A TENTATIVE CODE OF THE ANCIENT AND DERIVATIVE CHARACTERS OF POLLEN GRAINS OF ANGIOSPERMS

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ABSTRACT

For any studies in the comparative morphology of pollen, as well as for any application of palynological data to plant taxonomy, phylogeny and palaeopalynology it is very important to be able to estimate the antiquity of the more recency of characters.

The palynological code proposed is the first step in this direction. Similar codes have been published earlier by other authors for both vegetative and generative organs of Angiosperms.

For the establishment of the antiquity of characters it is necessary to take into consideration the phenomenon of heterochrony; therefore not a single character, but as many as possible should be used.

FOR any studies in the comparative morphology of pollen, as well as for any application of palynological data to plant taxonomy, phylogeny and palaeopalynology, it is very important to be able to estimate which characters are ancient and which are of recent origin.

The palynological code proposed is the first step in this direction. Similar codes have been published earlier by other authors for both vegetative and generative organs of Angiosperms, but this is the first code for pollen.

The code expresses my ideas about the evolution of Angiosperm pollen grains.

In this paper I shall restrict myself to one of the characters of pollen grains, viz. the character of aperture. The spore apertures had initially three fissures; they corresponded to the places of contact of spores in the tetrahedral mother tetrads. The unifissurate apertures developed in different groups later. They were derived fiom the trifissurate apertures in connection with the formation of the square tetrads. Later, in the end of Palaeozoic the spores began to appear with proximal and distal apeitures having three fissures or one. The appearance of the distal apertures in addition to proximal apertures was discovered in different groups of vascular plants.

The spores and the pollen grains of some recent Pteridophyta and Gymnospermae still retain the traces of bipolar apertures (*Abies* Mill., *Osmunda* L. PL. 1, FIGS. 5 & 6).

Distally and proximally trifissurate aperturable pollen were also observed in some fossil Angiospermae (*Duplosporis* Pflug., PL. 1, FIGS. 3 & 4). Rudimentary bipolar apertures can be also observed in the pollen grains of some recent species. For instance, one can see the trifissurate sign on the pollen grains of *Myrica gale* L.(PL. 2, FIG. 7). Rudimentary trifissurate signs are present in the pollen grains of many genera of Dicotyledons growing now in the Southern Hemisphere (*Balanophora capensis* Eckl. et Zeyh., PL. 2, FIG. 11, 12; many species of *Loranthus* L., PL. 1, FIG. 2, PL. 2, FIGS. 9, 10), as well as in the fossil pollen grains from the Upper Cretaceous deposits.

The evolution of the pollen grains of Dicotyledons proceeded in the direction of the gradual disappearance of the polar apertures and formation of the equatorial apertures. Initially the latter were closed (*see*, for instance, *Pemphixipollenites* Stover, PL. 1, FIG. 1), later they became open apertures.

In the pollen of the recent Dicotyledons the equatorial type of the apertures, typical for them only prevails. The apertures of the pollen grains of Dicotyledons have attained the highest level of specialization and the greatest diversity among the apertures of all the Cormophytes. As for the pollen grains of Monocotyledons, those of the recent species have no proximal apertures nor, at least, any traces of tetradscars. The pollen grains of the most ancient representatives of this group are radially symmetrical with a trifissurate aperture at the distal pole.

In the pollen grains of Monocotyledons in connection with the establishment of bilateral symmetry, the trifissurate aperture was transformed into unifissurate and later into sulcate.

As it is generally known, the pollen characters are the most conservative than those of many other plant organs. Consequently it might be assumed that the pollen of the most ancient Angiospermae had a spore-like appearance.

The fossil finds of the pollen of the first Angiospermae are still very scanty. Accordingly they cannot serve as a basis for the explanation of the entire process of the evolution of pollen grains and of their apertures. However, all the finds were taken into consideration in the course of the code.

CHARACTERS	ANCIENT	DERIVATIVE
Type of mother tetrads	tetrahedral	square and other types
symmetry	radial	bilateral
apertures		
position	polar	equatorial or global
form	fissure without membranes	colpate covered by membranes, porate, colporate, acolpate
size	large	small
number	1-3	4 and more
rudiments	non-functioning polar scares, arches, polar harmomegathus	absent
length of polar axis	less than equatorial diameter	more than equatorial diameter
exine		
nexine	rather thick	faintly perceptible scarcely seen or lacking
sexine	thin, equal to nexine	considerably thicker than nexine
sculpture	tuberculate medium sized	reticulate or spinose very conspicuous or minute with traces of reduction
columellae	simple	branched
tegillum	absent and thin	present and thick
suprategillum	absent	present
intine	thin	thick
exintine	absent or very thin	thick, under pores or layer of uniform thickness
pollen grains	solitary	in groups

For the establishment of the antiquity of characters it is necessary to take into consideration the phenomenon of heterochrony.

For example, the rudimentary polar aperture persisting in the pollen grains of *Carya* Nutt. (PL. 2, FIG. 13) is an ancient character, while the perceptible onci under the pores is the evidence of an advanced specialization in the direction of adaptation to anemophily. The pollen grains of the ancient family Lauraceae are characterized by a considerable reduction of the exine and by the total disappearance of the apertures.

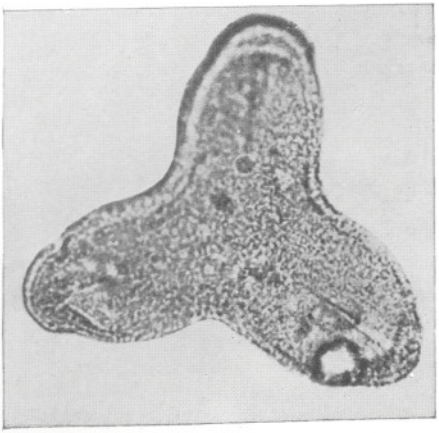
Therefore, the evolution of characters should never be based upon a single character, but upon as many as possible.

The establishment of affinities is greatly complicated by the phenomenon of convergence in the morphology of pollen.

Many families of Dicotyledons have tricolporate pollen grains that might have developed independently, by different pathways. One of those pathways that have led to the formation of the tricolporate type can be traced via the tricolpate (PL. 2, FIG. 14) to the tricolporate grains. This is proved by the fact that both types are encountered within the same family (e.g. in Molluginaceae, Papaveraceae, Linaceae) or even within the same genus (e.g. *Salix* L.).

The other direction can be traced from the bipolar trifissurate to the tricolporate pollen grains. This way is more complicated; it can be detected in the course of examination of fossil pollen grains. The evolutionary sequence thus established proceeds from the pollen grains of the *Duplosporis* Pflug type and leads to the bipolar trifissural grains, with the simultaneous presence of oroid equatorial apertures, or to the grains of the *Pemphixipollenites* Stover type. The further evolution of the apertures consists in the reduction of fissures at the points of their junction at the poles, while the free ends of these fissures directed meridionally cross the oroids equatorial apertures. This can be exemplified by the pollen grains of *Symplocacites* N. Mtchedlishvili. In the course of the further development the fissures are covered with membranes: they expand, the apertures of ores also be come wider. Finally the evolutionary sequence ends with usual tricolporate type (PL. 2, FIG. 9). Separate links of this evolutionary series can be seen in the pollen of Loranthaceae.

The further study of the comparative morphology of fossil and recent pollen, the



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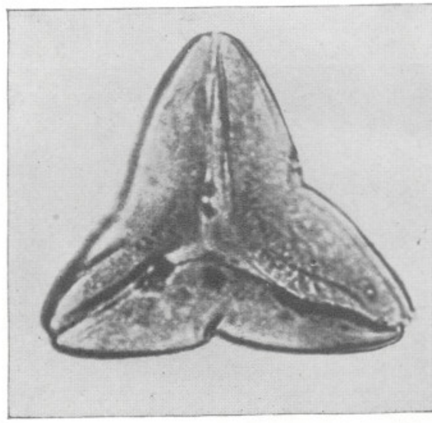

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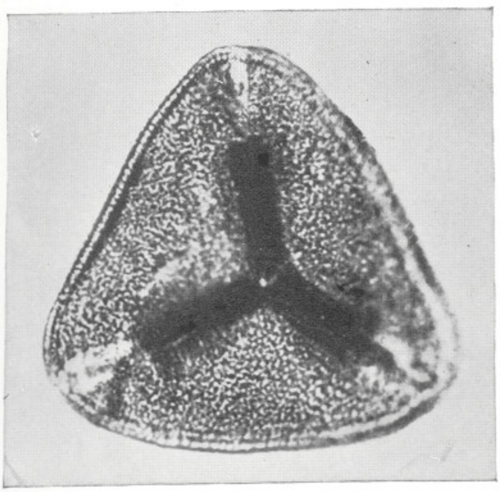

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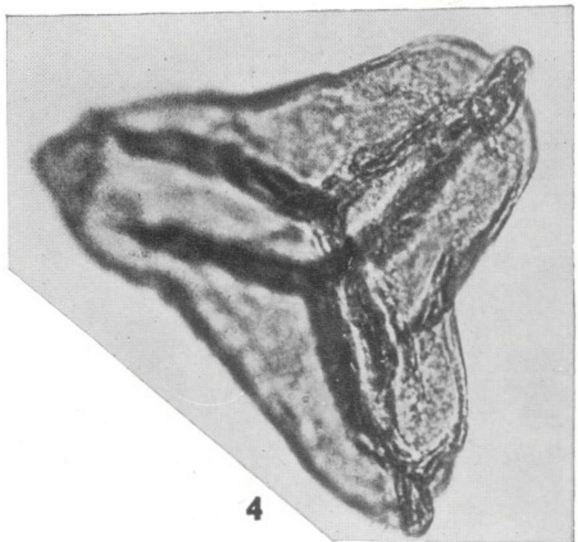

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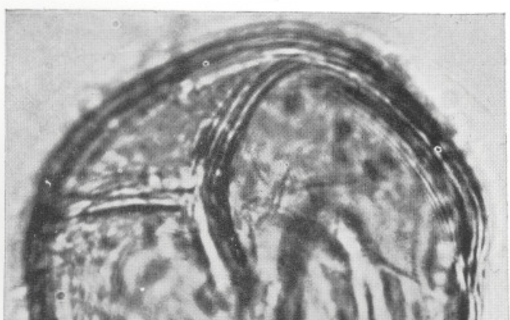

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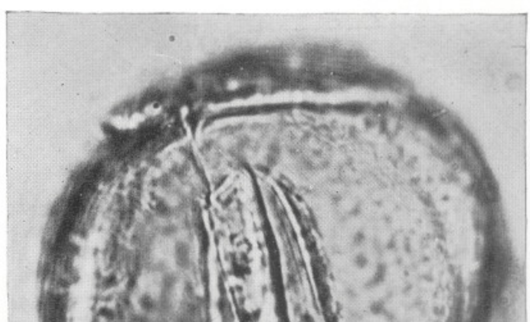

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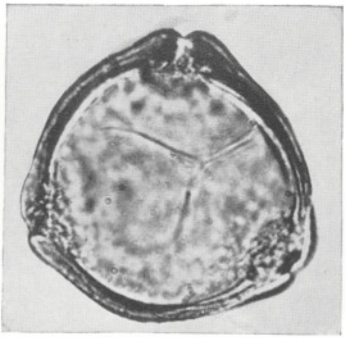

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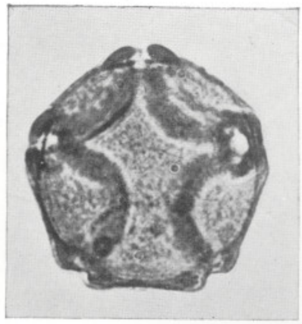

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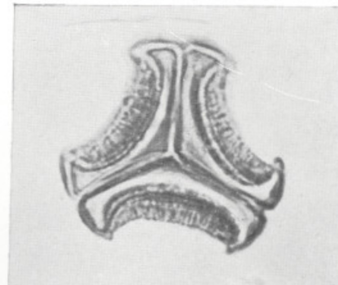

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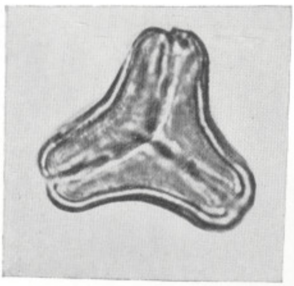

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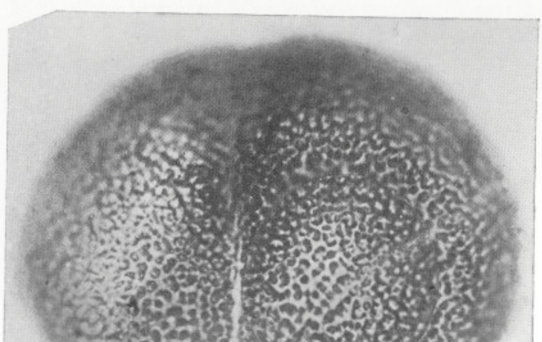

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study of the development of pollen grains and the study of the abnormalities in the structure of pollen due to hybridization, undoubtedly will lead the palynologists to the successful solution of these complicated, still mysterious and interesting problems.

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EXPLANATION OF PLATES

PLATE 1.

Photomicrographs of spores and pollen grains. × 1000.

1. *Pemphixipollenites sibiricus* Bondar.
2. *Loranthus dregei* Eckl. et Zegh.
3. *Duplosporis borealis* (Chlon.) Bondar.
4. *Duplosporis ocliferius* (Chlon.) Bondar.

5-6. *Osmunda cinnamomea* L.

PLATE 2.

Photomicrographs of pollen grains. × 1000.

7. *Myrica gale* L.
8. *Alnus glutinosa* (L.) Gaertn.
9. *Loranthus eugenioides* H.B.K.
10. *Loranthus punctatus* Ruiz et Pav.
11. & 12. *Balanophora capensis* Eckl. et Zeyh.
13. *Carya texana* Bukley.
14. *Dipterocarpus insignis* Thw.
15. *Cornus sanguinea* L.