Functional morphography of some palynomorphs from Permo-Triassic transition in India and its bearing on palaeoclimate

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The basic plan of morphography functions for survival of organism within the frame-work of effective delivery of output, economy of building-material, adaptability during stress, and meticulous procreation., A recasting in the pathways of vital components in certain spores and pollen had occurred at PTB transition which induced long-range evolutionary effects. Thus, a change from prevalence of striations to that of taeniae, safra to sulcus, protosaccus to eusaccus, Varitrileti to Cosmotrileti, and overall bigger size to smaller size was an episode of great significance at this datum plane. The subtle signal of such remodelling in micro-morphography are recorded as pre-adaptive phenomenon, just prior to PTB in the Changxingian Stage and their establishment in the Induan Stage. This fact may be utilized with high degree of confidence in locating the Permo-Triassic Boundary in nonmarine sequence on peninsular India.

Key-words - Morphography, Palynomorphs, Permian - Triassic, India

FORM and function of any component in an organ are intimately related with each other. Such relationship in the morphology of spores and pollen is expressed at the micro-architectural level. Although in fossil palynomorphs, only external coat, i.e. exine, is available for study, its high quality preservation exhibiting intricate details of structure and sculpture provides immense opportunity to recunstruct the bauplan (or building plan). As one analyses merely the configuration, shape, size, orientation, and arrangements of structure and sculpture, the Morphology is generally referred to as Morphography in the case of *Sporae dispersae*.

The basic plan of morphology operates within the frame-work of four functional factors, viz.— effective delivery of the output, economy of the building-material, adaptability during stress, and meticulous procreation. The importance of these factors is mutually complementary as well as interdependent. The survival, which incorporates continuity of progeny, of the organism is the most vital purpose (Fig. 1). Any function of a component in an organ is programmed within the basic laws of nature, to cause protection and to guard the fundamental effect of the life-system, i.e. the continuance of existence. The population of organisms changes due to inner and outer forces (Golubev 1995), and the components of the organs also

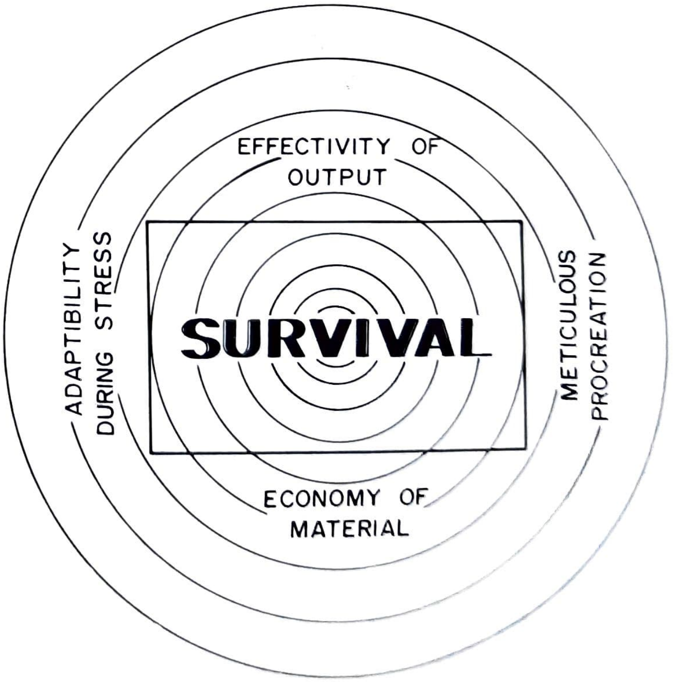

Figure 1. The plan of morphology of an organ, or an organ component, operates within the frame-work of certain factors, four of which are basically important. The ultimate aim of a function is survival. The factors are mutually dependent as well as complementary, as symbolised by circles within circles.

respond, may be at the micro-level, to the causal forces of evolution.

It is well understood that the effectivity of function is a mean to achieve the crucial goal of survival through reproduction. The nodal point of function, therefore, concentrates meticulously more at the reproductive system (procreation) than at the corpus system, because progenation — the key for continuance of species through time, is the most senstive phenomenon and it works only under strictly optimal conditions.

The economy of building-material implies the progressive simplification of structure, least wastage of matter, and availability of stand - by component in case a replacement is urgently required. Although on the path of evolution along the temporal line, many a times it appears that superfluous, apparently wasteful or unwanted building-material is present in a component or in an organ, but on a closer look of such a situation it appears that it had been there as a result of an inevitable requirement, or a specialization, to encounter a particular set of climate, ecology, environment and prevailing competition at that level of evolution. An organ with highly specialized function, or overloaded with extra building-material ultimately extincts.

The nature is never in a hurry, neither it jumps in leaps and bounds. Evolution is a slow and synchronized process of careful adaptations, selections, rejections, and innovations. The eco-stresses (term used here in a broader sense, including geodynamics and cosmodynamics) instigate the mutational forces to redesign and re-adjust the organs in order to meet the pressing need of suvival under the changing circumstances. The organisms, their organs, and their components respond to such demands, and with the adjustment in the masterplan blue-print of genetic material the newer forms of morphology come in to being.

The fossil spores and pollen found in dispersed condition in the sediments of Gondwana Sequence — representing Permian, Triassic, Jurassic, and Early Cretaceous periods, were produced by vegetation which existed on the Gondwanaland. This Supercontinent had a geography and environments unknown in the present time. The commencement of Gondwana deposits had witnessed an extremely cold, glaceogenic climate during Late Carboniferous- Early Permian times. The subsequent amelioration in the climate and an increased precipitation had resulted in the multi-directional evolutionary pathways, an advent and upsurge of the *Glossopteris* flora and termination of Carboniferous traits in plant communities. All this was the result of great stress-event at the Carboniferous- Permian transition (Vijaya 1996). This was followed by the favourable geotectonic conditions for the deposition of huge coal reservoirs during Permian. At the Permo-Triassic transition, the recurrence of a short spell of cool climate, a regression followed by transgression of seas, and a slight anticlock-wise rotation of the Supercontinent had occurred as major episodes, which triggered the path of plant evolution (Tiwari 1993). Thus, the Permian-Triassic Boundary (PTB) records an event of major shake-up after the Carboniferous-Permian Boundary — a gap of about 50 Ma.

Under the spell of new setup of warmer and relatively drier conditions, the *Glossopteris* flora declined and the *Dicroidium* flora evolved. Subsequently the *Ptilophyllum* flora came in to being, with which stablization of conditions continued upto Cretaceous.

Such a vast panorama of changing vicissitude of climates and environments encompasses the history of sequential alterations in plant life at several stages, but the one at the PTB was the greatest of all. This is well reflected in the distribution of palynomorphs through Gondwana time (Tiwari & Tripathi 1992).

A plant is an organism, the spores and pollen are organs functioning as units which are entrusted with a crucial role in the life-cycle of a plant as couriers of reproductive material. The body, the saccus, the germinal aperture, structures, exoexinal extentions, and several other morpho-features in the building-plan of spores and pollen are their morpho-components, which change with time.

In the present communication, some of the characters which qualify for recognizing the evolutionary shifts at PTB have been evaluated for their morphography and its functional effectivity during the period of transiliency at Palaeozoic-Mesozoic Systemic Boundary.

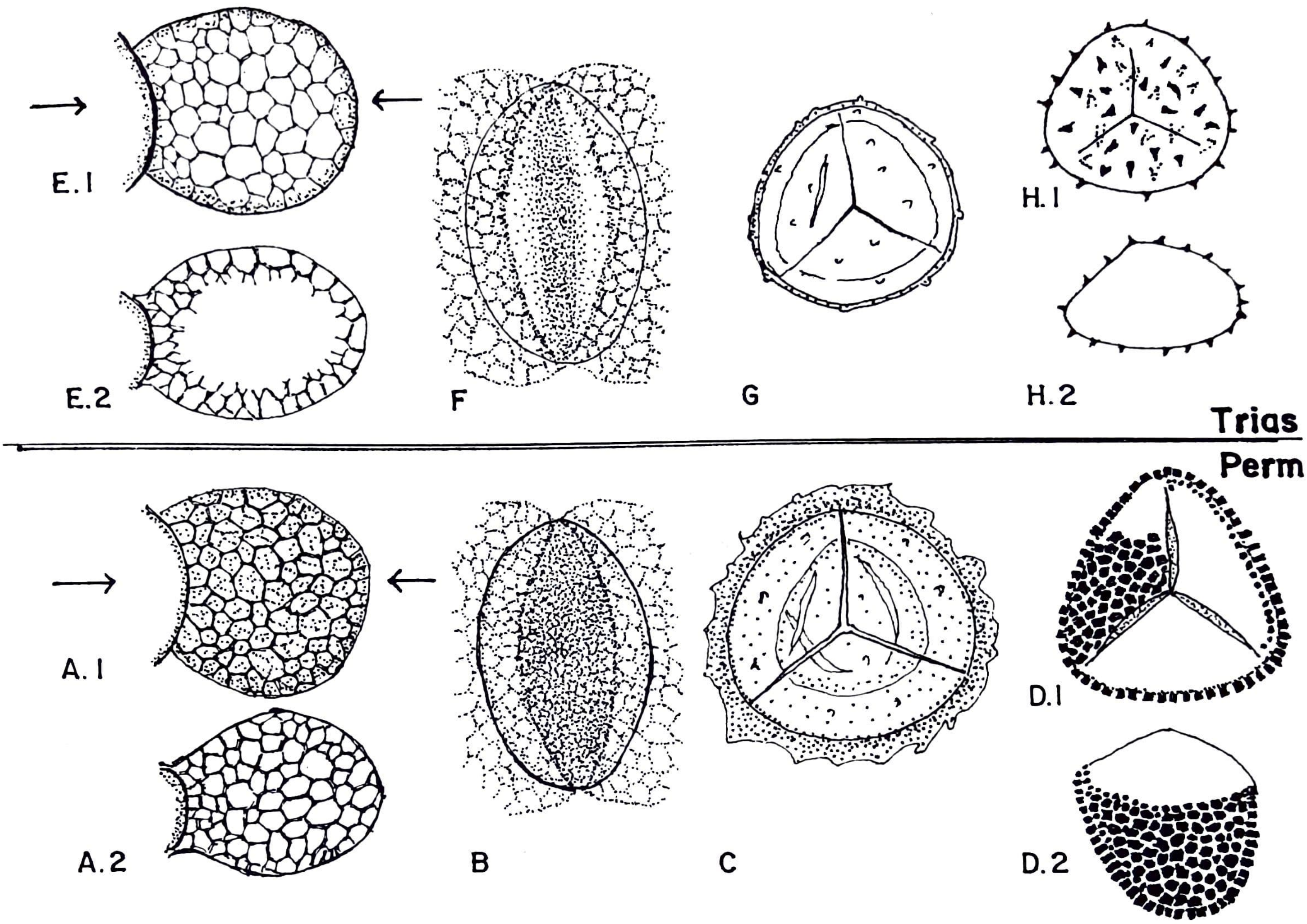

Figure 2. Certain characters in organ-components of spores and pollen which changed through the transient phase from Permian to Triassic A.1- Filled saccus (protosaccate condition) in surface view; a.2- Same in meridional section along the line of arrows in A.1, showing absence of cavity; B - Distal side of pollen body showing safra with fine infrareticulate structure, sacci encroachment and lines of attachment (sacci partially shown); C - *Dentatispora*, showing well developed cingulum and cavate bau-plan; D.1 - *Microbaculispora*, a representative of Varitrileti in proximo-distal view with distal ornament (on left sector) and psilate nature on the proximal side (right sector); D.2 - Same in lateral orientation; E.1 - Eusaccus in surface view (compare with A.1); E.2- Same in meridional section (compare with A.2) along the arrow line in E.1; F - Sulcus, a sunken, thin area on distal side of pollen body, sacci partially shown; G - *Lundbladispora* with narrow cingulum; H.1-A Cosmotrileti representative in proximo-distal orientation; H.2 - Same in meridional section (All figures are diagrammatic and not to scale).

SPORE POLLEN COMPONENTS

The mission of a pollen is to carry the male gametophyte, genetically haploid material, to the female gametophyte, and to germinate there in order to achieve ensured delivery of the male gametohyte for fertilization. For the whole process, the protection of the nucleic material, wider dispersal, effective landing and consequential germination must be precisely ascertained.

The task of a spore is more challenging than that of a pollen. It is a single nuclear-cell which after dispersal germinates and gives rise to gametophyte outside the exine. Thus it has to face greater hazards of extinction if it does not reach on to a suitable substratum. It is a risky chance, and hence the primitiveness of the system is evident.

The morphology of Permian spores and pollen was constructed to carry out such tasks, but they had primitive organizations in many ways, and have evolved only in slow pace during Permian. However, at the end of Permian and the beginning of Triassic a great change had occurred in the physical and biological systems on the earth (Sweet *et al.* 1992). The life on land sufferred a sort-of-mass-extinction crash, and the plant life swiftly (geologically speaking) changed its course of evolution to give rise to a new type of plant population. Such phenomenon has been termed as high turnover (Tiwari 1995). Appearance of certain Induan char-

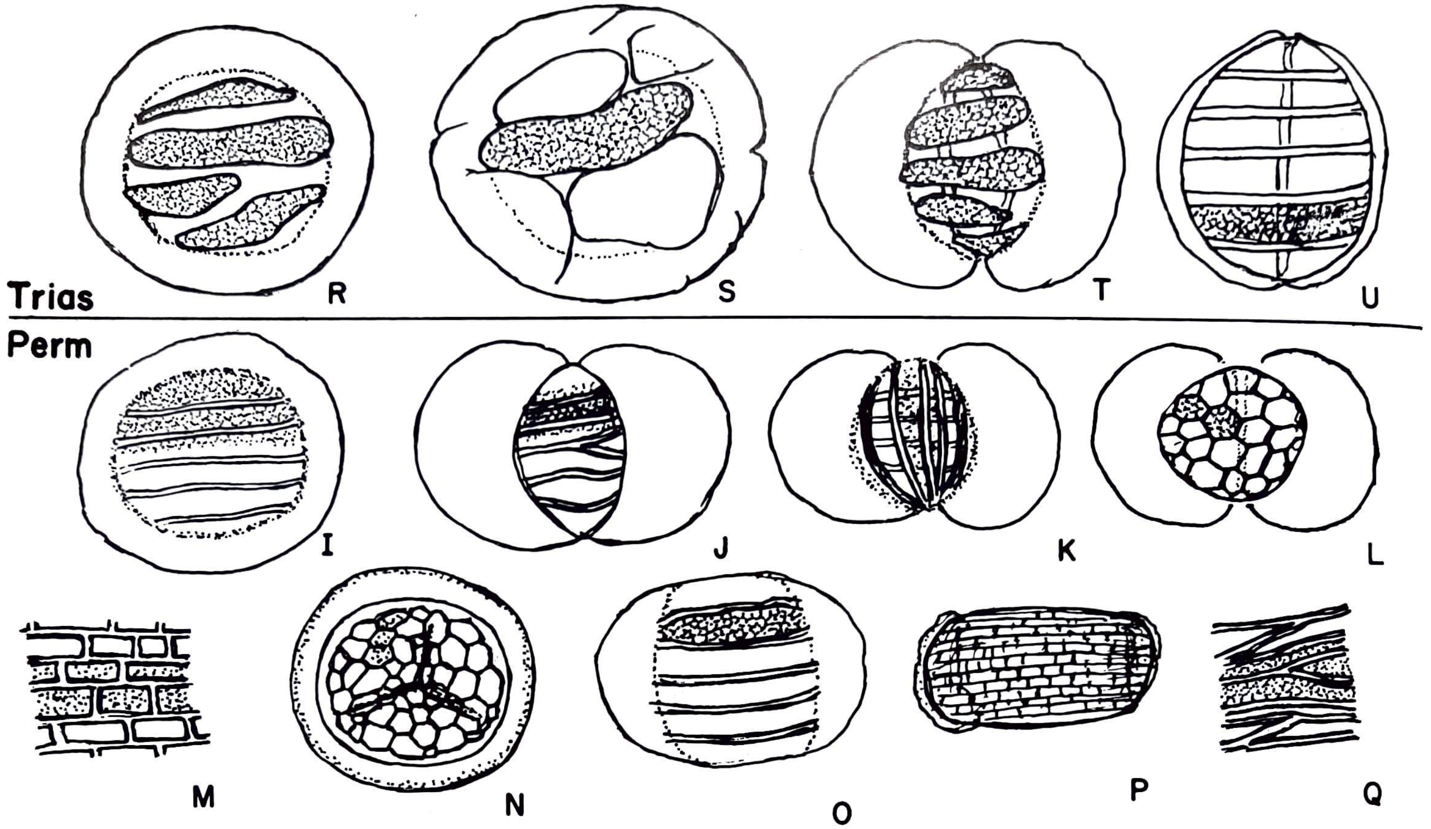

Figure 3. I - Striations on monosaccate, *Striomonosaccites;* J - Disaccate with simple horizontal striations, *Striatopodocarpites;* K Horizontal striations proximally and vertical striations on distal face, *Distriatites;* L- Reticuloid pattern of striations on disaccate, *Korbapollenites;* M - Brick-work pattern of striations; N - Reticulate striations on monosaccate, *Barakarites;* O - Simple, non-branching striations, *Faunipollenites;* P - Closely packed brick-work pattern on *Tiwariasporis;* Q - Branching and interconnections in striations; R - Taeniae on monosaccate, *Kamthisaccites;* S - Lobes of sexine, *Goubinispora;* T - Typical taeniae (stripes) leaving plateae inbetween, *Arcuatipollenites;* U - Slightly widened striations to make striniate character, *Trabeculosporites.*

acters in Changxingian palynomorphs, in other words - a foreshadowing of change during the time just preceding to PTB, is an example of pre-adaptation. Such events are reflected in the spore-pollen complexes which are true representatives of plant communities of any time (Traverse 1994).

Across the PTB, the changing morphology of palynomorphs had established, and so also their functions to face the alien climate and eco-stresses.

Following are certain group characters (Figs 2 & 3) which have undergone the transient phase (an alphabetic list of complete names of spore-pollen taxa, with authors name and year, is given in table 1):

Table 1. Alphabetic list of spore-pollen taxa named in the text.

Acanthotriletes Naum. *ex* Pot. & Kr. 1954
Alisporites Daugh. *em.* Janson. 1971
Apiculatisporis Pot. & Kr. 1956
Arcuatipollenites Tiw. & Vijaya 1995 (*partim* = *Lunatisporites* Lesch. *em.* Scheur. 1970)
Baculatisporites Thoms. & Pfl. 1953
Barakarites Bharad. & Tiw. 1964
Brevitriletes Bharad. & Sriv. *em.* Tiw. & Singh 1981
Crescentipollenites Bharad., Tiw. & Kar 1974
Densoisporites Weyl. & Krieg. *em.* Dettm. 1963
Dentatispora Tiw. 1964
Dicappipollenites Tiw. & Vijaya 1995 (*partim* = *Lueckisporites* Pot. & Kl. *em.* Kl. 1963)
Didecitriletes Venkatach. & Kar *em.* Tiw. & Singh 1981
Direticuloidispora Tiw. 1964
Distriomonosaccites Bharad. 1962
Distriatites Bharad. 1962
Faunipollenites Bharad. 1962
Gondisporites Bharad. 1962
Goubinispora Tiw. & Rana 1981
Guttulapollenites Goub. *em.* Venkatach., Goub. & Kar 1967
Horriditriletes Bharad. & Sal. 1964
Kamthisaccites Sriv. & Jha 1986
Korbapollenites Tiw. 1964
Krempipollenites Tiw. & Vijaya 1995 (*partim* = *Klausipollenites* Janson. 1962)
Lophotriletes Naum. ex Pot. 1954
Lundbladispora Balme *em.* Playf. 1965
Microbaculispora Bharad. 1962
Parastriapollenites Mahesh. 1970
Pityosporites Sew. *em.* Manum 1960
Playfordiaspora Mahesh. & Baner. *em.* Vijaya 1995
Plicatipollenites Lele 1964
Podocarpidites Cooks. & Coup. 1953
Protoeusaccites Tiw., Vijaya & Ram-Awatar 1994
Rhizomaspora Wils. 1962
Satsangisaccites Bharad. & Sriv. 1969

Scheuringipollenites Tiw. 1973
Sriatopodocarpites Soritch. & Sed. ex Sed. *em.* Bharad. 1962
Sriomonosaccites Bharad. 1962
Tiwariasporis Mahesh. & Kar 1967
Trabeculosporites Triv. & Misra *em.* Tiw. & Ram-Awatar 1987
Vitreisporites Lesch. *em.* Janson. 1962

1. *Striations and taeniae*- The body in a majority of Permian and Triassic pollen bears striations or taeniae. These two terms have been erroneously used in the past as synonyms. However, they are not even homologous. The striations are simple, linear, uniformly wide furrow-like groves, separated from one another by plateae of the infrareticulate sexine, while taeniae are over-grown, flabby stripes or bands of infrareticulate sexine, placed in more or less parallel orientation on the proximal face of the body; the inter-taenial spaces (plateae) are wide but not uniformly so, along their lengths (Vijaya 1990). Thus, striations and plateae could be homologous as both expose the nexine, having no sexinal layer over them.

The groves and the bands cannot have a function of hermomegathy because they are rigidly placed, well organized without any tendency to get flatten or smothered. No compensatory folds to accommodate the shrinkage of exine are found on the proximal face of the body; had they played a role in hermomegathic movements of the exine, there should have been some evidence in the preserved exine also. No indication of rupturing, collapsing, or fully or partial smothering of body on proximal side has ever been recorded. And in extant bisaccate pollen (e.g. *Pinus*) we do not have striations or taeniae; hence a key to the past cannot be found in the present.

Striations and plateae expose the nexinal part of the exine. This fact prompts to predict their function as emergency exits for pollen tube; probably, such multiple doors were required for these groups of pollen in which real sulcus on distal side had seldom developed and sulcoid channel is non-existent in striate forms. At this stage of evolution in pollen morphology, when typical sulcus had yet to evolve, the effective delivery of genetic material-output was exigent - even at the cost of building material. Hence, keeping the sole aim of survival in view, a plurality of germinal gate-ways seems to be an adaptive experimentation. This group of pollen was, however, wiped out of the scene by the end of Triassic, yet the striations and taeniae have a story to tell about their successful existence for nearly 80 Ma.

The striations are primarily a Permian character and taeniae aTriassic one. In Permian, an array of permutation and combination in linear groves is recorded in:

i. Monosaccate, simple striations on one of the faces of the body (*Striomonosaccites*),
ii. Monosaccate, simple striations on both the faces of the body (*Distriomonosaccites*),
iii. Monosaccate, reticuloid striations on proximal face of the body (*Barakarites, Parastriapollenites*),
iv. Disaccate, simple/branched striations on proximal face of the body (*Stiatopodocarpites, Faunipollenites, Crescentipollenites*),
v. Disaccate, simple striations on both the faces of the body (*Distriatites*),
vi. Disaccate, reticulate pattern of striations on proximal face of the body (*Rhizomaspora, Korbapollenites*),
vii. Disaccate, reticulate pattern of striations on both the faces of he body (*Direticuloidispora*),
viii. Disaccate - vestigial sacci, brick-work striations on both the faces of the body (*Tiwariasporis*).

Beside these basic patterns, variations in brachings, interconnections, vertical partitions giving rise to brick-work design or even polygonal arrangements have occurred in Permian striate pollen.

Such a matrix of diversification in striations culminates at the end Permian, but drastically declines across the PTB. Only a few taxa which were overwhelmingly dominating the population during most of the late Lower and Uper Permian meakly straddle across the boundary in to the Early Triassic; such morphos are *Striatopodocarpites, Faunipollenites, Crescentipollenites,* and *Tiwariasporis*. Loaded with their evolutionary exhaustion and faced with altered conditions, ultimately these taxa also waned away during the rest of Triassic. But, conccurrently a smooth change-over in the closing phase of Permian - at Changxingian level—from striate to taeniate population had taken place. Incoming and then the dominance of definitive stripe-bearing pollen are the characterizations of the PTB transition.

Such new-comers are:

i. Monosaccate, taeniae on one of the faces of the body (*Kamthisaccites*),

ii. Monosaccoid to disaccoid, taeniae-like islands of sexine on the body faces (*Goubinispora*),

iii.. Disaccate, taeniae on proximal face of the body (*Arcuatipollenites* = *Lunatisporites*),

iv. Disaccate, striniate- simulation of incipient taeniae (*Trabeculosporites*).

Obviously, the Triassic taeniae system is less diversified than the striation system of the Permian.

There are some off-shoot experimentation during Permian which tried to develop taeniae-like characters in *Corisaccites*, *Guttulapollenites*, *Dicappipollenites* (= *Lueckisporites*). However, they are not multitaeniate, like *Arcuatipollenites*, and also do not qualify for the identification of Permian-Triassic event on the Indian peninsula.

Why a basic character of about 50 Ma standing, produced by glossopterids, declined drastically across the PTB, and slowly died out thereafter ? Why it was coterminus with *Glossopteris* ? Rather, it could have been taken up by the genetically descendant groups of this flora. This organ-character seems to have changed in response to a need for different function. This may also lead to the conclusion that although the striations and plateae shared the task of poly-sulcate functional state, the bands of sexine in taeniate pollen had some other function to perform. It appears that a change in climate towards drier side caused the devlopment of a thickly-banded corpus to avoid desiccation.

The lush vegetation and rich forests of Upper Permian which gave rise to Raniganj coals indicate a high precipitation during that period. On the other hand, the Early Triassic Panchet Formation is almost devoid of coaliferous material and is characterized by khaki-green shale-sandstone cycles followed by red facies (Sastry *et al.* 1977). The vegetation was adversely effected by the declining precipitation. Additionally, the geotectonics governing the formation of coal on Indian peninsula had changed at the close of Permian, resulting into a non-deposition of peat during Triassic. The climate was not necessarily arid during Early Triassic on Gondwanaland since pteridophytes were still abundant, yet after a short spell of cooling near the boundary there was a trend towards warmer and drier side. Here survived the taeniate-pollen-bearing plants comfortably.

The taeniae — stripes or bands of sexine — could provide more weight and strength to the corpus. The extra weight, distributed on beam-like bands on convex surface, could prevent the pollen from landing upside-down, i.e. a help for pollination-friendly orientation; this also gave more strength to the body coat to save it from collapsing. And as already mentioned, the wider inter-taenial spaces with exposed nexine could provide better opportunity for opening, if required, to give way to pollen tube. The distal-side-down was a vital orientation to be achieved because yet the true sulcus was being evolved gradually in taeniate pollen.

The striations had to decline and to die out because of over-specialization; they functioned well in a cool to moderately cold climate but could not be effective in drier and warmer conditions.

2. *Saccus* — The Permian saccate pollen possess filled saccus, i.e. they were protosaccates. The eusaccate, or true saccate nature is initiated at the PTB zone with the occurrence of *Protoeusaccites* (Tiwari & Vijaya 1994; Tiwari *et al.* 1995), and *Playfordiaspora* (Vijaya 1995). And the saccus of subsequent time, i.e. PTB and younger horizons, is found to be consistently trying to become a true saccus; that means- several species in disaccate pollen acquired for a hollow saccus till it is completely achieved in more of less all the morphos by the end of Gondwana times. This aspect of evolutionary change has been discussed in detail by Venkatachala *et al.* (1992).

A transformation of the condition in which the cavity of the saccus is filled with reticulation or alveolae (*Crescentipollenites*, *Faunipollenites*, *Pityosporites*-stalk) to a state where it is hollow (in several species of *Arcuatipollenites*, *Alisporites*, *Podocarpidites*) is a big achievement in the form of an organ. It conserves the building material and, at the same time, gives better effectivity to bouyancy due to loss in weight and also a support of two cavities on either side of the body. After all, why a hollow saccus was not developed in the pollen right from the beginning, say - Carboniferous ? Why the pollen had carried a burden of filled saccus for more than 70 Ma ? Strange are the ways of nature. Yet it can be very well conjectured that at that low level of evolution — at the time of emergence of saccus — even to have filled saccus was a great achievement in an adaptive experimentation in the new territory of floating in the air. And it was a success for such a long period. The pollen at the PTB transition had obviously experienced a major change in a vital component which set a trend thereafter for all the time to come. The sacci of extant disaccate pollen are all hollow, i.e. eusaccus.

Whether it was a climatic need for such a change, is not clear. What stress could have made a group of plants to produce eusaccate pollen ? Obviously none. Only a saving of sporopollenin and, at the same time, better functioning — an aid to wide dispersal and consequently better chance of reproduction appear to be the underlying force of evolution. The long experience of filled saccus guided the organ to produce hollow saccus through chemical memory in the traits of plants.

3. *Sulcus* — Sulcus is a distally placed, wide germinal furrow or grove on the body of a pollen. Its function is to facilitate the exit of pollen tube, or the germ material, at the accurate time of requirement. True sulcus is an extremely thin sunken area, exposing the nexine, bounded by thicker regions of sexine. The paths of evolutionary trends in sulcus during Gondwana times have been discussed by Venkatachala *et al.* (1992).

The pollen of Permo-Triassic transition period had opted for another achievement, in addition to taeniae and eusaccus, in the enhancement of morphography of an important component, i.e. sulcus. There had been no true sulcus in Permian Gondwana pollen; only it was represented by safra (saccus-free-area), an area where nexine and sexine have not separated along the *Isolierschicht*. Safra is not a depression or a grove with organized weak-zone of nexine. It appears that pollen morphology had come to an age for take off to bear a vital structure which condtinued till today in saccate pollen. But taeniae also evolved side by side during the PTB zone on Gondwanaland to provide exit doors, alternative to sulcus-failure, because safra was undergoing a stage of transformation to become a true sulcus. This system of multiple possibilities continued for the whole of Triassic in taeniate pollen.

In non-striate, non-taeniate pollen, the true sulcus picked up relatively faster, as is the case in certain species of *Alisporites*, *Podocarpidites*, *Satsangisaccites*, and *Vitreisporites*. In such morphos, a narrow vertical fold is seen in the saccus-free-area on the distal face indicating thin nature of nexinal layer in this area. Such is not the case in the Permian non-striate pollen.

The non-striate, non-plateate pollen had to ensure the development of a perfect germinal device because there were no alternative arrangements for the exit of the tube. Such morphology has been effective in achieving the conservation of material, surer method of out-put delivery, and purposeful advancement in the progress of procreation. The true sulcus is the nodal point from where further lines of colpus and porus must have taken the clue for futuristic morphology.

The decline in frequency, or termination, of safra — bearing morphos, e.g. *Striatopodocarpites*, *Faunipollenites*, *Crescentipollenites*, *Plicatipollenites*, and several others, at and across the PTB zone, and the appearance of true sulcus-bearing morphology in the species of *Arcuatipollenites*, *Alisporites*, etc. point toward an elvoutionary shift in the components of morphos.

4. *Size* — There has been a basic change in the overall — size of the pollen groups, particularly the saccates, across the PTB. The termination of most of the large-sized monosaccates and disaccates (for example, *Plicatipollenites*, *Scheuringipollenites*) and advent of smaller morphos (*Krempipollenites*, *Vitreisporites*, and smaller species of *Striatopodocarpites*, *Arcuatipollenites*) at the boundary are indications of evolutionary manifestation for saving the building material. However, bigger pollen, as *Goubinispora* and few species of *Alisporites* also contributed to the population, yet a gradual reduction in size in most of the groups is prevalent.

During the whole of Permian, generally the bigger size was in vogue, but the reduction phase has been triggered at the end of Permian.

5. *Other Character Components* — The morphology of spores, i.e. of the pteridophytic morphos, is conservative in adapting major change in components. Then, how do they adjust in newer conditions ? Either they make very little adjustment, or they extinct.Why they are so non-adventurous even at the cost of their existence? It seems that they lack the genetic push for evolving on the faster track, because by inheritance they are the remnant of those stocks which could not evlove as others

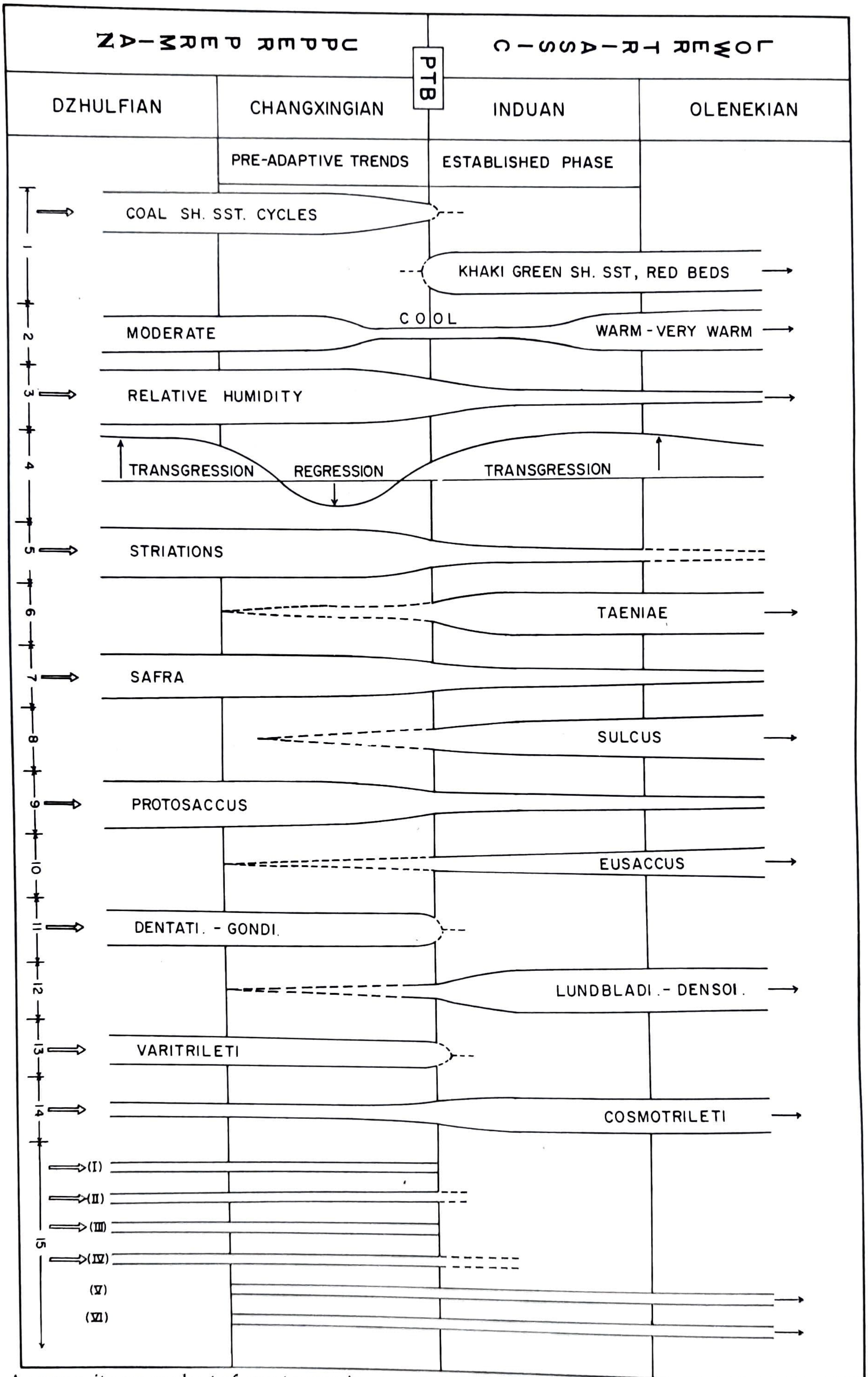

Figure 4. A composite range-chart of events covering a part of Dzhulfian, Changxingian-Induan and a portion of Olenekian. The pre-adaptive phase at the close of Permian and the established phase at the beginning of Triassic are highlighted. The course of alteration in spore-pollen morphology corroborates with changes in lithology, climate, sea-levels, and evolutionary shifts (exemplified by six taxa). PTB - Permian-Triassic Boundary; hollow arrows - continued occurrence from older horizons; solid arrows - continued in to younger horizons; broken lines - sporadic and unsteady; complete lines - steady; width of vertical range column - relative abundance/prominence; I. *Distriatites*, II. *Verticipollenites*, III. *Indospora*, IV. *Densipollenites*, V. *Playfordiaspora*, VI. *Krempipollenites* (Range bars suggest only range of occurrence and not the frequencey).

have done during Devonian-Carboniferous time. It could also be possible that the pteridophytes, in general, survive only in humid climatic nitches, and even in changed condition there exist humid pockets for the abode of this sensitive group; hence a change in organ-component might have not been compulsive.

At PTB, an example of termination of Varitrileti-group of spores (*Microbaculispora*, *Brevitriletes*, *Didecitriletes*, etc.) indicates that the Triassic descendants of the Permian Varitrileti-producing plants did not opt for continuing the same morphology in their spores. Most of the ornamented spores in the Triassic have a distribution of sculptural elements all over the body — unlike Varitrileti. Apparently, in the former group, such as *Lophotriletes*, *Acanthotriletes*, *Apiculatisporis*, *Baculatisporites* (Cosmotrileti — the term being introduced here to accommodate this group of spores) the distribution of ornaments seems to be an extravaganza of material when compared to those of Varitrileti where ornament is restricted to the distal face only. However, infact the latter often bears densely disposed ornaments while in the former they are sparsely spaced. Hence there is an overall saving of material in the case of Cosmotrileti.

The reductional change in the cingulum of cavate spores from the end Permian to the beginning of the Triassic (*Dentatispora* to *Lundbladispora*) is also evident. *Gondisporites*, a marker of Upper Permian, has a ridge-like broken cingulum, without a continuity all around the amb. This could be an off-shoot change in the direction of reductional trend, yet it did not survive beyond the PTB. Similarly, *Densoisporites* — a Triassic marker and not a seemingly cingulate spore, could be linked with this group in having thick equatorial exine and a cavate bauplan.

Probably these morphos belong to unrelated groups yet sharing a common cavate organization. The cavate spores encloses a freely hanging inner body (nexine) within a cavity made up of the sexine. Thus, the inner body, containing the genetic material for reproduction, is least effected by the stresses on the outer coat — a device to get better protection.

A cingulum is a heavy, clumsy and primitive component. A definitive morphological change, howsoever subtle it is, in this character at the transitionary period is noteworthy.

RELATIONAL MORPHOGRAPHY AND CLIMATIC CHANGE

Various patterns discussed above exemplify the succession of palynofloras in Gondwana Sequence. May be that elsewhere in the northern lands or in the Tethyan realm some morphos could have arisen earlier or later with relation to the PTB (Balme 1970). Thus, migration as a causal factor for appearance or disappearance of a particular morphos, bearing the components under discussion, cannot be ruled out. Yet the situation does not change because the effectivity of function of that component remains the same in the new setup across the Permian-Triassic Boundary on the Gondwanaland. Moreover, the Apparent-Form-similarity (Afsim factor) has to be kept in mind in making such deductions on migration (Tiwari & Vijaya 1995).

It has been derived in the previous pages that the following recasting in the pathways of vital character-components of certain spores and pollen had occurred, more or less concurrently, at the PTB datum:

1. Striations ————→ Taeniae
2. Protosaccus ————→ Eusaccus
3. Safra ————→ Sulcus
4. Big size ————→ Smaller size
5. Varitrileti ————→ Cosmotrileti
6. Cingulum ————→ Sub-cingulum

The first three of the above listed deviations are very crucial and critical. The taeniae lasted for the whole of Triassic while eusaccate state and the sulcus proved to be successful till the Recent. The condition of Cosmotrileti also prevails in the extant ferns. This character was established in all the groups of trilete-bearing pteridophytic spores at the Early Triassic level, although there were a number of Cosmotrileti morphos in Permian also, along with Varitrileti.

The pathways of changes in a set of components of an organ turn slowly in a well-charted direction. On such a turning point a mixing up of characters may also be noticed; such as - presence of sriations on taeniae. Also, reversal of characters after a lapse of time is not uncommon. Yet the most befitting features are retained and established under the frame-work of functional factors during the changing conditions. It does not mean that one morphology gave rise to another, in a classical sense of evolutionary paths of organisms. After all, spores and pollen are only organs, or entities of the life cycles of plants which actually gave rise to newer lines, or got extinct. But the reflection of definitive change in the character of an organ of a plant — such as, from striation-bearing to taeniae-bearing pollen population, is itself an evidence of evolutionary shift in plant communities. The continuum in record of spore-pollen occurrences through a profile of rocks along the time axis, their numerosity and independence, and a perfect preservational state make them most suitable objects for analyses of micro-level evolution.

The Permo-Triassic transition was a turning-point datum-plane for trigering of long-range evolutionary effects. The spore-pollen morphology had responded to a challenge of altered conditions by regulating itself to optimise the climatic and environmental systems which were created at the onset of Triasssic. It appears that at the PTB zone a chemical message was transmitted through several components of spore-pollen organs for a change and it was relayed at the pre-adaptive stage, i.e. one step before the actual main-stream change in lithology, climate and geotectonics at the Permo-Triassic boundary had occurred (Fig. 4). The subtle signals for morphological remodelling are recorded in Changxingian Stage and their establishment in Induan Stage. This phenomenon may be used with a high degree of confidence in locating the PTB in nonmarine sequence on peninsular India.

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