

AN APPROACH TO THE PROBLEM OF TAXONOMY AND CLASSIFICATION IN THE STUDY OF *SPORAE DISPERSAE*

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ABSTRACT

The present state of disagreement among spore workers with regard to the taxonomy and classification of *Sporae dispersae* has been reviewed. The taxonomic categories for *Sporae dispersae* have been defined and practicability of organ-genus concept over the form-genus concept for the circumscription of spore taxa has been discussed.

INTRODUCTION

DETAILED study of the dispersed spores and pollen, recovered from sedimentary strata, dates back to Reinsch (1881) when he described some of them from coals of the Carboniferous age. Thereafter, for several decades, these dispersed microremains attracted occasional attention of palaeobotanists and petrologists. However, it is only since the early thirties that the British, German, Russian, American and Indian palaeobotanists as well as geologists, realizing the importance of the *Sporae dispersae* in geological dating and stratigraphical correlation of sedimentary strata, set themselves to a serious study of these plant microremains. This increased research activity has resulted into very significant and substantial contributions on the study of *Sporae dispersae* of various ages and from many parts of the world.

Prompted by a desire for exactitude and clarity in description of the *Sporae dispersae*, spore workers have always adopted some system of taxonomy and classification to present their results. A number of these systems are a result of original thought but others are a sequel to synthesis of the then prevalent older conceptions. Each of these efforts on systematics of *Sporae dispersae* has its merits and also shortcomings. However, in spite of the latter these efforts are highly commendable inasmuch as they have been able to single out the numerous difficulties besetting the evolution of an ideal system.

From a perusal of the current literature on *Sporae dispersae* it becomes evident that the British spore workers mostly follow Knox's

(1950) system, the American workers prefer that of Schopf, Wilson and Bentall's (1944), in Germany, an amplification of Ibrahim's (1933) system is mostly in vogue and the Russian workers classify according to Naumova's (1937) system. This tendency to stick to one or the other of these systems, none of which excels the others, has unconsciously led to thwart the evolution of one such system of classification for the *Sporae dispersae* which may be universally followed. Of late, in view of the greater applied use of *Sporae dispersae* in coal and oil prospecting, the need for a universally accepted standard system of classification for these is being increasingly felt so that assimilation of data from all over the world can be more easily achieved.

THE PROBLEM

All the systems of classification proposed in the past, in spite of their diversities, tend to fall into two groups depending upon the differences in their taxonomic treatment of spore taxa:

1. Artificial (morphologic) systems which consider the morphologic characters of spores and pollen as the basis of specific, generic and suprageneric grouping (BENNIE & KIDSTON, 1886; IBRAHIM, 1933; NAUMOVA, 1937; ERDTMAN, 1947; KNOX, 1950; PANT, 1954 and POTONIÉ & KREMP, 1954).
2. Natural (phylogenetic) systems which emphasize circumscription of spore genera on the analogy of higher taxa (Orders-Classes) of the natural system of classification of plants (SCHOPF, 1938; SCHOPF, WILSON & BENTALL, 1944).

The real problem among palynologists today is to decide about the suitability of any of the two approaches between which most of the opinions tend to segregate. However, to choose between the two is not so easy unless we discuss the usefulness of one over the other in the light of scientific as well as practical needs and the limitations

imposed by the nature of the material handled.

ASPECTS IN THE STUDY OF *SPORAE DISPERSAE*

The study of *Sporae dispersae* has twofold applications, i.e. botanical and geological. The botanical aspect concerns primarily, with the taxonomy and phylogeny of spores and pollen and secondarily with ecology in so far as these plant microremains are representatives of the flora of that area. The geological aspect of stratigraphical correlation and dating of strata depends upon the applied use of the botanical knowledge so gained, especially that which concerns the changes in the distribution of *Sporae dispersae* or in other words their parent floras, during geological time.

Speaking of the botanical aspects of taxonomy and phylogeny, *Sporae dispersae* have limited value in view of their dispersed nature, because nothing definite can be stated about the identity of their parent plants. As a matter of fact, whatever we know today about the phylogeny of some of the dispersed spores has been a contribution from botany or palaeobotany rather than vice versa and it is doubtful if an independent study of *Sporae dispersae* would ever contribute anything more tangible than probabilities. However, for ecological studies, *Sporae dispersae* have proved to be of real help especially in Tertiary ecology where Pollen-analysis, in conjunction with the study of plant megafossils, has always enhanced accuracy of data and thereby its interpretation. This success of pollen studies of Tertiary strata is in a large measure due to the possibility of correctly identifying the parent genera or even species of the dispersed spores and pollen.

The application of the study of *Sporae dispersae* to stratigraphical (geological) problems especially of the pre-Tertiary strata depends on the detection of floral changes which have occurred in an area during the course of time due to migration and evolution of the species constituting its vegetation. Floral changes are normally imperceptibly gradual, but occasionally they are accentuated due to biotic or environmental factors and, accompanied with migration of species from and to the area, cause significant change in the composition of succeeding floras, thus interpolating floral-breaks in the vegetational history of the area. These floral-breaks are used for delimiting stratigraphic horizons.

Study of *Sporae dispersae* reveals these floral-breaks readily. It is for the detection of such floral-breaks and for fine stratigraphic correlation of coal seams as well as other strata, that this branch of palaeobotany is proving to be of great practical value.

From the studies of Mason (1936) and others it is now well known that floral changes are caused by the evolution or migration of such constituent species which, in view of their specialized needs of the environmental factors, behave as the borderline species in the population. Thus to detect the floral changes in a fossil flora it is imperative that the fossils of the borderline species should be distinguished from the other species. The same holds good in the study of *Sporae dispersae* and implies a taxonomic treatment which aims at distinguishing the spores belonging to each species and genus of the parent flora. Hence it can now be concluded that the primary need in the scientific study of *Sporae dispersae* is to define the taxonomic principles which may enable circumscription of the small, spore taxa as nearly equivalent to natural plant species and genera as possible.

TAXONOMIC CATEGORIES FOR *SPORAE DISPERSAE*

Spore-Species

A scientific definition of a plant species could be that it is a group of morphologically and physiologically similar individuals which are biologically isolated from those of the other closely related species. Among *Sporae dispersae*, in view of their isolated state, a fossil spore-species can be defined only as a group of morphologically (i.e. morphographically) similar individuals. The other features such as physiological similarity and biological isolation are beyond any means to establish in fossils. Thus, in effect, the only important basis of defining spore-species is the morphology of spore features as these are actually evidences of evolutionary morphology.

Theoretically, a species cannot be strictly genetically homogeneous population because no individual can contain all the hereditary factors which exist in allelic pairs and series. But we know that in nature, barring exceptions, mostly one set of either of the pair of allelic characters tend to be represented in a species. The more usual characters must, therefore, be accepted as the characters to define a spore-species.

Variation within a Spore-species — The characters tend to vary, within a species some varying more but others less. From my work (BHARDWAJ, 1952) on the spores of the living genus *Anthoceros* (L.) Prosk., the work of Knox (1950) on the spores of *Lycopodium*, *Phylloglossum*, *Selaginella* and *Isoetes*, Stokey & Atkinson (1956) on Osmundaceae and Wagner (1952) on *Diellia*, I have been able to infer that in Cryptogams the morphographic characters of mature spores, within a natural species, vary quantitatively but the range of variation is within definable limits. Likewise, as far as known to me, this generalization holds good in the case of pollen grains of Phaneogams as well.

It is worth pointing out here that while writing these generalized observations, I am not oblivious to the many exceptions noted so far by many colleagues, such as the occurrence of monolete as well as trilete spores in *Onoclea sensibilis* and others or the occurrence of abortive or giant spores in many natural fern-hybrids or the production of large and small spores as in *Notholaena affinis*. According to Wagner (1952) some fern species, known to be apogamous, such as *Pteris cretica* and others often show several size classes in spores. Likewise a number of similar, exceptional inconsistencies in the phanerogamic pollen grains are also on record. In my opinion the more usual features should be considered as more important in the taxonomy of fossil spores and pollen rather than the less common exceptions.

To ascertain the variation range for one of the variables such as the size, within species of *Sporae dispersae*, I carried out a large number of absolute size measurements of random specimens of several unquestionably distinct species of cryptogamic miospores ranging in size from 15 to 120 μ and some megaspores, from a coal seam in the Saar. This study not only revealed the range of size variation within these species but also a notable fact that this range shows more than proportionate increase as the size of the spore increases, e.g. in spores of 20 μ size, the range of variation may be only 25 per cent of absolute size, but in larger spores, e.g. of 100 μ average size up to 40 per cent and in megaspores, it may be 100 per cent or even more. These figures are only to give an approximate idea about the possible range of size variation within a species and should neither be taken as absolute nor universally applicable for other variables as

well. The size is a valuable variable in miospores of *Lycopsidea* but of less consequence for their megaspores, of indeterminate utility in spores of *Sphenopsida* and of problematic use in the taxonomy of gymnospermous pollen grains.

In other features, e.g. height and width of emergences as well as that of rays, the range of quantitative variation in a species is within definable limits. For delimitation of species within a genus it is important to work out the range of variation and the statistical mean of each variable, to enable comparison with that of the other comparable species. Unless as pore worker has a rational conception of these variations, he is very likely to split or lump together natural species.

Stratigraphical and geographical separation — An important consideration while delimiting species is the stratigraphical and geographical separation. Usually plant species remain unchanged only for short durations in geological time-scale and so to anticipate a long vertical range for a species may lead to taxonomic error. Likewise contemporary species recorded from two widely separated or even contiguous regions, having no common floral history, are more likely to be different. In such cases a very critical morphographical study is necessary which may reveal differences otherwise not discernible.

Spore-Subgenus

The status of a subgenus in the systematics of living plants has very frequently been ambiguous and for this reason this taxon has rarely received unanimous approval of taxonomists wheresoever attempts have been made to subdivide genera in this way. It is for such reasons that there are many cases on record where subgenera have ultimately been raised to the rank of genera or abolished to end a controversy. Likewise in *Sporae dispersae* a taxonomic treatment, envisaging creation of subgenera, is equally vulnerable or rather more so because here a taxonomist has recourse only to the morphological characters of spores. And an attempt to group together two sets of species, with qualitatively different association of characters only because they agree in one character which might have appeared in both of them due to parallel evolution, is bound to be hazardous.

Spore-Genus

In recent years, with better understanding of the nature of plant species and the modes of speciation, our concept of the various supraspecific taxa, especially the genus, has become more precise. In older times the genus-concept, as traced by Bartlett (1940), consisted merely in a tendency to group together plants of distinguishable but similar kind under one name. This morphographical concept continued through several centuries till Darwin's ideas of evolution added phylogenetic background to the morphology, emphasizing the morphological circumscription of a plant genus. Such an outlook on the genus-concept has not changed in the post-Darwin time. A modern definition of the genus by Buxbaum (1951) says that the genus is (in words of JUST, 1953), "the sum total of species belonging to a phylogenetic unit recognized as such by the unity of its morphological type (generic types)". With this definition it becomes clear that an agreement in the important morphological features between the type-species and other constituent species is an important criterion of the modern genus-concept and that is what Greenman (1940) also said that "the species of a genus must conform in all essential morphological characters to those of the type species of the genus". Such a genus, whose constituent species cohere round a type by the identity of their morphological characters, represents one evolutionary tendency and is a phylogenetically homogeneous, natural genus. In this connection it appears worthwhile to point out that in spite of such a clear understanding of the genus-concept there are many genera in the plant kingdom, especially among Lower Cryptogams which are still not natural genera (*sensu strictu*) but are composite, being groupings of convenience and any analogy from these while circumscribing spore genera, should preferably be avoided. Apparently these composite taxa are only awaiting detailed morphological and cytological study before they can be justly divided into natural genera.

In palaeobotanical taxonomy, in view of the fragmentary and difficult nature of material available for study, delimitation of genera has been more lax and two kinds of genera, i.e. organo-genera (*organo-genera*) and forma-genera (*forma-genera*) are officially recognized. The former are morphologically

circumscribed round a type and comprise only species of similar kind, thereby more or less approximating to a grouping of closely related species as in a natural genus or a family. Form-genera, on the other hand, are broadly defined including all forms, remotely related or even unrelated and thus represent highly artificial groupings. It is as well worth while to remark here that form-genus concept is older than the organ-genus concept as the former owes its inception to the earlier decades of palaeobotanical thought when limitation of the knowledge about the phylogeny of plants necessitated groupings of convenience, based on similarities in superficial characters. The organ-genera represent the modern trend where more and more effort is made to create generic groupings as nearly homogeneous and closely phylogenetic as possible.

As already discussed above, all natural plant genera are morphologically circumscribed, their phyletic homogeneity being accepted on the basis of the morphographic congruity of their constituent species. Likewise in *Sporae dispersae* where the nature of the parent plants is uncertain, the morphology of spores alone is the means to a phyletic grouping. The concensus of opinion by palynologists tends to recognize at least as much non-plasticity of the morphologic characters in spores as among other conservative organs of plant sporophytes. Therefore, it can be readily surmised that among *Sporae dispersae* morphologic circumscription of a genus, in faithful conformity to the type-concept, will automatically lead to more or less natural genera which in terms of palaeobotanical taxonomy can be called organ-genera. These spore organ-genera in exceptional cases may represent spores of a number of closely related natural genera instead of one, as has also been noted among living plants where sometimes spores of a sub-family or even a family are of the same type. Likewise instances are also not unexpected when a morphologic spore genus may represent only a section of some natural plant genus whose spores might have varied from the rest but the other gross morphology of the sporophyte would have continued to be like the rest. Irrespective of this, for our practical purposes such spore organ-genera are the ultimate ideal as these are the only possible phylogenetically homogeneous groupings that can be achieved on the basis of factual study of *Sporae dispersae*.

Form-genus vs. Organ-genus in the Taxonomy of Sporae dispersae — If we compare the history of systematics of *Sporae dispersae* to that of palaeobotany or botany in general, we find close correspondence in the way form-genus concept has gradually led to organ-genus concept. The history of systematics of *Sporae dispersae* dates back to Reinsch (1881) when he created the genus *Triletes* to include all rounded or triangular microscopic remains having a triradiate structure on one of their faces. Subsequently H. Potonié (1893) created *Sporites* to include all dispersed pteridophytic plant spores. Likewise Seward (1914) instituted *Pityosporites* for the coniferous pollen of the Abietinae-type. As these years constituted the beginning of the study of dispersed plant spores, lack of adequate knowledge about them necessitated broad groupings of convenience and these taxa were thus of the nature of form-genera. In 1933, Ibrahim introduced type method of circumscribing spore genera and created a number of morphographic genera. Subsequently Naumova (loc. cit.), Erdtman (loc. cit.), Knox (loc. cit.) and Pant (loc. cit.) as well as numerous others have also created morphographic genera although they did not take cognizance of the type method. Potonié and Kremp (loc. cit.) have strictly adhered to type method and have circumscribed narrow morphographic genera whose constituent species mostly agree to the type.

Schopf (1938), Schopf, Wilson and Bental (1944), Dijkstra (1946) and some others have preferred to maintain *Triletes* among the older form-genera after restricting it as the genus to include all triradiate megaspores presumably of lycopod origin and assigning a type to this emended genus. Apart from this Schopf *et al.* have redefined a number of other validly described genera and created a few new ones, all having the status of form-genera yet with generic types.

The purpose of the type concept in circumscribing a genus, as far as understandable to me, is to enable grouping of such constituent species which purport to be links of a single evolutionary chain and they are supposed to show same association of qualitative characters. In a form-genus which represents one or more plant classes, it is apparent that a large number of evolutionary tendencies may be included so that to designate any one form as the type, representing the whole genus, is not possible

as such a genotype can represent only one evolutionary tendency and not all. It is for such an anachronism that I have never been able to understand how form-genus concept and the type concept can be faithfully co-ordinated. For the same reason in the genus *Triletes* (Reinsch) Schopf, the large number of constituent species are not similar to its genotype *T. Reinschi* (Ibr.) Schopf. Actually in the system of Schopf *et al.*, the main emphasis in defining the spore genera is not on the type concept but on gross phylogeny, that its constituent species belong to one plant group each.

Now the question arises as to which concept, i.e. of the form-genera or the organ-genera, suits us better for our needs. It has already been made clear in the preceding pages that the study of *Sporae dispersae* has two applied aspects, i.e. botanical (floristic) and geological (stratigraphic). Considering the botanical aspect we can well imagine that form-genera, in view of their artificial nature and composition, are likely to over-emphasize similarities between floras of various regions even if their virtual congruity is only remote. Organ-genera, on the other hand, being homogeneous and natural, can depict the real floral affinities, neither over-emphasizing nor underrating similarities or dissimilarities. If the flora of two regions shows similar association of organ-genera, it is presumable without any doubt that the two are related and if otherwise, then unrelated. Among related floras how close the two may be is finally determined by the agreement or non-agreement among the species.

For stratigraphical purposes form-genera can rarely be of use as index-fossils because they have enormous vertical range usually extending through several geological periods. As their horizontal distribution tends to become artificially wide, they are equally useless for inter-regional correlations. Organ-genera are the only supraspecific category which being phyletic can correctly depict the evolutionary changes in the floras and, being smaller units, are better able to indicate the ecological changes in the floras. Spore organ-genera are thus of real importance for practical purposes. In another of my papers (in this volume) dealing with the systematics and stratigraphy of the Saar Coal Measures, the successful applied use of spore organ-genera for stratigraphical horizoning is well established.

It can be argued by those who want to retain form-genera in the systematics of *Sporae dispersae* that if the form-genera are not suitable for stratigraphical deductions, their species may well serve the need. Natural spore-species usually have very short vertical and horizontal range and are of real importance only for correlation of coal seams or other strata within a basin. Usually they are neither capable of defining stratigraphic horizons within the epochs nor are of use for inter-regional correlations. However, it is another question if one employs composite species which, being equivalent to organ-genera, will serve very well to define stratigraphical horizons, but in such cases the absence of natural spore-species will undermine successful correlation of coal seams and other strata.

It should be apparent from this discussion that natural spore-species and spore organ-genera are indispensable for the successful academic as well as applied study of *Sporae dispersae*, and that form-genus concept has outlived its utility for the present needs of palynologists and should be dispensed with. As such, it is necessary to redefine the existing spore genera, as far as possible, into narrowly circumscribed, morphological organ-genera.

SUPRAGENERIC CATEGORIES

Systematics of *Sporae dispersae* does not end merely after diagnosing species and genera but also raises the question of arranging the genera into a system of suprageneric taxa as in a system of classification.

So far most of the authors of morphological systems have suggested suprageneric categories on the basis of similarities in some

easily observable morphographic characteristics. The need is, however, to interpret these characters on grounds of comparative morphology and thereafter to circumscribe higher categories on the basis of agreement in phylogenetically more important characters. In this way the spore organ-genera, small as they are, can be grouped together into series (equivalent to Families), the latter into subdivisions, divisions and so on, on the basis of phyletic nearness of the various types of morphographic characters, whose elucidation is possible from a comparative study of *Sporae dispersae* and *in situ* spores from fossil and living spore-bearing organs. Such advanced studies are necessary to make the suprageneric groupings phyletic thereby leading to a phylogenetic system of classification for *Sporae dispersae*.

CONCLUDING REMARKS

Opinions can hardly be divided if I were to say that the ideal system of classification for *Sporae dispersae* can be that alone which is most phylogenetic. To achieve such an objective an easier course is to trace the phylogeny from species upwards through morphologically circumscribed species and genera that can be grouped into suprageneric categories equivalent to families, orders, etc., based on facts of comparative morphology. Such a taxonomic procedure will eventually lead to a classification, more or less corresponding to the natural system of classification used for plants in general. No doubt, such a system will stand parallel to, rather than be merged with, the natural system of plants, still this will be the closest possible approach to it in view of the difficult nature of *Sporae dispersae*.

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