Morpho-evolutionary biohorizon stratigraphy and cladistics in saccate pollen through Gondwana Sequence of India

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The morphographic characters of fossil saccate pollen and their evolutionary sequence through the span of Gondwana formations play a vital role in the biohorizon stratigraphy. Based on evolutionary changes in the morphology of the pollen group, their FADs (First Appearance Datums) and LADs (Last Appearance Datum) and the cluster levels, eleven biohorizons and ten inter-biohorizon Zones (Interval-zones) have been identified. The model of alliance among the prime morphographies has been acquired through simple character state analysis. By extrapolation of lineages, four unique monosaccate and one simple disaccate organizations could be identified to have their origin in the early Upper Carboniferous stock of Australia, which, in turn, were related with the Devonian progymnospermopsida complex. The five outgroup stocks continued as such into the late Early Asselian Talchir Formation of India and sprouted in the subsequent Permian time. A gap in the sequence has been identified during Upper Carboniferous of Australia and the lowermost Permian in India. The sixth major lineage of striate pollen branched off from the simple disaccate pollen lineage to appear in the Late Asselian. Cladistic analysis supports the applicability of the proposed biohorizons as important stratigraphic parameter. The congruence of derived and ancestral states of internally compatible and persimonically harmonious characters in pollen organizations has been used in drawing relationship trees. Thus, the cladograms and stratograms (nested diagrams of stratigraphic occurrences) together depict the maximum diversification at the lower Upper Talchir and the P/Tr boundary. The major extinction of monosaccates at the Lower Permian-Upper Permian boundary and that of the striate-disaccates in the basal Triassic have also been brought to light. The reasons of such a behaviour is attributed to environmental stresses caused by massive glaciations during Early Permian Talchir Formation, climatic changes towards warmer-drier situation at Lower/Upper Permian passage and global cooling and regression at the permo-Triassic level. Pollen features, like striations, taeniae, girdling monosaccus, clefts and remnant of germinal marks, etc. of the Permian and Triassic have perished completely by the end of Triassic. Most of the Jurassic palyno-assemblages contain the fag-end organizations of simple disaccate lineages; the experimentation seems to have attained a more simple state in the morphography of saccate pollen which continued thereafter.

Key-words—Evolution, Biostratigraphy, Saccate pollen, Cladistics, Gondwana (India).

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सारौंश

भारत के गोंडवाना अनुक्रम में कोष्ठीय परागकणों में क्लेडिस्टिक तथा आकार-विकासीय जैवमंडलन स्तरविन्यास

विजया एवं रामशंकर तिवारी

गोंडवाना शैल-समूहों में अश्मित कोष्ठीय परागकणों के आकारिकीय लक्षणों तथा उनके वैकासिक अनुक्रम की जैवमंडलीय स्तरविन्यास में महत्वपूर्ण भूमिका है। परागकण समूह की आकारिकी में विकासीय परिवर्तनों, इनके एफ-ए-डी० एवं एल-ए-डी० तथा समूह-स्तरों पर आधारित 11 जैवसंस्तर तथा 10 अंतरजैवसंस्तर मंडल अभिनिर्धारित किये गये हैं। सामान्य लक्षण-विश्लेषण के आधार पर सम्बद्ध मॉडल बनाये गये हैं। आस्ट्रेलिया के प्रारम्भिक उपरि कार्बनीफ़री कल्प में इनकी उत्पत्ति सुनिश्चित करने के लिए श्रृंखलाओं के बाह्यकलन के द्वारा चार विशेष एककोष्ठीय तथा एक सरल द्विकोष्ठीय संरचनायें अभिनिर्धारित की जा सकी हैं जो डिवोनी कल्प के प्रोजिम्नोस्पर्मोप्सिड् समूह से सम्बद्ध किये गये थे। ये पाँच बाह्य-समूह अर्नतिम प्रारम्भिक अँसेलियन तलचीर शैल-समूह में वैसे ही विद्यमान रहे तथा परमी कल्प में इनका प्रादुर्भाव हुआ। भारत के अधरितम् परमी कल्प में तथा ऑस्ट्रेलिया के उपरि

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कार्बनीफ़री कल्प में विद्यमान अनुक्रम में रिक्तता अन्वेषित की गई है। अनंतिम ॲसेलियन में विकसित होने हेतु रेखीय परागकणों की छठी मुख्य श्रृंखला सरल द्विकोष्ठी परागकणों की छठी मुख्य श्रंखला से अलग हो गई। क्लेडिस्टिक विश्लेषण प्रस्तावित जैवसंस्तरों के महत्वपूर्ण स्तरिकीय परिसीमन हेतु उपयोगी सिद्ध हुआ है। परागकण संरचनाओं के व्युत्पादित एवं पूर्वजी लक्षणों का उपयोग सगोत्रता-वृक्ष बनाने में किया गया है। अत: क्लेडोग्राम एवं स्ट्रेटोग्राम संयुक्त रूप से अधरि उपरि तलचीर एवं परमी/त्रिसंघी सीमा पर सबसे अधिक विभिन्नता प्रदर्शित करते हैं। अधरि परमी उपरि परमी सीमा पर एककोष्ठीयों तथा आधारी त्रिसंघी कल्प में रेखीय-द्विकोष्ठीयों के बहत्विलुप्तीकरण पर भी विवेचना की गई है। इस तरह का विलुप्तीकरण वातावरण में अत्याधिक परिवर्तनों के कारण हुआ है। इन परिवर्तनों का मुख्य कारण हिमनदन अथवा जलवायु में काफी उतार-चढ़ाव हैं। परागकणों के कई लक्षण जैसे रेखीयन, टीनी, मेखलन आदि त्रिसंघी कल्प के अन्त तक बिल्कुल समाप्त हो गये थे। जूराई कल्प के परागाणु-समुच्चयों में अधिकतर सरल द्विकोष्ठी श्रृंखलाओं के कुछ ही अंश शेष हैं। यह अध्ययन कोष्ठीय परागकणों की आकारिकी में अधिक सरल प्रतीत होता है, ये परागकण इसके बाद के कल्पों में भी मिलते हैं।

SPORES and pollen are unique entities in the life cycles of plants, because of their being complete units in themselves, beset with fine exinal characters and individualistic organizations. The building substance of the exine—the sporopollenin, a suitable material for preservation manifests into the structures, sculptures and modes of layer separation according to the blue-print of the genetic code in the mother cells (Heslop-Harrison, 1973). The large number in which they occur theoretically in all types of sediments (facies independent), adds a great value to the study of fossil spores and pollen. These assets make them more suitable than several other types of plant fossils for character analysis in time. When morpho-organizations of dispersed pollen and spores are tagged with stratigraphy, they could be effectively utilized in determination of evolutionary lineages, bench-mark events delineated by turnovers or by major innovations of organizations, genealogical pattern of descendence, and identification of major biohorizons and interbiohorizon zones for stratigraphic resolution (Hedberg, 1976; Levinton, 1988).

In the Indian Gondwana Sequence, extensive investigations in the field of palynofloral stratigraphy have been done (Lele & Makada, 1972; Bharadwaj & Srivastava, 1973; Tiwari, 1973; Bharadwaj, 1975b; Lele, 1975, 1984; Chandra & Lele, 1980; Vijaya & Tiwari, 1987; Tripathi *et al.*, 1990, and references cited therein). However, so far little has been done on the lines of morphographic character analysis in search of evolutionary trends. Lele (1964) and Lele and Shukla (1978) established morpho-variant lines in *Potonieisporites* and *Plicatipollenites* in the Lower Permian succession and derived composite variation trends; however, no biostratigraphic events were ascertained in this analysis. Although Bharadwaj (1975a) proposed a scheme to derive character lineages in spore-pollen groups mainly based on the nature of tenuitas, the generalized temporal reference made this proposal less useful for biostratigraphy. Kumar (1984) has attempted to evaluate the character variants in polysaccate pollen but again precise stratigraphic tagging could not be accomplished.

The present paper deals with the appearance of major morphographic building-plans of saccate pollen (Tiwari, 1975; Lele, 1975) at the beginning of Early Permian in the Indian peninsula, their diversification, multiple proliferation and declination through Permian, Triassic, Jurassic and Lower Cretaceous periods. During such a vast span of time passing through several changing climatic patterns (Lele, 1976; Kar, 1976; Shah, 1976; Tiwari & Tripathi, 1988; Banerji & D'rozario, 1990), the saccate pollen have undergone definitive experimentation due to severe stresses, in their saccus body architecture at several horizons. These biohorizons could be further tested for their compatibility with stratigraphic datums, using cladogram and stratogram (Fortey & Jefferies, 1982) of the stock lineage-trees, which are structured around similar organizations.

The saccate pollen have a remarkable edge over the trilete and monolete pteridophytic (incl. lycopsidean) spores and asaccate pollen of other types in respect of dispersal and subsequent preservation in synchronous sediments of varied lithofacies. The saccus is the most effective instrument for spatial dispersal of pollen by the mechanism of wind floating, while the non-saccate pollen and spores are handicapped for wider scattering; they are almost locally concentrated after shedding, and if carried away by waterflows they have a current biased distribution. Since the numerical abundance has not been taken as a criterion for datums, the saccate pollen have the best chance of representation in the widely separated regions at a given time. Their dispersal record is analogous to fragrance which could be detected in the same time plane in distant areas, may be that the degree of intensity varies. The FADs of innovation in character states in saccate pollen have, thus, a better prospect to provide control-lines for dating and correlation than that of the non-saccate morphos.

EVOLUTIONARY TRENDS AND BIOSTRATIGRAPHY

Speciation is the key event in evolution. The evolutionary trends are regarded as either variation in the rate of speciation or selective extinction of species in a biased morphological direction (Gould & Eldredge, 1977). The saccate pollen species are not the true biological species. They are morphographic groups of dispersed pollen specimens, based around a morpho-type which share similar characters amongst themselves. The circumscription of such morphographic taxa may not include, at times, the naturally affiliated forms; the ecological variants could be included into the group because of the apparent form similarity; or, inversely, the variants of a form can be mistaken for entirely separate species. Such a practice of identifying the non-statistically founded pollen species leads to the problem of biased identification. In a system where form-species could be sometimes arbitrarily defined, the incompleteness of geological record further adds to the difficulty of tracing ancestral or descendent lines, or character state (specific features) alliance (Joysey & Friday, 1982).

In order to circumvent these problems, the *gross organization and basic exine character* (morphos)—rather than the narrow quantitative parameters used for circumscription of pollen species—have been taken for the assessment of the character state relationship. The term "morphos" (singular and plural both, morphos) has been used in the text to denote the morphographic unit of characteristic building-plan and specified characters linked with it (morph, Gr., morphe, form); it is a supraspecific category of pollen—could be suprageneric or of a infraturma group. The supraspecific categories might give a very generalized picture in case where a whole fossil organism is dealt, but in case of palynotaxa they minimize the blurring effect of the taxonomic artifacts. The choice of the category "genus" for cladistic analysis has been rated as more effective than the "more-or-less species". It is more so when the "genus" is taken in terms of fundamental morpho-organizations. Such an approach has resulted into cohesive group patterns in pollen morphographies. And because the sequence of fossil occurrence is related with the time, the inter-connections of morphographic groups could be established by the criteria of relationship of descent and compatibility of derived characters.

The morphos have also followed definitive paths of innovation, diversification and extinction. It is not speculated here that one pollen group has given rise to another, but it is asserted that the phenomenon of evolutionary forces had always been in the backdrop which geared the morphological characters to alter in a certain direction, for better adaptation under changing conditions.

The biostratigraphic classification of strata is mainly based on the criterion of various distinguishable fossil assemblages. The morphological features of the fossils and their evolutionary sequence that had occurred, play a vital role in the development of fossil-based stratigraphy. The innovation of a mode in body-sac attachment, a novel character on body exine, or an unusual feature of the sulcus are remarkable character states, employed in the search of event datums. The consistent first appearance and the steady last appearance of a unique character or of a morpho-organization, or both, in a given population demarcate the major level of change in evolutionary flow, and referentially such FADs and LADs have important relation with the biochronology (Gradstein, 1983).

Through time, the gradual change within a character produces variants, but the mutational changes in genome contribute to speciation and such characters are reflected as apparent discontinuity in the chain of lineages. Although pure phyletic analysis cannot be advocated for pollen taxa dispersed in sediments of the geological past, such a discontinuity of characters had been generally observed in the run of lineages. The gross offsets in groups indicate rampant mutational changes that produced newer morphos, and refers to a catastrophy which exterminated the older ones.

CLADISTIC ANALYSIS

During the course of present study, the first occurrences of distinctive morphographic organizations were plotted along the stratigraphic span of Gondwana Sequence, and the range-line of occurrence for each form was drawn. Now the question was whether the clusters of these forms should be based intuitionally, or they be grouped in the light of their maximal character relationship. To adapt the latter approach, a simple cladistic analysis (Henning, 1966) has been done and its results are incorporated in the distribution chart (Text-figure 1). The cladistic approach (Greek *clade*, meaning a branch or younger shoot) for analysis of lineage in morphography deals with the relationship amongst a series of taxa grouped on the basis of their uniquely shared and evolutionarily derived similarities. The cladograms (branching pattern diagrams) based on fossils are not necessarily phylogenetic expression, unless the sequence of record in temporal aspect is continuous. But, if the trends of changes in group morphology through geological section are established, the broad phylogenetic sequence could be interpreted (Fortey & Jefferies, 1982; Hill & Crane, 1982). By the fixation of ancestral and derived character states in each pair of characters of a taxon, a further closeness with history of evolutionary connections can be achieved through cladistics. Such an attempt has been made here for saccate pollen through Gondwana Sequence.

The list of taxa, each representing a morphographic organization, is given in Table 1. Forty-four distinct morphographies (A to Z and AA to AV) were selected from amongst various genera. After repeated attempts for choosing the polarity of characters for outgroup comparisons, 28 character-pairs were finally enlisted (Table 2). In the list the italicised character represents the ancestral state, while the roman stands for derived state.

Table 1—Palynotaxa considered for morpho-evolutionary analysis

CODE NO.	PALYNOTAXA
A	*Potonieisporites* Bhardwaj emend. Bharadwaj 1964
B	*Plicatipollenites* Lele 1964
C	*Parasaccites* Bharadwaj & Tiwari 1964
D	*Virkkipollenites* Lele 1864
E	*"Pityosporites"* Seward emend. Manum 1960
F	*Caheniasaccites* Bose & Kar 1966
G	*Vestigisporites* Balme & Hennelly emend. Tiwari & Singh 1984
H	*Gondwanopollis* Lele & Maithy 1969
I	*Rimospora* Lele & Maithy 1969
J	*Rugasaccites* Lele & Maithy 1969
K	*Divarisaccus* Venkatachala & Kar 1966
L	*Crescentipollenites* Bharadwaj, Tiwari & Kar 1974
M	*Faunipollenites* Bharadwaj 1962
N	*Stellapollenites* Lele 1964
O	*Crucisaccites* Lele & Maithy 1964
P	*Circumstriatites* Lele & Makada 1972
Q	*Vesicaspora* Schemel emend. Wilson & Venkatachala 1963
R	*Pachysaccus* Lele & Maithy 1969
S	*Scheuringipollenites* Tiwari 1973
T	*Tuberisaccites* Lele & Makada 1972
U	*Parastriopollenites* Maheshwari 1967
V	*Rhizomaspora* Wilson 1962
W	*Sahnites* (Mehta) Mehta emend. Tiwari & Singh 1984
X	*Striatopodocarpites* Soritsch & Sedova emend. Bharadwaj 1962
Y	*Verticipollenites* Bharadwaj 1962
Z	*Striomonosaccites* Bharadwaj 1962
AA	*Barakarites* Bharadwaj & Tiwari 1964
AB	*Densipollenites* Bharadwaj 1962
AC	*Lueckisporites* Potonié & Klaus 1954
AD	*Corisaccites* Venkatachala & Kar 1968
AE	*Guttulapollenites* Goubin emend. Venkatachala, Goubin & Kar 1967
AF	*Schizopollis* Venkatachala & Kar 1964
AG	*Distriomonosaccites* Bharadwaj 1962
AH	*Klausipollenites* Jansonius 1962
AI	*Playfordiaspora* Maheshwari & Banerji 1975
AJ	*Alisporites* Daugherty emend. Jansonius 1971
AK	*Satsangisaccites* Bharadwaj & Srivastava 1969
AL	*Lunatisporites* Leschik emend. Scheuring 1970
AM	*Kamthisaccites* Srivastava & Jha 1986
AN	*Goubinispora* Tiwari & Rana 1981
AO	*Podocarpidites* Cookson *ex* Couper 1953
AP	*Minutosaccus* Mädler 1964
AQ	*Brachysaccus* Mädler 1964
AR	*Infernopollenites* Scheuring 1970
AS	*Staurosaccites* Dolby 1976
AT	*Samaropollenites* Goubin 1965
AU	*Podosporites* Rao emend. Kumar 1984
AV	*Callialasporites* Dev 1961

Taxa considered under discussion but not included in Table 1

Tiwariasporis Maheshwari & Kar 1967
Distriatites Bharadwaj 1962
Distriamonocolpites Bharadwaj & Sinha 1969
Hamiapollenites Wilson 1962
Aurangapollenites Srivastava 1977
Trochosporites Wilson 1962
Tumoripollenites Bharadwaj 1962
Platysaccus Naum. ex Potonié & Klaus 1954
Podocarpeaepollenites Thiergart 1949

Since we are dealing with the detached, exclusively fossil components of the plants which existed during Late Palaeozoic and Mesozoic eras, it is difficult to get clues for determination of character polarity in their living counterparts. It is more so, because almost none of the prime characters, viz., striations, taeniae, alveolae, endoreticulae, protosaccus, trilete or monolete marks, etc. is found in the extant saccate pollen. Therefore, we are left with two parameters, one—the stratigraphic levels of characters, and the other—the *in situ* pollen characters and their primitive or advance nature rated on the basis of parent plants. The little-known latter aspect is again syndromically tagged with stratigraphy, hence of no major consequence. The stratigraphical parameter is significantly authentic and irreversible in deciding the polarity in character

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Text-figure 1—Composite figure of Cladogram and Stratogram, showing character states relationship of morphos and their stratigraphic occurrence through Gondwana Sequence of India. Lower segment in the figure exhibits the primaeval stock level in Carboniferous (C1, C2) in Australia and their outgroup relation in Devonian (D), and the upper segment of the figure illustrates the sprouting and branching pattern of main six trees identified in the oldest strata of Indian Gondwana. *Solid-circle*—FAD's of each morphos; *thick lines*—main trunk of morphos-trees; *Dotted lines*—branching pattern of tree showing relationship amongst cladistically grouped morphos; *Continuous thinline*—consistent stratigraphic range of each morpho-organization; *Broken line*—inconsistent occurrence; *Cardinal numbers* are Morphos Index Numbers (MIN). Stratigraphic column not drawn proportionately, Permian sequence inflated.

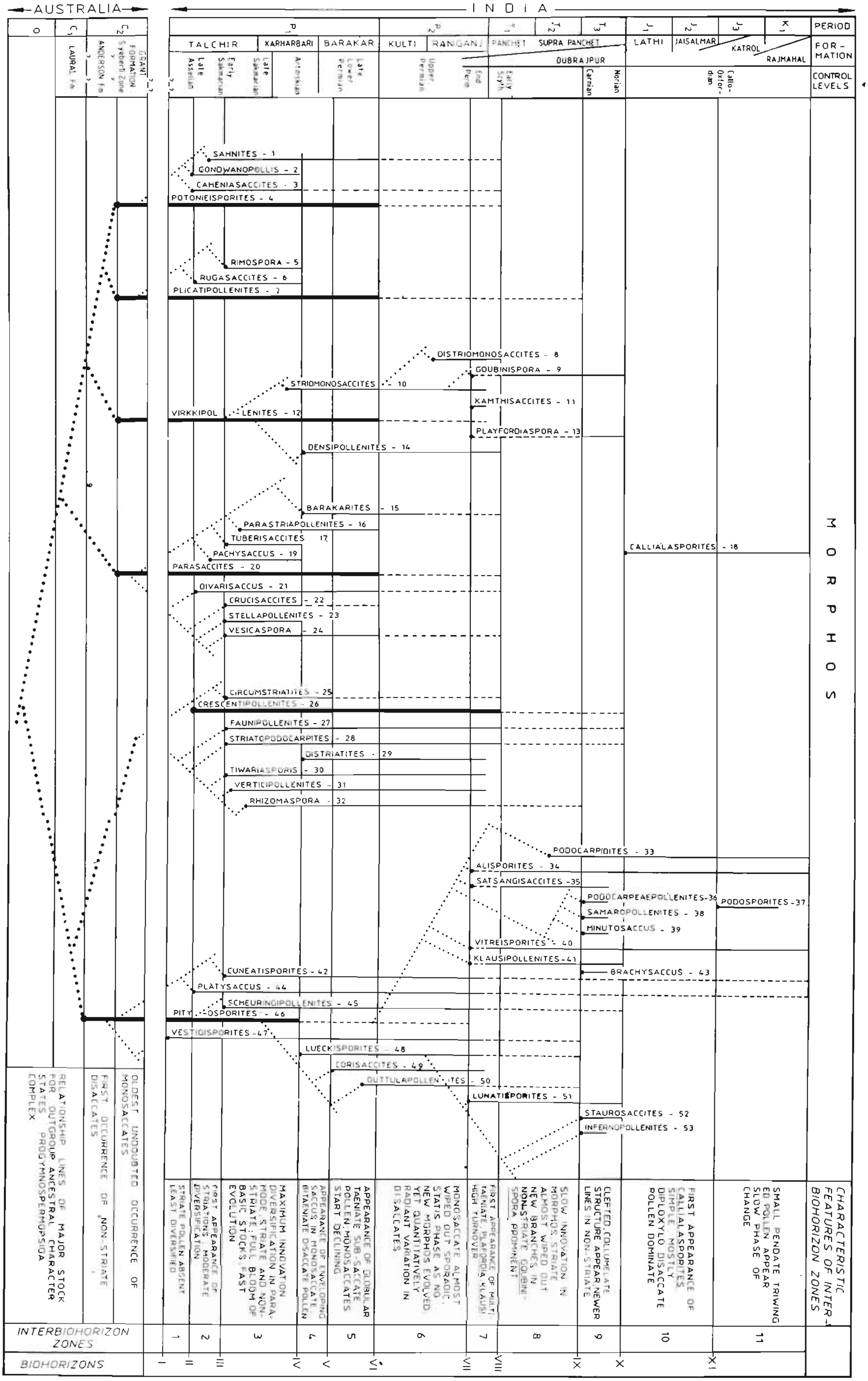

AUSTRALIA
INDIA
PERIOD
FOR-MATION
CONTROL LEVELS
O
C_1
C_2
P_1
P_2
T_1
T_2
T_3
J_1
J_2
J_3
K_1
LAURAL Fm
ANDERSON Fm
Syeberli Zone
GRANT FORMATION
TALCHIR
KARHARBARI
BARAKAR
KULTI
RANIGANJ
PANCHET
SUPRA PANCHET
DUBRAJPUR
LATHI
JAISALMAR
KATROL
RAJMAHAL
Late Asselian
Early Sakmarian
Late Sakmarian
Artinskian
Late Lower Permian
Upper Permian
End Perm
Early Scyth.
Carnian
Norian
Callo-Oxfor-dian
MORPHOS
SAHNITES - 1
GONDWANOPOLLIS - 2
CAHENIASACCITES - 3
POTONIEISPORITES - 4
RIMOSPORA - 5
RUGASACCITES - 6
PLICATIPOLLENITES - 7
DISTRIOMONOSACCITES - 8
GOUBINISPORA - 9
STRIOMONOSACCITES - 10
KAMTHISACCITES - 11
VIRKKIPOLLENITES - 12
PLAYFORDIASPORA - 13
DENSIPOLLENITES - 14
BARAKARITES - 15
PARASTRIAPOLLENITES - 16
TUBERISACCITES 17
CALLIALASPORITES - 18
PACHYSACCUS - 19
PARASACCITES - 20
DIVARISACCUS - 21
CRUCISACCITES - 22
STELLAPOLLENITES - 23
VESICASPORA - 24
CIRCUMSTRIATITES - 25
CRESCENTIPOLLENITES - 26
FAUNIPOLLENITES - 27
STRIATOPODOCARPITES - 28
DISTRIATITES - 29
TIWARIASPORIS - 30
VERTICIPOLLENITES - 31
RHIZOMASPORA - 32
PODOCARPIDITES - 33
ALISPORITES - 34
SATSANGISACCITES -35
PODOCARPEAEPOLLENITES-36
PODOSPORITES -37
SAMAROPOLLENITES - 38
MINUTOSACCUS - 39
VITREISPORITES - 40
KLAUSIPOLLENITES - 41
CUNEATISPORITES - 42
BRACHYSACCUS - 43
PLATYSACCUS - 44
SCHEURINGIPOLLENITES - 45
PITYOSPORITES - 46
VESTIGISPORITES - 47
LUECKISPORITES - 48
CORISACCITES - 49
GUTTULAPOLLENITES - 50
LUNATISPORITES - 51
STAUROSACCITES - 52
INFERNOPOLLENITES - 53
RELATIONSHIP LINES OF MAJOR STOCK FOR OUTGROUP ANCESTRAL CHARACTER STATES PROGYMNOSPERMOPSIDA COMPLEX
FIRST OCCURRENCE OF NON-STRIATE DISACCATES
OLDEST UNDOUBTED OCCURRENCE OF MONOSACCATES
STRIATE POLLEN ABSENT LEAST DIVERSIFIED
FIRST APPEARANCE OF STRIATIONS, MODERATE DIVERSIFICATION
MAXIMUM INNOVATION DIVERSIFICATION IN PARA-MODE, STRIATE AND NON-STRIATE; FULL BLOOM OF BASIC STOCKS, FAST EVOLUTION
APPEARANCE OF ENVELOPING SACCUS IN MONOSACCATE, BITAENIATE DISACCATE POLLEN
APPEARANCE OF GLOBULAR TAENIATE SUB-SACCATE POLLEN, MONOSACCATES START DECLINING
MONOSACCATE ALMOST WIPED OUT SPORADIC, STATIS PHASE AS NO NEW MORPHOS EVOLVED YET QUANTITATIVELY RADIANT VARIATION IN DISACCATES
FIRST APPEARANCE OF MULTI-TAENIATE, PLAFORDIA KLAUSI HIGH TURNOVER
SLOW INNOVATION IN MORPHOS, STRIATE ALMOST WIPED OUT NEW BRANCHES IN NON-STRIATE GOUBINI-SPORA PROMINENT
CLEFTED, COLLUMELATE STRUCTURE APPEAR, NEWER LINES IN NON-STRIATE
FIRST APPEARANCE OF CALLIALASPORITES SIMPLE, MOSTLY DIPLOXYLO DISACCATE POLLEN DOMINATE
SMALL PENDATE TRIWINGED POLLEN APPEAR SLOW PHASE OF CHANGE
CHARACTERISTIC FEATURES OF INTER-BIOHORIZON ZONES
INTERBIOHORIZON ZONES
1
2
3
4
5
6
7
8
9
10
11
BIOHORIZONS
I
II
III
IV
V
VI
VII
VIII
IX
X
XI

Table 2—Ancestral (in italics) and derived character states, selected for cladistic analysis of Gondwana saccate pollen

CHARACTER CODE	CHARACTER STATES
I.	Symmetry *Radial*/Bilateral (radial symmetry is the basic plan).
II.	Tetrad mark *Present*/Absent (remainié of primitive pteridophytic group).
III.	Tetrad mark *Trilete*/Monolete (tetrahedral tetrad had primitive configuration).
IV.	Body exine *Sculptured*/Structured (reference point pteridophytic exine).
V.	Proximal face of the body *Simple*/with Elevations (sexine forming islands, strips or discrete protuberances (result of secondary evolution in sexine).
VI.	*Non-striate*/Striate (striations are later development in evolutionary course).
VII.	Cleft on proximal face of body *Absent*/Present (Dolby & Balme, 1976; p. 150).
VIII.	Striations *Linear*/Reticuloid (tagged with stratigraphic occurrence).
IX.	Striations on *One face*/Both the faces of body (radiation in character as advance state).
X.	Striations *Loose-ended*/Joined-ended (Lele & Karim, 1972; p. 61).
XI.	*Non-striate*/Taeniate (Vijaya, 1990; p. 90; secondary evolution, a response to seasonality of climate).
XII.	*Taeniae two*/More in number (adaptation during course of evolution).
XIII.	*Monosaccate*/Disaccate (conservation of material and adaptation for better bouyancy).
XIV.	*Monosaccate*/Tri- or polysaccate.
XV.	Saccus *Sculptured*/Structured (general lineage of exine structure).
XVI.	Saccus *Infrapunctate*/Infrareticulate (exinal evolution lineage).
XVII.	Saccus *Infrapunctate*/Infracolumellate (further advancement in exinal evolution lineage).
XVIII.	Saccus *fully inflated*/little inflated.
XIX.	Saccus *Enveloping*/Non-enveloping (Pteridophytic spores and prepollen are reference points).
XX.	Distal attachment *Radial*/Bilateral (linked with basic lineage of radial symmetry).
XXI.	Distal attachment *Differential*/Para-mode.
XXII.	Para-mode *Circular*/Cruciform.
XXIII.	Para-mode *Circular*/Stellate (experiments in body-sac attachment relationship).
XXIV.	Sacci *Terminal*/Pendate (experimental line).
XXV.	Central body—Defined with *Haploxylon sacci*/Diploxylon sacci.
XXVI.	Central body—Ill-defined with *Haploxylon sacci*/Diploxylon sacci (reference point monosaccate as ancestral state).
XXVII.	In disaccates folds at root *Present*/Absent.
XXVIII.	In monosaccates folds at root *Present*/Absent (reduction in area of distal surface in central body—a conservation of material).

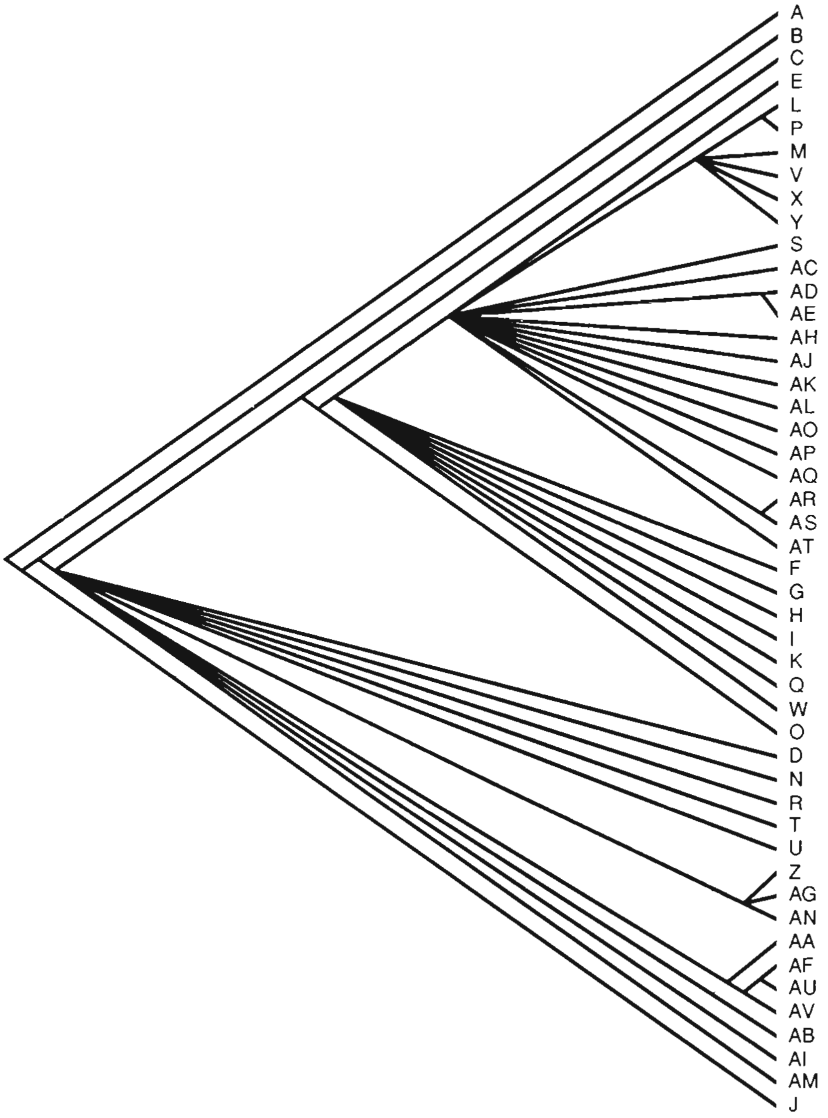
states of fundamental nature in a morphos. Stratigraphy, evolution and polarity in characters are linked with time, hence there can be no better parameter than stratigraphy for fixing the polarity of characters. However, the recurrence of primitive character in younger horizon may create problems in such considerations but they can be detected in conjunction with the entirety of characters; thus retrogressive trends or effect of parallel evolution can be sorted out on the basis of character compatibility.

The cladogram patterns are constructed from a matrix of taxa versus characters. In Table 3, the characters are taken along X-axis and the taxa on Y-axis. In Table 4, this arrangement has been reversed in order to project the result of different combinations. Table 3 depicts the outcome of sorting of taxa by taking monosaccate/disaccate (i.e., character XIII) as the primary key and striate-nonstriate (i.e., character VI) as the secondary key. Table 4 illustrates the results of sorting based on Column B representing *Plicatipollenites* as an outgroup for radiosymmetric monosaccate stock. The whole data was handled employing LOTUS software.

For the matrix, symbol-"1" is taken as ancestral (plesiomorphic) and "3" as derived (apomorphic) character state. The transitionary and mixed state is represented by symbol-"2". The root of each cladogram sector has been assumed to possess most ancestral character state. No numerical algorithms are employed here to generate cladograms as given in Text-figure 1. The correlation of simple cladistic pattern with the broad-frame stratigraphy reinforces the significance of various event-planes in saccate pollen through Gondwana Sequence.

To achieve a more compact picture of character state distribution in the matrix, the characters as well as taxa were shortlisted. As the parsimony demands, the majority set of internally consistent characters were chosen (Levinton, 1988). Such an arrangement (Tables 5, 6) reflects the alliance of character states which are based on minimum changes required for plotting the cladograms. Various segments of cladogram (see dotted lines in Text-figure 1) represent morphographic relationship lines, rather than the phyletic lines. It is our opinion that such an approach will considerably reduce the problem of homoplasy. No pollen morphos has been derived from the other but their basic similarities are suggested, hence the branching is not drawn in a direct manner, as in a typical cladogram.

In order to assess the results obtained by the above described method, an analysis was performed through the courtsey of Dr M. Muller of Florida Museum of Natural History. This analysis (Text-figure 2) was attempted on Apple MacIntosh IIci computer applying "Phylogenetic Analysis Using



Text-figure 2—Showing the results of Nelson algorithm analysis measuring evolutionary "cost" between character states. A supplementary figure to Text-figure 1 (MIN as in Text-fig. 1; courtsey D. Dilcher and M. Muller).

Parsimony (PAUP)" ver 3.0 (Swofford, 1990). The characters are ordered and reversible. An ordered character sequence is one which measures the evolutionary "cost" of acquiring a character as the absolute value of the difference between character states. Through this analysis, 1000 trees of length 132 were retained, and consensus tree (Text-figure 2) was drawn using the Nelson algorithm. This analysis provides a chance to compare the results of cladistic analysis done by us using a simple method (Text-figure 1) and by the algorithm method (Text-figure 2).

BIOHORIZON AND EVOLUTIONARY EVENTS

The analysis of data on appearances of new morphographies in saccate pollen through Gondwana Sequence of India has thrown light on several aspects of biostratigraphy. The advent level of derived features as well as termination or attenuation of lineages has been termed here as Biohorizon. In strict sense, a biohorizon is a surface (or distinctive bed) of biostratigraphic change, or a plane of distinctive characters. The identification of biohorizons is generally based on first appearance, last occurrence, change in frequency, evolutionary change, or change in character of individual taxon (Hedberg, 1976). In the present context, for recognising biohorizons emphasis is laid on the evolutionary changes in organizations and important characters which implicitly incorporate their FADs or LADs.

The second important natural outcome of the present analysis is the interbiohorizon-zones (or

Table 3—Elaborated data matrix of character states (1. Ancestral, 2. Transitionary, 3. Derived) and morphos; character codes are on X axis and morphos on Y axis. For morphos A-Av see Table 1, and for character states see Table 2

MORPHOS CODE	CHARACTER CODE													
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	XIII	XIV
AF	1	3		1	3	1	1							3
AU	1	3		1	1	1	1				1			3
AV	1	1	1	1	1	1	1				1			2
AN	1	3		3	3	3	1	1	1	1				2
R	1	1	1	3	1	1	1				1		1	1
O	2	1	3	3	1	1	1				1		1	1
A	2	1	2	3	1	1	1				1		1	1
N	1	3		3	1	1	1				1		1	1
AB	1	3		3	1	1	1				1		1	1
J	1	1	3	1	1	1	1				1		1	1
C	2	1	1	3	1	1	1				1		1	1
AM	1	3		3	1	1	1				3	3	1	1
B	1	1	1	3	1	1	1				1		1	1
T	1	3		3	3	1	1				1		1	1
AI	1	1	1	3	1	1	1				1		1	1
D	1	1	1	3	1	1	1				1		1	1
U	1	1	1	3	1	3	1	3	1				1	1
AG	1	3		3	1	3	1	1	3	1			1	1
AA	1	1	1	3	1	3	1	3	1				1	1
Z	1	3		3	1	3	1	1	1	1			1	1
K	3	3		3	1	1	1				1		2	
H	3	3	3	3	1	1	1				1		2	
F	3	1	3	3	1	1	1				1		2	
W	3	1	3	3	1	1	1				1		2	
G	3	1	3	3	1	1	1				1		2	
Q	3	3		3	1	1	1				1		2	
V	3	3		3	1	3	1	3	1				2	
I	3	1	3	3	1	3	1	3	3				2	
AT	3	3		3	1	1	1				1		3	
AD	3	3		1	3	1	1				3	1	3	
AQ	3	3		3	1	1	1				1		3	
AK	3	3		3	1	1	1				1		3	
AC	3	2	3	3	3	1	1				3	1	3	
AH	3	3		3	1	1	1				1		3	
AR	3	3		3	3	1	3				3	3	3	
AE	3	3		3	3	1	1				3	3	3	
S	2	3		3	1	1	1				1		3	
AL	3	3		3	3	1	1				3	3	3	
AS	1	3		3	3	1	3				3	1	3	
AO	3	3		3	1	1	1				1		3	
AJ	3	3		3	1	1	1				1		3	
AP	3	3		3	1	1	1				1		3	
E	3	3		3	1	1	1				1		3	
Y	3	3		1	1	3	1	1	1	1			3	
X	3	3		3	1	3	1	1	1	1			3	
P	3	3		3	1	3	1	1	1	3			3	
M	3	3		3	1	3	1	1	1	1			3	
L	3	3		3	1	3	1	1	1	1			3	

interval-zones), which by definition are the intervals between two distinctive biostratigraphic horizons (Hedberg, 1976). These zones represent a sequence between two identifiable biohorizons, and since the biohorizons are demarcated on the basis of morpho-evolutionary datums in the present work, the significance of interbiohorizon-zones is enhanced as a parameter for correlation and dating.

The earliest palynoassemblages from the Indian Gondwana are mainly constituted by radiosymmetric and bilateral monosaccates, and a few monosaccoid nonstriate-disaccate forms. Through time, during Late Permian and the Mesozoic, varied types of disaccates have evolved. The synthesis of data has

Table 3—Contd.

MORPHOS CODE	CHARACTER CODE													
	XV	XVI	XVII	XVIII	XIX	XX	XXI	XXII	XXIII	XXIV	XXV	XXVI	XXVII	XXVIII
AF	3	1	1	3	3	2	1							3
AU	3	1		3	3	1				3	1			3
AV	1			3	1									3
AN	3	3		1	3	1	1							3
R	3	1	1	1	3	1	3	1	1					3
O	3	3		1	3		3	3						2
A	3	3		1	3	1	1							1
N	3	3		1	3		3		3					3
AB	3	3		1	1									3
J	3	3		1	3	1								1
C	3	3		1	3	1	3	1	1					3
AM	3	3		1	3	1	1							3
B	3	3		1	3	1	1							1
T	3	3		3	3	3	3	1	1					3
AI	3	3		1	1									3
D	3	3		1	3	1	1							3
U	3	2		1	3	1	3	1	1					3
AG	3	3		1	3	1	1							3
AA	3	1	1	3	3	1	1							3
Z	3	3		1	3	1	1	3						3
K	3	3		1	3	3	3						3	
H	3	3		1	3	3				1	1		1	
F	3	3		1	3	3					1		3	
W	3	3		1	3	3	3			1	1		1	
G	3	3		1	3	3				1	1		3	
Q	3	3		1	3	3				1	1		3	
V	3	3		1	3	3				1	3		3	
I	3	3		1	3	3				1	1		1	
AT	3	3		1	3	3				3	1		3	
AD	3	1	1	3	3	3				2	1		3	
AQ	3		3	3	3	3				1	1		3	
AK	3	3		1	3	3				1	1		3	
AC	3	3		1	3	3				1	3		3	
AH	3	3		1	3	3				1	1		3	
AR	3		3	3	3	3				1	1		3	
AE	3	1	1	3	3					2	1		3	
S	3	3		1	3	3				1		1	3	
AL	3	3		1	3	3				1	2		1	
AS	3		3	3	3	3				1	1		3	
AO	3	3		1	3	3				1	3		3	
AJ	3	3		1	3	3				1	2		3	
AP	3	3		3	3	3				3	1		3	
E	3	3		1	3	3				1	1		3	
Y	3	3		1	3	3				1	3		3	
X	3	3		1	3	3				1	3		3	
P	3	3		1	3	3				1	1		1	
M	3	3		1	3	3				1		1	3	
L	3	3		1	3	3				1	3		1	

revealed 11 major episodes, each of which is diagnostic as a FAD for new organisations which could be linked for their relationship with an older plan of construction; similarly, LADs of characters were also demarcated for identification of their extinction.

Biohorizon-I : *Potonieisporites—Plicatipollenites* Phase

In terms of evolution, the earliest Talchir palynoflora is in a conspicuous primitive state of composition because it comprises less diversified

Table 4—Elaborated data matrix of character states (1. Ancestral, 2. Transitionary, 3. Derived) and morphos; Morphos are on X axis and character codes on Y axis. For morphos A-Av see Table 1, and for character states see Table 2

CHARACTER CODE	MORPHOS CODE																									
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X	Y	Z
XXVI													1						1							
XII																										
XXVII					3	3	3	1	1		3	1	3			1	3		3			3	1	3	3	
XXIII			1											3				1		1	1					
VIII									3			1	1			1					3	3		1	1	1
IX									3			1	1			1					1	1		1	1	1
X												1	1			3								1	1	1
XXIV					1		1	1	1			1	1			1	1		1			1	1	1	1	
XVII																		1								
XXII			1												3			1		1	1					
XXV					1	1	1	1	1			3				1	1					3	1	3	3	
XIII	1	1	1	1	3	2	2	2	2	1	2	3	3	1	1	3	2	1	3	1	1	2	2	3	3	1
XVIII	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1
XX	1	1	1	1	3	3	3	3	3	1	3	3	3			3	3	1	3	1	1	3	3	3	3	1
XIV	1	1	1	1						1				1				1		1	1					1
XXI	1	1	3	1							3			3	3			3		3	3					1
VII	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
XXVIII	1	1	3	3						1				3	2			3		3	3					3
V	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1
III	2	1	1	1		3	3	3	3	3					3			1			1		3			
I	2	1	2	1	3	3	3	3	3	1	3	3	3	1	2	3	3	1	2	1	1	3	3	3	3	1
XI	1	1	1	1	1	1	1	1		1	1			1	1		1	1	1	1			1			
VI	1	1	1	1	1	1	1	1	3	1	1	3	3	1	1	3	1	1	1	1	3	3	1	3	3	3
II	1	1	1	1	3	1	1	3	1	1	3	3	3	3	1	3	3	1	3	3	1	3	1	3	3	3
XIX	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
XVI	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1	3	3	2	3	3	3	3	3
XV	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
IV	3	3	3	3	3	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1	3

type of organizations, e.g., *Plicatipollenites, Potonieisporites, Parasaccites, Virkkipollenites* and *"Pityosporites"* (Figures 2-6). The *Vestigisporites*-type of pollen are also recorded at the Biohorizon-I but they are closely related in character states with *Pityosporites* stock (see Tiwari, 1975; the older assemblage of Dudhi River section *in* Lele, 1975; assemblage of Talchir Needle Shale, Athgarh Basin *in* Tiwari *et al.*, 1987). It could be, that in some isolated localities (viz., Jamunia River section, Jharia Coalfield) all the five basic morphos are not recorded. This phenomenon appears to be related with the ecological conditions where the vegetation could have been very scanty, or with taphonomy hence the total representation is not reflected.

Now the question arises as to how and from where the girdling monosaccate organization has evolved? It is a known fact that several groups of Late Carboniferous seed plants, viz., Cordaitales, Callistophytales and Coniferales, produced monosaccate pollen. Although there are no Carboniferous sediments on the Indian Peninsula, the other regions of Gondwana contain Carboniferous palynoassemblages in which the monosaccate pollen have been generally assigned to *Feleixipollenites* and *Potonieisporites* (Balme, 1988). In Australia, Lower Carboniferous Laural Formation exclusively contains small trilete spores with incipient cingulum, and no saccate pollen are on record (Balme, 1960; Kemp *et al.*, 1977). In the subsequent Anderson Formation, the first appearance of a non-striate disaccate pollen resembling *Pityosporites westphaliensis* is recorded (Balme, 1960; pl. 5, fig.35). This *"Pityosporites"* is taken here to represent an old stock of simple disaccate pollen with laterally separated sacci and probably with a thinner, linear area—an incipient scar, at the centre of the cappa. In all probability, this oldest occurrence of non-striate disaccate pollen has morphographical connections with similar forms in the lowermost Talchir palynoassemblage in India (Lele, 1975, pl. 1, fig. 15; Tiwari *et al.*, 1987, fig. 2d).

In Australia, the oldest undoubtedly saccate pollen comprising bilateral and radiosymmetric organizations (*Potonieisporites, Parasaccites*), found at the base of *Spelaeotriletes* (*Anabaculites*) *yberti* assemblage (Early Namurian; Kemp *et al.*, 1977, p. 182; Playford, 1985; Cooper, 1991), are in

Table 4—Contd.

CHARACTER CODE	MORPHOS CODE																					
	AA	AB	AC	AD	AE	AF	AG	AH	AI	AJ	AK	AL	AM	AN	AO	AP	AQ	AR	AS	AT	AU	AV
XXVI																						
XII			1	1	3							3	3					3	1			
XXVII			3	3	3			3		3	3	1		3		3	3	3	3	3		
XXIII																						
VIII	3						1							1								
IX	1						3							1								
X					1									1								
XXIV			1	2	2			1		1	1	1			1	3	1	1	1	3	3	
XVII	1			1	1	1											3	3	3			
XXII																						
XXV			3	1	1			1		2	1	2			3	1	1	1	1	1	1	
XIII	1	1	3	3	3		1	3	1	3	3	3	1		1	3	3	3	3	3		
XVIII	3	1	1	3	3	3	1	1	1	1	1	1	1	1	1	3	3	3	3	1	3	3
XX	1		3	3		2	1	3		3	3	3	1	1	3	3	3	3	3	3	1	
XIV	1	1				3	1		1				1	2							3	2
XXI	1					1	1						1	1								
VII	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	3	1	1	1
XXVIII	3	3				3	3		3				3	3							3	3
V	1	1	3	3	3	3	1	1	1	1	1	3	1	3	1	1	1	3	3	1	1	1
III	1		3						1													1
I	1	1	3	3	3	1	1	3	1	3	3	3	1	1	3	3	3	3	1	3	1	1
XI		1	3	3	3			1	1	1	1	3	3		1	1	1	3	3	1	1	1
VI	3	1	1	1	1	1	3	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1
II	1	3	2	3	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	1
XIX	3	1	3	3	3	3	3	3	3	1	3	3	3	3	3	3	3	3	3	3	3	1
XVI	1	3	3	1	1	1	3	3	3	3	3	3	3	3	3	3				3	1	
XV	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1
IV	3	3	3	1	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1	1

association with lycopsoid and apiculate trilete forms. This zone also contains nonstriate-disaccate pollen, but no striate pollen has been recovered (Text-figure 3). In Biohorizon-I, the striate-disaccate pollen are absent (Lele, 1975; Tiwari *et al.*, 1987). In this repsect it resembles the Stage 1 of Australia (lower part of *Potonieisporites* assemblage, in Kemp *et al.*, 1977; Playford, 1985). However, Biohorizon-I is relatively younger than the latter because of the dominance of *Plicatipollenites-Parasaccites* (instead of *Potonieisporites*).

At this level the prominence of well-organized tetrad mark in monosaccates has a bearing on the phenomenon of continuance of a primitive character of a prepollen. Although the polarity for germination had shifted to the distal surface by this time, yet the distal saccus-free-area remained non-sulcoid in nature as it shows distinct infra-reticulate structure, and there is no thinning of sexine. The trilete mark appears to have functioned as an emergency exit for pollen tube. This is a case of conservation of a primitive character which continued through time for providing better chance of survival. This contention is supported by the fact that in subsequent time, although radiosymmetric monosaccates continued to occur till the Permian end, the tetrad mark lost its prominence to become a vestigial imprint. The bipolar germination mechanism appears to be an important evolutionary character at this biohorizon.

Stratigraphically, these stocks are the oldest in the Indian Peninsula. They are found in the lowermost beds of the Talchir Formation (Text-figure 1). Biohorizon-I is dated as Asselian but older in relation to the *Eurydesma*-bearing Manendragarh beds (Shah & Sastry, 1975) which are of Late Asselian age. The latter contains a much diversified palynoflora including striate-disaccate pollen types.

Biohorizon-II : *Crescentipollenites-Rugasaccites* Phase

The FAD for striate-disaccate (Figure 30) is identified in Penganga assemblage (Lele, 1984). In terms of symmetry, the bilateral construction of monosaccate pollen starts gaining ground at this datum plane (*Gondwanopollis, Caheniasaccites, Rugasaccites,* bilateral forms of *Parasaccites* as *P.*

Table 5—Selected and short-listed data matrix of character states and morphos; character codes are on X axis and morphos on Y axis. For morphos A-AV see Table 1, and for character states see Table 2

	II	IV	V	VI	VII	VIII	XI	XIII	XIV	XV	XVI	XVII	XIX
AU	3	1	1	1	1		1		3	3	1		3
AV	1	1	1	1	1		1		2	1			1
AB	3	3	1	1	1		1	1	1	3	3		1
D	1	3	1	1	1		1	1	1	3	3		3
AI	1	3	1	1	1		1	1	1	3	3		1
C	1	3	1	1	1		1	1	1	3	3		3
B	1	3	1	1	1		1	1	1	3	3		3
A	1	3	1	1	1		1	1	1	3	3		3
Z	3	3	1	3	1	1		1	1	3	3		3
AA	1	3	1	3	1	3		1	1	3	1	1	3
W	1	3	1	1	1		1	2		3	3		3
AQ	3	3	1	1	1		1	3		3		3	3
AL	3	3	3	1	1		3	3		3	3		3
AR	3	3	3	1	3		3	3		3		3	3
E	3	3	1	1	1		1	3		3	3		3
AD	3	1	3	1	1		3	3		3	1	1	3
AC	2	3	3	1	1		3	3		3	3		3
L	3	3	1	3	1	1		3		3	3		3

Table 6—Selected and short-listed data matrix of character states and morphos: character codes are on Y axis and morphos on X axis. For morphos A-AV see Table 1, and for character states see Table 2

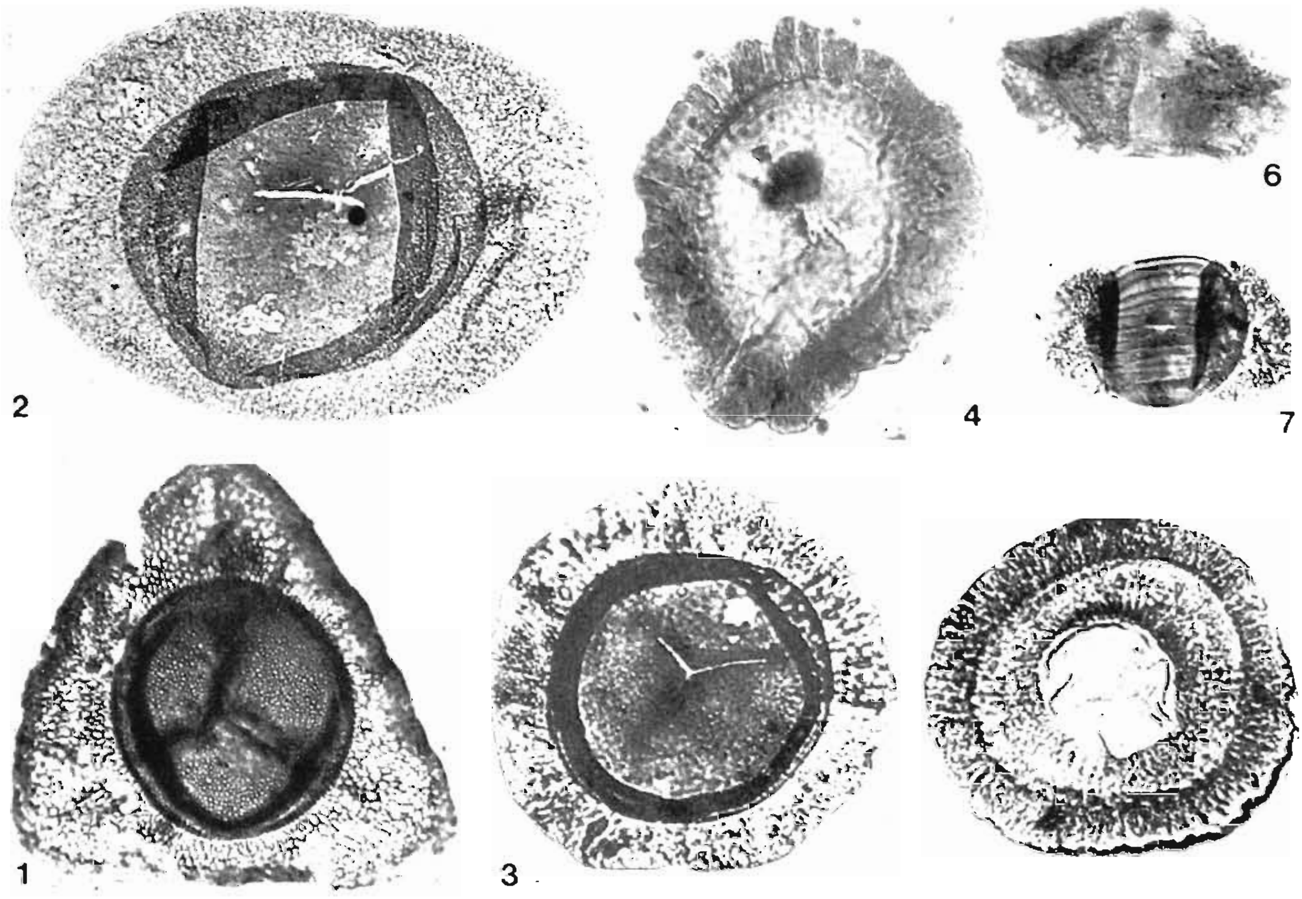
	A	B	C	D	E	L	W	Z	AA	AB	AC	AD	AI	AL	AU	AR	AU	AV
VIII						1		1	3									
XVII									1			1			3	3		
XI	1	1	1	1	1		1			1	3	3	1	3	1	3	1	1
VII	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1
XIV	1	1	1	1				1	1	1			1				3	2
VI	1	1	1	1	1	3	1	3	3	1	1	1	1	1	1	1	1	1
II	1	1	1	1	3	3	1	3	1	3	2	3	1	3	3	3	3	1
V	1	1	1	1	1	1	1	1	1	1	3	3	1	3	1	3	1	1
XIII	1	1	1	1	3	3	2	1	1	1	3	3	1	3	3	3		
XV	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	1
XVI	3	3	3	3	3	3	3	3	1	3	3	1	3	3	3	3	1	1
IV	3	3	3	3	3	3	3	3	3	3	3	1	3	3	3	3	1	1
XIX	3	3	3	3	3	3	3	3	3	1	3	3	1	3	3	3	3	1

bilateralis). With the bilateral monosaccate lineage (i.e., *Potonieisporites*) the morphologies of *Cabeniasaccites* and *Gondwanopollis* are closely related. Such a trend flows from typical monosaccate towards the disaccoid organization with a tendency of reduction in the lateral spreads of the saccus. Thus *Gondwanopollis*-type of organizations are intimately related with *Sahnites*-kind of morphos (Figures 8-11). In natural sequence of incidences it also appears logical that from radial monosaccate having para-mode of body-sac attachment (*Parasaccites*) such steps might have led to derivation of ovoidal, nonstriate-disaccate bilateral forms (Figures 21-23) assigned to *Vesicaspora* and *Divarisaccus* (Venkatachala & Kar, 1966; Lele & Shukla, 1978; Meyen, 1987).

The basic nature of body exine is infra-reticulate in monosaccates. The appearance of vermiculate or rugose sculpture at this biohorizon (*Rugasaccites*; Figure 13) is an example of re-appearance of an ancestral character state of exine.

The earliest occurrence of striate-disaccate equates this biohorizon with the part of *Potonieisporites* assemblage (base of Stage 2) in Australia (Kemp *et al.*, 1977). The sequence of FADs suggests that striate-disaccates had their fore-bearers in the older sequence which were closely related with the simple disaccate stock of "*Pityosporites*" type; the latter precedes the striate forms on temporal scale (Text-figures 1, 3). These are considered to have a remote ancestral relationship (Figures 6, 7).

This biohorizon has been established by incorporating the Penganga and Manendragarh



Figures 1-7—Oldest mother stock complex represented by **1.** *Teichertospora* McGregor & Playford 1990, and the morphos of six basic lineages which share ancestral character states of the stock in different combinations, i.e., prominent germinal mark, non-sulcoid distal saccus-free-area and body-in-fold system, as seen in fig. **2.** *Potonieisporites*, in Kemp *et al.*, 1977; **3.** *Plicatipollenites*, **4.** *Parasaccites*, **5.** *Virkkipollenites*, **6.** *"Pityosporites"*, in Balme, 1960; **7.** *Crescentipollenites*, in Kemp *et al.*, 1977.

palynoassemblages (Lele, 1984; Lele & Chandra, 1972; Chandra & Lele, 1980). The age of Manendragarh beds is Late Asselian. It has been indicated by the occurrence of *Eurydesma* fauna (Shah & Sastry, 1975).

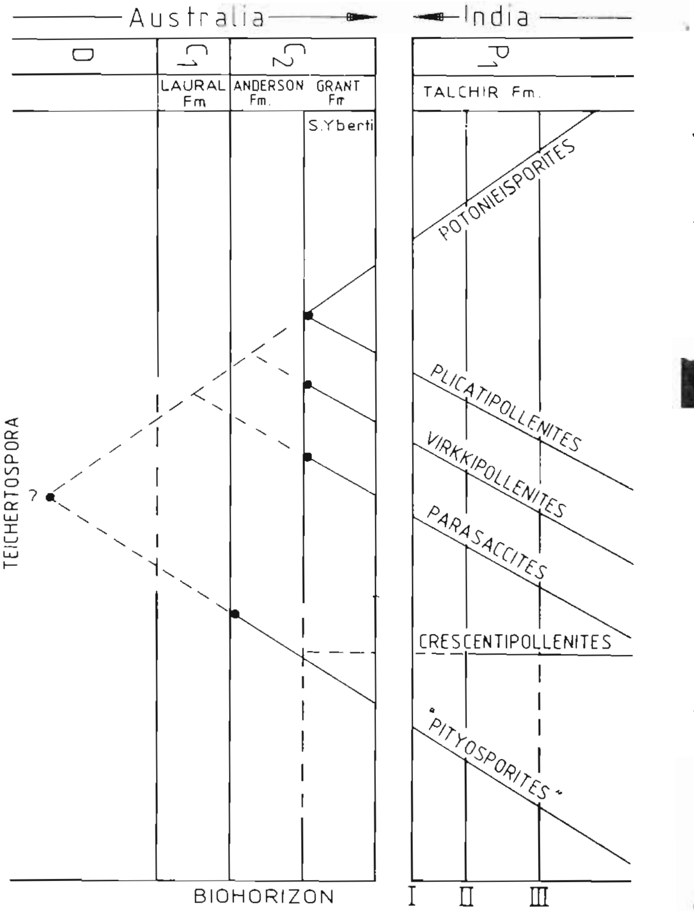
Biohorizon-III : *Crucisaccites-Tuberisaccites* Phase

This level of morphographic evolution in saccate pollen qualifies for a unique status in the Indian Gondwana. Many new characters derived from the preceding stock branch-off from three main organizations—monosaccate, non-striate-disaccate and striate-disaccate, including six basic lineages.

The composition at Biohorizon-III comprises diversified striate-disaccate pollen (such as *Circumstriatites, Striatopodocarpites, Faunipollenites,* Figures 31, 34, 33), nonstriate (*Scheuringipollenites*; Figure 45; *Platysaccus*) and monosaccates (*Tuberisaccites*, Figure 28; *Crucisaccites, Stellapollenites*; Figures 26, 25) and *Rimospora*, Figure 14). Subsequently, the reticuloid pattern of striations in mono- and disaccates also appears. The pitcher-shaped saccus develops both in striate and nonstriate-disaccates (*Verticipollenites, Aurangapollenites*). Furthermore, a unique variability is observed in a pseudo-striate form where extreme reduction of sacci has taken place (*Tiwariasporis*, Figure 37).

The basic bauplan of circular para-condition of saccus attachment is manifested in stellate, cruciform and amphi-saccate organizations at this biohorizon. By way of character state matching, these morphos appear to have been derived from the circular para-mode of body-sac attachment, as in *Parasaccites* (Figures 23-26).

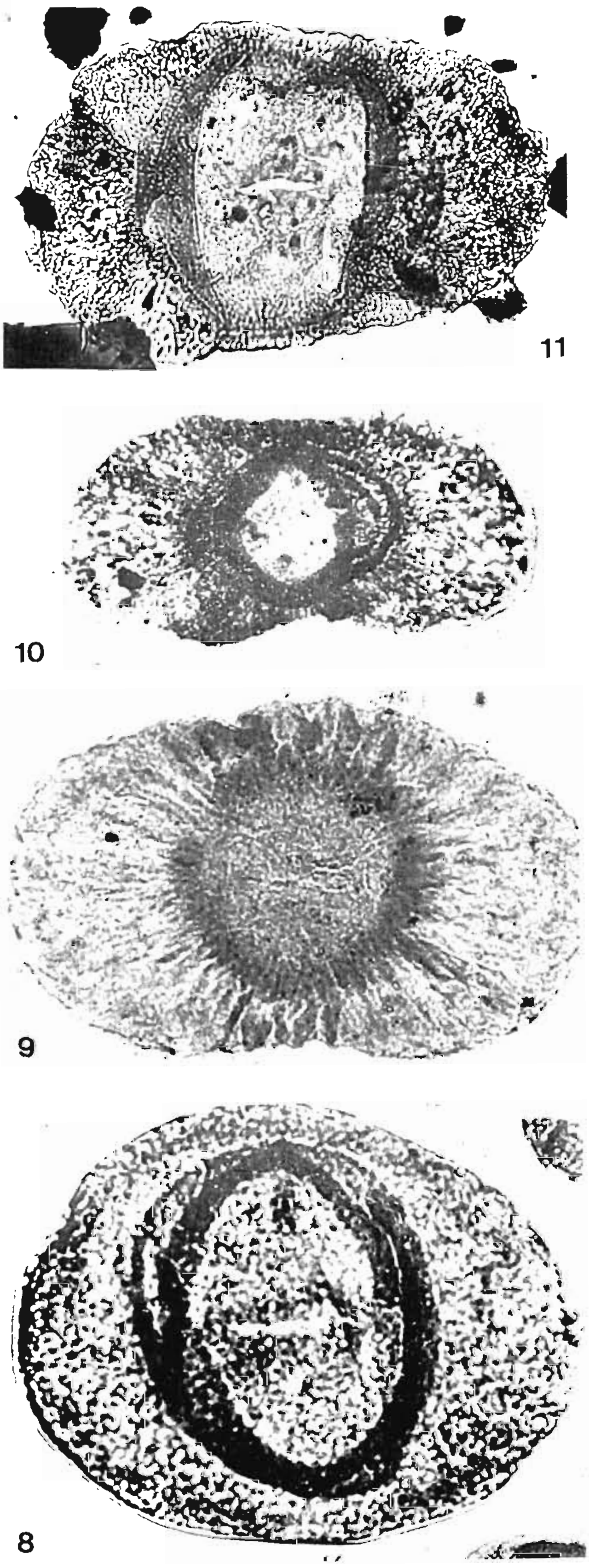
In the radiosymmetric para-mode lineage, further manifestation in the sexinal distribution has



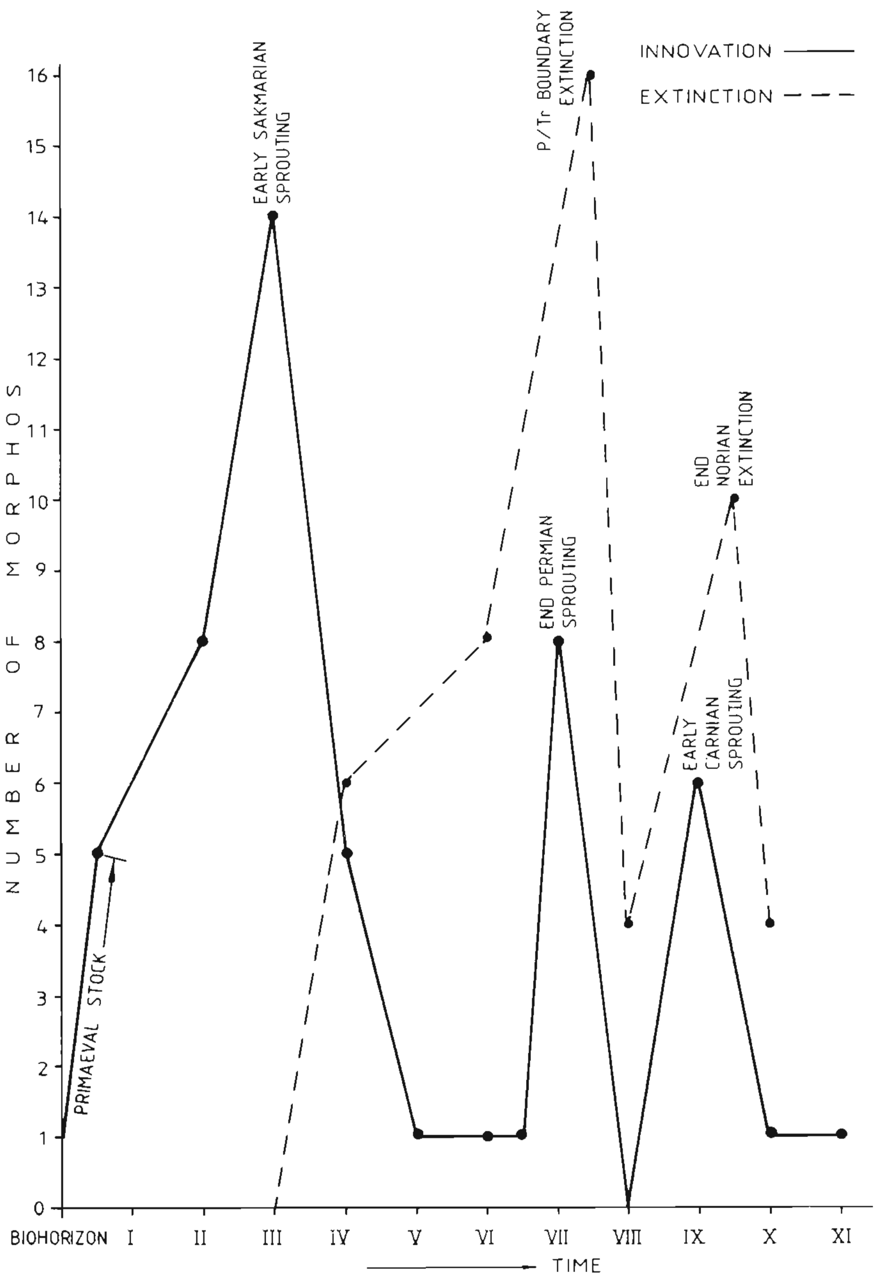
Text-figure 3—Cladogram showing relationship of stock morphos based on congruence of parsimonically compatible character states. Out-group presumably located in Progymnospermous group of Devonian in Australia.

occurred by development of conspicuous protuberances and reticuloid pattern of grooves on the body (*Tuberisaccites, Parastriopollenites*; Figures 28, 29). This seems to be the starting plane for subsequent reticuloid striation-bearing monosaccates (*Barakarites*). The humble start of striate-disaccate line in Biohorizon-II has branched-off radiantly giving rise to a complex of combinations in striation pattern (Vijaya, 1990).

In the wake of sprouting of newer morphography at several levels, some trisaccate and



Figures 8-11—Showing morphos of *Potonieisporites* lineage in sequence of evolutionary states. The derived character state in each morphos is the resultant of changes. **8.** *Potonieisporites*, the stock of this tree possessing mainly ancestral character states of prominent germinal aperture, distal non-sulcoid saccus-free-area and double body-in-fold system; **9.** *Caheniasccites* and **10.** *Gondwanopollis* are the morphos which acquired derived state in the characters of having reduced body-in-fold and also attaining bilateral symmetry; **11.** *Sahnites* showing retained prominent nature of germinal aperture and represents ultimate derived character state of the lineage.

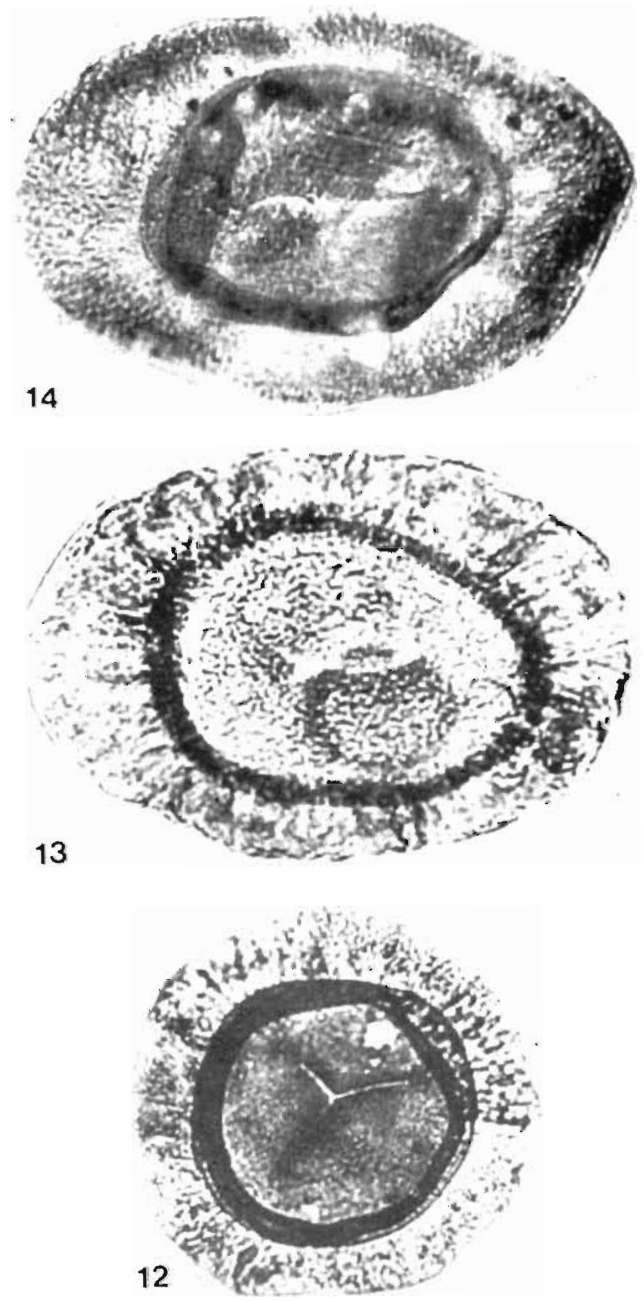


Text-figure 4—Graphic representation of mode of *innovation* (solid lines) and *extinction* (broken lines) in number of morphos through Gondwana Sequence of India; only the incoming and outgoing morphos are depicted at each biohorizon, and not their total sum. Stratigraphic succession represented by *Biohorizon numbers* from I to XI. This represents three innovation events and two extinction events. The high turnover of morphographies at P/Tr transitional zone as well as Carnian/Norian level are well-projected. The Early Sakmarian sprouting represents the highest innovation in saccate pollen.

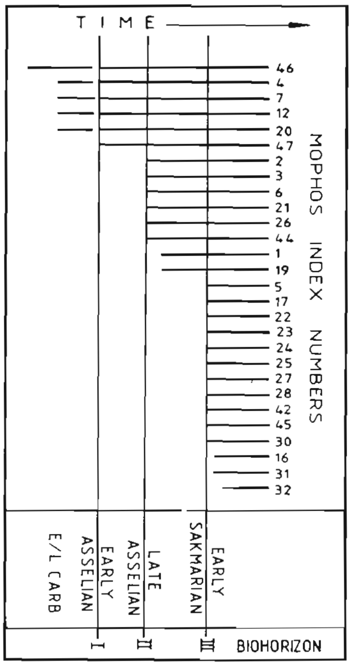
tetrasaccate forms (Figure 65) also occur but without any special exine characters (i.e. striations, islands, taeniae or a tetrad-mark). Their sporadic inconsistent incidences and anomalous features suggest that they are morpho-variants of disaccates rather than naturally affiliated groups in themselves (viz., *Trochosporites* in Lele, 1975; *Tetrasaccus* in Maithy, 1969; Tripathi *et al.*, 1990; Vishnu-Mittre, 1954; Sukh-Dev, 1980). Also a trisaccate pollen specimen with indistinct thin striation-like grooves has been assigned to *Crustaesporites* sp. by Lele and Karim (1971) from the younger beds of Talchir Formation.

The experimentation of nature to produce new and unusual combinations of building plans in pollen in the lower part of Upper Talchir Formation is well documented (Text-figures 1, 5).

Biohorizon-III derives the data from the



Figures 12-14—Morphos of *Plicatipollenites* lineage: **12.** *Plicatipollenites*, the out-group stock of this lineage is characterised by prominent germinal aperture and the body-in-fold system. The aperture becomes vestigial in subsequent time; **13.** *Rugasaccites*; and **14.** *Rimospora*, the morphos although appear at younger level than *Plicatipollenites* (with structured body exine) yet possess sculptured exine which is an ancestral character state.



Text-figure 5—A spread diagrame of sequential distribution of morphos through Biohorizons-I, II and III with respect to Australian primaeval stock in L/U Carboniferous (MIN as in Text-figure 1).

palynoassemblages studied from the younger horizon in Dudhi River Section (Lele, 1975) and Jayanti Coalfield (Lele & Karim, 1971; Lele & Makada, 1972; Chandra & Lele, 1980). The Umaria Marine bed assemblage (Lele & Chandra, 1972) is relatively younger to Manendragarh assemblage. The Umaria bed overlies the Talchir boulder bed and passes upward into the Karharbari rocks without any visible break (Sastry *et al.*, 1977). The productids make predominating elements of Umaria bed where *Eurydesma* are very rare, hence dated as Late Sakmarian. By these parameters, Biohorizon-III is assigned an Early Sakmarian age.

Biohorizon-IV : *Densipollenites-Barakarites* Phase

This biohorizon is recognised by the first appearance of four distinct morphographies in saccate pollen. In one group, the saccus envelops the body from all sides and is attached at one point (*Densipollenites*). This new organizational architecture is a remarkable episode in which the saccus is filled with endoreticulate alveolae to make it a protosaccus. It provides better protection to the central body which nurtures the genetic material. In other group, the body-sac attachment is a girdling kind, and a circumsulcus develops at the equatorial region of the body which bears reticuloid striations (*Barakarites*). The singular morphos having an enveloping saccus (*Densipollenites*) although does not possess any haptotypic mark, in most of the character state comparability this organization comes closest to *Virkkipollenites* (Figures 18, 19).

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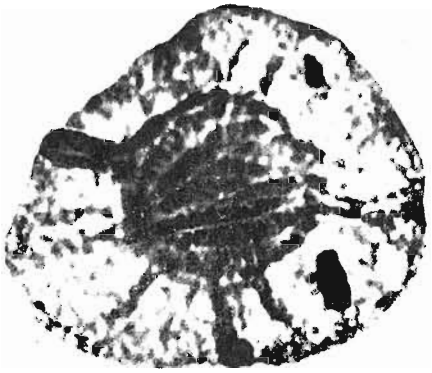

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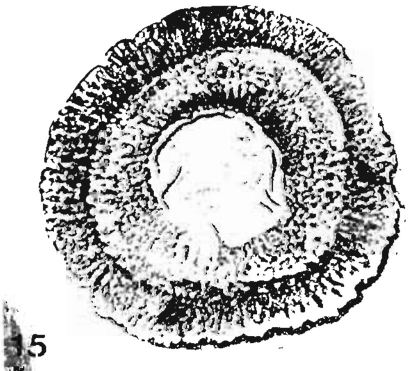

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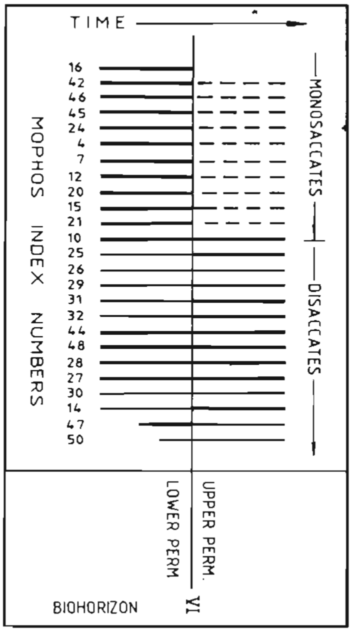
Figures 15-17—Morphos of *Virkkipollenites* lineage: **15.** *Virkkipollenites*, definitely a line of experimentation from the mother stock, lacking body-in-folds. Simple linear grooves develop on one of the faces of the body as seen in **16.** *Striomonosaccites*, and in another direction the sexinal islands also develop on other face of the body as in **17.** *Goubinispora*, a derived character state of out-group stock.



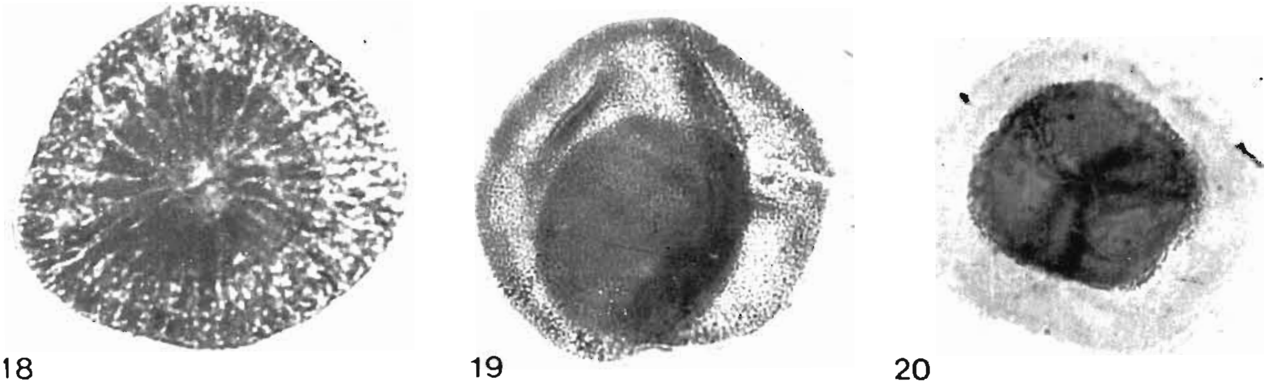
Text-figure 6—Sequential distribution of morphos across Lower/Upper Permian boundary at Biohorizon-VI to depict the major declination in monosaccate lineages at beginning of Upper Permian. Line thickness is indicative of relative prominence; broken line for inconsistent occurrence (MIN as in Text-figure 1).

The relationship derivation of the former from the latter can be traced through *V. densus* (Lele, 1964; pl. 2, fig. 19) and *Virkkipollenites* sp. (*in* Venkatachala & Kar, 1968; pl. 2, fig. 21).

The reticuloid striations-bearing monosaccate has its linkage in the comparable forms of older Biohorizon-III (i.e., in *Parastriopollenites, Tuberisaccites*). Similarly, the simple monosaccate pollen (*Virkkipollenites*) has relationship with the striate-monosaccate (*Striomonosaccites*) which occurs at slightly older level than the Biohorizon-IV.

The FAD for taeniate pollen (*Lueckisporites*) is also identified at the Biohorizon-IV. This bilateral bitaeniate, disaccate pollen has a greater degree of similarity in character states with nonstriate-disaccate "*Pityosporites*" stock in which the two sexinal bands could have developed on the proximal face of the body, presumably in response to the climatic changes. Such a derivation of relationship is simple, without involving many steps and in tune with the stratigraphic occurrence. The occurrence of striations on both the faces of the central body in disaccates is also recorded at this phase (*Distriatites*, incl. *Hamiapollenites*; Kar, 1973). This marks the diversification trends at their peak in the disaccate pollen.

The other important event which took place at this juncture is the extinction of unique lineage of monosaccate stellate body-sac attachment and also that of the monosaccate forms with tuberculoid sexinal protuberances, rugulate or reticuloid



Figures 18-20—Morphos, thought to be remotely allied with *Virkkipollenites* tree (**18.** *Virkkipollenites* sp.) but retaining a primitive state of saccus attachment which could give rise to a total covering as in **19.** *Densipollenites*, and almost total covering of the body as in **20.** *Playfordiaspora*.

sculpture on body surface (*Tuberisaccites, Pachysaccus, Rugasaccites* and *Rimospora*). The cruciform body-sac organization also loses it impact. All these events contributing to a high morphographic turnover correspond with the change of palynoflora at the Artinskian/Kungurian transition (Text-figure 1).

In the Australian Gondwana sediments, the earliest record of alete enveloping monosaccate organization and that of morphos with the circumsulcus and reticuloid striations are from *Acanthotriletes* Assemblage-Zone dated as Early Artinskian (High-cliff Sandstone Formation; Segroves, 1970). However, with reference to Umaria Marine bed, the Biohorizon-IV occurs at a higher level than the Early Artinskian, and hence is dated as early Late Artinskian. The Biohorizon-IV is identified at the uppermost Karharbari Formation represented in several sections (Tiwari, 1973; Lele & Makada, 1974; Bharadwaj & Srivastava, 1973).

Biohorizon-V : *Corisaccites* Phase

The FAD of globular taeniate form (*Corisaccites*) is the characteristic feature of this phase. The taeniate line of relationship appears to branch-off from older, simple nonstriate-disaccate. This new character has an alliance with a more complex unit of similar morphography (*Guttulapollenites*) in Late Permian, at a level slightly younger to Biohorizon-V. Parsimonically, *Lueckisporites, Corisaccites* and *Guttulapollenites* (Figures 60; 57 61) represent important character states. In some of the localities (South Rewa Gondwana Basin; Tiwari & Ram-Awatar, 1988) multitaeniate-disaccate pollen with massive sexinal bands have also been recorded, which exhibit gross similarity with *Lueckisporites*. However, this line does not survive in the subsequent horizons and hence seems to be a stage of experimentation at this level. After a gap represented by Kulti and Lower Raniganj formations the morphos with multi-taeniate body make their entry again at the Biohorizon-VII which is the derived state from the older stock of this group.

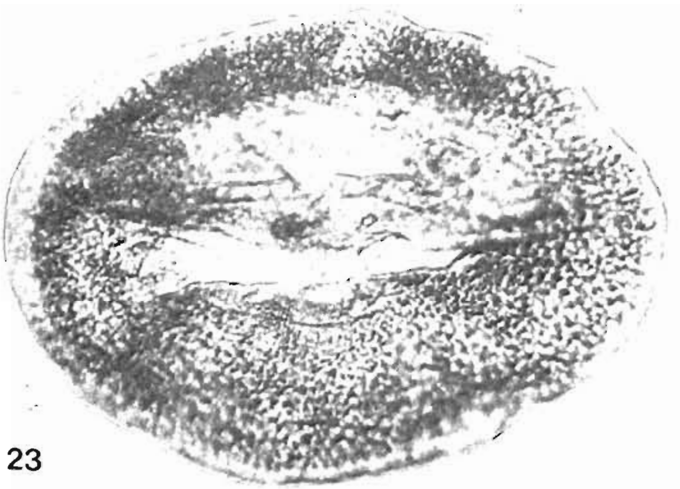
In globular taeniate form *Corisaccites*, the body exine is finely microverrucose (Venkatachala & Kar, 1966b) which makes a deviation from the generally found infra-structured exine of the body. This apparently represents homoplasy in a character, showing retrogressive evolutionary trend. The saccus is also indistinctly structured, rather than having well organized endo-reticulation. The indistinct structure of saccus is an ancestral character state. FADs of these morphos are identified by Kar (1973) and Bharadwaj and Srivastava (1973).

Distriamonocolpites, a unique pollen with oval configuration and striations on both the faces and a sulcus-like saccus-free-area, also appears at this level (identified in Bharadwaj & Dwivedi, 1981). It demonstrates the trend of specialization in striate pollen with non-expression of sacci.

In Australian sediments, the earliest globular forms with taeniate organization (*Corisaccites*) are recorded from *Quadrisporites* Assemblage dated as Late Sakmarian (Segroves, 1970). On the face value of data available the Australian record of *Corisaccites* is much earlier than the Biohorizon-V.

Biohorizon-VI : Monosaccate extinction Phase

It is evident from Text-figure 1 that no new morphographical feature has appeared at this level. On the contrary, most of the singular monosaccate organizations either became extinct or almost disappeared (Text-figure 6). At the same time, the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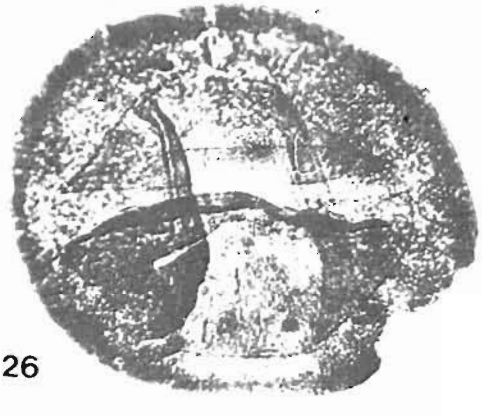
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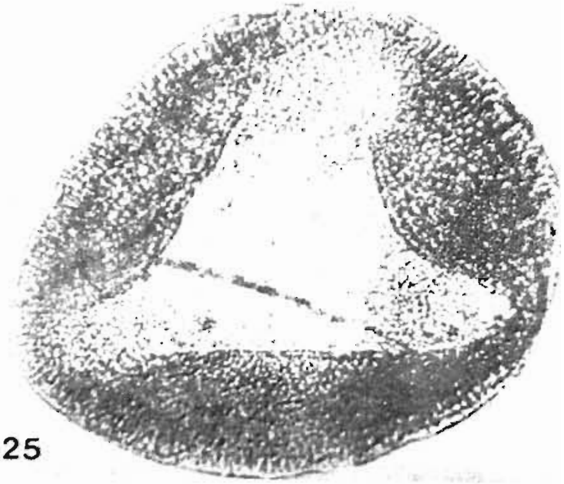
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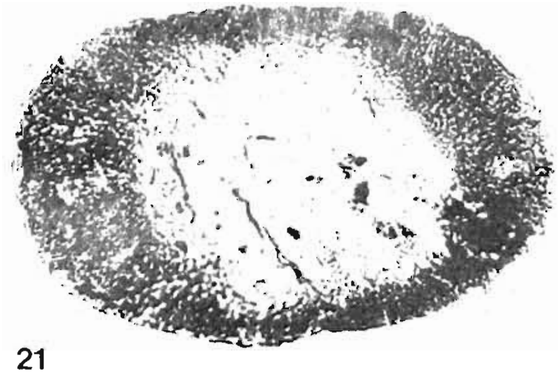
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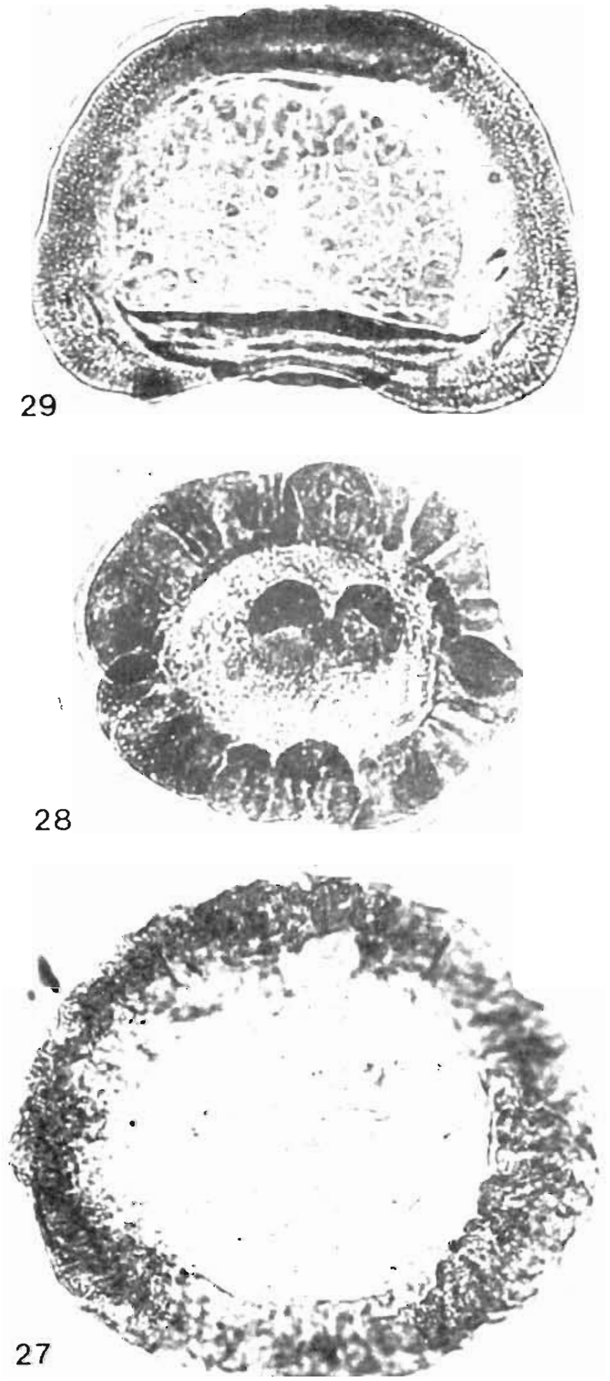
Figures 21-26—*Parasaccites*-lineage is variously diversified in terms of derived character states of body-sac attachment as well as symmetry. **21.** *Parasaccites bilateralis*—the derived character state from radial symmetry, **22.** *Vesicaspora* is the other morphos of this state. The amphi-saccate, cruciform and stellate modes of body-sac attachment, as in **23.** *Divarisaccus*, **26.** *Crucisaccites*, and **25.** *Stellapollenites*, again are derived character states of para-mode (**24.** *Parasaccites*)

striate-disaccates exhibit immense proliferation in quantitative characters resulting into an array of form-species. The characters in striations, central body and the sacci follow multivariant paths at this biohorizon (Kar, 1973; Lele & Shukla, 1978; Tiwari, 1973; Srivastava & Jha, 1988).

This is considered as a great event for the extinction or landslide decline of monosaccate

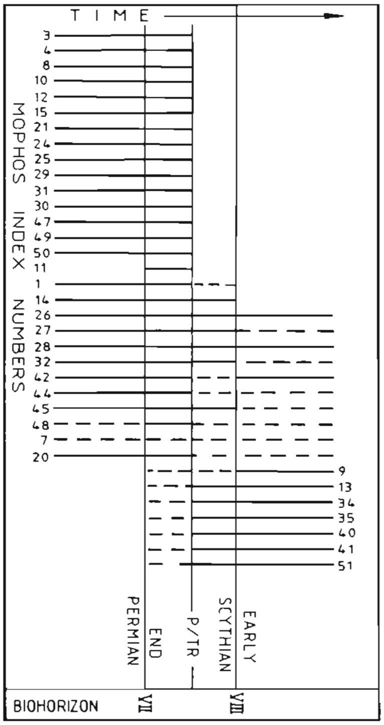


Figures 27-29—The branched-off morphos of **27.** *Parasaccites* out-group showing manifestations in the development of newer features in the exine character as seen in **28.** *Tuberisaccites*; and **29.** *Parastriopollenites* but the para-mode in body-sac attachment is retained.

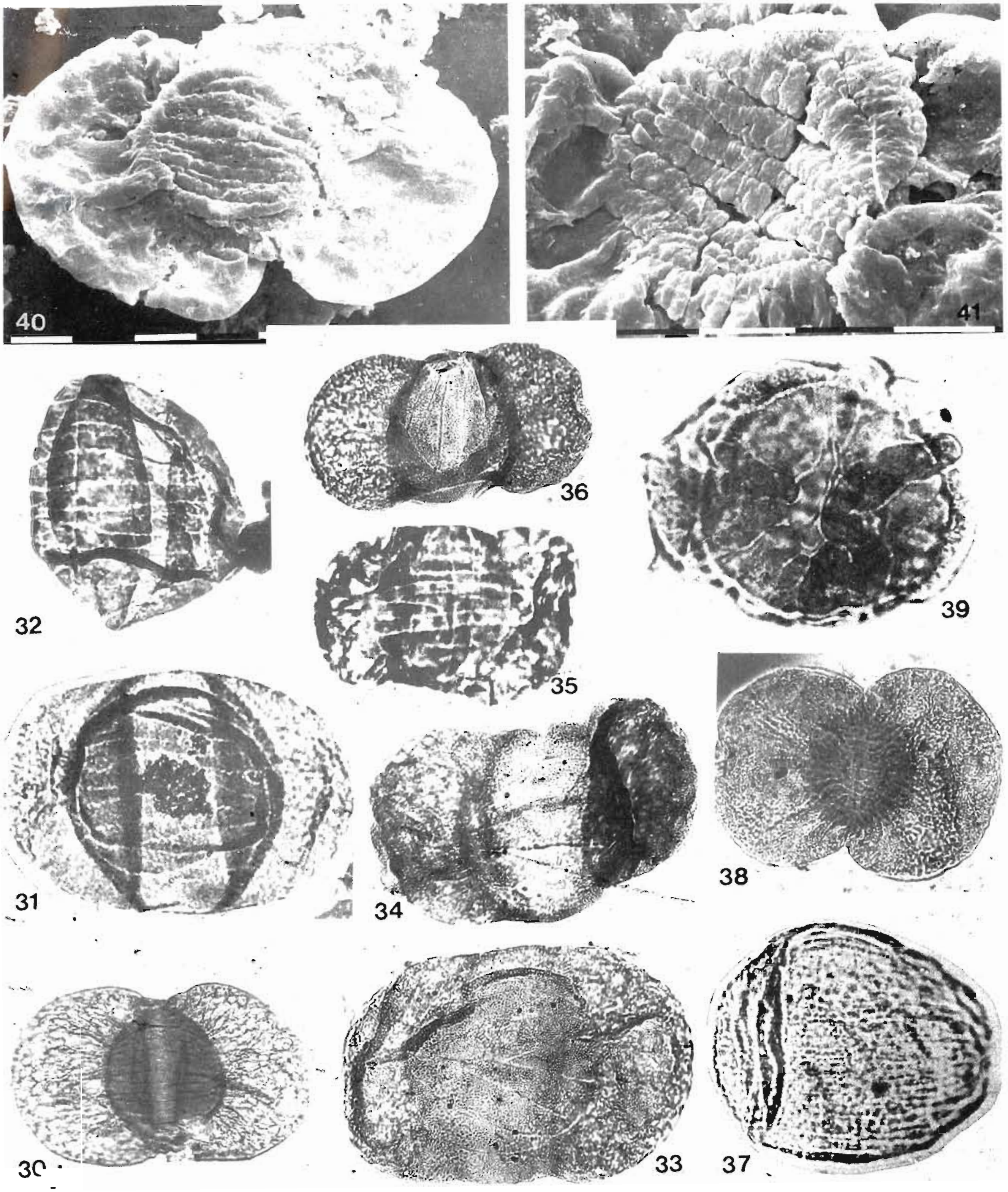
which dominated the Early Permian scenario. Virtually, the quantitative acme-zones of monosaccate pollen taxa cease at the end of Karharbari Formation (i.e., Biohorizon-IV), thus bracketing the Talchir and Karharbari palynofloras into one package, but the qualitative occurrence of monosaccates continues into the Barakar, whereafter they record a major decline (at Biohorizon-VI) and disaccates dominate the pupulation. The shift from monosaccate to disaccate domain and termination of several lineages of older sequence markedly denote a major change in the floral components delineating the Early and Late Permian epochs. The morpho-evolutionary trends in pollen group support the demarcation of Barakar and Kulti interformational boundary and also denote the Lower Permian-Upper Permian boundary.

Biohorizon-VII : *Lunatisporites-Playfordiaspora* Phase

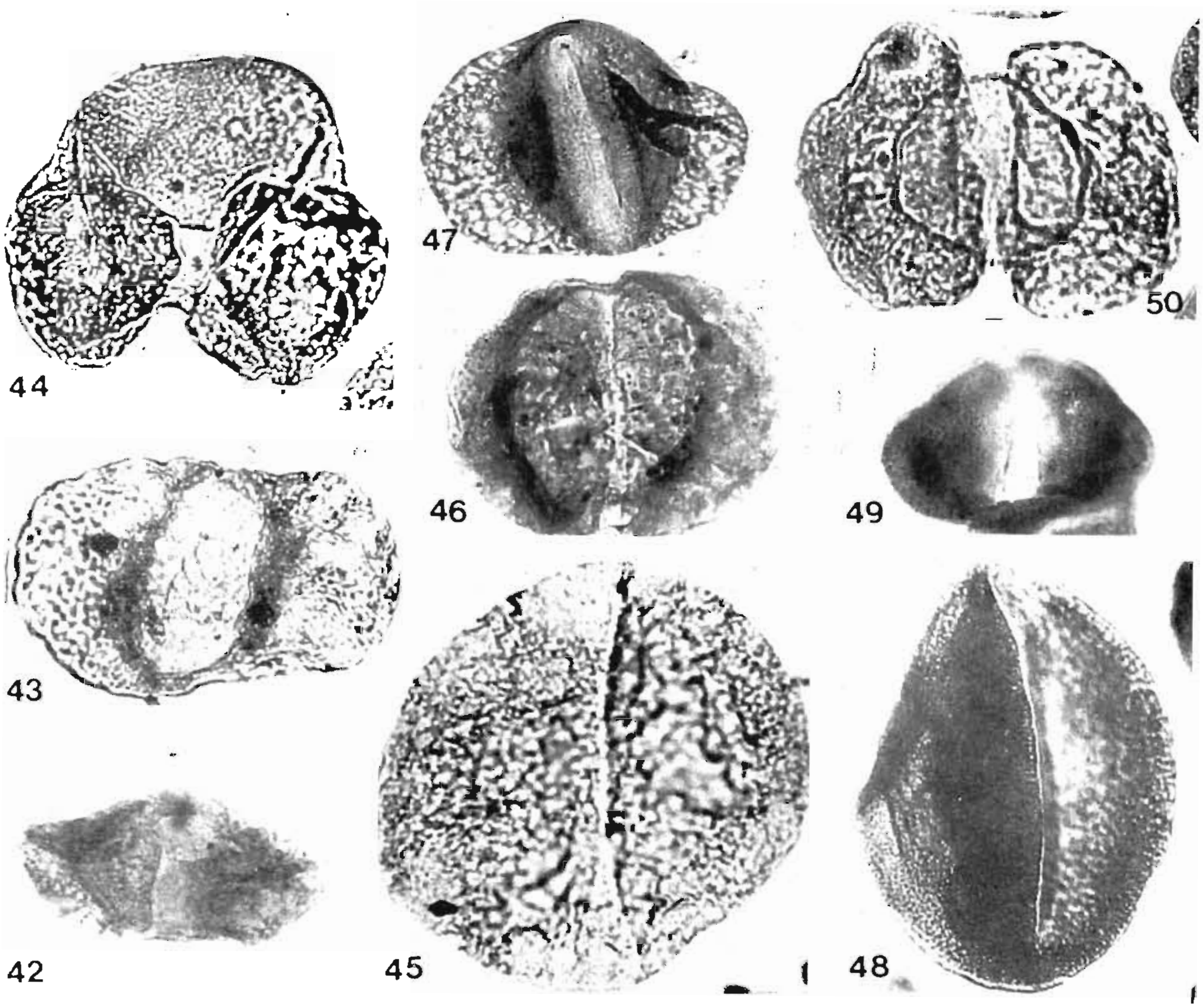
This biohorizon is identified by FAD of typical multi-taeniate pollen (Figures 58, 59). This new lineage has its form-relationship with bitaeniate stock of the Biohorizon-IV (Text-figure 1). Other entrants at this level are the monosaccates with several sexinal elevations on the cappa (*Goubinispora, Kamthisaccites*). Cladistically, *Goubinispora*-kind of morphos have their alliance with *Striomonosaccites*. The taeniate monosaccate organization has its maximum nearness to the *Virkkipollenites* stock; by way of minimum steps



Text-figure 7—Distribution of saccate morphos from end Permian (Biohorizon-VII) to Early Triassic (at Biohorizon-VIII) revealing the high degree of turnover at P/Tr boundary. Solid lines—consistent occurrence; broken lines—inconsistent and sporadic occurrence (MIN as in Text-figure 1).



Figures 30-41—*Crescentipollenites*-lineage (Fig 30) with its allied morphos The possible closely affiliated morphos of this tree is **31.** *Circumstriatites* experimenting a step towards joining the striation-ends to form a circum-striate pattern. Other morphos with varying combinations of ancestral and derived character states are: **32.** *Striasulcites*, **33.** *Faunipollenites*, **34.** *Striatopodocarpites*, **35.** *Distriatites*, **36.** *Striapollenites* Beside the horizontal and vertical grooves on body surface, a new line of experimentation, i.e. the non-linear pattern of the grooves is also observed which gives rise to a reticuloid pattern or its derived state, as seen in—**37.** *Tiwariasporis*, **38.** *Rhizomaspora*, and **39.** *Schizopollis*. Specimens under SEM to evaluate the nature of horizontal grooves in fig. **40** and vertical partitions in between the horizontal striations as in fig. **41**. bar 10 μm



Figures 42-50—Morphos of "*Pityosporites*" lineage: **42.** "*Pityosporites*", a stock for the out-group of disaccate pollen which has adapted diversified lines in morphography of nonstriate-disaccates as well as taeniate and clefted kind of patterns in exine character; **43.** *Vestigisporites*, first step from the out-group morphos in terms of evolution; **45.** *Scheuringipollenites*, the most simplified morphos—a combination of primitive (indistinct nexine) and advanced (absence of germinal mark and thinning of saccus-free-area) character states. Further adaptations in shape, size of sacci and their attachment with body is illustrated in Figures **46.** *Alisporites*, and **47.** *Satsangisaccites*. In **48.** *Brachysaccus*—the derived character state in exine structure having reticulate-columellate nature is a much advanced situation. In other characters, however, it seems to be distantly allied with *Scheuringipollenites* morphos. **50.** *Podocarpidites* shows a state adapted towards bigger size; the uniquely changed orientation of sacci is seen in figures **44** and **49**—*Samaropollenites* group of morphos, where the sacci become small and pendate.

these derivations can be achieved (Figures 15-17).

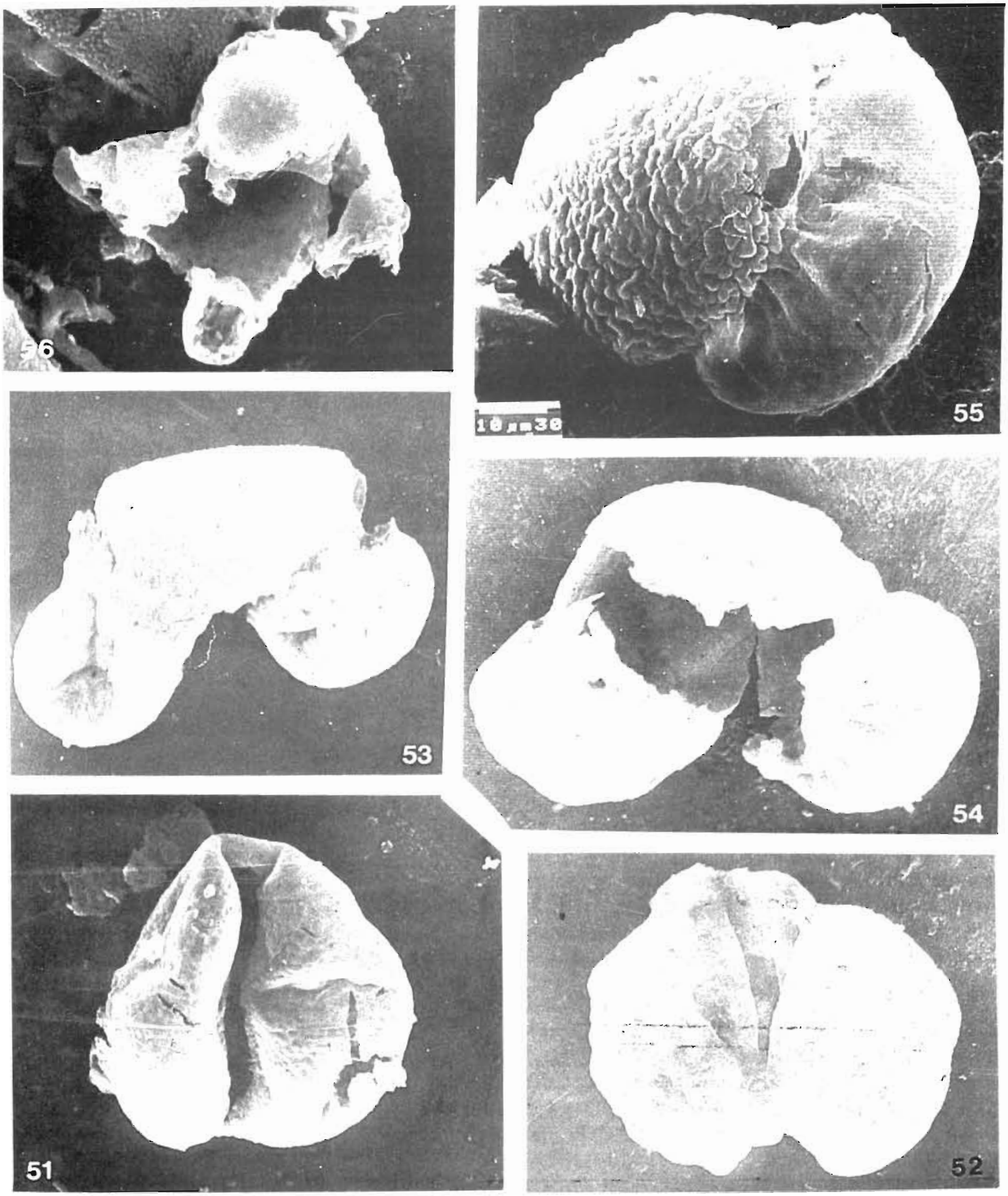
A unique organization, recorded for the first time at Biozone-VII, is represented in monosaccate pollen (*Playfordiaspora*, Figure 20) which does not have any intermediate linkage for its correlation with the older stock. The nature of saccus structure, its coverage over the body, and the presence of trilete mark may reflect a remote ancestral relationship with trilete monosaccate pollen of pre-Permian. The reappearance of such character states is baffling. Nevertheless, by way of comparison its affinity lies with *Virkkipollenites* (Figure 18).

Simple, disaccate, nonstriate pollen with individualistic features also appear at this line (*Klausipollenites, Satsangisaccites, Alisporites*; Figures 51, 46, 47). Cladistically the alete, nonstriate-disaccate lines of the Early Permian are the possible outgroups which are related at different temporal levels, with this group of pollen. The Biohorizon-VII is demarcated at the end of Permian horizon in the Indian Gondwana (Vijaya & Tiwari, 1987).

Biohorizon-VIII : Striate-disaccate extinction Phase

Between Biohorizon-VII and VIII several characters and some organizations of long-standing

Permian history met their extinction gradually (Text-figure 7). At the level of Biohorizon-VIII, forms with striations on both the faces of body, vertical partitions between horizontal striations, reticuloid striations, and pitcher-shaped saccus terminated completely from the scenario. The character state of



Figures 51-56—Morphos of "*Pityosporites*" stock under SEM showing modified nature of sacci in relation to their attachment to the body in disaccate as well as trisaccate forms **51.** *Klausipollenites*; **52.** *Satsangisaccites*; **53, 54.** *Samaropollenites*; **55.** *Podocarpidites*; **56.** *Podosporites*. Bar represents 10 μm in each figure

enveloping saccus, para-attachment of body-sac, and the monosaccate with reticuloid striations and circumsulcus also vanished from the population of saccate pollen. Thus, all radially and bilaterally symmetrical monosaccate or monosaccoid forms which had their spread in Early Permian disappeared at Biohorizon-VIII. Evidently the morpho-organizational turnover (sum total of dying-out and incoming forms) is very high at this level of time (Text-figures 1, 4).

The span of time between Biohorizon-VII and VIII has been identified as Permo-Triassic transition; based on many other parameters as well (Vijaya & Tiwari, 1987; Tiwari & Vijaya, 1992) the P/Tr boundary has been recognized between these biohorizons, precisely at the Raniganj-Panchet interformational boundary where steady occurrence of taeniate pollen and cavate spores begins.

The Biohorizons-VII and VIII resemble in several aspects of FADs and LADs with *Protohaploxypinus microcorpus* Assemblage-Zone (Late Permian) and the *Lunatisporites pellucidus* Assemblage-Zone (Griesbachian) of Australia, respectively (Helby *et al.*, 1987).

Biohorizon-IX : *Staurosaccites-Brachysaccus* Phase

There is a considerable gap in the data from the Indian Peninsula between the Biohorizon-VIII and IX, as sequential palynofloras are not yet known. However, the singularity of this zone is reflected in the record of some unusual organizations.

In nonstriate-bisaccate forms small sacci attached to a relatively bigger body (e.g., *Minutosaccus*; Figure 49) are recorded. A related disaccate with moderately developed distally inclined and laterally joint sacci (*Samaropollenites*; Figure 44) is also found. In another disaccate, the sacci are least inflated and remain adhered with the body inclining distally to mark a narrow sulcus (*Brachysaccus*, Figure 48). The transitionary stage of saccus structure in between the infrareticulate to infracolumellate nature is also reported in the latter two pollen groups (Dolby & Balme, 1976).

Another new lineage of disaccate pollen includes forms with cappa which is finely columellate and dissected into two equal halves by a sharp cleft, and little inflated sacci having similarity in structure with cappa (*Staurosaccites*, Figure 63). Further diversity is seen in the forms having two clefts but more inflated sacci resulting into diploxylonoid construction (*Infernopollenites*, Figure 62). By way of comparison, the clefted pollen share many character states with taeniate forms of older lineage. Therefore, cladistically this is the only probable relationship, but the clefted form had acquired a derived character of columellate structure in body exine as well as saccus. This is a significant step in the evolutionary sequence of exine characters observed at this datum which could have acted as progenitor of angiospermoid trends in sexinal structure.

The disaccates with small, pendate sacci are morpho-organizationally related with *Klausipollenites* stock. The *Brachysaccus* organization had its outgroup in *Scheuringipollenites* stock of nonstriate-disaccates but with a derived character of columellate structure in the sacci. Some radiosymmetric alete monosaccate pollen of indeterminate organization (referred to *Enzonalasporites* and *Pseudoenzonalasporites*) are reported from this biohorizon (Kumaran & Maheshwari, 1980). They could have some linear development in the younger strata also, but no evidence of well-studied forms is available.

In Australia, the FAD of *Staurosaccites* is at the latest Anisian level on the top of *Triplexisporites playfordi* Oppel Zone while that of *Infernopollenites* is at the earliest Ladinian level (*Staurosaccites quadrifidus* Oppel Zone). The assemblage containing the organizations typical of Biohorizon-IX in the Indian Peninsula makes its beginning at early Late Carnian and continues up to Early Norian (Kumaran & Maheshwari, 1980; Tiwari *et al.*, 1984).

Biohorizon-X : *Callialasporites* Phase

At this level a very significant morphography, viz., *Callialasporites* Complex, appeared in the lineages of saccate pollen representing an assembly of close-knit forms generally described as *Callialasporites, Tsugaepollenites, Cerebropollenites* and *Triangulopsis*—a group of subsaccate pollen (Sukh-Dev, 1961; Dettmann, 1963; Singh & Kumar, 1969). The sporadic but marked record of these subsaccate morphos, generally with granulose microsculpture on exoexine extended to form frilled or flat, continuous to tri-notched, vestigial or uninflated saccus, characterises this biohorizon (Figures 64, 67). No other significant morphology in the saccate pollen has made its beginning. On the contrary, a large number of organizations record their extinction; the older disaccates with striations, taeniae and clefts do not show at this level, so also the simple disaccate (*Klausipollenites*) group. The *Goubinispora* and *Playfordiaspora* lineages also disappear. However, the diploxylonoid disaccate simple nonstriate pollen group (*Alisporites, Podocarpidites*) continues to survive. Evidently, the *Callialasporites* phase is remarkable in recording the extinction of the saccate pollen morphography of long standing which started at Biohorizon-VII.

The FAD of *Callialasporites* from the Indian Mesozoic sequence is from *Gliscopollis* Zone dated as Lower Jurassic, which overlies the *Taeniaesporites* Zone (Koshal, 1975; Ramanujam, 1987). In Australia, the definite FAD of *Callialasporites* is recorded in *Corolina torosa* Zone and dated as Hetinginian (Lowermost Jurassic).

Biohorizon-XI : *Podosporites-Dacrycarpites* Phase

Small pollen with three sub-hemispherical, distally subequatorially attached, pendate sacci and micro-granulate microrugulate to microverrucose sculpture on the body appear at the Callo-Oxfordian level represented by the Biohorizon-XI (Figures 55, 68; Text-figure 1). No other significant saccate pollen morphology has appeared. The *Callialasporites* and the simple non-striate-disaccate (*Podocarpidites, Alisporites*) type of organizations continue to prevail. The triwinged pollen complex makes its FAD at the Callo-Oxfordian level (Srivastava, 1966; Lukose, 1972). It has a form-similarity with triwinged pollen, generally identified as *Podocarpeaepollenites* (Figure 66), of the Upper Triassic (Kumaran & Maheshwari, 1980).

In Australia, *Murospora florida* Oppel Zone exhibits the first appearance of *Microcachrydites* group of triwinged pollen (Helby *et al.*, 1987); hence equation of this level to Middle Callovian is corroborated. There is no distinct alteration in the saccate pollen organization after the Biohorizon-XI, a trend which continues from Upper Jurassic to Lower Cretaceous.

INTERBIOHORIZON ZONES

The recognition of 11 Biohorizons leads to the delimitation of 10 Interbiohorizon Zones (Biointerval Zones, Biostratigraphic Interval-Zones, or Interval-Zones; Hedberg, 1976). In accordance with ISG, the names of these zones have been given after a taxon (distinctive morpho-organization in the present context), typical of the zone. It is not obligatory that designated taxon is confined to a particular zone.

Following is the brief characterization of each Interbiohorizon-Zone proposed here and illustrated in Text-figures 1 and 8.

1. *Potonieisporites* Interbiohorizon Zone

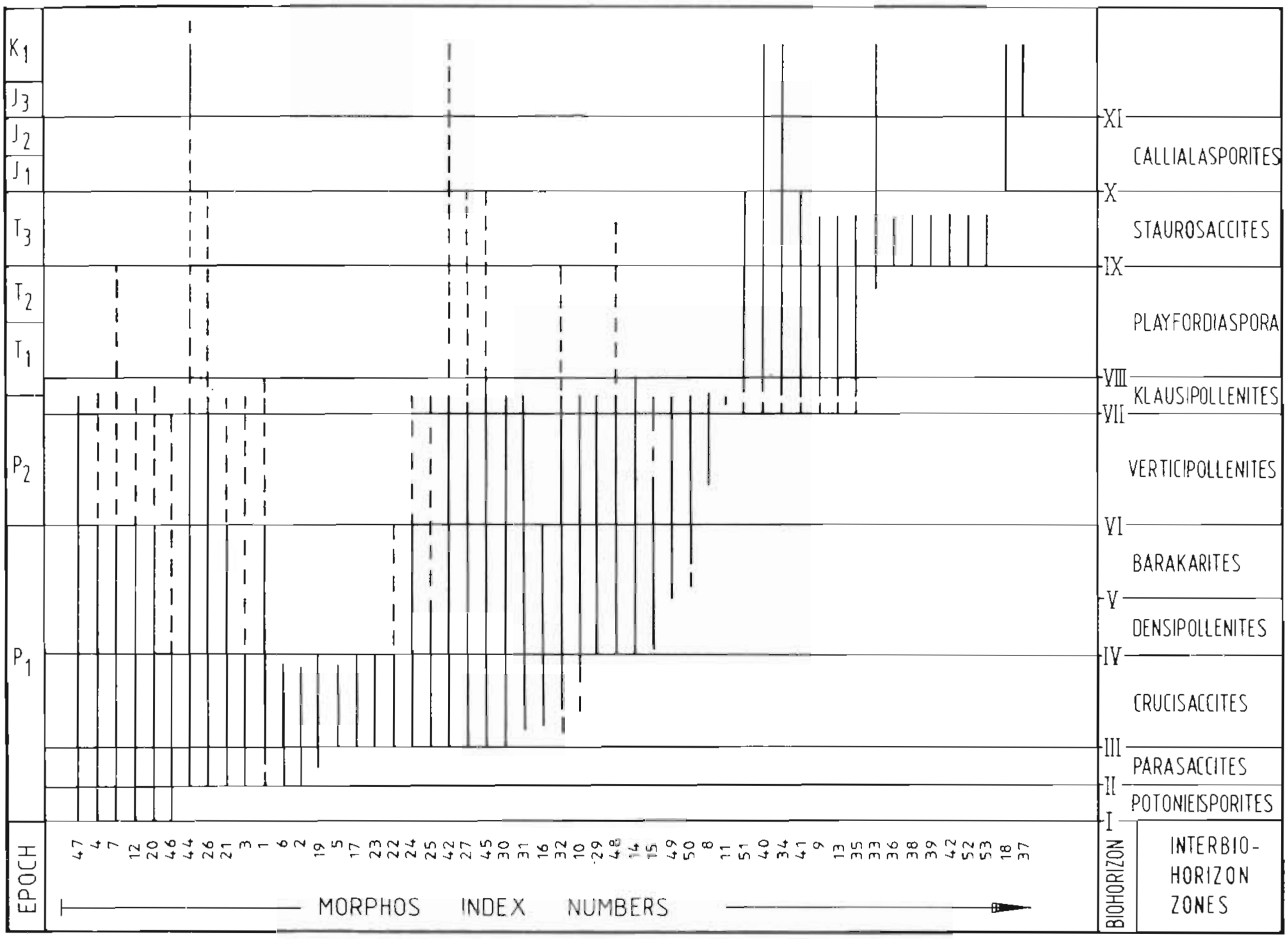
It is the oldest as well as the least diversified zone (between Biohorizon I and II) in the Indian Gondwana. It is represented by four elements of basic stock having monosaccate organization (*Potonieisporites, Plicatipollenites, Parasaccites* & *Virkkipollenites*), and a simple disaccate (*Pityosporites*). The forms with a vestigial monolete mark are also recorded but they make a related auxilliary group to "*Pityosporites*" (Text-figures 3, 5). The absence of striate-disaccate pollen is diagnostic for this zone. The subsequent younger Interbiohorizon-zones are progressively complex in their components. The present zone is equated with the lowest part of Lower Talchir Formation having Early to early Late Asselian age relationship.

2. *Parasaccites* Interbiohorizon Zone

The first appearance of striations on the body cappa of disaccate pollen marks the identity of this zone, i.e., between Biohorizon-II and III. *Parasaccites* is numerically dominated and diversified in organizations in the next younger zone. The striate group progressively diversifies at the top of this zone. Also, the new trends of evolution in the reduction of body curvature on distal face are seen; thus the double body-fold system in the body of monosaccate pollen *Potonieisporites* of older lineage has a morpholinkage with *Gondwanopollis* which has a single fold system in the same pattern; this circular body-fold system further acquires bilateral convex arrangement alongwith lateral axis indicating further change in distal surface area. The width of lateral continuations of saccus also reduces considerably. These lines are major trends of bilateralism with a path line towards the monosaccoidal bisaccate form (*Sahnites*) in having narrow lateral continuity, which in time disappears to give such a form with perfect disaccate configuration. From the preceding *Potonieisporites* Interbiohorizon-Zone, the present zone is distinguished in having the FAD of striate pollen and increased complexity in the morphos. The lithological sequence of Lower Talchir to lower part of the Upper Talchir Formation is represented in the *Parasaccites* Interbiohorizon Zone. In age relationship, this zone ranges from Late Asselian to Early Sakmarian.

3. *Crucisaccites* Interbiohorizon Zone

It is a zone between Biohorizon-III and IV. In this zone, maximum innovation and inflexion in the characters have been recorded among the basic group characters of the older stock. This zone spans from lower Upper Talchir Formation to the Upper Karharbari Formation, short of Karharbari-Barakar boundary. This means that in terms of morphographic evolution in saccate pollen there is a consistency of lineages from lower Upper Talchir Formation through most of the Karharbari Formation



Text-figure 8—Summary diagram to depict Inter-relationship of Biohorizons, Interbiohorizon-zones and stratigraphic distribution of morphos. Permian sequence inflated out of proportion (MIN as in Text-figure 1).

without appearance of any significant new morphography. The age relationship for this zone is indicated with Early Sakmarian to late Late Artinskian.

4. *Densipollenites* Interbiohorizon Zone

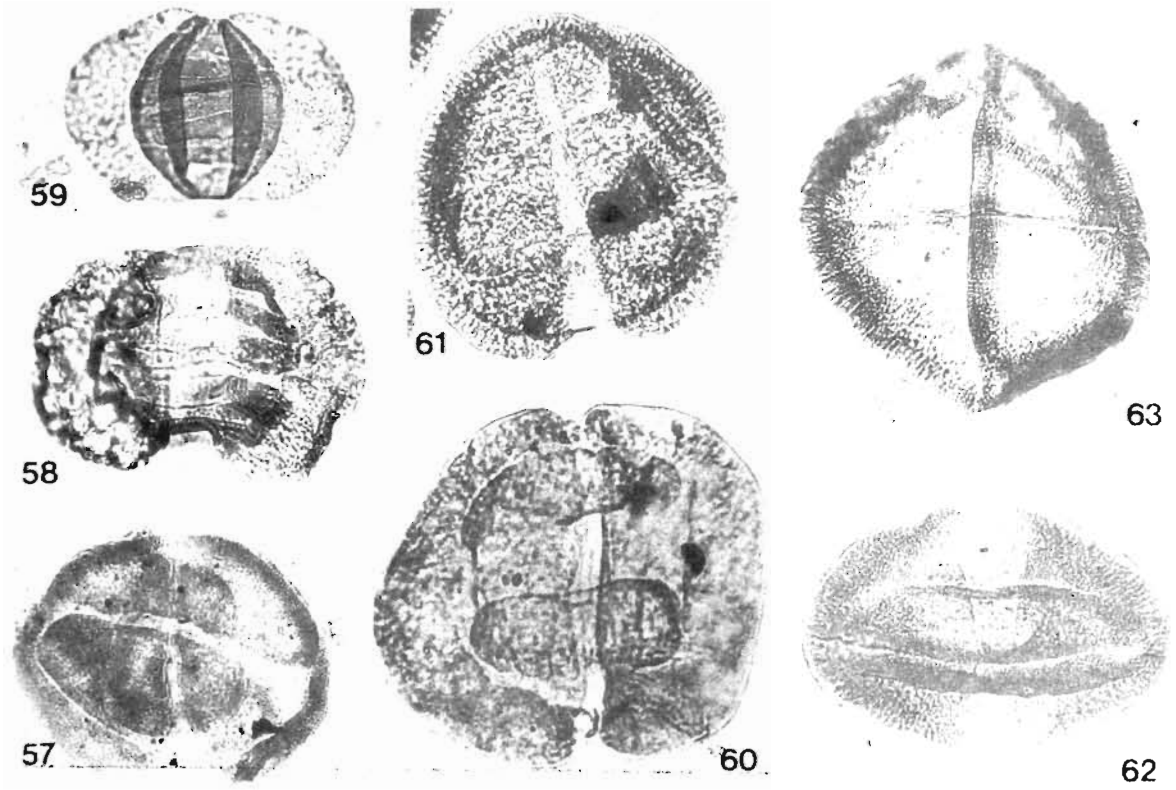
This zone is delimited by Biohorizon-IV at the base and V at the top. In the lithostratigraphic sequence, it represents a narrow span of the uppermost Karharbari Formation and the lowermost Barakar Formation. This is a significant transitional zone for demarcating the Karharbari-Barakar boundary and represents the Artinskian-Kungurian passage. The age relationship is suggested on the basis of lithostratigraphic comparisons with the control levels. The absence of *Rimospora, Rugasaccites, Tuberisaccites, Pachysaccus, Stellapollenites, Distriomonosaccites, Corisaccites* and *Guttulapollenites* qualifies this zone to be distinguished from the adjacent lower and upper zones. The continuity of occurrence of several older morphos, particularly the monosaccates, characterize this zone.

5. *Barakarites* Interbiohorizon Zone

It encompasses most of the late Early Permian Barakar Formation and lies between Biohorizon-V and VI. The palynoassemblages contain a number of monosaccate lineages struggling from the preceding zones, which suddenly decline or become extinct at its top. The non-striate disaccates with simple organization (*Cuneatisporites, Platysaccus, Ibisporites* Group) also diversify within this zone. Qualitative sproutings have not been observed but quantitatively the characters have immensely diversified.

6. *Verticipollenites* Interbiohorizon Zone

This zone is demarcated by Biohorizon-VI at the base and Biohorizon-VII at the top. Except for the appearance of a rarely recorded character of sexinal protuberances on body surface (*Tumoripollenites*)



Figures 57-63—A line of experimentation in the off-shoot morphos of *"Pityosporites"* stock, is seen in **57.** *Corisaccites* possessing a combination of ancestral and derived character states, i e. exine sculptured but having thick sexinal bands, respectively The other morphos with micro-intrareticulate sexine but bi-taeniate; **60.** *Lueckisporites*, and the globular multi taeniate state in figure **61.** *Guttulapollenites* The most advanced state of multi-taeniate organization is represented by Figures **58** and **59.** *Lunatisporites* Other morphos illustrated here in Figures **62.** *Infernopollenites* and **63.** *Staurosaccites* represent mainly the congruence of derived character states in body exine nature (clefted and columellate).

in the later half of the zone, no new morphogrpahy in saccate pollen appears during the span of this zone. The entire zone represents Kulti Formation and most of the Raniganj Formation, except for the uppermost part of the latter. The older monosaccate stock dies out or declines considerably at the bottom of this zone. The younger elements of Triassic affinity mark the upper limit of this zone. This interbiohorizon-Zone represents most of the Upper Permian period and terminates at its end.

7. *Klausipollenites* Interbiohorizon Zone

This zone is a transitional passage between upper reaches of the Raniganj Formation (Biohorizon-VII) and the Lower Panchet Formation (Biohorizon-VIII). It encompasses the events which took place at the Permo-Triassic boundary. Striate-disaccates continue in this zone, but most of them disappear at its top level. The progressive increase in the newer types of nonstriate as well as taeniate disaccate morphos is the characteristic feature of this zone.

When viewed in totality of events in Gondwana Sequence, the *Klausipollenites* Interbiohorizon-Zone represents a period when major shift of organizations have been towards newer type of nonstriate-disaccates, in contrast to the monosaccates and striate-disaccates of the Permian time. Thus, the offset of lineage trees is the characteristic feature of P/Tr boundary.

8. *Playfordiaspora* Interbiohorizon Zone

The interval zone between Biohorizon-VIII and IX is regarded as a unique zone encompassing upper part of the Lower, the Middle and beginning of the Upper Triassic formations. The paucity of data does not allow a detailed analysis but morpho-evolutionary trends suggest a continuation of saccate forms which appeared at the P/Tr boundary. This is a phase of slow evolutionary alterations in morphographies of saccate pollen. From the older Interbiohorizon Zone, the present zone differs in the absence of major lines of the Permian lineages. So also in the younger Interbiohorizon Zone where several new lines appear

9. *Staurosaccites* Interbiohorizon Zone

It is a zone between Biohorizons-IX and X. The Upper Triassic (excl. Early Carnian of which data is not known) palynoassemblage is represented in the span of this interval zone. New morphographies, including clefted body and columellate exine structure, appear for the first time at the base of this zone. On the basis of available data it appears that the Rhaetic assemblage does not contain several of the forms which otherwise mark the Carnian assemblage (Koshal, 1975; Tripathi *et al.*, 1990).

10. *Callialasporites* Interbiohorizon Zone

This is an Interval-Zone between Biohorizon-X and XI. The singular organization of *Callialasporites* defines the starting point of this zone, while the appearance of triwinged *Podosporites* group demarcates its upper limit. Most of the saccate forms of this zone are simple nonstriate-disaccates, generally having diploxylon construction of sacci; they continue from the earlier Interbiohorizon Zone. The offshoot lineage of nonstriate-disaccate pollen of Biohorizon VII is wiped out from its base line. A complex unit of sub-saccate forms has been on record within this Interbiohorizon Zone. Random occurrence of striate-disaccates seems to be an indication of recycling.

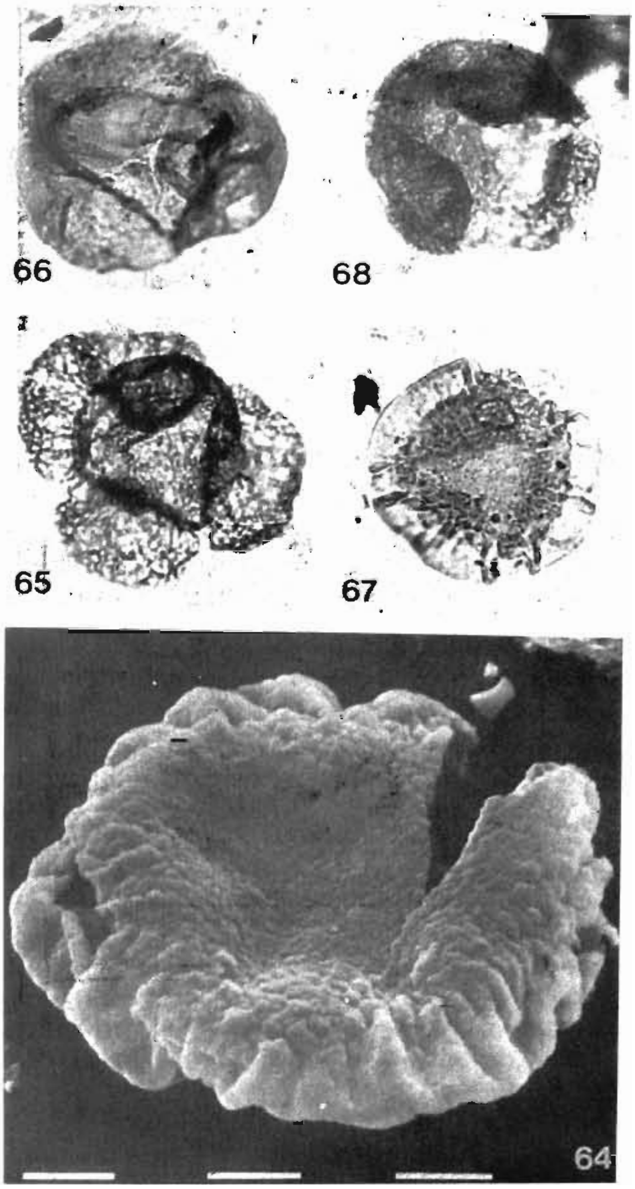
MORPHO-ORGANISATIONAL ALLIANCE : CLADOGRAMS AND STRATOGRAMS

The outcome of cladogenesis has been interpolated with the stratigraphic occurrence of each character states through Gondwana Sequence. After such a synthesis of cladograms and stratograms (stratigraphically arranged morphos forming the trees) the final picture crystalizes the biostratigraphic events.

Six basic organizations considered as the oldest stocks are discussed below for their morpho-evolutionary relationships. These stocks are subsequently represented in the form of individual tree, structured on the basis of data matrix given in Tables 3 to 6, which evidence the degree of morpho-evolutionary allinace among the ancestral and derived character states. The placement of related morphographies in these trees is made in terms of stratigraphic occurrences as well as synapomorphy (relative akinness).

Pre-Permian Lineage

The character state matrices given in Tables 3 and 4 clearly indicate that the ancestral character states are shared by six major lineages (Figures 2-7), as given in Text-figure 3. At the level Biohorizon-III, with reference to *Potonieisporites* type of organisations as the oldest lineage, the radiosymmetric monosaccate pollen with body-fold system (*Plicatipollenites*) are closer to it; while others (e.g., *Virkkipollenites, Parasaccites*) are



Figures 64-68—Morphovariants of mono-and di-saccate organizations, probably the transforming states to tri- as well as tetrasaccate forms having microreticulate exine structure as in **65.** *Tetrasaccus* and **66.** *Podocarpeaepollenites.* The morphos with retrogressive step in the character of exine and nature of saccus is represented by Figure **67.** *Callialasporties.* **64.** SEM of *Callialasporites* to evaluate granular pattern on body surface as well as non-structured state of the saccus; bar—10 μm. A triwinged morphos with shifted sacci root from the body equatorial position towards the distal body face as in Figure **68.** *Podosporites.*

relatively and progressively distant in relationship. The disaccates are still remotely related to the monosaccate block. They could have had a common origin because stratigraphically the simple disaccate morphos is older than the monosaccates—as per the present data.

The definite stratigraphic occurrences of these lineages (solid circles in Text-figure 3) indicate their relationship in Pre-Permian horizons of Australia and South America (Kemp *et al.*, 1977; Archangelsky & César, 1986). The oldest occurrence of *Potonieisporites, Plicatipollenites, Virkkipollenites* and *Parasaccites* organizational groups is from Early Namurian (base of *S. yberti* zone; Playford, 1985, p. 125) while that of "*Pityosporites*" is recorded in the assemblage of Anderson Formation; this assemblage is closely related with that of Lower Carboniferous Laural Formation (Balme, 1964, p. 56). The segment of cladogram (Text-figures 1, 3) in Carboniferous is incomplete and hence less parsimonious. Still the congruence of character states as well as their stratigraphical incidences support the topology proposed here.

On the basis of relationship pattern it is presumed that the oldest mother stock of saccate pollen was in existence in the Progymnospermopsida complex and through *Teichertospora*-type of organization (Figure 1) in Devonian (Balme, 1988; Mc-Gregor & Playford, 1990), various lineages might have arisen during the Lower Carboniferous. The palynofossils normally included under the Suprasubturma *Pseudosaccititriletes* Richardson 1965 seem to be the ancestral stock for the monosaccate pollen. Such a complex of diverse suite of trilete cavate miospores of this group, such as—*Auroraspora, Grandispora, Endosporites*, etc. in Lower Carboniferous (Viséan) of the Bonaparte Gulf Basin, north-western Australia, has been recorded by Playford and Satterthwait (1988).

The progymnosperms are a group of vascular plants intermediate in morphology and age between Early Devonian pteridophytes and seed plants of Late Devonian and later ages (Stein & Beck, 1987). The prominent nature of the tetrad mark in these basic lineages up to the level of Asselian-Sakmarian is a continuation of prepollen character of pteridosperms (in broad sense including Glossopteridales) and Cordaitales. It is interesting to note that the trilete mark in the same group of pollen becomes almost vestigial in the younger strata.

Potonieisporites-lineage

Taking this lineage as a trunk of the morphostratigraphic tree in the form of a stratogram at Biohorizon-II, the maximum character states of this stock are shared by three forms (Figures 8-11; Text-figure 1). The possible branching of *Potonieisporites* tree has occurred with in the time span of Late Asselian to Early Sakmarian and its flourishing period lasted only up to the end of Lower Permian Barakar Formation.

The palynomorphs normally included under the Suprasubturma *Pseudosaccititriletes* Richardson 1965 seem to be the ancestral stock for radiosymmetric building plan of *Parasaccites, Plicatipollenites* and *Virkkipollenites* trees; the *Potonieisporites* lineage is a branched-off line from the original plexus (Figures 1, 2).

Plicatipollenites-lineage

By way of determining the assembly of comparable character states, two forms (*Rugasaccites* and *Rimospora*) appear to have close relationship with the *Plicatipollenites* trunk. Although *Rugasaccites* is a closely related branch with the main lineage, it shows one primitive character state of rugate exine sculpture which is a retrogressive step in the course of evolution. *Rimospora*, on the other hand, is a step ahead in having derived character states of bilateral symmetry and incipient grooving on the body surface. This corroborates with the stratigraphically younger appearance of this form (Figures 12-14; Text-figure 1).

The branching of the *Plicatipollenites* tree has taken place during the Late Asselian to Early Sakmarian period and lasted up to the early Late Artinskian; however, the elements of *Plicatipollenites* continued impressively up to the top of Lower Permian Barakar Formation, thereafter it dwindled and disappeared at P/Tr boundary.

Virkkipollenites-lineage

With *Virkkipollenites* as out-group morphos, this lineage seems to have branched off into affiliated comparable forms with derived character states. The deviations in characters took place later in the sequence. The important shoots of relationship are connected with the forms having striations (Figures 15-17). The futuristic organization of enveloping saccus also seems to be linked with the main trunk of the tree. These events have taken place at transition phase encompassing Late Artinskian to the earliest Kungurian time (Figures 18, 19).

The next event, supposed to be allied with this tree, had occurred at the latest Permian (Biohorizon-VII) where newer characters of body and saccus have come into being, although the basic organization remained the same. A singular form

(*Playfordiaspora*) with zona-like thin reticulate saccus, a trilete mark and the coverage of saccus on body could be remotely connected with the main tree, as some characters had ancestral affinity in this taxon. Parsimonically, the *Virkkipollenites*-lineage seems to be the best suited stock of relationship for *Playfordiaspora*. The organizations which sprouted from this lineage at P/Tr boundary transition continued up to Upper Triassic (Figures 18-20; Text-figure 1).

Parasaccites-lineage

The tree of *Parasaccites* affinity attains a maximum diversification of new morphographies among all groups of monosaccates. The para-condition of saccus attachment remaining a principal character state, eight new forms have branched-off from this lineage, most of which appear in Early Sakmarian (Biohorizon-III). This tree flourishes with its branches up to the end of Artinskian where four of the unique lines disappeared; the other continued up to the close of Early Permian. The only trend which persisted into Late Permian is that of the monosaccoid bisaccate configuration—a derived character state (Figures 21-29; Text-figure 1). The *Parasaccites* tree is the most dominating factor in the Lower Permian Sequence; it loses its grip by the end of Lower Permian Barakar Formation, although stray branches struggle to continue up to P/Tr boundary.

Crescentipollenites-lineage

The above described four trees, comprising monosaccate organization stand apart from the two trees of the disaccate pollen. The first occurrence of striate-disaccate, with lunar folds at the sacci roots on distal face of the body, at Biohorizon-II, heralds an event of great significance of a distinctive morphology.

At Early Sakmarian Biohorizon-III, most of the relation-branching in this lineage had sprouted. Subsequently, this complex ramifies to give rise to some more evolutionary lines up to Biohorizon-IV. In totality, the striate complex predominates the scenario from Early Kungurian to P/Tr boundary. The major thrust of *Crescentipollenites* tree gets denuded by Scyathian (Tiwari & Singh, 1986) yet few straddlers continue till Liassic (Koshal, 1975)—see Figures 30-41 and Text-figure 1.

Pityosporites-lineage

The term "*Pityosporites*" used here has no conservative taxonomic connotation in the present context; it represents a stock of simple disaccate pollen architecture without striations. The genus *Vestigisporites*, also recorded from the lowermost Talchir is considered to be the branched-off lineage from the *Pityosporites* main tree at an older level. The suspected vestigial scar in the *Pityosporites* recorded from Anderson Formation (Balme, 1960; pl. 5, fig. 35) supports this contention. The FAD of this morphos predates the occurrence of monosaccate stocks. Analysis of the data reveals that there seems to be a convergent point of relationship between simple disaccate and the monosaccate organizations in the Lower Carboniferous, as shown in Text-figure 3.

The tree with "*Pityosporites*"-type of organization in a broader aspect of construction and in course of time has given rise to a line of relationship at Biohorizon-I (late Early Asselian) into a pollen with monolete slit on the proximal face of the body. As stated earlier, the "*Pityosporites*" form of Carboniferous (Figure 42), in all probability, possesses a vestigial linear thinning, which could be an outgroup character of ancestral state in this lineage.

The alterations in sacci shape towards haploxylon and indistinct nexinal differentiation define a group (*Faunipollenites, Scheuringipollenites*) at the base of *Crucisaccites* Interbiohorizon-Zone, which had maximum characters sharing with the main trunk (Figure 43; Text-figure 1). The origin of taeniae is an event of great morpho-stratigraphic significance. By assembly of character states, the taeniate pollen have a close relationship bondage with the nonstriate-disaccate tree. Such forms make their appearance at Late Artinskian-Early Kungurian. The further manifestation of these derived characters had taken place at the close of Permian where multiple taeniate forms are recorded for the first time (Figures 57-61).

The clefted and columellate character states (*Infernopollenites, Staurosaccites*) which are much advanced with relation to the taeniate pollen of this tree, appear at late Early Carnian. Cladistically, however, these forms share maximum character relationship with bitaeniate pollen (Figures 62, 63; Text-figure 1).

The main trunk of the simple disaccate morphos is further related with a prime group of similar forms with, of course, variable individualistic features, which appeared at the Permian-Triassic transition zone. This complex persisted during the whole span of Triassic. The other allied forms which joined these branching pattern at the late Early Carnian acquired some of the advance character states in their morphography (e.g. reduction of size and transitional columellate structure in sacci.

During Jurassic and into the Lower Cretaceous, only a few of the nonstriate-disaccate morphos—mainly diploxylonoid, continued to occur. At Callo Oxfordian time plane, a triwinged organization with a shift of sacci roots on distal side from the equator and a recurrence of ancestral character states (sculptured body) emerges (Figures 64, 67, 68). In view of common trend in character states, these younger triwinged morphos had a relationship with *Podocarpeaepollenites* type of forms (Figure 66) of Carnian age (Kumaran & Maheshwari, 1980; pl. 9, fig. 13).

From a glance at the "*Pityosporites*" lineage it becomes evident that except for taeniate branching no new morphographies had appeared up to the latest Permian. The tree of striate-disaccate complex flourished during Permian while the nonstriate-disaccate lineage offsets it in prominence at the P/Tr datum and continued till close of the Gondwana.

DISCUSSION

Primaeval outgroups

The oldest six morphographic stocks of saccate pollen in the Gondwana Sequence of India, when cladistically extrapolated for their lineages, anchor their primaeval outgroup in the Carboniferous of Australia (Text-figures 1, 3). But evidences and opinions differ regarding the dating of various palynological zones in the Upper Carboniferous of Australia (Balme, 1964; Kemp *et al.*, 1977; Playford, 1985; Gilby & Foster, 1988; Foster & Waterhouse, 1988; Cooper, 1991).

The Lower Carboniferous assemblage from Po-Formation of Tethys Himalaya (Khanna & Tiwari, 1983) does not contain any saccate pollen so also the Viséan assemblage of Australia. The *Grandispora maculosa* Zone (Kemp *et al.*, 1977) of Late Viséan to earliest Namurian age (brachiopod control) contains exclusively Early Carboniferous palynotaxa (*Grandispora, Auroraspora, Anabaculites yberti, Raistrickia, Hymenozonotriletes*). No such palynoflora is on record from the Indian Peninsula. In the subsequent younger zone, i.e., *Spelaeosporites (Anabaculites) yberti* Zone (Early Namurian), additionally nonstriate-disaccate pollen make their humble appearance. However, Foster and Waterhouse (1988) recorded striate pollen as well, and if this be accepted, the absence of striate-disaccate in Stage 1 of Australia still remains intriguing because Stage 1 is younger to the *S. yberti* Zone. The arguments putforth by Foster and Waterhouse (1988, p. 143) that Stage 1 is probably a facies controlled palynoflora and hence the striate-disaccates are absent; this needs further verification because similar situation has been recorded in *Potonieisporites* Interbiohorizon proposed here.

The Stage 1 Assemblage has more akinness with the Early Asselian Talchir palynoflora (*Potonieisporites* Interbiohorizon) rather than with the Early Namurian *S. yberti* assemblage. Yet the pattern of diversity of forms in Stage 1 suggests that the monosaccates might have their ancestry in Late Viséan/Early Namurian time-transition. Obviously, Stage 1 has a greater bond of age relationship with Early Permian rather than the Carboniferous. In view of this Permian affinity of Stage 1, it is indicated that in Australia the succession between uppermost Namurian to Asselian could be incomplete.

Biostratigraphy and cladistics

The record of sedimentary deposition is, no doubt, incomplete and recognised or inferred hiatuses exist at several levels in the Gondwana Sequence. In order to minimize the blurring effect of discontinuity of strata on the changes that had occurred in pollen morphography, the gross organizations and basic exine characters (morphos) have been taken as units for alliance determination. The major innovations and appearance of newly derived character states tagged with stratigraphic sequence have revealed eleven definite datum lines—termed as Biohorizons. These levels, in terms of saccate pollen morphography, represent important events. At places these morpho-evolutionary biohorizons precede the lithostratigraphic boundaries as if they foreshadow the incoming change in the whole set-up (e.g. Karharbari/Barakar, Raniganj/Panchet boundaries). Ten Interbiohorizon Zones delimited on the basis of eleven Biohorizons record the floral changes in the Gondwana Sequence. These zones and the biohorizons are important reference units for correlation. The FADs, LADs and diversification of characteristically identifiable morpho-evolutionary groups in saccate pollen are implicitly reliable parameters of precision in correlation and age connotation.

The viability of the proposed zonations and biohorizons in stratigraphy is reinforced by cladistic analysis. The character polarity is based on primitive (ancestral) and advanced (derived) states in each pair. These terms are relative expressions and could have a stratigraphic bias. Nontheless, stratigraphy has been taken to be a dependable guide in deciding the character states because the richness of sequential palynological data available for Gondwana of India has lessened the pit-falls of stratigraphically biased polarity.

In terms of polarity of a character state, the present observations have revealed that distinct proximal germinal aperture (trilete, monolete) and lack of distal sexinal thinning (sulcus) are the ancestral character states. This fact is collated with the older stratigraphic occurrence of these features in comparison to the vestigial mark and thinning of distal sexine in younger sequences, which are derived characters. At Biohorizons I, II and III, the forms *Plicatipollenites, Potonieisporites, Parasaccites* and *Sahnites* possess prominent proximal aperture with well-defined labra and vertex, suggesting their functional nature for germination. This character transforms into a vestigial imprint in the subsequent biohorizons. Similar is the behaviour of the distal saccus-free-area in these pollen; it is a structured sexinal layer in the older sequences. In younger horizons it ultimately becomes unstructured.

The distinct germinal mark and clearly structured distal sexine of the body are the prepollen characters (Mapes & Rothwell, 1984; Kerp *et al.*, 1990). As other Late Palaeozoic conifers produced prepollen (Clement-Westerhof, 1984), it is probable that most of the early saccate pollen with a prominent proximal aperture, were prepollen as well as zoidogamous rather than siphonogamous.

Innovation, evolution and extinction

The massive glaciation of early Lower Permian, the time of Talchir sedimentary deposits, had its history in the Carboniferous glaciation of Australia. The wide-spread ice sheets generated intensive cooling and left little open space for the growth of vegetation during Lower Talchir. In this climatic set-up the five types of stock organizations in saccate pollen were found, which vouch for reduced diversity in the organizational architecture at Biohorizon-I.

The lower part of Talchir experienced a sustained period of refrigeration resulting into extremely stressing condition. This invoked the force of evolution to generate enormous newer morphographies in younger horizons by the level of Biohorizon-III (Text-figure 5). Although the glaciers had yet not completely retreated, as recorded in Jayanti and West Bokaro coalfields, they had melted away to a greater extent to leave wider habitat areas for plants. It provided a platform for radiation in morphography and inflation in species output at the close of Tālchir, at Biohorizon-III. It was a great event in the evolution of morphography of pollen, which is collated with Early Sakmarian (Text-figures 4, 5). The climate continued to ameliorate in the subsequent time, and the morpho-lineages flourished. There is an evidence of cooling down of the climate at the proximity of Biohorizon-IV (Bharadwaj, 1975; Mitra, 1988). There is no evidence of mass extinction at second cooling phase of Upper Karharbari but definitely some bizarre organizations (*Rugasaccites, Rimospora, Stellapollenites, Gondwanopollis, Crucisaccites*) met their extinction. Thus it may be termed as a regional extinction, as defined by Donovon (1988), in terms of episodic and fast termination of few morphos in a broad area.

This event is again followed by incoming of new organisations (*Barakarites, Densipollenites, Lueckisporites, Distriatites*) which provide evidences for one more step in the course of evolution; the Biohorizon-VI again experienced a regional termination of long standing lineages (*Potonieisporites, Caheniasaccites, Parastriopollenites* and *Divarisaccus*).

The cool-loving morphos of older sequence are either terminated or their overall impact is highly attenuated, and this event is connected with a change in climate which was warmer and drier during the Kulti Formation (Text-figure 6). The seasonality in climate is apparent in the latter because striate disaccates immensely diversify.

In the Upper Permian, from the Lower Permian-Upper Permian boundary till the end Permian, the process of evolution has been slow as no new organizations have come into being. The statis nature of evolutionary changes during this vast period is reflected in the monotony of assemblages in the coalseams of Barakar and Raniganj formations.

Two important phenomena were observed during the Upper Permian—one, protracted and gradual extinction of straddling monosaccates and two—increase in the numerosity of striate disaccate pollen. The influence of warm and increasingly humid climate during most of the Upper Permian is thus reflected in the morpho-evolutionary trends of saccate pollen.

The end Permian Biohorizon-VII marks the innovation of new characters (Text-figures 4, 7), which continued into the Triassic; this event is followed by a line of episodic, fast extinction of numerous morpho-lineages (Biohorizon-VIII) so that most of the major trees terminated and only few new offshoots captured the scenario in younger horizon, till Biohorizon-IX. The P/Tr boundary lies between the closely placed Biohorizon-VII and VIII (*Klausipollenites* Interbiohorizon-Zone). The turnover of forms is very high at this level as depicted in spread diagram (Text-figure 7). But the end Permian mass extinction, the greatest crisis to effect the marine biota for which several causes have been discussed (Maxwell, 1989), is not reflected in the patterns of saccate pollen occurrence. The extensive regression of Late Permian sea must have caused the greater continentality which induced drier climate than the Permian resulting into the high turnover of plant species.

Recently Stanley (1984, 1988) has emphatically suggested that the frigid condition of poles resulting into the cooling of continental margins must have spread the cool temperatures from high latitudes towards the equator in Upper Permian. Such a situation could have triggered a high degree of extinction of forms in the end of Permian. Palynologically there are indicative evidences of cooling of climate in the Upper Permian, more so in Godavari Graben (Srivastava & Jha, 1988). This is concluded on the basis of increased frequency of *Parasaccites*, a cool-loving taxon primarily associated with glacigene sediments of Early Permian Talchir Formation. The continuance of this cooling effect is indicated across Permo/Triassic transition as reflected by the fair occurrence of *Callumispora* (Bharadwaj, 1975; Bharadwaj & Tiwari, 1977). The subsequent time in Upper Panchet (Biohorizon-VIII onwards) has again experienced warmer and drier climatic condition which is reflected in red bed formations. The proposition of Stanley (1988), in general, supports the pattern of spore-pollen extinctions due to cooling at P/Tr boundary and thereafter by an immense warming.

At Biohorizon-IX again the post P/Tr lineages modified to give rise to several new morphos (Text-figure 1) with totally novel characters which reflect a relationship to the angiospermoid characters in sexine structure (incipient columellae). These Carnian-Norian off-shoots remained on scene for a short time and were out at the end of Norian. This could be correlated with Triassic-Jurassic boundary (Norian event, Orth, 1989, p. 61). With regard to various saccate pollen, the end Norian event is a high extinction level in which all the nonstriate-disaccates, taeniates and monosaccates of P/Tr origin and the weakened branches of striate-disaccate of the Permian affinity die out. Although the clefted and columellate forms of the Carnian also vanish from the scenario but they seem to have given rise to newer branches of columellate morphos.

At Lower Jurassic Biohorizon-X the amazing start of *Callialasporites* group is noteworthy because the recurrence of several ancestral character states (trilete mark, saccus covering on body, zona-like flattened saccus) are identified. Similarly at the *Podosporites-Dacrycarpites* phase, Biohorizon XI, the primitive character state of sculptured body exine reappears, which is a reversal of features in stratigraphically younger morphos.

The summary diagram of innovation and extinctions (Text-figure 4) reveals that there have been three peaks of maximum incoming of new morphos and two of extinctions. The Early Sakmarian sprouting is the most prominent maximal in the whole of Gondwana Sequence. The end Permian and Early Carnian sprouting maximals are immediately followed by extinctions, thus raising the turnover values of mophos at these two levels.

Biohorizons—the tie-points of stratigraphy

The morphographic organizations in pollen tagged with singular characters, i.e., morphos, are as good indicators of datums in terrestrial sequence as the faunal remains are in the marine strata. The pollen have additional credentials of numerosity, wider distribution leading to facies-independence and miracle material sporopollenin which make them "omnipresent" and suitable for preservation of finer characters. In effect, spore-pollen make a more practical and authentic tool than the other types of fossils. Generally, the long range of occurrences are taken as negetive point for dating reliability of pollen as compared to very short range in majority of animal fossils. This may be true for certain groups of palynofossils but, as is clear from the present study, there are several forms which have relatively short stretch of incidences, viz., *Stellapollenites, Crucisaccites, Rimospora, Rugasaccites, Tuberisaccites, Kamthisaccites, Brachysaccus, Staurosaccites*, etc.

When precisely identified and objectively determined the short-ranging taxa could be of great value. Above all, the FAD for morpho-organization groups in pollen are most effective parameters in stratigraphy, so also the mass extinction plane and high turnover datum can be easily demarcated with the help of the morphos. The major episodes in the evolutionary sequence of saccate pollen are discussed for their synchroneity with biochronological and lithostratigraphic datums.

The Biohorizon-II is a reliable datum as it is tagged with the Manendragarh palynoassemblage. Manendragarh marine fauna consists of well-studied bryozoa, brachiopods, lamellibranchs and gastropods. It is dominated by *Eurydesma* and its age is suggested to be late Early Asselian (Shah & Ghosh, 1977; Shah & Sastry, 1975). Recent studies of a rich fauna from Calytrix, in marine glaciogene sequence of Grant Formation, Australia (Foster & Waterhouse, 1988) have brought out a Mid to Late Asselian age for the strata, but the palynoassemblage of the same is highly diversified and it compares closely with the Biohorizon-III level identified here and dated as Early Sakmarian. However, in the

Calytrix palynoflora the lowermost sample (354 m) which is 50 m above the basal line of Grant Formation, yielded a least diversified assemblage mainly having apiculate trilete and monosaccates with *Protohaploxypinus* spp.; this level could be equated with Biohorizon-II of the present study.

The second important datum is Umaria Marine bed which is dated as Late Sakmarian (Sastry *et al.*, 1977) on the basis of productids dominance. However, no new morphos in saccate pollen have appeared at this level, hence no line of biohorizon could be identified. But in the sequence of Jayanti and West Bokaro coalfields, the Biohorizon-III has been demarcated. By comparison of totality in pollen-spore assemblages and on stratigraphic grounds (Chandra & Lele, 1980) the Umaria beds are taken to be younger to the Jayanti beds; hence Biohorizon-III represents a definite Early Sakmarian level.

The palynofloral assemblages recorded from the Intertrappean beds of Abor Volcanics from various localities in Arunachal Pradesh (Prasad *et al.*, 1989) are comparable to that of Upper Talchir, resembling to Biohorizon-III. The first volcanic flow in the Agglomerate Slate sequence in Kashmir also represents Sakmarian level (Kapoor & Shah, 1979) which is followed by an Artinskian flow below the Nishatbagh beds. These episodes of north-west and north-east India have apparently no deteriorating effect on the flora of the peninsula, because no mass extinction, as could be expected, has been recorded in the morpho-evolutionary sequence presented here (Text-figure 4).

The Permo-Triassic event is very well documented between Biohorizon-VII and VIII. The changing pattern of the sequence records innovation of forms at the end Permian level, extinction of older lineages at P/Tr boundary (Text-figure 7) and radiation of newer forms at Early Scythian level. There has been a high degree of extinction but newer forms have also come into being. The palaeontological datums (palynofossils, plant megafossils, estheriids) almost conicide with the Raniganj-Panchet interformational boundary (Tiwari & Vijaya, 1992). Thus with higher degree of confidence, the entrance of *Goubinispora, Playfordiaspora, Klausipollenites, Lunatisporites* and exit of *Densipollenites, Corisaccites, Distriatites* and *Verticipollenites* can be taken as biochronologic datum for P/Tr boundary.

The Biohorizon-IX stands for the well-dated Carnian. The assemblage from Tiki Formation is linked with the fauna consisting of *Unio, Tihkia* and reptilian remains like *Hyperodapedon, Parasuchus,* etc. In the present study well delineated Biohorizon-IX is characterised by the pollen having columellate exine structure and clefted body. The appearance of these morphos makes an event of evolution in itself.

The FADs of *Callialasporites* and *Podosporites* complex are linked with the Lower and Middle Jurassic sequence. The tie-point for these data is linked with the well known fauna of Lathi and Jaisalmer formations. Although the former is poor in vertebrates, the latter formation has rich and diverse bivalves, ammonoids, etc. (Krishna, 1987).

CONCLUSIONS

1. The events in evolutionary sequence of morphographies of saccate pollen found in the Gondwana formations are definite indicators of biochronological datums.
2. The FADs of new organizations, or LADs of older lineages, have led to identify eleven Biohorizons and consequently ten Interval-Zones through the wide span of Gondwana Sequence.
3. The cladistic analysis, based on ancestral and derived character states, has carved out the relationship clusters of morphos and the stratogram patterns which have emerged into a mosaic of morpho-organizational trees with their patterns of sprouting as well as off-sets through time.
4. The saccate pollen groups are more reliable for time plane identity than the nonsaccate spore-pollen because of their wider dispersal capabilities, and the stratigraphically linked character polarity is highly authentic since the Gondwana flora is intensively studied from oriented profiles representing wide geographic areas.
5. The Upper Talchir Formation experienced the peak activity of radiation in morphos because the intensive climatic stresses invoked the forces of evolution.
6. The P/Tr boundary zone was the biggest episode in terms of turnover of forms during the whole Gondwana Sequence.
7. The rate of evolution during Upper Permian was slow and so also in the post P/Tr boundary phase of the Triassic.
8. The congruence of character states and sequence of stratigraphic occurrences suggest that the glossopterid palynoassemblages of Early Permian in India had their roots in the Lower Carboniferous of Australia. The least diversified palyno-morphographies of earliest available strata of India had only six stocks which branched-off and sprouted into the

plexus of organizations in the subsequent Permian Period.

9. The Upper Carboniferous-Lower Permian gap in stratigraphy is indicated by the comparative assessment of palynodata and their outgroup relationship.
10. Morphographically, the prominence of well organized trilete and monolete mark, and that of a non-sulcoid distal saccus-free area on body in the monosaccate pollen of Talchir Formation make them probable candidate for prepollen representative, even at the Lower Permian level. The monosaccates could have had their main root of origin in the progymnospermopsida—mainly with a trilete mark and flabby flange characters which appeared during the Upper Devonian-Lower Carboniferous time.

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