
Pollen spore morphology and plant evolution

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Nair PKK 1996. Pollen spore morphology and plant evolution. *Palaeobotanist* 45: 130-133.

Spores and pollen grains both are resistant to environmental stress and diagnostic by virtue of the unique exine characteristics, by which it has emerged as a reliable tool in evolutionary biology, both of fossils and present day plants, at various taxa levels. "Sporae Dispersae" being the only morphological material reflecting continuity of evolutionary lineage through geological time, there is new scope for its application in fixing stratigraphic successions and phyletic origins. The triphyletic theory of the origin and evolution of angiosperms has been explained to demonstrate the value of pollen grains and spores in phylogenetic taxonomy, and further, the emerging areas of application of the principles of morphological evolution of pollen grains have been indicated.

Key-words—Palynology, Morphology, Sporae dispersae, Evolution, Triphyletic theory.

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सारांश

परागकण बीजाणु आकारिकी एवं पादपविकास

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बीजाणु एवं परागकण दोनों ही सभी पर्यावरणीय परिवर्तनों में यथावत् बने रहते हैं तथा बाह्यचोल के विशेष लक्षणों द्वारा पहचाने भी जा सकते हैं जिसके फलस्वरूप विकासीय जीवविज्ञान में अशिमत और वर्तमान पौधों में ये महत्वपूर्ण सिद्ध हुए हैं। विकीरित बीजाणुओं के आधार पर स्तरिकीय अनुक्रम तथा जातिवृत्तीय उद्भव अन्वेषित करना सम्भव है। आवृतबीजी पौधों के उद्भव एवं विकास के त्रिजातिवृत्तीय सिद्धान्त की विवेचना की गई है तथा परागकणों के आकारिकीय विकास के सिद्धान्तों की बढ़ती उपयोगिता पर भी प्रकाश डाला गया है।

POLLEN grains and spores are reproductive propagules of diagnostic value by virtue of the characters embodied in the exine (Erdtman, 1952). The pollen grains can be a useful tool in evolutionary considerations has been demonstrated by Wodehouse (1935, 1936), since when the pollen unit has been taken as a parameter of merit in phylogenetic taxonomy and comparative morphology. With the revolutionary developments in optical technology, leading to the introduction of electron microscopy, the use of pollen and spores at micromorphological levels has become relevant in biodiversity studies at genetic levels (Ravikumar & Nair, 1986). The unique structural characterisation of "Sporae dispersae" was presented by von Post as early as 1930 (see Erdtman, 1954), and later for a variety of purposes (Faegri & Iversen, 1975; Moore & Webb, 1978), but it may be noted that the combination of morphotypes in any one "Sporae dispersae"

group reflected the bio-diversity of plants (Potonié 1967; Chaloner, 1967), they belonged to, a large majority of which are represented by spores alone, the vegetative counterpart having been totally destroyed during the process of fossilisation.

PRINCIPLES

The pollen grain or spore is a 'special cell' enveloped within a wall, rendering protection to the protoplasm, by virtue of an outer layer composed of sporopollenin, a material which is resistant to destruction and decay, with the result that it withstood the environmental hazards through geological time, visible since Precambrian times (see Nair, 1966). The exine also embodies a combination of characteristics rendering taxonomic identities, enabling a variety of applications, for both the extinct (Barghoorn *et al.*, 1954) and extant plants (Erdtman, 1952; Nair, 1970).

The scheme of reproductive biology provides a picture of the variety of spore and pollen forms, the differences in number produced by any one taxon/individual, the characteristic modes of dispersion resolved into anemophilous, entomophilous and hydrophilous, and the universality of occurrence of individual or combination of forms, thereby projecting their importance as a tool in evolutionary biodiversity studies, both of form and function, at various levels and stages (Nair, 1970). The very fact that the process of meiosis, the most crucial event in the very sustenance of life, is the basis of variations, natural selection, and origin of new life (species) and that the reproductive units—the pollen grains and spores to be precise—are the primary sites and repositories or genomic changes, may be taken to suggest that the exine is a true reflection of evolutionary morphology, to merit consideration as the fundamental morphological unit in phylogenetic studies. It is generally understood that the plant body is a harmonious combination of a variety of structures and functions, the evolution of each of which being at various rates and levels of progression, studies in comparative morphology (Faegri, 1937); are beset with limitations, and this is particularly so with vegetative structures. The pollen and spores being the products of a high degree of protection during development, and of its being the gene as the most conservative and basic unit in the reproductive system for evolving phylogenetic projections through time and space.

MORPHOLOGICAL CHARACTERISATION AND EVOLUTION

The morphological characters are resolved into five groups, covered under three levels in the order of their importance, namely *primary* (germinal aperture), *secondary* (exine ornamentation) and *tertiary* (exine strata, grain size and shape). A certain combination of the five characters gives identity to a particular taxon, whether of fossil or of present day plants (Erdtman, 1952).

The apertural system is of primary importance, as it is the most conservative morphological component of the exine, to which the principle of protection as the basic phenomenon in evolutionary biology could be extended. The apertural area is weak and hence vulnerable to environmental hazards, needing natural protection whether through developmental orientations or structural features, enhanced further

by the sculptural patterns. While the primary and secondary characters are considerable stable and reliable, the tertiary characters, barring a few, are plastic and hence not of stable value in comparative studies, but useful in substantiating the findings from the study of the basic character components.

With the apertural system as the basic of morphological evolution of the pollen grains and spores, several propositions on plant evolution at various taxa and even cultivar levels have been put forward (Lam, 1950; Kuprianova, 1966; Muller, 1970; Walker, 1974) correlating also cytological characteristics (cytopalynology: Nair & Ravikumar, 1984; Swaminathan & Rao, 1970) in some instances. The apertural system is not well organised (Mahabale, 1969) in the lower groups (algae, fungi) and hence may be considered *amorphous*. The organisation of the spore unit perhaps became stable at the bryophyte level as evident from the formation of three definite character groups, the trilete, monolete and alete, and hence *trimorphous*. This situation continued for a long period of plant evolution, covering the pteridophytes, gymnosperms and a part of the angiosperms, but for the appearance of new structures and characteristics, in conformity with the changing needs at the various level of evolution during the long period of geological time.

To begin with, the spores were morphologically similar (homosporous) and the difference in sexual characteristics were visible only in the prothallus, and the first sign of morphological differentiation of sex was expressed in heterospory (Petit, 1970), in some pteridophytes like *Isoetes*, *Marsilia*, *Selaginella*, *Lycopodium*, etc. (Nair, 1976). The next notable change was the conversion of the position of the aperture from the proximal as in cryptogams, to distal (in terms of the tetrad) in spermatophytes (gymnosperms and angiosperms), and this change occurred at the level of Cycadofilicales, which originated during the Permocarbiniferous period. With the change from proximal to distal, the aperture came to be strengthened by a membrane, in the light of which the terms *trilete*, *monolete* and *alete* has been changed to *trichotomocolpate* (sulcate), *monocolpate* and *acolpate* or *inaperturate*.

With the origin and evolution of the angiosperms, an array of apertural forms together with the trimorphous forms appeared both with regard to Number (N), position (P) and Character (C) particularly so with a majority of the dicotyledons and hence the

situation may be described as *Polymorphous*. Thus, the general trend of morphological evolution was from amorphous through trimorphous to polymorphous. Within the trimorphous, the trilete form was primitive as evident from the living primitive taxa (*Riccia*) and also of extinct plant groups (Rhyniaceae) from which evolved the monolete and the alete. Within the polymorphous, the tricolpate form was primitive, as in Ranunculaceae, from which evolved a variety of new apertural forms. However, some authors believed that the monolete-monocolpate was the most primitive from which evolved other forms (Wodehouse, 1935).

TRIPHLETIC THEORY

Nair (1968, 1970), propounded the triphyletic theory of the origin and evolution of angiosperms on the strength of his findings in morphological evolution of apertural forms in spores and pollen. The trimorphous condition of pre-angiosperms, when present in the angiosperms, ought to suggest primitiveness, and in such a consideration, the subclass Magnoliidae of Cronquist's (1968) system of classification, consists of trimorphous grains alone, and hence the most primitive. The monocotyledons also contain taxa with trimorphous forms, together with others such as the many porate (*Alisma*), spiraperturate (Eriocaulaceae), and monoporate (Gramineae) condition. In all the dicotyledons except the subclass Magnoliidae, the grains are new, consisting of the primitive tricolpate, and/or their variants (colporoidate, colporate, spiraperturate), etc., the apertural position being either equatorial or global. On the above basis, the angiosperms were considered to have originated and evolved along three lines namely the Magnolian stock (Subclass Magnoliidae), the Monocot stock, and the Ranalian stock (all dicots except the subclass Magnoliidae) in the order of evolutionary hierarchy. This is the palynological basis for the triphyletic theory of angiosperms (Nair, 1979).

ORIGIN AND SPREAD OF ANGIOSPERMS

The origin of angiosperms has been an enigma for evolutionary biologists all through botanical history (Arber & Parkin, 1907; Lam, 1950). From the knowledge generated for fossil pollen and other materials, the angiosperms are supposed to have made a sudden origin in the Cretaceous Period

(Muller, 1970). All discoveries of pre-Cretaceous angiosperms have been disputed. But, the view of Eames (1961) that the angiosperms and gymnosperms have a common origin in the Cycadofilicales is substantiated by palynological facts. The change from the proximal position to the distal occurred at that level, together with the origin of the flower (flowering plants). If that were so, there must have been pre-Cretaceous angiosperms, down to the Permo-Carboniferous Period, and what happened to them?

Origin must have been a slow process, although suddenness can be assigned to limited cases under special circumstances. The origin of a whole group, of the magnitude of angiosperms can not be sudden and therefore the situation presented by the Cretaceous Period may be false. It has been presumed that the appearance of suddenness must have been the end result of the decline in dominance of the pre-Cretaceous gymnosperms, some of which have even become extinct (e.g., Cycadofilicales, Cordaitales, among others, Florin, 1951) and the process is still on, as evident from the living fossil *Ginkgo*, although it was dominant (e.g., *Ginkgoites*) during the Jurassic Period in India (Rajmahal Hills) itself. Thus the decline of one group, leads to the dominance of another group living along with, and that is what might have happened in the case of early angiosperms (Nair, 1974).

SPORAE DISPERSAE

Although spores and pollen occur throughout the period of geological history, the taxonomic identification could be possible only when they are found in organic connection, except for those in recent geological times (Nair, 1960), in which comparison with the pollen of the present day equivalents is feasible. The principles of morphological evolution can be applied to the 'spora dispersae', in order to throw light on the evolutionary levels of geological horizons, as projected in spore morphology (Bharadwaj, 1963) and phylogeny (Potonié, 1967). The principles and methods of applying morphological evolution of spora dispersae in plant phylogeny and stratigraphy has been demonstrated (Nair & Saxena, 1974) and the application of fossil pollen in the study of vegetational succession and past environments are well known (Faegri & Iversen, 1975).

CONCLUDING REMARKS

Pollen grains and spores being omnipresent (Nair, 1985), resistant to environmental stress and strain, and diagnostic, they have become a very reliable and handy tool for application in a variety of areas, of which the strongest advantage is in the study of evolutionary biology for the reason that there is hardly any other morphosystem with such a continuity in evolutionary lineage. With the advancements in electron microscopy, the scope of application of pollen in evolutionary studies has been vastly extended to micromorphological levels, with the result that the unit is useful in resolving the breeding system of crops (Ravikumar *et al.*, 1979) and their wild allies (Srivastava *et al.*, 1977; Nair *et al.*, 1990), and in population genetics. Perhaps, the pollen and spores constitute the single morphological projectile of biodiversity in plants, protected by nature and handed down the scale of phylogenetic time, to the advantage of scientists in gaining an insight into the process and direction of evolution.

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