CHAPTER - I

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PALYNOCLOGICAL SCIENCE - A SHORT SKETCH

That pollen grains constitute a partner in the reproductive biology of plants, and have been realised as early as 717 B.C., as evidenced from the stone carvings of the Assyrian Winged Beings pollinating the datepalms. That was a time when there was no possibility of gaining an insight into the internal structures because of the nonavailability of proper magnifying apparatus. The beginning to the study of micro-morphology was made only in 1667 when Robert Hooke discovered the compound microscope and also discovered the structure of the cork cells. In course of time, structural details of various plant and animal materials including pollen grains came to light. Before the close of the 19th century, a fair degree of knowledge on the architecture of pollen walls has been presented and its value to taxonomy and phylogeny has been demonstrated (Wodehouse, 1935).
The contemporary beginning in the study of pollen morphology started with the publication of the "pollen grains" by Wodehouse (1935), to which may be associated the publication "Pollen Morphology and Plant Taxonomy - Angiosperms" by Erdtman (1952). The contemporary progress in the study of pollen morphology has been reviewed and presented in the book "Pollen morphology of Angiosperms - A historical and phylogenetic study" by Nair (1970d).

One of the most significant developments during the last two decades is the progress in the technology of the electron microscope which made a strong impact on the study of pollen morphology, particularly with regard to the developmental morphology to the exine by TEM and on the fine morphology of exine surface by SEM. Further, the application of pollen morphology in plant phylogeny has been amply demonstrated at various taxonomic levels. For example, Nair (1970d; 1974c-d) in a series of communications laid the principles and methods for applying pollen morphology in phylogenetic treatises and also enunciated the triphyllatic theory of Angiosperms. The theory suggests that the angiosperms has its phylogenetic root in the pteridosperms, at which level the group diverged along three directions, namely the Monocot stock, Magnolian stock and the Ranalian stock.
respectively. Of the above three lines, the Magnolian stock and Monocot stock by having the dominance of monocolpate grain have been considered to be nearer to the preangiosperms, while the Ranalian dicots with the tricolpates and its derivatives represent new evolution in the plant kingdom. From the facts prescribed on the morphological evolution of pollen grains, it has become clear that the pollen grains reflect in them to a fair degree, the trends and directions of plant evolution as a whole which led to the proposal of pollen based plant research (Nair, 1969).

While pollen morphology occupied the main stream of palynological studies, several lines of applied interest took shape at different times along the course of growth of the science. These lines of interest are in conformity with the ramifications in the cycles of pollen biology which have been presented by Nair (1974) in an illustrative chart. It has been pointed out that the biological cycle in a flowering plant, for example, is constituted of the pollen phase and the seed phase, the former of which is further divisible into three stages, namely the developmental stage, free life stage, and the fertilization stage. Considering the free life stage alone, it may be noticed that the pollen
grains which are dehisced from the anther are carried by various agencies like wind, the water and insects such as the honey bees. The air borne pollen are either deposited on open surfaces of water leading to its final preservation as fossils in the mud bottom, or else they find entry into the nostrils of the human beings producing allergy. The insect collected pollen are carried to hives, where these serve as food to the larvae. Also, such pollen find entry into the honeys and provide an index to the plants visited by the concerned insects in collecting nectar and pollen. The direct transfer of pollen by the pollinating agencies to the stigma of the equivalent female results in fertilization and seed production. The above course of events suggests that pollen grains are omnipresent, being dispersed all over the earth's surface, and in every area of their occurrence they become an important instrument for scientific enquiries. Thus, the study of air borne pollen is of ultimate application to the problem of human allergy; study of honey pollen provides an index of bee pasturage, and the study of fossil pollen through time and space provides a picture of the vegetational succession and distribution. In this way every branch of palynological science has an interest and identity of its own and the
present concept of the scope and circumscription of the science is far wider than the one envisaged by Hyde in 1946. It is contended that every structure and function directly or indirectly involved in pollen biology come within the purview of palynology. For example, the developmental stage prior to the formation of pollen is considered to have a bearing on development of pollen itself by virtue of the fact that the origin and organization of pollen are achieved only after the protective floral leaves and the anther walls are fully formed.

While it is possible to mark out narrow areas of studies, the science has been categorised broadly into Morphographic palynology, Agricultural palynology, Forest palynology, Medical palynology and Palaeopalynology (Nair, 1968c), although Erdtman (1952 and later) delineated several aspects of interest, namely morphology, aero-palynology, iatropalynology, copropalynology, palaeopalynology etc. A detailed consideration of the various aspects of the study is of no particular relevance to the present investigation. A critical analysis of the pollen morphology of angiosperms alone is given here, giving particular emphasis to the value of pollen morphology in plant taxonomy and evolution and also to utilitarian aspects involving plant materials of economic significance to man.
ASPECTS OF POLLEN MORPHOLOGY

(i) Pollen morphology & taxonomy

The separation of Paeoniaceae from Ranunculaceae, of Nelumbonaceae from Nymphaeaceae, of Fumariaceae from Papaveraceae, of Bombaceae from Malvaceae, and Cuscutaceae from Convolvulaceae, finds support from pollen morphology (Nair, 1966). However, pollen morphology does not lend evidence for the breaking of the Liliaceae into several families, as suggested by Hutchinson and other phylogenetic taxonomists. On the other hand, the taxonomic circumscription as defined by Bessey, Hallier and Engler, may be considered natural, because of the fact that eurypalyny as observed in the family, represented an early stage in the evolution of the monocotyledons. Similarly, the splitting of the Scitamineae with inaperturate pollen, is hardly justified as the family is unipalynous. So is the case with the splitting up of Urticaceae into Moraceae, Cannabinaceae and Ulmaceae, although Cannabinaceae shows some difference in its pollen than the rest to merit a separate taxonomic status. A study of the Indian species of Dephne (Nair, 1965d) leads to the conclusion that the species *D. bholua* and *D. papyracea* should be united under a single species *D. cannabina*, as originally believed by Hooker.
(ii) **Pollen morphology & geographical distribution:**

Of special importance is the observation of 3-colpate pollen in the var. *normalis*, as against the pantoporate pollen in the var. *alba* of *Caltha palustris* (Nair, 1961a). The species grows along the northern temperate belt of the world; and only in the Kashmir valley var. *alba* characterised by pantoporate pollen could be noticed. The Kashmir flora constitutes a synthesis of plants that migrated into the valley during early Pleistocene times, consequent to the exposure of land covered previously by the 'Karewa' lake. In the wake of these migrations, new geographic mutations and breeding might have produced new bioforms, one of which is represented by the variety *alba* with pantoporate pollen grains.

The species *Argemone mexicana* is an exotic weed that found its way into India during historic times and presently it has spread to the entire country. Pollen studies have shown an array of morphological variations in the various geographic forms (Nair and Sharma, 1962). Similarly, the specimens of *Daphne papyracea* from Mussorie and Kud (Kashmir) respectively have shown differences (in the nature of pollen variations) in pollen morphology (Nair, 1965d).
(iii) Pollen morphology & cytology:

A study of the *Sisymbrium irio* complex (Nair and Sharma, 1966-67) has shown that the pollen grains are 3-zonocolpate in the diploid. In all other cytological forms, the fundamental 3-zonocolpate form as in diploid occurs, along with new forms, namely 3-synocolpate in the triploid, 4-zonocolpate and synaperturate-operculate in tetraploid-caulis (grown in moist sun), 4-zonocolpate and 4-parasynocolpate in tetraploid-caulis (grown in dry shade) and spiraperturate in tetraploid-subcaulis. The hexaploid stands apart with 2 'aperturate-operculate' pollen type along with a few 4-zonocolpate and abnormally spiraperturate types. Polyploidy has been suggested as the possible reason for the changes in pollen morphology.

A study of 10 species belonging to the *Taraxacum* complex (Nair and Chopra, 1964) has shown that the extent and nature of pollen variations (in germinal apertures) are irrevocably tied up with the interesting genetic system of the genus.

(iv) Pollen morphology and plant evolution:

The evolutionary significance of pollen morphology has been explained in a series of publication on the subject (Nair, 1965c, 1968a, 1970d, 1974d). In laying the principles
of morphological evolution of pollen grains, it has been proposed that the characters relating to germinal aperture are. Primary, of exine ornamentation Secondary and other characters Tertiary in the order of their degree of importance. In a morphological analysis of the spore-pollen morphiorms in the plant kingdom, it has been observed that the germinal apertures in the spores of Thallophyta are not well-marked; in the Archegoniatae composed of Bryophytes, Pteridophytes and Gymnosperms, there are three well-marked morphotypes, namely trilete, monolete and alete; in the angiosperms there is an array of apertural morphotypes. The above observation led to the suggestion, that the plant kingdom could be classified palynophylogenetically into three divisions, namely Primorphosporophyta (Syn. Thallophyta), Trimorphosporophyta (Syn. Archegoniatae) and Polymorphosporophyta (Syn. Anthophyta or Angiospermae, Nair, 1977).

Regarding the phylogeny and evolution of the primitive angiosperms, it has been argued that those taxa which reflect the trimorphous trend of morphological evolution as that in the Trimorphosporophyta (Archegoniatae), should be considered primitive and should form the base for gaining an understanding of the phylogeny and evolution of the angiosperms. Among the various systems of plant classification, the Magnoliidae of Cronquist (1968) has been found to
approach the facts of pollen phylogeny; and further, two evolutionary stocks of dicotyledons, one represented by the fundamental monocolpate pollen, and the other by tricolpate pollen, designated as the "Magnolian stock" (Magnoliaceae and its allies), and the "Ranalian stock" respectively, have been noticed. Further, the Ranalian stock represents new evolution, being completely devoid of the ancient monocolpate form. The monocots, being dominantly monocolpate, might have evolved parallely with the Magnolian dicots.

(v) Pollen morphology of cultivated plants:

A study of the pollen morphology of 48 varieties of Canna (Nair, 1961b), indicated the occurrence of pollen variations which could conveniently be used as a measure in interpretations of cultivar taxonomy. The pollen in the species are fundamentally inaperturate and spinate, and with indistinct stratification. An evolutionary reduction series starting from the spinate to the psilate and pilate (showing clear stratification) pollen could be observed in the cultivars, and further, a few porate grains were observed in just two varieties (Flamingo & M.S. Thacker) which indicated the taxonomic uniqueness of those two varieties.
The work initiated with the pollen grains of Canna, was continued with regard to other ornamentals, such as Hibiscus, Bougainvillea, and Euphorbia pulcherrima (Nair, 1961c); and it has been found that a statistical analysis of pollen morphology would be an effective basis for cultivar taxonomy.

Pollen morphology of several crop plants, of food or medicinal values, namely cereals, vegetables, oil crops, such as Brassica (Nair and Sharma, R.K. 1976), Linum (Nair and Sharma, R.K., 1975), Cocos, (Nair and Sharma, M., 1963), and Rauwolfia (Nair and Kaul, 1965), has been done. Among the cereals pollen grains are fundamentally monoporate, and it has been observed that a graphical presentation of size range provides a clue to the separation of varieties of Zea mays (Nair, 1962); a monographic account on the pollen morphology of Indian vegetable crops, has demonstrated the use of pollen morphology in cultivar taxonomy of several plants. Of particular importance is the finding that the effect of acetolysis itself is an index of varietal taxonomy, the grains enlarging along specific directions when acetolysed. Further, the grains without protoplasm (morphologically sterile) offer a clue to assort the cultivars into related groups.
The study of the cultivated Brassica (Nair and Sharma, R.K. 1976) and Linum (Nair and Sharma, R.K., 1975) has indicated the potential use of electron replicas of pollen in differentiating the varieties. The pollen grain of Linum has been found to be made up of islands of various sizes and shapes, each with a central spine, and with or without lateral spines at the corners forming the circumference of the island. The islands are broadly divisible into mega-islands and micro-islands; in L. usitatissimum alone, the various varieties could be differentiated on the basis of electron replica patterns.

In Rauwolfia serpentina (Nair and Kaul, 1965), a solitary gigantic plant has been observed to contain a certain percentage of larger grains, which suggested that the particular individual is a 'pollen mutant'. Pollen morphology is an index in checking the adulteration of such drugs as those constituted of flowers and with this aim in view the pollen morphology of Indian medicinal plants was done and a pollen key was provided.

The cultivated plants do represent an advanced level of plant evolution and this fact is more or less confirmed by the presence of advanced pollen morphoforms, namely
tricolporate and pantoporate in most families of the
dicotyledonous crops and monoporate in monocotyledonous
ones. The Gramineae (cereals) among the monocotyledons,
and the legumes (pulses) among the dicotyledons consti-
tute a majority of the crop plants, and both possess highly
evolved pollen forms, namely the monoporate and the tricol-
porate respectively. Thus, crops being the result of
breeding, are "a significant link in evolution controlled
by man", which is reflected amply in pollen morphology
(Nair, 1970f).

(vi) Other information:

The above analysis on pollen morphology is mainly
based on the work done in India during the last two decades.
However, in order to complete the file, mention may be made
of the earlier work and also those which are not covered
in the above review concerning only applied morphology of
pollen. In our Puranas and Upanishads there is mention
of pollen; as for example there is a mention of the bath
with the pollen of Cassia fistula by Lord Shiva. In
recorded history the value of pollen morphology has been
for the first time understood by O'gnaunarty (1846) in
the Bengal dispensatory in which pollen have been conce-
zived as globules and also as bearing external ornamentation.
In the flora of British India, Hooker recorded his findings on pollen morphology of *Nymphaea*, Malvaceae, Asclepiadaceae and several other plants, and his findings bear much meaning even under present approach to the study of pollen morphology. He separated *Nymphaa alba* from *N. stellata* on the basis of the absence of spines in the former and similarly he recorded that the Malvaceae is characterised by spines on the exine walls. In other Indian floras also, there are records on pollen morphology, as for example Gamble (1934) separated the various genera of the Convolvulaceae on the basis of pollen characters.

As early as 1948, a time when the study of pollen morphology entered into its contemporary phase of growth initiated with the publication of the book "Pollen grains" by Wodehouse (1935), Birbal Sahni recorded that the material for palynological research is vast but trained workers are lacking in India. By about the same time Bhaduri (1948) presented a monographic work on the pollen morphology of Acanthaceae and similarly Sayyed Udein et al (1948) published their findings, though poor at the present standards, on the pollen flora of the Hyderabad. With the publication of the book "Pollen Morphology and Plant Taxonomy/Angiosperms" (Erdtman, 1952), there has been a wave of interest shown
to the study of pollen morphology in India as elsewhere, with the result that a large volume of publications, both descriptive and analytical, have appeared. Of these, particular mention may be made of the "Pollen Flora of Western Himalayan Plants" by Nair (1965), "Pollen Flora of Rajasthan" by Jain and Nanda (1966-67), "Pollen Flora of Upper Gangetic Plains," by Rao and Shukla (1976) and a series of papers on the pollen grains of Indian plants by Nair and his colleagues, Vishnu-Mitter and his colleagues and Chanda and his colleagues. In addition, Nair made a comprehensive analysis of the pollen morphology of angiosperms and provided a base for applying pollen morphology in phylogenetic taxonomy and evolution of plants. Apart from the demonstration of the application of pollen morphology to cytology, geographical distribution and other aspects of applied morphology important information has been provided on terminology for exine morphology and also new methods and means of using pollen morphology to advantage. Nair (1968) proposed new terms for exine strata, namely, ectine (abbreviation of ectoexine) and endine (abbreviation of endoexine), synonymous with the terms sexine and nexine of Erdtman (1952) for the outer and inner layers of the exine respectively. Similarly, he proposed a replacement of the terms ora of Erdtman (1952) by the terms endocolpium and endoporium whenever the inner
apperture (endoaperture) relate to colpate or porate apertures respectively. It has further been suggested (Nair, 1970d) that the porate apertures may be categorised into megaporate (when the pore diameter is more than half the diameter of grain), normaliporate (when the pore diameter is equivalent to half the diameter of the grain) and miniporate (when the pore diameter is less than half the diameter of grain). Also, the terms stenopalyny and eurypalyny (Erdtman, 1962) have been replaced by the terms unipalyny and multipalyny respectively. The approach in proposing these changes has been to provide simpler alternatives so that a new entrant to the science can easily comprehend the morphology of the exine.

It has already been mentioned that the application of pollen morphology to unipalynous taxa is somewhat difficult and in such circumstances a consideration of morphology in its totality is important. In such considerations, it becomes important to make a statistical analysis of pollen size and also the variations in the various taxa of any one genus or species for example. It has been demonstrated that the graphs showing size range is of importance in the delineation of species of Crotalaria, (Tewari, unpublished) or of
Quercus (Vishnu Mittre and Singh, 1967). It has also been demonstrated that the size range graphs provide a picture of the taxonomic differences among cultivars of Zea mays (Nair, 1962; Vishnu Mittre and Gupta, 1966) and also many vegetable crops (Nair and Kapoor, 1974). It has been found that the very effect of acetolysis on pollen size provides interesting information on taxonomic differences, the enlargement due to acetolysis being longitudinal (along the length of the colpus), lateral (along the breadth of the colpus), or peripheral (all over the grain; Bamzai and Randhawa, 1965).

Although, the study of pollen by the use of electron microscope has become a necessary fashion of the day, the use of such technology in India is yet gaining momentum because of the lack of sufficient facilities to cater to the needs of scientists in a large country like ours. However, the studies of the pollen grains of Linum by Nair and Sharma, R.K. (1975) and of Brassica by Nair and Sharma, R.K., (1976) have served to provide an idea about the immense potential in initiating such investigations.

The finding that pollen morphology is a reflection of the functional potential of pollen in any one pollen mass (Nair, 1970b) is of immense application, at a time when the
technology of plant breeding would involve the selection of desired pollen from desired taxa of plants on a morphophysiological basis, for storage and use in breeding.

Thus, the contributions made by Indian workers, are considerable, new lines and directions on the applications of pollen morphology to human advantage having been presented and demonstrated.

SCOPE OF PRESENT INVESTIGATION

The study of pollen morphology has come to occupy an important place in the realm of comparative morphology of plants, owing to the growing conviction that the pollen being a gene pool of all variations during the life cycle of plants reflect in them, to a fair degree, the trends and directions of evolution and interrelationships among plants. With the advances made in the technology of the microscope, it has become possible to gain a deeper understanding of the fine structure of the pollen walls which have given an additional index to studies of plant taxonomy and evolution. The successful application of the evolutionary morphology of pollen and spores is amply reflected in the enunciation of the triphyletic theory of the angiosperms on the basis of an
analysis of germinal apertures alone. Further, the technique and procedure of morphological analysis have reached such new heights of perfection that it is now possible to apply pollen morphology to plant taxonomy, down to the level of cultivars. It is in this background that the present study of pollen morphology of Rosales has been undertaken.

In order to project the importance of the problem, it is significant to explain the facts relating to the primitive angiosperms. In a series of articles on the subject by Nair (1965-1974) argued that the taxonomic system of Cronquist as evidenced in the fact that the order Magnoliiales, Piperales, Nymphaeales and Aristolochials together of the subclass Magnoliidae contains families with the trimorphic apertural condition (trichotomocolpate, monocolpate, inaperturate) which brings the group closer to praeangiosperms. He has further suggested that the angiosperms originated and evolved along three directions; namely: the Monocot stock, Magnolian dicot stock, and the Ranalian dicot stock.

In the evolutionary scheme given by Cronquist, the Magnoliidae constitutes the basal taxon, from which evolved the Hamamelidae, the Rosidae and other subclasses except that Asteridae have their phylogenetic root in
the Rosidae. It is, therefore, clear that along the evolutionary line, Magnoliidae-Rosidae-Asteridae, the Rosidae forms the second tier in the evolution of the majority of dicotyledonous angiosperms. This finding is corroborated by the evolutionary chart explaining the phylogenetic system of Bessey (see Lawrence, 1958) in which also the Rosales has been shown to link the Ranalian taxa below and higher dicot taxa including the sympetalae above. Further, the monographic account on floral evolution provided by Wernham (1912) provides striking proof for the evolution of sympetalous taxa from the Rosalian plexus. It is, therefore, imperative that the Rosales constitute the second step in the evolutionary radiation of the dicotyledonous angiosperms.

In a correlative analysis of the pollen morphology and floral evolution, Nair (1969 and 1972) provided further proof to show that Rosales constitute the second tier in the evolution of dicotyledons. Tewari (1976; unpublished) has given further proof from a study of some leguminous plants, in support of the above contention. It is, therefore, imperative that Rosales need have to be given the much deserved attention, not only with regard to pollen morphology but also with regard to other aspects of the floral morphology in particular and plant morphology in general.
The present study is envisaged to take into consideration the families of Indian plants as given in the Flora of British India by Hooker. While every genus and species could not possibly be taken, an attempt has been made to represent various families to the extent possible. The data obtained from the present investigation are pooled with the totality of information available from literatures and a complete analysis of the pollen morphology of the group has thus been attempted.