

# COMPARISON OF THE LATE PALAEOZOIC SACCATE MIOSPORE ASSEMBLAGES OF ANGARALAND AND THE INDIAN PART OF GONDWANALAND

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## ABSTRACT

Unlike plant megafossil assemblages of the Late Palaeozoic of Angaraland and Indian part of Gondwanaland, the miospore assemblages of both areas look much more similar. A more detailed comparison of saccate miospores shows that this similarity is more seeming than real. There are also differences in proportion of miospore types at various intervals of the Upper Palaeozoic sequence.

## INTRODUCTION

Plant megafossil data suggest that, during the Late Palaeozoic, Eurasia was divided into large and distinct phytochorias (in a rank of area or even kingdom) viz., Angara, Gondwana, Euramerian and, from the Late Carboniferous on, Cathaysian. These phytochorias were mainly developing autochthonously; the isolation of the Gondwana flora in India being especially significant (MEYEN, 1969, 1970a, 1972; CHALONER & MEYEN, 1973). The Angara flora of the U.S.S.R. and the Gondwana flora of India were once considered to be closely related, but more recent investigations have led me to challenge this opinion (MEYEN, 1969, 1971). It has been shown that dominants of both floras are distinctly different (glossopterids in India; cordaitalean leaves in the Asiatic part of Angaraland and in the Petchora Basin, conifers and other gymnosperms in the area of the Russian platform and the Cis-Ural). Genera common to Angara and Gondwana are form genera and resemblances between the vegetative parts of several Angara and Gondwana plants are the result of parallelism (MEYEN, 1969, 1971; SURANGE, 1971).

The relation of the late Palaeozoic floras of Angaraland and the Indian part of Gondwanaland takes on a different aspect when one compares assemblages of miospores. The number of common genera and morphological types greatly increases and the two floras appear, from a casual survey, much more similar. The reasons for this apparent discrepancy between data provided by plant mega and microfossils is a subject of the present paper. As both floras consisted mainly of gymnosperms, it seems appropriate to lay stress on saccate miospores that probably belonged to these plants. The author has studied slides kept in Birbal Sahni Institute of Palaeobotany, Lucknow, India. Angara saccate miospores were studied on material from the Tunguska and Petchora Basins, the Russian Platform and the Cis-Ural.

Observations on the relation between saccate miospores of Angaraland and India have already been presented in the literature. ZAUER, SALUJHA AND SAMOILOVICH (1969) analysed large taxonomic units of Late Permian miospores and concluded that their assemblages from India, the Russian Platform and Siberia were essentially different but relations at generic level were not considered. LUBER (1970) in a brief review of Upper Palaeozoic miospore assemblages mentioned the presence of a large number of Euramerian and Angara elements in Gondwana assemblages. DIBNER (1971) after a revision of Angara

monosaccate miospores, referred some of them to Gondwana genera known from India (*Crucisaccites*, *Divarisaccus*, *Striomonosaccites*, *Plicatipollenites*) or Australia (*Bascanisporites*), but correctly remarked that this generic unity "indicates only morphological similarity of pollen grains, but not direct genetic connections between plants producing them". Relation of several Gondwana and Angara miospore genera (including saccate ones) have been analysed by HART (1965), BALME (1970) and others.

Considering the unity of miospore assemblages of Angaraland and the Indian part of Gondwanaland one should clearly distinguish the possibilities of referring similar Indian and Angara miospores (1) to the same form genera on the basis of certain characters, or (2) to the same natural groups, whose presence in both floras may serve as a basis for phytogeographical and stratigraphical conclusions.

Let us begin with the question of the taxonomic relation of Angaran and Indian monosaccate miospores. Unfortunately, the systematics of the group leaves much to be desired. Before about 1960 nearly all Gondwana monosaccate miospores were included in *Nuskoisporites*, and those from Angara in either *Cordaitina* or *Zonales*. Since that time detailed investigations have made it evident that distinct genera of narrower concept could be distinguished. Considering the outline, mode of attachment and structure of sacci, body infold system, body structure and other characters, many new genera have been established (*Cannanoropollis-Virkkipollenites*, *Parasaccites*, *Plicatipollenites*, *Striomonosaccites*, etc.). Instead of wide and highly polymorphic genera of limited or no stratigraphical significance, palynologists obtained more closely defined genera with more restricted stratigraphical distribution. It should be noted, however, that the growing tendency to establish genera on the basis of every variation in the combination of the enumerated and other characters, threatens to confuse the taxonomy of saccate miospores. About 200 form genera have already been proposed.

Let us now compare the genera of Angara and Indian monosaccate miospores. Both in Siberian and in the European parts of Angaraland monosaccate miospores usually placed in *Cordaitina* are very common (ZAUER, 1960, 1965; PALEOPALINOLOGIA, 1966; DIBNER, 1971). In many of them the line of attachment of saccus to central body is obscure or indiscernible, so that to establish the topographical relation between the saccus and body is often impossible. In saccate miospores the nexine is often not preserved, and the body outline cannot be recognized (VISSCHER, 1971). The holotype of *C. uralensis* (Luber) Samoil. appears to be preserved in this way. A contour which is commonly taken to be the equatorial outline of the central body may, in reality, represents the line of attachment of the saccus. It appears that monosaccate miospores preserved in this way should be referred to a single form genus, e.g. to *Cordaitina* Samoilovich (if the present interpretation of its type species morphology is correct), or *Virkkipora* Pant & Srivastava, the type specimen of which is also devoid of a central body. *Cordaitina*-like miospores lacking a central body are very common in both Angaran and Indian assemblages.

Many Angaran *Cordaitina* in which the body is preserved look very similar to *Parasaccites* and *Cannanoropollis* (*Virkkipollenites*) of India. I incline to agree with DIBNER (1971), who refers some Angara monosaccates to the Indian genera *Plicatipollenites*, *Divarisaccus* and *Striomonosaccites*. Other Angara miospores having rugate exine resemble the Indian genus *Rugasaccites*. Miospores fitting the diagnosis of *Potonieisporites* are widely distributed in the Angara, Euramerian and Gondwana Upper Palaeozoic. Morphological types, resembling the Gondwana genera *Pachysaccus*, *Gondwanopollis*, *Densipollenites*, *Caheniasaccites*, *Stellapollenites*, *Rhimospora* and some other genera, known in India, have not so far been

found in Angara assemblages. Miospores with polygonal areas on body exine and a distinct triradiate slit (e.g. *Barakarites* and *Parastriopollenites*) are not found in Angara assemblages and there are no miospores with striations on both proximal and distal sides of the body (as in *Distriomonosaccites*). DJUPINA (1971) and DIBNER (1971) referred several Angara miospores, including *Cordaitina ornata* Samoil., to the Indian genus *Crucisaccites*. It is possible that some Angara miospores do possess the characters of *Crucisaccites*, but this is not the case with *Cordaitina ornata*, which has subequatorial saccus attachment, unlike para-condition in *Crucisaccites*. The similarity between *C. ornata* and *Crucisaccites* is merely superficial (MEYEN, 1973).

It is difficult to find morphological types and corresponding form genera that are endemic to Angaraland. Among such endemics may be the pollen grains that have been extracted by MAHESHWARI AND MEYEN (1971) from *Cladostrobus*. This genus represents the male fructification of plants that bore *Rufflora* leaves which are one of the dominants among Angara plant megafossils. Pollen grains of *Cladostrobus* have an intrareticuloid monosaccus, a promonosaccus in Maheshwari's opinion. In immature grains the saccus is closely adpressed to the body, and it would be difficult to recognise that dispersed grains in this condition were saccate. The saccus covers the proximal side, the sulcus is rather large and oval or circular. Dispersed miospores of this type belong to the genus *Cladaitina* Maheshwari & Meyen (type species: *C. dibnerae* Mahesh. & Meyen, 1975). Such miospores are often represented solely by either the isolated body or saccus folded into a fusiform shape. They thus resemble monocolpate miospores of the *Ginkgocycadophytus* type. In Angaran miospore assemblages the content of *Ginkgocycadophytus* is usually rather high, especially in the Upper Permian. Careful investigation of these miospores under high magnification has convinced me that many specimens may be the isolated and folded bodies and sacci of *Cladaitina*-like monosaccate miospores.

Comparison of Angaran and Indian disaccate miospores is even more difficult than with monosaccate forms. Over 100 disaccate form genera have been defined. Many of these lack adequate diagnoses and type material. In addition, many Permian disaccate miospores from the U.S.S.R. were described under names which had been originally applied to fossil leafy shoots (such as *Ullmannia* and *Lebachia*), fructifications (*Caytonia*) or living conifers (*Podocarpus*, *Cedrus*, etc.).

Some Indian disaccate miospores are referred to form genera previously established in Euramerian (*Illinites*, *Lunatisporites*, *Jugasporites*, *Limitisporites*, *Strotersporites*, *Cuneatisporites*, *Vesicaspora*, *Rhizomaspora*, *Sulcatisporites*) and Angara (*Striatopiceites*, *Striatopodocarpites*) areas. The genera *Faunipollenites*, *Hindipollenites*, *Primuspollenites*, *Verticipollenites*, *Striatites*, *Distriatites*, *Striapollenites*, *Lahirites*, *Corisaccites*, *Ibisporites*, *Schizopollis*, *Gondwanipollenites* are considered as Gondwana endemics.

In their general habit, Indian and Angara disaccate miospores have much in common, because in both areas one can see different combinations of a small number of the same characters (outline and type of attachment of sacci, type of striations, character of sulcus etc.). It is natural that the simplest morphological types, corresponding to the genera *Striatopodocarpites*, *Limitisporites*, *Striatites*, *Platysaccus*, *Vesicaspora* and others are found in many phytochorias. But some morphological types are more localised. Among Indian miospores there are few forms with distinct triradiate mark (as in *Illinites*) and miospores with a proximal slit, such as *Strotersporites* and *Limitisporites*, although rare in India, are characteristic of western parts of Angaraland. In contrast to Angaraland, in India one seldom encounters miospores with wide flat thickenings on the proximal side of the body

(as in *Taeniaesporites*), or like *Hamiapollenites* with transverse bands on the distal side of the body and reduced sacci. Such miospores have been assigned in Soviet literature to several genera and species as "*f. connectivalis*". The latter type of miospore, with or without striations, is very common in the European part of Angaraland. On the other hand miospores with pitcher-shaped sacci (*Hindipollenites*, *Verticypollenites*), with vertical striations on the proximal side (*Striapollenites*), with a double system of striations (*Distriatites*), with polygonal structures on the body (*Primuspollenites*), with indistinct body equator (*Faunipollenites*, *Sulcatisporites*), or with complex folding of the body (*Schizopollis*) are characteristic of Indian assemblages.

Some Indian and Angara miospores which at first glance look very similar, show important differences when closely examined. For example, the northern genus *Lueckisporites* is only superficially similar to the Indian *Corisaccites* (BALME, 1970; MEYEN, 1973), and their synonymy, suggested by HART (1969) and VISSCHER (1971), cannot be maintained.

There is a good deal of uncertainty in the relation between the genera *Striatopodocarpites* and *Lahirites*. BOSE AND MAHESHWARI (1968) rightfully disputed the validity of the former, but this does not solve the question of the relation between Angara and Indian miospores of this type. If we consider the holotype of the type species of *Lahirites* (*L. raniganjensis*) it is certain that such miospores are absent from Angaraland. This species was originally described rather schematically, without noting that the striae are not straight, but undulating or even discontinuous with perpendicular offshoots and transverse anastomoses. Such striation is not known in *Striatopodocarpites*-type spores of Angaraland. It is true that other Indian *Lahirites* show a more usual type of striation. BALME (1970) referred some of these to *Striatopodocarpites*.

The relation between *Distriatites* and *Hamiapollenites* also needs clarification. The study of *Distriatites* in the collection of Sinha (1972) has convinced me that the multiple ribs on the distal side of the body may be related to the widening and splitting of a distal band, like that in *Hamiapollenites*. In some specimens this band bears only one groove, sometimes not completely crossing the distal side of the grain. These look very similar to *Hamiapollenites*. BALME (1970) placed *Distriatites* into synonymy with *Hamiapollenites*, but later he (personal communication of 5.3.1973) has come to the conclusion that the genera can be separated on the basis of the small constricted sacci of the type species of *Hamiapollenites*.

Indian miospores described under the generic name *Faunipollenites* are very similar to the northern genera *Striatopiceites* (= *Striatopiceipites*) and *Protohaploxipinus*. In all three genera the body outline may be indistinct, the principal diagnostic character of *Faunipollenites*. However, in some specimens of *Faunipollenites* the body is clearly seen, although in others it cannot be recognized even under the phase-contrast microscope. HART (1965) included *Faunipollenites* in the synonymy of *Protohaploxipinus*. This was a comparison between distinct morphological types and relating them to form genera of Angara and Indian miospores. If such an approach is adopted one may claim a certain unity between Angara and Indian saccate miospore assemblages. But this apparent unity will decrease if we compare not only separate form genera but also transitional forms between them, and if we also consider the distribution of taxa in time and space, especially in different parts of Angaraland.

It was recognised long ago that form genera of miospores occurring in the same area and bed show mutual transitions. In the Permian of the Cis-Ural, the transition between

*Vittatina* and certain striate disaccate miospores was repeatedly described (SAMOILOVICH, 1953; ZAUER, 1960; ABRAMOVA & MARCHENKO, 1964). In India such transition has never been reported. Besides in the Indian *Vittatina*-like pollen, which I examined, the exine is either structureless, minutely coniculate or with irregularly distributed intramicroreticulation on the proximal side. Angara *Vittatina* normally shows distinct intramicroreticulation throughout the whole proximal side.

Lele has drawn my attention to the transition between the Indian representatives of *Potoniisporites*, *Plicatipollenites*, *Limitisporites* and *Sahnites*. In Euramerian assemblages the first genus is transitional with different genera, such as *Candidispora*, *Nuskoisporites* and *Guthoerlisporites* (NYGREEN & BOURN, 1967). In Angara assemblages *Plicatipollenites* and *Potoniisporites*-like pollen are also known but are transitional with *Cordaitina*-like pollen showing the para-condition of saccus attachment, and are morphologically close to *Parasaccites*. Disaccate striated miospores in India are linked through certain *Lahirites* (related to *L. raniganjensis*) and *Hindipollenites* with the genus *Primuspollenites* which has polygonal areas instead of striations. Such transition and *Primuspollenites*-like miospores are not known from Angaraland assemblages.

Indian representatives of the genera *Rugasaccites*, *Pachysaccus*, *Gondwanopollis*, *Caheniasaccites* and *Rhizomaspora*, which have a similar exine structure, show a transition from monosaccate to disaccate condition, that does not occur among Angara miospores. Some *Vesicaspora*-type pollen have a monosaccus divided into two strongly inflated portions with equatorial connections which may be displaced towards the proximal side (the present author's and A. V. Gomanjgov's observations). The miospores then look typically disaccate, but here the transition from monosaccate to disaccate condition is only an apparent one. Pollen of this type is very common in the Upper Permian of European Angaraland, and may belong to plants bearing *Phylladoderma* leaves (MEYEN AND GOMANJKOV, 1971).

Forms intermediate between monosaccate and disaccate are rare in the Permian of Angaraland. They are, however, known from the Cis-Ural and Siberia (e.g. the genus *Samoilovichisaccites* Dibner). One may observe a series, linking mono- and disaccate miospores in Siberian Carboniferous assemblages viz., *Florinites venustissimus* Medv.—*F. viluensis* Medv.—*Protohaploxipinus ineptus* Medv. from Tunguska basin (MEDVEDEVA, 1960). This series is clearly different from those observed in India, though *F. venustissimus* is very similar to *Plicatipollenites indicus* Lele.

The number of such variation series could be multiplied. It is possible that in some places we will find parallel series in different phytochorias if the analogy with plant megafossils is valid (MEYEN, 1971). But this cannot be conclusive evidence of natural relationships of parent plants, because similar trends in variation may well be present among different plant groups (cf. pollen of conifers and certain pteridosperms).

Let us now consider the distribution of similar miospores of India and Angaraland in time and space. During the late Palaeozoic the Angara palaeofloristic area underwent significant differentiation (MEYEN, 1970a, 1972; CHALONER & MEYEN, 1973), especially between European and Asiatic parts of the area. Transitional plant assemblages occur in the Petchora Basin. Several palynologists have regarded western Angaraland as part of the Euramerian area. I cannot agree with this. In assessing the phytogeographical relation between different territories we must consider more or less synchronous plant assemblages. Those who regard the assemblages from the Artinskian, Kungurian, Ufimian, Kazanian and Tatarian stages of the Russian Platform as Euramerian ones, ignore two factors. Firstly, undoubted Artinskian and Kungurian miospore assemblages

are not known in Western Europe, and are known only in those parts of North America which cannot be certainly assigned to the Euramerian area (or Atlantic area according to my scheme of zonation of the Lower Permian) because of the lack of plant megafossils. Secondly, assemblages from the Zechstein and those from the Upper Permian of the Russian Platform look very different. *Cordaitina*, *Vittatina* and monocolpate miospores of the *Ginkgocycadophytus* type are very common in assemblages from the Russian Platform and virtually absent in the Zechstein. *Lueckisporites* and *Taeniaesporites*, on the other hand, although typical of the Zechstein, occur only in the westernmost parts and only in the uppermost Permian of the Russian Platform.

The spatial distribution of Angara saccate miospore assemblages is generally speaking as follows (PALEOPALINOLOGIA, 1966; DIBNER & LUBER, 1968). In the Asiatic parts of Angaraland monosaccates are dominant in Upper Palaeozoic strata; disaccates occur in small numbers throughout almost the whole section, their frequency slightly increases in the Upper Permian in which a few striate miospores also occur. The genera *Lueckisporites* and *Taeniaesporites* are very rare. In the European part of Angaraland and in Western Kazakhstan i.e. Ural-Kazakhstan area of the Lower Permian, and East-European area of the Upper Permian (MEYEN, 1970a, 1972; CHALONER & MEYEN, 1973), monosaccates range throughout the Permian, but their abundance gradually decreases, whereas a number of disaccate, including striate forms increases. The western part of Angaraland is especially characterized by a high diversity and large numbers of *Vittatina*, which sometimes shows, as mentioned earlier, a transition to striate disaccates. Thus in Angaraland, the proportion of mono- and disaccates reflects mainly geographical differentiation.

Quite different distributional patterns are observed in India (BHARADWAJ, 1966, 1969). Radial monosaccates dominate in the Talchir and Karharbari Groups, but in the Barakar, Barren Measure (BM) and Raniganj Groups their percentage is rather low. Striate disaccates are comparatively rare in the Talchir and Barakar, more common in Karharbari, and very abundant in the Barren Measures and Raniganj Groups. Non-striate disaccates are rare in the Talchir, about as common as striate disaccates in the Karharbari and Barakar and less abundant than striate forms in the Barren Measures and Raniganj. In other words the relative proportions of mono- and disaccate forms in India depends on the age of the assemblage.

Summing up the data on morphology and variation of Angara and Indian saccate miospores, and considering their distribution in time and space, we may conclude that the unity of the assemblages may well be more apparent than real. On the basis of morphology we are forced to refer some Angara and Indian miospores to the same form genera. But as in plant megafossils, the same generic name does not imply that we are dealing with representatives of the same natural group at generic rank, or indeed even at the level of family or order. We may hope that with the application of SEM, phase contrast and UV-microscopes, we shall be able to investigate in greater detail the morphology of Angaran and Indian representatives of the same form genera and this may disclose significant differences. It will not, however, free us from the burden of widely distributed form genera because the critical details cannot be observed on every specimen. Most specimens will always have to be classified on the basis of characters seen under an ordinary light microscope. Therefore, in future palynological taxonomy and nomenclature should embrace taxa, established for different modes of preservation (cf. *Lepidodendron-Aspidiaria-Bergeria-Knorria* in plant megafossils).

Unfortunately, the natural affinities of the overwhelming majority of Angara and Indian miospores are still unknown. Arguing that the dominant forms in the micro- and megafossil assemblages are likely to derive from the same plant group, we may suggest that most of saccate miospores of India belong to glossopterids. There is a satisfactory correlation between occurrences of monosaccate miospores and *Gangamopteris* leaves, and disaccate (including striate) miospores and *Glossopteris* leaves (LELE, 1963-1964; BHARADWAJ, 1966). Miospores resembling *Faunipollenites* have been found inside the micropyle of seeds of the fructification genus *Senotheca* corresponding to certain *Glossopteris* leaves (BANERJEE, 1969).

Angara monosaccate miospores are usually referred to the Cordaitales on the basis of their similarity to the pollen of true Euramerian cordaitaleans although similar pollen is also known from sporangia of the European pteridosperm genera *Dictyothalamus* and *Schuetzia* (REMY & REMY, 1968). Some Angara monosaccate miospores (*Cladaitina*) were connected with plants producing *Ruflorea* leaves (see above). But both the male strobili and leaves of these plants, as well as the exine structure of their miospores, are very different from those of *Cordaites* and *Cordaianthus*. Angara disaccates are usually referred to conifers (by analogy with living conifers and with pollen found *in situ* in fossil coniferalean fructifications) or to Caytoniales. Indeed, as was mentioned earlier, the coniferalean (?) genus *Phylladoderma* (established on leaves) may be linked with miospores having a monosaccus divided into two inflated hemispheres which give it a disaccate look. Zauer (1960) concluded that some Angara disaccates belong to pteridosperms. It seems that the Permian peltaspermaceous pteridosperms of Angaraland produced such miospores. It is suggestive that, in miospore assemblages obtained from rocks with abundant *Tatarina* leaves (fam. Peltaspermaceae, MEYEN, 1970b), disaccates predominate, and monocolpate asaccate miospores known in Mesozoic peltasperms are either rare or absent.

Nearly all previous schemes of palaeofloristic zonation of the Late Palaeozoic are based on plant megafossils (but see SULLIVAN, 1967) whose natural affinities are often unknown or doubtful. We are thus dealing with the spatial distribution patterns not of clearly defined systematic groups of complete plant organisms, but those of certain morphological units (organ and form genera) the natural affinities of which may differ in various phytochorias. Fortunately, these morphological types, like systematic groups, have a fairly regular spatial distribution. Meanwhile the resulting maps are closer to phenogeographic than to true phytogeographic ones. Of course, phenogeographic maps are interesting in themselves, but they cannot be used with full confidence for the solution of problems of florogenesis, or for palaeoclimatic and palaeogeographic reconstructions. For future phytogeographical analysis of Palaeozoic floras we need firstly to combine data obtained from plant micro- and megafossils, and secondly to pay more attention to recognition of the natural affinity of both miospores and plant megafossils.

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