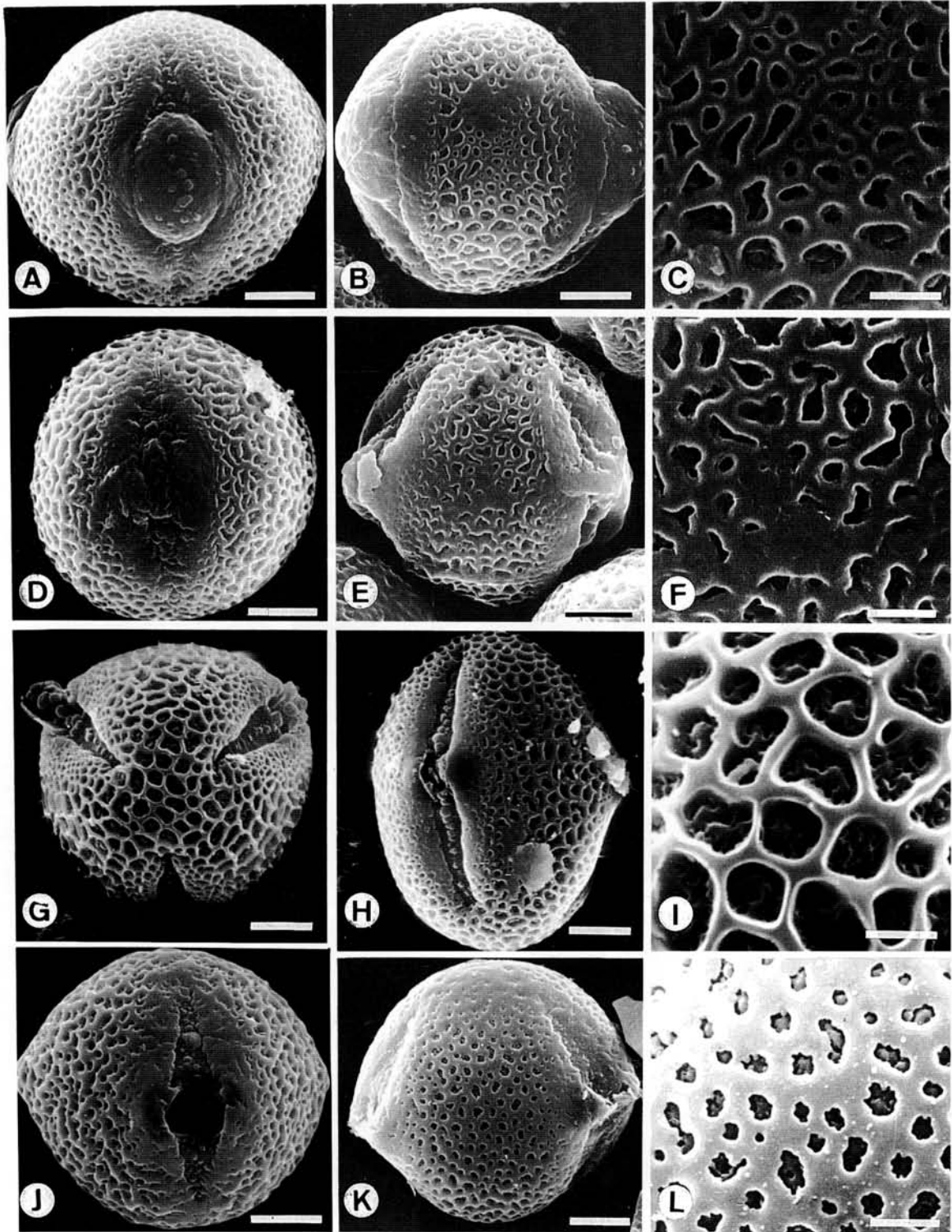


Fig. 7: A-C: *Lespedeza pubescence*. A,B. Equatorial view showing granular colpus membrane, operculum-like structure and undifferentiated colpus margins, bar=4.3 μ m; C. Detail of reticulate tectum, bar=1.5 μ m. D-F. *L. virgata*. D,E. Equatorial view showing not well developed coplus margins and mesocolpial pouches, bar=4.3 μ m; F. Detail of reticulate tectum, with irregular lumina, bar=1.5 μ m. G-I. *Phylloidium pulchellum*. The pollen showing mesocolpial pouches, lalongate endoaperture and granular colpus membrane, bar=5 μ m; I. Detail of coarsely reticulate tectum, bar=1.5 μ m. J-L. *Tadehagi triquetrum* subsp. *pseudotriquetrum*. J,K. Equatorial view showing undifferentiated colpus margins, densely granular colpus membrane and slightly mesocolpial pouches, bar=4.3 μ m; L. Detail of finely reticulate tectum, bar=1.5 μ m.

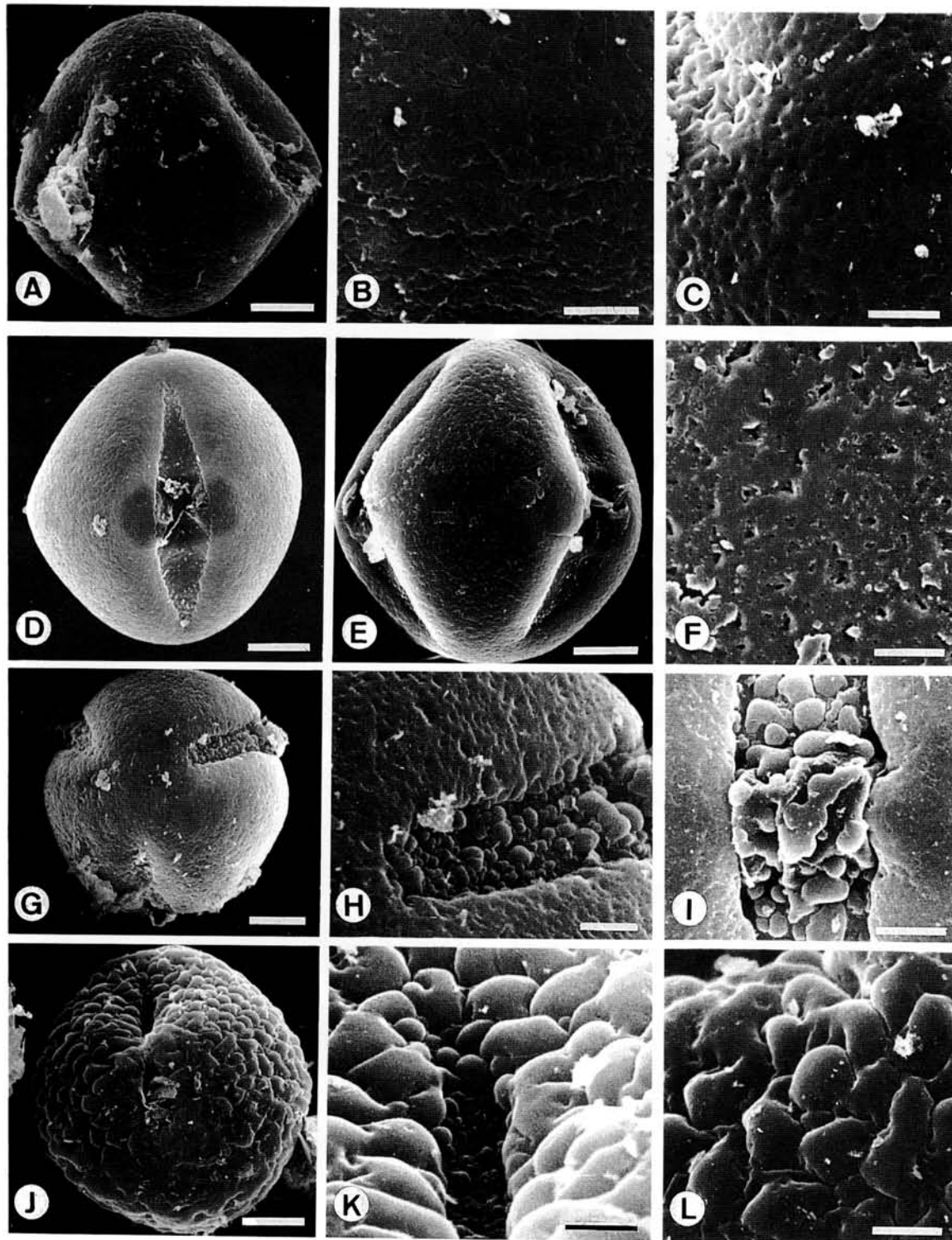


Fig. 8: A-C: *Pycnospora lutescence*. A. Equatorial view showing granular colpus membrane, bar=4.3 μ m; B,C. Detail of intermesocolpium with finely reticulate/weakly rugulate tectum, bar=1.5 μ m. D-F. *Uraria crinita*. D,E. Equatorial view showing lalongate endoapertures and well developed coplus margins, bar=7.5 μ m; F. Detail of finely reticulate tectum, bar=1.5 μ m. G-L. *U. largopodioides*. G. Polar view showing tricolporate pollen, bar=6 μ m; H,I. Detail of densely granular colpus membrane, slightly mesocolpial pouches and psilate. microperforated tectum, bar=2.1 μ m. J. Equatorial view showing another type of pollen of one species, bar=6 μ m; K,L. Detail of densely granular colpus membrane and coarsely granular/verrucate tectum, bar=2.1 μ m.

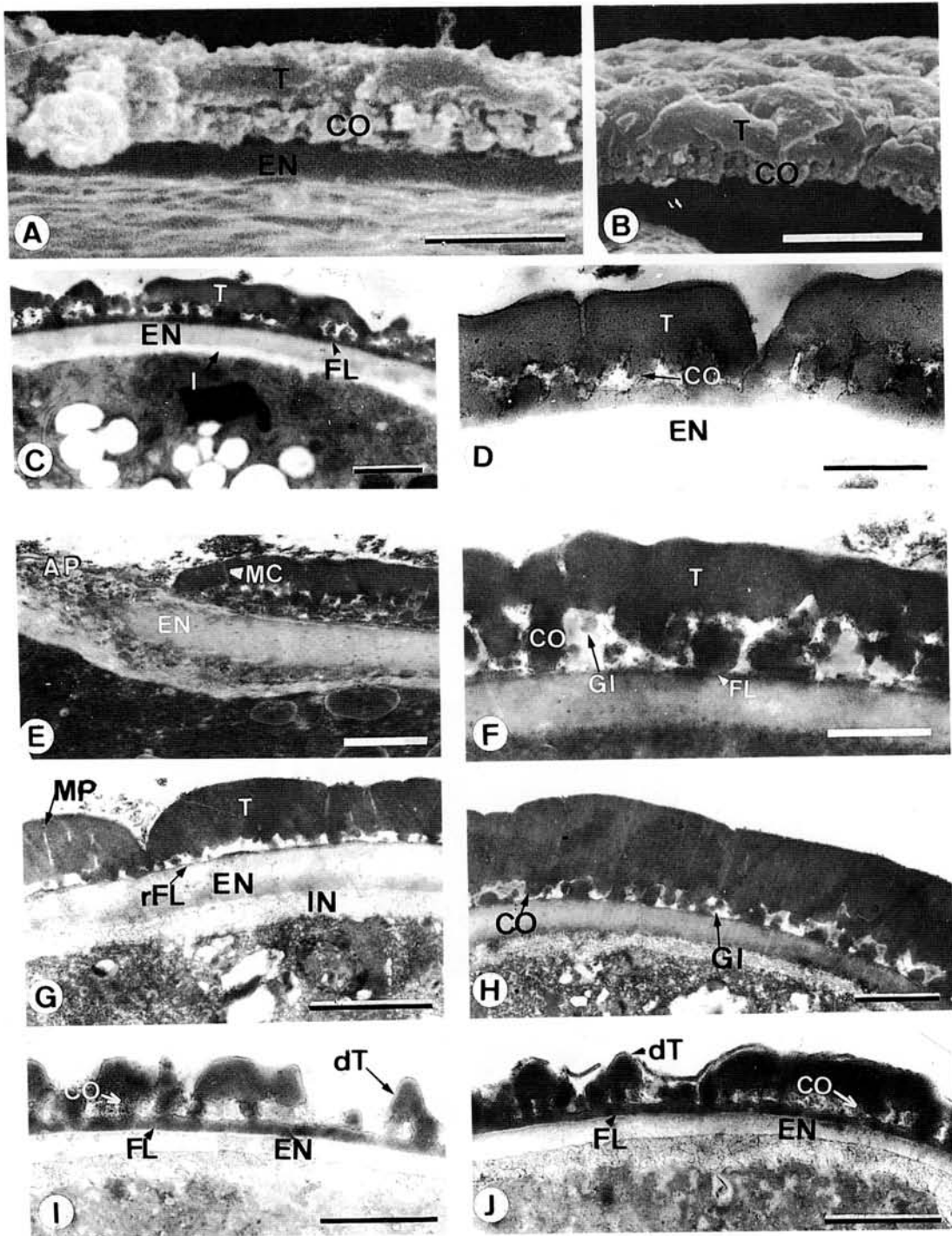


Fig. 9: A-B: *A. vaginalis*. In SEM showing exine stratification of the fractured wall with simple columellae, well developed endexine and verrucate tectum, bar=1.5 μ m. C-J: TEM micrographs. C-D: *Campylotropis giraldii*. C,D showing the endexine nearly as thick as the tectum, the foot layer being well developed. The simple columellae without granular interstitia. E-F: *Christia obcordata*. E. The endexine near the aperture is not well developed, foot layer discontinuous and columellae reduced. F. The tectum has sparse microperforation and the interstitium has both columellae and granules. G-H: *Codariocalyx motorius*. Exine under intermesocolpium showing the obscure and discontinuous foot layer. The short columellae gradually substituted by granular interstitium; the tectum often sparsely microchannelled. I: *Dendrolobium dispersum*. J: *D. umbellatum*. Both of two with the continuous foot layer. The discontinuous tectum is of not microchannels. The collumellae without granular interstitium. Bars=1 μ m.

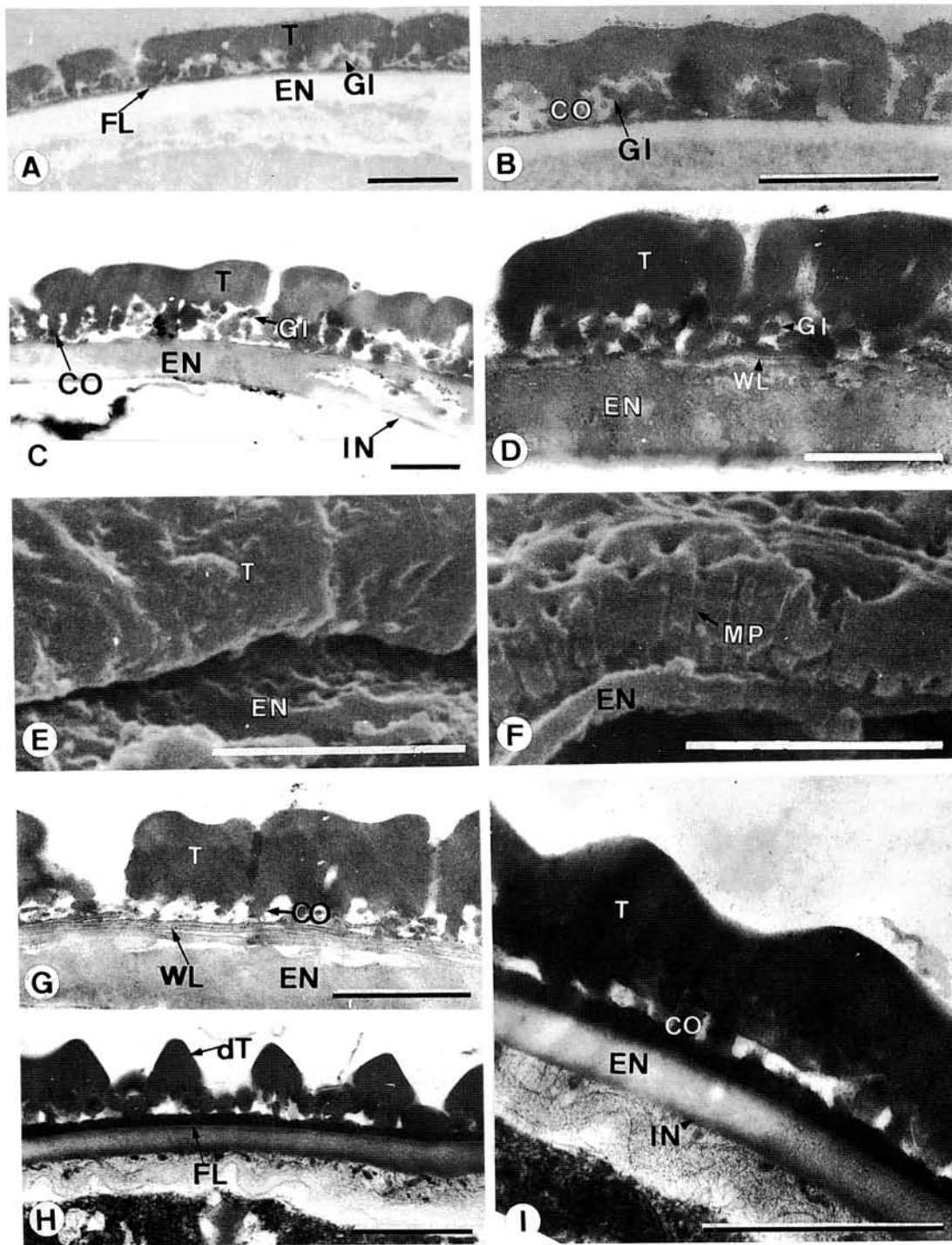


Fig. 10: A,B: *Desmodium gangeticum*. In TEM showing thin foot layer, the endexine is thicker than the tectum. The columellae are reduced, substituted by granular interstitium. C,D: *D. heterocarpon* var. *heterocarpon*. The tectum is as thick as endexine, with microperforations. There are fragmented white lines between the columellae and the endexine. The columellae are reduced, substituted by granular interstitium. E,F: *D. microphyllum*. In SEM the fractured pollen showing the tectum with microperforation, gradually disappeared at mesocolpium. The endexine is one half of tectum. G: *Lespedeza cuneata*. The endexine well developed and as thick as the tectum, the columellae often connected with the endexine by white lines. The discontinuous foot layer is reduced. H,I: *L. pubescence*. The endexine is half of the tectum; the columellae without white lines; the foot layer is distinct. Bars=1 μ m.

In SEM, we observed the pollen wall of *D. microphyllum*, the tectum is very thick, about 1-1.5 μm ; the columellae are as thin as the endexine, without a granular interstitium; the endexine is thinner than the tectum. Under the colpus regions, tectum is thickened four to six times in thickness.

Group 5. *D. gangeticum* (Fig.10, A-B), *D. heterocarpon* var. *heterocarpon* (Fig.3,G-L; Fig.10, C-D), *D. heterocarpon* var. *strigosum* (Fig.3, J-L) and *D. velutinum* are representatives.

The amb type of these pollen is circular to semi-angular, and the equatorial view is prolate to suboblate. The endoapertures are lalongate, and mesocolpial pouches are well defined. Sometimes, they protrude toward the equator to form rhomboidal and partially covered endoapertures. The colpus membrane is densely covered by fine granules. The tectum is finely reticulate and markedly rugulate, but that of *D. gangeticum* is only finely reticulate. The colpus margins are well differentiated.

The tectum has a few microperforations. The columellae are reduced, substituted by a granular interstitium. This feature is markedly present in this group. In the pollen of *D. heterocarpon* var. *heterocarpon* has obvious fragmented white lines to form lamellar zone between the columellae and the endexine. The foot layer is absent. The endexine is thicker than the tectum, about 0.25-0.35 μm . Under the colpus regions, it is gradually reduced.

Kummerowia -- Fig.6, D-F. There are two species of herbs in this genus in Taiwan. The pollen grains of *K. striata* have been examined in this study. The pollen is circular in polar view and prolate to oblate spheroidal in equatorial view. The endoapertures are lalongate. The mesocolpial pouches are obvious, partially covering the endoapertures. The colpus membrane is sparsely speckled with fine granules. The colpus is 4/5 of the polar axis in length, about 20-25 μm . The colpus margins are not well differentiated, weakly canaliculate and microperforate. The tectum is reticulate, with irregular lumina. There are a few granular remnants between the lumina.

The tectum is as thick as the columellae and the endexine, about 0.5-0.7 μm . The endexine is granulated and has a distinctly undulate margin. The thickness of the tectum of the colpus margins is thinner than other portions.

Lespedeza -- Fig.6, G-L; Fig.7, A-F; Fig.10, G-I. There are six species of herbs or undershrubs of this genus in Taiwan. The pollen of four species are examined here. All of these species have smaller pollen than other genera of this tribe. The amb type is circular to semiangular. The equatorial view is subprolate to spheroidal. The endoapertures are larger, and circular to elliptic. In LM, they can be easily observed. The mesocolpial pouches of *L. cuneata* and *L. virgata* are obvious and partially cover the endoapertures, but in another two species they do not. The colpus membrane is covered by coarse granules. Operculum-like structures cover the endoapertures. The colpus margins are undifferentiated and jagged. The tectum is more coarsely reticulate than that of *Kummerowia striata* in the same subtribe. The lumina are irregular and polygonal. The baculae are obvious on the lumina.

The tectum of *L. cuneata* (Fig.10,G) is continuous and thick. The columellae are short and irregular, about 0.15-0.2 μm . They often connect with the endexine by white lines. The foot layer is replaced by white lines. The endexine is well developed and as thick as the tectum, about 0.6-0.9 μm . At the colpus region, the endexine is twice thicker.

The exine stratification of *L. pubescence* shows the long and regular columellae. There are no white lines. The foot layer is distinct and continuous, about 0.15-0.2 μm . The thickness of endexine is half than that of the tectum, thinner than that of *L. cuneata*.

Phyllodium --Fig.7, G-I. This is a monotypic genus of shrubs of Desmodieae in Taiwan. The pollen morphology of *P. pulchellum* differs greatly from that of the other genera of Desmodieae. The pollen is circular in polar view and prolate to oblate-spheroidal in equatorial view. The endoapertures are large and lalongate, and mesocolpial pouches are well developed. After acetolysis, they protrude toward the equator to form a rhomboidal aperture. The colpus membrane has a row of coarse granules arranged in the middle of the colpi. The tectum is coarsely reticulate, and there is finely reticulate sculpture inside the rectangular lumina. This feature is present only in this genus. The colpus margins is not well differentiated.

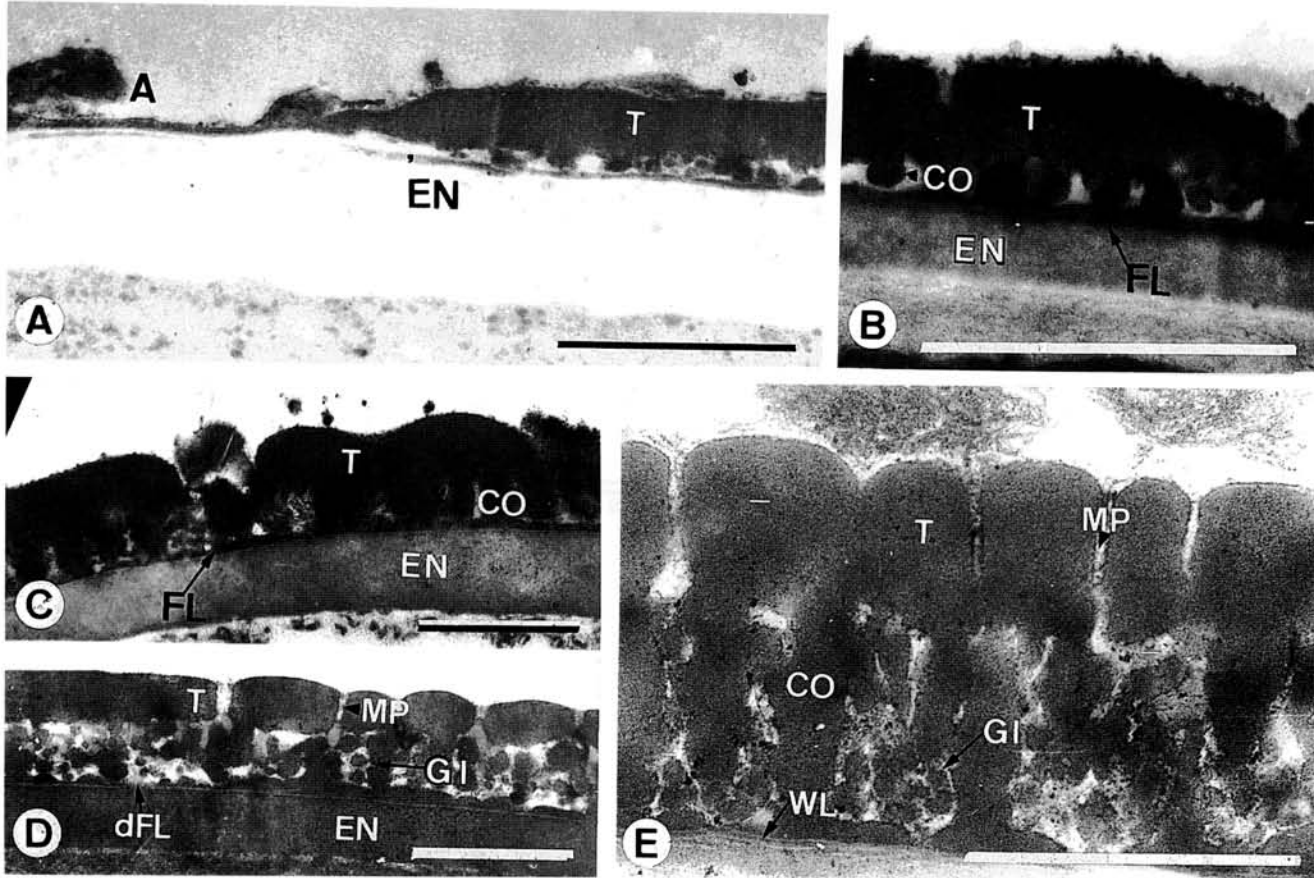


Fig. 11: A,B: *Pycnospora lutescens*. In TEM showing the endexine is well developed under mesocolpium. The columellae are reduced. The foot layer is distinct and continuous. The tectum has no microperforation. C: *Tadehagi triquetrum pseudotriquetrum*. The well developed endexine thicker than the tectum, without microperforation; the foot layer is thin but distinctly continuous; the simple columellae with little granular interstitium. D: *Uraria crinita*. The well developed endexine thicker than the tectum; the foot layer disappeared and replaced by white lines; the columellae are reduced and almost replaced by granular interstitium; the tectum with microchannells. E: *Uraria lagopodioides*. Same as above. Bars=1 μ m.

The tectum is thick, about 0.8-1.0 μ m. It is equal in thickness in anywhere in the pollen wall. The foot layer is continuous. The columellae are shorter than the tectum, about 0.2-0.3 μ m. The endexine is gradually thickened under the colpus area.

Pycnospora -- Fig.8,A-C; Fig.11,A-B. This is another monotypic genus of herbs of Desmodieae in Taiwan. The pollen of *P. lutescens* is closely similar to that of *Codariocalyx* species of the same subtribe. The polar view is circular and the equatorial view is prolate to oblate spheroidal. The endoapertures are subcircular to lalongate. The mesocolpial pouches are not very obvious. The colpus membrane is densely covered by coarse granules. The tectum is finely reticulate and weakly striate, with microperforations. The colpus margins are undifferentiated and undulate.

Tectum is thicker than other parts of the exine stratification, 0.8-1.3 μ m. The columellae are reduced, gradually replaced by the coarse granules, about 0.2-0.3 μ m in length. The foot layer is thin, distinct and undulate. It is a continuous layer without microchannells. The endexine is well developed, not thickened by the colpial margins, about 0.2-0.3 μ m. The intine is gradually thickened, twice thick under the colpus regions.

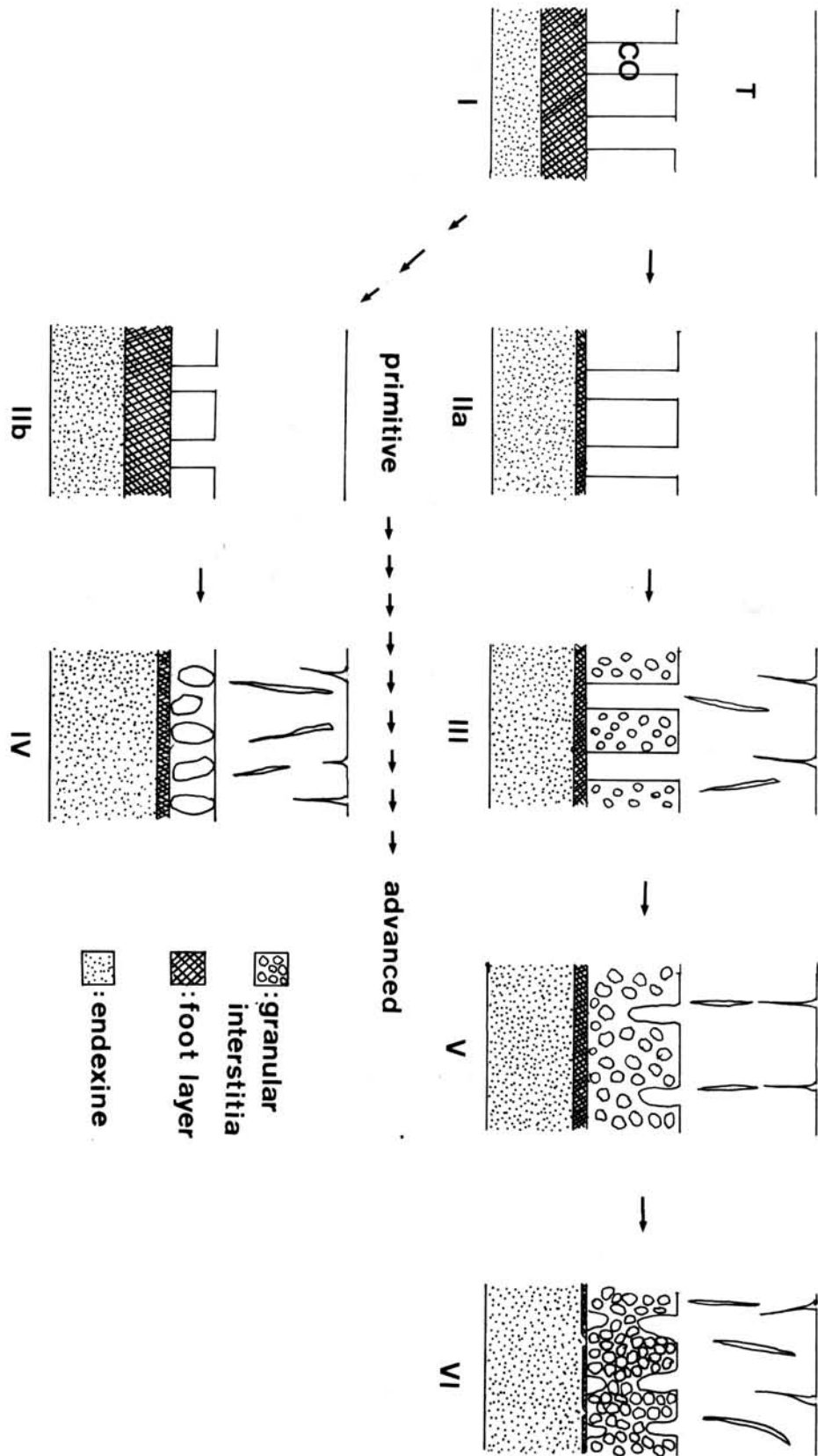


Fig. 12. The evolutionary pathway of pollen of Desmodieae in Taiwan.

Tadehagi --Fig.7,J-L; Fig.11, C. As another monotypic genus of shrubs of Desmodieae in Taiwan. The pollen of *T. triquetrum* subsp. *pseudotriquetrum* is dissimilar from that of close relatives, but like *Kummerowia* in a different subtribe.

The pollen grains are semiangular in polar view and subprolate to suboblate in equatorial view. The endoapertures are lalongate, and the mesocolpial pouches are obscure. The colpus membrane is sparsely covered unevenly coarse granules. The tectum is reticulate, with irregular lumina. The colpus margins are not well developed and jagged.

The tectum of this taxon is thinner than that of the others taxas in this tribe. The columellae are gradually reduced. The granular interstitia are visible. The foot layer is thin, distinctly continuous and undulate. It has no microchannels. The endexine is well developed, thicker than the tectum, 0.6-1 μm . The intine thickened under the endoapertures.

Uraria --Fig.8, D-L; Fig.11, D-E. There are four species of herbs of *Uraria* of the Desmodieae in Taiwan. The pollen grains of *U. crinita* and *U. lagopodioides* were examined in this study. The pollen of *U. lagopodioides* is dimorphous.

The pollen is circular to semiangular in polar view and prolate to prolate spheroidal in equatorial view. The endoapertures are lalongate, and mesocolpial pouches are not well developed. The colpus membrane is smooth. The tectum is psilate and microperforated in *U. crinita* and the colpus margins are well developed. In contrast, the colpus membrane is densely covered by coarse granules in *U. lagopodioides*. The tectum is of two different types: one is psilate and microperforate, and the other is coarsely granulate to verrucate.

The tectum is thinner than in other parts of pollen wall, with microperforations. The columellae are reduced and the granular interstitia are increased. The foot layer has disappeared and is replaced by white lines to form lamellar zone. The endexine of this genus is well developed, thicker than the tectum. It is gradually thickened toward the colpi.

DISCUSSION AND CONCLUSION

The pollen grains of Desmodieae show many different features, nevertheless, there are some similitaries among them. Examination of the pollen of some species of three genera, i.e. *Christia*, *Desmodium* and *Uraria*, found degenerated columellae and foot layer (Fig.9,E-F;10,A-D). The pollen of *Christia* species has many granular interstitia between the tectum and the columellae. This feature had been found in *Alysicarpus* (Fig. 9,A-B), but the columellae of this genus were well developed. The characteristic is different from the former three genera. Van Campo & Lugardon (1973) described the pollen of *Acacia* as having granular interstitia among the colmellae, then called "structure grenue". They suggested that the granular interstitium was deposited by global sporopollenin. Walker & Walker (1981) proposed that the "interstitium" is located between the tectum and endexine, sometimes with granular interstitia. Ferguson & Skvarla (1979, 1981) examined the pollen of Papilionoideae, and found the pollen of many species with granular interstitia, reduced columellae, and foot layer. Horvat and Stainer (1979,1980) had found these characteristics in *Phaseolus* and *Vigna*.

Codariocalyx is a monotypic genus in Taiwan. It was placed in *Desmodium*, but Ohashi(1973) classified it a separate genus. It has two species, one in Taiwan and another in the Himalayan region. The pollen of *Codariocalyx* has psilate tectum. This feature was not found in the pollen grains of the other genera in this tribe. It has short and reduced columellae, often substituted by many coarse granules (Fig.9, G-H). *Pycnospora* is another monotypic genus, which pods have many seeds like those of *Crotalaria*. Ohashi(1973) included *Pycnospora* in Desmodieae because it has the same characteristics of floral parts. The pollen of *Pycnospora* was found to be similar to that of *Codariocalyx*.

In general, taxonomists have suggested that *Christia* and *Uraria* are close relatives. Examination of the pollen of those two genera revealed that they have very different tectum sculpture, but with the same exine stratification. Reduced columellae and many granular interstitia are both present. The former taxon has an entomophilous flower, the latter is self pollinated. The floral parts of *Christia campanulata* are similar to those of *Uraria*.

Ferguson and Skvarla(1979) found the pollen of Bryinae and Desmodiinae to have granular interstitia. They did not describe the Lespedezinae as having this feature. Ohashi (1971) used LM to examine the pollen morphology of Desmodiinae with exception of exine stratification. We found the pollen of Lespedezinae being closely relative to that of *Dendrolobium*. Pollen of both has a coarsely reticulate tectum and simple columellae without granular interstitia, but their floral parts are different. Ohashi(1973) has studied the Desmodiinae and its close relatives. He thought that *Dendrolobium* is the most primitive genus of Desmodiinae. We found a closer relationship between *Dendrolobium* and Lespedezinae in pollen characteristics.

We have divided the pollen of Desmodiinae into six types (Table 2). (I) The thick tectum is coarsely reticulate, without microperforations. The remnants of ektexine are present on the lumina. The simple columellae have no granular interstitia, and the foot layer is continuous. The colpus margins are undifferentiated. There is an operculum-like structure. The pollen grains of Lespedezinae (*Campylotropis*, *Kummerowia* and *Lespedeza*) have the above characters. (II) The tectum has no microperforation. This type is divided into two subtypes. (a) The tectum is finely reticulate. The simple columellae have no granular interstitia. The foot layer is reduced. The pollen of *Desmodium multiflorum*, *D. sequax*, *D. velutinum* also have these features. (b) The thick tectum is coarsely reticulate. The foot layer is obvious and continuous, and the colpus margins have microperforations, and the colpus membrane is finely granulate. The pollen grains of *Dendrolobium* species, *Desmodium caudatum*, *Phyllodium* have these characteristics. The pollen of *Tadehagi* is similar to that of these taxa but lacks the foot layer. (III) The tectum is coarsely verrucate or weakly rugulate. Only the pollen grains of *Alysicarpus* species have mesocolpial pouches partially covering the endoapertures and colpus membranes that are coarsely granulated. The tectum, collumellae and endexine have the same thickness. There are a few granular interstitia, and the foot layer is thin. The pollen grains of *Alysicarpus* species, *Desmodium intortum* and *D. scorpiurus* have these above features. (IV) The tectum is thick, psilate,

Table 2. The characteristics of pollen grains of Desmodiinae in Taiwan.

Types	Endoapertures	ektexine			sculpture	ratio		representatives
		T	Col.	FL		ex/in	t/col	
I	lalongate	no (microperforation)	simple	continuous	coarsely-reticulate	2/1-3/1	1/1-2/1	<i>Campylotropis</i> sp. <i>Kummerowia</i> sp. <i>Lespedeza</i> sp.
Ia	lalongate	no	simple, thick	continuous	finely-reticulate	2/1-3/2	1/1	<i>Desmodium multiflorum</i> <i>Desmodium velutinum</i>
Ib	lalongate or lolongate	no	simple, thin	continuous	coarsely-reticulate	2/1-4/1	2/1-4/1	<i>Dendrolobium</i> sp. <i>Tadehagi</i> sp.
III	round or lalongate	with	granular	continuous; gradually reduced	microperforated; weakly striate	1/1-2/1	2/1-4/1	<i>Alysicarpus</i> sp. <i>Desmodium intortum</i> <i>Desmodium scorpiurus</i>
IV	lalongate	with	granular	continuous; thin	verrucate; psilate	2/1	1/1-2/1	<i>Codariocalyx</i> sp. <i>Desmodium microphyllum</i> <i>Pyconspora lutschense</i>
V	lalongate	with	granular or reduced	fragment reticulate or weakly striate	finely-	1/1-2/1	1/1	<i>Christia obcordata</i> <i>Desmodium gangeticum</i> <i>Desmodium heterocarpon</i>
VI	lalongate	with	granular or reduced	reduced or coarsely-granular	psilate or	2/1-3/1	1/1-1/2	<i>Uraria</i> sp.

microperforated or weakly rugulate. The columellae are reduced and substituted for with granular interstitia. The pollen grains of *Codariocalyx*, *Desmodium heterophyllum*, *D. microphyllum*, *D. podocarpon* subsp. *oxyphyllum*, *D. triflorum* and *Pycnospora* have these characteristics. (V) The tectum is finely reticulate or weakly rugulate, and has microchannels. The reduced columellae are reduced. The granular interstitia are increased. The foot layer is discontinuous and obscure. There are many white lines to form lamellar zone between the endexine and ekexine. The colpus membrane is densely covered by coarse granules. Good examples are the grains of *Christia obcordata*, *Desmodium gangeticum* and *D. heterocarpon* var. *heterocarpon*. (VI) The tectum is psilate and microperforated, and the endexine is as thick as the tectum. The reduced columellae are replaced by granular interstitia. The foot layer has disappeared and white lines are visible. All this is illustrated by the pollen of *Uraria*.

Heslop-Harrison (1976) has suggested that the pollination has relationship with pollen morphology. Pollen morphology and tectum sculpture are related to the propagation of plants. Ferguson and Skvarla (1982) studied the relationship between the pollen of legumes and their pollinators. They discovered that the pollen of entomophilous flowers has coarse verrucae and complicated exine stratification. In examining the pollen of Desmodieae, we found that the pollen of *Uraria lagopodioides* has dimorphic pollen types (Fig.8,G-L). One type has a psilate tectum, the other obvious verrucate. *Uraria* is a self-pollinated genus. This diversity will be investigated by examining the microsporogenesis of *Uraria lagopodioides* in the future.

Graham and Tomb (1977) thought the pollen wall being genetically controlled by the sporophytic and gametophytic generations. The transitional tendency of evolution in plants through pollen morphology and exine stratification has to include many variations of diploidy and haploidy generations. Ferguson and Skvarla (1983) interpreted the evolutionary pathway of Papilionoideae through granular interstitia. They suggested that the advanced legumes have pollen with granular interstitia and flowers with more specialized floral parts, but Afzelius (1956) found that the pollen of gymnosperms had granular interstitia. According to the granular interstitia both present the primitive and advanced plants, we suggested that the pollen sculptures have convergent and divergent evolution. We made an interpretation of the evolutionary pathway of the pollen characteristics in Desmodieae plants. Figure 12. represents an evolutionary pathway. It is proposed that the pollen of Type I has not perforated tectum, with short columella, prominent foot layer and endexine, showing a primitive type. It evolved toward type II. The Type II proceeds two directions. Subtype IIa has finely reticulate tectum, simple columellae and reduced foot layer, then specialized to form Type III. The Type III has the microperforated tectum, granules filled within the columellae, then evolved toward Type V. Type V is modified as reduced columellae, and increased granular interstitia. Finally, Type VI is advanced type in the continuous evolutionary pathway. The pollen of this type has filled with granular interstitia. Another pathway is subtype II b that has reticulate tectum, simple columellae and thick foot layer, then specialized by reduced columellae and formed as single layer of granules as Type IV.

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台灣山螞蝗族植物花粉的研究

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摘 要

本文以台灣山螞蝗族 (Desmodieae) 中十二個屬三十四種植物的花粉為材料，應用光學及電子顯微鏡來觀察花粉外部形態及內部層次構造中所展現的特徵差異，這一族植物的花粉形態變異很大，雖然都是三溝孔粉，但外壁花紋及層次結構在種與種之間卻各異其趣。

山螞蝗族植物之花粉依目前所觀察的結果，由外部形態及層次結構將其分為六個類型。第一類型：外壁粗網紋，明顯雙緣溝，具孔蓋似的構造，單純的圓柱層並無孔間顆粒存在。第二類型又分兩種亞型：A外壁皆為粗網紋，雙緣溝，溝緣外壁雕紋微細穿孔，溝孔處有細顆粒覆蓋，基層則逐漸消退；B外壁細網紋，壁層沒有微細管道及柱間顆粒，最內層厚度大增。第三類型：外壁具粗瘤狀突起，蓋頂明顯半圓紋。第四類型：外壁微細穿孔或具有輕微的網狀散條紋，基層不連續或逐漸消退。第五類型：外壁皆細網紋，基層不連續，最內層厚度與蓋頂相當。第六類型：外壁具微細穿孔，圓柱層被柱間顆粒取代，基層消失。

分類學者比較各屬間之外部形態，將山螞蝗族又分為三個亞族，台灣僅產兩個亞族即螞蝗亞族及胡枝子亞族，但是由花粉形態上的差異來看，反在其間尋到一些相似性，可能是演化的過程中適應環境而在外部形態上產生變化，內部構造如花粉粒卻未及改變而保持相似的特徵。