Differential morphographic identity of Gondwanic palynomorphs

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The exine structures, bauplan and germinal apertures are the basic characters for the morphographic identification of fossil spores and pollen, The apparent but unreal form-similarities of some bisaccate pollen taxa of *Sporae dispersae* from Gondwanaland on one hand and those in the contemporary Euromerian sequences on the other, have been sorted out in this paper. Trends of different exine structures and saccus organizations have been identified in pollen. This concept has been exemplified by the fact that the pollen taxa *Lunatisporites, Lueckisporites* and *Klausipollenites* of the north possess mostly imperfect reticulae, compactly placed grana, columnar elements, rodlets, vermiculae, verrucae or similar elements mixed together, rounded or multifaceted islands of various shapes and sizes, incomplete or even isolated closely packed muri as exinal elements which make the infra-structure of the sexine in the corpus. In contrast to this trend, the major pattern of exine structure in apparently similar taxa of the Gondwanaland is different; most of the pollen groups exhibit perfectly infrareticulate structure on corpus with complete muri and distinct meshes.

Such a differential morphographic identity may lead to a more rational model of the palaeo-phytogeography based on palynofossils, because the genuine similarities and differences could be effectively used in delimiting the floral provinces. The distinctions in the mother vegetations, which have had produced pollen and spores in two regions,corroborate the distinctions in the groups of palynotaxa discussed here. This paper proposes the theory of the Apparent Form Similarity (AFSIM factor) and highlights certain lines of differentiation amongst the similar-looking but basically different spore-pollen components produced by unrelated plant groups. Some aspects of palynofloral distribution *vis-a-vis* climatic changes through Gondwana have also been discussed.

Key-words— Palynology, Morphology, Gondwana.

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साराँश

गोंडवाना के परागाणविकरूपकों की अन्तरात्मक आकारिकीय पहचान

रामशंकर तिवारी एवं विजया

अश्मित परागकणों एवं बीजाणुओं की आकारिकीय पहचान के लिए बाह्यचोल, बोप्लान एवं जननिक छिद्र जैसे कुछ विशेष लक्षण हैं। गोंडवानाभूमि एवं समकालीन यूरोमेरियन अनुक्रमों के विकीरित परागाणुओं में से कुछ द्विकोष्ठीय परागकण वर्गकों के स्पष्ट सदृश-प्ररूपों को इस शोध-पत्र में छाँटा गया है। परागकणों में विभिन्न बाह्यचोल संरचना की प्रवृत्तियाँ एवं कोष्ठ-निर्माण अभिनिर्धारित किये गये हैं। यह अवधारणा इस पर आधारित है कि उत्तर क्षेत्र के वर्गकों *ल्यूनाटिस्पोराइटिस, ल्यूकिस्पोराइटिस* एवं *क्लॉसिपोलिनाइटिस,* में अधिकतर अपूर्ण रेटिकुली, सुसंगठित ग्रेना, स्तम्भी अवयव, दंडिकायें, वर्मिकुली, वेरुसी अथवा सदृश मिश्रित अवयव, गोल अथवा विभिन्न आकार के बहुआयामी द्वीप एवं सघन रूप से गठित मुरी विद्यमान हैं ये सभी कोर्पस में सेक्साइन की अन्तरासंरचना का निर्माण करते हैं। इसके विपरीत गोंडवानाभूमि के एक जैसे वर्गकों में बाह्यचोल संरचना विभिन्न प्रकार की है। परागकण समूहों में से अधिकतर में कॉर्पस पर पूर्ण मुरी एवं विभिन्न प्रकार की जालिका सहित पराजालिकावत् संरचनायें विद्यमान हैं।

इस प्रकार की अन्तरात्मक आकारिकीय पहचान से परागाणविकरूपकों पर आधारित पुराभौगोलिकी का एक विशेष मॉडल प्राप्त हो सकता है जिसका विभिन्न वनस्पतिजातीय प्रदेशों के परिसीमन में वास्तविक समानताओं एवं अन्तरों का यथार्थ उपयोग किया जा सकता है। मातृ-वनस्पतियों के पारस्परिक भेद, जो कि इन दो क्षेत्रों के बीजाणु एवं परागकणों में विकसित हो गये हैं, परागाणु-वर्गकों के समूहों जो इस शोध पत्र में वर्णित हैं, की पुष्टी करते हैं। इस शोध-पत्र में "स्पष्ट प्ररूप सदृशता" का सिद्धान्त प्रस्तावित किया गया है तथा असम्बद्ध पौधों के समूहों द्वारा उत्पादित एवं एक ही जैसे लगने वाले परन्तु विभिन्न बीजाणु-परागकण अवयवों में पारस्परिक अन्तरात्मक रुपरेखा इंगित की गई है। गोंडवाना में परागाणुवनस्पतिजातीय एवं जलवायवी परिवर्तनों के कुछ पहलुओं पर भी प्रकाश डाला गया है।

IN the later half of fifties and the beginning of sixties of the present century, the foundation of detailed morphography and taxonomy for *Sporae dispersae* was laid down in India. The major fields of activities covered by palynological studies in the Gondwana sequence are : delimitation of taxa and their identity as Gondwanic population; diagnostic assemblage-delineation for each formation; correlation of coalseams in complex geological set-up; identification of climatic phases during Lower Gondwana; demarcation of Permo-Triassic boundary in nonmarine deposits; cladistically constructed morpho-evolutionary tree and biohorizon demarcation; identification of time transgressive lithostratigraphic units, viz., formations in Gondwana basins; palynofloral affinity of Tethyan sequence in north-west India with the peninsular Gondwana *vis-a-vis* northern provinces (Tiwari, 1991a, 1991b; Vijaya & Ram-Awatar, 1994).

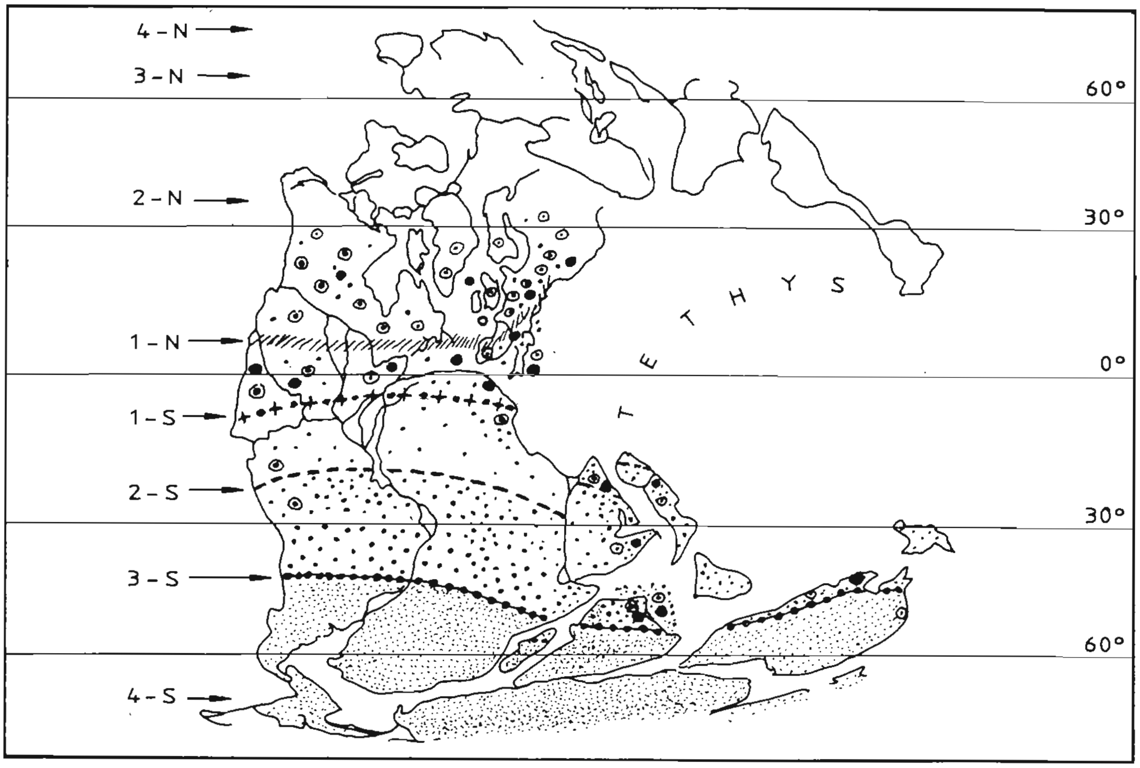
The intricate nature of exine structure and the bauplan (i.e., building plan, or organization) of palynomorphs are important for their real identity. This line of analysis makes the theme of the present paper.

Morphotaxonomy is the foundation of palaeopalynology and, implicitly that of correlation, age determination and delineation of past floral provinces. Because of the historical reasons, the Gondwana palynologists had always a bias for the taxonomy practiced in Europe which resulted in the allocation of several genera of *Sporae dispersae*, found in the Permian and Triassic Gondwana, to the pegion-hole assortment-scheme of spore-pollen taxa which was developed for the northern hemisphere (Balme & Hennelly, 1955, 1956). The identification of *Nuskoisporites* in Talchir Formation (Early Permian in India) by Potonié himself in 1959 (Potonié & Lele, 1961) is an example of the beginning of this syndrome. The European bias continued because the gross "comparability" of shape and arrangement of various morphographic characters was very "impressive" to put them under the same names! Thus the finer differences were not identified fully in the early days of palynological studies (1940-1962). However, with the advancement in concepts and resolutionary approach for organization as well as structure of exine in palynomorphs, several new characters were recognised for Gondwana spores and pollen; consequently, numerous generic categories were identified which, although had Apparent Form Similarity (AFSIM) with some northern taxa, basically differed from that stock.

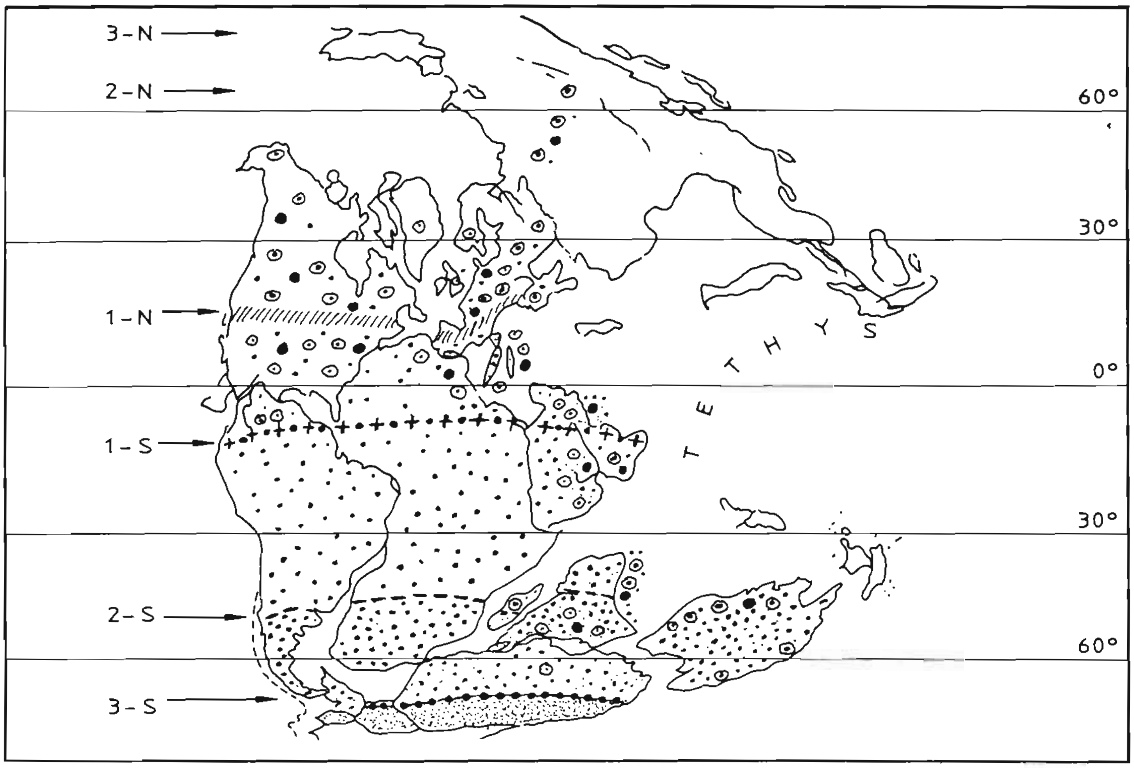
It is important to note here that recognition although at times with sceptic remarks, has been given to these new proposals (Balme, 1970; Foster, 1979; Conti *et al.*, 1986; Demelia, 1983; Playford, 1990; Eshet, 1992), and sequel to this the Gondwana palynofloras are emerging effectively for delineation of provinciality. Examples of segregation of such taxa on the basis of organization and structure are as given below :

Later segregation	**Earlier assigned to**
Plicatipollenites Lele 1964 *Virkkipollenites* Lele 1964 *Parasaccites* Bharadwaj & Tiwari 1964 *Barakarites* Bharadwaj & Tiwari 1964	*Nuskoisporites* Potonié & Klaus emend. Klaus 1963 *Cordaitina* Samoilowich 1953
Indotriradites Tiwari 1964 *Dentatispora* Tiwari 1964	*Cirratriradites* Wilson & Coe 1940 *Kraeuselisporites* Leschik emend. Scheuring 1974
Microbaculispora Bharadwaj 1962 *Microfoveolatispora* Bharadwaj 1962 *Brevitriletes* Bharadwaj & Srivastava emend. Tiwari & Singh 1981	Several species of *Granulatisporites* Potonié & Klaus 1954 *Leiotriletes* (Naum.) Potonié & Klaus 1954 *Lophotriletes* Potonié & Klaus 1954
Scheuringipollenites Tiwari 1973	*Sulcatisporites* Leschik 1956
Vestigisporites Balme & Hennelly emend. Tiwari & Singh 1984 *Sahnites* Pant emend. Tiwari & Singh 1984	*Jugasporites* Leschik emend. Klaus 1963 *Limitisporites* Leschik emend. Potonié 1958 *Illinites* Kosanke emend. Klaus 1964
Playfordiaspora Maheshwari & Banerji emend. Vijaya 1995	*Guthoerlisporites* Bhardaj 1954

A comparative study of several type materials from Europe and India has been done by the authors (Leschik, 1956; Schaarschmidt, 1963; Grebe, 1957; Reinhardt, 1964; Reinhardt & Schön, 1967; Mädler, 1964a, 1964b; Klaus, 1960, 1963, 1964; Potonié & Klaus 1954; Schulz, 1964, 1965, 1967; Mykura & Schön, 1967; Scheuring, 1970; Goczan - P-Tr in Southern Hungary : *Pers. obs.*, 1980; Bharadwaj, 1962; Playford & Dettmann, 1965; Sinha, 1972; Bharadwaj & Tiwari, 1977; Tiwari & Rana, 1980; Tiwari & Ram-Awatar, 1989). It has been a practice that the world-wide occurrence of strate and taeniate bisaccate pollen during Permian-Early Triassic time is explained by the palynologists as a probable result of "parallel evolution". But it has to be kept in mind, that there existed a great latitudinal disparity between the northern and southern floras; the palaeogeographic configuration of continents (Maps 1, 2) of that time had also played a major role in shaping the climatic stress which was instrumental for evolutionary trends. The migration could be effective leading to the occurrences of similar forms in widely separated regions but the time-lapse involved in the movement of vegetation has to be determined for such common occurrences. The important factor was the mother-stocks of the vegetations which were individualistic in the Permian time in each region. Inspite of these situations which favour for a major distinction in two floras of north and south (Euromeria and Gondwana), why it is so that the bisaccate pollen are built on the similar basic plan of architecture? The inherent genetic-push could possibly be the reason. However, because of their seemingly-identical gross features, the significant differences in exine structure and its differential distribution on the corpus, the eusaccate or protosaccate construction of sacci and the manifestation of remnant germinal slit, true sulcus, or saccus-free-area (SAFRA), and saccus-cover were hardly brought to



Map 1— Palynofloral influence lines, 1-S to 4-S in the southern hemisphere and 1-N to 4-N in the northern hemisphere, from equator towards poles, suggesting the areas of general impact of various palynofloras controlled by broad climatic zones during Early Permian time on Pangea. Fine and densely stippled-- Glossopterid regime; coarsely stippled - decreasing effect of southern palynoflora towards equator; Solid circles -- tropical and highly wet equatorial palynoflora; Dot in circle --Euromerian palynoflora. 1-N line marked by short oblique lines, beginning of drier and warmer zone northward; 1-S line, plus-and-dot-mark, southern limit of tropical zone. 2-S broken-line - northern limit of warm temperate with cooling effect from south; 3-S lines with bold dots-in-chain - line of cool temperate to cold climate of the southern region. Rest of the arrows are levels of further changes in climate. The intermixing along Tethyan region, and in general, depicted by symbols, whose density indicates the degree of migration as well (Map adapted from Stanley, 1993).



Map 2 — Palynofloral influence lines in Early Triassic. Symbols as in Map 1. Note the narrowing of southern cool temperate zone and widening of tropical and warm temperate areas, suggesting the beginning of uniformity in the climate. The Tethyan region has more of mixed palynoflora in Triassic than in the Permian (Map adapted from Smith *et al.*, 1994).

light. Obviously, the indiscriminate dumping veiled the differences of finer characters. The problem of superficial form-similarity lies in the simplicity of construction in some of the bisaccate pollen. The gross characters, however, do not provide many chances of distinction in characters, and hence only the saccus-body proportions or the nature of striations were thought to be variables. It is strange that even at the present state of our advanced knowledge of morphography, difference between striations and taeniae is not recognised effectively. It is a significant observation that taeniae are dominant in northern palynoflora and striations in the southern.

The simple trilete spores, all the more, do not have wider degree of character-expressions, hence they are mostly dumped taxonomically even though they are the product of widely separated plant populations of different composition.

The trickling *in situ* records of spores and pollen (Pant & Basu, 1973, 1979; Pant & Nautiyal, 1960; Pant *et al.*, 1985; Grebe & Schweitzer, 1962; Adloff & Doubinger, 1969; Doubinger, 1961; Clement-Westerhof, 1974; Grauvogel-Stamm, 1978) continue to assert the distinctive identities of miofloras when tagged with megafloras. Some interesting occurrences of *Sporae dispersae* taxa in fructifications are examined to drive at the main theme of this article that finer differences in exine and organization of palynomorphs can be effectively utilized in establishing the identity of the otherwise-apparently-comparable forms. Clement-Westerhof (1974) recovered pollen grains-closely comparable to *Jugasporites delasaucei, Lueckisporites virkkiae, Lunatisporites* sp., from cones belonging to *Ullamannia* Göppert 1850. The plant megafossils in that assemblage are assigned to *Ullamannia Pseudovoltzia, Ortiseia* and *Quadrocladus*. None of these elements are so far reported in Gondwana flora. Obviously, the occurrence of the genus *Lunatisporites* in the Indian assemblage has to be sceptically reassessed; it has a chance of being unrepresented in the Gondwana sequence. And this has presently been identified and confirmed on the basis of sexine structure. Similarly, Tiwari and Singh (1984) have established that *Jugasporites, Limitisporites* and *Illinites* (cf. Grebe & Schweitzer, 1962) do not occur in Gondwana palynofloras. The typical northern forms of this group of pollen have an island of unstructured exine (i.e., nexine) which bears a slit on the proximal polar region of corpus (Pl. 1, figs. 1-7). These forms were earlier recorded in the cone of *Ullamannia frumentaria* by Grebe and Schweitzer (1962, pl. 6, figs 1-15). Beside other forms, *Illinites kosankei* Klaus 1964 was recovered in the cone of *Aethophyllum* by Grauvogel-Stamm (1978). Later, *Illinites* was proved to possess laterally situated two tenuitates (Jansonius & Staplin, 1962). However, the taxa *Jugasporites, Limitisporites* and *Illinites* were continued to be identified in the Indian as well as Australian palynofloras of Permian age, although *Ullamannia* or *Aethophyllum* has never been recorded. The identity is now established on the basis of exine character of the corpus in these taxa, and similar-looking forms from Gondwana (Pl. 2, figs 1-5) are referred to *Vestigisporites* and *Sahnites* (Tiwari & Singh, 1984).

The recognition of *Satsangisaccites* in *Nidistrobus* and *Lelestrobus* (Bose & Srivastava, 1973a, 1973b; Srivastava, 1984) and other *in situ* saccate pollen (comparable to dispersed pollen) in typical Gondwana fructifications (Pant *et al.*, 1985; Pant & Basu, 1973), is an indication that the very basic identity of Gondwana dispersed spores and pollen lies in the aspect of floral provinciality and structural diversity.

This contention has been reinforced by precious data on plant megafossils (Chaloner & Meyen, 1973; Meyen, 1972, 1987; Chaloner & Lacey, 1973; Lacey, 1975; Lele, 1961, 1976; Maithy, 1974; Chandra & Chandra, 1988; El-Khayal & Wagner, 1985; Srivastava, 1992) by which the delineation of *Glossopteris* flora *vis-a-vis* other floras has become more effective. An overview of the Permian floral community of typical Gondwana and those of Euromerian and Angarian region clearly identifies the basic differences in the major components of the population. The Lower Gondwana flora is characterized by the prominence of *Glossopteris, Gangamopteris, Vertebraria, Rubidgea, Palaeovittaria, Rhabdotaenia, Pteronilsonia, Trizygia, Raniganjia, Barakaria, Gondwanophyton, Damudopteris, Paranocladus, Buriadia*, etc. Most of these forms are restricted to the Gondwana region. Their complexity, proliferation and dominance remain significant inspite of the fact that sporadic occurrences of a few genera belonging to northern regions may be recorded in the southern region, and *vice versa*.

The panorama of Euromerian flora is different. There, the Carboniferous elements such as *Sigillaria, Calamites, Cordaites, Lebachia, Ernestiodendron, Ullamannia, Pseudovoltzia, Sphenobaiera* and several others continued into the Permian. In the Upper Permian there were two plant associations in the north, a hygrophylic *Neocalamites*-sphenopterid association and a xerophytic *Callipteris*-conifer association (Schweitzer, 1986). True *Calamites* are not known from India. Basically Indian Gondwanic ferns are distinct from the Euromerian ferns, and Cordaitales are also supposed to be different. In Angaraland also, the endemic Carboniferous plants continued into the Permian. The genera *Paragondwanidium, Angaridium, Angaropteridium, Viatscheslavia, Angarodendron, Demetria, Rufloria, Tschernovia, Phyllopitys, Paraschizoneura, Umbellaphyllites, Zamiopteris, Vojnovskya*, etc., are the supporters of a different pool of plant-group, grossly in contrast with the Gondwanic floras.

The *Sporae dispersae* produced by such a vegetation must reflect the identity of their mother plants. With more and more distinctions being recognised in the mother megafloras, the basic individualities of microfloras must be recognized. However, this never intends to mean here that there exists a total differentiation, or no mixing of forms has taken place (see Vijaya & Tiwari, 1991). But it is intended positively that the characters in the widely unrelated spores and pollen population have to be sought for their distinctiveness, inspite of Apparent Form Similarity (AFSIM) in superficial matching. AFSIM is a factor which simulates gross similarity, although finer differences are present. The conservation of certain characters inherited from the remote past appears to be the cause of AFSIM, yet the differences are manifested at a much finer level of structure. We are aware that the *in situ* records are still meagre, which could otherwise make a more sound basis for such an approach.

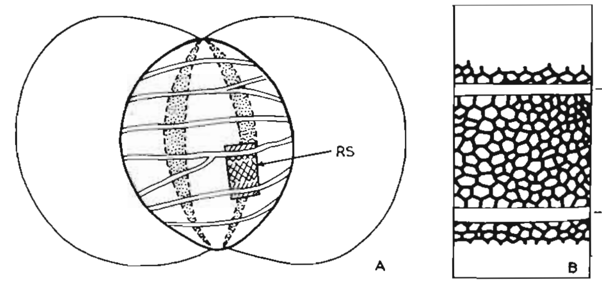
THE APPROACH

The mechanism of sporopollenin deposition on the primary walls of spore and pollen in the initial stages of development is controlled by genetic material of the cell-contents which guides the pattern of exine sculptures as well as structure. The cell-inclusions (e.g., endoplasmic reticulum, or mitochondria) located at peripheral cytoplasm and the plasma membrane exert a possible influence on the specific patterning of exine (Heslop-Harrison, 1973; Skvarla & Larson, 1966; Larson, 1965). Further in the tetrad, the callose wall dissolves to release the microspore in isolation, hence the information concerning the ultimate exine morphology must reside in the isolated microspore. The structural characters of sexine in the gymnospermous pollen of extant plants show differences in the nature as well as finer pattern; the sexine in this case is rod-bearing or tegillate but their nature is variable in Coniferae characterising for generic group (Ueno, 1960a, 1960b).

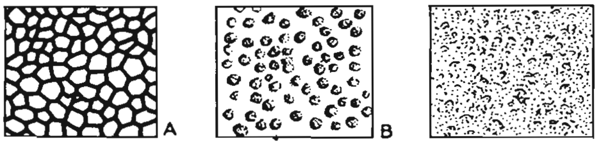
It is, therefore, derived that the dispersed palynomorphs produced by basically different floras may apparently look similar in gross morphography of form, shape, size, etc. (i.e., form-similarity), but the key of their identity lies in their exine structure which is the finer expression of their genetic character operating through distinct groups of plants. Thus the gross characters alone may be elusive to decide the individuality of palynofossil groups.

The following basis, which exhibited differential lineage in morphography, has been formulated for discussion.

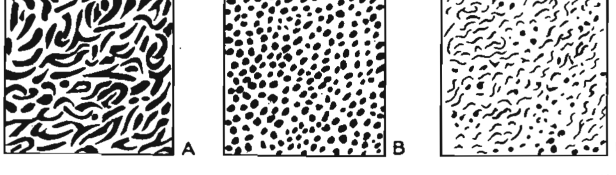
Exine structure — The central body, or the corpus, of saccate pollen possesses varied types of infrastructures in sexine. The Gondwana pollen exhibit mostly microinfrareticulate structure constituted by perfect muri and complete meshes giving rise to a network of fine nature (e.g., *Faunipollenites, Crescentipollenites, "Lunatisporites"*, Pl. 3, figs 1, 2, 4, 6); the uniformly wide muri, enclosing fine meshes of polygonal- variant shapes and sizes can be identified by L-O analysis (Text-figure 1). In few groups of pollen infrapunctate structure is also found, e.g., *Lahirites* (Bharadwaj, 1962; pl. 12, fig. 172). The genus *Striatites* as interpreted by Bharadwaj (1962) possesses microverrucose sculpture. Thus, there are three main patterns of exine characters mainly perfect infrareticulum, rarely infrapunctation or microverrucose sculpture (Text-figure 2). On the other hand, it has been observed that in several of the striate, taeniate and non-striate saccate pollen groups from the Euromerian Permian and Triassic have basically different lines of structure pattern. In these cases, the infrastructure of the cappa, or taeniae, mostly consists of relatively big faceted, rounded in outline or variably-shaped, island-like elements, vermiculae, grana, ridge-shaped, columnoid exinal elements which are connected in subtectum, imparting a look of channel or drainage system. In some cases, these elements could be regular, irregular, compact, partially fused or discrete (Pl. 3, figs 3, 5). Imperfect reticulum with hanging or isolated muri may also make the structure of cappa, but it is highly irregular and a broken system of meshes (Text-figure 3). In case where relatively bigger exinal elements are seen in the subtectate region, they impart a pattern of wavy, irregular, prominent bodies placed in irregular manner but closely packed leaving narrow inter- elemental spaces which look like interconnected channels. The variation of this basic structure is seen in fine elongated, irregular, simple or bifurcated ridges, rodlets, or even granulose internal structures, e.g., *Taeniaesporites noviaulensis* Leschik 1956 (Text-figure 4c; Pl. 3, fig 3). This array of subtectate exinal elements is termed here as *"infravermiplexate"* because no other term satisfactorily defines the variations observed (Text-figures 3, 4). The infravermiplexate structure of exine is not at all the typical "reticulate network-like" structure having meshes constructed by perfect muri in the subtectate region. However, as stated above, there are a very few pollen taxa in



Text-figure 1 — Details of infrareticulate exine structure, on the cappa of saccate pollen, generally occurring in Gondwana palynomorphs; A, Proximo- distal view of *Crescentipollenites* — a rectangular sector (RS) marked to enlarge in; B, showing ideal infrareticulum, portions of two striations (S) and their relationship (upper and lower part of rectangle left unfilled).



Text-figure 2 — Main characters of exine on cappa in saccate pollen generally found in Gondwana; A, Infrareticulate (most common); B, Infrapunctate (structured as pits C, Microverrucose (sculptured as chagrinate or microverrucae as in *Striatites*).



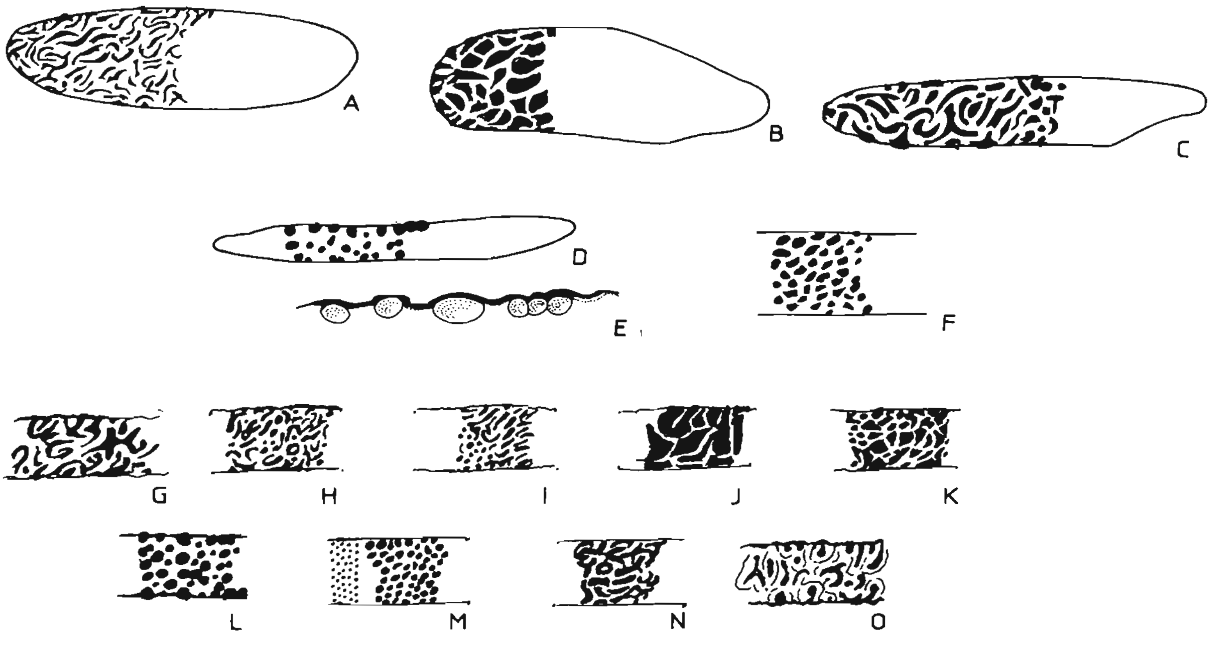
Text-figure 3 — General pattern of exine structure in cappa of saccate pollen of Euromerian Permian and Triassic; A, Infravermiculate; B, Infragranulose to infraverrucose; C, Fine ridges and dots as infrastructure.

the northern assemblages also, which have fine infrareticulation or infrapunctation in the cappa. But in case of Gondwana pollen, the perfect infrareticulation is a rule, rather than an exception.

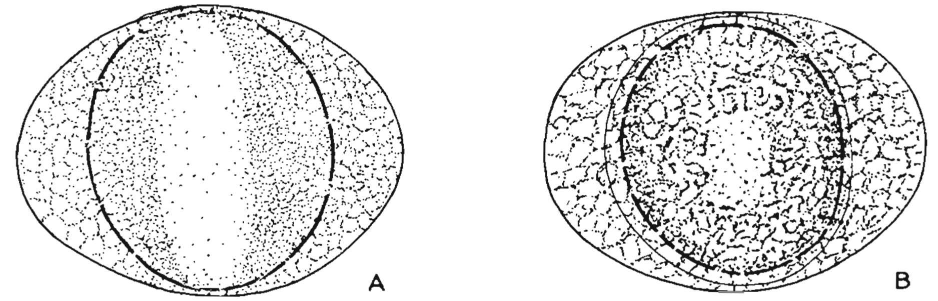
The distinction in the above mentioned two lineages of structures is so perfect that it can be easily identified under oil-immersion objective. In this respect it is important to note that from the Lower Permian of Son Valley Gondwana Basin, Lele and Maithy reported a monosaccate pollen genus *Rugasaccites* (Lele & Maithy, 1969; pl. 1, figs 7-11; pl. 2, figs 13-17; p. 300) which possesses a structureless to faintly infrapunctate sexine but with a sculpture of low vermiculae on both the faces of the body. This type of sculpture never occurred in the Upper Permian pollen, and morphographically it appears to be a primitive character-state. With the trend of sexine character in European forms, the Son Valley taxon makes an entirely distinct line of specialization because in the former, the elements are subtectate (*structure*) while in the latter we are dealing with the supratectate pattern (*sculpture*). Further, in the species of *Striatites* from Gondwana (Text-figure 2C), the exine of the body has chagrinate to microverrucose sculpture (Bharadwaj, 1962).

Cappa — Cappa is the cap-like sexinal layer developed over the corpus of a saccate pollen. The sexine on cappa is normally reduced, but relatively speaking, this character is generally prominent in the northern forms (Pl. 10, fig. 1), e.g., taeniae in *Lunatisporites* Leschik 1955, *Lueckisporites* Klaus 1963; cappa in *Cristatisaccus, Alisporites* in Mädler, 1964a. In laterally preserved specimens, the comparison between Gondwanic and European forms can be better demonstrated. In Gondwana Permian pollen, it has been observed that not much prominent, flabby or inflated layer of sexine (Pl. 2, figs 1-5) develops over the nexine on body surface (Text-figure 5A). The difference in the nature of exine structure described above appears to be responsible for manifesting remarkable prominence in the cappa of northern forms where subtectate exinal elements are well developed, irregular and varied.

Striations and taeniae — These two characters are basically different from each other (Text-figure 6); striations are very narrow, furrow-like linear grooves, with regular and evenly uniform, less than 0.5 µm width all



Text-figure 4 — Details of "Infravermiplexate" structure of exine --- collectively showing the array of variation; **A** and **B**, range of size and shape in vermiplexate structure; **C**, *Taeniaesporites noviaulensis* Leschik 1956, Holotype, pl. 22, fig. 1; **D**, *Taeniaesporites antiquus* Leschik 1956, Holotype; **E**, enlarged view of **D** to show exinal subtetate elements at taeniae margin which make it wavy; **F**. *Illinites unicus* in Leschik 1956; **G** to **O**, in relatively low magnification; **G**. *Crustaesporites globossus* Leschik 1956, Holotype; **H**. *Falcisporites zapfei* Leschik 1956, pl. 22, fig. 7; **I**. *Sulcatisporites* sp. Leschik 1956, pl. 22, fig. 29; **J**. *Sulcatisporites spendens* Leschik 1956, pl. 22, fig. 10; **K**. *Lueckisporites virkkiae* Leschik 1956, pl. 21, fig. 17; **L**. *Taeniaesporites antiquus* Leschik 1956, pl. 22 fig. 4; **M**. *Labiisporites granulatus* Leschik 1956, pl. 22, fig. 12; **N**. *Falcisporites*, specimen in Pot. & Kl. 1954; **O**. *Strotersporites jansonii* in Klaus 1963, pl. 10, fig. 74.

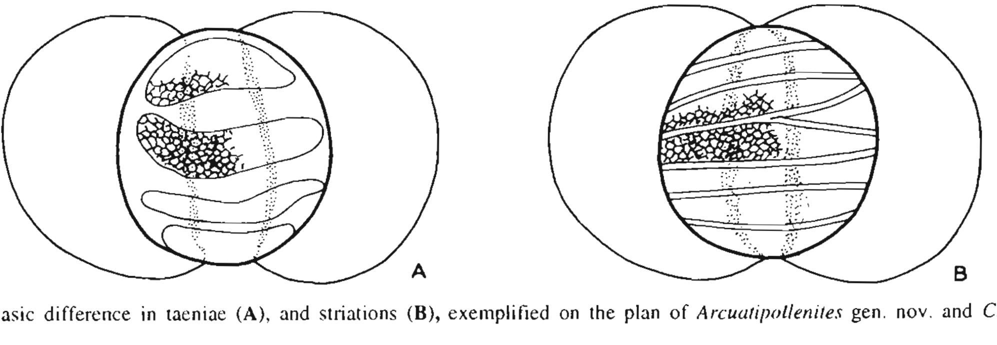


Text-figure 5 — **A,** *Krempipollenites* gen. nov. showing full length merging SAFRA without a median weaker zone (Body structure finely infrareticulate — not shown in figure); **B,** *Klausipollenites,* line drawing based on Holotype (Potonié and Klaus 1954, pl. 10, fig. 7) and other European specimens to sho distal encroachment of sacci from all sides of body resulting into the formation of circuloid diffused SAFRA (compare 5A).

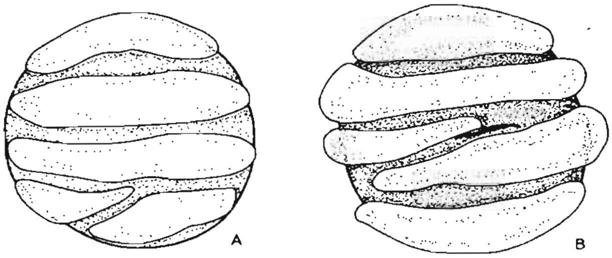
along their length (Pl. 4, figs 1, 3; Text-figures 1, 6B, 14), while the taeniae are the irregularly wide strips or bands of sexinal material (Pl. 4, figs 2, 4; Text-figures 6A, 7, 9, 10) leaving unevenly broad, one to several micron wide unstructured "paths" of nexine between them (Tiwari, 1982; *Platea* termed by Vijaya, 1990). During the examination of various materials by the present authors, a line of distinction has been identified that although in the European taxa true striations are also found (Pl. 3, fig. 5), e.g., *Fevisporites tenuis* Leschik 1956; *Striatites keuperi, Mesostriatites hercynicus* and *Thuringisaccus multistriatus,* all in Mädler 1964a, and species of *Strotersporites* Wilson 1962, but in majority of the cases they are not linear furrows with uniform width, viz., *Lunatisporites (Taeniaesporites) noviaulensis,* in Leschik, 1956, pl. 22, figs 1, 2; *Striatites* in Schaarschmidt, 1963, pl. 14, figs 6, 8. In a few cases they may appear to be "striate" but the grooves have irregular width along their length, e.g., *Strotersporites jansonii, S. wilsonii, Striatites angulistriatus, S. marginalis, S. minor,* all in Klaus, 1963; Ineffect they are also taeniate forms but with narrower "paths", between wide sexinal strips, which, however, are not uniformly linear.

The northern taeniate pollen generally possess very well developed, flabby and inflated, prominently raised taenial bands with massive appearance (Text-figure 7B; see Scheuring, 1970, 1978). Such elevated bands have obviously been resulted from the prominent subtectate exinal elements termed here as infravermiplexate, e.g., *T. noveaulensis* in Leschik, 1956. On the contrary, the taeniae in Gondwanic Permian-Triassic pollen, so far assigned to *Lunatisporites* or *Lueckisporites,* are generally less pronounced, not massive, or feebly inflated (Pl. 3, fig. 6; Pl. 9, figs 1-10; Pl. 10, figs 4-8; Text-figure 7A).

Slit on the body — The striate and taeniate pollen of Gondwana palynoflora normally do not possess a slit or a germinal mark, e.g., *Faunipollenites, Crescentipollenites, "Lunatisporites".* If at all a seemingly comparable feature is present, that too in very rare cases, it is either a compressional fold, a slight widening of a median striation for a short stretch of its length, or a vague linear opening between two taeniae; such features are not related with well defined mono-, bi-, or trilete mark. Besides, certain pollen have been reported to possess a monolete mark (Lele & Karim, 1971; pl. 3, figs 32, 33) but in these cases such a mark is located on the sexine of central body, and not on the nexine. In other



Text-figure 6 — Basic difference in taeniae (**A**), and striations (**B**), exemplified on the plan of *Arcuatipollenites* gen. nov. and *Crescentipollenites,* respectively.



Text-figure 7 — A, Nature of less inflated taeniae (Gondwana) and B, more inflated, prominently raised taeniae (European); prominent monolete on nexinal path shown (M).

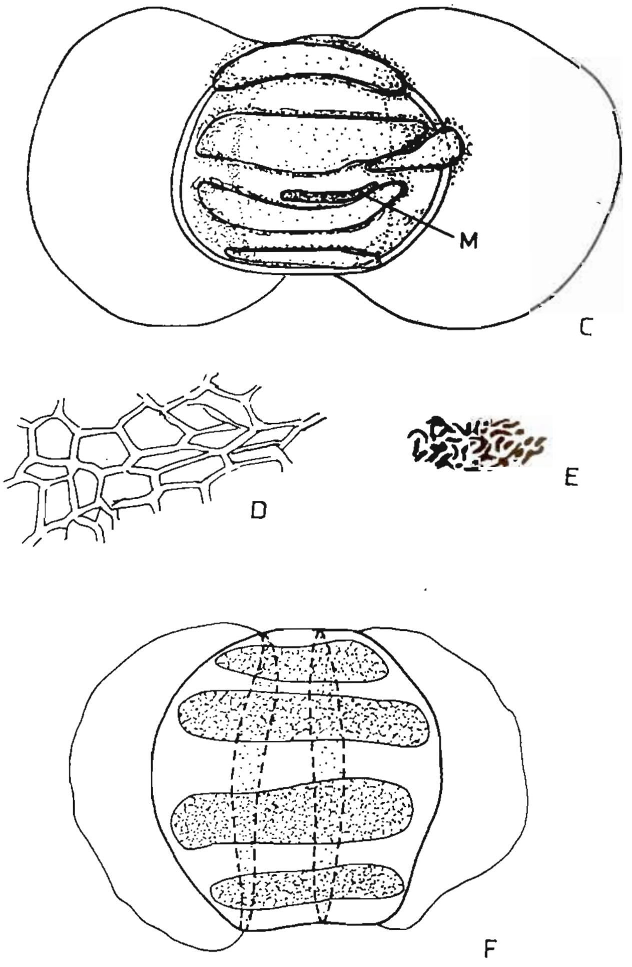
cases, the mark-like opening has resulted from the rupturing of exine along a striation, simulating a monolete mark (Lele & Karim, 1971; pl. 3, fig. 34). The typical striate grains with median striation simulating a monolete mark are also present in the Gondwana material, but they are very rare and may be compared to *Strotersporites* Wilson 1962 for this character.

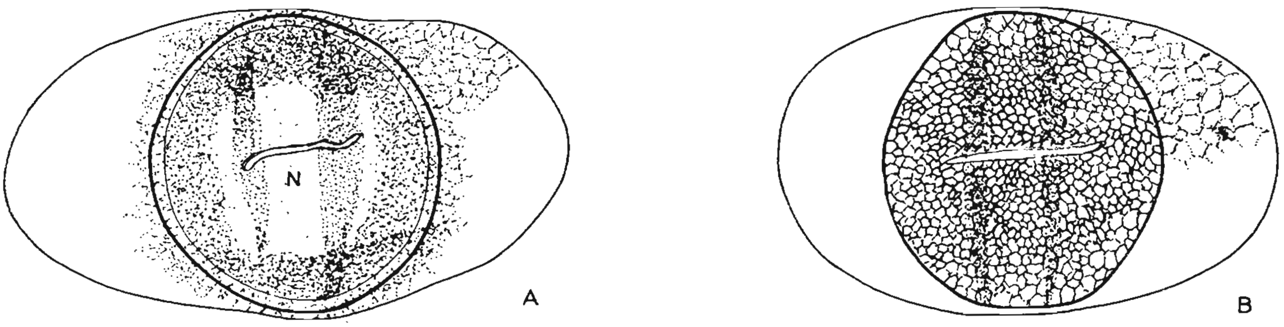
In the pollen of comparable configuration from the northern floras, a distinct slit occurs in a number of simple and striate/taeniate taxa (*Limitisporites, Lueckisporites, Lunatisporites, Strotersporites, Striatites* spp.). Such a mono-, bent mono-, or reduced trilete mark, short and vestigial remnant of proximal functional germinal aperture is situated on the nexinal layer, and not on the sexine (Pl. 1, figs 1-7; Text-figures 8A, C, 11A). This can be very well ascertained in *Lueckisporites virkkiae* Potonié & Klaus 1954 (pl. 10, fig 3) and *Strotersporites* Wilson 1962 (pl. 2, fig 1). Jansonius (1962) and Scheuring (1970, 1978) have very rightly emphasized the importance of such a mark in morphotaxonomy. The continuance of the slit in time is a dragging primitive tendency in the pollen of northern hemisphere, while their general absence is an advanced step of evolution in the southern hemisphere.

In non-striate and non-taeniate genera, the presence of mono-, bi-, or trilete mark on the sexine-free central region of the nexine in *Limitisporites, Jugasporites* and *Illinites,* respectively, has been effectively demonstrated (Tiwari & Singh, 1984). In *Sahnites* and *Vestigisporites* the mark is situated on the sexine of the cappa, as there is no sexine-free region in these Gondwanic pollen (Pl. 2, figs 1-5; Text-fig. 8A, B).

Differential sexine development — Almost all the pollen groups of Glossopterid origin have a uniform development of sexine all over the Cappa (proximal face) of the central body (e.g., *Vestigisporites, Sahnites,* etc.; Pl. 2, figs 1-5). This means -- it is never absent from, or ill-developed in, any region of the surface of corpus. In contrast to this phenomenon, several similar-looking pollen taxa of the northern flora possess differential distribution of sexine, that means, the exine has not developed a structured layer in some areas, mostly in the central portion of the cappa (Pl. 1, figs 1-7; Text-figure 8); the example can be cited in *Jugasporites, Limitisporites, Illinites*-group (see Tiwari & Singh, 1984), and *Gardinasporites* Klaus 1963.

Saccus — The protosaccate (saccus filled with alveoli) construction of sacci occurs in the pollen of Permian and Triassic times (Scheuring, 1974; Tiwari, 1981). The details of saccus structure have not been given due importance so far, except by Scheuring (1970)





Text-figure 8 — Comparative characters in **A,** *Limitisporites rectus* Leschik 1956, pl. 1, fig. 15 — Central region of body develops no sexine and bears a monolete on nexine (N); **B,** *Salnites* Tiwari & Singh, 1984, body develops sexine all over the body surface proximally with a monolete mark; nexinal island not present (compare 8A); **C,** *Lunatisporites noviaulensis* Leschik 1956, Holotype showing well defined monolete on the inter-taenial nexinal path (M); **D,** Saccus structure with coarse infrareticulation; **E,** Sexine structure of taeniae; **F,** *Arcuatipollenites ovatus* (Goubin) comb. nov. — no mark present.

who discovered the protosaccate condition in Triassic pollen, but further studies by him (Scheuring, 1978) have revealed that *Lunatisporites acutus* and *L. noviaulensis mollis* are not protosaccate pollen, as they have a cavity in the sacci forming a true saccate organization (eusaccate). On the other hand, the striate and taeniate pollen from the Permian and Triassic Gondwana had a protosaccate fill in the saccus (Pl. 3, figs 1-2, 6; Text-figure 9). Such important differences in morphology were masked due to the delayed conceptual understanding, which led to indiscriminate dumping. Recently, Vijaya (1995b) has opined that *Playfordiaspora* is a eusaccate pollen (Pl. 6, fig. 3) , and Tiwari, Vijaya and Ram-Awatar (1995) have proposed that *Protoeusaccites* gen. nov. is a transitionary bisaccate pollen where cavity has just started to be formed (Pl. 5, fig. 3).

The continuity (or discontinuity) of saccus-covering, with alveolar or endo-reticulate structure, on to the proximal or distal face of corpus gave initial clue to identify *Parasaccites-Plicatipollenites*- group (Pl. 5, fig. 1) from *Nuskoisporites*- group (Lele, 1964; Bharadwaj & Tiwari, 1964). Recently, *Cordatina* has also been identified to differ from the above mentioned genera on the basis of its construction and saccus-like sexinal covering (Pl. 6, fig. 1) adhering to the body (Vijaya *et al.*, 1988). Further, it has been observed that the northern palynoflora contains several groups of pollen with saccus covering on to the body having a continuity of coarsely aloveolate structure, e.g., species of *Triadispora, Gardinasporites*, etc. The relative displacement of central body with respect to saccus outline in flattened specimens determines the degree of attachment-continuum of saccus layer with the body. In the Gondwanic pollen, the comparable configuration is also known, e.g., *Densipollenites, Playfordiaspora* (Pl. 6, figs 2, 3).

Organization or the Bauplan — The secondary features, such as infold system, body shifting, common

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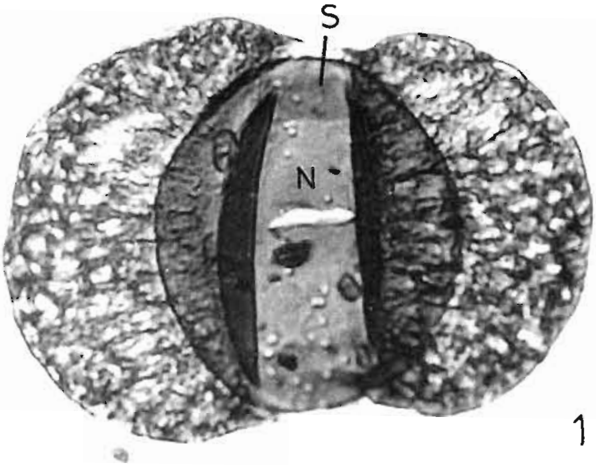
PLATE 1 ⟶

All specimens illustrated in Pl. 1 are from the Zechstein of Europe, to show differential development of sexine on central body, and presence of slit in nexine.

1. *Limitisporites latus* Leschik, 1956; Holotype in proximal view to show monolete mark on nexine (N), and sexinal bands (S) at two lateral regions of the body. x 775.
2. A portion of the specimen in fig. 1, enlarged to highlighten infragranulose sexine structure (S) at the lateral regions on central body and its merger with sacci (M), leaving nexinal part (N) free in the centre with a monolete mark; in proximal view. x 2000.
3. Central body of the specimen in fig. 4, enlarged to show infragranulose structure in sexinal bands (S) at the lateral regions on the central body merging with sacci; proximal view. x 2000.
4. Holotype of *Ilinites spectabilis* Leschik, 1956; pl. 21, fig. 7, in proximal view to show presence of trilete mark in the nexine (N); and sexinal bands seen at slightly lower focus. x 1000.
5. Holotype of *Limitisporites rectus* Leschik, 1956; pl. 21, fig. 15, in proximal view to show sexine (S) at lateral regions on the central body and a monolete mark in nexine (N). x 1000.
6. Holotype of *Illinites purus* Leschik, 1956; pl. 21, fig. 6; showing encroachment of sacci (S) independent of folds, trilete mark on nexine. x 1000.
7. Specimen of *Jugasporites delasaucei* in Leschik, 1956; pl. 21, fig. 11; in median focus exhibits distinct monolete mark on nexine, (sexinal band at lateral regions on the central body (not in focus); proximal view. x 1000.



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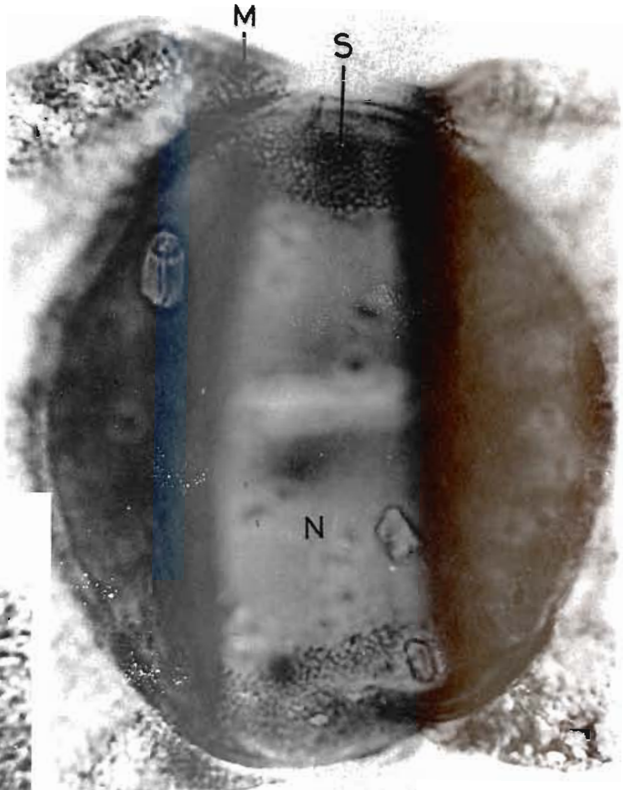

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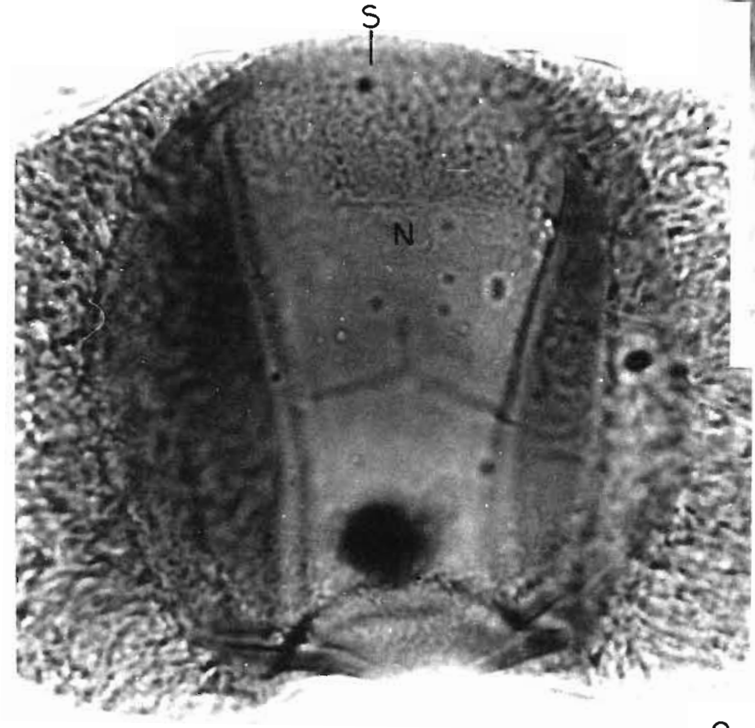

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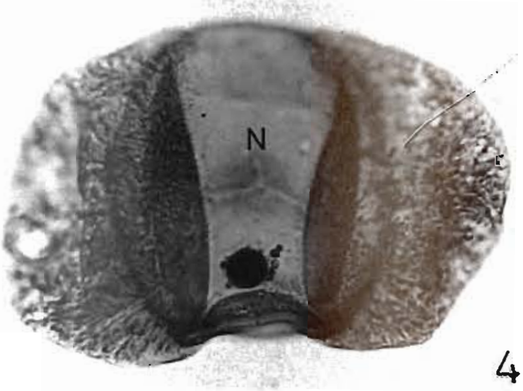

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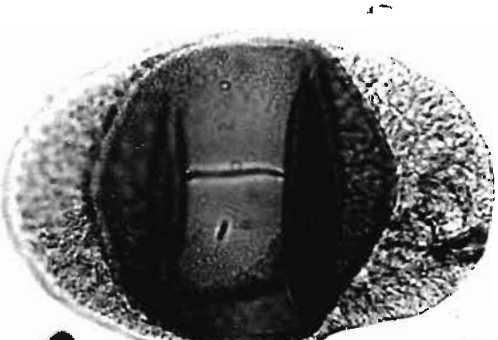

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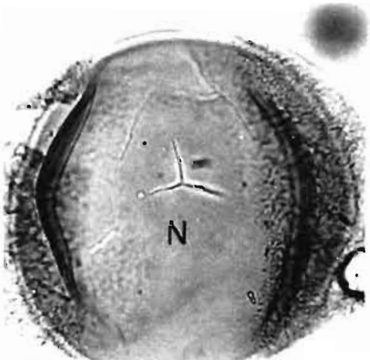

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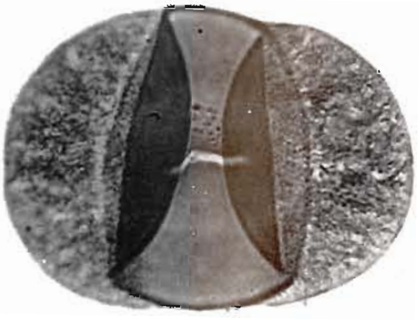

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PLATE 1

orientation in plane of flattening, etc., in fossilized spore-pollen are predetermined by three-dimensional organisation or "Bauplan" of the specimen in its original form. When folds of a particular pattern are consistently found in a large number of specimens of a coherent population, they cannot be set aside as mere preservational artefacts. Thus, the ring-forming or polygonal infold-system in *Plicatipollenites* Lele 1964, or set of lunar body folds along the distal zones of sacci attachment in *Crescentipollenites* Bharadwaj, Tiwari & Kar 1974 (Text-figure 1A); *Sahnites* Pant emended Tiwari & Singh, 1984 (Text-figure 8B); *Protoeusaccites* Tiwari *et al.*, 1995, are the manifestation of the pollen body-shape in 3D which on flattening accommodates the extra wall-space and gives rise to regular pleats in the nexine (Pl. 5, figs 1-3). The absence of such compensatory folds in *Parasaccites* and *Lahirites*, for example, is also equally significant because it indicates that originally the proximal-distal axis of the body is not long and the body could be lensoid in shape in meridional view. By extrapolation, therefore, the organization of plant microfossils can be reconstructed. Similarly, the folds along the three trilete rays of a trilete mark, having otherwise low vertex or thin labra, expresses the raised nature of the contact region near the mark (e.g., *Varitrileti*-group, *see* Tiwari & Singh, 1981).

Tenuitas — The true sulcus or its equivalent structure has been demonstrated to be very useful criterion for sorting out finer morphographic identity (Scheuring, 1970). The tenuitates are identified with careful observation as they are not always delineated (e.g., lateral tenuitates in *Ovalipollis*, by Scheuring, 1970, and in *Illinites* by Jansonius & Staplin, 1962; and circumpolar tenuitas in *Barakarites* by Foster, 1979). In bisaccate pollen, the distal saccus-free-area (SAFRA) may or may not represent a true sulcus. In several Gondwana saccate pollen, the true sulcus, i.e., thinning of the exine with a channel-like depression forming a groove (*Falcisporites*), or a weak zone (*Klausipollenites* in Jansonius, 1962), is generally rare.

The distal saccus-free-area in the earliest Permian monosaccates of Gondwana is not a sulcus (Vijaya & Tiwari, 1992), but as we go up in time, similar forms with thinner and depression-like unstructured distal area simulating a sulcus-like organization are found. The nature of sulcus in the Permian and Triassic pollen must be ascertained by examining the thinning, and groove-like nature of unstructured exine in the distal saccus-free-area (Pl. 5, figs 2, 3). It is very important to differentiate between the saccus-free-area (SAFRA) and a true sulcus (Venkatachala, Tiwari & Vijaya, 1994).

MORPHOTAXONOMY

The areas to be explored for intensive study are suggested above. These lines of thinking lead to the concept of Apparent-Form-Similarity factor (AFSIM-factor) which is based on the analysis that in similar-looking pollen forms real differences can be sought in their exine structure, development of cappa, nature of striations and taeniae, presence or absence of a monolete, bilete or trilete slit on the body, its location on sexine or nexine, differential development of sexine on the proximal body face, saccus covering on to the body, protosaccate or eusaccate nature of the saccus, nature of the distal SAFRA, presence or absence of true sulcus and tenuitas, and the organization as resolved by the compensatory secondary folds consistently found in the form of lunar, lanceolate or of other configuration in the nexine of compressed specimens.

The above concept has been exemplified by two taeniate and one nonstriate, bisaccate pollen taxa of the Indian Permian and Triassic Gondwana assemblages, which were so far described under *Lunatisporites*, *Lueckisporites* and *Klausipollenites*, and are now differentiated from these northern taxa.

For these forms following new names have been proposed :

1. *Arcuatipollenites gen. nov.* (based on some species assigned so far to *Lunatisporites* Leschik 1955).
2. *Dicappipollenites* gen. nov. (based on some species assigned so far to *Lueckisporites* Potonié & Klaus 1954).
3. *Krempipollenites* gen. nov. (based on some species assigned so far to *Klausipollenites* Jansonius 1962).

Arcuatipollenites gen. nov.

Synonym

Species described under following genera from the Late Permian and Triassic of Gondwana :

1955 *Lunatisporites* Leschik emend. Scheuring 1970
1955 *Taeniaespoites* Leschik
1965 *Taeniaesporites in* Goubin
1965 *Protohaploypinus in* Goubin

Type species — *Arcuatipollnites ovatus* (Goubin, 1965) comb. nov.

Generic diagnosis — Bisaccate pollen. Corpus proximally bearing three or more taeniae extending fully or partiall along its terminal axis. Sexine of taeniae showing mostly finely infrareticulate structure formed

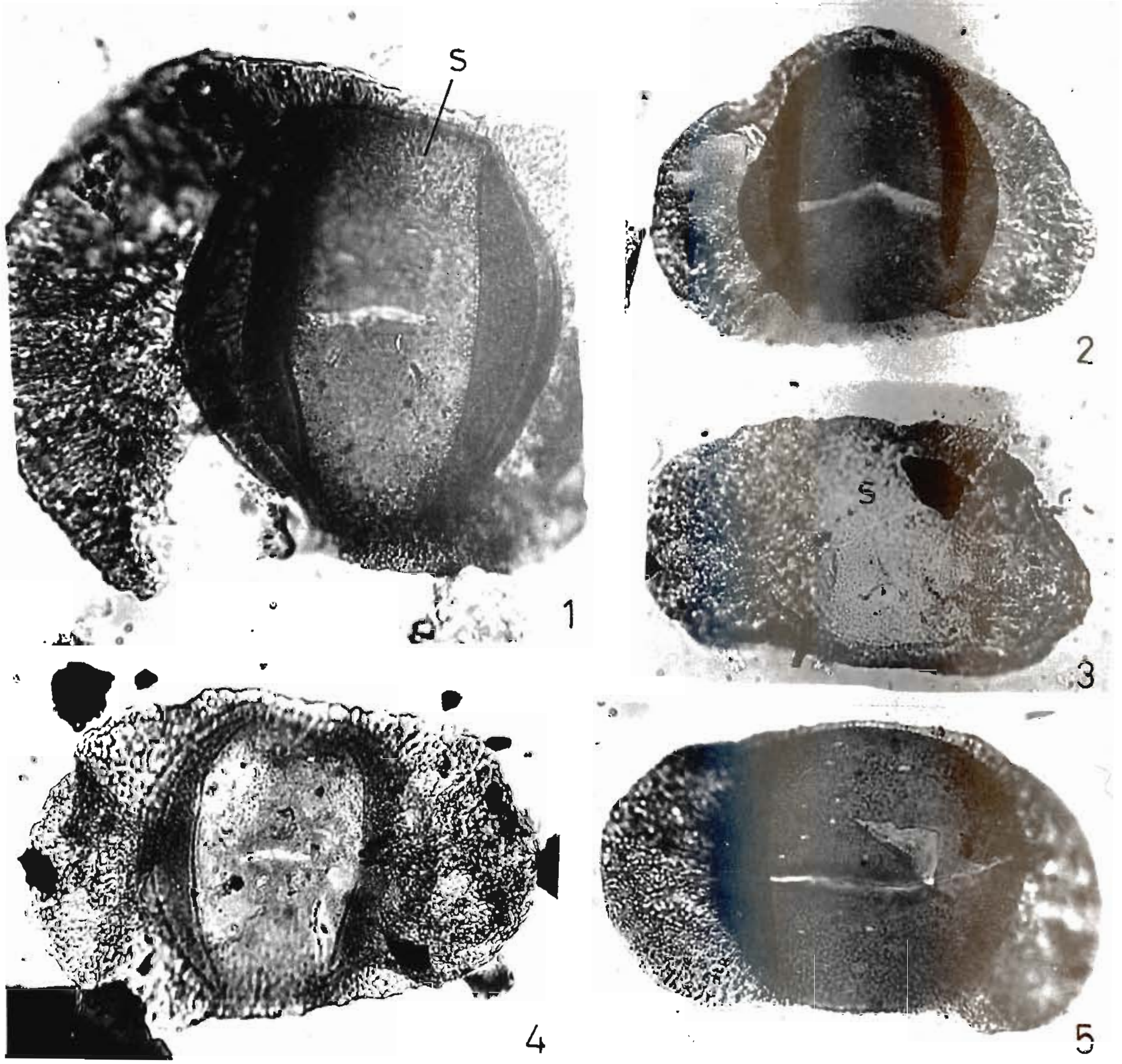


PLATE 2

Sahnites Pant emend. Tiwari & Singh 1984, and *Vestigisporites* B & H. emend.

1. Tiwari & Singh 1984 showing uniform development of finely infrareticulate sexine (S) all over the central body, and the presence of a monolete or bilete mark on it.

1, 4. *Sahnites barrelis* (Tiwari) Tiwari & Singh 1984. x 1000, x 750. BSIP Slide no. 3993, 8415.

2. *Sahnites jayantiensis* (Lele & Karim) Tiwari & Singh 1984. x 750. BSIP Slide no. 4003.

3. *Vestigisporites* rudis Balme & Hennelly 1955. x 500.

5. *Sahnites methois* (Hart) Tiwari & Singh 1984. x 750. BSIP Slide no. 3993.

by complete muri enclosing perfect meshes resulting into a net-like infrastructural pattern; inter-taenial spaces (platea) variedly and unevenly wide, exhibiting nexine. No mark or slit present on taenae or on inter-taenial nexinal spaces. Sacci poximally attached to equatorial or slightly within the region of corpus, distally inclined encroaching the distal area leaving well delineated SAFRA extending over full-length along lateral axis of the corpus; lines of sacci attachment on distal side accompanied by feebly or prominently developed lunar or lensoid folds; no germinal furrowor weaker zone developed between two folds in the SAFRA, but partially unstructured exine may be seen in the centre. Sacci alveolate with protosaccate-fill having muri and meshes of varied sizes.

Comparison — *Arcuatipollenites*, being a taeniate form (*sensu* Vijaya, 1990), excludes comparisons with striate pollen genera *Crescentipollenites, Striatites, Faunipollenites*, and others. In apparent-form-similarity this genus compares with *Lunatisporites* Leschik emnd. Scheuring 1970. Detailed morphographical analysis of *Lunatisporites* by Scheuring (1970, 1978) has established that the type specimen as well as other specimens of that population from the type material bears a well defined monolee mark on the central nexine pth. This slit may be variabe in nature, placement or prominence but it is almost invariably present in the central inter-taenial pathway (i.e., platea, *see* Vijaya, 1990) where exine does not show any structure. The occurrence of a slit, a remainié of the once-a-functional aperture, in *Lunatisporites* Leschik 1955 is the conservation of a character in evolution. The proximal mark is the indicator of proximal germination (viz., very well defined in *L. noviaulensis*) but even when the germination polarity has shifted distally, this relic remains in the northern forms. Obviously, its absence from the comparable pollen from Late Permian and Triassic of Gondwana (*Arcuatipollenites* gen. nov.) is a distinctive line of morphology.

Arcuatipollenites further differs from *Lunatisporites* because it has been established that the type species *L. acutus* and *L. noviaulensis mollis* show a hollow saccus, i.e., they are eusaccate (Scheuring, 1978, pp. 60-62, pl. 30, figs 424-440; pl. 31, figs 441-445). Also, the type specimen of *Lunatisporites noviaulensis* Leschik 1956 (pl. 22, fig 1, here illustrated in Pl. 7, figs 1-3) is a eusaccate pollen. On the other hand, *Arcuatipollenites* includes protosaccate pollen with complete fill of alveoli in the saccus. Even without the TEM study, this feature can be identified through L-O analysis (Scheuring, 1978; here Pl. 8, figs 1, 2).

The structure of taeniae in the genera under discussion is basically not the same and the pattern of differentiation is obvious. In *Acuatipollenites* the infrareticulation is extremely fine, regular, complete or perfect with uniformly 0.5 µm wide muri and 0.5 µm across polygonal, circuloid or radially elongated meshes (Pl. 8, figs 1-3; Text-figure 9). However, our analysis and study of several specimens of *Lunatisporites* from the type material from Europe (Leschik, 1956; Schaarschmidt, 1963; Clarke, 1965; Visscher, 1971; including the holotype of *Taeniaesporites noviaulensis* Leschik 1956) has revealed that the structure of taeniae is different from that of the Gondwana forms; the sexine is not perfectly and uniformly infrareticulate but with a difference in overall composition of exinal elements in the subtectate region. The infrastructure in the taeniae of

PLATE 3 →

Specimens illustrated to highlighten the nature of sexinal elements in body-exine structure in the striate and taeniate bisaccate pollen found in Euromerian and Gondwanan regions.

1 A bisaccate pollen frm Early Permian of Gondwana, having thin nexine (*Faunipollenites*), and narrow linear grooves (striations) on proximal face of body which get merged laterally; exine structure between these grooves is finely infrareticulate, a character of Gondwana pollen. x 750.

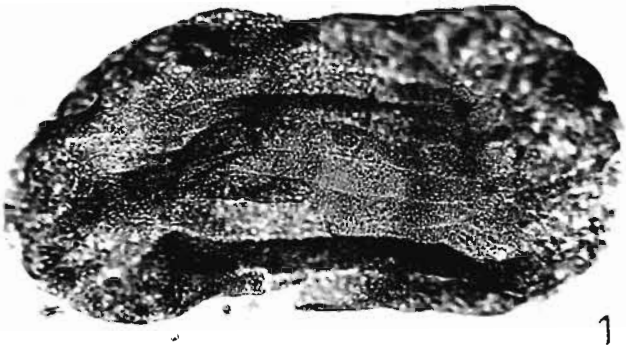
2. Another striate bisaccate pollen (*Crescentipollenites*) from Gondwana, possessing perfect infrareticulate structure in sexine on body surface, and crescent-shaped body-folds at the dista zones of sacci attachment. x 750.

3. A portion of the holotype specimen of *Lunatisporites noviaulensis* Leschik 1956; pl. 22, fig. 1; enlarged to show "infravermiplexate" structure of sexine in two of the taeniae. x 2000.

4. A portion of central body in a striate bisaccate pollen (*Faunipollenites*) from Indian Gondwana, enlarged to show perfect and finely infrareticulate structure (S) of sexine. x 2000.

5. A portion of the central body in *Striatites microcorpus* Schaarschmidt, 1963; pl. 14, fig. 6, from Zechstein of Europe, enlarged to highlighten the "infravermiplexate" nature of sexine (compare with fig. 4); linear grooves tending to form taeniae. x 2000.

6. Specimen of taeniate bisaccate pollen *Arcuatipollenites* gen. nov. earlier assigned to "*Lunatisporites*" from peninsular India, to show perfectly fine infrareticulate structure of sexine in taeniae. x 750.



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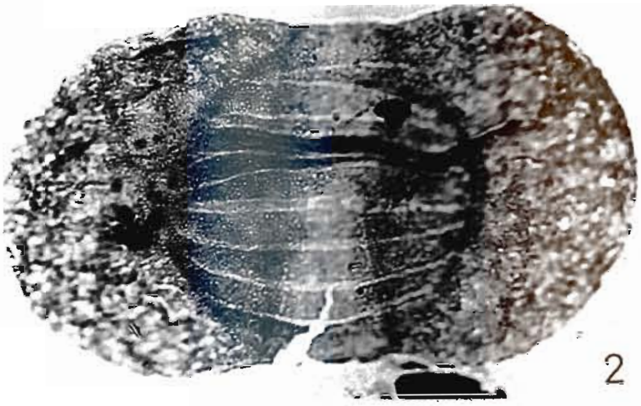

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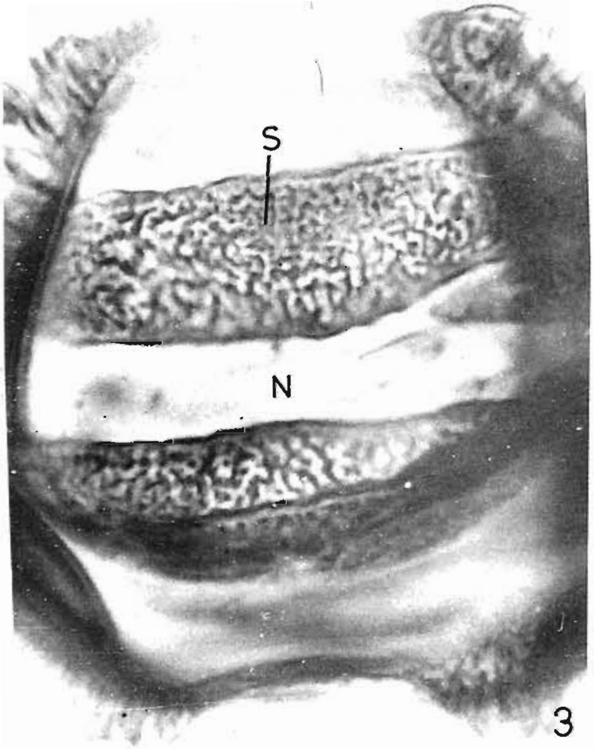

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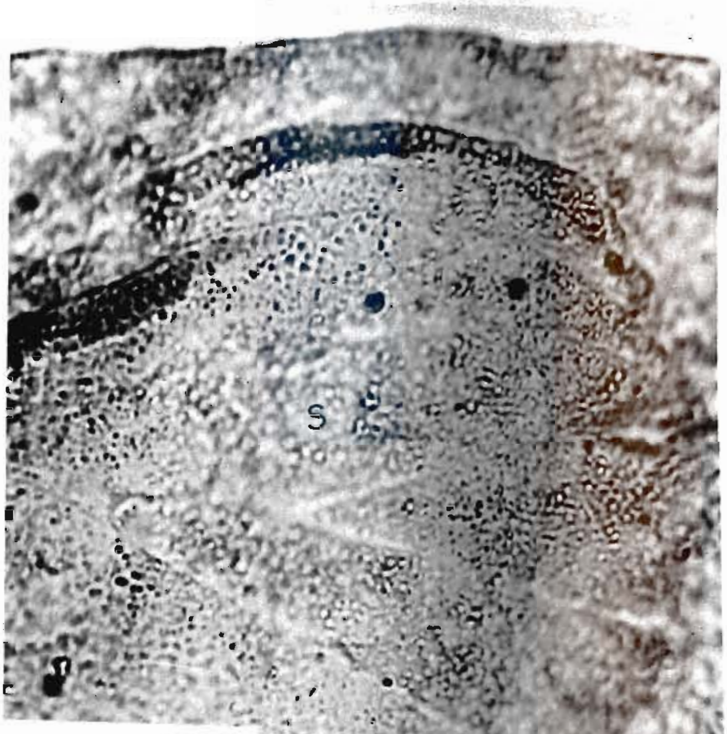

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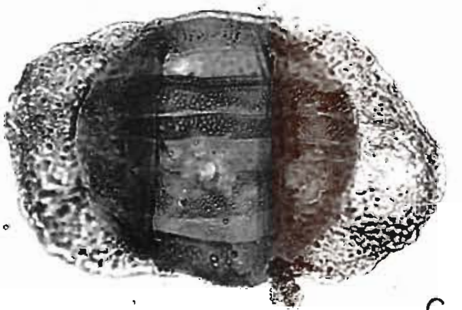

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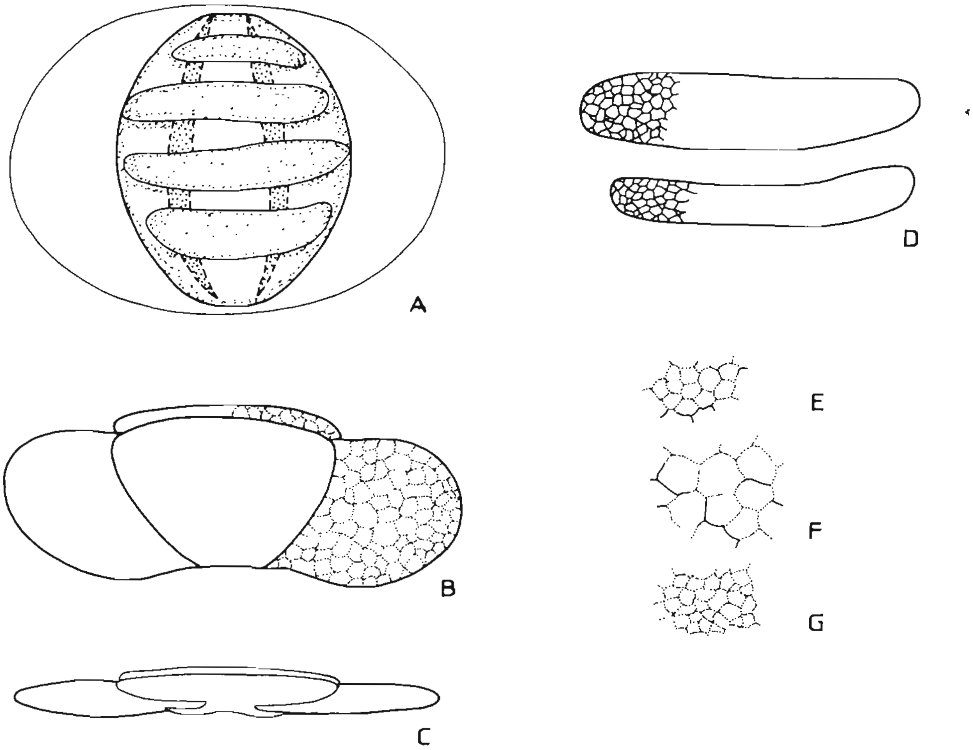
PLATE 3



Text-figure 9 — Generalised outlay of organization in *Arcuatipollenites* gen. nov., **A,** Proximally showing taeniae, distally arcuate folds along SAFRA border, **B,** Meridional sketch across central line showing saccus filled with alveolate structure, and a taenial thickening on proximal side of body, **C,** Highly compressed specimen to postulate formation of folds, **D,** Partially drawn structure of taeniae; **E, F, G,** L-O, analytical drawings of high, middle and low foci, respectively of saccus to decipher protosaccate nature.

Lunatisporites is basically "vermiplexate", at times in some specimens incomplete infrareticulation may be developed (Scheuring, 1978; pl. 30, fig. 434). Fine infravermiculate structure includes ridge-like bodies, rodlets, irregular islands, verrucoid, partially fused or discrete isodiametric rounded objects, grana and T-shaped or wave-shaped small bodies. These are optically opaque, less than 0.5 µm, rarely bigger, disposed close to each other leaving optically lighter areas between them (Text-figure 4; Pl. 7, figs 1, 3). These charactes can be easily recognised under high-power or oil immersion objective. Several photomicrographs published earlier also decipher them clearly (Clarke, 1965; Visscher, 1971), and many observations indicative of such structures have already been recorded in the past (Scheuring, 1970, 1978; Visscher, 1971).

Scheuring (1978, p. 60) describes structure of taeniae in *Lunatisporites noviaulensis mollis* as "Die Scheidenwandchen des taeniaten Alveolensystems können sehr oft zu isodiametrischen, apophysenartigen Stutzelementen reduziert sein". The structure of exine showing "apophysis" protuberances, columnoid growth, grana or similar mixed structure in subtectate region, islands of various shapes, pillar-like elements can be clearly seen in photomicrographs illustrated by Scheuring (1978, pl. 29, figs 412, 416, 419, 423; pl. 30, figs 430, 431, 434; pl. 31, figs 441-443, and other figures on these plates). Our observation reveals that the structure results into a canal-system like pattern with big and small channels. The sacci in *Lunatisporites* are eusaccus (or echtsaccat) as concluded by Scheuring (1978, pp. 60, 62, illustrations on plates 28 to 30).

Derivation of name — After unique nature of *Arcuate* folds at saccus attachment zone on distal face of the body.

In view of the shape of central body, distinctness of nexine, nature of arcuate folds, and taeniae, following species have been resolved under the genus *Arcuatipollenites* gen. nov.

A. ovatus (Goubin) comb. nov. (Type species)
A. pellucidus (Goubin) comb. nov.
A. damudicus (Tiwari & Rana) comb. nov.
A. asansoliensis (Tiwari & Rana) comb. nov.

A. tethyensis (Vijaya & Tiwari *in* Vijaya *et al.*) comb. nov.

A. paliensis (Tiwari & Ram-Awatar) comb. nov.

Lunatisporites gopadensis is striate rather than taeniate species (Bharadwaj & Srivastava, 1969, p. 127). *Lunatisporites karii* Vijaya & Tiwari in Vijaya *et al.* (1988) appears to be a variant of *Lunatisporites pellucidus* with under-developed sacci.

Arcuatipollenites ovatus (Goubin) comb. nov.

Pl. 3, fig. 6; Pl. 9, figs 1, 6, 9

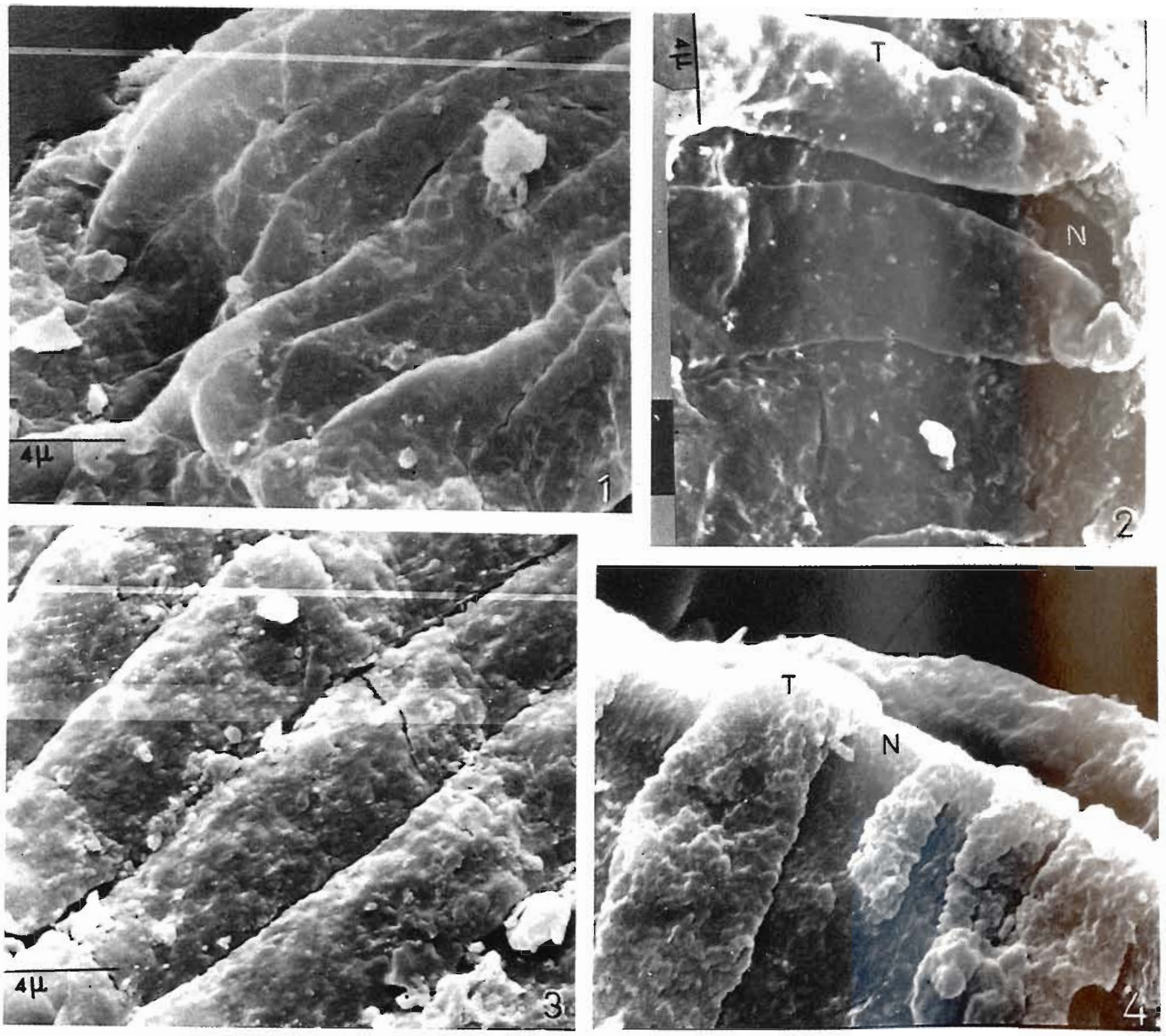
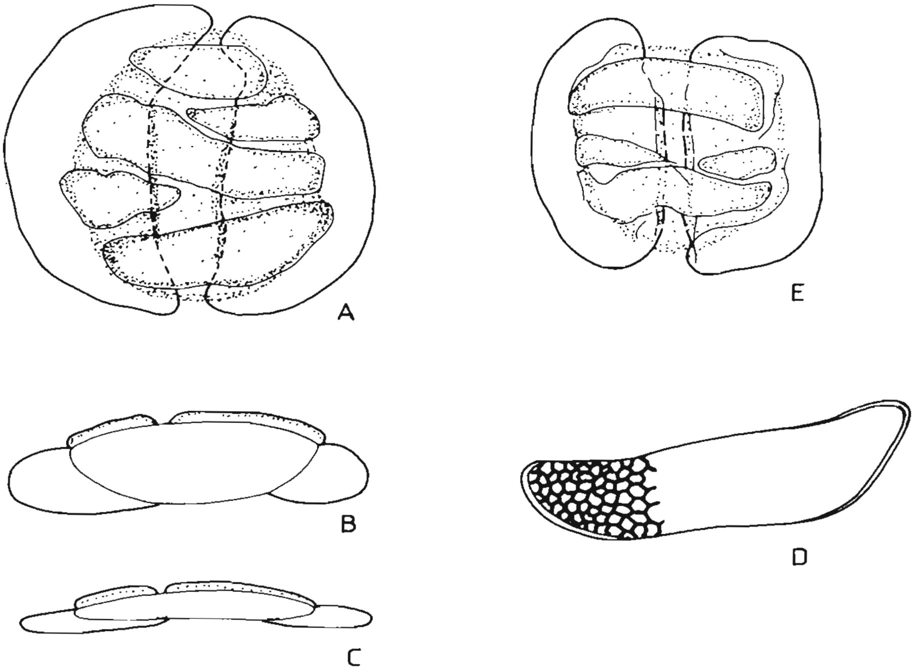


PLATE 4

Nature of striations and taeniae in the population of bisaccate pollen; under SEM.

1, 3 Linear and uniformly wide (<1 µm) narrow grooves termed as "striations", on the proximal face of body; the ends of striations merge with the body-saccus junction at the body equator; under SEM.

2, 4 Inflated sexinal bands of varied sizes and width on proximal face of central body (T) leaving unevenly wide, nexinal parts (N) between two such sexinal bands termed as "Taeniae"; under SEM. Fig. 2 — proximal view, Figure. 3 — taeniae on a folded body.



Text-figure 10 — Holotype of *Arcuatipollenites paliensis* Tiwari & Ram-Awatar (1989) comb. nov., **A**, Characteristic massive taeniae nd shape of sacci; **B**, Meridional section across line of arrows; **C**, Compressed meridional section; **D**, Coarse and distinct infrareticulate structure on taeniae partially drawn; **E**, Another specimen of the same species in Tiwari & Ram-Awatar, 1988.

Synonym

1965 *Taeniaesporites ovatus* Goubin; pl. 2, fig. 2.
1975 *Lunatisporites ovatus* (Goubin) Maheshwari & Banerji; pl. 5, fig. 68
1977 *Lunatisporites rhombicus* Bharadwaj & Tiwari, *partim*; pl. 5, figs 57, 59.

Holotype — Goubin, 1965; pl. II, fig. 2

Type locality — Morondova Basin, Madagascar IDI 2484 m.

Horizon & age — Group Sakamena, Trias Moyen.

Diagnosis (enlarged after Goubin, 1965; p. 1423)— Haploxylon or slimly diploxylon bilateral bisaccate pollen, 55-90 µm; central body distinct, ovalish-circuloid with slightly curved or flat lateral ends. Taeniae 4-6 in general, may be more, having finely infrareticulate sexine. Sacci laterally apart, distally leaving distinct

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PLATE 5 →

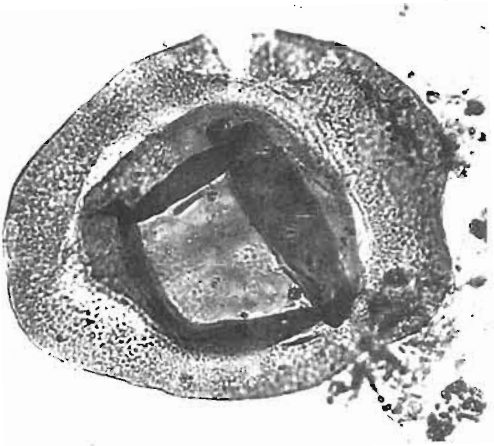
Specimens illustrated to show the bauplan among saccate pollen, i.e., mode of body-saccus attachment, body folds, and saccus structure.

1. A monosaccate polle (*Plicatipollenites*) from Early Permian of Gondwana characterized by having saccus filled with alveoli, and saccus-free-area on both the faces of central body; the body-folds are on the distal face along the body-saccus attachment. x 500.
2. A non-sriate bisaccate pollen (*Satsangisaccites*) in Early Triassic of Gondwana showing the protosaccate nature of sacci, and full length SAFRA with a weak-zone along the lateral axis on distal face. x 750.
3. A non-striate bisaccate pollen (*Protoeusaccites*) from Late Permian sequence in India, characterized in having partial cavity in the centre of saccus — a transitionary character-state in saccus structure, from protosaccate to eusaccate. x 1000.

PLATE 6 →

Monosaccate pollen exhibiting varied kinds of bauplans in northern and southern regions.

1. A monosaccate pollen (*Cordaitina*) from Permian of Tethys Himalaya having enveloping saccus on one of the faces of central body, and leaving saccus-free-area on the other face; a basic character in the pollen of northern hemisphere; protosaccate. x 750.
2. A monosaccate pollen (*Densipollenites*) from Permian Gondwana possessing a saccus enveloping the central body, attached only at one point as evidenced from the position of body in variously flattened specimens. x 750.
3. A monosaccate pollen *Playfordiaspora*) from Early Triassic Gondwana, characterized by eusaccate nature of saccus (the arrow); the spread of sexine continues up to the trilete mark proximally on to the body surface and with distal face covered with saccus. x 1500.



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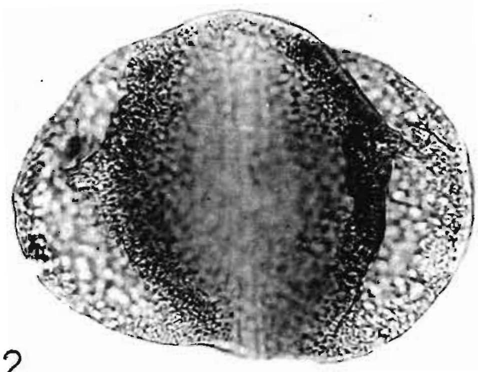

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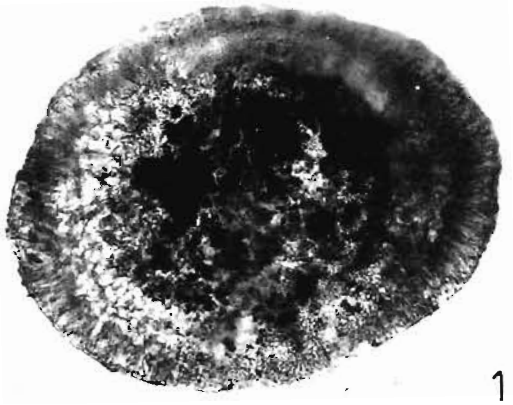
PLATE 5



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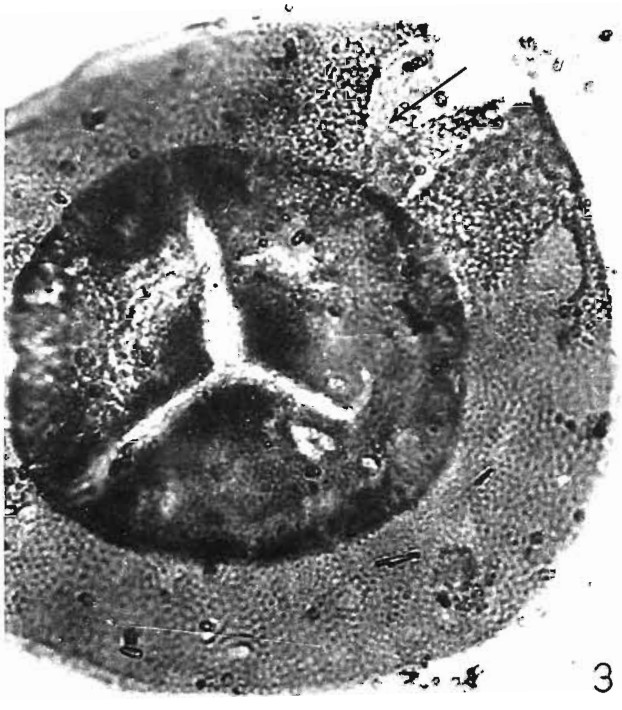

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PLATE 6

SAFRA, zone of saccus attachment accompanied with lunar folds. Saccus alveolae variable in size, filling the chamber to form protosaccus.

Remarks — This species is circumscribed on the basis of ovalish-circuloid shape of the corpus (Vijaya *et al.*, 1988).

Arcuatipollenites pellucidus (Goubin) comb. nov.

Pl. 8, figs 1, 2; Pl. 9, figs 4, 10

Synonym

1965 *Protohaploxypinus pellucidus* Goubin; pl. 2, fig. 4
1970 *Taeniaesporites pellucidus* (Goubin) Balme; pl. 13, figs 8-10.
1975 *Lunatisporites pellucidus* (Goubin) Maheshwari & Banerji; pl. 5, fig. 74.
1977 *Lunatisporites diffusus* Bharadwaj & Tiwari; pl. 5, fig. 63; pl. 6, figs 64-66.
1988 *Lunatisporites diffusus* Bharadwaj & Tiwari *in* Vijaya *et al.*; pl. V, fig. 12.

Holotype — Goubin 1965, pl. 2, fig. 4.

Type locality — Morondova Basin, Madagascar, LW2 202m.

Horizon & age — Group Sakamena, Trias Inferieur

Diagnosis (enlarged after Goubin, 1965, p. 1423)— Haplo- to slimly diploxylon, horizontally oval pollen 68-85 X 51-60 µm; central body almost indistinct, thin, broadly oval to rhombish, taeniae vary in number (4 to 9 or more) and width; sexine finely infrareticulate. Distally SAFRA wide. Distal zones of saccus attachment associated with very narrow, thin arcuate folds. Saccus-structure protosaccate with fine alveolae.

Remarks — The nexine being thin, the outline of the corpus is not prominent. Broadly oval to rhomboid body, wide SAFRA, and feebly-developed lunar folds distinguishes *A. pellucidus* from *A. ovatus*.

Arcuatipollenites damudicus (Tiwari & Rana) comb. nov.

Pl. 9, fig. 5

Synonym

1980 *Lunatisporites damudicus* Tiwari & Rana; pl. 2, figs 48, 49.

Holotype — Tiwari & Rana, 1980, pl. 2, figs 48, 49

Type locality — Borehole RNM-4, Sample no. 5, depth 59 m, Raniganj Coalfield, West Bengal, India.

Horizon & age — Supra-Panchet (Mahadeva) Formation, Middle Triassic.

Diagnosis (enlarged after Tiwari & Rana, 1980, p. 41) — Small pollen with pronounced diploxylonoid construction; holotype 60 X 30 µm; central body horizontally oval, dense, 36 x 26 µm; sexine infrareticulate. Taeniae 4-5, may be more, prominent; SAFRA 10 µm wide straight-sided. Sacci laterally apart, subspherical, 15 µm wide from body equator along terminal axis, 40 µm along lateral axis, finely infrareticulate with relatively thick muri; protosaccate fill present.

Remarks — *A. damudicus* is typical in its shape, fully blown sacci without cavity, distinct taeniae and well defined thick central body.

Arcuatipollenites asansoliensis (Tiwari & Rana) comb. nov.

Pl. 9, fig. 3

Synonym

1981 *Lunatisporites asansoliensis* Tiwari & Rana; pl. 4, figs 59, 61.
1977 *Lunatisporites rhombicus* Bharadwaj & Tiwari; pl. 5, figs 60- 62.

Holotype — Tiwari and Rana, 1981, pl. 4, fig. 59.

Type locality — Bore hole RD-1, Sample no. 5, depth 600.58 m, Raniganj Coalfield, India.

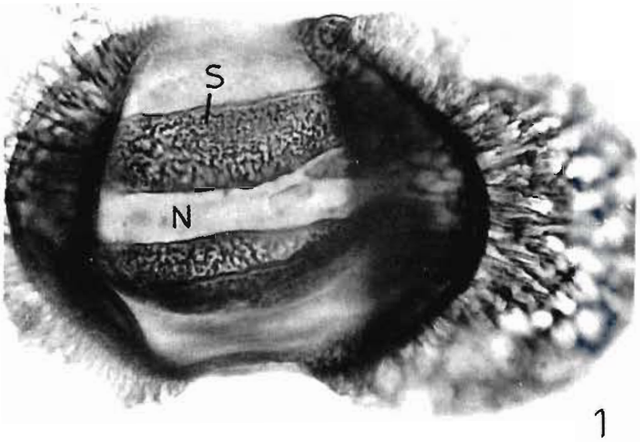
Horizon & age — Panchet Formation, Early Triassic.

PLATE 7 ⟶

1 Holotype of *Lunatisporites noviaulensis* Leschic 1956; pl. 22, fig. 1, in top focus showing the nature of sexinal "infravermiplexate" structure in the taeniae. x 1122.

2. Presence of sharply defined monolete mark in the nexinal path in the same specimen, i.e., in Figure 1, illustrated in median focus. Eusaccate nature of saccus also clear. x 1122.

3. A portion of the specimen in Figure 1, enlarged to show "infravermiplexate" structure of sexine in taeniae with dots, dash, islands, vermiculae, etc.; two central taeniae in focus, the lateral ones are out of focus; a short taenia seen on right-side; in top focus. x 2000.



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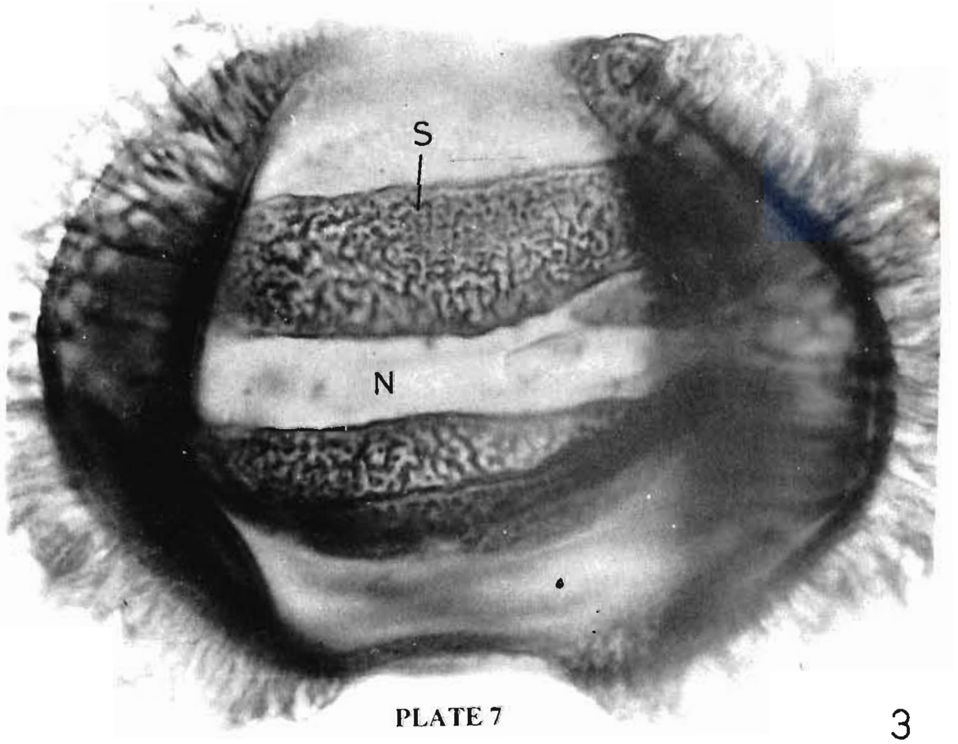


PLATE 7

3

Diagnosis (base on Tiwari & Rana, 1981, p. 204) — Mainly haplo- to slightly diploxylon 60-85 X 50-60 µm. Central body vertically elongated with trapezoid tendency of shape, 43 x 54 µm in holotype, equatorial rim 3-6 µm thick around the body; number of taeniae observed 3-6, finely infrareticulate. Sacci kidney-shaped or crescent-like, not fully blown, forming 15-27 µm wide distal biconvex SAFRA with prominent secondary folds at the zone of attachment. Saccus finely alveolate with protosaccate fill.

Remarks— The construction of very small sacci, trepezoid tendency of the corpus shape and prominent peripheral thickness in the corpus characterises this species.

Arcuatipollenites tethysensis (Vijaya & Tiwari) comb. nov.

Pl. 9, fig. 8

Synonym

1988 *Lunatisporites tethysensis* Vijaya & Tiwari *in* Vijaya *et al.*; pl. 5, figs 7, 8, 10, 11, 14.

Holotype — Vijaya *et al.*, 1988, pl. 5, fig 7.

Type locality — Sample No. 1, Kalapani Limestone, Malla Johar area, Tethys Himalaya, India.

Horizon & age — Kalapani Limestone Formation, Triassic (Anisian-Carnian).

Diagnosis (based on Vijaya et al., 1988, p. 76)— Haploxylonoid, 86 X 68 µm; central body distinct, 60 x 68 µm in size in holotype, oval with broader lateral ends, proximally having 5-6 taeniae, infrareticulate, each of the taeniae bearing 2-4 faint horizontal striation-like lines. Sacci less than hemispherical, distally inclined, leaving a 5-20 µm wide saccus-free-area; lunar folds at the zone of saccus attachment clear. Sacci mediumly coarse in reticulate structure; protosaccate.

Remarks — The presence of faint striation-like lines on prominent taeniae is an interesting character. Since the taeniae are prominently developed, this species has been treated under the genus *Arcuatipollenites.*

Arcuatipollenites paliensis (Tiwari & Ram-Awatar) comb. nov.

Pl. 8, fig. 3; Pl. 9, figs 2, 7

Synonym

1989 *Lunatisporites paliensis* Tiwari & Ram-Awatar; pl. 1, figs 14, 15.

Holotype — Tiwari & Ram-Awatar, 1989; pl. 1, fig. 14.

Type locality — Bore-hole no. JHL-23, depth 203.0-204.0 m; about 9 km east from Birsinghpur-Pali, Johilla Coalfield, M.P., India.

Horizon & age — Barakar Formation, Early Permian.

Diagnosis (based on Tiwari & Ram-Awatar, 1989, p. 101) — Pollen horizontally circuloid, 110-140 µm; central body faintly demarcated, big, subcircular to oval, bearing 3-5 prominently inflated and massive taeniae which being thickened at their margin having fine infrareticulate structure with relatively thick muri. Sacci proximally equatorially attached, distally inclined leaving a 10-20 µm broad SAFRA, folds at attachment line slim, not typically lunar, sometimes very narrow or indistinct. Sacci less than hemispherical, giving a circuloid shape to the grains, infrareticulate, meshes not coarse, muri compact and perfect filling the saccus.

Remarks — *A. paliensis* is distinct from other species of the genus *Arcuatipollenites* in having massive taeniae, but compares with *A. pellucidus* in thin nature of nexine.

The salient features of species in the genus *Arcuatipollenites* are :

1.1 Central body distinct, nexine thick and prominent arcuate distal body folds at the zone of saccus attachment.

A. ovatus — Ovalish-circuloid central body with apparently flat lateral ends.

A. damudicus — Horizontally oval, dense central body with diploxylon sacci.

A. asansoliensis — Trapezoid central body with prominent peripheral rim.

A. tethysensis — Vertically oval central body having faint striations on taeniae.

1.2 Central body not prominently defined, nexine thin, arcuate body folds narrow and feeble.

A. pellucidus — Central body vertically elongated and broadly oval to rhombish, nexine very thin, outline faint.

A. paliensis — Vertically roundly oval, relatively big central body with crescent-shaped sacci and massive taeniae.

Dicappipollenites gen. nov.

Synonym

Species reported under *Lueckisporites* Potonié & Klaus from Permian of India are:

1954 *Lueckisporites* Potonié & Klaus *partim.*
1970 *Lueckisporites in* Balme
1972 *Lueckisporites in* Sinha.

Type species — *Dicappipollenites crassus* (Sinha) comb. nov.

Generic diagnosis — Bisaccate pollen; central body bearing two horizontal taeniae, separated by unevenly wide nexinal space in between. Structure of taeniae finely infrareticulate with perfect muri and complete meshes, forming distinct net-like pattern, rarely variable tending to be finely infrapunctate. Taeniae rarely massive, their shape being strip-like, or kidney-like, or bean-like, or variables of half-circle. Central nexinal path (platea) varying in width along its terminal extent across the horizontal axis of the body. No slit or mark present on the nexinal space (platea) between two taeniae. Sacci kidney-shaped or crescentic, rarely hemispherical or bigger then half-circle, proximally attached to equator, distally invading the body to leave the "SAFRA" of variable width free, without regular, taper- end folds at the lines of attachment, or ring-fold. At times, attachment zone may be ill-defined. Distal saccus-free-area relatively thin, unstructured or indistinctly structured. No defined germinal furrow in the form of a groove or weaker area present. Sacci mostly showing a tendency to remain small, being variously structured; protosaccate.

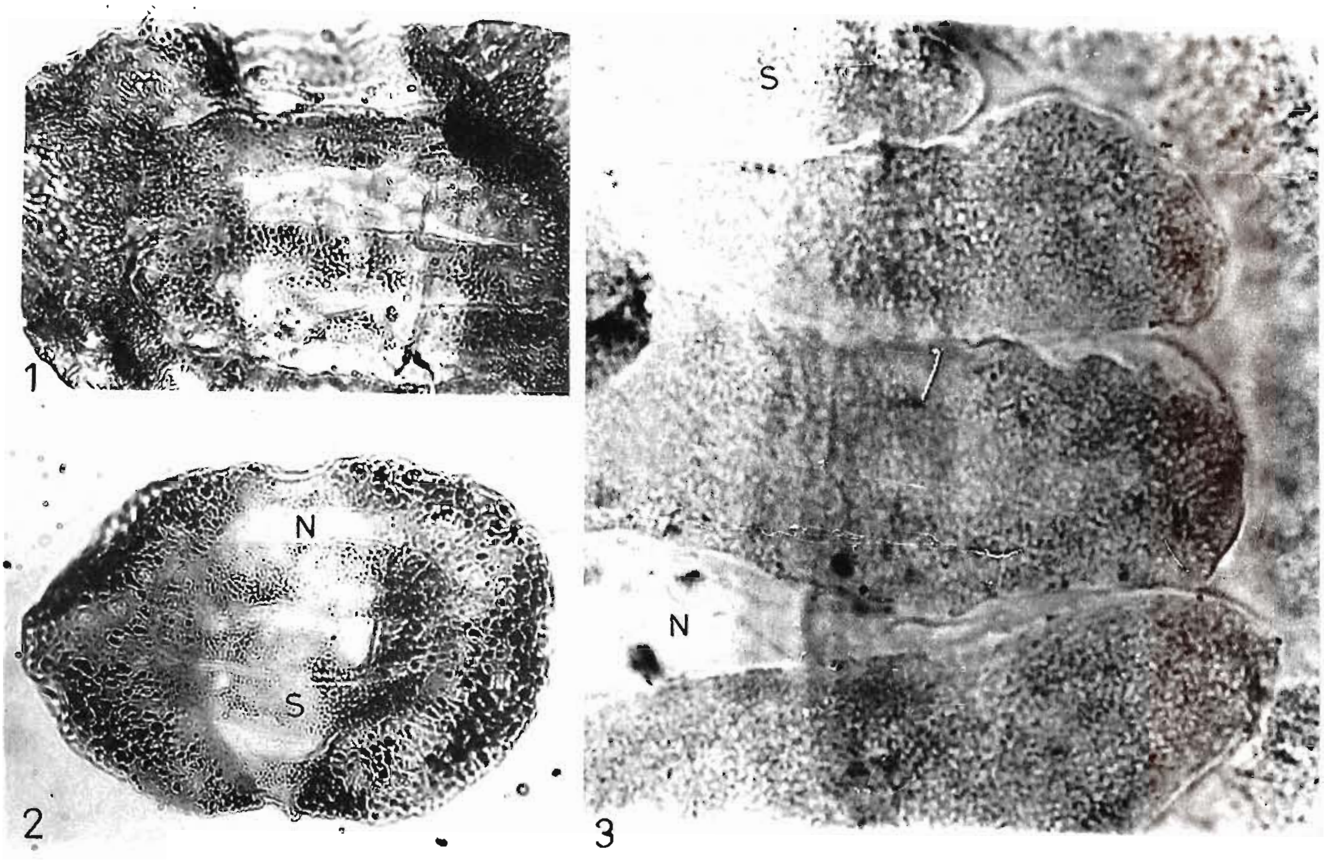


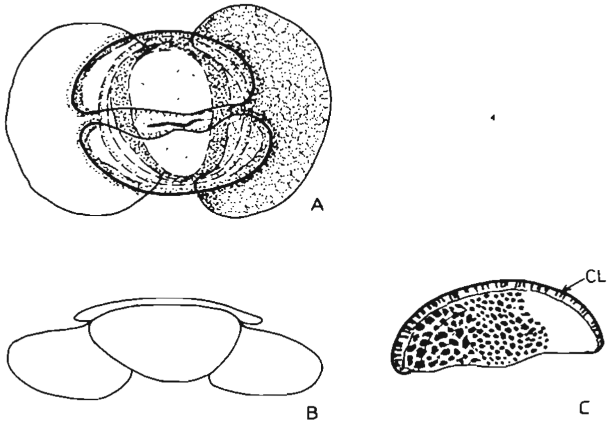
PLATE 8

Specimens of taeniate bisaccate pollen *Arcuatipollenites* gen. nov illustrated to show very fine and perfectly infrareticulate structure (S) in the sexine of taeniae - a character of exine structure in Gondwana saccate pollen, leaving irregular nexinal path (N)

1, 2. *Arcuatipollenites pellucidus* (Goubin) comb nov x 1000,

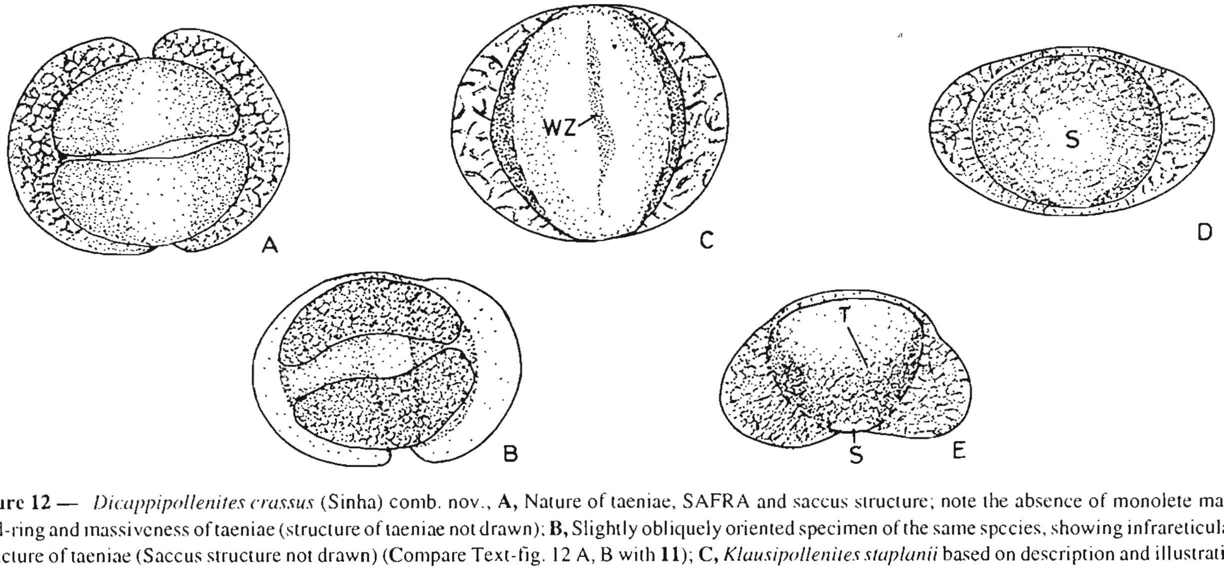
3. *Arcuatipollenites paliensis* (Tiwari & Ram-Awatar) comb nov. x 2000

Comparison — *Dicappipollenites* gen. nov. is proposed to exclude all those forms which possess striation, or more than two taeniae on their body.



Text-figure 11 — *Lueckisporites virkkiae* Potonié & Klaus, line- drawing based on specimen in Leschik 1956, pl. 21, fig. 17; **A** showing circular central body (broken lines), an oval prominent fold-ring (dark-stippled), two massive horizontally placed taeniae extending beyond the body equator, a prominent, bent monolete mark on nexine between the two taeniae and inflated kidney-shaped sacci; **B,** Sacci proximally originate from below the taeniae, as seen in meridional section cutting across one of the taeniae (arrows); **C,** Exine structure of taeniae and collumnoid layer (CL) at marginal zone which is thicker at periphery on outside of the body.

Lueckisporites Potonié & Klaus, 1954 (based on type species *Lueckisporites virkkiae* Potonié & Klaus, 1954) is a comparable genus in form-similarity. However, distinct morphographic lines have been recognised in these two genera; *Dicappipollenites* differs by the absence of a slit or any type of mark (bent monolete, bilete, trilete or their variables) on taeniae or on the inter-taenial nexinal path, and in the infrastructure of taeniae which is fundamentally of different type in being perfectly and finely infrareticulate, forming complete network-like pattern, or rarely infrastructured with micropunctation. The examinations of several specimens of *Lueckisporites* found in the European palynofloras (*Lueckisporites virkkiae* in Leschik 1956, pl. 21, fig. 17; specimens in slides of the material - Potonié & Klaus 1954; Leschik, 1956; Grebe, 1957) have revealed that this population includes specimens which possess monolete, or a bilete mark (rarely trilete with unequal rays), in the nexinal space (platea) between the two taeniae. Moreover, the taeniae are more pronounced, elevated, prominently crossing over to the proximal sacci roots as well as beyond body equatorial line (Pl. 10, figs 1-3; Text-figure 11); the structure of taeniae is infravermiplexate, i.e., granulose, baculose, verrucose, fine rod-lets, islands, curved bodies, verminculae-like exinal elements present in a layer at the subtectate region forming an irregular canal system - an entirely different pattern, when compared to in-



Text-figure 12 — *Dicappipollenites crassus* (Sinha) comb. nov., **A,** Nature of taeniae, SAFRA and saccus structure; note the absence of monolete mark, fold-ring and massiveness of taeniae (structure of taeniae not drawn); **B,** Slightly obliquely oriented specimen of the same species, showing infrareticulate structure of taeniae (Saccus structure not drawn) (Compare Text-fig. 12 A, B with **11**); **C,** *Klausipollenites staplanii* based on description and illustration of Jansonius 1962 pl. 12, figs. 21-27, showing prominent arcuate thickening at equator of body. full length diffused SAFRA, a median weak-zone (WZ) and incomplete muri in sacci; **D,** *Klausipollenites (Pityosporites) schaubergeri* (Potonié & Klaus 1954) Jansonius 1962, the Holotype. Drawing based on Potonie & Klaus 1954, pl. 10, fig. 7, and several other specimens studied, to show encroachment of sacci from all sides on to the distal face of the body leaving a circuloid SAFRA (S), and absence of a weak zone in the centre; **E,** based on Potonié & Klaus 1954, pl. 10, fig. 8 laterally flattened specimen showing continuous wide track of saccus (T) on equatorial and distal face excepting a small area on the distal most region in the centre (S).

frareticulum with complete muri found in *Dicappipollenites* (Pl. 10, figs 4-8; Text-figure 12B). The exine structure as described above for *Lueckisporites* has also been noted in the description by Potonié and Klaus (1954) and Scheuring (1970). The infravermiplexate structure is present in the taeniae of *Lunatisporites* also but in *Lueckisporites* it is much finer in nature attaining infraverrucose to infragranulose pattern.

The morphographic details of *Lueckisporites* are figured here, based on the study of the specimens of *L.*

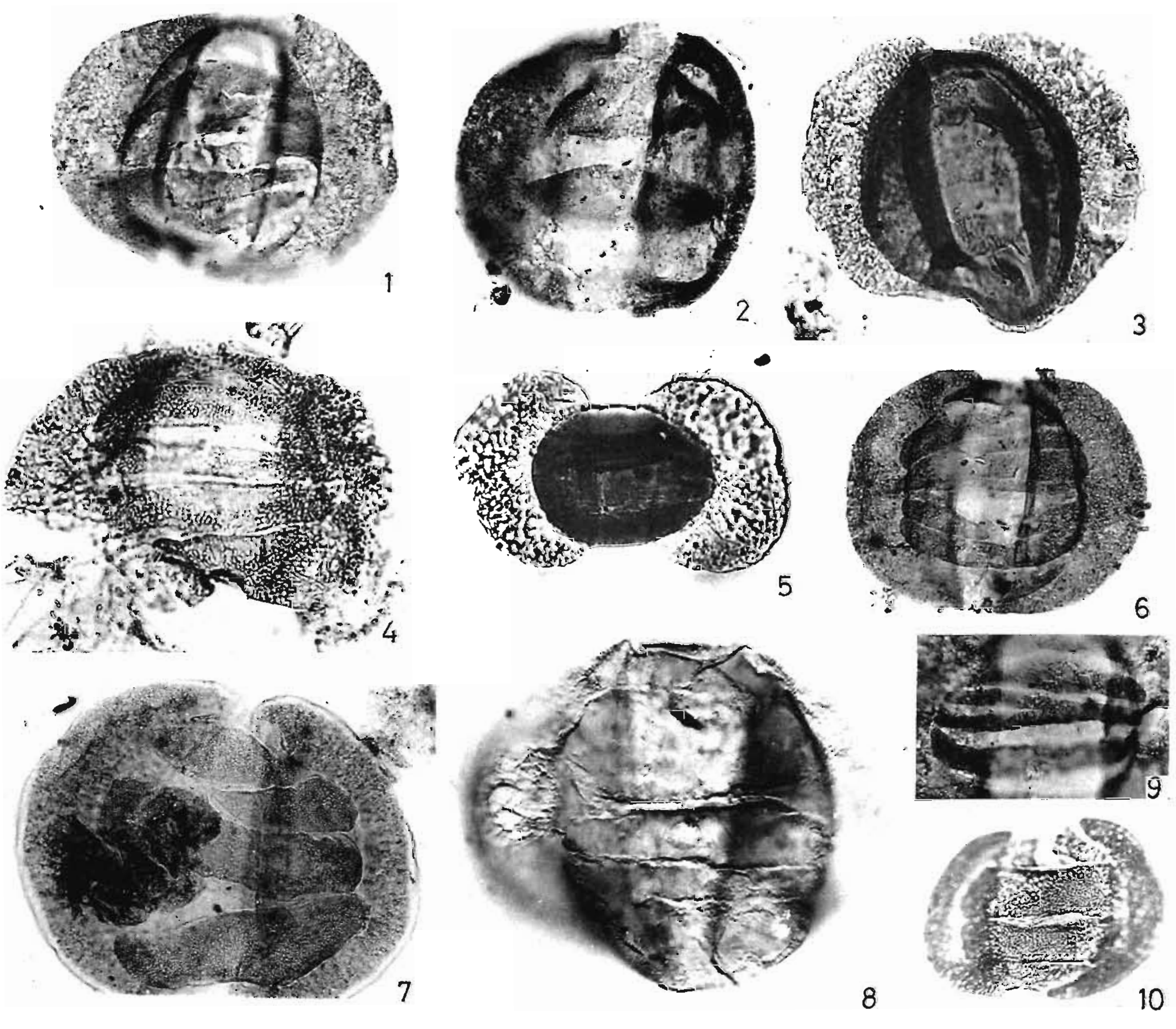


PLATE 9

Specimens referred to various species of the genus *Arcuatipollenites* gen. nov., -- to show finely infrareticulate structured sexine in taeniae, varied overall shapes, central body, and the nature of arcuate folds.

1, 6. *Arcuatipollenites ovatus* (Goubin) comb. nov. x 750.

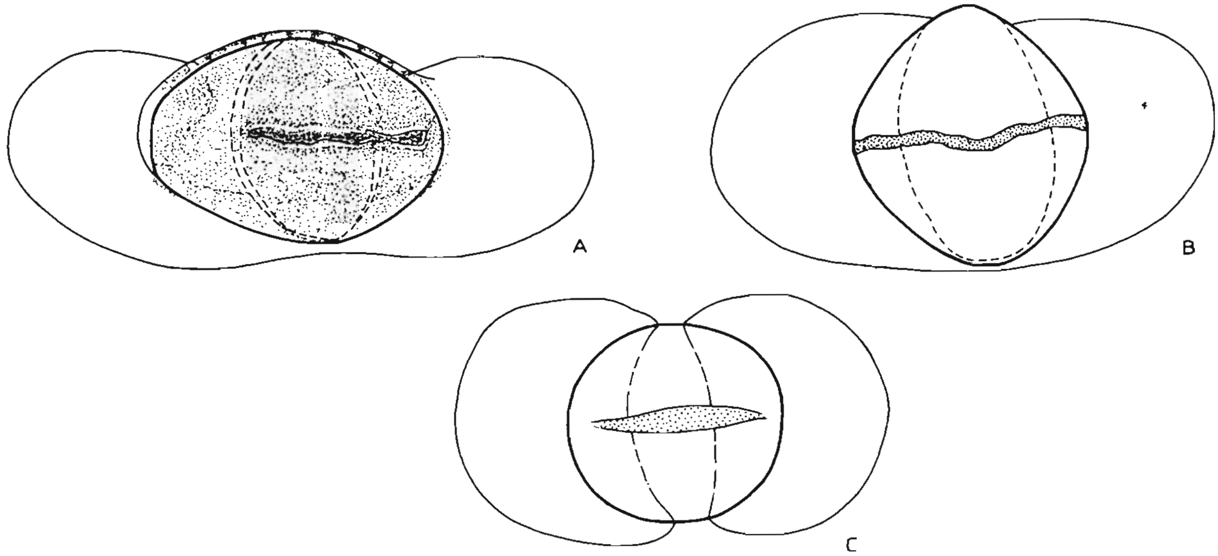
2, 7. *A. paliensis* (Tiwari & Ram-Awatar) comb. nov. 7. Holotype in Tiwari & Ram-Awatar, 1989; pl. 1, fig. 14 x 550; 2. x 500.

3 *Arcuatipollenites asansoliensis* (Tiwari & Rana) comb. nov. Holotype, Tiwari & Rana, 1981; pl. 4, fig 59, x 750.

4,9,10. *A. pellucidus* (Goubin) comb. nov. x 750, 500, 500.

5. *A. damudicus* (Tiwari & Rana) comb. nov., Holotype, Tiwari & Rana, 1980; pl. 2, fig. 48. x 750.

8. *A. tethysensis* (Vijaya & Tiwari) comb. nov., Holotype, Vijaya *et al.*, 1988; pl. V, fig. 7. x 750.



Text-figure 13 — **A,** *Chordasporites singulichorda* Klaus 1960. Holotype based on Klaus, 1960, pl. 53, fg. 45, sublaterally flattened with thick cappa, oval marked SAFRA and a ridge-like thick "chord"; body structure not clear, infragranulose?; **B,** Chor*dasporites magnus* Kl. 1964; Holotype, Klaus, 1964, pl. 4, fig. 43 to show nature of prominent "chord" extending across the terminal axis of body; **C,** Specimen apparently comparable to *Chordasporites* with a fold rather than a true "chord" as in A and B.

virkkiae Potonié & Klaus in Leschik (1956, pl. 21, fig. 17). *Arcuatipollenites* gen. nov. and *Lunatisporites* Leschik emend. Scheuring 1970 differ from *Dicappipollenites* in possessing more than two taeniae.

Organisation — Text-fig. 12A, B.

Derivation of name — *Di* meaning two and *cappa* denotes cover.

The following species are resolved under the genus *Dicappipollenites* on the basis of nature of taeniae and central body :

D. crassus (Sinha) comb. nov.
D. nyakapen densis (Hart) comb. nov.
D. balmei sp. nov.
D. singhii (Balme) comb. nov.
D. singrauliensis (Sinha) comb. nov.

Dicappipollenites crassus **(Sinha) comb. nov.**

Pl. 10, figs 4-8

Synonym

1972 *Lueckisporites crassus* Sinha, pl. 5, figs 63, 64.

Holotype — Sinha, 1972, pl. 5, fig. 63 (could not be traced in type slide).

Neotype — Pl. 10, fig. 7; BSIP Slide no. 6653.

Remarks — The type specimen of the holotype species *Lueckisporites crassus* Sinha and so also the second specimen (1972, pl. 5, fig. 63, 64) are missing in the Type Slide no. 4136 (BSIP Repository). Therefore another closely matching specimen has been searched from the type material (reference : Sinha, 1972), and designated as Neotype for this species. The Jhingurdah seam was assigned to Barakar Formation by Sinha

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PLATE 10 →

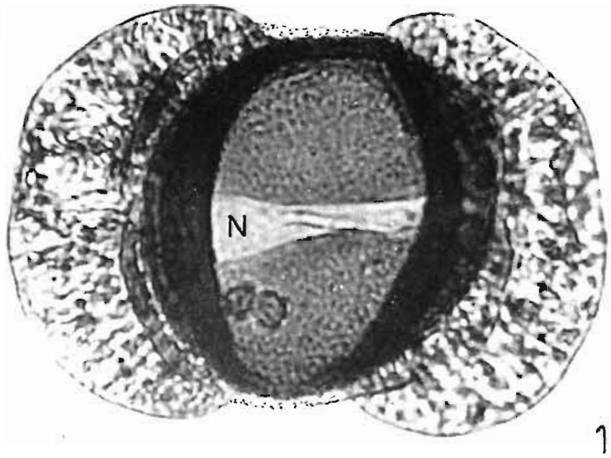
1-3. **1.** General view of the specimen of *Lueckisporites virkkiae* Potonié & Klaus in Leschic, 1956; pl. 21, fig. 17; Slide n. B 10295/1 (x 11, 3) showing two massive sexinal bands (taeniae T) on body leaving an unstructured nexinal path (N) in the centre which bears a prominent monolete mark. Taeniae extending much beyond the body equator (x 1000). **2.** Body enlarged in edian focus to show well developed monolete mark in nexine (x 2000); **3.** Same in top focus to show incomplete reticulation and irregular net-work leading to variant of "infravermiplexate" pattern in subtectate layer; extension of taeniae, ring-fold in body and body thickness (x 2000).

4. *Dicappipollenites crassus* (Sinha) comb. nov. Holotype, Sinha, 1972; pl. 5, fig. 63. x 750 (reproduced from original photograph).

5. A portion of specimen in fig. 8, enlarged to show infrareticulate structure of sexine in taeniae. x 1500.

7. Neotype specimen for *D. crassus* (Sinha) comb. nov., Slide no. BSIP 6653 (Tiwari & Srivastava, 1984). x 750.

6, 8. *D. crassus* (Sinha) comb. nov., Slide no. BSIP 6660 (Tiwari & Srivastava, 1984), 4141 (Sinha, 1972). x 750, 1000.



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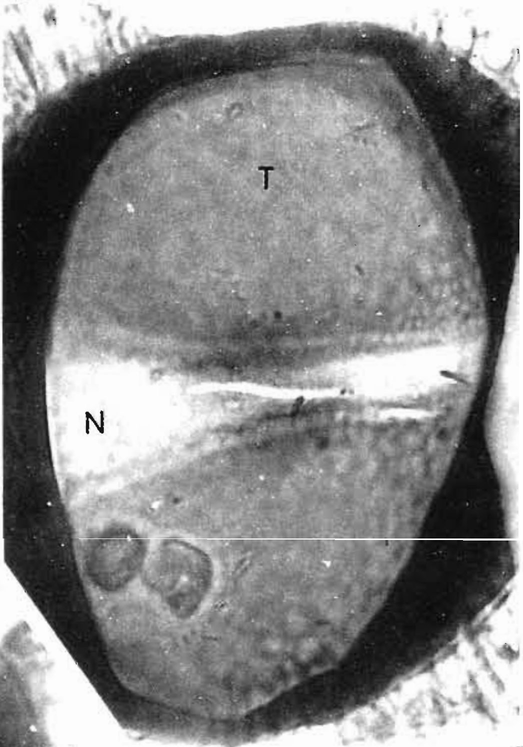

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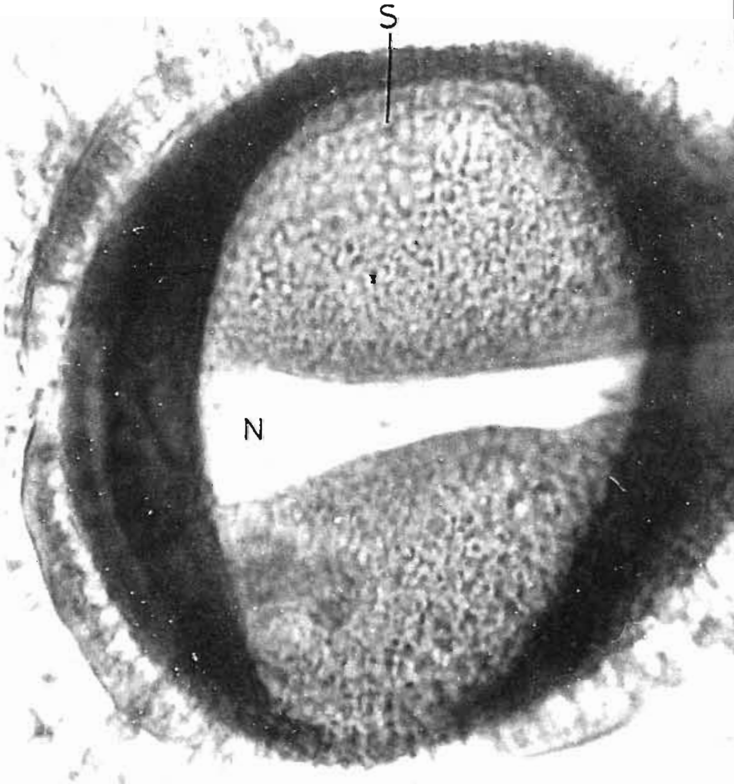

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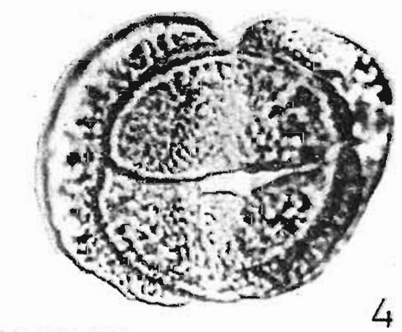

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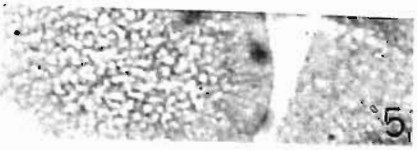

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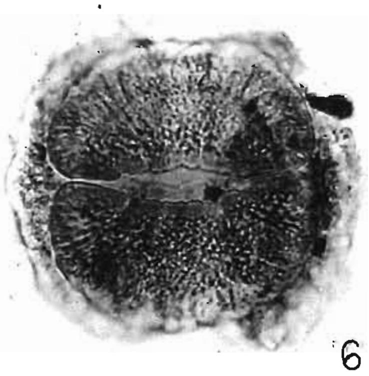

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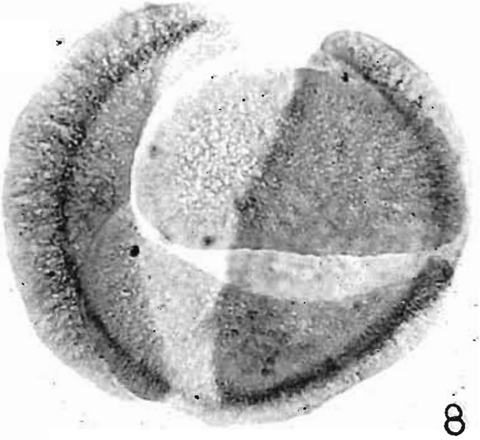
PLATE 10

7



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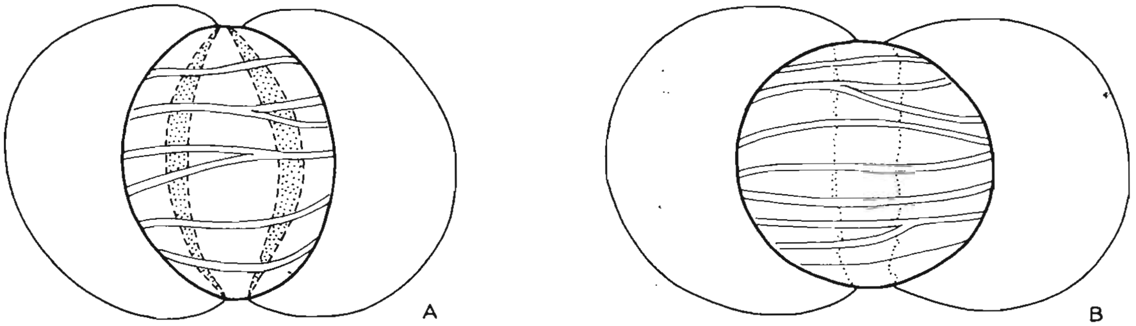


Text-figure 14 — Simple striate bisaccate pollen to show nature of striations and SAFRA. **A**, *Crescentipollenites* Bharadwaj., Tiwari & Kar - marked lunar folds at margin of delineated SAFRA; **B**, *Striatopodocarpites* Sed., SAFRA without lunar folds (structure not drawn).

(1972), but Tiwari and Srivastava (1984) re-studied the material and found that it contains a palynoflora similar to that of Raniganj Formation. Based on other stratigraphical evidences also, Jhingurdah seam is now considered to be the part of Raniganj Formation. Hence, presently the horizon given for the Neotype is Raniganj Formation.

Type locality — Borehole NCSJ-4, Jhingurdah Seam, Singrauli Coalfield, Madhya Pradesh, India.

Horizon & age — Raniganj Formation, Late Permian.

Diagnosis (enlarged after Sinha, 1972, p. 187) — Slimly diploxylon, subcircularly bilateral pollen, 42-48 x 88-70 µm. Central body thin, distinct, ovalish-circuloid, 40 x 50 µm in holotype, (60 x 55 µm in Neotype), possessing two reniform equal- sized taeniae, placed at lateral ends, leaving 2-7 µm wide unstructured space in centre, sexine in taeniae finely infrareticulate. Sacci less than hemispherical, reniform, crescent or bean-shaped, proximally equatorially attached distally inclined; SAFRA distinct, straight-sided, 5-20 µm wide. Saccus infrareticulation fine, looking similar to that of the strips, filled.

Remarks — D. crassus is characterised by its circuloid-oval shape, shape of sacci and two big taeniae.

Dicappipollenites nyakapendensis **(Hart) comb. nov.**

Pl. 11, figs 3, 6

Synonym

1960 *Lueckisporites nyakapendensis* Hart; pl. 1, fig. 12.

Holotype — Hart, 1960, pl. 1, fig. 12.

Type locality — Nyakapenda River Valley, coal three feet from the top of C.S. 34 ("Middle Seam") of McKinlay, South Africa.

Horizon & age — Early Permian.

Diagnosis (enlarged after Hart, 1960, p. 9) — Horizontally oval central body, possessing two sexinal-strips at each lateral-end leaving a central nexinal path. Taeniae finely infrareticulate, not massive, more or less bean-shaped. Sacci more than hemispherical in shape, laterally apart, protosaccate in nature, saccus intrareticulation coarse.

Remarks — Hart (1969) elaborately gave an account of variation in the dimensions, but included several diversified forms in this species (Hart, 1969; pl. 1, figs 2, 3, 4, 6). Based on the type specimen, it is opined here that the forms having subcircular to oval body, well-developed more than half-circle sacci, distinct straight-sided saccus-free-area, infrareticulate sexine of the taeniae — which are not massive, and absence of slit on the inter-taenial path of unstructured exine should be included in this species.

Dicappipollenites balmei **sp. nov.**

Pl. 11, figs 4, 5, 7, 8

PLATE 11 →

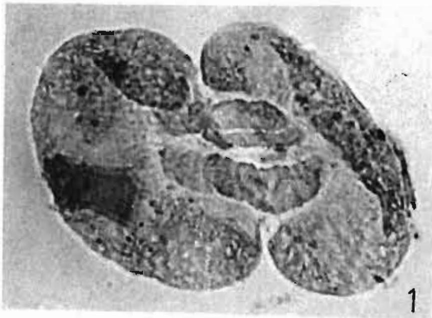
Specimens of *Dicappipollenites* gen. nov., studied presently are illustrated to show variation in over-all shape, nature of taeniae, and the sulcus among the species.

1, 11, 12. *Dicappipollenites singrauliensis* (Sinha) comb. nov. specimens in Sinha, 1972; pl. 5, figs 62, 61; Slide no. BSIP 4134; x 625.

2, 9, 10. *D. singhii* (Balme) comb. nov. x 500, x 750, x 500.

3, 6. *D. nyakapendensis* (Hart) comb. nov. x 500.

4-5, 7-8. *D. balmei* sp. nov. x 750, 5. x 1875, 750.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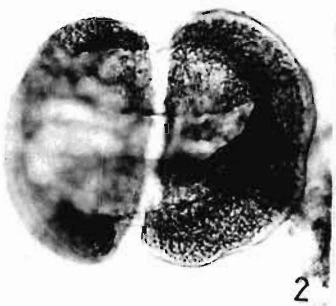
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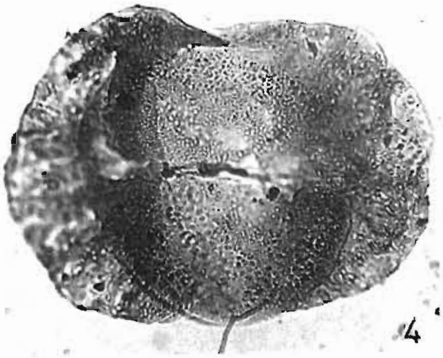
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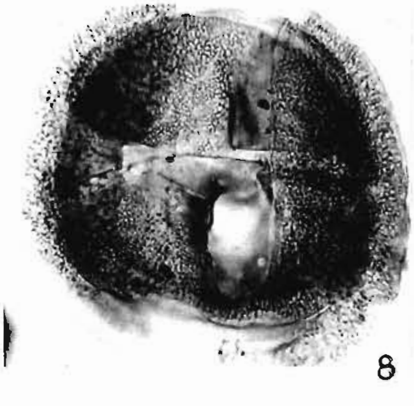
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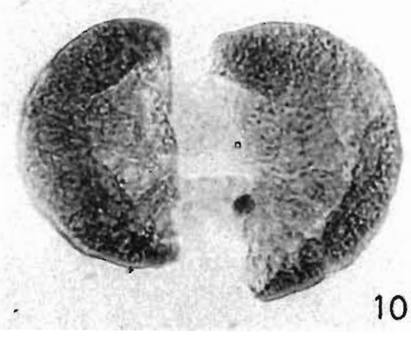
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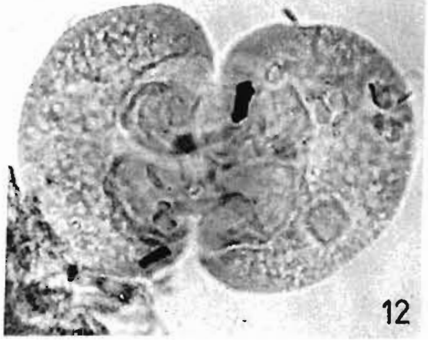
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PLATE 11

Synonym

1970 *Lueckisporites virkkiae in* Balme; pl. 13, figs 4-5.

Holotype — Balme, 1970; pl. 13, fig 4.

Type locality — Wargal Limestone, Field no. K11-6A, Salt Range.

Horizon & age — Chhidru Formation, Late Permian.

Diagnosis — Haploxylon 58-74 μm; central body horizontally oval, big, 40-54 μm along the longer axis, distinct, bearing two bean-shaped taeniae, equal to body width, no mark in centre on nexinal parth, sexine on taeniae finely infrareticulate. Sacci hemispherical, distally leaving unstructured wide, straight-sided SAFRA, saccus structure densely infrareticulate, protosaccate.

Remarks — *D. balmei* is distinct by having horizontally oval central body with prominent taeniae.

Dicappipollenites singhii (Balme) comb. nov.

Pl. 11, figs 2, 9, 10

Synonym

1970 *Lueckisporites singhii* Balme, pl. 13, figs 1-3.

Holotype — Balme, 1970, pl. 13, fig 2, UWA 57919.

Type locality — Wargal Limestone, Field no. KII-6D, Salt Range, West Pakistan.

Horizon & age — Chhidru Formation, Late Permian.

Diagnosis (enlarged after Balme, 1970, p. 376) — Slimly diploxylon, horizontally-oval, bilateral pollen, holotype 55 x 75 μm. Central body thin, vertically ovalish, distinct, bearing two broad ragged taeniae. Sexine structure finely infrareticulate, may be infragranulose, taeniae not massive. Sacci hemispherical, distally inclined subequatorially leaving wide, straight "SAFRA". Saccus infrareticulation medium-sized; protosaccate.

Remarks — Balme (1970; pp. 374, 376) mentioned that in the population of disaccate bitaeniate pollen from Salt Range, not a single specimen is similar in morphology to *Lueckisporites virkkiae* of Europe, although in the centre on nexinal path seldomly faint monolete mark may be simulated in this species. *L. singhii* is included in the genus *Dicappipollenites* gen. nov. because of its structure of taeniae. This species differs from *D. crassus, D. nyakapendensis* and *D. singrauliensis* in having vertically oval central body and ragged taeniae.

Dicappipollenites singrauliensis (Sinha) comb. nov.

Pl. 11, figs 1, 11, 12

Synonym

1972 *Lueckisporites singrauliensis* Sinha; pl. 5, figs 61, 62.

Holotype — Sinha, 1972, pl. 5, fig. 61.

Type locality — Borehole NCSJ-4, Sample no. 112, Jhingurdah Seam, Singrauli Coalfield, Madhya Pradesh, India.

Horizon & age — Raniganj Formation, Late Permian.

Diagnosis (enlarged after Sinha, 1972, p. 187) — Diploxylon, horizontally oval bilateral pollen, 65 x 90 μm; holotype measures 87 x 60 μm. Central body small, 36 x 52 μm thin, distinct, circular, bearing two reniform taeniae with uneven thickness, almost equal to body width; in centre nexine has no mark. Sexine on taeniae finely infrareticulate. Sacci diploxylonoid, more than

PLATE 12

Specimens of *Klausipollenites schaubergeri* from the Zechstein of Europe illustrated to show the nature of sexinal elements in body exine, and encroachment of saccus on proximal and distal faces of the body.

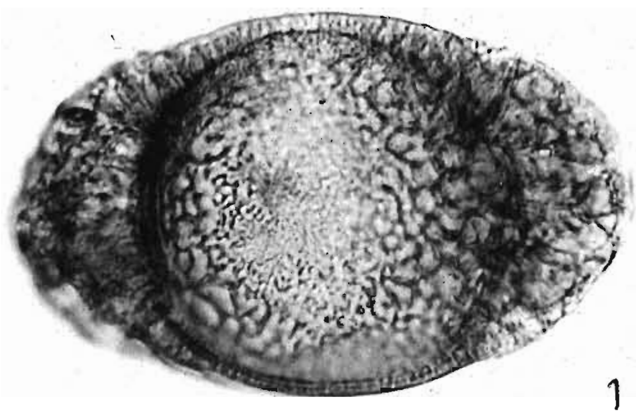
1, 2, 3. Specimen in the preparation of Leschik, 1956; Slide no. B 10295/6 (XII, 9), in 1. top 2. middle, and 3. low foci to highlighten the encroachment of sacci to leave only a circuloid SAFRA on distal face; all x 2000.

4. Another specimen in the preparation of Leschik 1956; Slide no. B 10295/1 (XIII, 2) showing encroachment of saccus on distal face of body leaving ovalish SAFRA, which, however, is not full length along the lateral axis. x 2000.

5. A specimen in the preparation of Leschik 1956; Slide no. B 10295/5 (XII, 8) to show "infravermiplexate" nature of sexinal elements. x 2000.

6. Holotype of *Klausipollenites schaubergeri* in Potonié & Klaus, 1954; pl. 10, fig. 7 to show encroachment of saccus from all sides, with coarser reticulae of sacci on distal face of body leaving a circuloid SAFRA. x 800.

7. Another specimen of *Klausipollenites schaubergeri* in Potonié & Klaus 1954; pl. 10, fig. 8; (laterally flattened) showing saccus continuity on lateral and distal face on body suface, leaving a small, thin circuloid area free at distal pole. x 800.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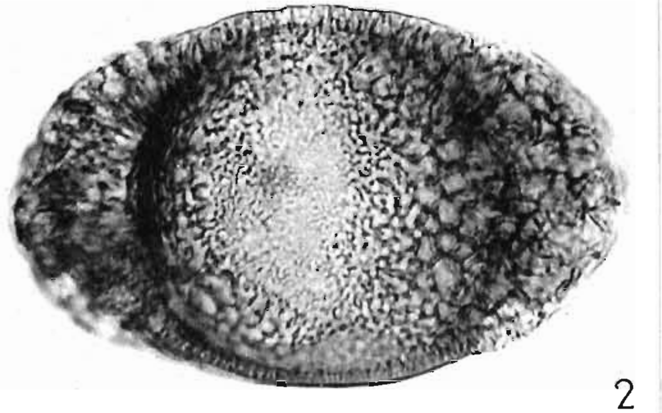
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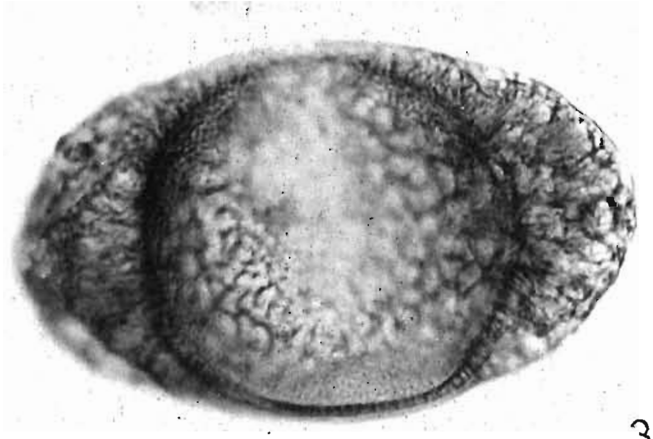
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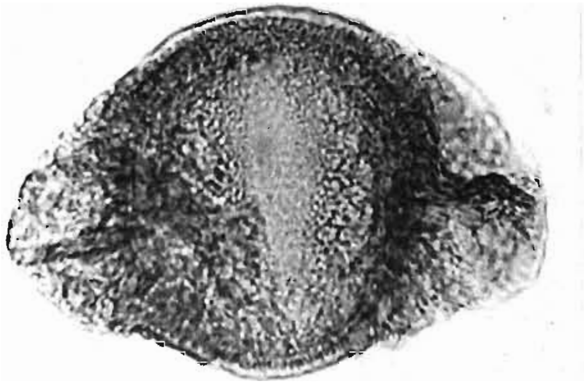
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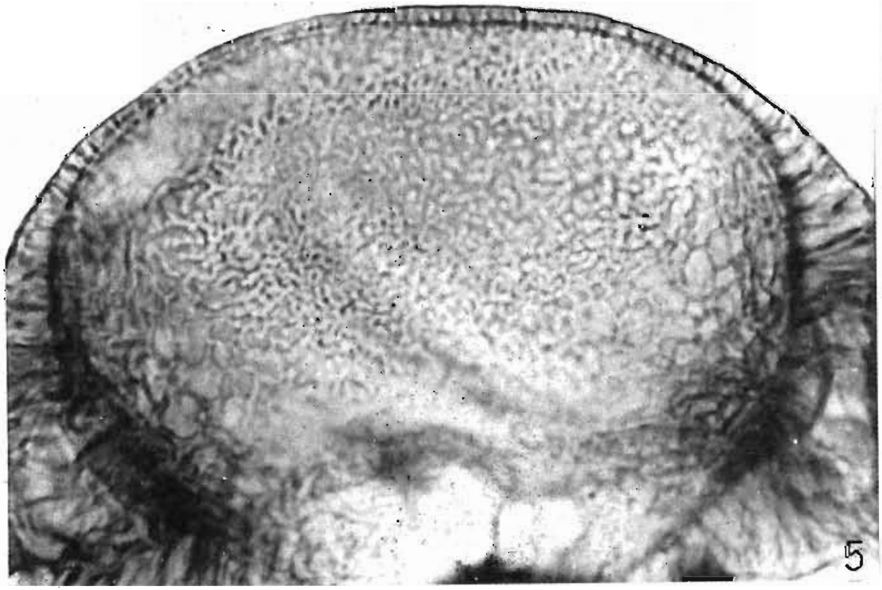
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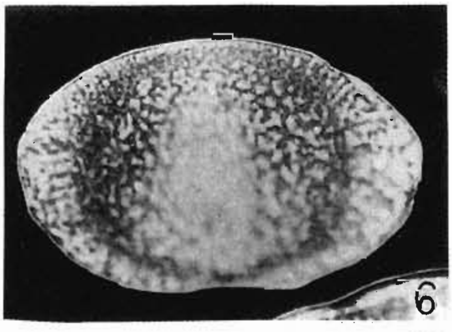
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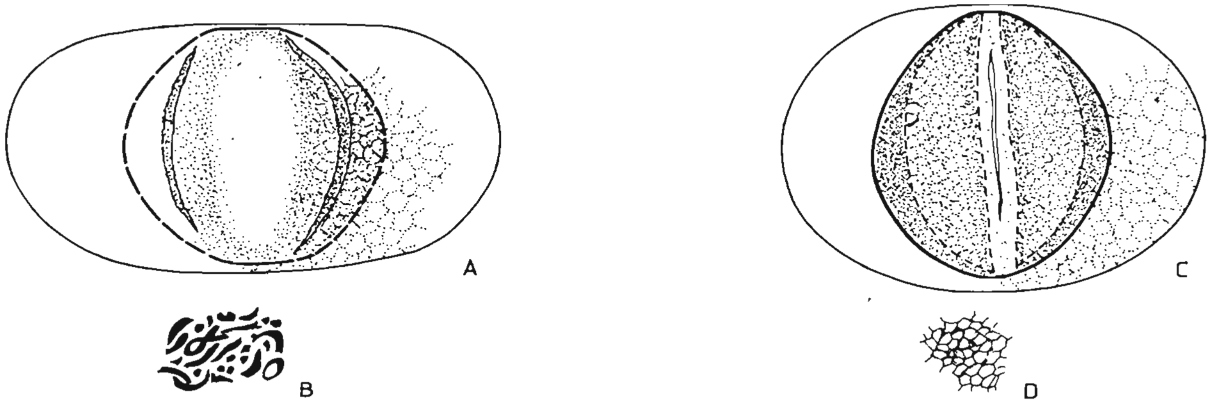
PLATE 12



Text-figure 15 — A, *Falcisporites (Pityosporites) zapfei* based on specimen in Leschik 1956, pl. 22, fig. 7 showing lunar folds at the proximal saccus attachment line, distal SAFRA with subovate round-ended sulcus, coarse reticulation of sacci (partially drawn) and **B,** structure of cappa. Compare **A** with C - Satsangisaccites Bharadwaj & Srivastava, 1969; **D**. structure of cappa of C.

half-sphere, proximally equatorially attached, distally inclined forming narrow, straight, indistinctly structured SAFRA. Saccus infrareticulum fine, apparently similar to sexine of taeniae; protosaccate.

Remarks — *D. singrauliensis* is distinguished by its big diploxylon sacci and small subcircular central body with two bean-shaped taeniae.

The salient features for the species of the genus *Dicappipollenites* are as under :

Central body bearing two taeniae; sexine finely infrareticulate; sacci shape variable

D. crassus — Ovalish-circuloid central body with two big taeniae; sacci crescent - shaped.

D. nyakapendensis — Horizontally oval small body; sacci *more* than hemispherical.

D. balmei — Horizontally oval central body, taeniae prominent; sacci less than hemispherical.

D. singhii — Vertically oval central body, taeniae wide, sacci ± hemispherical.

D. singrauliensis — Prominently diploxylon shape, central body subcircular, small; taeniae of uneven width and thickness.

Krempipollenites gen. nov.

Synonym

All the species described under the genus *Klausipollenites* Jansonius 1962 from the Permian and Triassic of India.

Type species — *Krempipollenites indicus* sp. nov.

Generic diagnosis — Bisaccate small pollen without striations, taeniae or any type of mark; strongly haploxylon in shape with circuloid, horizontally oval to obovate outline. Corpus well-defined, proximally finely and uniformly infrareticulate with complete and perfect muri forming very fine polygonal meshes. Cappa not prominently developed. Sacci haploxylon, crescent-form to variable of less than half-circle in polar view, smaller than the corpus, appearing like ear-lobe extensions, may be with smooth constrictions but no notches at the contour at body-saccus junction, and having a broader attachment base; proximally equatorially attached, distally inclined, laterally smoothly continuous with a very narrow sexinal layer. Distal saccus-free-area (SAFRA) not sharply delineated by folds or defined lines; distal bases of sacci gradually merging with the fine structure and ultimately with nexine of SAFRA; apparently a subovate, thin, elongated narrow saccus-free-area extending full length of lateral axis of the central body seen. Sacci relatively coarser than cappa in structure; protosaccate.

Comparison — Although sharing a form-similarity, the genus *Klausipollenites* Jansonius 1962 based on the holotype of *Pityosporites schaubergeri* Potonié & Klaus (1954, pl. 10, fig. 7), is considered to be a different lineage than *Krempipollenites* gen. nov.

The specimens assignable to *Klausipollenites schaubergeri sensu* Jansonius 1962, from the materials studied by Leschik (1956), Klaus (1963, 1964), Mädler (1964a, 1964b) and Schaarschmidt (1963), have a distinctive exine structure and typical tendency to bear a restricted distal sulcus which does not extend up to the lateral margin of body outline, but remains as circuloid area at the centre.

The photomicrograph of holotype of the type species (Potonié & Klaus, 1954, pl. 10, fig. 7 here illustrated Pl. 12, fig. 6; Text-figures 5B, 12D) shows encroachment of coarser saccus infrareticulation from all the sides on to the central body distally which restricts the distal SAFRA as a very small circular to subcircular sulcus in the centre. This trend is also depicted in the second specimen illustrated by Potonié and Klaus (1954, pl. 10, fig. 8; here in Pl. 12, fig. 7; Text-figure 12E), which is laterally flattened and where the lateral continuation of saccus is prominent in the form of a broad continuous layer of coarsely structured covering on most of the lateral region of the corpus distally. Thus distally only a small, thin, sulcoid area remains uncovered by sacci. On the other hand, the specimens included in *Krempipollenites* gen. nov. do not possess such a prominent invasion of the sacci on to the body over the distal region; they have full-length SAFRA in the centre of the body (Text-figures 5, 12D, E; Pl. 13, figs 1-3, 5-10).

Jansonius (1962) included such forms in the genus *Klausipollenites* which show full length, wide saccus-free-area on distal face of the body, two prominent folds or thickenings in the body at the equatorial region along the saccus bases, and a line of "apparent weakness over the distal pole, often causing folding along this line or secondary folds in the area"; this median vertical fold has apparently "germinal significance" (Jansonius, 1962, pl. 12, figs 21, 23-26 here in Pl. 13, fig. 4; Text-figure 12c). Besides, the forms having a monolete, trilete or tetralete type of thick ridges have also been proposed to be included in *Klausipollenites* (Jansonius, 1962, pl. 12, figs 28-30, 34, 36). There is no evidence of saccus encroachment from all sides on distal face of the body to a greater extent to leave a very small SAFRA — a character so well seen in *Pityosporites schaubergeri* Potonié & Klaus 1954; the latter species, however, also possesses thicker areas along the equatorial region of the central body at sacci bases which may be comparable to the folds seen in the specimens illustrated by Jansonius (1962). But in *P. schaubergeri sensu* Potonié & Klaus 1954, the median vertical fold in the centre of the SAFRA is not present. Moreover, in the type as well as other several specimens (in the slides of Leschik, 1956; Klaus, 1964) it is clear that distally saccus encroaches the body surface from all sides leaving only a small circuloid oval area free, which also seems to develop finer reticulum (a careful examination of photomicrograph given by Potonié and Klaus, 1954, pl. 10, fig 7, reveals this clearly). In *Krempipollenites* gen. nov., neither of these characters (equatorial sharp folds or thickenings, or a median vertical fold in SAFRA) is present (see Pl. 13, figs 1-3, 5-10; Text-figure 5A).

The structure of sexine had two lines of distinction in the population of these pollen, (i). finely and perfectly infrareticulate, and (ii). inframicroverrucose, irregular sort of infragranulose, infravermiculate or its variation — termed here as *Infravermiplexate* (with dots, islands, rod-lets, etc.). The material studied by us from European assemblages (*loc. cit.*) contains pollen with second type of structure, i.e., very fine infravermiplexate. But some of the species described by Jansonius (1962) have, in all probability, the infrareticulate structure. Visscher (1971) also illustrated comparable forms from Ireland. In Indian material, however, no such structure which could be classified in the second category, mentioned above, had ever been found. So also other Gondwanic materials exhibit the infrareticulate structure rather than infragranulate, infravermiculate (or infravermiplexate) one.

The genera *Falcisporites* Leschik 1956, *Alisporites* Daugherty emend. Jansonius 1971, *Satsangisaccites* Bharadwaj & Srivastava 1969, and *Labiisporites* Leschik 1956 differ from *Krempipollenites* gen. nov. in body-saccus construction and resultant shape, nature of SAFRA, its delimitation and the shape of sacci, apart from other details.

Raniganjiasaccites Kar 1969, apparently a comparable genus, includes subsaccate pollen with a proximal monolete-like mark or a thinner area to that effect (Kar, 1969, pl. 1, figs 18, 19). It is thus a synonym of *Vestigisporites* Balme & Hennelly 1955 emend. Tiwari & Singh 1984.

Organization — Text-figure 5A.

Derivation of name — In the honour of Late Professor Dr G.O.W. Kremp, the doyen of palynology.

Krempipollenites indicus sp. nov.

Pl. 13, figs 1-3, 5-10

Synonym

1977 *Klausipollenites schaubergeri* in Bharadwaj & Tiwari.

1984 *Klausipollenites schaubergeri* in Tiwari *et al.*; pl. 1, fig. 5.

Holotype — Pl. 13, fig. 1, Slide no. BSIP 11459.

Isotype — Pl. 13, fig. 6, Slide no. BSIP 11459.

Type locality — Borehole PGD-2, depth 358.50 m; Panagarh Basin, West Bengal, India.

Horizon & age — Panchet Formation, Early Triassic.

Diagnosis — Horizontally oval outline with smooth contour and crescent-shaped haploxylon sacci, size of the type 44 x 66 µm. Central body exine finely infrareticulate proximally, cappa not inflated. Sacci bases distally merging with sexine which become increasingly finer in infrareticulate structure, or even unstructured; attachment lines on distal side of sacci not defined; in proximo-distally flattened specimens a 1-2 µm wide continuation of saccus may be present on lateral sides. SAFRA thin, apparently wide and full-length along lateral axis of the body. Sacci with protosaccate fill infrareticulate.

Remarks — The tendency of specimens to get preserved sublaterally or laterally suggests that sacci are not aligned in same line with the body but are slightly distally pendate (see Pl. 13, figs 7, 10 for organization).

SOME MORPHOGRAPHICAL REMARKS

A time-to-time re-study of any type-material contributes to our understanding of many characters of the specimens which could have been thought to be less significant at the time of their first description. Implicitly, such a process reduces the degree of subjectivity which, otherwise, would continue to cloud the concepts of taxonomic delimitations. The authors of this article had several opportunities to study the European materials; their continuous efforts to understand the Gondwanic and Tethyan palynology made a backdrop to search for fundamental lines of deviations in northern assemblages. Partly, these materials were also studied earlier by several workers (Jansonius, 1962; Scheuring, 1970, 1974, 1978; Grebe & Schweitzer, 1962; Visscher, 1971; Visscher *et al.*, 1974) and valuable observations were recorded by them. In the following account, additional descriptions of certain type specimens, or comments on some important taxa as they have been understood now, are given. This will further give an insight into the theme (AFSIM) proposed in this paper.

Kraeuselisporites Leschik 1955

Kraeuselisporites, as re-defined by Scheuring (1974), is an acavate spore in which the trilete rays do not enter the zona; moreover, the ornaments consist of bulbous-headed, round tipped cone and finger-like processes. In *Indotriradites* Tiwari 1964, the trilete rays enter on to the zona and reach up to its outer margin. It is distinctly cavate (Text-figure 17A, B). Comparisons of these taxa had been the matter of biased opinion (Balme, 1970), but Foster (1979) meticulously straightened out the tangle.

The occurrence of both these forms in one assemblage from Tethyan Triassic (Vijaya *et al.*, 1988) indicates that there has been a two-way influence of vegetation on this region.

Cordaitina Samoilovich 1953

Pl. 6, fig. 1

As stated earlier, the organization of *Cordaitina* Samoilovich 1953 is different than all apparently similar looking radial monosaccate pollen described from Gondwana (viz., *Parasaccites* Bharadwaj & Tiwari 1964; *Plicatipollenites* Lele 1964, etc.). This difference has been identified by Vijaya *et al.* (1988). The sexinal layer bearing coarser structure of alveoli in saccus continues on to the nexine as a blanket cover on one of the faces, while in Gondwana forms the corpus is finely

PLATE 13 →

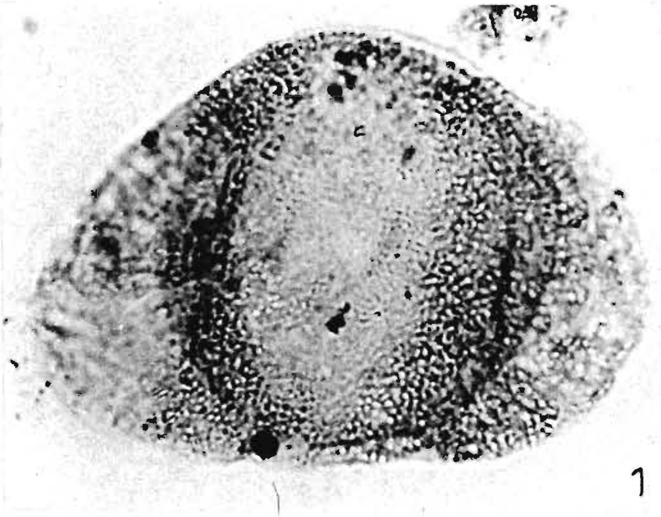
Specimens presently studied as *Krempipollenites indicus* sp. nov., are illustrated to show basic organization, structure of sexine on body surface, and full-length "SAFRA"

1-3. Holotype specimen in -- 1. mid, 2. top, and 3. low foci to show the merger of saccus along the zone of attachment, fine infrareticulation of sexine on body and wide full-length SAFRA; 1 & 2. x 1365; 3 x 750; Slide no. BSIP 11459.

4. *Klausipollenites staplinii* Jansonius, 1962; pl. 12, fig. 21. x 1500.

5, 7-10. *Krempipollenites indicus* sp. nov. x 750, 7. x 1500; Slide nos. BSIP 11459, 11460.

6. Isotype specimen in proximal focus showing fine infrareticulation. x 1000; Slide no. BSIP 11459.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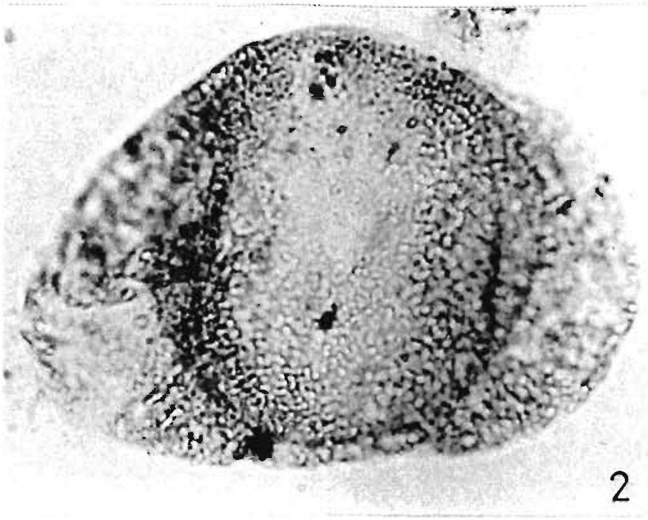
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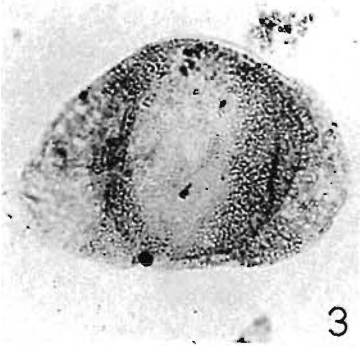
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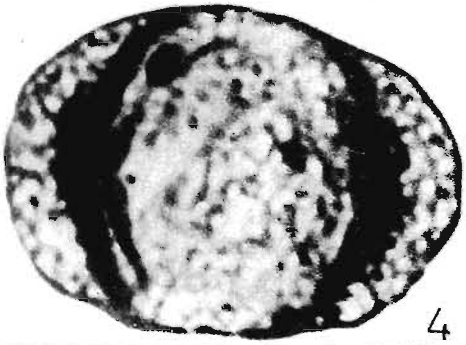
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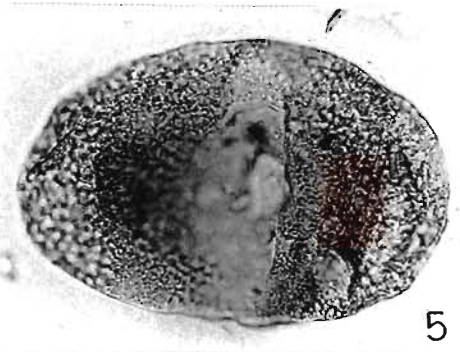
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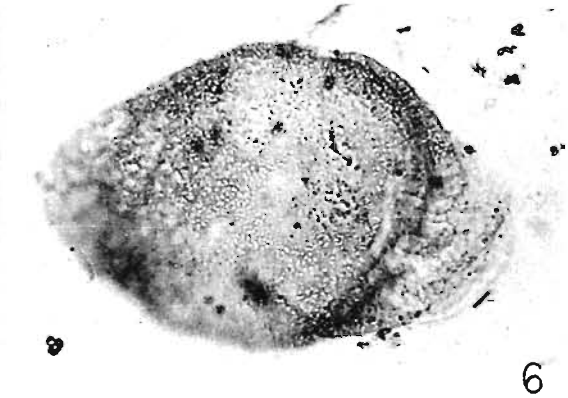
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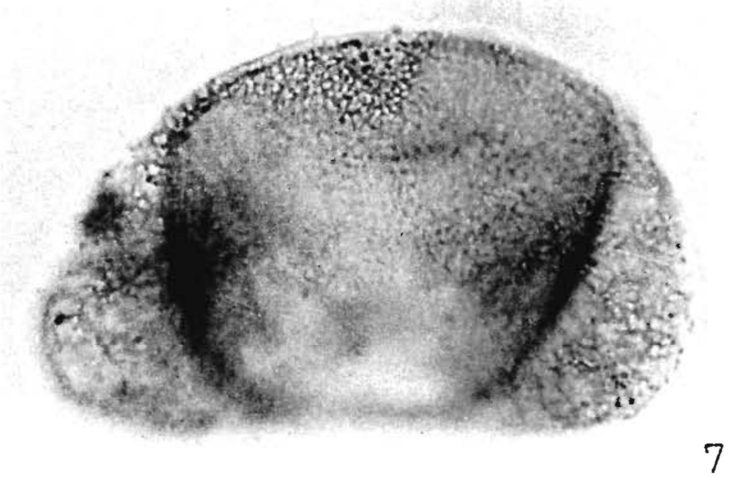
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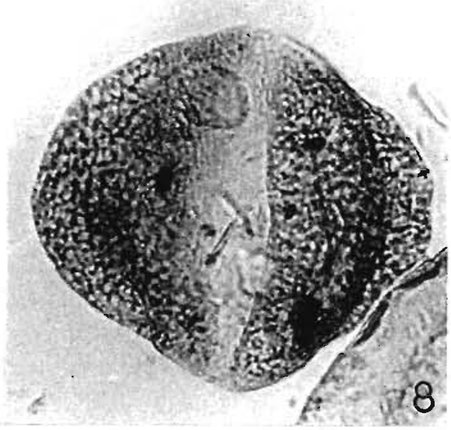
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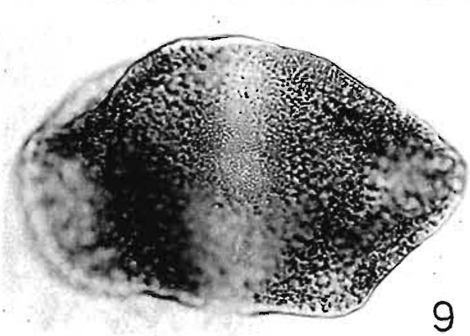
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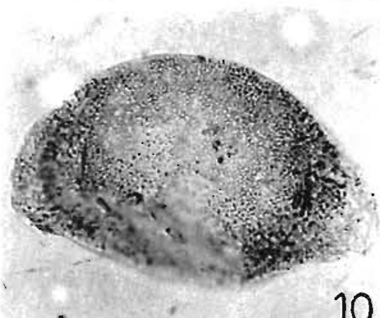
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PLATE 13

infrareticulate and in sharp contrast with coarser alveolate structure of the saccus. In *Plicatipollenites,* the zone of saccus attachment is associated with nexinal infold system of regular polygonal format (Pl. 5, fig. 1); in *Parasaccites* the attachment is merging but leaving free 70 to 80 per cent of distal face of the body at polar region.

No pollen similar to *Cordaitina* has been identified from the Gondwana continents; the Tethyan belt of Salt Range and Malla Johar Himalaya (Balme, 1970; Tiwari *et al.*, 1984; Vijaya *et al.*, 1988), however, do show the incidences of this taxon.

Hexasaccites Reinhardt & Schmitz 1965

Hexasaccites muelleri–type of pollen grains have been earlier assigned to *Triadispora* (Visscher, 1966), *Nuskoisporites* (Schulz, 1965) and *Stellapollenites* (Visscher, 1971). However, they do not belong to the first two genera because of organisational differences (refer Scheuring, 1970; Reinhardt & Schmitz, 1965; Adloff & Doubinger, 1969). *Hexasaccites* possesses a girdling monosaccus with symmetrical invasion of body from three regions on one of the faces (say first face), while on the other face (second face) the invading saccus-lobes change the angle by 60° with respect to those of the saccus lobes on the first face. The resultant organisation makes a star-shaped pattern with 6 saccus-free lanes, 3 on first face and other 3 on the second face. Thus basically *Hexasaccites* had a resemblance with *Stellapollenites* Lele 1965, but the invalidity of the former as a junior synonym of the latter (Visscher, 1971) is uncertain. Pollen included in *Hexasaccites* possess trilete mark on the nexine (Demelia, 1983), while those in *Stellapollenites* do not exhibit any such mark (Pl. 15, fig. 1). *Dacrycarpites europaeus* Mädler 1964b also shows a stellar organisation of sacci (*pers. obs.* 1980).

Crucisaccites Lele & Maithy 1964

Pl. 14, fig. 1

Another important marker of Early Permian in the Indian Gondwana is the genus *Crucisaccites* Lele & Maithy 1964 which is an unmistakable morphographic entity (Tiwari *et al.*, 1989). Apparently comparable forms have been reported from the European assemblages of Lower Thuringian (Visscher *et al.*, 1974). It is, however, notable that in the European *Crucisaccites* the saccus is extremely stunted (Pl. 14, fig. 7), hence the saccus structure is indeterminate. The Gondwana *Crucisaccites* is protosaccate, with alveolate-fill and fully blown, big saccus (Pl. 14, fig. 1).

Sulcatisporites Leschik 1956

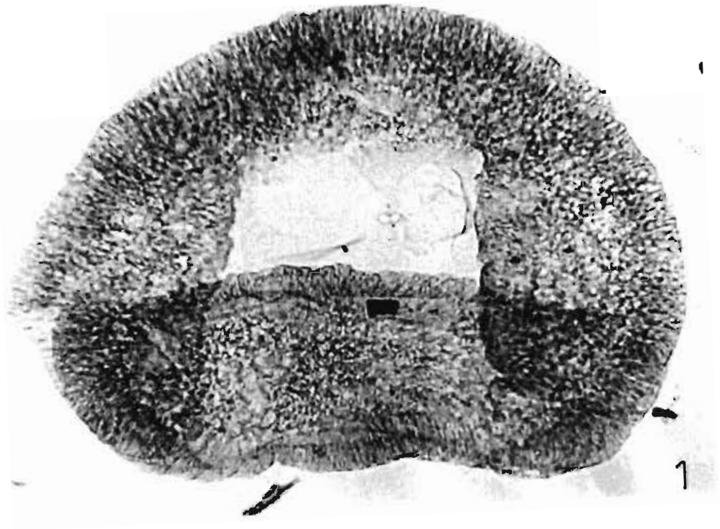
The holotype of the type species *Sulcatisporites interpositus* Leschik 1955 bears a bilete mark and well-defined body and is considered to be an abnormally preserved specimen of *Ovalipollis.* Thus, *Scheuringipollenites* was instituted by Tiwari (1973) to accommodate bisaccate pollen from Gondwana, till then assigned to *Sulcatisporites* Leschik; the former possesses indistinct thin nexine, no germinal mark, haploxylonoid sacci and infrareticulate structure of corpus.

The trend of sexine structure differentiation is further evidenced in the holotype of *Sulcatisporites splendens* (Leschik, 1956; pl. 22, fig. 10, p. 137) as : "Bilaterally oval pollen without lateral notches; a nicely preserved specimen is distal side up in the slide, 70 x 58 µm. Corpus well marked, vertically rhombish-oval, 40 x

PLATE 14

⟶

1. A specimen of *Crucisaccites indicus* Srivastava, 1970; a monosaccate pollen from Early Permian of India is characterized by cruciate mode of body-saccus attachment and protosaccate nature of fully blown saccus. x 720.
2. Holotype specimen of *Falcisporites zapfei* Leschik, 1956; pl. 22, fig. 7; from Zechstein of Europe, in distal focus showing sunken sulcus in "SAFRA" x 1000.
3. A portion of the specimen in Figure 2, enlarged, in proximal focus to show incomplete reticulae and "infravermiplexate" structure with prominent exinal elements in subtectum on central body. x 1500.
4. A portion of central body of the specimen in Figure 3, further enlarged to show nature of sexinal elements. x 3000.
5. Holotype of *Labiisporites granulatus* Leschic, 1956; pl. 22, fig. 11; enlarged to show "infravermiplexate" (incomplete reticulum, infragranulose to infraverrucose) structures in sexine, presence of a bent monolete mark in nexine covered with sexine, and protosaccate nature of saccus. x 1500.
6. Specimen of *Satsangisaccites* in the preparation of Bharadwaj & Srivastava, 1969; to show finely infrareticulate structure in sexine, presence of body folds on distal face, a median weak-zone and protosaccus - fill in sacci. x 750.
7. Specimen referred to as *Crucisaccites* in Visscher *et al.*, 1974; pl. 6, fig. 3; from Lower Thuringian of Europe which shows stunted sacci with indeterminate saccus structure (compare Figure 1). x 1310.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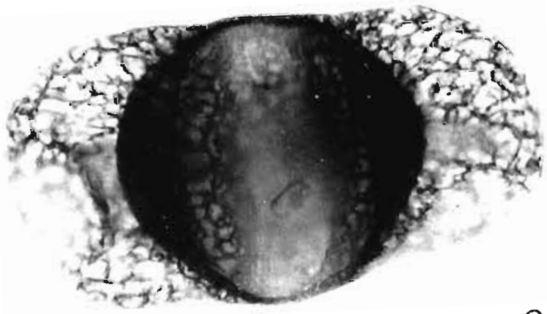
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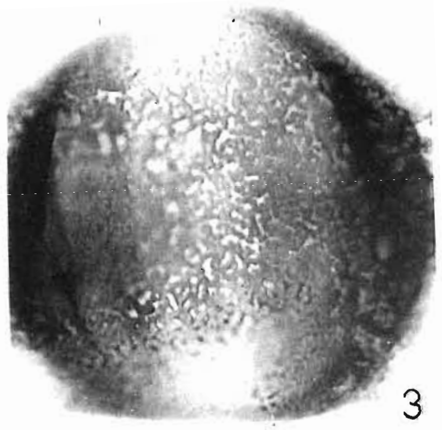
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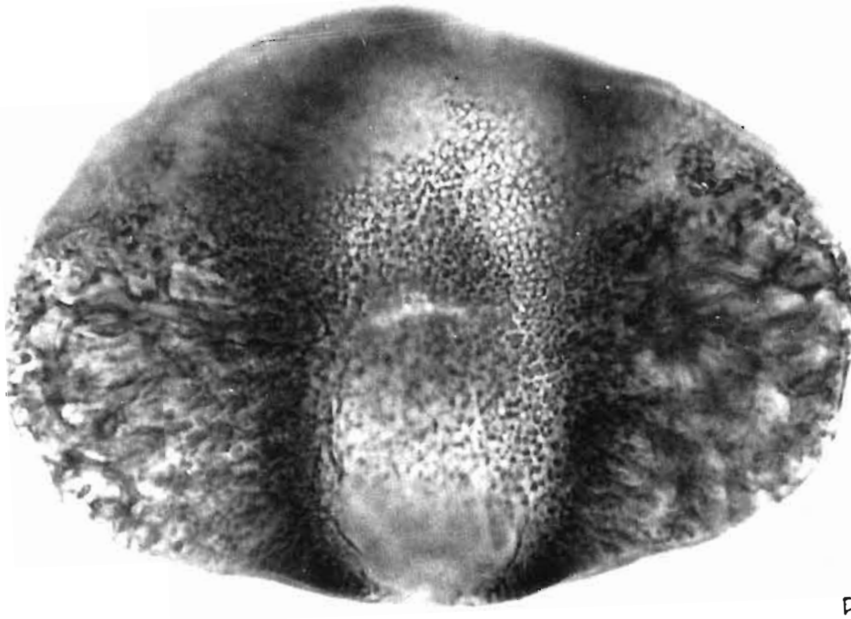
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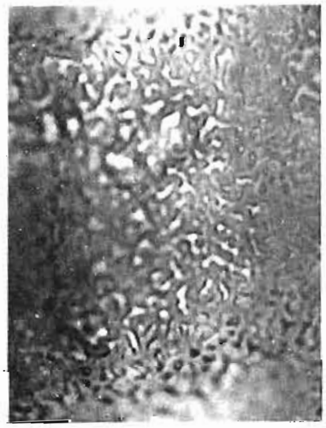
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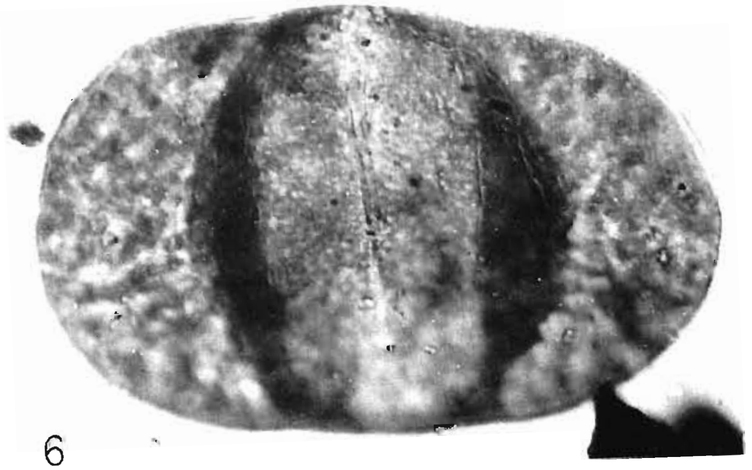
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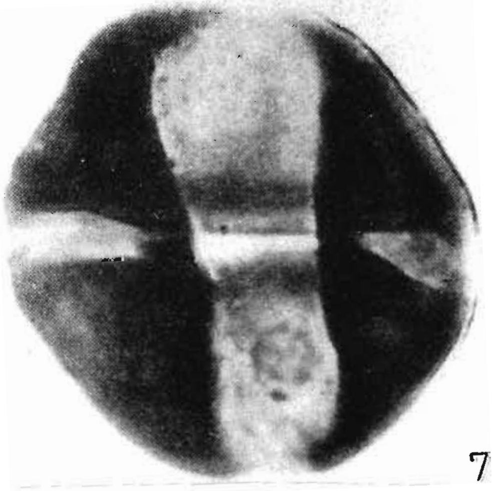
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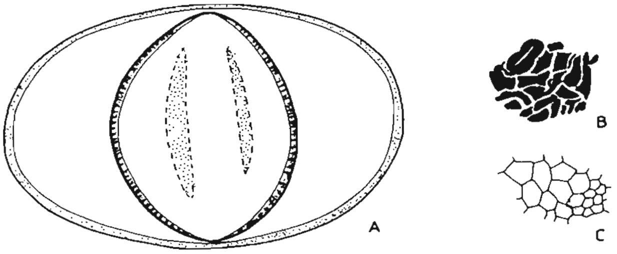
PLATE 14

54 µm. Cappa 3 µm thick, infravermiplexate with thick vermiculae and verrucae as structure in subtectate layer; in the central part of cappa the structure becoming obscure; on the margin column-like structure seen in optical section. Sacci less than hemisphere, perfectly infrareticulate, meshes 1-6 µm wide, muri 1 µm thick, coarser on distal side, limbus-like 2 µm wide zone seen at the periphery of the sacci; laterally this zone is continuous without notches. Distally sacci roots 6 µm apart from each other forming straight-sided, wide channel; attachment zones of sacci accompanied by 7 - 10 µm wide planoconvex nexinal folds (as in figure) which are 5-7 µm short of length to reach the lateral body margin; distally sacci encroaching the body. Structure of the saccus not protosaccate (Text-figure 16).



Text-figure 16 — *Sulcatisporites splendens* Leschik 1956, pl. 22, fig. 10 **A**, to show well defined body with prominent structure, limbus-like zone at sacci periphery and lunar folds at SAFRA lines; **B**, massive nature of infrastructure, **C**, perfect reticulation of eusaccate sacci.

The infravermiplexate structure of cappa is very prominent. The structure of saccus and the sulcoid SAFRA is also characteristic. No similar forms have been encountered in the Permian-Triassic of Gondwana. Another specimen described as *Sulcatisporites* sp. by Leschik (1956, pl. 22, fig. 9) although a badly preserved specimen shows infravermiplexate structure of cappa.

Falcisporites Leschik, 1956

Pl. 14, figs 2, 3, 4

Holotype — *Falcisporites zapfei* (Potonié & Klaus 1954) Leschik 1956.

This genus is understood to encompass the population of bisaccate, alete pollen with distinct distal sulcus. However, a careful study of the specimen illustrated and described by Leschik (1956, pl. 22, fig. 7) under this species revealed very interesting diversions from the normal contention regarding this taxon :

"Specimen bilateral, bisaccate; central body circulo-hexagonoid, with flatish lateral sides, darker than the sacci, 1 µm thick. Exine structure of the central body consisting of irregular, narrow, U-shaped, T-shaped, sickle-shaped or circular, discrete exinal elements in the subtectate region as infra-structure forming infravermiculate to infragranulose pattern, collectively termed as infravermiplexate.

Sacci encroaching the central body proximally from both the terminal sides up to 7 µm and attached subequatorially along with 2-3 µm wide lunar folds; distally sacci entering to a greater extent on to the body (up to 13 µm from body equator) and attached to the body leaving an ovoid, true, sunken sulcus (thin and unstructured). Laterally sacci showing 1 µm wide connectives. Sacci structure infrareticulate, with 3-5 µm hexagonal-polygonal perfect reticulation. Protosaccate condition not evident in L-O analysis".

It is thus derived that the specimen assigned to the genus *Falcisporites* by Leschik 1956 has proximal subequatorial body folds in a lunar fashion to which region the sacci bases are attached; the distal saccus-free-area is clearly defined as a sulcus. The most important character is the structure of central body exine. It makes the differentiation from similar-looking pollen of the Gondwanic origin where the body exine is perfectly infrareticulate (Text-figure 15). The genus *Falcisporites* is circumscribed on the type specimen of the Holotype *Pityosporites zapfei* Potonié & Klaus 1954, pl. 10, fig. 9 (see also another specimen of the same species : pl. 10, fig. 10). These two specimens are somewhat different than the one which is illustrated by Leschik (1956) and described above in having a narrower SAFRA and consequently narrow sulcus (as seen here in Pl. 14, fig 2), and proximal body structure as distinct narrow-meshed reticulum often with incomplete nature. The saccus construction, proto- or eusaccate, is indeterminate.

Another species *Falcisporites granulatus* Leschik 1956 (pl. 22, fig. 3; p. 136, type specimen) is a variant from the one described above. The type is a small pollen grain, 42 x 30 µm, with oval outline. Central body (nexine) is ovate with round ends 27 x 23 µm. Cappa is uniformly, finely infragranulose in structure; a small trilete mark is present on the nexine, covered with sexinal layer. Distal sulcus biconvex, 11 µm wide in the centre. Two lunar folds (5 µm wide) are present at the body equator bordering the sulcus. Sacci fine to mediumly coarse in structure, alveolate, protosaccate, inclined distally and reaching up to inner margin of the nexinal folds.

Falcisporites granulatus Leschik 1956 thus possesses finely infragranulose structure on cappa as revealed through the study of its type. Besides, the grain possesses a distinct trilete mark, two thick folds at body periphery, and polygonal areas on body surface (this, however, appears to be preservational artefact).

Satsangisaccites Bharadwaj & Srivastava 1969

Pl. 14, fig. 6

It is a distinct line of morphography in being bisaccate, usually haploxylonoid, with fully inflated half-circular sacci, having crescentic folds in nexine, situated at two terminal sides of the body along the equatorial region, and a distinct sulcoid groove which results into a thin linear, vertical fold in the centre of narrow SAFRA (Bharadwaj & Srivastava, 1969, pp. 130-133). The nexinal folds at body equator make a significant character which reflects the organisation of the body. So also, the narrow SAFRA with a narrow median furrow or a true sulcus represented by a weak-zone median fold which is an important feature developed in these bisaccate pollen. The fine infrareticulate structure of the cappa, which is not prominent, and the protosaccus-fill of sacci are additional diagnostic characters of the genus (Text-figure 15C, D). On the basis of this circumscription, *Satsangisaccites* could be differentiated from *Alisporites* Daugherty emend. Jansonius 1971 which has a tendency to become diploxylonoid with sacci bigger than the faintly outlined body, and a much broader SAFRA of diffused nature. *Satsangisaccites* is usually equated with *Falcisporites* Leschik 1956. They are excellent examples of apparent form similarity (AFSIM). But *Falcisporites* described above has a well-delineated elongated oval sulcoid groove-like depression occupying the entire SAFRA; the sexine in this specimen of *Falcisporites* is also not infrareticulate type, as in *Satsangisaccites*, but exhibits infraverrucose to infravermiplexate structure (Text-figure 15B). However, the type specimen of *Pityosporites zapfei* Potonié & Klaus 1954 has narrower sulcus, incomplete reticulum as body structure but no weak-zone median fold.

Labiisporites Leschik, 1956

Pl. 14, fig. 5

Type species — *Labiisporites granulatus* Leschik 1956.

Remarks — Few apparently similar forms found in Gondwana have been assigned to this genus (Lele & Karim, 1971; Lele & Makada, 1972). In order to understand the morphography of this taxon, the Holotype of the type species of this genus (Leschik, 1956; pl. 22, fig. 11) is being described in detail.

"A nicely preserved, proximally up, dark brown specimen without detritus. Bisaccate, bilaterally oval, 51 x 75 µm. Sacci smaller than the body height, but terminally elongated. Central body outline not sharp, apparently oval elongated with broad round ends, exine infragranulose to infraverrucose having islands, dots, dashes and irregular-shaped fine discrete exinal elements in the subtectate layer; slightly bent, not sharply delimited monolete mark present on intexine, and the sexine layer covers this mark. Sacci proximally invading the body equator to quite some extent and merging with it; distally also up to the same extent but with a sharp line of attachment; no lunar folds present; distal sulcus well marked, thin elongated area. Sacci laterally 2 µm wide and continuous at one of the sides, with fine-coarse-fine reticulation as deciphered in L-O analysis in top-middle-bottom foci from the surface, respectively, suggesting a protosaccate condition, meshes up to 7 µm wide, muri 1-1.5 µm thick, unevenly thickened, massive in nature; limbus-like structure not seen."

The second specimen referred to this species by Leschik (*Labiisporites granulatus* Leschik 1956; pl. 22, fig. 12; p. 13) is also a nicely preserved specimen : light brown distally up, 66 x 55 µm; body vertically oval with rounded lateral sides, less than 1 µm thick; mark represented by a 12 x 4 µm triangular vent in the centre. Body cappa infragranulose, infraverrucose or with small island-like exinal elements in the subtectate region which are fine, may be fused but not forming rod-lets; lunar folds very narrow along the distal zone of saccus attachment. Sacci proximally equatorially attached distally leaving a 14 μm wide, groove - like sulcus, laterally 1 μm wide continuation on both sides. Structurally sacci protosaccate with coarse muri and thick meshes, columnar in optical section."

In the Indian Gondwana material such conditions of monolete, being present in the nexine covered with sexine, the infragranulose to infraverrucose structure of the body, and the true sulcus are never recorded in the otherwise-similar-looking pollen.

Crescentipollenites Bharadwaj, Tiwari & Kar 1974

Pl. 3, fig. 2

Type species — Crescentipollenites fuscus (Bharadwaj) Bharadwaj, Tiwari & Kar 1974.

Remarks — Striate bisaccate pollen group is a very complex repository of taxa. During Permian and Triassic, the striate and taeniae-bearing pollen and the alveolate protosaccate fill of saccus appear to be cosmopolitan. Inspite of their form similarities, however, several differences do exist. The genus *Crescentipollenites* stands on the features of striations, distinctly fine infrareticulate sexine of corpus and tapering fold at distal sacci roots. The description given by Bharadwaj, Tiwari and Kar (1974, p. 143, 144) are elaborated below in order to add new observations :

"Bisaccate pollen with horizontal striations (not taeniae with nexinal inter-spaces). Cappa normally not inflated. Striations are linear grooves of generally less than 1 μm wide with uniform width all along their lengths, simple or branched with or without connections between them. SAFRA is well delimited by sacci-base attachment. Two, mostly semi-lunar, crescentic or taper-end vertical folds run parallel with each other, in the nexine distally, normally lying in the region of saccus attachment zone and extending laterally up to full-length of the body. Typical groove or furrow as a true sulcus not developed. Saccus with infrareticulate- or alveolate-fill forming protosaccus (Pl. 3, fig. 2).

The structure of cappa shows fine infrareticulation with thin, narrow, perfect muri and complete, polygonal meshes which contrast with the coarser structure of sacci beyond the equatorial region. Slit or mark on the cappa are absent.

Foster (1979) considers that *Crescentipollenites* is a synonym of *Striatopodocarpites* Zoricheva & Sedova *ex* Sedova 1956 emend. Hart 1964. However, in originally designated type of *Striatopodocarpites* (Sedova, 1956, photo. 3), semilunar folds do not appear to be present in nexine. In the line drawing (Sedova, 1956, drawing 3) such folds are drawn but this drawing does not seem to be based on photo 3. The end-to-end typical lunar folds with curved alignment of sharp SAFRA makes *Lunatisporites* a unique organization. Type specimens of *Striatoabietites* and *Striatopinites* (Sedova, 1956), although possess lunar folds, have monolete mark on the body. The central body with longer polar axis develops compensatory folds on flattening to accommodate larger surface area. Elongately oval, rhomboid body with long polar axis develops perfect lunar folds. The central body with shorter polar axis does not develop such folds.

Chordasporites Klaus 1960

Type species — Chordasporites singulichorda Klaus 1960.

Remarks — Vijaya *et al.* (1988) have opined that the specimens from Gondwana palynofloras assigned to *Chordasporites* Klaus 1960 do not find their place in this genus because they do not exhibit the typical "chord" (variant spelling of "cord"; a straight line connecting two points); mostly a compressional fold (Pl. 15, fig. 3) on the central region of cappa is depicted, which generally has been taken as "chord". In some of the Australian and Indian forms, however, suspected chord needs confirmation.

In order to understand this genus, a brief description of the Holotype of the Type species (Klaus, 1960; pl. 33, fig. 45) is being given below :

A badly preserved, sublaterally oriented specimen, having a well-defined, horizontally elongated, trapezoid corpus. Cappa well developed, 2-4 μm thick, as seen in optical section, apparently corroded, unevenly thickened, divided into many irregular and faint areas of 2-4

PLATE 15

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1. Specimen of *Stellapollenites* Lele, 1965; pl. 1, fig. 2 to show stellate mode of body-saccus attachment. x 500. Slide no. BSIP 694.
2. *Scheuringipollenites* Tiwari, 1973; showing thin nexine and protosaccate structure of sacci. x 750.
3. Specimen referred to "*Chordasporites*", which possess a compressional fold rather than a chord on proximal face of body. x 750

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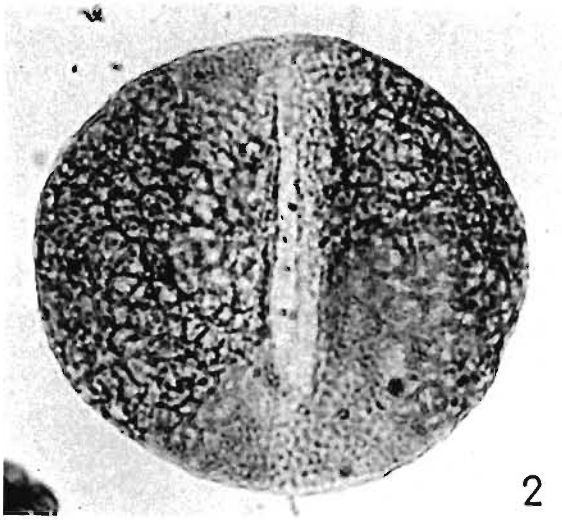

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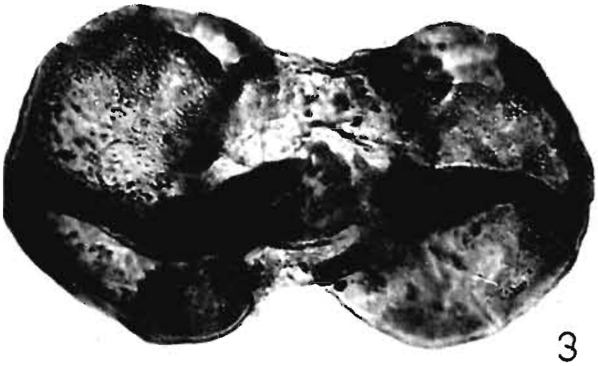


3

PLATE 15

μm size, by fine grooves forming a coarse reticulate pattern; this feature is clearly seen on the cappa outline at places. Cappa structure not clear, amorphous to indistinctly infragranulose. In the central region two vague, horizontally running narrow thickenings can be located, between which a linear, slightly wavy, chord-like thickening is present. It is half of the body's horizontal axis in length. Sacci dislocated sublaterally, equal to corpus in size, proximally equatorially attached, distally invading the corpus leaving a well-defined, broad, oval area bound by thin narrow folds of nexine. Saccus structure indistinct, hardly perceptible, faintly infrapunctate.

It is thus clear that in *Chordsporites* the "Chord" is a short, narrow, solid, wavy linear thickening of exine in the centre of cappa, rather than a fold. Besides, typical broad oval sulcus, a thick cappa and indistinctly structured sacci make this genus distinctive. The specimen is, however, badly preserved and exine pattern could be secondary. No comparable chord is yet known in Gondwana pollen. To illustrate these observations, a line drawing based on the Type specimen of the Holotype is given as Text-figure 13A.

Lueckisporites Potonié & Klaus 1954

Pl. 10, figs 1-3

Several specimens of this genus were studied from the Zechstein material. In order to achieve an understanding of the detailed representative characters, the specimen of *Lueckisporites virkkiae* Potonié & Klaus, described by Leschik (1956; pl. 21, fig. 17, p. 133) is described here :

Diploxylon construction, 76 x 53 μm, distally up, dark brown pollen. Corpus subcircular, 46 μm, well defined, 2 μm thick, proximally bearing two distinct massive taeniae expanding 2-6 μm beyond the corpus outline reaching over to the sacci, slightly less than half-circle, with inner margin mildly and irregularly concave, each measuring 53 x 23 μm. Taeniae thickened in their circumferential region with radially arranged column-like structural elements as seen in optical section; the inward facing margins of taeniae unthickened. Structure in surface view infragranulose to infraverrucose. Intertaenial nexinal path bears a 10 μm long slightly bent prominent monolete mark.

Distally a prominent ring like nexinal fold present, the ring being roundly oval, encircling 27 μm wide area at the centre; the ring-fold being continuous, 5 μm wide. Sacci bigger than the corpus, kidney shaped but fairly blown, 15 μm wide x 53 μm along the lateral axis, laterally ± 10 μm apart from each other; fine-coarse-fine alveolar structure evident in L-O analysis at top-middle-bottom foci, protosaccate. Distally sacci attached in the fold-ring region; proximally sacci subequatorial in attachment appearing to emerge from below the taeniae.

Remarks — Grossly comparable forms are known from the Gondwana flora. But the massive taeniae with radial pattern of columnar subtectate elements as seen in optical section, and the prominent monolete slit on the inter-taenial unstructured exinal path is unique for this species (Text-figure 11).

Lunatisporites **Leschik emend. Scheuring 1970**

Pl. 7, figs 1-3

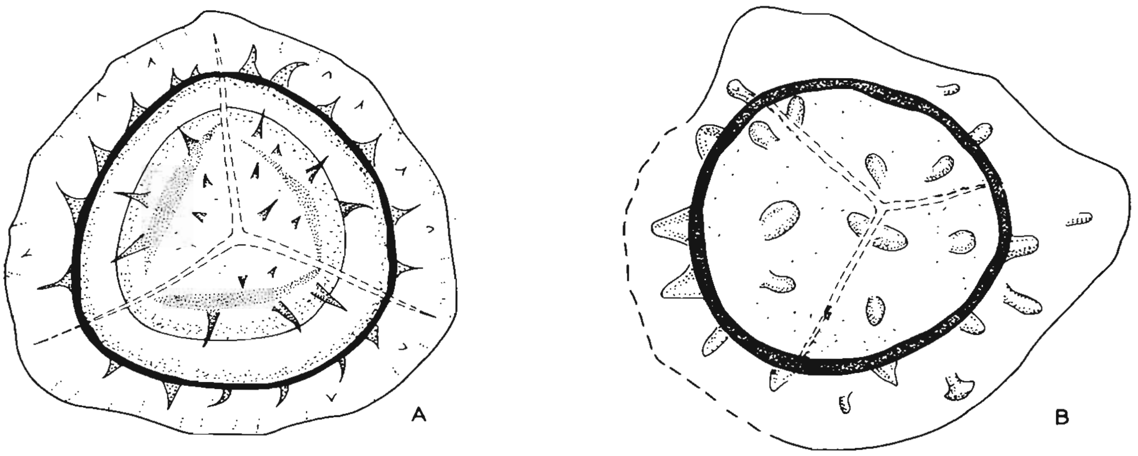
Scheuring (1970, 1978) studied the *Taeniaesporites -Lunatisporites* complex in detail and described the type material of this group. He recognised *Lunatisporites* as a valid name and incorporated *Taeniaesporites* under this genus as a junior synonym.

Some of the specimens of this taeniae-bearing pollen complex from Leschik's (1956) material are described below in order to decipher the basic characters.

Taeniaesporites noviaulensis **Leschik 1956**

Holotype — (pl. 22, fig. 1, p. 134) A nicely preserved specimen, bilateral, diploxylonoid, distally up in slide; corpus horizontally ovoidal-circuloid, with one lateral side being flat; 46 μm vertical axis x 61 μm horizontal axis. Corpus nexine 1.5 μm thick, sharply defined. Proximally bearing 5 prominent taeniae, two of the laterally situated taeniae transgressing the nexine outline, two median taeniae broad and fully grown but the remaining one taeniae in the middle is short and placed near the equator of body. Taeniae leaving 1 to 7 μm wide inter-taenial nexinal space in between themselves. Sexine structure infravermiplexate, appearing as rodlets, islands or sickle-shaped elements forming a channel-like pattern by exinal elements in the subtectate region.

The nexine between taeniae smooth, unstructured, median path bearing a 19 μm long, sharply defined monolete mark. SAFRA 32 μm wide in centre, biconvex,



Text-figure 17 — **A,** *Indotriradites* Tiwari 1964 showing cavate construction, distal ornament (spines) and trilete rays reaching on to the flange; **B,** *Kraeuselisporites* Jansonius em. Scheuring showing acavate construction, distal ornament (verrucae and finger-like rounded cones, etc.) and trilete rays not reaching onto the flange.

laterally 16-20 μm wide. Nexinal folds not apparent, except two short olds at the margin of corpus as in Text-figure 8C. Sacci fully blown, coarsely infrareticulate, meshes 5-8 μm wide, muri simple, straight less than 1 μm thick, uniform, radially elongated near the body; sacci proximally ± rially attached to the body, laterally continuouσ βψ 1 μm wide connection. Eusaccate (Text-figure 8C-E).

Another specimen referred to *Taeniaesporites noviaulensis* by Leschik (1956; pl. 22, fg. 2) bears four prominent taeniae whose structure is similar to the Type specimen (i.e. infravermiplexate). In other characters also it closely compares with the latter.

The species which are so far described from the Indian Gondwana material (Maheshwari & Banerji, 1975; Bharadwaj & Tiwari, 1977; Tiwari & Rana, 1980, 1981) as *Lunatisporites* do not find their place in this taxon, because in the Gondwanic forms the sexine of taeniae is finely and completely infrareticulate, the monolete mark is absent, taeniae are not massive, and sacci are alveolae-filled. As discussed in the preceding account, the Gondwana pollen of apparent-form-similarity have been now included under the genus *Arcuatipollenites* gen. nov. (Text-figure 8F).

The holotype of *Taeniasporites antiquus* Leschik (1956; pl. 22, fig. 4; p. 134), bears several taeniae, 10 in number short of horizontal span of body or full-length, irregularly arranged, wedge-shaped, knotty, wavy in appearance. The structure of taeniae exhibits infragranulose pattern in subtectate region, with unequal grana, discrete or fused, imparting wavy appearance to the margins of the taeniae (Text-figure 4D, E). Sacci are proximally finely infrareticulate but internally and distally with coarse reticulate structure having up to 8 μm wide polygonal or elongate meshes and thin wavy muri, appearing to be protosaccus.

The specimen is not well-preserved yet the prominent infragranulose structure of taeniae is distinct. No such structure is ever found in the taeniate pollen of the Gondwana palynofloras.

DIFFERENTIAL MORPHOGRAPHIC FLOWS

When the Euromerian and Indian Gondwana palynofloras of Permian and Triassic are analysed from the AFSIM (Apparent Form Similarity) point of view, the distinct flows of morphographic pools become evident (Table 1). This does not mean, however, that there is no real inter-mixing of morphographic features amongst palynomorphs of two regions. Yet because of the differences in the mother vegetation and in climatic conditions due to latitudinal disparity, the flows of characters, in several cases, are not same as they appear to be (Table 2).

Major groups of spores and pollen are discussed below :

Monosaccate pollen — Four basic organizations make the main lines of the morphos in the earliest Permian Lower Gondwana monosaccate pollen.

Table 1—Characterisation of northern and southern spore-pollen composition in Permian and Triassic sequences.

EUROMERIA			GONDWANA	
Aratrisporites	Monosulcites	T_3	Aratrisporites	Minutosaccus
Camerosporites	**Ovalipollis**		Arcuatipollenites	Playfordiaspora
Cicumpollis	Paracirculina		Araucariacites	**Podocarpidites**
Doubingirispora	**Parillinites**		Brachysaccus	Samaropollenites
Enzonalasporites	Patinasporites		**Densoisporites**	Satsangisaccites
Eucommiidites	Ricciasporites		Enzonalasporites	**Staurosaccites**
Heliosaccus	Saturnisporites		Goubinispora	Striate-few
Kyrtomisporites	Striatoabieitites		**Infernopollenites**	Vitreisporites
Labiipollis	Triadispora		Krempipollenites	
Leschikisporis	Vallasporites		**Lundbladispora**	
Lunatisporites	Zonate-types			
Microsaccus				
Minutosaccus				
Araucariacites	**Ovalipollis**	T_2	Aratrisporites	Nevesisporites
Camerosporites	Parillinites		**Arcuatipollenites**	Orbella
Chordasporites	Parvisaccites		Auracariacites	**Playfordiaspora**
Costatisulcites			Carnisporites	**Podocarpidites**
Doubingirispora	Presacculina		Crescentipollenites	Pretricolpipollenites
Eucommiidites	Saturnisporites		**Densoisporites**	Ringosporites
Falcisporites	Scutasporites		**Dicappipollenites**	**Satsangisaccites**
Illinites	Strotersporites		Faunipollenites	Simeonospora
Infernopollenites	Sulcosaccispora		Goubinispora	Striatopodocarpites
Jugasporites	**Triadispora**		Guttatisporites	Tigrisporites
Klausipollenites	Tsugaepollenites		Infernopollenites	Vitreisporites
Kugelerina	Vitreisporites		**Krempipollenites**	
Lagenella	Zebrasporites		**Lundbladispora**	
Lunatisporites	Zollerella		Murrigerisporites	
Alisporites	Labiipollis		Alisporites	Krempipollenites
Aratrisporites	Lunatisporites		Apiculate group	Lundbladispora
Aulisporites	Lundbladispora		Aratrisporites	**Playfordiaspora**
Araucariacites	Microcachryidites		**Arcuatipollenites**	Ringosporites
Brachysaccus	Minutosaccus		Araucariacites	Satsangisaccites

EUROMERIA			GONDWANA	
Carnisporites	Orebella	T_1	**Callumispora**	Striatopodocarpites
Colpectopollenites	Perisaccus		**Densoisporites**	Vitreisporites
Conaletes	Striatisaccus		Dicappipollenites	
Cordaitina	**Triadispora**		Goubinispora	
Falcisporites	**Voltzeaceaesporites**		Indotriradites	
Illinites				
Klausipollenites				
Cordaitina	**Lueckisporites**	P_2	Arcuatipollenites	Parasaccites
Corisaccites	**Lunatisporites**		Corisaccites	Playfordiaspora
Falcisporites	Lundbladispora		Crescentipollenites	Plicatipollenites
Gardinasporites	**Nuskoisporites**		Densipollenites	Sahnites
Gigantosporites	Paravesicaspora		Dicappipollenites	Satsangisaccites
Illinites	Perisaccus		**Faunipollenites**	Scheuringipollenites
Jugasporites	Playfordiaspora		Gondisporites	**Striatopodocarpites**
Klausipollenites	Striatopodocarpites		Indospora	Striomonosaccites
Labiisporites	Strotersporites		Indotriradites	**Verticipollenites**
Limitisporites	Vittatina		Krempipollenites	Vestigisporites
			Microbaculispora	Vitreisporites
			Navalesporites	
Apiculates	Lunatisporites	P_1	**Barakarites**	Plicatipollenites
Endosporites	**Nuskoisporites**		**Callumispora**	Potonieisporites
Florinites	Strotersporites		Corisaccites	Rugasaccites
Gigantosporites	Triquitrites		Crescentipollenites	**Sahnites**
Juli Group	Tuberculatisporites		**Crucisaccites**	Scheuringipollenites
Klausipollenites	**Vesicaspora**		Densipollenites	**Stellapollenites**
Lueckisporites			**Dentatispora**	Striatopodocarpites
			Dicappipollenites	Tiwariasporis
			Distriatites	Verticipollenites
			Faunipollenites	Vesicaspora
			Indotriradites	Vestigisporites
			Microbaculispora	Virkkipollenites
			Parasaccites	

Table 2 — Morphos shared by the palynoassemblage of Permian and Triassic in the northern and southern regions.

EUROMERIA		GONDWANA
Aratrisporites Brachysaccus Carnisporites Minutosaccus Playfordiaspora	T_3	Aratrisporites Brachysaccus Infernopollenites Lundbladispora Minutosaccus Playfordiaspora Podocarpidites Staurosaccites Vetreisporites
Araucariacites "Parasaccites" "Stellapollenites" Vitreisporites	T_2	Aratrisporites Auracariacites Carnisporites Guttatisporites Lundbladispora Murrigerisporites Orbella Playfordiaspora Simeonospora
Aratrisporites Carnisporites Lundbladispora Playfordiaspora "Crucisaccites" "Stellapollenites" "Striatites" "Striatopodocarpites"	T_1	Aratisporites Carnisporites Lundbladispora Playfordiaspora Striatopodocarpites Vitreisporites
"Corisaccites" "Crescentipollenites" "Crucisaccites Lundbladispora "Parasaccites" Playfordiaspora "Plicatipollenites" "Striatopodocarpites"	P_2	Corisaccites Crescentipollenites Indospora Gondisporites Playfordiaspora Striatites Striatopodocarpites "Strotersporites" Vitreisporites
Potonieisporites Vesicaspora	P_1	Corisaccites Crescentipollenites Crucisaccites "Labiisporites" Potonieisporites Stellapollenites Striatopodocarpites Vesicaspora

1. *Parasaccites* Bharadwaj & Tiwari 1964
2. *Plicatipollenites* Lele 1964
3. *Virkkipollenites* Lele 1964
4. *Potonieisporites* Bhardwaj 1954

An array of various lines of modifications from these organizations is seen in *Barakarites* Bharadwaj & Tiwari 1964; *Crucisaccites* Lele & Maithy 1964; *Vesicaspora* Schemel emend. Wilson & Venkatachala 1963; *Caheniasaccites* Bose & Kar 1966; *Divarisaccus* Venkatachala & Kar 1966; *Parastriapollenites* Maheshwari 1967; *Stellapollenites* Lele 1965; *Sahnites* Pant emend. Tiwari & Singh 1984, etc. (see Vijaya & Tiwari, 1992).

The identification of *Cordaitina-Nuskoisporites* as a separate stock from *Para-Plicati-Vikkipollenites*-complex has sorted out the basic identity in the north-south palynofloras. Specimens referred to *Crucisaccites* by Visscher *et al.* (1974, pl. VI, figs 2-4) from European Lower Thuringian possess stunted saccus with non-protosaccate nature. Can they be matched with the fully blown protosaccus-bearing *Crucisaccites* of the Karharbari Formation of Early Permian Indian Gondwana?

Demelia (1983) has described *Stellapollenites muelleri* (Reinhardt & Schmitz) Demelia, after examining several specimens under SEM. This makes a very good example of AFSIM factor, exhibiting the stellar organization of saccus in the Gondwana and European morphos. However, *S. muelleri* bears a well-defined trilete mark on the nexine of body. Such mark has never been reported in Gondwanic *Stellapollenites*. Besides, the structure of the body appears to be infravermiplexate in *S. muelleri* rather than infrareticulate (Pl. 15, fig. 1). It is also to be noted that *Stellapollenites* occurs in the Early Permian Gondwana while in northern flora similar looking forms have been reported from Triassic, e.g., *Dacrycarpites europaeus*, *Podocarpae-pollenites thiergartii* in Mädler, 1964a.

Several of the monosaccate species from Gondwana are conventionally assigned to the genera *Potonieisporites* Bhardwaj 1954 emend. Bharadwaj 1964 and *Vesicaspora* Schemel emend. Wilson & Venkatachala 1963. Lele and Shukla (1978) made an indepth analysis of the fold-patterns in the former genus and traced some linkage with *Plicatipollenites* in its organizational variability. Our study of such monosaccate pollen indicates that *Potonieisporites-Plicatipollenites-Sahnites* make one morphos group of transitional characters (Vijaya & Tiwari, 1992). *Vesicaspora*, on the other hand, does not have many characters which could significantly show variations leading to some of these morphos. The occurrence of these two taxa, or their "identification", in the Permian of north and south probably relates to their history in the Carboniferous stalk. The differences at species level in the population of these taxa in two areas under discussion are, however, significant and thus provide a working system for stratigraphy in each region.

Parasaccites-like pollen have been reported by some workers (e.g., Scheuring, 1978) in Middle Triassic, or studied by the authors from the European Permian material (e.g., in slides of Potonié & Klaus, 1954). However, they make distinct line of morphology either in unequal saccus encroachment on spheroid rather than disk-shaped body, or in having infraverrucose structure of the body exine. Typical *Parasaccites* are not yet recorded from Europe or North America.

In the Upper Permian, the Gondwana monosaccate pollen diversify into newer lines of character-states. The genera *Densipollenites* Bharadwaj 1962; *Goubinispora* Tiwari & Rana 1981; *Kamthisaccites* Srivastava & Jha 1988; *Striomonosaccites* Bharadwaj 1962; *Distriomonosaccites* Bharadwaj 1962 and *Playfordiaspora* Maheshwari & Banerji emend. Vijaya 1995b are some of the examples; most of the forms transgress into the Early Triassic as well. Recently, with a re-interpretation of eusaccate nature of *Playfordiaspora* its wide distribution in Euromerian as well as Gondwana Late Permian-Triassic sequences has been recognised by Vijaya (1995b). Rest of the morphographic lines represented by the taxa listed above appear to be restricted to Gondwanic region.

Bisaccate pollen — Simple striate bisaccate pollen with two prominent lunar folds at distal saccus attachment zones - *Crescentipollenites,* and non-striate bisaccate — *"Pityosporites"*, make two basic lines of morphography in Early Permian Gondwana. The occurrence of several taeniate and striate bisaccate pollen appears to cut across the boundaries of palaeogeographic regions. However, with the proposition of the AFSIM factor, the genera *Arcuatipollenites, Dicappipollenites, Faunipollenites* and *Crescentipollenites* become identity taxa for Gondwanic Permian-Triassic sequence. *Lueckisporites virkkiae* remains a distinct northern form. Some of the other forms appear to remain post-bag genera. Distinction in *Faunipollenites* Bharadwaj 1962 on one hand and *Protohaploxypinus* and *Striatoabieites* on the other lies in the fact that in the former the nexine is extremely thin due to which the body outline remains diffused and the sacci merge with the body at their attachment lines without any zone of demarcation (Pl. 3, fig. 1); the platea on body are also finely and perfectly infrareticulate in structure (Tiwari *et al.*, 1989). *Striatoabieites* possesses strineae or taeniae and infragranulose structure of body sexine (Scheuring, 1978).

With the distinction in the basic nature of striations and taeniae outlined by the present authors in this work (Pl. 4, figs 1-4) or in the past (Tiwari, 1982; Vijaya, 1990), most of the pollen earlier dumped as striate from the Euromerian region, now find their place in the taeniate group, e.g., *Striatoabieites* in Scheuring, 1978. However, there are some forms in the northern assemblages also which bear true striations (and not taeniae). For example (*pers. obs.*, 1980), *Striatites keuperi* Mädler 1964a (Triassic) bears ten striations (out of which one is branched) with infrapunctate sexine in between them and resembles *Striatopodocarpites*-type of forms of the Gondwana. *Fevisporites tenuis* Leschik 1956 and *Fastigatisporites cruciatus* Leschik 1956 reported from Zechstein, are again the examples which cannot be differentiated from the species of striate bisaccates from Indian Permian; they bear true striations but the structure of exine between the striations is infragranulose. However, the cappa in *S. keuperi* and *F. tenuis* is distinctly inflated and project out beyond the outline of the body as uniformly wide (2 µm) collar which is not a body thickening or an equatorial rim.

The main stock of striate bisaccate pollen in Early Permian Gondwana is *Crescentipollenites*. The diversity of forms related to this line is seen in *Circumstriatites* Lele & Makada 1972, *Faunipollenites* Bharadwaj 1962, *Distriatites* Bharadwaj 1962, *Striapollenites* Bharadwaj 1962, *Tiwariasporis* Maheshwari & Kar 1967, *Verticipollenites* Bharadwaj 1962, *Hindipollenites* Bharadwaj 1962 and *Rhizomaspora* Wilson 1962. One specimen of *Crescentipollenites* with true striations, infrareticulate exine and lunar folds has been noted by the authors while scanning the slides of Zechstein material of Grebe (1957); so also *Mesostriatites hercynicus* reported from the Lower Triassic by Mädler 1964b cannot be separated from *Striatopodocarpites decorus* Bharadwaj & Salujha 1964 of Upper Permian of India.

Distriatites Bharadwaj 1962 apparently resembles *Hamiapollenites* Wilson 1962 but it is confirmed that the former bears striations, while the latter possesses well-defined taeniae (strips of uneven width). However, the palaeogeographical distribution of these taxa is not fully known. *Rhizomaspora* has been widely identified in almost all the Permian assemblages of the world, and the genus appears to be a post-bag taxon, although no serious morphographical analysis has been done so far on this group. Another important genus, *Strotersporites* Wilson 1962, has to be circumscribed on the basis of a monolete mark or mark-like slit in the central region of the cappa generally associated with the median striation. The monolete mark appears to be a constant feature in the Permian pollen population of the northern hemisphere. In 'original' *Strotersporites*, the monolete, straight or bent, shows well-defined suture and prominent lips. In others, a pseudo-monolete is formed due to partial or full rupturing of the median striation, which results due to flattening of the curved surface of cappa. Well-defined lips and suture decide the true nature of mark.

The distinction of *Sahnites* and *Vestigisporites* for Gondwana and *Jugasporites, Limitisporites* and *Illinites* (Juli-group) for the Euromerian assemblages has cleared many of the AFSIM problems in the bisaccate pollen population (Tiwari & Singh, 1984; present work).

Pollen comparable to *Satsangisaccites* Bharadwaj & Srivastava 1969 have been reported from a microsporangiate organ of *Pteruchus* from the Early Triassic of India. This pollen genus makes an identity line of its own for Gondwanic region.

Klausipollenites, as redefined to bear a small circuloid SAFRA, an inflated cappa and a wide belt of saccus around the body, could be distinguished from *Krempipollenites* which is a population of simpler forms with full-length, diffused saccus-free-area and finely infrareticulate exine of the non-inflated cappa. Only extremely rare forms with infrareticulate corpus encounter in the Zechstein. The distribution pattern of these morphologies are not yet fully worked out, but the lines of AFSIM are visible. Similarly, *Scheuringipollenites* Tiwari 1973 makes a Gondwanan trait rather than that of the north.

Trilete spores — There appears to be a widespread matching ' in taxa reported from all palaeophytogeographic provinces, e.g., *Acanthotriletes, Lophotriletes, Leiotriletes, Verrucosisporites*, etc. The simplicity of exine structure does not provide multiple areas in morphographic comparisons. The Filicales, as such, are conservative in the expression of characters in spore exine manifestation.

However, notwithstanding such a situation of least diversification in fern-allied spores, the concept of Varitrileti Group (Tiwari & Singh, 1981) based on differential distribution of ornament on proximal and distal faces of spores makes real identity of otherwise-similar-looking forms. The Infraturma Varitrileti broadly includes — *Microbaculispora, Microfoveolatispora, Brevitriletes, Didecitriletes, Imperitriletes, Lacinitriletes,* etc. The lacinate folds associated with trilete rays and the differential distribution of ornament (where present) make these taxa unique. The creation of folds along vertex on flatening is a bauplan manifestation, the restricted distribution of ornament on distal face is a genetic expression. Such spores are normally not recognized outside of the Gondwana Province. So also, *Gondisporites* Bharadwaj 1962, a cavate, sculptured, typically having a ridge-like narrow cingulum is a Gondwanic element.

Monolete spores — The situation is not different in monolete spore group. *Latosporites, Laevigatosporites, Verrucososporites,* etc., are cosmopolitan. The genus *Navalesporites* Sarate & Ram-Awatar 1984, however, could be a distinct line of morphography and be used for phytogeographic determinations when its distribution is fully known.

The discussion given above has been summarised in Tables 1 and 2. The intermixing of forms in the region of Tethys shore, and the pattern of mutual occurrence in two regions are given in Maps 1 and 2. These data are not exhaustive so also not very specific in terms of stages or formations, yet a broad mosaic of provinciality can be derived from them.

Palaeoclimate and palynofloral structuring

The Late Carboniferous-earliest Permian witnessed the high intensity Gondwana glaciers whose cooling effect was felt up to the Palaeo-equator (Dickins, 1984; Cleal, 1991; Visscher, 1993; Wopfner, 1991; Wagner, 1993). The evidences of Asselian glacigene sediments are on record up to 30° S (Audley-Charles, 1988; Gonzalez, 1990; Vijaya & Tiwari, 1991). By the time of Early Sakmarian, the Carbono-Permian Gondwana glaciation had almost vanished from all the continents, except on the Antarctica. Fair to substantial occurrence of vegetation, i.e., *Gangamopteris- Glossopteris* flora, reflected in diverse palynoflora, during Asselian indicates that there were wide tracks of openland without the ice cover, which sustained the flora. The glaciers were not of sheet-type but localized on highlands, moving on to the lowlands and seas (Vijaya, 1995a). The withdrawl of glaciers initiated the amelioration of climate, proliferation of glossopterid forests and consequently the formation of coal swamps during Sakmarian through end Permian.

Recently, Kutzbach and Ziegler (1994) have used a climate model to simulate the climate of Late Permian and compared the model with Walter's climate-biome classification scheme. According to these authors, Antarctica, Australia, Indian Peninsula, Madagascar and South Africa experienced a cool temperate climate with a large regional climatic difference during Late Permian, while Tethyan (Himalayan) region including Salt Range, had a warm temperate climate. The climate of Middle East was mainly subtropical humid, or subtropical arid in localized areas. The southern Euromerian region of the Pangea had precipitation in all seasons in the north of equator due to east-west mountain range. The mainland Euromeria experienced subtropical to temperate dry climate with variation to arid conditions during Late Permian.

Ziegler *et al.* (1994) while dealing with the Early Mesozoic phytogeography and climate have opined that temperate latitude swamps disappeared about the beginning of Triassic in both the hemispheres, and cordaitids nearly became extinct from the north and so also glossopterids from the south. The area of Tethyan shore south of equator had a warmer climate in the Early Triassic. In the north, the latitudinal gradient ranged from dry subtropical to warm or cool temperate biomes. During the Early and Middle Triassic the biomes are less distinct with a warm temperate belt extending up to 70° N in the Euromerian region. On the Gondwanaland also similar situation appears to have had existed.

The northern limit of Gondwana flora is not easy to decide. Yet on the basis of dominance of *Glossopteris* the relative boundary is well accepted, inspite of sporadic report of the occurrence of *Glossopteris* leaves near low latitudes (Ash, 1981; Archangelsky & Wagner, 1983; Maheshwari & Bajpai, 1988).

An attempt has been made here to draw influence lines 1-S to 4-S in south and 1-N to 4-N in north of equator during Permian (Map 1) and Triassic (Map 2). These lines are neither Walter's biome lines (Walter, 1984) nor climatic lines in strict sense. They suggest the areas of influence of particular palynoflora, its intensity and gradient of paucity. Thus, for example, in Map 1 the southern most belt between 4-S and 3-S lines (densely stippled) is the region of *Glossopteris* vegetation characterised by certain group of spores and pollen; as we go up towards equator the influence of this zone becomes lesser and lesser (black dots with increasing sparsity) till the mainland Euromeria. Reversely, similar is the case of European palynoflora which shows its influence in the region of Tethyan shores in Middle East and northeast India. The belt between 1-S and 1-N lines is tropical but wider than the expected because the east-west mountain ranges in this area must have caused high rainfall making it a wider wet zone. In Map 2 the shifting and widening of influence 1-N : 2-N and so also 1-S : 2-S are based on the warming up of general climate, more intermixing of palynomorphs, presumably caused by migration of plant communities and northward movement of Pangea.

The Early Permian palynofloral structuring and distribution patterns of major morphos reveal that the typical Gondwanic elements were predominant between 3-S and 4-S lines (Map 1). This area was under the influence of glaciation and experienced a cool temperate climate. The palynomorphs mainly consist of girdling monosaccate pollen *Plicatipollenites, Parasaccites, Virkkipollenites, Potonieisporites,* and rare striate and non-striate bisaccate pollen, and pteridophytic spores. This assemblage is mainly associated with glacigene suites of Talchir Formation in India. The influence of the palynoflora which is found between 4-S and 3-S lines was felt in the region northward up to 2-S line although the cool temperate climate must have been changing to warm temperate due to the latitudinal gradient towards the equator (Singh, 1964; Hemer, 1965; Balme, 1970; Kar, Kieser & Jain, 1972; Chateauneuf & Stampfli, 1979).

The occurrence of rare and sporadic representatives of Gondwanic Early Permian in the region delimited by 2-S and 2-N lines is depicted by increasing sparsity of dots in Map 1. Such an impact is associated with the cooling effect produced by Gondwana glaciers.

The Late Permian witnessed almost complete vanishing of glaciers from the Gondwanaland and a cool temperate climate with warming trend prevailed. The palynoassemblage in India records the dominance of striate (not taeniate!) without monolete and non-striate bisaccate pollen; pteridophytic spores are common but the monosaccates decline drastically. The pattern of spatial distribution remains the same, as in Early Permian.

During Permian, the tropical region (1-S to 1-N line) and the main Euromerian subtropical belt (1-N - 2-N line) shows a different palynological composition when compared to the southern one, in having *Nuskoisporites, Cordaitina,* Juli group, *Lueckisporites,* taeniate (*Lunatisporites*) bisaccate (not striate) with monolete and *Klausipollenites.* The tropical belt has a slightly different aspect (solid circles) than the germanic and other European belt (Klaus, 1963; Scheuring, 1974) (dots in hollow circle : Map 1). In general, the Early Permian palynoflora is dominated by *Nuskoisporites* and *Lueckisporites,* while Late Permian shows predominance of *Lunatisporites, Klausipollenites* and the *Juga-Limiti-Illinites* Group. With the identity of AFSIM flows, the palynofloras between the lines 1-S and 2-N are considered to be different than those between 1-S to 4-S. The exine structure discussed in this paper makes the difference from Gondwana belts all the more clear. However, various degrees of intermixing has also been identified and shown in Map 1.

The Early Triassic had, by and large, experienced a global warming and drier conditions. In India it was not a drier period as was thought earlier, because diversified hygrophytic spores have been reported from the Early Triassic. The situation of influence lines are shown in Map 2. A comparative view from Permian time (Map 1) reveals a major widening of tropical/wet season belt (1-S to 1-N) and also that of the middle latitude and warm temperate belts (1-N to 2-N and 1-S to 2-S) in the Triassic. The Gondwana palynoflora between 2-S and 3-S lines, mainly contains *Playfordiaspora, Krempipollenites, Satsangisaccates* and *Arcuatipollenites,* beside cavate and apiculate spores. Apparently forms saccate pollen *Lunatisporites, Klausipollenites, Falcisporites,* are dominant in the Permian of Euromeria rather than in Triassic as *Arcuatipollenites, Krempipollenites, Satsangisaccites* are on Gondwanaland. The Middle Triassic palynoflora did not change remarkably from the Early Triassic, but in Late Triassic more elements of the north have entered into the region of high latitude of the southern hemisphere.

In Euromerian Early Triassic, the composition of spores and pollen is qualified by newer elements than the Permian. The Middle and Late Triassic had further differentiation (see Table 1). There had been no mass extinction at P/T boundary in the floral components of the globe.

MELTING-POT: MIDDLE EAST AND HIMALAYAN TETHYS

Inspite of divergent trends in many groups of pollen and spores, there are morphos which are shared by north and south (Table 2). However, in such determinations the post-bag genera — *Cuneatisporites, Platysaccus, Alisporites, Podocarpidites, Cycadopites*, several trilete spores and other groups of broader circumscriptions, cannot be considered as they appear to be "omnipresent". Similarly, the taxa representing minor variation or based on quantitative characters only, have little value in such comparisons. Considering the AFSIM factor, the major palynomorphs are enlisted in Table 1, which relieve the differences in two regions under discussion.

The Tethyan region on Indian Plate has proved to be a melting pot during Permian-Triassic period for Gondwanic vegetation on one hand and the European vegetation on the other, although the major influence in Kumaon, Garhwal, Kashmir and Salt Range is that of the glossopterid flora. Tiwari and Vijaya (1988) have identified the reflection of such a trend. The Middle East Permian and Triassic also show the impact of Gondwanic flora, but with a greater influence of the northern flora in having *Parasaccites, Indospora, Densipollenites, Faunipollenites, Arcuatipollenites, Sahnites* on one hand and *Cordaitina, Gardinasporites, Perisaccus, Nuskoisporites*, Juli-group on the other.

During Early Permian, the extreme cold condition and prevailing dominance of well-adapted Glossopteris flora on the southern Gondwanaland presumably did not permit the migration of plants from the area across the equator which was under much warmer climate. In Late Permian, however, invasion of some plant groups from the north could have been possible along the shore-line region of the Tethys (Map 1) which was relatively warmer than the main Gondwanaland. Because of the northward movement of Pangea, which started in Early Triassic, the latitudinal belts shifted southward; the resultant warming of the south could possibly have prompted more plants to migrate on to the Gondwanaland from Euromeria where much aridity and warming came up.

The route of migration must have been along the Tethys bank and island chains, in the Middle East and the north west Indian subcontinent. The Triassic witnessed more of two way traffic but the one towards south was more prominent in all periods of Permian and Triassic because of the changing climatic conditions. From south to north, there was steep upgradation in temperature at the equator which permitted only selected taxa to cross over. This disparity became somewhat subdued in Triassic yet the higher temperatures on northern region pushed the floral elements to the south where it was still not that warm.

CONCLUSIONS

In the taxonomy of *Sporae dispersae*, the "splitting" results in population boom and the "dumping" causes masking of differential characters. But complimentarily both can be purposefully utilized in achieving the progressive refinement of phytogeographic provinciality. The recognition of basic differences in sexine structure of taeniae and cappa of pollen in Gondwanan and Euromerian Permian-Triassic floras unmasks the finer character expressions which now defines the segregation of the unrelated populations having apparent-form-similarity. The megafossils and the *in situ* records indicate to corroborate these proposals by which the degree of intermixing, extent of migrations and alteration due to adaptations can be more effectively deciphered. The differential morphography of taxa suggested here reinforces the uniqueness of Gondwana flora. The patterns of intermixing of forms, more along the Tethys shore were controlled by the changing belts of climate. The Tethyan realm had been the region of migratory traffic as well as intermixing of morphos.

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