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THE ROLE OF POLLEN MORPHOLOGY IN PLANT SYSTEMATICS

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SUMMARY. A short historical background to the subject is given. The role of pollen morphology as a taxonomic character is discussed and various approaches to the study of pollen are considered and described. The importance of studying the whole pollen grain and its potential contribution to the understanding of the overall biology of the plant is emphasized. Examples illustrating these points are drawn from a number of groups. For example in the subfamily **Papilionoideae** (**Leguminosae**) the exine stratification and aperture structure are shown to be more significant characters for distinguishing tribal and generic categories while ornamentation is of more importance at specific level. The apparent adaptation of exine characters for bird pollination and the potential significance of pollenkitt in the family are discussed.

The necessity to establish a large pollen data base especially in the large tropical plant families of economic importance is emphasized. The value of such a data base in understanding structural and functional homology is demonstrated in **Papilionoideae** and its importance in the interpretation of the fossil record in **Palmae** is outlined.

The value of pollen morphology in groups like **Restionales**, which have very reduced macromorphological characters, is shown.

The very uniform pollen morphology of the small family **Moringaceae** is used as an example of how useful information can be deduced from data of this kind.

Mandragora (**Solanaceae**) with cryptoaperturate pollen exemplified how structure can be properly interpreted by resorting to a wide range of techniques for preparation and study.

Recent advances in techniques for study of pollen development and comparative ontogeny and functional roles of pollen are considered briefly.

Pollen of some representatives of the tribe **Vicieae** (**Papilionoideae**) are illustrated to show the variation in exine ornamentation and stratification and to emphasise the need for more TEM in this group.

An extensive bibliography in included.

RESUMEN. Se da una breve revisión del tema. Se discute el papel de la morfología polínica como carácter taxonómico, considerando y describiendo diversos aspectos del estudio del polen. Se resalta la importancia del

estudio del grano de polen como un todo único y su potencial contribución al entendimiento de la biología de las plantas. Se dan ejemplos que ilustran estos aspectos en una serie de grupos vegetales. Por ejemplo, en **Papilionoideae** (**Leguminosae**) la estratificación de la exina y la estructura de las aperturas son los caracteres mas significativos para la segregación de las categorías tribales y genéricas, mientras que la ornamentación es de mayor importancia a nivel específico. Se discute también la adaptación aparente de los caracteres de la exina para la polinización por pájaros y el significado potencial del pollen-kitt en la familia.

Se resalta la necesidad de establecer una adecuada base de datos polínicos en las grandes familias tropicales de importancia económica. Se demuestra en **Papilionoideae** el valor de tal base de datos en el entendimiento de las homologías estructurales y funcionales, y se subraya su importancia en la interpretación de los restos fósiles de **Palmae**.

Se muestra el valor de la morfología en grupos como **Restionales**, que tiene muy reducidos caracteres macromorfológicos.

La muy uniforme morfología polínica de la pequeña familia **Moringaceae** se usa como ejemplo de como se puede deducir útil información de datos de este tipo.

Mandragora (**Solanaceae**) con polen criptoaperturado ejemplifica como la estructura puede ser interpretada con el empleo de un buen número de técnicas de preparación y estudio.

También se consideran recientes avances en técnicas de estudio para el mejor entendimiento de la ontogenia comparada y la funcionalidad del polen.

Se ilustra el polen de algunos representantes de la tribu **Vicieae** (**Papilionoideae**) para mostrar la variación en la ornamentación y estratificación de la exina y para resaltar la necesidad de mas estudios a TEM en este grupo.

Se incluye una extensa bibliografía.

INTRODUCTION

Pollen morphology is an expression of part of the genome and like any character be it cryptic or macromorphological it may be useful in some groups for taxonomic studies and less valuable in others. In many groups valuable information can be derived from a full and careful study leading first to an understanding of both the morphology and where possible the functional role of the characters of the pollen grain. An understanding of the ontogeny of the pollen grain and of the deposition and fundamental structure of sporopollenin are of significance for comparative pollen morphologists by contributing to the understanding and interpretation of some of the structures used as distinguishing features, as for example the differential staining of the exine in this section. The pollen grain may be studied not only for comparative morphological data alone but also for clues to unexpected aspects relating to breeding systems, pollination biology and hybridisation. In this way a better understanding of the whole biology of the group under investigation may result. Another aspect is the the relating of morphological data to fossil pollen and the fossil record and where this is possible additional insight may be obtained into evolution. These are some of the points that this paper will try to demonstrate.

HISTORICAL BACKGROUND

A brief resume of the history of comparative pollen morphology

and taxonomy may enable one to understand better to-day's philosophy and practice of the subject. The study of pollen in inevitably linked with the history of microscopy but is also associated with fashion. Comparative pollen morphology has been studied for about 150 years beginning with workers like MOHL (1835) and HASSELL (1842). The subject was adopted by workers in the classical German school of plant taxonomy of the late 19th and early 20th century as for example the works of HALLIER (1893) on Convolvulaceae and URBAN (1916) on Bignoniaceae show. Laterly two workers have made outstanding contributions in providing the foundation for the study of pollen morphology in relation to systematics. First WODEHOUSE (1935) who provides the classical background to the importance of the study of the "whole" pollen grain. A view almost forgotten by a majority of workers until comparatively recently where it has been so strongly advocated by DAHL (1976) and followed by MULLER (1979, 1981) and is now rapidly becoming the accepted approach. The second great worker is of course ERDTMAN (1952) who provided the work which is rightly regarded as the corner stone of modern comparative pollen morphology. Erdtman's work centred around the study of the acid resistant sporopollenin exine. The shape, size, apertures, ornamentation and the stratification of the wall are the characters which proved so useful in distinguishing pollen grains of different species genera, tribes, families and orders. Treatment whit acids, the acetolysis method, arose from the techniques used to prepare fossil pollen from the Quaternary and earlier epochs. Erdtman began his studies in the field of palaeopalynology and carried the methods of the Scandinavian school of pollen analysis of the 1920's into his studies of the pollen morphology and taxonomy of angiosperms. The method allowed careful and detailed observations and descriptions of pollen grains to be made with the light microscope with the technique of "LO analysis" (see ERDTMAN, 1969). Erdtman's influence and contribution are enormous and numerous workers benefitted from his training and inspiration. The period from 1950-1970 saw a great development in the subject parallel with but distinct from pollen analysis. The Paris/Montpellier school under Van Campo made significant contributions also at this period and the journals Grana palynologica and Pollen et Spores were founded. In these are numerous papers on the structure and significance of the exine of recent pollen.

The early 1970's saw a new era with the ready availability of the scanning electron microscope (SEM). The value of the transmission electron microscope (TEM) in comparative pollen studies had already been shown by ROWLEY (1959, 1960), LARSON (1964), LARSON & SKVARLA (1961), SKVARLA (1965) and others. Many laboratories and institutions working in the field of plant systematics set up units of comparative pollen morphology and it became recognised that pollen was a valuable and significant character important in taxonomy.

Many workers to-day study acetolysed pollen using LM, SEM & TEM. While others confine their investigations to unacetolysed freshly fixed or reconstituted herbarium material. Obviously the techniques used for study depend on the primary aim of the investigation and also on the nature of the pollen grains. The main case for justification of study of acetolysed pollen is that the results are more directly or easily compared with fossil material as is so elegantly demonstrated by WALKER & WALKER (1985). However, also the details of the exine stratification and inner views of the endoapertures can be studied with SEM. Information may be lost or overlooked by failure to consider the

complete pollen grain, for example some assessment of viability can be made even from herbarium material as for example in **Melanophylla** (**Cornaceae**) (FERGUSON, 1977) and likewise the occurence of differing levels of pollenkitt (FERGUSON, 1984).

EXAMPLES OF THE STUDY OF POLLEN AND ITS TAXONOMIC SIGNIFICANCE

Leguminosae (subfamily **Papilionoideae**)

The group is comprised of some 440 genera and 12000 species in some 32 tribes. A very important point relevant to comparative palynological investigations is that the taxonomy has been recently reviewed using macromorphology and cryptic characters (see POLHILL & RAVEN, 1981). There have been a lot of recent investigations of pollen morphology incorporating electron microscopy for example FERGUSON (1978, 1980, 1981b, 1984), FERGUSON & SKVARLA (1979, 1981, 1982, 1983), FERGUSON & STRACHAN (1982), GRAHAM & TOMB (1974, 1977), HORVAT & STANIER (1979, 1980), KAVANAGH & FERGUSON (1981), MARECHAL & al. (1978), POOLE (1979) and STANIER & HORVAT (1978, 1983). Detailed pollen information is available for some 2500 species from these works and FERGUSON & SKVARLA (unpublished). This represents a minimum data base from which an attempt can be made to reach general conclusions on the pollen morphology and evolution of the subfamily as a whole. From these studies it is clear that pollen apertures and exine stratification are conservative characters consistently of the greatest value in tribal classfication as well as at generic and specific level while size, shape and exine ornamentation are found to be characters of secondary importance more of value at the generic and specific levels. Together with the well established trend from tricolporate to porate (see PUNT, 1975) there is a rather unusual tendency for reduction of the endoaperture to a tricolpate aperture with an associated development of an operculum over the colpus (FERGUSON & SKVARLA, 1981; FERGUSON, 1984). There are trends towards increase in thicknees of the endexine and loss of the foot layer and on the otherhand loss of the endexine (except for a thin layer in the apertural area) and a very thin foot layer. Together with these two trends in exine stratification is the development of a complex interstitium. The complex granular interstitium appears to be a derived pollen character in the group (FERGUSON & SKVARLA, 1983). Great variation may occur in the exine stratification in some groups with otherwise relatively unremarkable tricolporate pollen and very little variation in exine ornamentation. This is particularly so in **Indigofera** (FERGUSON & STRACHAN, 1982) and in **Swartzia** (FERGUSON & SKVARLA, in prep.). These genera particularly demonstrate the importance of TEM in pollen studies of this subfamily.

In the comparative pollen morphology of the subfamily **Papilionoideae** there are few or no complete discontinuities in pollen characters except at species or sometimes at generic level. There is a gradual increase in complexity of pollen through the more derived tribes which have more genera with complex pollen than occurs in less derived tribes. Some genera in, what on taxonomic evidence are, the derived tribes can have comparatively unspecialised pollen. The only complete discontinuity in pollen morphology associated with tribal boundaries is between **Psoraleae** and **Amorpheae** (FERGUSON & SKVARLA, 1981; FERGUSON & STIRTON, in prep.; FERGUSON, in prep.).

Even within some genera a gradual increase in complexity occurs, especially in exine stratification, with a wide range of variation and

few clear cut discontinuities as for example **Indigofera** and also in **Psophorcarpus** (see POOLE, 1979). However, STANIER & HORVAT (1978) have found pollen characters and exine stratification valuable in distinguishing **Phaseolus** and **Vigna** and groups within **Vigna**.

In the genus **Vicia**, **V. faba** has a granular interstitium (see Plate 2) while **V. cracca** shows a slight tendency towards break up of the columellae into granules, they also differ in exine ornamentation, the former having a rugulate/reticulate tectum on the mesocolpia (Plate 1) while the latter has an almost complete smooth or slightly rugulate tectum. **Lathyrus vernus** and **L. latifolius** have pollen with a columellate interstitium (Plate 2). FERGUSON (1984) has suggested that exine stratification may prove as a useful pollen character to separate these closely related genera. However, a fuller survey may show that continuous variation from columellate to a densely granular interstitium somewhat similar to that found in **Indigofera**. Other genera in the tribe **Vicieae** as **Pisum** and **Lens** (Plates 1 & 2) have a distinctly columellate interstitium and there is some variation in the exine ornamentation which may prove useful in distinguishing species and species groups.

Another important observation that arose from the survey of subfamily **Papilionoideae** is the fact that closely related species sometimes were found to have rather different exine ornamentation, some with a reticulate tectum, others with rugulate/verrucate ornamentation. Similar rather characteristic rugulate/verrucate ornamentation occurs in species and genera taxonomically far apart. Verrucate ornamentation in the pollen of subfamily **Papilionoideae** is associated with flowers adapted for bird and bat pollination (see FERGUSON & SKVARLA, 1982; FERGUSON, 1984). It is emphasized that it was only possible to make this type of observation with a good taxonomic background and a large palynological data base.

A detailed study of the pollen of the genus **Erythrina** (HEMSLEY & FERGUSON, 1985) well documented as a bird pollinated genus showed that the New World species with long, slender, horizontally presented, tubular flowers and vertical inflorescences known to be pollinated by hummingbirds have uniform, regularly reticulate pollen ornamentation. The pollen of this group is dry and powdery when dissected from anthers of herbarium specimens. On the other hand species with more or less gaping flowers held reflexed with the standard petal enlarged and horizontal inflorescences which allow for pollination by perching birds and are predominantly Old World have much more varied pollen with sexinous granules, coarse muri and even a finely reticulate tectum in some species. The pollen in this group is very often rather sticky with a lot of pollenkitt in comparison with the pollen of the hummingbird pollinated group (see FERGUSON, 1984). This shows two things; first the sort of information careful study of herbarium material can yield and second the importance of studying the whole pollen grain.

Pollenkitt is a potentially very valuable character little understood and apart from the interesting work of HESSE (1981) it has scarcely been studied. A few results for **Papilionoideae** are included in FERGUSON (1984). Likewise variation in pollen colour well known to bee keepers (see HODGES, 1952) has received little recent attention in taxonomy. The biochemical nature, function and distribution of the surface coatings of pollen grains could in some groups prove to be extremely valuable in contributing to an understanding of the taxonomy and evolution.

Restionales

The group has palynologically been studied quite well (CHANDA, 1966; CHANDA & ROWLEY, 1967; LADD, 1977). In a group such as this cryptic characters can be of considerably importance where both the floral characters and vegetative morphology are very reduced. However, careful reexamination of the pollen morphology by LINDER & FERGUSON (1985) show that thin sectioning of the apertures for TEM study and fracturing for SEM study together with light microscopy suggests that palynologically **Centrolepidaceae** is very distinct from **Restionaceae** and **Flagellariaceae**. The previous workers had been unable to elucidate the differences due to the limitations of light microscopy or due to oversimplification of SEM data. The importance of these recent findings is not only in taxonomy but also has phytogeographical implications by the fact that Restionaceae-type fossil pollen occurs in the Palaeocene of Europe as well as in southern hemisphere fossil deposits.

Moringaceae

A small family with a single genus and some 13 species of great potential importance because of the flocculating properties of the foliage. It has recently been revised taxonomically by VERDCOURT (1985) and a detailed pollen study carried out in parallel (see FERGUSON, 1985a). This exemplifies collaboration between taxonomist and comparative pollen morphologist and almost essential approach to systematic studies to-day. Similar collaboration has been common place in many laboratories in the past and continues to-day, these include for example MULLER & LEENHOUTS (1976) in **Sapindaceae**, SKVARLA, RAVEN & al. (1978) in **Onagraceae**, SKVARLA, TURNER & al. (1978) in **Compositae**, VERDCOURT & HALLIDAY (1978) and POOLE (1979) in **Psophocarpus**, VERDCOURT (1981) and FERGUSON (1981b) in **Macrotyloma** and the long series of works of FORMAN (1975, 1978) and FERGUSON (1975, 1978) and FORMAN (1982) and HARLEY & FERGUSON (1982) in **Menispermaceae**.

The pollen morphology of **Moringa** is very homogeneous but very characteristic being tricolporate with very distinctly costate apertures, a smooth tectum (an uncommon feature in angiosperm pollen) and a granular interstitium. Small differences in pollen size correlate with floral characters perhaps indicating an increase in DNA in the cell and possible polyploidy. Here pollen size may give a clue to the need for further investigation but care is always needed in applying pollen size as a taxonomic character. Work of VAN DER PLUYM & HIDEUX (1977) have shown that pollen grain size in **Eryngium maritimum** is related to age and position of the inflorescence.

The pollen morphology of **Moringaceae** throws no light on the families supposed affinities with **Resedaceae** and **Capparaceae** on the one hand and **Leguminoseae** subfamily **Caesalpinioideae** on the other.

Mandragora (Solanaceae)

The pollen morphology of the genus **Mandragora** is both remarkable and unique in the **Solanaceae**. DIEZ & FERGUSON (1985) have attempted to elucidate the structure of the pollen. The work is of particular interest not only for the results but for the range of techniques used in the study. Acetolysed and unacetolysed pollen were studied with LM then with SEM both with and without critical point drying. Likewise both acetolysed and unacetolysed pollen were examined with TEM. The pollen has pentagonal or hexagonal shaped areas bounded by apertural thinnings in the endexine. The thinnings are covered with a complete

and ornamented ektexine.

Palmae

A survey of the pollen of the **Palmae** is currently being carried out at Kew with the object of supplementing and expanding the overviews of THANIKAIMONI (1970) and SOWUNMI (1972) using techniques of electron microscopy (see FERGUSON, 1981a). The study is in parallel with the preparation of a Genera Palmarium (MOORE & al., 1985) and with taxonomic guidance from Dr. J. Dransfield at Kew. In addition to providing taxonomic data for this economically very important tropical family it is hoped that the study may give clues to profitable areas for investigation of pollination biology. Furthermore, palm pollen is well represented in the fossil record and a better knowledge of the pollen morphology of the extant species is very important for palaeopalynology. Preliminary results demonstrate far more variation than had hitherto been suspected, as for example in the taxonomically well defined genus **Pinanga** (FERGUSON & al., 1983). Remarkable parallelism and superficial resemblances occur in exine ornamentation and stratification between a wide range of not only genera and tribes but also subfamilies (FERGUSON, 1985b). These results demonstrate the need for more work and extensive surveys incorporating detailed studies with SEM and TEM and for careful comparative observations on fossil palm pollen before these fossils are attributed to extant genera of **Palmae**. The work of FREDERIKSEN & al. (1985) on the Eocene pollen genus **Diporokonia** is a good example of this type of work. Similar work has been carried out by COETZEE & PRAGLOWSKI (1984) in confirming the occurrence of **Casuarina** and **Myrica** in the Tertiary of South Africa and there are the classical works by MULLER on **Sonneratia** (1969, 1978). MORLEY (1982) has shown most elegantly how the comparison of pollen from extant species with fossil finds can considerably increase our knowledge of the evolution of the **Alangiaceae**.

COMPARATIVE POLLEN ONTOGENY

Although there have been an increasing number of studies of pollen development few have attempted to be essentially comparative except those of DICKINSON (1976) and CERCEAU-LARRIVAL & al. (1981). Some general features can be recognised which may have significance in understanding relationships between higher categories for example families and orders but really the coverage or angiosperm pollen is very small. There is a need as well for a review of the existing works and an analysis of results bearing in mind the fine structural features different groups have in common and evaluating their taxonomic significance.

The work of ABADIE & HIDEUX (1979, 1983) on the ontogeny of pollen of species of **Saxifraga** with very different exine architecture demonstrates how pollen development can give a clearer insight into the relationships between species, species groups and sections within a genus. The recently described techniques of BARNES & BLACKMORE (1984) for fracturing, osmium digestion and examination with SEM perhaps will open the prospect of more rapid surveys of ontogeny.

OTHER ASPECTS

Study of the fine structure of the exine and the arrangement of the sporopollenin molecules (ROWLEY & al., 1981) and relationships

between architecture and harmomegathic stress (BOLICK, 1978, 1981 and BLACKMORE, 1983) contribute to a deeper understanding of the pollen grain and in consequent a better evaluation of the structures used in systematics.

CONCLUSION

Pollen studies have much to contribute to taxonomy. The techniques of electron microscopy can complement light microscopy and enable morphology to be studied in great delail. However, it is desirable and often essential to consider the whole pollen grain and its relationship with and role in the biology of the plant. In tropical groups where living material is not easily available much information and many ideas can be derived or infered from herbarium material. Data analysis should include possible functional significance as well as form. Some pollen features have been demonstrated to be under adaptive selection in both closely related groups and in disparite groups (**Papilionoideae**). Remarkable parallelism in ornamentation and exine stratification occur (**Palmae**) and these as yet need careful evaluation. Some pollen structures as for example apertures in relation to harmomegathic movement are almost certainly the result of convergent evolution in response to common functional requirements. It is necessary to try to distinguish between structural and functional homology and to be aware of those features which may cause taxonomic confusion. An essential requisite for such understanding is a sound taxonomic framework supported by an adequate pollen morphological data base. Multidisciplinary studies, collaboration and exchange of ideas and information are advocated both with the taxonomist, other specialist studies of cryptic characters as well as workers in fine structure and ontogeny and with palaeopalynologists. Only this type of approach to pollen morphology in taxonomy is likely to yield the greatest return to systematics and evolution.

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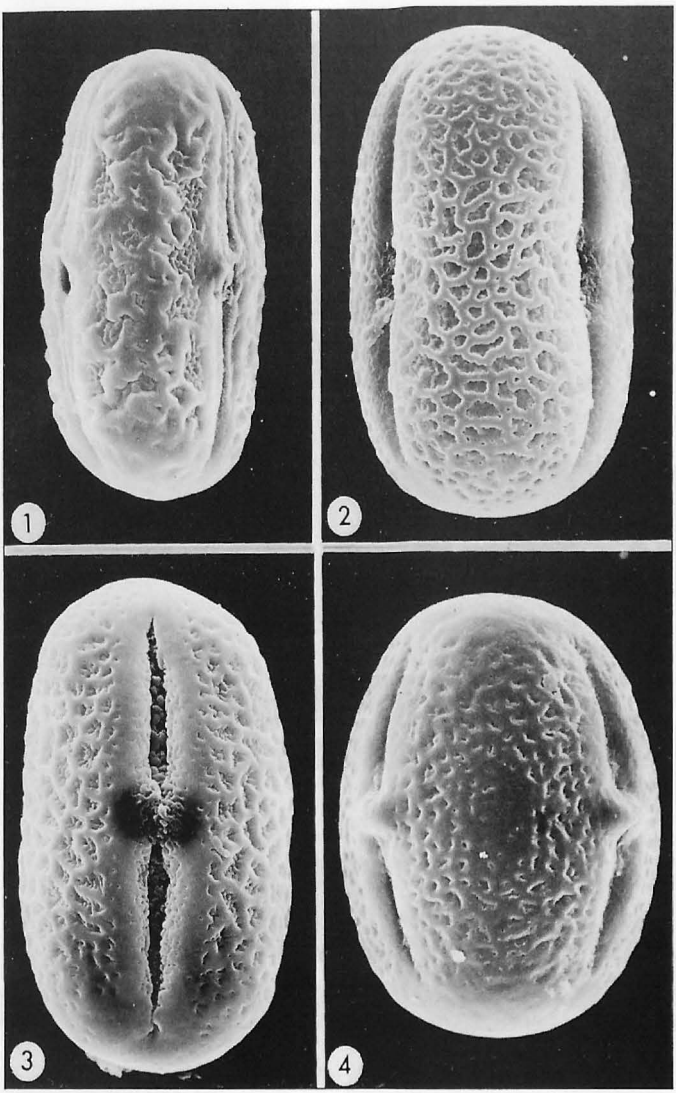
Plate 1. Figs. 1-4 SEM micrographs. 1.- **Vicia faba** L. (from Tuli 57, Austria) showing smooth tectum on poles and reticulate/rugulate tectum on mesocolpium with sexinous granules x 1600. 2.- **Pisum sativum** L. (from Syngranides 1276, Cyprus) showing reticulate tectum with sexinous granules in lumina x 1800. 3.- **Lens culinaris** Medicus (from Meebold s.n., Italy) showing the outline of the endoaperture as an area darkened by the electron beam on colpus at equator; distinct, smooth colpus margins and reticulate tectum on mesocolpium with sexinous granules in lumina and a smooth tectum on poles x 2400. 4.- **Lathyrus latifolius** L. (from Last 178/1, England) showing smooth tectum on poles and rather finely reticulate tectum on mesocolpium with sexinous granules in lumina, bulging mesocolpial pouches are pronounced on the colpi at equator x 1800.

Plate 2. Figs. 1-7 TEM micrographs. 1-2.- **Pisum sativum** L. (from Syngranides 1276, Cyprus). 1.- Showing whole pollen grain cut in longitudinal section, note endexine absent at polen and thickened towards equator forming costae x 1400. 2.- Detail showing thick endexine, narrow foot layer, columellate interstitium and thick tectum x 14000. 3.- **Lens culinaris** Medicus (from Meebold s.n., Italy) showing similar stratification to **Pisum sativum** Fig. 2 x 19000. 4.- **Lathyrus vernus** (L.) Bernh. (from Cox s.n., Finland) stratification similar to Figs. 2-3 but cut nearer polar area and slightly thinner endexine; thicker sparser columellae and thick, smooth tectum x 26000. 5.- **Lathyrus latifolius** L. (from Last 178/1, England) columellate interstitium with very thin foot layer x 17500. 6.- **Vicia cracca** L. (from Little s.n., England) endexine thickening towards aperture but note tendency for some columellae to become somewhat granular x 26000. 7.- **Vicia faba** L. (from Tuli 57, Austria) showing a granular interstitium and almost complete loss of the foot layer x 14000.

Pollen from all specimens examined taken from the Herbarium, Royal Botanic Gardens, Kew. (K).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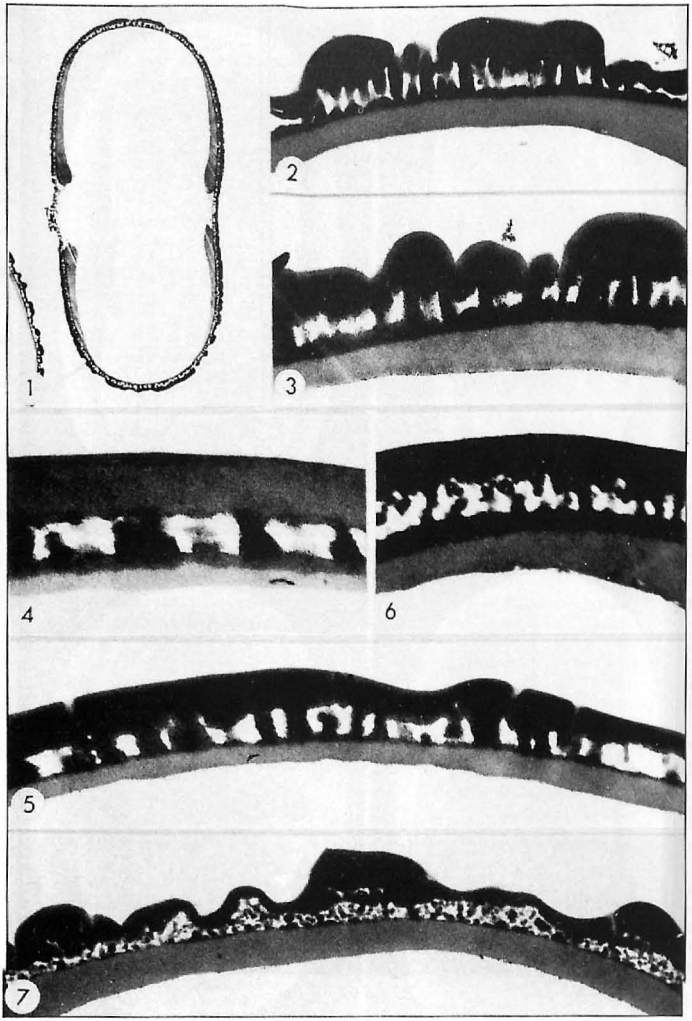
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