Protoeusaccites gen. nov.—A case of transitionary character-state in saccus structure in the Late Permian bisaccate pollen

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A new non-striate, bisaccate pollen genus—*Protoeusaccites* gen. nov., is described from the Middle Member of the Pali Formation, South Rewa Gondwana Basin, Madhya Pradesh, India. The grains are diploxylonoid with a prominent central body having a monoletoid mark or a thin area. The sacci with partial cavity in their chamber show a unique transitionary character-state, between the "Protosaccate" and "Eusaccate", in their structure.

Key-words—Palynology, *Protoeusaccites*, Middle Pali Member, Sohagpur Coalfield, Gondwana, Late Permian, India.

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सारांश

प्रोटोयूसेक्काइटिस नव प्रजाति—अनंतिम परमी द्विकोष्ठीय परागकणों की कोष्ठीय संरचना में परिवर्तनशील वर्ण-अवस्था का एक प्रमाण

रामशंकर तिवारी, विजया एवं राम-अवतार

मध्य प्रदेश (भारत) मे दक्षिण रीवा गोडवाना द्रोणी में पाली शैल-समूह के मध्य सदस्य से एक नयी अरेखीय द्विकोष्ठीय परागकण प्रजाति—**प्रोटोयूसेक्काइटिस** नव प्रजाति वर्णित की गयी है। ये परागकण एकअरीय चिन्ह् अथवा कृश क्षेत्र से युक्त विशिष्ट केन्द्रीय काय वाले डिप्लोक्सीलोनॉयडी हैं। इनके प्रकोष्ठ मे आँशिक गुहा से युक्त कोष्ठ इनकी संरचना में "प्रोटोसेक्केट" एवं "यूसेक्केट" के मध्य विशिष्ट परिवर्तनशील वर्ण-अवस्था प्रदर्शित करता है।

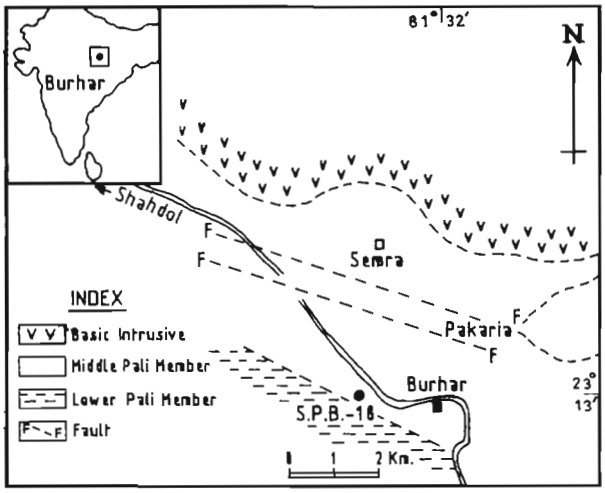
SACCATE pollen are the dominant components in the *Sporae dispersae* of Late Palaeozoic and Mesozoic sequences of the Indian Gondwana. Although detailed morphology of this group has been studied in the past, little attention was paid to the structure of the saccus. Scheuring (1974, 1978) published the landmark discovery in which he differentiated between eusaccate (true-saccate) and protosaccate (saccus filled with reticulum) conditions in the sacci of pollen from the Swiss Gips Keuper, Alpine Triassic. While the eusaccate condition is the character of saccate pollen of extant gymnosperms (Klaus, 1977), the protosaccate condition is the basic saccus-plan most frequently found in the pollen of geological past (Tiwari, 1981). The eusaccate condition, however, also occurred in the extinct pollen group (Coniferales and Cordaitales) but only few reports are published (Couper, 1958; Dettmann, 1963; Scheuring, 1978; Taylor & Taylor, 1987; Vijaya, MS).

The present paper describes the morphography of *Protoeusaccites*, a new pollen genus from the Late Permian Pali Formation, South Rewa Gondwana Basin, India (Map 1; Text-figure 1). It shows a unique character-state between a Protosaccate and Eusaccate saccus structure.

MORPHOLOGY AND TAXONOMY

The pollen of extant *Pinus* (Pl. 4, figs 1, 3) is a typical example of true saccus (Erdtman, 1957; Scheuring, 1974); the surface of the saccus is irregularly sculptured and the saccus cavity is surrounded by a system of regularly arranged endoreticulum in two or three layers, i.e., a three-tier arrangement of large, medium and small reticulum in centripetal order (Text-figure 2A). This composition varies from species to species and sometimes also becomes complex (Klaus, 1977). In such pollen, the cavity occupies almost 9/10 of the total internal space of the saccus. Thus the saccus becomes a pouch-like, hollow structure with a thin sexinal layer as its outer wall (Text-figure 2B, C).

The trends of evolution in any organism appear to act in multi-pronged direction. Through time, the



A PORTION OF THE GEOLOGICAL MAP OF PAKARIA BLOCK, SOHAGPUR COALFIELD DISTRICT SHAHDOL, MADHYA PRADESH

Map 1—Showing the location of the Bore-hole S.P.B.-18 in South Rewa Gondwana Basin, India.

morphological diversification may appear to be extravagant, in producing apparently useless and abnormal component in an organism. However, in nature, such experiments go on but ultimately a minimum production of building material of an organism with a threshold point for maximum efficiency seems to be the goal of evolution. However, nothing can be said as "ultimate" because the evolution is a continuous process and still better perfection can be achieved in future. In the case of saccus structure, the eusaccate condition in all extant taxa has been achieved. The protosaccate condition (Text-figure 3A, B) involves more building material and adds heaviness to the pollen grain, whereas eusaccate condition (Text-figure 2) needs lesser material, resulting in more effective buoyancy of pollen. In view of this, a stage between completely filled saccus and the hollow saccus is an important character-state (Text-figures 2-4) which needs attention of the morphologists.

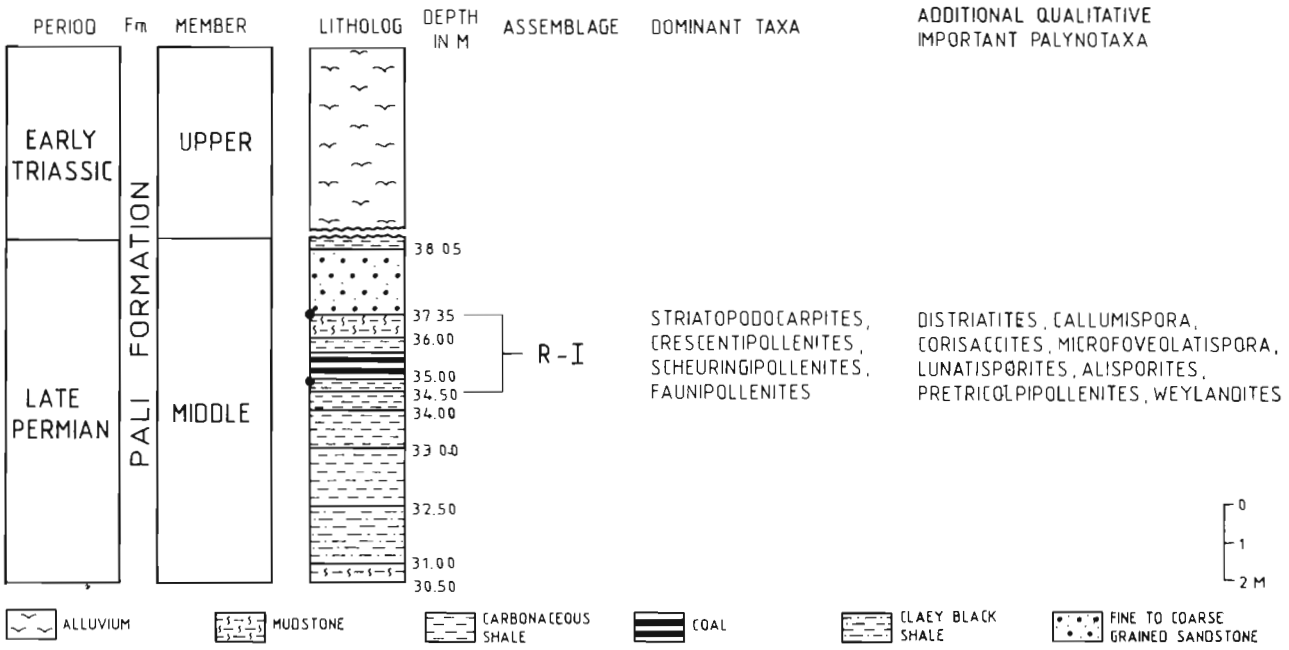
Infraturma—*Disaccitriletes* Leschik 1955

Genus—*Protoeusaccites* gen. nov.

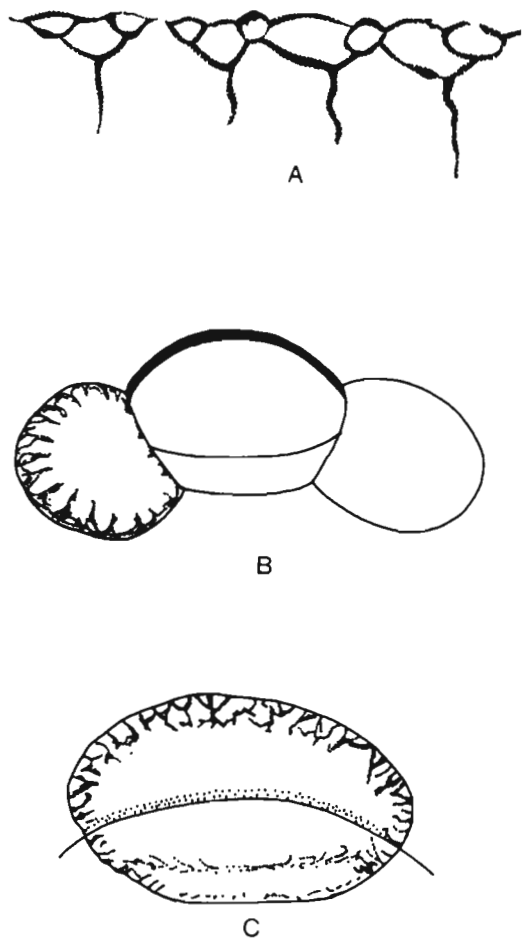
Type species—*Protoeusaccites rewaensis* sp. nov.

Generic diagnosis—Bisaccate, non-striate pollen with central body having intrareticulate structure of cappa. A thin, ill-defined vestigial monoletoid mark or a thin area could be located on the proximal face of the central body. Sacci proximally attached to the equatorial region of central body, distally inclined and attached along the lateral axis of the body leaving a well-defined bilateral saccus-free-area (SAFRA). Distal sulcus represented by a thin area within the region of SAFRA. Sacci partially filled with alveolae, leaving a cavity in the internal central region, thus attaining a protoeusaccate condition.

Description—The main characteristic feature of this non-striate bisaccate pollen is the development of partial cavity in the central region of sacci chambers. The



Text-figure 1—Schematic representation of lithology in Bore-Core S.P.B.-18, at the level of Late Permian-Early Triassic Pali Formation. The black dots in litho-column indicate depth of the samples, which show the presence of *Protoeusaccites*. R-I is the youngest palynoassemblage recognised in latest Permian Raniganj Formation of Damodar Basin, India (Tiwari & Singh, 1986). The characteristic taxa of this palynoassemblage are given.

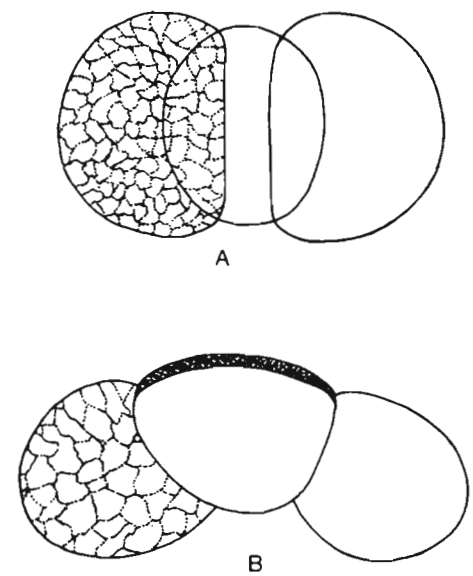


Text-figure 2—Sketches adapted after Klaus (1977). **A**. Diagramatic representation of the nature of reticulum in sectional view within the saccus of *Pinus* pollen hanging from the inner wall of saccus and extending into the saccus chamber; lumen shape and size vary gradationally, and getting radially elongated, in three-tier arrangement. **B**. Sectional view of *Pinus* pollen to show the partial in-fill of endoreticulum in saccus chamber leaving a cavity to form true saccus. The inner surface of saccus possesses two to three-tier endoreticulum leaving the saccus cavity in centre without any in-fill. **C**. Sectional view of saccus to show the hanging endoreticulate rodlets forming an alveolar system of such two to three-tiered irregular reticulum. The saccus cavity is surmounted by a thin layer of endoreticulum resulting into a pouch-like hollow structure. The attachment of saccus with body is shown by dotted line.

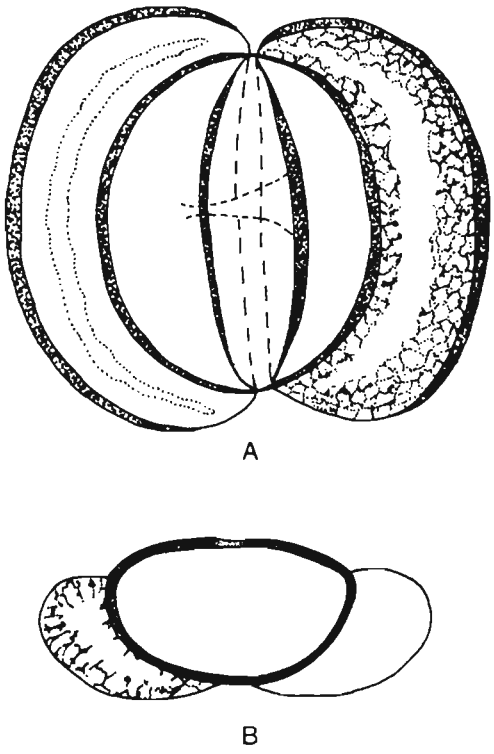
alveolar layers are arranged in the peripheral region of the cavity. In the proximo-distally flattened specimens, the internal-fill appears as thicker zone adjacent to the saccus outline. This feature is the result of compactness of meshes on the internal surface of the saccus cavity. The outline of the central body also shows alveolar layers attached on to it in the region of saccus cavity (Plates 1, 2). Thin area on the proximal surface of the body, simulating a diffused and ill-defined monolete-like mark is present. The saccus-free-area is well delineated and extends distally all along the lateral axis of the central body.

Comparison—In general organization, the genus *Protoeusaccites* compares with *Alisporites* Jansonius 1971, *Cuneatisporites* Leschik 1956, *Abietineaepollenites* Potonié 1951 ex Delcourt & Sprumont 1955, *Brachysaccus* Mädler 1964, and such other taxa having non-striate, non-taeniate bisaccate construction. However, the development of partial cavity inside the saccus chamber gives a unique organization to the genus *Protoeusaccites,* which distinguishes it from other bisaccate pollen. Although not described originally, the presence of partial eusaccate condition could be noted in few species referred to *Alisporites* (e.g., *A. similis*, in Dettmann, 1963, pl. 15, figs 5, 6), *Podocarpidites* (e.g., *P.* cf. *multesimus*, in Dettmann, 1963, pl. 15, fig. 15), and probably in *Abietineaepollenites* (e.g., *A. microalatus* in Couper, 1958, pl. 28, fig. 11). However, in these forms no proximal tetrad mark has been reported. Besides, *Protoeusaccites* differs in general organization nature of sacci, saccus-free-area and the sulcus.

The eusaccate condition of saccus has been recorded in some species of *Lunatisporites* by Scheuring (1978) but these taxa differ from *Protoeusaccites* in having taeniae on the proximal face of the central body. Recently, *Playfordiaspora* Maheshwari & Banerji 1975 has been identified to be a true eusaccate pollen (Vijaya, MS), but it is a trilete monosaccate pollen with a single layer of reticulum underneath the tectum and hence it differs from the present genus. Other eusaccate pollen, viz., *Vesicaspora, Florinites, Flexipollenites, Sullisaccites,* are monosaccate and can be differentiated from *Protoeusaccites.*



Text-figure 3—Semi-diagrammatical presentation of the saccus structure in a Protosaccate bisaccate pollen. **A**. As seen in median focus the saccus chamber is filled with endoreticulum; **B**. Meridional sectional view of the same specimen to show the saccus-in-fill and attachment mode.



Text-figure 4—Semi-diagrammatic presentation of the specimen in surface view of *Protoeusaccites rewaensis*. **A**. Specimen in proximo-distal orientation to show the nature of alveoli in saccus chamber, irregular partially incomplete, thick meshes and narrow lumen. Proximally saccus extends along the equatorial length, distal-saccus-cover is up to 2/3 of the total surface area on corpus. On proximal face of central body, a vestigial monoletoid mark is present. Partial in-fill of sacci leaving a hollow cavity in central region, a proto-eusaccate condition; **B**. Same specimen in meridional section to show the details of saccus structure and body-saccus attachment.

Organization—Text-figure 4A, B.

Derivation of name—A character-state between protosaccate condition with alveolae filled saccus and the eusaccate condition having a cavity: Proto-eusaccate.

Protoeusaccites rewaensis sp. nov.

Plates 1-3

Holotype—Pl. 1, fig. 1; size 59 × 64.5 µm; Slide no. BSIP 11251.

Isotype—Pl. 1, fig. 2; size 55 × 56.0 µm; Slide no. BSIP 11252.

Type-locality—Bore-hole S.P.B.-18 (Sample no. 18/82, depth 34.50 m and 37.35 m) about 1.1 km southwest of Burhar Town near Katkona Village, Sohagpur Coalfield, South Rewa Gondwana Basin, Madhya Pradesh, India.

Horizon & age—Middle Pali Member, Pali Formation, Late Permian.

Description—Pollen grains diploxylonoid, brown to dark brown; central body 1-2 µm thick, outline generally distinct, brownish-yellow, roundly oval; body exine thin, finely intrareticulate, structure obscure at places due to thick muri and small lumen. Saccus attachment proximally at equatorial region, distally bilateral; sacci coming close to each other at lateral ends of the body but not connected with each other, bigger than body along lateral axis, less inflated, less than hemispherical, ear-lobe-shaped. Distal saccus-free-area forming up to 20 µm wide, bilateral channel, converging at lateral ends. Exine in saccus-free-area thin, somewhat chagrinate in nature appearing as true sulcus. Saccus alveoli medium-sized with 1-2 µm thick walls and narrow lumen, some partially incomplete meshes also seen; a hollow crescent-shaped space surrounded by alveolar fill can be clearly seen through L-O analysis, revealing the protoeusaccate condition of the saccus. Saccus cavity extending laterally along the saccus length on lateral axis occupying about one-third of the total saccus space.

Diagnostic characters

1. Diploxylonoid, bilateral, bisaccate pollen, broadly oval.
2. Structure of cappa finely intrareticulate, body thin but equatorially tending to be thickened.
3. Zone of saccus attachment generally well-marked.
4. Sacci less inflated along horizontal axis, ear-lobe-shaped, closely adjacent laterally.
5. An elongated narrow hollow space in the centre of saccus chamber present forming a partial eusaccate condition.

REMARKS

The structure of saccus in bisaccate pollen of extant Pinaceae and Podocarpaceae is eusaccate (Pl. 4, figs 1, 3). No protosaccate condition of saccus is known in the pollen of extant Coniferales (Erdtman, 1952). On the other hand, the pollen of extinct gymnosperms, particularly from the Late Palaeozoic, are predominantly protosaccate (Pl. 4, figs 2, 4). However, through the temporal scale, the eusaccate pollen have also been recognised in Palaeozoic, Mesozoic and Cenozoic times (Taylor & Taylor, 1987; Couper, 1958; Dettmann, 1963).

In recent years, conditions comparable to eusaccate organization have been recorded in a few taxa from Devonian, Permian and Triassic sequences. Balme (1988) reported a single-layered endoreticulate structure of the sexine enclosing a cavity in the miospore genus *Teichertospora*. This was proposed to be the oldest record of a eusaccate-like condition of the sexine. *Teichertospora* has a prominent trilete mark on the proximal face of the body which might have acted as

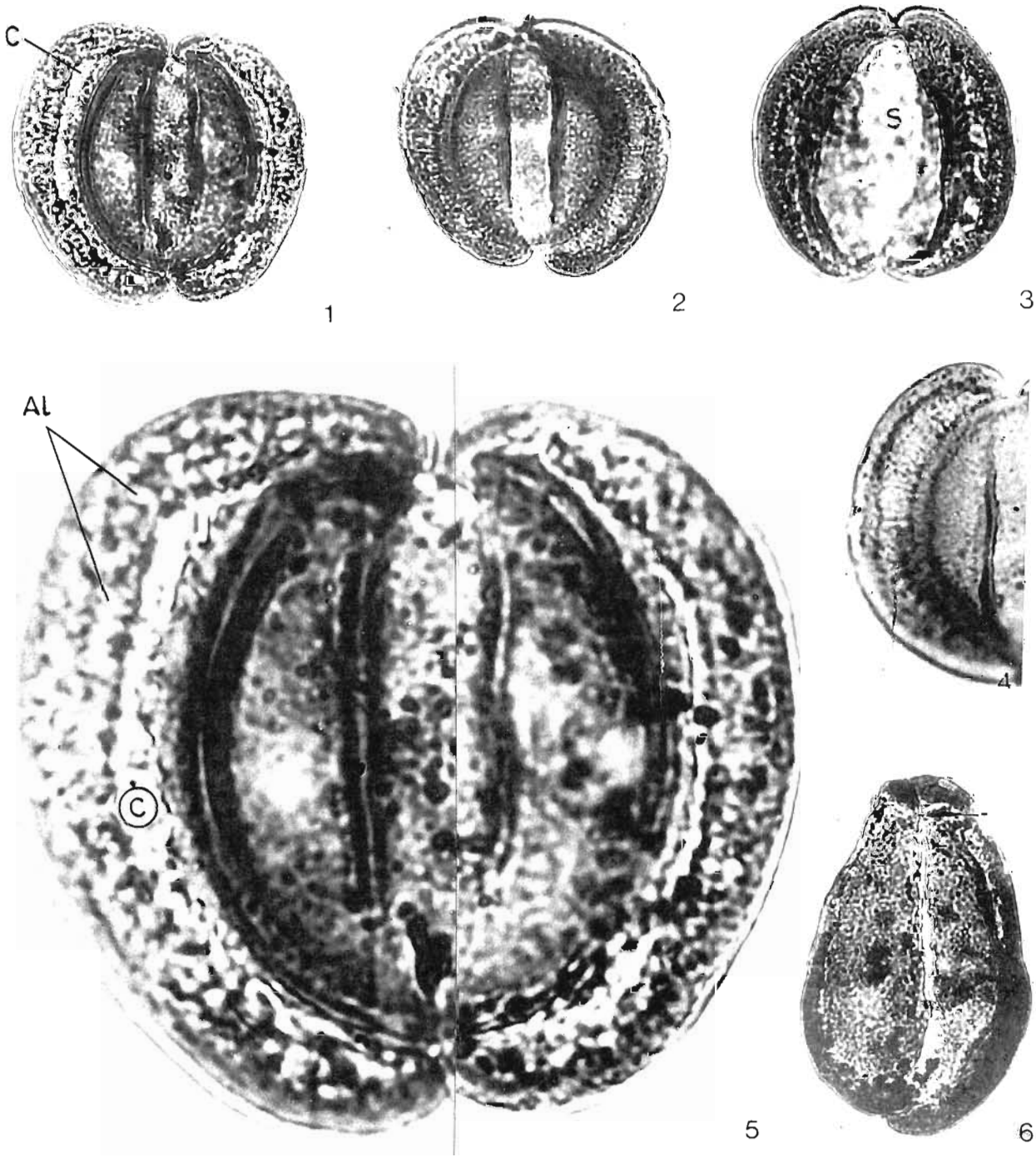


PLATE 1

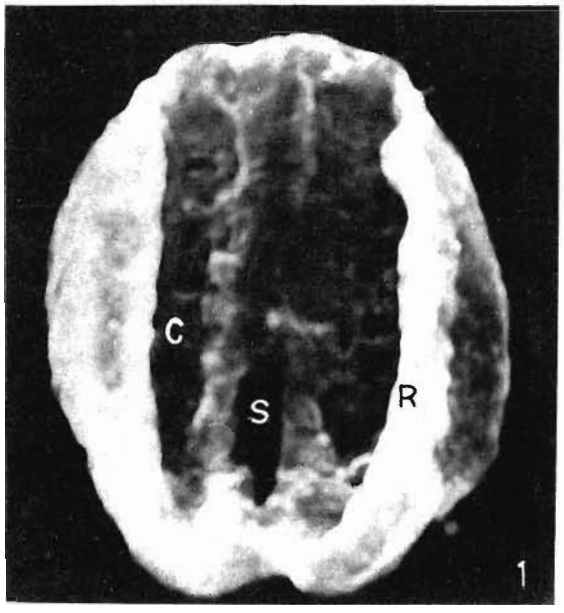
1 Overall view of Holotype specimen of *Protoeusaccites rewaensis* sp nov., distal face of the specimen showing prominent distal zone of saccus attachment. Sacci adjacent laterally but not connected, and ear-shaped enclosing a partial cavity (marked as C) in the central region of the saccus chamber, along the lateral axis (Proto-Eusaccate condition), appearing as crescentic, thin area occupying less than one-third of total saccus space. Saccus-alveoli compact and thick, arranged at the periphery of the cavity. Very faint thin area present on the cappa. Saccus-free-area (SAFRA) delimited as bilateral channel, × 750; BSIP Slide no. 11251.

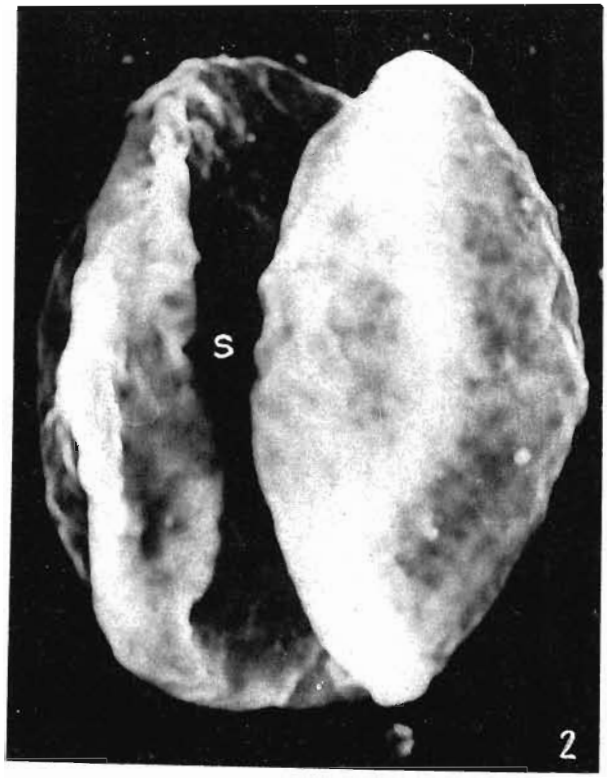
2 Distally-up Isotype of *Protoeusaccites rewaensis* sp. nov., showing monoletoid thinning on cappa. Saccus-spread on body surface is distinctly seen up to the distal zones of saccus attachment, which seem associated with narrow vertical folds. Prominent thickening around body equator. × 750, BSIP Slide no. 11252.

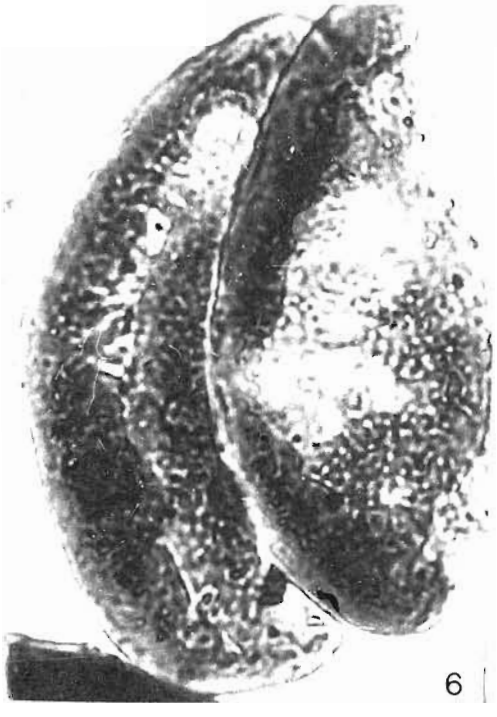
3,6. Specimens of *Protoeusaccites rewaensis* sp. nov. showing variation in overall shape, sulcus (wide to narrow) and nature of sacci inflation, × 750; BSIP Slide nos. 11253, 11254.

4 An enlarged part of fig. 2 to highlighten the mediumly fine alveoli in saccus structure and the elongated crescent-shaped cavity enclosed within the saccus chamber. × 1000.

5. Specimen in 1, enlarged (× 2000) to illustrate thick muri and irregular lumen spaces in saccus-alveoli and cavity (C) in saccus chamber. Nature of alveoli at the peripheral region of saccus (Al). Nexial thickening present around body-equator.







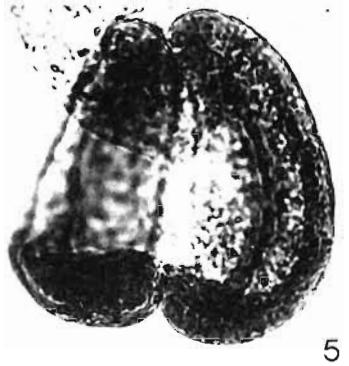


PLATE 2

Specimens studied under SEM and transmitted light, referred to *Protoeusaccites rewaensis.*

1.2. Under SEM cavity in saccus (C) bilateral channel as sunken area—SAFRA (S), and peripheral thickness in sacci resulted from the compactness of the meshes (R), × 1000, 2000.

3-7 Variations in overall shape, width of sulcus, nature of partial cavity in saccus chamber and the saccus-alveoli, × 750, except (6), × 1000; BSIP Slide nos. 11257, 11256, 11255, 11258, 11256.

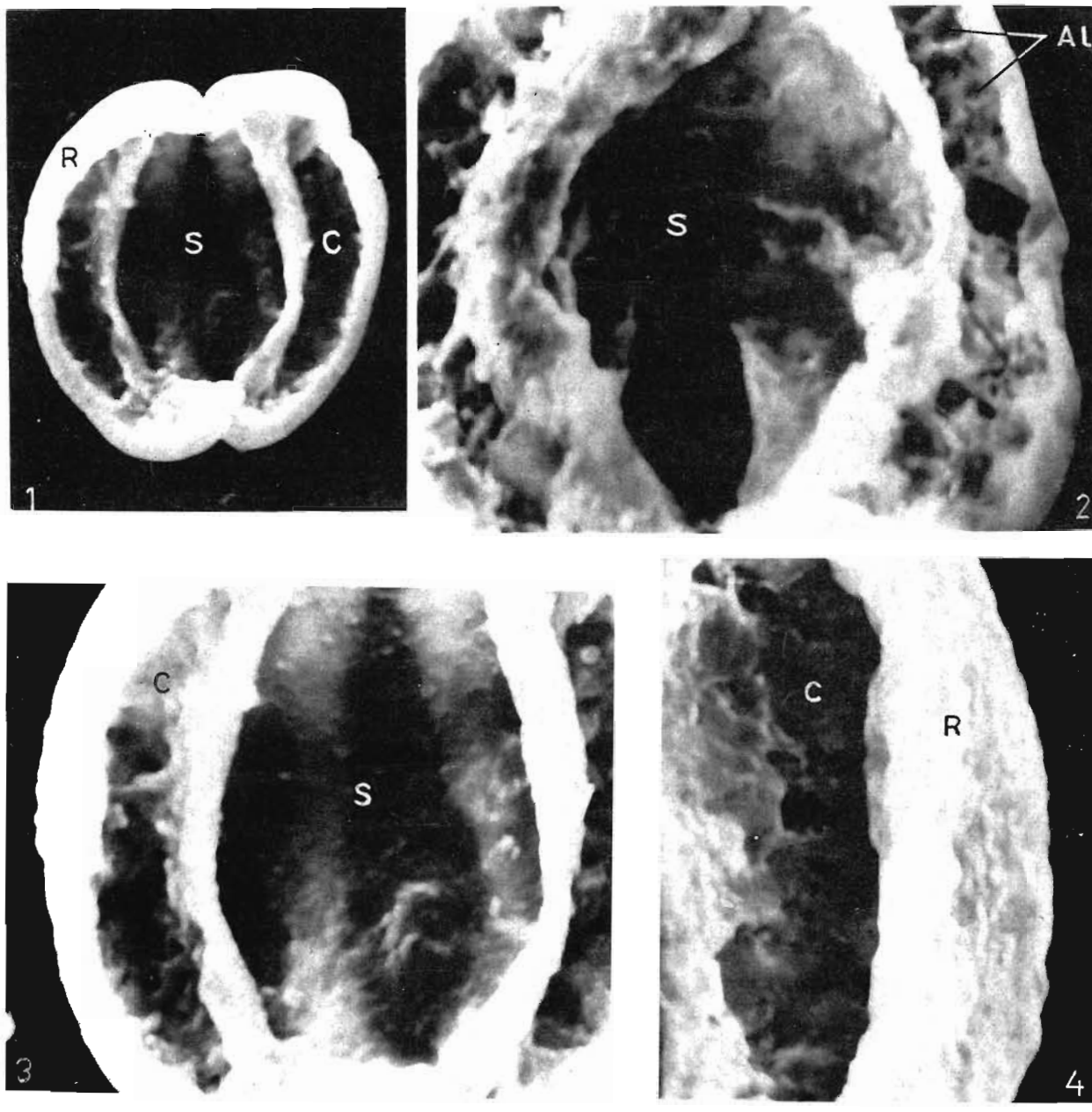


PLATE 3

1 Specimen under SEM to illustrate the nature of sulcus (S) and elongated crescent-shaped hollow cavity (C) in saccus area, seen here as depressions in surface view, × 1000

2 The sunken area (S) does not show any structure on surface, saccus broken at peripheral region showing nature of alveolae (A1) with thick meshes and varied spaces in lumen, × 2000

3. Well-delineated nexinal thickening (N) around body equator, saccus periphery thick, × 2000.

4 Thick and compact nature of meshes of the alveoli fills (R) in saccus chamber appears as thick crescentic area along the saccus outer margin. saccus in the area of hollow cavity (C) is irregularly patterned without any in-fill of alveoli (Proto-eusaccate condition).

a functional germinal apparatus. In this regard it is considered to be a pre-pollen of the Pro-gymnosperm Group. From the latest Permian and Triassic palynoassemblages, the organization of the saccus in the trilete-bearing monosaccate genus *Playfordiaspora* Maheshwari & Banerji 1975, has recently been re-interpreted to possess a true saccus (eusaccate condition; Vijaya, MS). In the structure of the sexinal cavity *Teichertospora* and *Playfordiaspora* are comparable to each other to a certain extent. However, recently Foster and Balme 1994, re-interpreted the organization of *Teichertospora* and opined that eusaccate condition is secondary in this genus. If this is so, we are not left with any eusaccate miospore from Devonian.

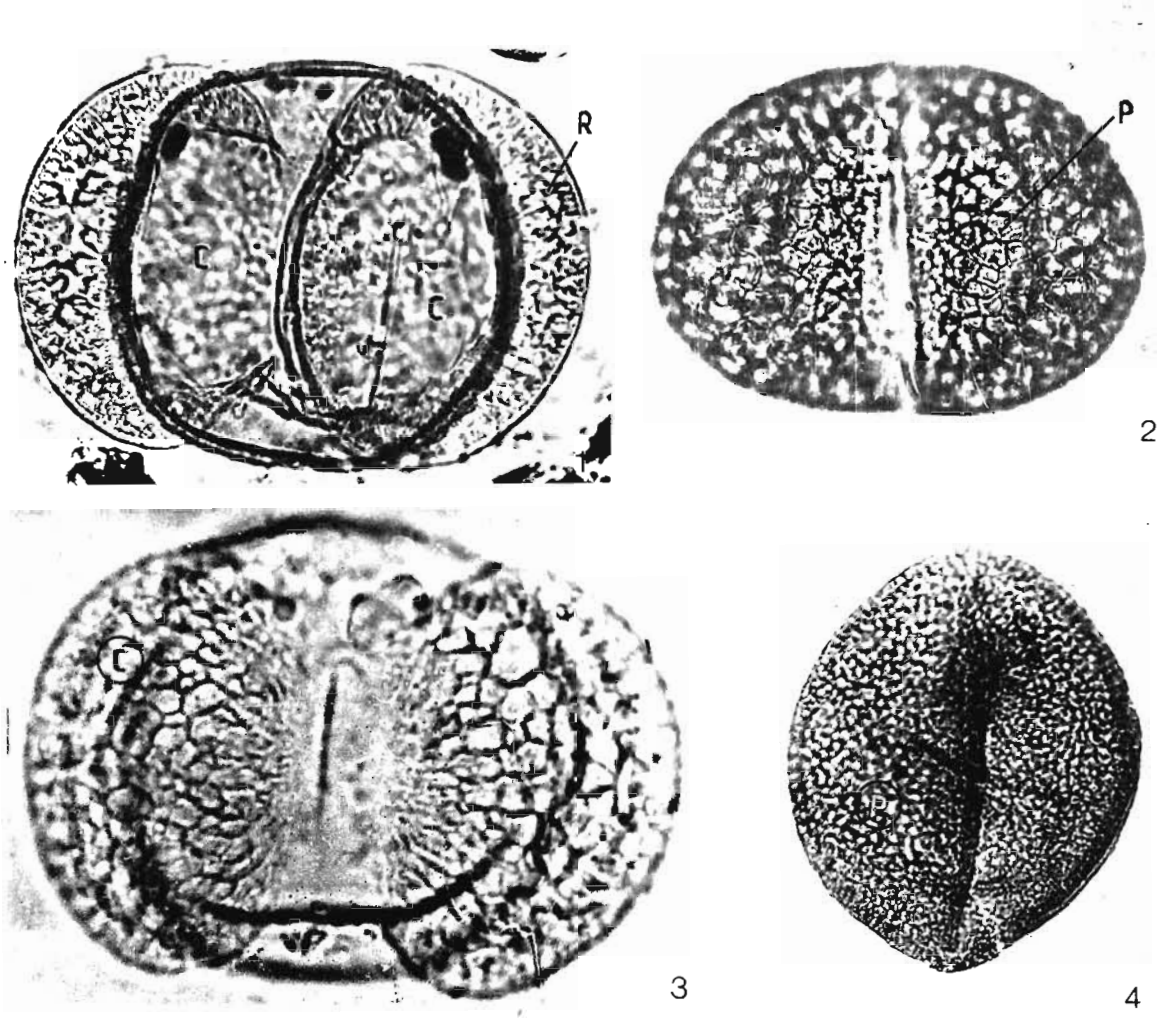


PLATE 4

To illustrate a comparative state of saccus structure in bisaccate pollen of extant *Pinus*, and the non-striate bisaccate pollen in the Permian and Triassic.

1,3. Pollen of *Pinus*, cavity (C) in sacci chambers, without any infill of reticulum attaining a eusaccate condition; peripheral thickening (R) seen because of the superimposition of the two sexinal layers; thickening around corpus also present.

2. Bisaccate pollen (*Satsangisaccites*) found in the Permian-Triassic sequence, having protosaccate nature (P) of sacci chamber.

4. Bisaccate pollen (*Scheuringipollenites*) of Permian age with protosaccate nature (P) of saccus.

Thus it has become evident from the analysis of available information that eusaccate condition of saccus was existing during Carboniferous time. Yet in view of the limited data on saccus study, it may not be very fruitful to hypothesise the evolutionary trends of this character-state through geological time. Nonetheless, from the presently identified *Protoeusaccites* in the Late Permian Gondwana Sequence it may be said that the eusaccate condition initiated for the first time at this level in bisaccate pollen. All the records of eusaccate condition—prior to Late Permian, come from monosaccate pollen. The Upper Carboniferous Pteridosperms (Callistophytales) and Carboniferous and Permian Cordaitales produced eusaccate monosaccate pollen. The taxa *Vesicaspora* Schemel emend. Wilson & Venkatachala 1963; *Felixipollenites*, *Sullisaccites* and *Florinites* are beset with a monosaccus having a cavity within.

Although abundant occurrence of bisaccate pollen is on record from Pre-Late Permian time, there seems to be no evidence of eusaccate nature of sacci in these groups. The taxa *Pityosporites* Mehta 1944 emend. Potonié & Klaus 1954, *Striatopodocarpites* (Soritsch & Sedowa) emend. Bharadwaj 1962, *Cuneatisporites* Leschik 1955, *Platysaccus* (Naum.) Potonié & Klaus 1954, *Striatites* Pant emend. Bharadwaj 1962, *Ibisporites* Tiwari 1964, *Faunipollenites* Bharadwaj 1962, and such other forms do not have a cavity in their sacci. Several monosaccate pollen of Late Carboniferous to Early Permian, viz., *Parasaccites* Bharadwaj & Tiwari 1964, *Plicatipollenites* Lele 1964, *Virkkipollenites* Lele 1964 also do not exhibit eusaccate condition.

It may be argued that without the TEM study the nature of saccus-fill cannot be determined. Definitely, such is not the case. The L-O analysis is the most effective method for deciphering the internal structure of sacci. From high-focus to low-focus levels one can very clearly decide whether a cavity is present or the whole saccus is filled with reticulum/alveoli. It is needless to explain the details of L-O analysis to the expert readers, but it can be emphasized that TEM should not necessarily be chosen as the only method for determining the eusaccate condition in a saccus.

On these lines of thinking, hundreds of specimens from Gondwana as well as northern palynofloras were examined by careful L-O analysis. The eusaccate condition in *Playfordiaspora* and *Protoeusaccites* has been ascertained by SEM of broken specimens and LM of variously preserved specimens. The level of origin of eusaccatism in bisaccate pollen, as observed here, is thus evidenced at the Late Permian on peninsular India. The other records of this character are from the Late Triassic of the Alpine sequence (Mädler, 1964; Scheuring, 1978). In subsequent younger horizons, the eusaccate state is established in more forms within the population of protosaccate bisaccate pollen. The record of *Abietineaepollenites*, *Podocarpidites* (Couper, 1958; Dettmann, 1963) in Jurassic and Cretaceous sequences suggests the proliferation of eusaccatism at the end of the Mesozoic.

The eusaccate nature of saccus in *Playfordiaspora* is in line with the occurrence of this important character in the Carboniferous and Permian monosaccate pollen. But *Protoeusaccites*—a distinctly bisaccate pollen, is a bench mark occurrence for eusaccate structure in the pollen of Disaccites group. With the point of initiation at Late Permian level, further in time, the eusaccate nature proliferated while protosaccate nature gradually disappeared to attain the climax in extant groups where only eusaccate structure is found. The "protosaccatism" has been obviously rejected during the course of evolution.

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