

TRENDS IN THE MORPHOLOGICAL EVOLUTION OF POLLEN AND SPORES*

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INTRODUCTION

POLLEN grains and spores form a unique entity in plants, both with regard to their structure and function. The morphological characteristics of pollen and spores are contained in their protective coat formed of two main layers, the intine and the exine (including the perine occurring in some spores). The significance of intine in pollen and spore morphology is comparatively negligible, although in the pollen of some plants (*e.g.*, Scitamineae), there is a considerably thick internal layer (medine; Saad, 1963), and thus a variety of morphological forms is exhibited by the exine.

The value of exine morphology in studies relating to the phylogeny and also taxonomy of plants has been understood since the beginning of the studies in pollen and spore morphology (*cit.* Wodehouse, 1935). In such considerations, the germinal aperture among the different morphological characters of exine has been the focus of attention of palynologists. Thus, Wodehouse (1936) indicated the possible lines of pollen evolution in which he envisaged phylogenetic changes in the germinal furrow in relation to its function. Apart from the 1-colpate form, the trichotomocolpate (trilete), and the 3-zonocolpate forms have been taken to be of basic significance in apertural evolution. Further, it has been pointed out that the trichotomous aperture in the pollen of primitive gymnosperms closely resembles that in the ferns, and that the furrow, characteristic of the Bennettitales and Cycadales, has its equivalent in the primitive angiosperms. It is also important to note that the prothallial tissue showed gradual reduction from the Cycadofilicales to Bennettitales, before it was completely eliminated in the Cycadales. Major evolutionary changes in aperture have been assumed to have started from the 1-furrowed forms of primitive gymnosperms (Bennettitales, Cycadales), by the processes of "modification, protection, or elimination of the wide open furrow". Similarly, Kuprianova (1948) considered the form of apertures alone, for evaluating the significance of pollen morphology in the evolution of mono-

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cotyledons. Recently, Erdtman (1964) has presented a scheme showing the possible lines of evolution of the various apertural types in pollen and spores. According to this scheme, grain forms having pore-like (ill-defined) proximal aperture(s) have given rise to those with zonal, distal, or global apertures (colpate, colporate, porate, or pororate). In the scheme proposed by Vishnu Mittre (1964), the trilete form is most primitive, and from this have evolved the inaperturate type, followed by the aperturate types. Kuprianova (1964) advanced certain principles of evolution of morphological characters.

Although the germinal apertures are of primary importance in the morphology of pollen and spores, there are also other morphological characters in which evolutionary phenomena are expressed. Wodehouse (1935) observed a gradual reduction in the exinous processes of the pollen grains in plants belonging to the Compositae. In the evolution of the saccate pollen forms of the Pinnaceae, those with a single saccus are considered to have given rise to those with two or more sacci. Within the family Polygonaceae (Wodehouse, 1931), pollen types with a thick and heavily ornamented exine have been taken to be primitive to those with a thin and unornamented (smooth) or lightly ornamented exine. Among the cultivated varieties of *Canna* (Nair, 1960), a gradual reduction in the processes, followed by a radial splitting of exine, producing free columellae, has been found possible. Evolutionary trends in pollen morphology have been traced for Linaceae (Saad, 1961) and also Convolvulaceae (Nair and Rehman, 1963). Thus, the phylogenetic views of pollen and spores have varied with individual workers, and also have been limited in scope, being often confined to a single morphological character.

The present attempt is to lay the principles that might be considered to govern the morphological evolution of pollen and spores.

POLLEN AND SPORE CHARACTERS

The morphological characters of pollen and spores are those relating to the germinal apertures, grain size and shape, exine strata, and exine ornamentation. Of these characters, those of apertures may be considered as *Primary*, of exine surface patterns as *Secondary* and others as *Tertiary*, in their degrees of importance (Nair, 1966).

A. Aperture

The various apertural forms in pollen and spores are the result of differences in the nature (circular, elongate, etc.), number (1-many), and distribution (polar, zonal, equatorial, or global) of apertures in individual sporomorphs. The various apertural types (*see* Nair, 1965) are as follows:

(1) *Trilete* (hypocolpate).—Aperture proximal in individual grains with reference to the tetrad; (trichotomocolpate; aperture distal);

(2) *Monolete*; aperture proximal; (monocolpate; aperture distal); (3) *Zonocolpate* (colpi 2-many); (4) *Zonoporare* (pores 2-many); (5) *Zono-colporate* (apertures 2-many); (6) *Zonoporare* (apertures 2-many); (7) *Pantocolpate*; (8) *Pantoporare*; (9) *Pantocolporate*; (10) *Pantoporare*; (11) *Spiraperturate*; (12) *Syncolpate*; (13) *Syncolporate*; (14) *Parasyncolpate*; (15) *Parasyncolporate*; and (16) *Inaperturate*.

Of subsidiary importance are the characters relating to the shape, size, margin, membrane, etc., of the various types of apertures.

B. Exine Ornamentation

The exine surface presents patterns which may broadly be considered as either depressions or processes. The surface patterns are conditioned by the arrangement and distribution of the columella that compose the sculptured layer (*ectine*; Syn. *Sexine*; Erdtman, 1952) of the exine. The various pattern types are as follows: (1) *granulose*; (2) *spinulose*; (3) *baculate*; (4) *verrucose*; (5) *gemmate*; (6) *clavate*; (7) *fimbriate*; (8) *foveolate*; (9) *scrobiculate*; (10) *fossulate*; (11) *rugulate*; (12) *areolate*; (13) *reticulate*; (14) *lophate*.

C. Other Characters

The tertiary characters include size, shape, and the exine strata. Considering the entire vascular plants, pollen or spore size varies from $10\ \mu$ to $200\ \mu$, and rarely more or less. Sometimes there is a wide range of pollen size in the individual taxon itself. Pollen and spore shapes (in different views) vary in the various sporomorphs, within the same taxon. The stratification of exine is sometimes very distinctive. They are either thick or thin; the columella composing the *ectine* are either free or united, either in part or completely, or there occurs a peripheral layer (*perine*) as in some ferns.

LINES OF EVOLUTION

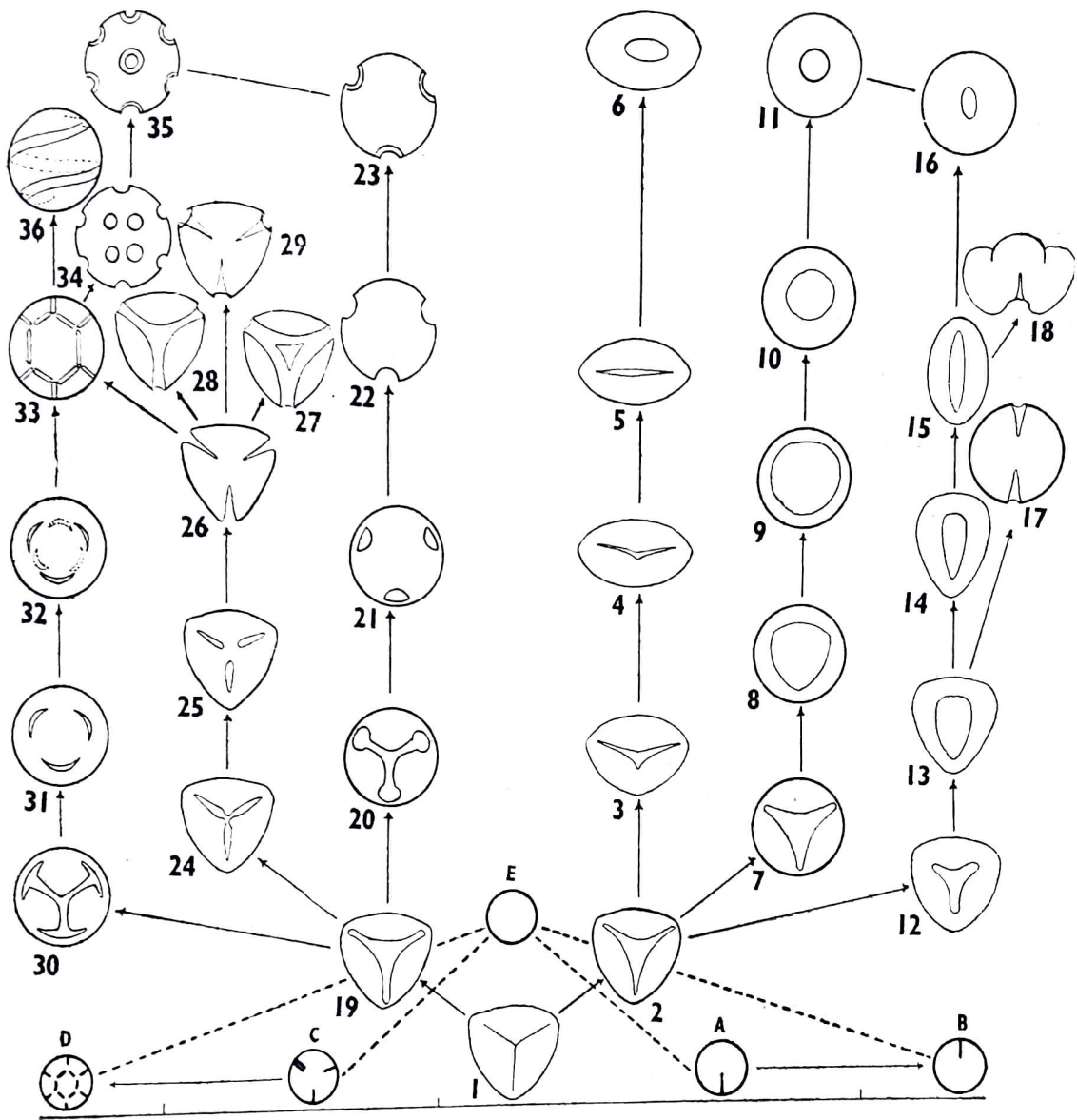
In studies relating to the phylogenetic relationships of plants, it is the total morphology of any particular sporomorph that is important. However, conclusions on total morphology have to be preceded by a scrutiny of the evolutionary tendencies in individual characters, comprising the primary, secondary and tertiary groups.

The theory and supporting evidences of apertural evolution (Text-Fig. 1), as conceived here, are as follows:

(1) The trilete type of aperture is perhaps the basic form, from which evolution proceeded along two lines, namely (a) the monolet-monocolpate plexus and (b) the tricolpate plexus. The grain with trilete aperture is tetrahedral and those with monolete are bilateral.

That the trilete form is basic in apertural evolution is evidenced in all the major groups of vascular plants. The aperture is triletous (or

trichotomous) in the grains of primitive pteridophytes (Rhyniaceae), gymnosperms (Cycadofilicales and even in some winged grains occurring as fossils; (e.g., *Fuldaesporites** and *Parasporites*), and angiosperms (some species of Schisandraceae; Wodehouse; 1935).



TEXT-FIG. 1. Chart showing the evolution of apertural types.

1-36. Types of apertures. 1. Trilete (basic form); 2-18. *Monocolpate* plexus. 2. Trilete (broadening). 3-6. Gradual reduction of one arm of the trilete and the change in shape of grain from tetrahedral to bilateral. 7-11. Widening of trilete produces a wide pore which gradually reduces. 12-16. Asymmetrical widening of the colpus and its reduction. 17. 2-colpate condition. 18. Saccate condition; 19-37. *Tricolpate* plexus. 19. Widening of the trilete aperture. 20-23. Evolution of 3-zonoporate aperture. 24-26. Evolution of the 3-zonocolpate aperture. 27. Para-syncolpate grain. 28. Syncolpate grain. 29. 3-zonocolpate grain; 30-36. Evolution of the pantocolpate (30-33), pantoporate (34), pantoporate (30-33), and spiraperturate (36) apertures. A-D. Position of apertures. A. proximal; B. distal; C. zonal; D. global; E. inaperturate.

* The evidences relating to fossil spores have been gathered from the drawings provided by Potonic (1956 and 1958), unless otherwise mentioned.

(2) The monolete (monocolpate) form might have evolved in two ways, namely, (a) by the reduction and final loss of one of the arms of the trilete, and (b) by asymmetrical widening of the trilete. Both the above conditions are accompanied by a change of symmetry from tetrahedral to bilateral.

Evidences for the gradual reduction of the arms of the trilete is apparent in the abnormal apertural conditions observed in *Loxogramma* (Nayar, 1963). In *Pityrogramma hybrida* var. *maxima* (Erdtman and Praglowski, 1959) the above condition is apparent. Among the angiosperms there are several species which provide substantial evidences to the possible widening of the trichotomous aperture, to form the monocolpate condition. In Piperaceae (*Schizostegia osmundacea*; Erdtman, 1952; also author's observations), and in several monocots (e.g., *Arenga obtusifolia*; personal observations), the trichotomous, monocolpate, and intermediate conditions between the above two are clearly evidenced, within the same species.

(3) In another line along the monolete-monocolpate plexus, the trilete aperture widened symmetrically to produce a wide pore, covering the whole of one face of the grain, which gradually reduced to a smaller size. The small-porate condition shall be reached also by the reduction of the colpus. Evidences for these evolutionary possibilities are again found in Piperaceae and in a majority of monocots, in which both the monocolpate and monoporate grains (pore wide) occur together. Evidences of reduction of the elongate aperture to the circular one is seen also in species of *Alnus* (Erdtman, 1953).

(4) The two-colpate condition might have been produced, by the secondary development of an aperture at the distal pole. In some species of *Riccia*, an aperture is reported (Pande, 1924; Ram Udar, 1958) to be secondarily produced for the protrusion of germinal tube, even though a trichotomous mark occurs on the proximal face. Two colpi on one face alone is perhaps reached by the constriction in the middle of the single colpus, and subsequent separation of the two parts. Such conditions are found in the fossil pollen grains *Gynkaletes*, *Cycadaceaelagella* and *Ginkgocycadophytus*.

(5) Along the tricolpate plexus, the three colpi have been produced by the constriction at base, and separation of the three arms of the trilete. That the three colpi represents three arms of the trilete is evidenced in the fossil grains like *Minerisporites* and *Remysporites*, in which the arms of the trilete are constricted at the base, and also in *Reinco-spora*, *Perotriletes*, *Equisetostachys* and *Maxisporites* in all of which the arms are fully separate. Tendencies to such a constriction are observed also in some present-day genera of Liliaceae and Palmae (Erdtman, 1944). In the fossil spore *Divisisporites* and also in some abnormal grains of *Pityrogramma hybrida* var. *maxima* the ends of the arms are divided, and extend laterally. By the dissolution of the central region of the trilete, 3 colpi lying parallel to the equator shall be deemed

to have evolved. Similarly, in the grains of *Phlebopteris hirsuta*, and *Cibotiumidites*, the ends of arms bulge and become club-shaped, in which case, the porate form shall be considered to have evolved by the dissolution of the central region of the trilete. Erdtman (1944), commenting on the 3-porate condition in *Vanilla*, expressed that, "theoretically, a triporate condition of a pollen grain would ensue in consequence of a coalescence of the central parts of the three slits in a pollen grain with a three-slit opening".

(6) After constriction and separation, transfer of colpi to the equator occurred and thus the 3-zonocolpate type evolved. The occurrence of apertures at varying distances from the poles is observed in the fossil grains like *Anacolsodites* and *Interporo-pollenites*, and in some living genera.

(7) From the three-zonocolpate form all other forms have evolved. In the predominantly 3-colpate sporomorphs, 4 or more zonocolpate grains are commonly found occurring (Erdtman, 1952) which evidently shows that the extra number of colpi are of secondary origin.

From the zonocolpate evolved the pantocolpate, pantoporate, zonocolporate and zonopororate, and spiraperturate conditions. The possible origin of the spiraperturate condition from the pantocolpate is evidenced in *Crocus sativus* (author's observations) in which all the intermediary conditions have been seen to occur. The complete fusion of colpi ends produced the syncolpate and the partial fusion produced the parasyncolpate conditions.

The ultimate product of reduction processes is the inaperturate form. This inaperturate type does not occur among the living ferns, although nearly alete (exine thinner on one side) spores occur in *Equisetum*. But, among fossil 'spora dispersae', there are form genera in which the trilete is small and almost becoming lost as in *Perianthospora* and *Bascanisporites*, and there are also 'alete' spores. Based on the principles advanced here, the phylogenetic position of the apertural types are as mentioned in Table I.

Apart from the above general principles, there are also other apertural characteristics which should be considered from the phylogenetic point of view. The possible evolutionary tendencies of these apertural characters are shown in Table II.

D. Exine Surface Patterns

A variety of exine, ornamentation types are observed in the sporomorphs belonging either to the pteridophytes, gymnosperms, or angiosperms, and as such the formulation of a basis to provide suggestions to the phylogeny of ornamentation types is rather complicated. Protection of germ plasm should be considered to have been of a higher magnitude among the lower plants, and likewise, the protective coat should be considerably resistant. Indications in exine ornamentation

TABLE I

Trends in the evolution of aperture types

Primitive	Advanced
1. Trilete	Monolete
2. Trilete (arms unconstricted)	Trilete (arms constricted)
3. Trichotomocolpate	Monocolpate
4. Colpate	Porate and colporate
5. 3-colpate (colpi proximal)	3-colpate (colpi zonal or distal)
6. 3-zonocolpate	4-(a) zonocolpate
7. Zonocolpate	Panto-colpate or porate
8. Pantocolpate	Spiraperturate
9. Nomotremel (aperture, present)	atreme

TABLE II

Trends in the apertural characters

Primitive	Advanced
1. Triangular	Elongate
2. Elliptical oovovate	Circular
3. Irregular distribution	Regular distribution
4. Crustate	Non-crustate
5. Tenuimarginate	Crassimarginate
6. Non-operculate	Operculate
7. Non-aspidote	Aspidote

with a higher magnitude of protection may be considered more primitive, and from this other forms might have evolved by the processes of reduction. Such a possibility is evidenced in the pollen grains of *Canna*, in which the exine normally does not have a clear stratification and, the surface carries spinous processes. Among the variation types of pollen occur evidences of gradual reduction of spines, before they were

completely lost, followed by a radial splitting of exine to their individual columella (Nair, 1961). The possible phylogenetic position of the various ornamentation forms is indicated in Table III.

TABLE III
Trends in the ornamentation types

Primitive	Advanced
1. Processes	No processes (psilate)
2. Spinose	Spinulose, baculate, verrucate or gemmate
3. Spinulose	Granulose
4. Granulose	Psilate (smooth)
5. Non-pitted	Pitted
6. Irregular (rugulate)	Regular (foveolate, scrobiculate, etc.)
7. Lesser pitting (depression)	More pitted (depression)
8. Scrobiculate	Foveolate
9. Reticulate	Foveolate
10. Areolate	Reticulate
11. Reticulate	Reticulate
12. Retipilate	Pilate

E. Other Characters

(i) *Exine strata*.—The same principles suggested for the ornamentation shall be applied to the stratification also, and the possible evolutionary lines are indicated in Table IV.

Pollen and spore shapes do not apparently possess much phylogenetic significance. Regarding the size of grains, larger size may be considered to be more primitive to the smaller.

POLLEN SPORE MORPHOLOGY AND PLANT EVOLUTION

A significant conclusion, emerging from the above account, is that the morphology of pollen and spores gives evidence to the possibility of parallel evolution of the major plant groups. The primitive tri-

TABLE IV
Trends in the exine strata

Primitive	Advanced
1. Exine thick	Exine thin
2. Non-perinous	Perinous (perinous condition may be considered specialised)
3. Indistinct stratification	Distinct stratification
4. Tegillate	Integillate
5. Homogeneous sexine (columella not clear)	Heterogeneous sexine (columella distinct)

radiate aperture is found among the primitive pteridophytes, gymnosperms, dicotyledons, and in the family Palmae (mainly) of the monocotyledons. The occurrence of the 1-furrowed pollen type in gymnosperms (Bennettitales, etc.), dicotyledons (Magnoliaceae, Piperaceae, Nymphaeaceae, etc.) and in monocotyledons, have often been taken to denote the phylogenetic affinities of the above plant groups. The very fact that the triradiate (trilete), and the 1-furrowed (monolete) condition occurs together in the major groups suggests that the 1-furrowed form in the ferns, gymnosperms, dicotyledons, and the monocotyledons have evolved independently of each other from a primitive microspore form with a triradiate mark. Also, it should be noted that there is no clear evidence to prove the similarities in the form of the furrow in the 1-furrowed sporomorphs of the gymnosperms, dicots and the monocots. Moreover, there is no evidence at hand to trace the origin of a large array of aperture types found in the angiosperms.

SUMMARY

Pollen-spore characters relate to germinal apertures, exine ornamentation, exine strata, grain size and shape, of which the first may be considered primary, second as secondary and the rest as tertiary characters in the order of their importance. The apertural evolution seems to have originated from a trilete (trichotomous) form. Subsequent evolution proceeded in two main directions to result (i) in the formation of the monocolpate form, by the widening and elongation of the trichotomous aperture and (ii) the trizonocolpate form, by the separation of the three arms of the trilete and their subsequent zonation. From these two main forms all others evolved by the processes of secondary development, reduction, or degeneration. The primitiveness or other-

wise of the other characters of aperture is also indicated. In tracing the evolution of exine ornamentation, such characters, which increase the protective value of exine, are considered primitive, and based on this principle, the phylogeny of the characters relating to ornamentation is shown. The significance of pollen morphology in plant evolution is discussed. The triradiate aperture which is considered most primitive occurs in all the primitive families of the ferns, the gymnosperms, and the angiosperms (Ranalian stock), which indicates an independent evolution of apertural forms in the different plant phyla, from a trilete form.

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REFERENCES

- ERDTMAN, G. 1944. Pollen morphology and plant taxonomy. *Svensk bot. Tidskr.* **38**: 163-68.
- . 1952. *Pollen Morphology and Plant Taxonomy. Angiosperms.* Almqvist and Wiksell, Stockholm, Sweden.
- . 1953. On the difference between the pollen grains in *Alnus glutinosa* and those in *A. incana*. *Svensk. bot. Tidskr.* **47**: 449-50.
- . 1964. On classification of pollen grains and spores. *Palynological Bulletin* **1**.
- AND PRAGLOWSKI, J. R. 1959. Six notes on pollen morphology and pollen morphology techniques. *Bot. Notiser* **112**: 175-84.
- KUPRIANOVA, L. A. 1948. Pollen morphology and phylogeny of the monocotyledons. *Komarov Inst. Acad. Sci.* **1**: 7 (in Russian).
- KUPRIANOVA, L. A. 1964. A tentative code of the ancient and derivative characters of pollen grains and spores. Palaeobotanical Society, Special session: Abstracts (Birbal Sahni Institute of Palaeobotany, Lucknow).
- NAIR, P. K. K. 1960. Pollen grains of cultivated plants I. *Canna*. *J. Indian bot. Soc.* **39**: 373-81.
- (Ed.). 1964. *Advances in Palynology.* National Botanic Gardens, Lucknow.
- . 1965. *Pollen grains of Western Himalayan Plants.* Asia Publishing House, Bombay and London.
- AND REHMAN, K. 1963. Pollen grains of Indian plants.—VI. Convolvulaceae. *Bull. nat. Bot. Gdns.* (Lucknow, India), No. 83.
- NAYAR, B. K. 1963. Spore morphology of *Loxogramme*. *Grana Palynol.* **4**: 388-92.
- PANDE, S. K. 1924. Notes on the morphology and life-history of *Picea sanguinea* Kashyap. *J. Indian bot. Soc.* **4**: 117-28.
- POTONIE, R. 1956. Synopsis der Gathunge der sporae dispersae. Part I. Sporites. *Beih. Geol. jb.* **23**: 1-103; Synopsis der Gathunge der sporae dispersae. Part II. *Ibid.* **31**: 1-114.

- RAM UDAR. 1958. Culture studies on the genus *Riccia* (Mich.) L. III. Sporeling germination in *R. trichocarpus* Howe. A reinvestigation. *J. Indian bot. Soc.* **37**: 70-74.
- SAAD, SHOKRY. 1961. Phylogenetic development in the apertural mechanism of *Linum* pollen grains. *Pollen Spores* **3**: 33-43.
- . 1963. Sporoderm stratification. The 'Medine', a distinct third layer in the pollen wall. *Ibid.* **5**: 17-38.
- VISHNU MITTRE. 1964. Contemporary thought in Palynology. *Phytomorphology* **14**: 135-47.
- WODEHOUSE, R. P. 1931. Pollen grains in the identification and classification of plants. VI. Polygonaceae. *Am. J. Bot.* **18**, 749-64.
- . 1935. *Pollen Grains*. McGraw-Hill & Co., New York.
- . 1936. Evolution of pollen grains. *Bot. Rev.* **2**, 67-84.