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THE CLASSIFICATION AND NOMENCLATURE OF FOSSIL MEGASPORES

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ABSTRACTS

The classification of trilete and alete fossil megaspores is discussed in the light of the study of megaspore characters in some living plants, as well as in dispersed fossil specimens. The influence of various macerating fluids and mounting media on the characters of megaspores is also discussed.

It is a well known principle of modern taxonomy that all classifications which are based on a single or a small set of characters tend to be more uncertain and unnatural. For example, the delimitation of genera and species of the higher plants, where the relatively large and well differentiated plant body presents a wide range of variable characters, on which to base a classification, is much less problematic than that of the lower forms which have less differentiated or undifferentiated plant bodies. A taxonomist trying to classify plants merely on the characters of their spores or conversely, attempting to delimit the taxa of dispersed spores suffers from a similar and sometimes a more serious handicap against systematists who classify plants on the basis of the diversities of form presented by the plant body as a whole. The small mass of a spore or pollen grain provides an extremely limited ground for the play of morphological variations. Naturally, the taxonomy of spores and pollen grains as such has a number of limitations but the classification of fossil spores tends to become even more uncertain because a fossil spore is often partially disorganised and its form is generally greatly distorted during fossilization. Moreover, it presents no physiological characteristics and practically no cytological details.

Three categories of spores can be distinguished among the higher living plants, *viz.*, (i) megaspores, (ii) microspores and (iii) isospores but among fossils one can usually distinguish only two (i) megaspores and (ii) "small spores" (or "miospores" of Guennel, 1952). In the normal course all spores larger than $200\,\mu$ are regarded as megaspores while smaller ones are called "small spores" or "miospores" since they could include both isospores as well as microspores, the two categories of spores being generally in the same size range. It may, however, be pointed out that the boundary line between fossil megaspores and "small spores" is arbitrary. Spores having a size range in the vicinity of $200\,\mu$ could possibly have an equal claim to be included in either of the two categories. Moreover, there are some well known exceptional megaspores which are smaller than $200\,\mu$, e.g *Didymosporites scottii* or the megaspores of *Stauropteris burntislandica* whose diameter ranges between 146-257 μ (*see* Chaloner, 1958 *b*) and there are also some exceptional microspores (pollen grains), e.g. those of some pteridosperms whose diameter ranges between 170 to 500 μ (Florin, 1937). As I can suggest no solution of this problem of distinguishing between megaspores and small spores I accept the present arbitrary distinction between the two categories and proceed further to discuss the classification of dispersed megaspores.

EARLY RECOGNITION OF MEGASPORES

In the early phases of Palaeobotany when it was largely a science of the naked eye and fertile imagination, tiny objects like fossil megaspores must have been missed by many and the few workers whose sharp eyes noticed them confused these with other things, e.g. Reinsch (1881, 1884) included diverse objects like algae and fossil spores under a common title and Carruthers (1869) confused them with sporangia. Still others, e.g. Zeiller (1895) and Lundqvist (1919) merely called them spores or megaspores and set them aside.

THE NAME TRILETES

Possibly the first man to give a name to fossil megaspores was Reinsch (1881, 1884) but as he also assigned a number of diverse objects to *Triletes* we cannot attribute its generic status to him. Subsequently, Bennie & Kidston (1886) suggested a restriction of the name *Triletes* to all kinds of spores formed in tetrahedral tetrads although they actually included only megaspores under the title. In the following period David White (1899), Rina Scott (1906) and Seward (1910) grouped dispersed and undispersed lycopod megaspores under the designation *Triletes*. In 1928 Bartlett, for the first time, used the word *Triletes* as a generic designation in a few binomial epithets but even he did not give any redefined generic diagnosis of *Triletes*. In 1930 Zerndt, not only followed Bartlett in using *Triletes* as a generic name but he also referred for the first time some of the types of Bennie & Kidston (1886) to named species. Harris (1935) interprets Bennie & Kidston's restriction of the name *Triletes* to megaspores of possible lycopod alliance as making it a form genus for such megaspores. However, as pointed out by Winslow (1959), even though Bennie & Kidston (1886) are the first effective authors of the form genus *Triletes* yet it has been validated only in 1930 by Zerndt. This publication by Zerndt is, no doubt, quoted by Schopf (1938) but he once again proceeds to validate the name *Triletes* as a generic title by giving a fresh emended diagnosis and by proposing *Triletes reinschi* as its type species. According to Potonie & Kremp (1954) this generic status of *Triletes* as proposed by Schopf is invalid because in the meantime Ibrahim (1933) had already suggested another name *Laevigatisporites* for megaspores of the same type. Nevertheless, as already pointed out above, *Laevigatisporites* (Ibrahim) Potonie & Kremp is a later synonym of the valid generic designation, *Triletes* (Bennie & Kidston) Zerndt.

SUBDIVISIONS OF TRILETES

Besides grouping various megaspores under *Triletes* Bennie & Kidston recognized its three subdivisions, *viz. Laevigati, Apiculati* and *Zonales.* These or other subgroups, e.g. *Auriculati, Aphanozonati, Triangulati* have also been recognized by many a later author like Zerndt (1930), Sahabi (1936), Schopf (1938), and Schopf, Wilson & Bentall (1944) etc., sometimes as separate generic entities but at other times merely as sections of the large genus *Triletes.*

OTHER NAMES OF MEGASPORES OR MEGASPORE-LIKE BODIES

Dispersed megaspores or objects like them have also been described under other names. Schopf (1938) proposed the name *Cystosporites* for certain distinctive trilete megaspores of the type found in the sporangia of *Lepidocarpon.* The spores of *Cystosporites* are large oval sacs sometimes up to one centimeter long. Their proximal end is greatly reduced and shows a distinct triradiate mark. A number of species of the genus have since been described by other authors. In addition, there are some alete bodies of the size of megaspores. As early as 1875 Newton described some megaspore-like, punctate, spherical bodies from Tasmanite or Australian white coal under the name *Tasmanites.* These objects, however, do not show any triradiate mark and their actual nature is uncertain. Some authors have suggested that they might be algal bodies but they might as well be seed megaspores. Another genus of seed megaspores described recently by Dev (1961) is *Saccarisporites.* This genus includes alete sacs possibly belonging to seeds of gymnosperms as is shown in a recent study by Pant & Srivastava (in press 2).

CHARACTERS USED IN THE CLASSIFICATION OF MEGASPORES

The characters which are used in classifying dispersed fossil megaspores are various; some of them are more constant but others are very variable. Possibly the only methods of assessing their value in classifying megaspores would be to determine the ranges of variation of the different characters of a megaspore in individual species of living heterosporous Pteridophyta and also to look for fossil megaspores enclosed in sporangia which are comparable with dispersed ones and then to determine their range of variation in a species on the basis of such enclosed specimens. In the former course, if we treat the megaspores of living plants in the same manner as the fossils, during extraction, we can also get a rough estimate of the changes that are introduced in the megaspores by macerating reagents. Some work of this type which was done by me and one of my students is the investigation of Lower Gondwana pollen sacs and seeds (Pant 1958, Pant & Nautiyal 1960) but so far we have not come across any megaspores enclosed in undehisced sporangia. However, Kräusel's (1961) discovery of casts of enclosed megaspores in attached sporangia of *Cyclodendron leslii* should raise our hopes of finding undehisced megasporangia in Lower Gondwana material. The work of Chaloner (1952, 1953 a, 1953 b, 1953 c, 1958 a, 1958 b) on the enclosed megaspores of fossil lycopods and *Stauropteris burntislandica* is quite important in this context and his studies have revealed that the form of megaspores and their surface characters are usually characteristic for individual species or genera.

The determination of constant and variable characters of megaspores in species of living plants was undertaken by me in collaboration with Dr. G. K. Srivastava, and we studied the megaspores of a number of heterosporous pteridophytes. So far we have studied megaspores of *Isoetes* (five Indian species), *Selaginella* (two species), *Marsilea* (one species), *Azolla* (one species) and *Salvinia* (one species). In addition Dr. Nautiyal and I have worked upon the seed megaspores of some living cycads (Pant & Nautiyal, 1962). The characters which we analysed during our studies are the general form of megaspores; the nature and presence or absence of triradiate and arcuate marks, the form of pyramic areas; the surface sculpturing, the number of layers in the spore coat, their thickness and physical and chemical nature.

The general form of a megaspore is often characteristic for a genus or group of higher rank. The form of the megaspores of *Marsilea* (and other Marsileaceae), *Azolla* and *Salvinia* is distinct. The megaspores of *Selaginella* and *Isoetes* although distinct from others are of the same general form (triangular or rounded). Gymnosperm megaspores, at least those of the living Cycadales, have the same general form in all genera. The presence of triradiate marks is a characteristic feature of all megaspores of the living Pteridophyta and these are, so far as we know, typically absent in the megaspores of the gymnosperms. The form of the triradiate mark, pyramic areas, etc. are usually characteristic of a genus or species, e.g. the small triradiate marks of *Azolla, Marsilea* or *Salvinia* have characteristic size and form although in the dimorphic or polymorphic spores of *Isoetes* the trilete rays are sinuous in the smaller spores and straight in the larger ones or they may be bifid in some and simple in others. Surface sculpturing of a spore is as a rule one of the most reliable characteristics for determining species. The work of Pfeiffer (1922) on the species of *Isoetes* in general and our own work on the various Indian species of the genus (Pant & Srivastava, 1962 a) shows that one could possibly distinguish the different species entirely or mainly on the basis of megaspore sculpturing. The number of wall layers of a spore and their chemical composition may again be a generic character, e.g. the presence of a silicious perispore and other wall layers are characteristic of the genus *Isoetes* although the number of inner wall layers is variable in the larger and smaller megaspores of the same species. The number of wall layers, their structural features and chemical composition are again generic characteristics for megaspores of other living heterosporous pteridophytes.

An important point which must be remembered about the analysis of fossil megaspore characters is the method of studying them. Our work (Pant & Srivastava, 1962 b) has shown that a megaspore, e.g. *Dijkstraea brasiliensis* may appear almost smooth when studied dry in incident light but if the same spore is mounted in glycerine jelly it starts showing well marked papillae (*cf.* Figs. 5, 6, 7). The method and amount of maceration may result in the complete or partial dissolution of the ornamented outer spore coat of a spore to such an extent that one of its inner layers may come to the surface and make it appear quite smooth. Incident light examination of a dry spore shows no details beyond those obvious on its opaque surface but if these very specimens are mounted in glycerine jelly or Canada balsam they become translucent and reveal many an internal detail (Fig. 5). The size of macerated megaspores too is affected very considerably by the mounting media (Fig. 9). Acid and alkali treated specimens, if they are mounted in glycerine jelly or dilute NH_4OH swell to slightly less than double their size in the dry condition but if the same are immersed in Canada balsam they almost completely shrink back to their dry size. Specimens of megaspores must therefore be compared only when they are studied under identical conditions and in order to get to know more details preferably by a combination of various methods of study.

SUGGESTIONS FOR THE CLASSIFICATION AND NOMENCLATURE OF FOSSIL MEGASPORES

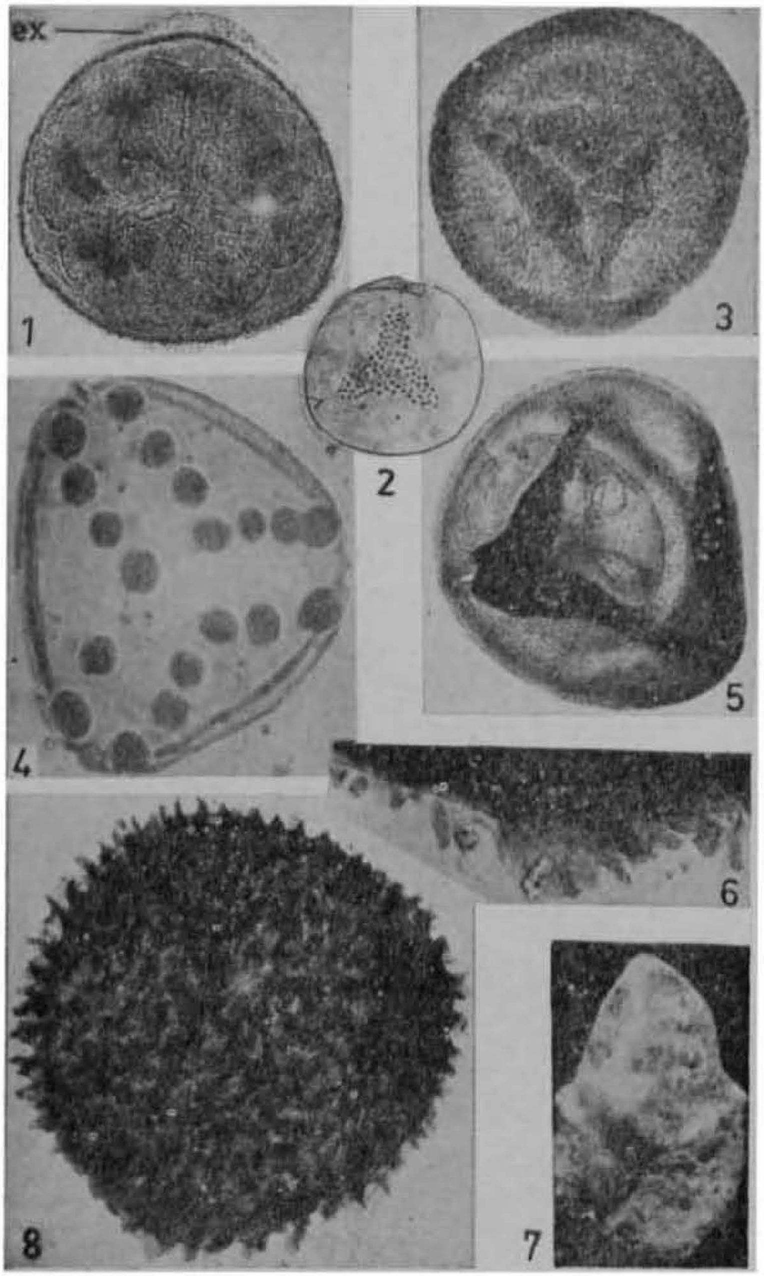
The primary grouping of megaspores, like that of the other kinds of spores may be based on the absence or presence of the tetrad marking and its nature, as suggested by me already (Pant, 1954). In the present paper I propose the group name *Megasporites* for megaspores of all kinds and under this name are included two subdivisions (i) *Triletes* for spores with a triradiate mark and (ii) *Macroaletes* for those without it. The subclassification of the group *Triletes* has already been suggested in another paper (Pant & Srivastava, 1961) wherein it is pointed out that the form genus *Triletes* or the names of its subdivisions as proposed by Bennie & Kidston (1886), Schopf (1938) and others be restricted to megaspores whose external features alone are described but if the internal details of megaspores, like the number and character of the various wall layers, be known they should be included in genera based on these details. The first genus of this type *Duosporites* was proposed by Høg, Bose & Manum (1955) and Pant & Srivastava, (1961, 1962 b, in press 1) have proposed five others, *viz. Carruthersiella* (Fig. 3), *Mammilaespora* (Fig. 8), *Dijkstraea* (Fig. 5-7), *Zeillerisporites* and *Talchirella* (Figs. 1, 2). The forms included under *Macroaletes* at present belong only to two form genera, *viz. Saccarisporites* Dev (1961) and *Tasmanites* Newton. The genus *Saccarisporites* Dev includes rounded or oval sacs possibly representing isolated seed megaspores. The genus *Tasmanites* includes punctate spherical bodies of uncertain nature. A key distinguishing the various megaspore taxa is given below:—

Megaspores of all kinds—*Megasporites*[1]

- α Megaspores without a triradiate mark—*Macroaletes*
  - A. Rounded bodies with a punctate wall—*Tasmanites*
  - B. Rounded sacs without punctate wall (possibly seed megaspores)—*Saccarisporites*
- β Megaspores with a triradiate mark—*Triletes*
  - A. Trilete megaspores with two wall layers
    - I. Spores rounded or sub-triangular
      - 1. Surface smooth or granular—*Duosporites*
      - 2. Surface with branched mamillate processes *Mammilaespora*
      - 3. Surface with simple papillae—*Carruthersiella*
    - II. Spores lageniculate
      - 1. Surface with processes—*Dijkstraea*
  - B. Trilete megaspores with three wall layers
    - 1. Surface smooth or granular—*Zeillerisporites*
    - 2. Surface papillate—*Talchirella*

As and when other types of megaspores are found they may be added to the above list. One must, of course, emphasize that the classification of fossil megaspores suggested here is an artificial grouping of sporomorphs having certain common characters. In the present stage of our knowledge a natural system can neither be a possibility nor even an aim.

[1] "Small spores" found in the fossil condition may be similarly grouped under the name *Miosporites*.



Figs. 1-8. 1, *Talchirella trivedii* Pant & Srivastava, macerated mounted megaspore showing the outer layer (*ex*) ×80. 2, *Talchirella trivedii* Pant & Srivastava, mounted inner sac showing pits. ×80. 3, *Carruthersiella trivalis* (Dijkstra) Pant & Srivastava, macerated mounted megaspore showing papillate surface layer and inner sac. ×51. 4, *Duosporites endosporitiferus* (Singh emend Dijkstra) Pant & Srivastava, inner layer of inner sac showing a uniseriate border of large pits. ×224. 5, *Dijkstraea brasiliensis* (Dijkstra) Pant & Srivastava, macerated mounted megaspore showing inner sac with pits. ×41. 6, *Dijkstraea brasiliensis* (Dijkstra) Pant & Srivastava, a portion of megaspore margin magnified to show processes. ×450. 7, *Dijkstraea brasiliensis* (Dijkstra) Pant & Srivastava, dry megaspore showing almost smooth surface ×61. 8, *Mammilaespora waltonii* Pant & Srivastava, macerated mounted megaspore ×80. (All after Pant & Srivastava).

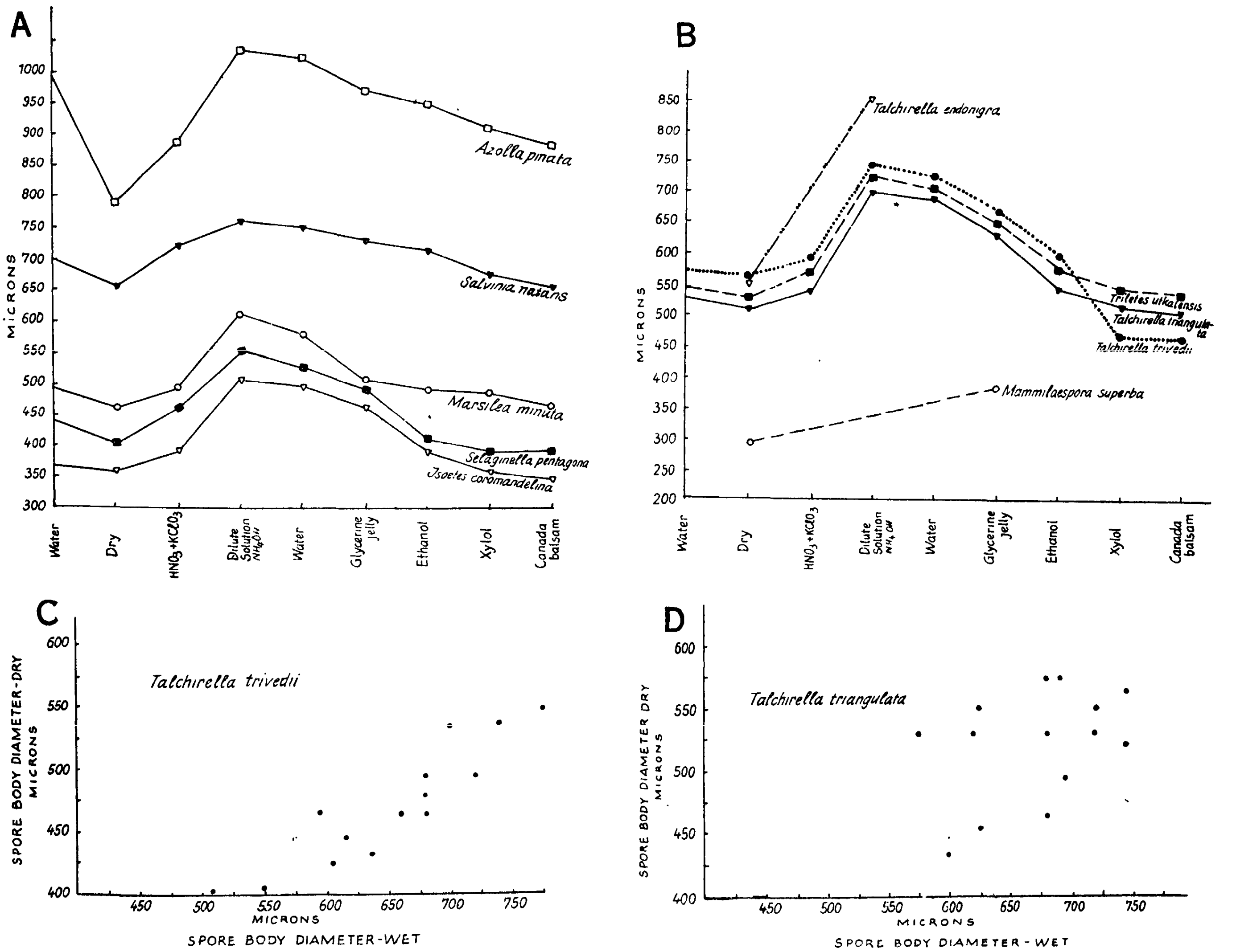


Fig. 9. A, graphic representation of change brought about by various mounting media and macerating fluids in the size of some living plant megaspores. B, graph of size changes brought about by mounting media and macerating fluids in the size of some fossil megaspores. C, D, scatter diagrams showing the dimensions of individual dry and glycerine jelly mounted megaspores of *Talchirella trivedii* and *T. triangulata*, respectively. (After Pant & Srivastava).

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