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Contributions of palynological characters to plant systematics

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Introduction

Palynology is the study of pollen and spore, mainly on the point of their morphology. It is not surprising that palynology increasingly plays an important role in the plant systematics because so little materials provide a great amount of information, i.e. pollen bears so diverse morphological characters such as pollen unit, shape, polarity, symmetry and grain size, the surface sculpture pattern, the wall stratification, the aperture type, number, size, arrangement and margin thickening, etc. As compared with other pollen characters and even floral characters, evolutionary trend of aperture type and number is so conservative and important that the phylogenetic as well as phenetic relationships of innumerable taxa have been elucidated (Erdtman 1969, Walker and Doyle 1975).

Many kinds of angiosperms produce enormous number of pollen grains, which are dispersed into the air and sink evenly and widely like a rain (so-called pollen rain) to cause the allergy to man. An analysis of samples taken from the air can provide the annual calendar of the kinds and amounts of the pollen rain and help the medical treatment. Owing to the high chemical resistance of the pollen wall, on the other hand, air-borne pollen grains can remain as microfossils when they sink in an acid bog or a lake. An analysis of the pollen from the peat or the sediment can facilitate the reproduction of the paleovegetational assemblages. Floristic as well as vegetational history of many parts of the world is well understood by this mean (Faegri and Iversen 1964, Graham 1972).

Although the studies on the biochemical, physiological, cytological, developmental points in addition to the pollen analysis, are important fields of palynology, its contribution to the plant systematics will be concentrated in this presentation.

Principal pollen characters and terminology

Pollen grain size: Pollen grain size ranges broadly between 15μ (*Myosotis*) and over 300μ (*Cymbopetalum*) in diameter. It is somewhat affected by the physiological conditions of the plant, the environmental factors, and even the method of preparation. Grain size is positively correlated with the length of style and dimorphic in the distylous species. In

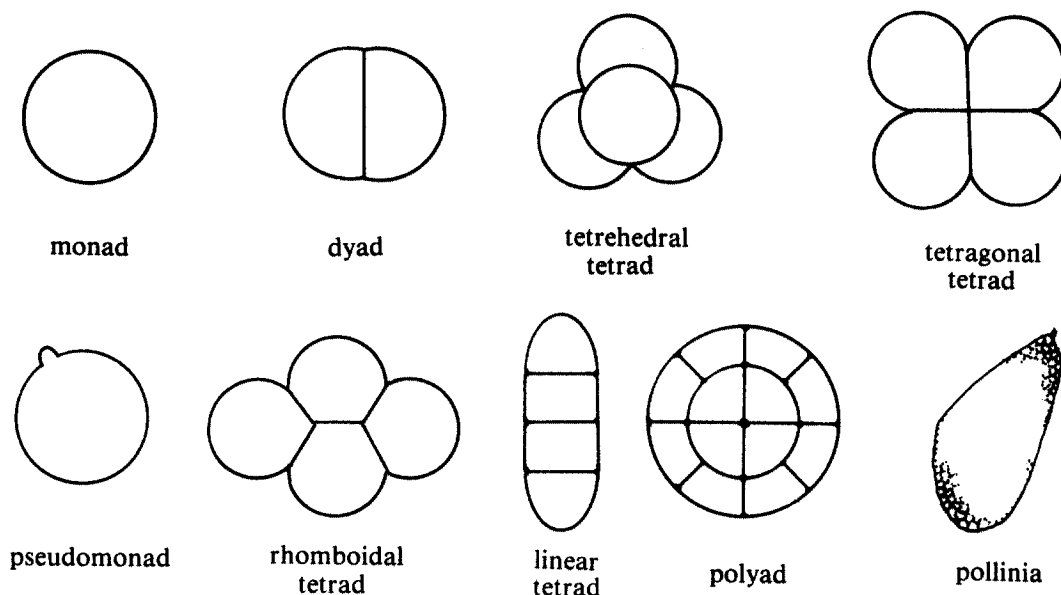


Figure 1. Principal types of cell unit of pollen grains (From Walker and Doyle 1975).

general, grain size is relatively small and ranges narrow in the anemophilous plants (15-45 μ), whereas large and wide in the zoophilous ones (15-120 μ). Erdtman (1969) divided grain size into six classes: minute (<10 μ), small (10-24 μ), medium-sized (25-49 μ), large (50-99 μ), very large (100-199 μ), and gigantic (\geq 200 μ). Although grain size seems a rather unstable character, it may often serve as a diagnostic character and may play a role in the construction of phylogenetic tree.

Pollen unit (Fig. 1): At maturity in the anther, pollen grains are mostly found solitarily (monad) but sometimes in groupings of two (dyad), four (tetrad), many (polyad) and mass (pollinia). A pollinium consists of the entire pollen mass of one or two pollen chambers fused together as a unit (found only in the Asclepiadaceae and Orchidaceae). The most common pollen unit besides monads is tetrad, which represents a retention of four pollen grains meiotically produced from a pollen mother cell. According to the spatial arrangement of the grains, there are five types: tetragonal, rhomboidal, linear, T-shaped and tetrahedral. A pseudomonad in the Cyperaceae looks like a monad but actually not, because it is formed by a disintegration of three of the tetrad grains. Pollen units other than monads are represented in some or all members of 43 dicot and 12 monocot families (Walker and Doyle 1975).

Wall stratification (Fig. 2): Pollen wall consists of two layers, an outer layer, exine, and an inner layer, intine. Exine is composed of the chemically resistant sporopollenin (an oxidative polymer of carotenoids and carotenoid esters) and remains after acetolysis. Intine is destroyed upon acetolysis and not so important in the pollen morphological viewpoint. Exine consists of two layers, ectexine and endexine; the former again consists of three layers: a roof-like tectum, a basal foot-layer, and rod-like columella between the two. the primitive type of exine possesses a fully covered tectum (tectate). Tectum gradually diminishes as an evolution progresses and the type shifts to semitectate and then to intectate, although the

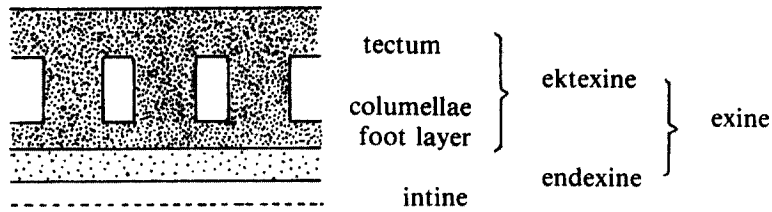


Figure 2. Pollen wall stratification (From Walker and Doyle 1975).

reversed trend is less frequently observed. There is a wide variety of modification in the stratification. In some taxa, exine is almost lacking. The proportion of ektexine and endexine, which can be distinguished by the electron density, is variable.

Surface sculpturing (Fig. 3): Pollen grain surface exhibits amazingly diverse sculpturing patterns. Major types include: psilate (smooth), foveolate (pitted), fossulate (grooved), scabrate (finely projected), verrucate (warty), baculate (rod-like), clavate (club-shaped),

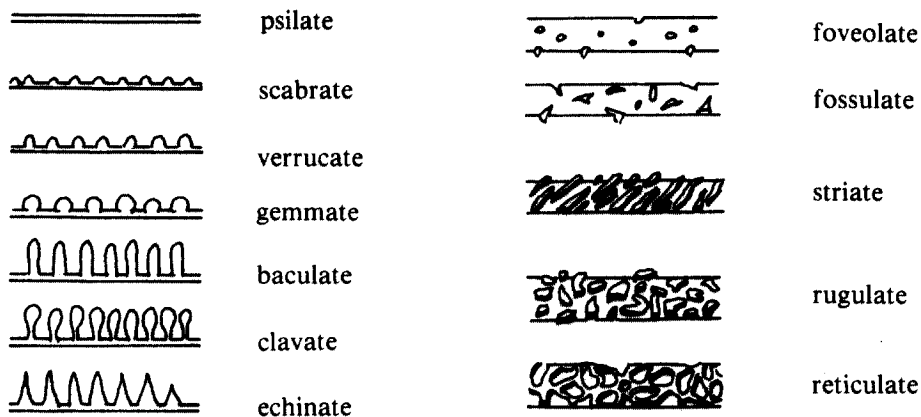


Figure 3. Sculpturing types of pollen grain wall (From Faegri and Iversen 1964).

gemmate (head-shaped), echinate (spiny), rugulate (with elongate sculpturing elements irregularly distributed), striate (with elongate elements parallel-oriented) and reticulate (with element forming networks). These sculpturing patterns may appear over the tectum or in the intectate pollen over the footlayer. A scanning electron microscope demonstrates the details of the patterns explicitly.

Grain shape: At the tetrad state, in which four pollen grains meet together, polarity of the pollen is determined. From the center of the four grains to the center of each grain we can draw a straight line, polar axis. Polar axis then extends between the inward pole or proximal pole and the outward pole or distal pole of the grain. The equatorial plane perpendicularly bisects the polar axis and form a boundary or equator between the proximal and distal faces of the grain (Fig. 4). If the polar and equatorial axis are the same in length, the grain is spherical; if the polar axis is shorter than the equatorial axis, the grain is oblate; and if the polar axis is longer than the equatorial axis, the grain is prolate. Actually varying degrees of

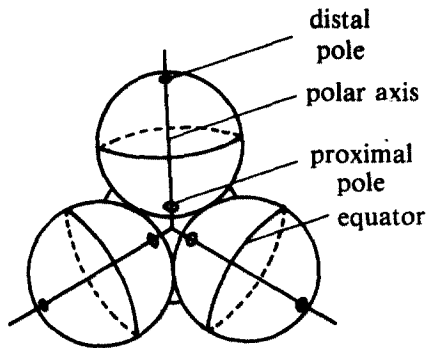


Figure 4. Pollen tetrads showing some terms related to the position in the tetrad (From Walker and Doyle 1975).

the ratio of polar/equatorial axis (P/E ratio) give further terms: prolate (≥ 2.00), euprolate (1.34-1.99), subprolate (1.15-1.33), prolate spheroidal (1.01-1.14), spherical (1.00), oblate spheroidal (0.88-0.99), suboblate (0.76-0.87), euoblate (0.51-0.75), and peroblate (≤ 0.50). On the other hand, a grain with a certain P/E ratio may exhibit various equatorial shapes according to its polar outline. Mostly grains are circular or oval, whereas less frequently they may be rhomboidal, apiculate, compressed oval, depressed oval, etc. In addition, the equatorial outline or amb shape is usually circular or some modifications appear such as triangular, lobed, subangular, hexagonal, etc.

Pollen aperture (Fig. 5): Apertures are specially delimited thinwalled areas in the exine through which pollen tube emerges at the time of germination. Aperture serves as an exit for the pollen tube emergence, as a harmomegaphic apparatus (it allows for a volume-change accommodation of the grain subjected to changes in humidity), and as an entrance of the pollen water absorption from the stigmatic surface. Morphology and terminology of pollen aperture depends largely on the number, shape, position and structure. With respect to

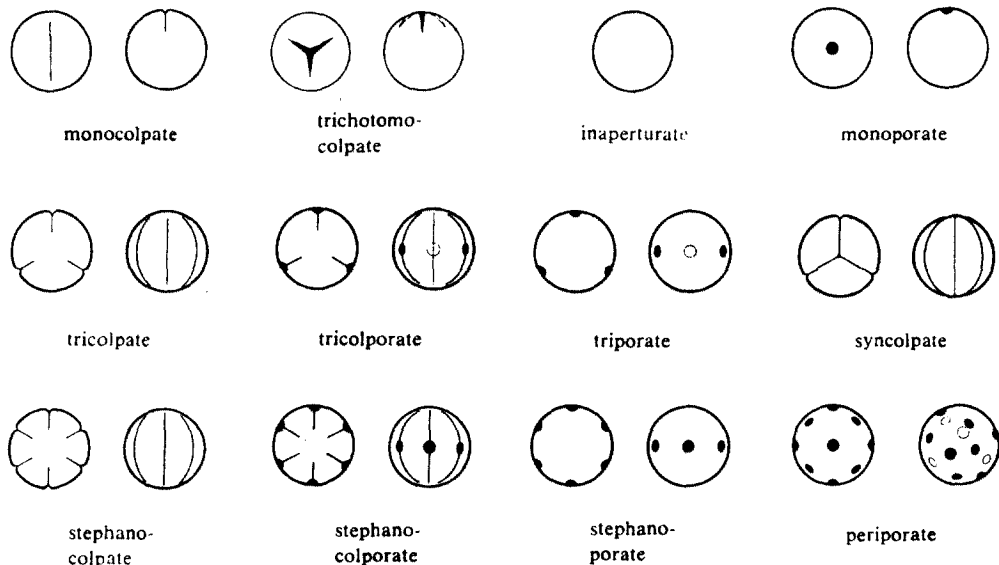


Figure 5. Principal types of pollen apertures (From Faegri and Iversen 1964).

number of aperture, the following prefixes are applied: in-aperturate (none), mono- (one), di- (two), tri- (three), poly (more than three). With respect to shape, there are two basic aperture types; elongate, furrow-like aperture, colpus, and round aperture, pore. When both colpus and pore exist together, the pollen is colporate; when colpus is weakly defined, colpoidate; and when pore is weak, colpoidate. The evolutionary trend is known to advance from colpus to pore in type and from one to many in number. The most primitive aperture of the angiosperms is monocolpate (or monosulcate) from which tricolpate aperture was derived. Tricolpate aperture is the basic type of dicots pollen whereas monosulcate aperture is the basic type of monocots and primitive dicots. Since there is no intermediate form between monosulcate and tricolpate, three hypotheses were proposed on the origin of the tricolpate aperture: through inaperturate (Walker 1970), through trichotomosulcate (Wilson 1963, Straka 1963) and directly from monosulcate (Kuprianova 1979).

The above introduction of pollen morphology, evolutionary trends and terminologies seems to be complicated, however, so diverse morphology of pollen grains from wide range of taxa needs even much more terms. Some more detailed explanation might be referred in Erdtman (1969), Faegri and Iversen (1964), and Walker and Doyle (1975).

Palynological role in plant systematics

Since the late 18th century, the subdivision of angiosperms into monocots and dicots has been believed to be natural. No disagreement has arisen on this historical treatment. The Bessey's phylogenetic system of the monocots and dicots is widely accepted, which has undergone some modifications or improvements later by Takhtajan and Cronquist. Ranales or Magnoliidae as an ancestral group is supported palynologically as well because they possess the most primitive monosulcate pollen (evidenced by the geological records and strongly inferred by a reasoning of logical parsimony). The monosulcate type derives to other types in the advanced taxa, via the tricolpate type in the dicots whereas directly in the monocots (Muller 1970). Since the Amentiferae, which was understood to be the ancestral group by Engler, possesses the tricolpate or tricolpate-derived pollen types, its primitiveness is readily disputed.

Pollen morphology has proved of value in the classification of the Saxifragaceae. *Berenice arguta* of the family was shown to have companulaceous grains and further investigation of its other features showed that it would indeed be better accommodated in the Campanulaceae. *Adoxa* was once placed in the Saxifragaceae due to its distinct style but its sympetalous feature made confusion with the Caprifoliaceae. After it was known that *Adoxa* has the *Sambucus*-type pollen, however, its own family Adoxaceae was moved next to the Caprifoliaceae. Cronquist (1981) points out that the embryological and chemical evidence also strongly supports its position near the Caprifoliaceae.

Trisyngyne, a New Caledonian tree, was placed in the Euphorbiaceae by the feature of male plant. Female plants were later found and *Trisyngyne* transferred to the Fagaceae. Examination of the pollen grains would have shown, however, that they are exactly the same type as those of *Nothofagus* and moreover precisely of a special kind of which the oldest

geological finds were made in the Cretaceous.

Generic limits within the Polygonaceae have long proven problematical. Several authors insisted the separation of *Polygonum* s.l. Hedberg (1946) investigated the pollen grains and distinguished ten different pollen types. He compared the result with the chromosome number and agreed with the generic separation into seven genera. This position has widely been followed by recent authors.

Taxonomic recognition of the genera of the Juglandaceae is based to a large extent on floral and seed characters as in most other families. Stone and Broome (1975) examined the pollen of seven genera and 57 species and recognized four major pollen types: triplicate-isopolar *Engelhardia*-type, triplicate-isopolar-pseudocolpate *Platycarya*-type, triplicate-paraisopolar *Carya*-type, and stephanoporate to anazoni-porate *Pterocarya*-type. Generic relationships were elucidated by the pollen characteristics, which are well matched with phylogenetic speculations based on other features.

Lythraceae, consisting of about 26 genera and 500 species, was monographed by Koehne (1903). The family was subdivided into two tribes Lythreae and Nesaeae, based on the degree of completeness of the ovary septa. The tribes were again divided into subtribes and series on the basis of other floral characters. Palynological study of 25 genera and 62 species of the Lythraceae (Lee 1979) revealed that the family is divided into three groups which are characterized by having a non-, 3-, and 6-pseudocolpate pollen grains. It was shown that not only the two tribes are mixed with all three kinds of pollen, but also most small groups do not have the same type of pollen (Table 1). The close relationship among the 6-pseudocolpate genera was also recognized by the result of numerical taxonomy (Lee 1973) in which 60 floral and vegetative characters, including only two pollen characters, were assessed. On the contrary, the numerical taxonomic study did not support the Koehne's taxonomy. It was suggested that the Koehne's treatment is not natural and needs a revision.

Table 1. Koehne's classification associated with the number of pseudocolpi in parenthesis (From Lee, 1979).

Tribe Lythreae	
Subtribe 1. Lythrinae	
Series I.	<i>Rotala</i> (6), <i>Ammannia</i> (6), <i>Peplis</i> (3), <i>Lythrum</i> (3) <i>Woodfordia</i> (0), <i>Didiplis</i> (0)
Series II.	<i>Cuphea</i> (0), <i>Pleurophora</i> (6)
Subtribe 2. Diplusodontinae	
Series I.	<i>Galpinia</i> (0), <i>Pemphis</i> (3), <i>Diplusodon</i> (0), <i>Alzatea</i> (0)
Series II.	<i>Physocalymma</i> (3), <i>Lafoensia</i> (0)
Tribe Nesaeae	
Subtribe 1. Nesaeinae	
Series I.	<i>Crenea</i> (6)
Series II.	<i>Nesaea</i> (6), <i>Capuronia</i> (0), <i>Heimia</i> (0), <i>Decodon</i> (0), <i>Grislea</i> (0), <i>Adenaria</i> (0)
Series III.	<i>Tetrataxis</i> (?), <i>Ginoria</i> (6), <i>Haitia</i> (6)
Subtribe 2. Lagerstroeminae	
	<i>Lagerstroemia</i> (6), <i>Lawsonia</i> (6), <i>Rhynchoalix</i> (3)

The Empetraceae have variously been referred to the Ericales, Sapindales, and Celastrales (Cronquist 1981). The affinity of the Empetraceae with the Ericaceae is supported on the basis of embryological as well as habitual resemblance. They also share the common feature of the susceptibility to particular rusts. Erdtman (1969) pointed out that the tetrad pollen is similar to that of the Ericaceae, especially to that of the *Ledum*. While Hutchinson still maintains the Empetraceae in the Celastrales, in the Engler Syllabus the family was moved into the Ericales.

Recently, an increasing number of palynotaxonomic researches are published. Some noteworthy examples include Ferguson (1981), Graham and Barker (1981), Nowicke and Skvarla (1974, 1983, 1984), etc. Suggestions from these studies, however, would await the taxonomist's evaluation and treatment such as rearrangement and separation in future.

An excellent palynological survey of angiosperm families is given by Erdtman (1969). He summarized what was known about the pollen morphology of every family up to about 1950. This monumental work demonstrates the value of palynology in taxonomic studies. Extensive palynological studies have been well documented in various bibliographies, Tralau (1965), Bibliography of Actinopalynology, 1961-1966 (Review of Palaeobotany and Palynology, Vol. 12, 1971), and Thanikaimoni (1972). None-the-less, increasing number of systematic palynological papers have been published every year in the palynological journals such as Grana, Pollen et Spores, Review of Palaeobotany and Palynology, Journal of Palynology (India), and Japanese Journal of Palynology and other journals of botany, plant systematics, etc.

Conclusion

As presented above, the palynological characters contribute enormously to the plant systematics. This is possible because pollen grains bear so many characters which are relatively conservative and phylogenetically useful. In angiosperms, the most important trends at the higher taxonomic levels involve the number, position, and structure of aperture, exine structure and stratification, and in some cases size and sculpture. Palynological evidence may contribute to place taxa of uncertain affinities, to suggest rearrangements, withdrawals and separations, as well as corroborating other lines of evidence. That is now possible to study even fine structural details in fossil pollen, opens up possibilities of new sources of phylogenetic evidence. It is confidently expected that pollen morphology plays an increasing role in both comparative phenetic taxonomy and in evolutionary interpretations.

Although palynological evidence plays such an important role in plant systematics, it must be treated with caution and not interpreted without reference to other lines of evidence. The interpretation of certain structures, the extent of variation and the elucidation of trends are still causing concern and it must be remembered that pollen characteristics are subject to parallelism, convergence or probably reversal, as are other characters employed by the taxonomist (Davis and Heywood 1973).

References

- Cronquist, A. 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
- Davis, P. H. and V. H. Heywood. 1973. Principles of Angiosperm Taxonomy. Krieger Publ. Co., Huntington, N.Y.
- Erdtman, G. 1969. Handbook of Palynology. Hafner Pub. Co., New York.
- Faegri, K. and J. Iversen. 1964. Textbook of Pollen Analysis. Hafner Publ. Co., New York.
- Ferguson, I. K. 1981. The pollen morphology of *Macrotyloma* (Leguminosae: Phaseoleae). Kew Bull. 36: 455-461.
- Graham, A. (ed.). 1972. Floristics and Paleofloristics of Asia and Eastern North America. Elsevier Publ. Co., New York.
- _____ and G. Barker. 1981. Palynology and tribal classification in the Caesalpiniodideae. Advances in Legume Systematics (ed. R. M. Polhill and P. H. Raven). pp. 801-834.
- Hedberg, O. 1946. Pollen morphology in the genus *Polygonum* s. lat. and its taxonomic significance. Sv. Bot. Tidskr. 40: 371-404.
- Kuprianova, L. A. 1979. On the possibility of the development of tricolpate pollen from monosulcate. Grana 18: 1-4.
- Koehne, E. 1903. Lythraceae. In Engler, Pflanzenreich VI. 216 (Heft 17).
- Lee, S. 1973. Palynology and numerical taxonomy of the Lythraceae. M.S. thesis of Kent State Univ., Ohio, U.S.A.
- _____. 1979. Studies on the pollen morphology in the Lythraceae. Korean J. Bot. 22: 115-133.
- Muller, J. 1970. Palynological evidence on early differentiation of angiosperms. Biol. Rev. 45: 417-450.
- Nowicke, J. W. and J. J. Skvarla. 1974. A palynological investigation of the genus *Tournefortia* (Boraginaceae). Amer. J. Bot. 61: 1021-1036.
- _____ and _____. 1983. A palynological study of the genus *Helleborous* (Ranunculaceae). Grana 22: 129-140.
- _____ and _____. 1984. Pollen morphology and the relationships of *Simmondsia chinensis* to the order Euphorbiales. Amer. J. Bot. 71: 210-215.
- Stone, D. E. and C. R. Broome. 1975. Juglandaceae A. Rich. ex Kunth. World Pollen and Spore Flora 4, Almqvist & Wiksell Per. Co., Stockholm.
- Straka, H. 1963. Über die mögliche phylogenetische Bedeutung der Pollen-morphologie der madagassischen *Bubbia perrieri* R. Cap. (Winteraceae). Grana Palynol. 4: 355-360.
- Thanikaimoni, G. 1972. Index bibliographique sur la morphologie des pollens d'angiospermes. Inst. France Pondichéry. Trav. Sect. Sci. Techn. XII: 1-337.
- Tralau, H. 1974. Bibliography and Index to Paleobotany and Palynology, 1950-1970. Stockholm.
- Walker, J. W. 1974. Aperture evolution in the pollen of primitive angiosperms. Amer. J. Bot. 61: 1112-1137.
- _____ and J. A. Doyle. The bases of angiosperm phylogeny: Palynology. Ann. Mo. Bot. Garden 62: 664-723.
- _____ and A. G. Walker. 1981. Comparative pollen morphology of the Madagascan genera of caceae (*Mauloutchia*, *Brocheneura*, and *Haematodendron*). Grana 20: 1-17.
- Wilson, T. K. 1964. Comparative morphology of the Canellaceae. III. Pollen. Bot. Gaz. 125: 192-197.