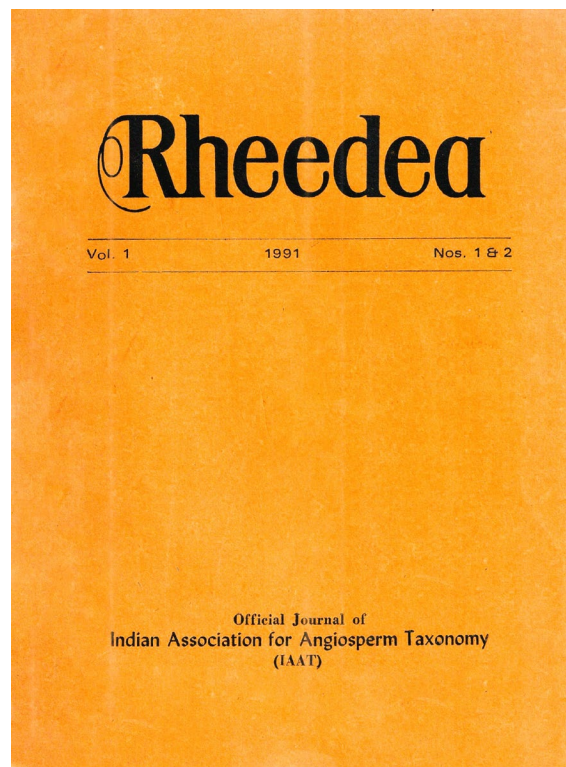




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## Pollen morphology, Plant taxonomy and Evolution

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### Abstract

The present is a key to the past, and the pollen-spore microfossils constitute perhaps the only record through geological Time, projecting the continuum of change in the diversity of flora, phytogeography and plant evolution. The above theme is explained in the light of our understanding of the principles of pollen - spore morphology and of morphological evolution of both the present day plants and fossil "Sporae Dispersae".

### Introduction

That the present is a key to the past has been the basic principle governing palaeofloristic and palaeostratigraphic interpretations (Erdtman, 1956; Faegri and Iversen, 1964, Nair, 1977). In one of the notes the late Prof. R. Potonie (1965) advised the stratigraphers to follow morphographic approach in making circumscription of "Sporae dispersae" (form species), because each morphoform represents the plant it belonged to. Today, the above advice is still relevant, considering the fast advances made in gaining knowledge on spore-pollen architecture, their taxonomic and phylogenetic value and relevance in linking the Present with the past, in terms of plant evolution.

The array of pollen grains and spores, produced by the various plants, are carried to different destinations, by carrier agencies like the air, the insects and water. Regarding pollen, the main destination is the stigma of the female counterpart, in which only an insignificant number of the pollen produced by any individual plant,

is required and the rest are wasted, but carried to various places, in each of which they, become important indices of value for gaining new information. The insect carried pollen finds entry into beehives, where it provides the food to the developing larvae; the airborne pollen are dispersed everywhere, and when it enters the bronchial system of man it produces allergy; the anemophilous, entomophilous and also the hydrophilous pollen together constitute a comprehensive entity of dispersed pollen getting into the mud bottom of sediments to become fossils (Nair, 1985 a). The above short account indicates that the study of dispersed pollen has a wide spectrum of applications, in gaining knowledge on allergenic plants, honey plants, and vegetational composition of the place where a sedimentary deposit occurs.

The pollen or spores when detached from the mother plant, loses its identity, if not found *in situ*. The identifications of the dispersed pollen/spores, is therefore, of basic importance, in using such units to advantage. This is made possible

by the pollen and spore units having an outer wall, the exine, which embodies such morphological characteristics, that are typical of the mother plant it belongs to. Further, the exine is resistant to decay, and are therefore preserved in almost every sedimentary conditions they are brought in, by virtue of their chemical composition being made up of "Sporopollenin", a polymer with the chemical formula  $C_{90}H_{129}(OH)_5$ . All the same, some exines are too fragile to stand environmental hazards, but by and large, the pollen of a very dominant section of the vegetation is preserved, such as to allow palaeofloristic interpretations.

During the last few decades, a new dimension to the study of pollen morphology has been added, through scanning electron microscope investigations, serving to provide an understanding of the fine structure of the exine wall, and the consequent enhancement of the application of pollen - spore morphology in plant taxonomy at micro-taxa levels. The development of suitable methods for scanning *spora dispersae* will provide a greater understanding of the morphology of those units, leading to a totally new approach to the circumscription of form species, and to their application in stratigraphic and palaeofloristic studies.

In addition to the above, the laying of the principles of pollen morphological evolution (Nair, 1970) and its demonstration in the origin and evolution of angiosperms (Nair, 1970, 1979) is of potential application in establishing the evolutionary status of any one "Spora dispersae" unit (Nair, 1966, 1974, 1977), which it can be hoped, will have a new impact on stratigraphic studies itself, based on a phylogenetic approach.

### Morphological characterisation of pollen and spores

The morphological characters of pollen and spores, are embodied in the exine, the outer resistant layer of the microspore wall (Erdtman, 1952). These characters are resolved into 5 general groups, namely Aperture, Exine strata, Exine ornamentation, Size and Shape in the order of their importance in plant taxonomy and evolution.

**Aperture** : The aperture characterisation is abbreviated as NPC (N: Number; P: Position in tetrad and C: Character). In character, the aperture (sometimes represented as a thinner area of the exine), is either present (*aperturate*) or absent (*inaperturate*). When present, the aperture is either elongate (*colpate*) or circular (*porate*), and in the lower plants triradiate aperture (*trilete*) forms also occur. The variants of the colpate and porate forms, are colp-orate, por-orate, spiraperturate, synaperturate etc. The number of apertures vary from 1 - many, and their position is either proximal, distal, equatorial or global in terms of the tetrad. The apertural characteristics are of primary importance in plant identifications relating to dispersed pollen, occurring detached from the mother plant.

**Exine Ornamentation** : The exine ornamentation is of secondary importance in phylogenetic taxonomy. The exine surface is either smooth (*psilate*, *leavigate*) with depressions (*reticulate*, *foveolate*, *scrobiculate*, *striate*), or with projections (*spinulate*, *verrucate*, *gemmate*, *baculate* etc.).

**Exine Strata** : The Exine is stratified into various layers, which is most pronounced in pollen walls. The strata consists of an inner homogeneous layer, superimposed by a columella layer carrying

a roof (tectum), fortified sometimes with an additional layer (supratectum or *suprategillum*), over which are the ornamentation patterns.

**Size :** The grains are either radiosymmetric (e. g. tricolpate) or bilateral (e. g. monocolpate) and accordingly the size is measured. For example, in a 3-colpate grain, the colpi are arranged along the equatorial zone, and the distance parallel to the colpi connecting the two poles is the Polar diameter (P), while that diametrically opposite is the Equatorial diameter (E). A monocolpate grain, which is like a boat, has three diameters (P, E1, E2), while the grains with global apertures, the E & P can not be specified and hence the size is expressed as the largest diameter.

**Shape :** Erdtman 1952 (1), suggested size classes on the basis of the equation  $\frac{P \times 100}{E}$  for radiosymmetric grains. The sharp inbilateral grains, may be expressed by general terms used for other morphological entities.

**Characterisation :** A combination of the various characters provide the grain a definite entity, enabling the fixing of taxonomic identity with regard to the mother plant it belongs to. Apart from the exine, the intine is sometimes very useful; It may also be pointed out that the general structure of the aperture and exine, are different in spores (cryptogamic Archegoniatae), as compared to the pollen grains (Spermatophyta). The 'letes' (e. g. fern spore) is a cleft with no floor (lack of aperture membrane), while the colpus (e. g. pollen) has a floor (colpus membrane). Similarly, the exine strata is not resolved into various constituent structures in spores as those of the pollen walls.

### Morphological evolution of pollen spores

A firm morphological organisation of the spore body may be considered to have begun at the level of the Bryophytes, in which the trilete, the monolete and the alete (trimorphous) forms occur. Most palynologists agree that the trilete form is the most primitive (Chaloner, 1970; Potonie, 1967; Mehra, 1974), and that it is from this the monolete and the alete have evolved, through a process of reduction (Nair, 1965; Miyoshi, 1966).

The trilete and the monolete are proximal in position in the tetrad, as known from microsporogenesis (Mehra, 1968). In terms of NPC, the number is *one*, position is *proximal*, and character is *trilete* and this apertural combination is considered the most primitive (Nair, 1965 a; Mehra, 1974).

While the trimorphous situation is present throughout the Cryptogams, and in Gymnosperms, an array of new apertural morphoforms appeared in the angiosperms. In terms of morphological evolution, the tricolpate is considered primitive to other apertural forms (Nair, 1970) in the Flowering plants.

The apertural evolution is the most significant aspect of morphological evolution of spores and pollen, and which has been applied in resolving problems of plant taxonomy and evolution. However, it may be pointed out that the ornamentation forms have evolved along two lines, namely the depression forms and the projection forms, from the psilate level, and these along with the morphological evolution of other characters, are of use in lower level taxonomy.

### Palynological basis of plant evolution

As mentioned earlier, the Bryophytes

marks the beginning of the structural organisation of the spore, and the evolutionary diversification from the trilete-monolete-alete, together making a trimorphous situation, was the conceivable beginning of spore evolution. Functionally, the spores are not 'dioecious', the antheridia and archegonia occurring in in the same thallus. It is only at the level of the Lycopods, that a combination of structural and functional features, become manifest by the occurrence of heterospory, the larger spores marking the female and the smaller marking the male. But for the above evolutionary change, the trimorphous condition initiated in the Bryophytes continued to remain at the Pteridophyte level also (Nair, 1970).

A major change in spore evolution occurred at the level of the Gymnosperms (Nair, 1976). The heterospory set in motion, in the lycopods, became more pronounced with the megaspore having been enclosed in an ovule, and the microspore (pollen) having been carried by pollinating agencies and particularly the insects. Rather, the pollen remained, mobile and the egg remained immobile thus setting off a major functional change in reproductive biology. Structurally, the position of the aperture shifted from proximal to distal, consequent to which the aperture developed a floor (aperture membrane), apparently as a protection against exposure of the weak apertural area. The new morphological structure that developed during the course of Gymnosperm; evolution was the winged pollen, characteristic of the pines and podocarps. otherwise, the trimorphous condition, as in pre-gymnosperms, continued to persist in the Gymnosperms.

At the Angiosperm (Anthophyta) level, the trimorphous situation suddenly

changed, with the origin of several new apertural morphoforms, starting with the tricolpate, followed by the tricolporoidate-tricolporate and other forms, the highest level of which was the monoporate, characteristic of the grasses.

From the above facts, Nair (1970, 1979) propounded the triphyletic theory of angiosperm evolution suggesting that the Angiosperm originated from the Pteridosperms, and evolved along three directions namely the Magnolian line (Subclass Magnoliidae of Cronquist, 1968), the Ranalian line (Subclass Ranunculidae & other subclasses other than Magnoliidae of Cronquist, 1968) and the Monocot line, from a primitive group, the 'Magno-Ranalian Complex'. On the basis of the fact that the Magnolian stock contained trimorphous forms along as in the pre - angiosperms, the group was considered the most primitive, while the total absence of the trimorphous forms in the Ranalian stock was considered to show its advanced status. The Monocots with a prepondorence of trimorphous forms, but also with newly evolved forms like pantoporate (*Alisma*), spiraperturate (*Eriocaulon*), and monoporate (*Typha*; grasses), branched off from the primitive Magno-Ranalian complex at a very early stage (Nair, 1979).

#### "Spore dispersae"

The fossil pollen and spores (Moore & Webb, 1978) are not in physical connection with the vegetative structures, as a general rule. However, the spores of *Rhynia*, and some other spore forms have been obtained *in situ* and which helped establish the fact that the trilete form is the most primitive spore form. However, the pollen grains recovered from Cretaceous onwards and particularly the

Quaternaries (Nair, 1965 b), could be related to several of the extant taxa.

From the principles governing the morphological evolution of pollen and spores, an attempt has been made in reconstructing the pattern of evolution of the 'Sporae dispersae' from some of the geological formations (Nair, 1966, 1974, 1974). The botanical identity of some of the Tertiary and Quaternary pollen and spores, which were originally described arbitrarily, were established and it has been noted that the flora was rich, comprised of both primitive and advanced families, reflecting the general belief of the sudden origin of the Angiosperms. It was possible to suggest that the Jurassic flora was dominated by the Gymnosperms which gradually gave way to the Angiosperms.

A morphological and phylogenetic analysis of some Gondwana "Sporae Dispersae" (Nair and Saxena, 1974) showed the dominance of the triletes, both in the lower and upper Gondwanas, represented by the Raniganj and Rajmahal geological formations respectively. From the trilete non-saccate primitive form, evolved the monolete - saccate forms (characteristic of some of the Gymnosperms) on the one hand and the monolete-non - saccate form (characteristic of Bennettitales), on the other. Along the above evolutionary directions, the modern gymnosperms (e.g. pines & podocarps with sacs, and cycadophytes without sacs) have apparently evolved.

### Concluding remarks

Studies on pollen biology indicate that the pollen grains and spores are carried to a variety of situations by agencies like air, insects and water, and at the destinations they provide an index for

generating new information of interest and application in a wide variety of scientific pursuits. The very fact that the morphological characterisation of the exine wall of pollen is of diagnostic value making it possible to identify the plants represented by the "Sporae dispersae", is the fundamental basis for using pollen in both phylogenetic taxonomy, and, "Pollen Analysis".

The exine wall being resistant to decay and destruction, the pollen and spores occur in geological sediments of all Ages, making it possible to use them in both palaeostratigraphy and palaeo-environment studies. Pollen and spores being omnipresent, it is important to gain information of them for using as a key to the Past environments, palaeoecology and palaeoclimate, on the one hand, and as a precaution in checking contaminants of fossil pollen preparations, from sedimentary samples of Tertiary and later Geological Areas, in particular. A new dimension to the fossil microflora studies *vis-a-vis* the pollen of the extant taxa is the study of the nature of the exine wall in relation to the geological Age (pollen wall maturation), and laying new standards for geological dating.

In order to make a near correct interpretation of the data on "Sporae dispersae" (palaeopalynology) of the later geological periods particularly, it is a pre-requisite to gain knowledge on the pollen and spore morphology of the Present day plants, their pattern of distribution in air and in sub-surface samples, including the long distance transport by air, water or by other means.

All the same, the interpretation of botanical affinities of 'Sporae dispersae', is difficult in the absence of sporangial/

vegetative connections of the spores. However, an understanding of the trends in morphological evolution of the 'Spore dispersae' has been made possible by knowledge gained on that of the present day plants. The triphyletic theory of Angiosperms, based mainly on the pattern of morphological evolution of pollen and spores of present day plants, do find substantiation from a reconstruction of the pattern of morphological evolution of the 'Spore disperse', which has conclusively proved that the trilete form has been the most primitive, from which the monolete and the alete forms evolved.

The knowledge of the pollen morphology of the present day plants is applicable not only for the interpretation of palaeofloristic data, but is also of relevance for the identification of pollen contained in air, honey, and in various other seen or unforeseen materials and places, and thereby, the science of palynology has come to be recognised as an aspect of environmental science (Nair, 1985b) of critical value as bioindicators, with application in a variety of areas such as geology, agriculture, forestry, criminology, biochemistry, pollution studies and even biophysics.

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