Morphological and Phylogenetic Studies on the Ornamentation of Pollen and Spores, with Special Reference to their Projected Groups

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In palynology, one of the most important problems is to describe the ornamentation of pollen and spores precisely. Therefore, many investigators have been studying about this problem and reporting their characteristic works in

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their special fields. Potonié (1934), Erdtman (1943), Kuprianova (1948), Faegri and Iversen (1950), Iversen and Troels-Smith (1950), Kosanke (1950), Pokrovskaya et al (1950), Thomson and Pflug (1953), Harris (1955), Potonié and Kremp (1955), Zaklinskaja (1957), Couper (1958), Norem (1958), Krutzsch (1959) and Couper and Grebe (1961), have already reported on the ornamentation of pollen and spores, but I am not contented with these publications even though most of them are quite splendid works. I have been working on the morphology and phylogeny of fern spores and the description of the characters of spores which I have done chiefly according to Norem's method (but not completely; more or less, I added my ideas to it). In brief, I have used next 38 patterns for the description of fern spores, as follows.

1. ACC (Aciculate)=with needle-like spines.
2. ACI (Acinate)=with closely-packed bulbous sculpturing like Tsuga (Hemlock) pollen.
3. ARE (Areolate)=with a network of narrow grooves surrounding small, more-or-less flat areas or islands; a negative reticulum.
4. BAC (Baculate)=Moderately high elements with more-or-less flat tops and parallel sides; ratio of height to width < 1.0.
5. CAP (Capitate)=with more-or-less slender projections tipped by small caps.
6. CLA (Clavate)=with small swollen or club-like rods; longer and less spherical than gemmate.
7. COL (Columnate)=with column like spines with blunt or flat tops and parallel sides; ratio of height to width > 1.0.
8. CON (Conulate)=Elements with more-or-less irregular conical shape and rounded or blunt tops.
9. COV (Convolute)=with closely-packed, irregular wall-like structures having the appearance of irregular reticulations in vertical view and overlapping scales in oblique or side view.
10. CRI (Cristate)=with rather short, irregular, often knobby ridges.
11. CUN (Cuneate)=Elements with sides flaring out from a restricted base (wedge-shaped).
12. EXV (Extervermiculate)=with rather short, low, narrow, irregular and sometimes branched projections.
13. FIL (Filiform) = with thread-like or filamentous ornamentation.
14. FOV (Foveolate) = with broad irregular depressions.
15. FRU (Fruticose) = with long, branching or anastomosing projections as on some hystrichosphaerids.
16. GEM (Gemmate) = More-or-less globoid elements supported on short, distinct stalk-like bases with a tangential diameter < head; height of stalk equal to or less than radial diameter of head. Sides of stalk straight or concave, never an acute angle as in granulate.
17. GRA (Granulate) = More-or-less globoid elements with a base diameter equal to or less than any other tangential (horizontal) diameter; angle of intersection between exine surface and element right or acute, never rounded; no stem or stalk. Granules differ from gemmae in the absence of a distinct stalk.
18. GRP (Grapnelate) = with projections resembling grapnel hooks.
19. LEP (Lepidote) = with scale-like projections.
20. LOB (Lobate) = with large rounded or lobe-like projections.
21. LOP (Lophate) = with the surface thrown into ridges, anastomosing (joining together into a network) or free; lophate ridges are usually higher than those of a reticulum.
22. MAM (Mammilate) = with nipple-like projections raised on rounded or wart-like bases.
23. PAP (Papillate) = with small blunt or rounded, never pointed, nipple-like projections; sides tapered or convex, and may be slightly constricted. Ratio of height to basal diameter > 0.5 < 2.0.
24. PIL (Pilate) = more-or-less globular elements supported on tall, straight-sided (never diverging) stalks or stems; height of stalk > radial (vertical) diameter of head. Pilate differs from gemmate in the height of the stalk.
25. PSI (Psilate) = with a smooth surface.
26. PUN (Punctate) = with minute depressions or perforations.
27. RET (Reticulate) = with the surface thrown into a network of anastomosing ridges enclosing lacunae or luminae.
28. RIV (Rivulate) = with narrow grooves or furrows separated by parallel ridges that are equal to or narrower than the grooves.
29. RUG (Rugate) = wrinkled.
30. SCA (Scabrate) = with low projections less than 1μ in diameter.
31. SET (Setose) = with long, slender bristle or hair-like projections.
32. SPI (Spinate) = with tapering, straight or slightly convex sided, and more-or-less pointed projections. Spines with ratio of height to basal diameter $\geq 2.0$ (hence, taller, than papillae) may have more-or-less blunt or rounded tips. Differs from columnate in the tapering sides.
33. SPS (Subpsilate) = surface irregular but without well-defined sculptural elements.
34. STR (Striate) = with long very narrow parallel grooves separated by wider ridges.
35. TUB (Tuberose) = with projections very densely packed, and lower and more rounded than verrucae.
36. VAL (Vallate) = with rather short broad furrows separated by ridges.
37. VER (Verrucose) = with low irregular wart-like projections.
38. VEM (Vermiculate) = with narrow irregular depressions resembling worm holes.

But with this method I sometimes had trouble describing a fern spore, because I was not able to draw a clear line between VER and PAP, CAP and PIL, GRA and PAP, PIV and STR, LOB and GEM, ARE and BAC, GRA and BAC, VAL and FOV, and RET and LOP, etc. In other words, I was not sure of the fundamental difference between them, and I could not distinguish them clearly in some cases, so I was at a loss what to do. Finally, I tried next classification of fern spores and have thought about their morphological, phylogenetic relations.

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**Material and Method.**

All of materials used are the specimens of Geochronology Laboratories of University of Arizona and the microscope a Leitz (Ob. $\times 100$, PL 40: 1, A. 0.65, Ok. $\times 15$, Periplan). I saw most of materials by 1500 times magnification and I drew their shape principally from optical section of ornamentation. Considering
the convenience of comparison of their shape, I made their drawing in same size intentionally. Further, in isodiametric groups like Echinoid, Baculoid, Granuloid, Gemmate etc., I showed only their shape of optical section and in elongated groups like Rivulate, Striate, Reticulate, etc., I added a part of airscape to the drawing of optical section. In Perispore, I drew both front view and side view in one compartment.

Results and Discussion.

As shown in Table 1, I was able to classify the ornamentation of fern spores. First, in these groups, I attached importance to the ratio of height to width. Namely, I divided like these, 1 \(0.01 < \frac{H}{W} < 0.5\), 2 \(0.51 < \frac{H}{W} < 1.01\), 3 \(1.01 < \frac{H}{W} < 1.0\), 4 \(2.01 < \frac{H}{W} < 3.0\) and 5 \(3.01 < \frac{H}{W}\). For instance, E1 means Echinoid group and its \(\frac{H}{W}\) is between 0.01 and 0.5, B3 means Baculoid group, its \(\frac{H}{W}\) goes in between 1.01 and 2.0, G5 means Granuloid group and its \(\frac{H}{W}\) is more than 3.01, as shown in Fig. 1.

Table 1.

A. Surface Psiloid.............Psilate (surface not ornamented)
B. Surface Non-Psiloid ..........(surface ornamented)
   I. Surface depressed. 1. Fossulate
   2. Alveolate
   3. Obervermiculate
   4. Wrinkled
   II. Surface projected
       a. Fundamental group
           1. Echinoid.........E1, E2, E3, E4, E5
           2. Granuloid .......G1, G2, G3, G4, G5
           3. Baculoid........B1, B2, B3
           4. Elongated Baculoid......LB1, LB2
           5. Elongated Granuloid .....LG1, LG2, LG3
       b. First varied group
           1. Gemmate........G’1, G’2, G’4, G’5
       c. Second varied group
           1. Echinoid Echinoid.......E. E2, E.E3, E. E4
           2. Echinoid Granuloid ......E. G2, E. G3, E. G4
           4. Granuloid Granuloid......G. G1, G. G2, G. G3
           5. Interstice Granuloid.....IG3
           6. Baculoid Granuloid ......B. G1
Therefore, it seems to me that these E₁, G₁, B₁, LB₁, and LG₁ have a quite close relation to the Psilate group and E₅, G₅ etc. are very far from the Psilate group. G' means Gemmate and E.E. means a group which has Echinoid on the Echinoid (Fig. 1–23). Similarly, E.G. means Granuloid on the Echinoid (Fig. 1–24), G.E. means Echinoid on the Granuloid (Fig. 1–25), G.G. means Granuloid on the Granuloid and so on so forth.

Secondly, I took care in the relationship among the Echinoid group, Granuloid group, Baculoid group etc. Of course, typical Echinoid, typical Granuloid, etc. are completely independent groups, but in some spores, sometimes, I could find Granuloid which seems to me quite near to Echinoid, or, Conversely, I found some Echinoid which should be completely near to Granuloid. Observing similar relationships among Granuloid and Baculoid, Baculoid and Elongated, I thought of a three dimensional relationship as in Figs. 2 and 3 among them. In Fig. 2., I put vertically the groups of \( \frac{H}{W} \), crossways, I put a, b, and c. groups. This b. means typical one and other a. and c. mean similar ones to another group.
Fig. 1

Three dimensional relationship between $H/W$ and morphological changes of ornamentation.

Fig. 3. are collected ones of each of Fig. 2 (Echinoid, Granuloid etc.) centering around P-S axis. According to these figures, it is understandable that Echinoid a group has a near relationship to Granuloid c group. Furthermore, dividing these groups by the value of $H/W$, it is shown that Echinoid a1 is quite near to Granuloid c1, but Echinoid a2 is not so closely related to Granuloid c5. These relationships are similar in other Granuloid and Baculoid, Baculoid and Elongated, Elongated and Perispore (abbreviation of this group is M.). As proof explaining these relationship, I can give an example, Pessopteris (169) in Ec3 compartment, Dictyocline (195) in Ea4, Ampelopteris (196) in Gc4, Pyrrosia (207) in Ga5, Polystichum (206) in Bc5, Lastrea (239) in Ba3, Leucostegia (240) in Lc3, Diacalpe (242) in La3, Polystichum (241) in Mc3 and Campyloneulon (284) in Ma3. (These numbers are author's species number).

Next, comes a problem of Infra-Granulate, Infra-Baculate, Infra-Striate, Infra-
Fig. 3
Fig. 4 1=Elongated Granuloid, 2=Elongated Baculoid, 3=Baculoid Granuloid, 4=Granuloid, Granuloid, 5=Interstice Granuloid, 6=Granuloid, Echinoid, 7=Echinoid, Granuloid, 8=Echinoid Echinoid.

Fig. 5 1=Gemmate Echinoid, 2=Gemmate, 3=Branched Gemmate 4=Gemmate Granuloid.

Fig. 6 1=Elongated Granuloid, 2=Interstice Elongated Granuloid, 3=Elongated Granuloid, Elongated Granuloid, 4=Elongated Baculoid, Elongated Granuloid, 5=Interstice Elongated Baculoid, 6=Elongated Baculoid, 7=Elongated Baculoid Baculoid, 8=Elongated Baculoid Granuloid, 9=Elongated Baculoid, Granuloid, Granuloid, 10=Elongated Baculoid, Echinoid Granuloid, 11=Elongated Baculoid Echinoid.
Striate, Infra-Reticulate groups. But the surface of the body of these groups is Psilate, so these groups should be put into Psilate category in their symmetrical position of upper part as a special type like in Fig. 3. Still more, it seems natural to put negative ornamentation groups like Fossulate, Alveolate, Obermicate, Wrinkled just under the Psilate compartment (Fig. 3.).

A strong point of this classification is I think, first, it is quite easy because their characters are very large (everyone can distinguish among Echinoid, Granuloid, Baculoid etc.) and second, the value of $\frac{H}{W}$ is not different by personality. Even if its value of measurement is different by individuality, owing to their minute gradation, it might not be so different fundamentally. Then will be seen no more such a ridiculous difference that yesterday it was A group but next day it changed to D group, which was often seen in Adjective grouping until now.

But this orange-like schema has problems in containing Second varied group (E.E., E.G., G'.G., etc.), and Third varied group (G.G.E., LB.E.G., LB.G.G.). On them now, I have thought just the skin of orange like Figs. 2 and 3. The skin has a relation to both groups. Accordingly, all of them could be contained like Figs. 4 and 5. Additionally, Fig. 5 is a figure from the reverse side.

In Elongated group, La means Elongated Echinate, Lb means Elongated Baculate in optical section. Of course, Reticuloid group should be contained in this group. La gradually approaches to Perispore (M) groups. Troulesome is LB. G., LB.G.G., LB.E., etc. groups. I would like to give them a branch which has two roots originating in both separated groups as Fig. 6. In this way, no matter what sort of groups may appear (e.g. by hybridization etc.), they will be able to be grouped by making a new branch indefinitely.

References


