Evolutionary pattern of striations and taeniae in the Indian Gondwana saccate pollen

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Striations and taeniae are genetically controlled morphographic characters of *sporae dispersae*. The sequential pattern of evolution in striations through Lower Gondwana has revealed that the earliest Permian is the starting plane for these characters which proliferate to a diversified and complex mosaic, in the subsequent time, culminating in Late Permian. The global occurrence of striations and taeniae in saccate pollen of Permian-Triassic times is an episode of evolution in organisation which appears to attain the fittest situation for exine protection, germination gates, or moisture regulators.

Key-words—Palynology, Morphography, Permian Gondwana (India).

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साराँश

भारतीय गोंडवाना के कोष्ठीय परागकणों में धारीयों एवं टीनीयों का वैकासिक स्वरूप

विजया

विकीरित बीजाणु-परागकणों की धारीयाँ एवं टीनीयाँ आनुवंश द्वारा नियंत्रित आकारिकीय लक्षण हैं। अधरि गोंडवाना में धारीयों में विकास के अनुक्रमिक स्वरूप से व्यक्त होता है कि ये लक्षण प्रारम्भिक परमी कल्प से विकसित हुए हैं तथा बाद में अनतिम परमी कल्प में इनमें और अत्याधिक परिवर्तन एवं विकास हुआ। विश्व में परमी-त्रिसंधी काल में कोष्ठीय परागकणों में धारीयों एवं टीनीयों की उपस्थिति विकास की एक घटना है जब वे बाह्यचोल रक्षक, अंकुरण छिद्र, अथवा नमी नियंत्रक के रूप में अपनी भूमिका निभाने में अपने को तदनुरूप विकसित कर रहे थे।

STUDY of palynofossils from the Indian Gondwana sediments reveals a range of variability in their morphographic characters in kind as well as number. Phylogenetic studies (Heslop-Harrison, 1971) of spore-pollen complexes indicate that the major qualitative patterns are genetically controlled. In course of evolution each event is followed by a set pathway, e.g., an organisation in any form starts with simpler and less diversified level—the base line, and enters progressively into more complex and diversified levels. Thus, there is a *Starting plane* at which the appearance of a trait is recognised which, in time, is accompanied by experimental diversification in its nature. In course of diversification, variations attain their maxima, and normally no further alteration appears to be acquired. This phase is a *Stabilizing plane*. In the ultimate phase the proliferation of characters starts declining. Such a change may occur gradually, or all of a sudden. This last phase of existence of a particular character is the *Dying-out plane*, and is always accompanied with the starting plane of other character. Such sequence of changes is noted in the Gondwana palynofossils through time.

Saccate pollen constituting the major share of Lower Gondwana palynofloras bear a central body and two sacci attached juxtaposed to each other on either side of the central body, or a monosaccus attached to the body in various modes. A variation is generally found in saccus-body relationship.

Saccus is the isolated sexine from nexine which gets blown up resulting into a bladder-like organ. This sexinal layer appresses the nexine of body and covers it in various degrees. The proximal surface of this part of a pollen is either without any mark or furrows (Pl. 1, figs 1, 15, Text-fig. 2A, M), or with linear grooves or irregular furrows (Text-fig. 2B), giving rise to ribbon-shaped elevations (Pl. 1, fig.

10) arranged in an array of patterns to produce distinctive feature for group identification in the dispersed pollen (Text-fig. 2A-R).

MORPHOLOGY

Presence of regular linear grooves (striations) or irregular furrows (resulting into taeniae) on the body of a pollen is recorded only in fossils, that too mainly of Permian and Triassic times; obviously this span of geological time is unique in respect of global phenomenon of the occurrence of "striate pollen". Word *striation* is derived from *Stria* (Pl. -*ae*, Latin, a furrow). This term has been defined in different ways by various workers, such as, "elongated ridges" by Thomson and Pflug (1953), "grooves between elongated sculpturing elements in striate grains" by Faegri and Iversen (1950); very fine "parallel microridges" by Kosanke (1950) and linear of "finger print pattern" by Harris (1955). In its objective meaning, however, the term striae is used most commonly in the sense of "furrows".

The manifestations of simple linear grooves (Pl. 1, fig. 5; Text-fig. 2B) result in various arrangement. Branching of horizontal striations is one line of variability leading to an increase in their number. Vertical partitions or connections in between these striations is another path of diversification which leads to brick-work pattern and then to reticuloid arrangement (Pl. 1, figs 3, 7; Text-fig. 2C, D, E, G, H, N, P, Q).

Another line of diversity in simple striations has been observed where sexine in between two striations become more flabby and relatively loose (Text-fig. 2F). In other words, the sexine is relatively more developed between the area delimited by two striations. The groove which is linear in normal case becomes somewhat irregular in width (Pl. 1, figs 8, 9). This appears to be a bridging phase in between the conditions of "striations and taeniae". Beside this, there is a group of pollen where striations have been found to be very faint and feeble; they cannot be traced all along their lengths (Pl. 1, fig. 4; Text-fig. 2I) but their presence can be marked.

As understood during the present analysis, the striations are defined here as linear, extremely narrow ($< 0.5 \mu$), uniformly wide, simple grooves running on the body forming various patterns of arrangements, such as—parallel, sub-parallel, simple, bifurcated, polygonal, brick-work, reticuloid, etc. These may be simple or branched, with or without vertical partitions. In between these grooves, sexine could be variously structured or sculptured (Bharadwaj, 1962; Kar, 1968; Tiwari, 1974; Lele, 1975).

Another major line of distinction in saccate pollen is the presence of taeniae (*taenia*, Pl.-*ae*; Latin, a ribbon-like strip). These are structured sexinal bands on proximal face of the body of saccate pollen leaving unstructured exinal region of uneven width in between two bands (Pl. 1, figs 10, 13; Text-fig. 2L). A number of genera are on record which bear such structure, e.g., *Lueckisporites, Lunatisporites* (Leschik, 1955; Potonié, 1970; Scheuring, 1970, 1978) and *Kamthisaccites* (Srivastava & Jha, 1986). Recently a species of bisaccate pollen is identified which bears striations on taeniae (Vijaya *et al.*, 1988). This might represent a stage of an experiment in the course of evolution (Pl. 1, fig. 14; Text-fig. 2K). In few palynotaxa instead of several bands of sexine only two such bands are present on both the lateral regions of the body, leaving a wide unstructured area free in the centre of the body (Pl. 1, fig. 6; Text-fig. 2J).

From the above discussed conventional usage of terms it becomes evident that striations and taeniae are two different characters; striations represent linear furrows—like grooves, in which sexine is least

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PLATE 1

(All photomicrographs. × 500)

1. *Satsangisaccites* sp. : Non-striate bisaccate pollen.
2. *Striatopodocarpites* sp. : Horizontal striations bifurcated at places.
3. *Rhizomaspora* sp. : Reticuloid striations.
4. *Striatopodocarpites* sp. Faint, incomplete striations.
5. *Crescentipollenites* sp. : Simple horizontal striations.
6. *Lueckisporites* sp. : Two sexinal bands (Taeniae) on lateral region of central body.
7. *Lahirites* sp. : Vertical partitions in between striations at places.
8. *Striatites* sp. : Striations loosing its linear nature, becoming somewhat irregular spaces.
9. *Lunatisporites* sp. : Elevated sexinal bands tending to be taeniae.
10. *Lunatisporites* sp. : Distinct irregular sexinal bands (Taeniae).
11. *Striatites* sp. : Flabbiness in sexine, transforming towards taeniae organization.
12. *Striomonosaccites* sp. : Horizontal striations, bifurcated at places.
13. *Kamthisaccites* sp. : Elevated irregular sexinal bands (Taeniae).
14. *Lunatisporites* sp. : Taeniae, bearing striations on them.
15. *Parasaccites* sp. : Non-striate monosaccate pollen.

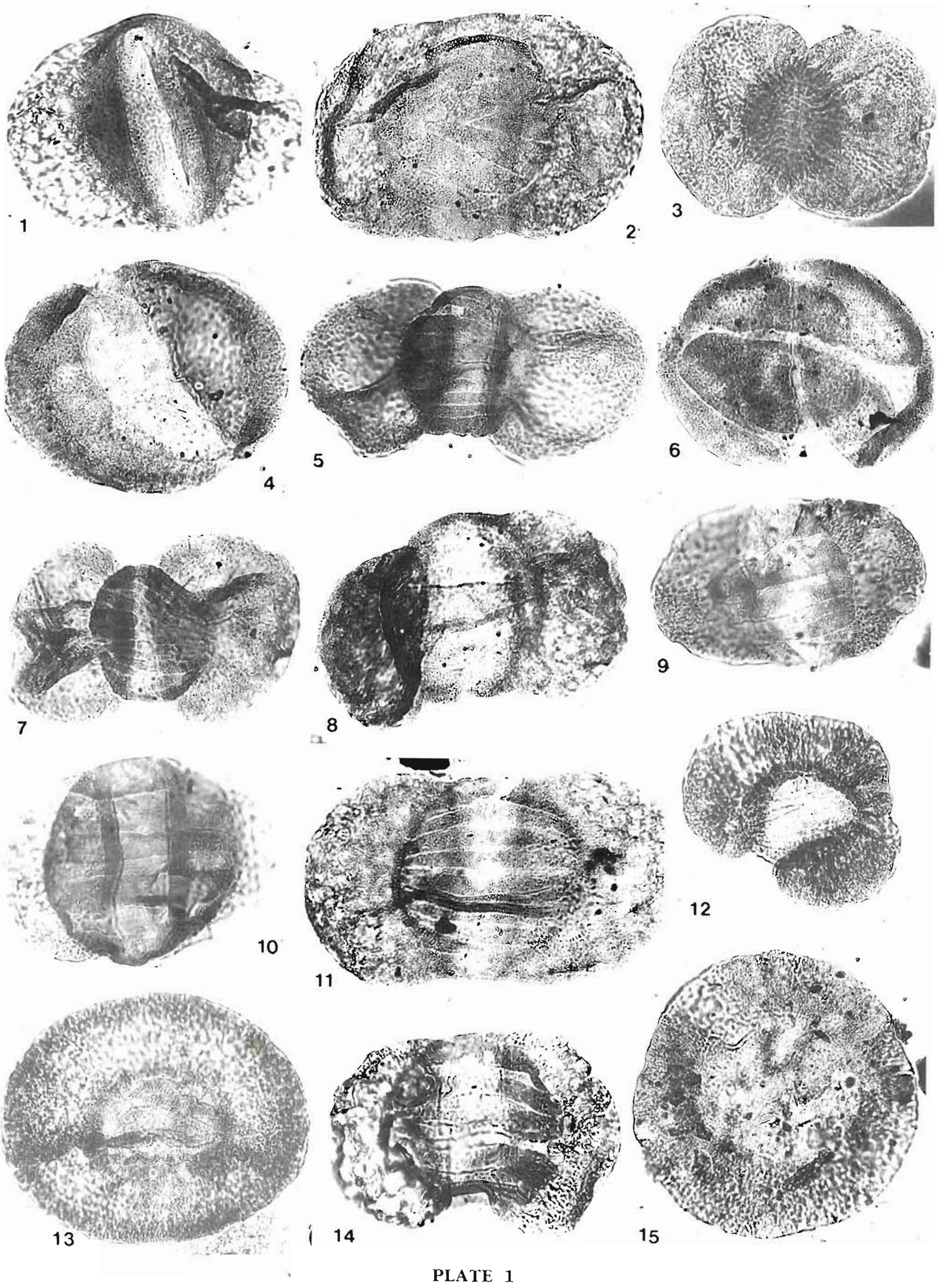
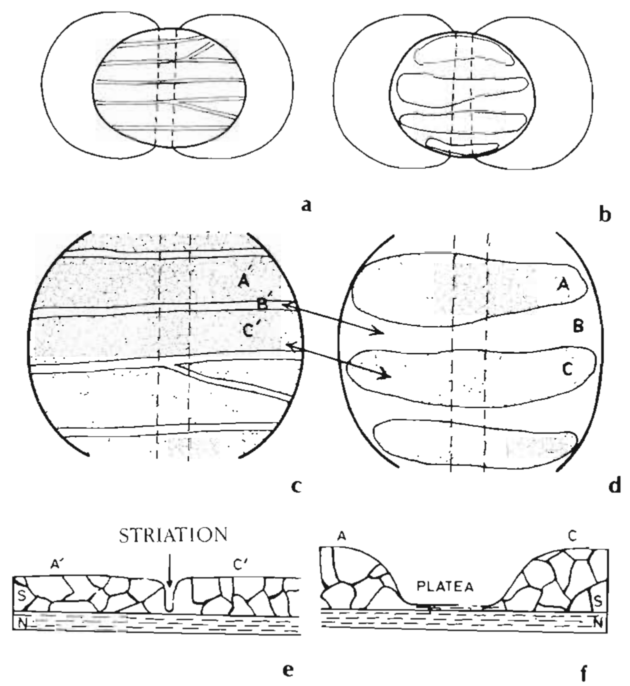


PLATE 1



Text-figure 1—Suggested terms for the distributional pattern of sexine on the body surface on saccate pollen. **a.** Simple linear furrows, striations; **b.** Well-developed sexinal bands, taeniae; **c.** A' & C'—Uniformly wide, broad, inter-striation spaces of structured sexine termed as Plaga; B'-linear, narrow furrows of unstructured sexine, termed as striations; **d.** A & C-Structured sexinal bands termed as Taeniae; B-irregularly wide unstructured sexinal inter taeniate space termed as platea; **e, f.** Schematic representation of sectional view of the exine layer along lateral axis of body. **e.** passing across striations and. f. across taeniae. A', C'—Plagae and striation; A, C-Taeniae and platea.
Section of mature exine consisting of inner lamellated nexine (N) and structured sexine (S). Arrows indicate reduced sexine in a striation (e) and a platea (f).

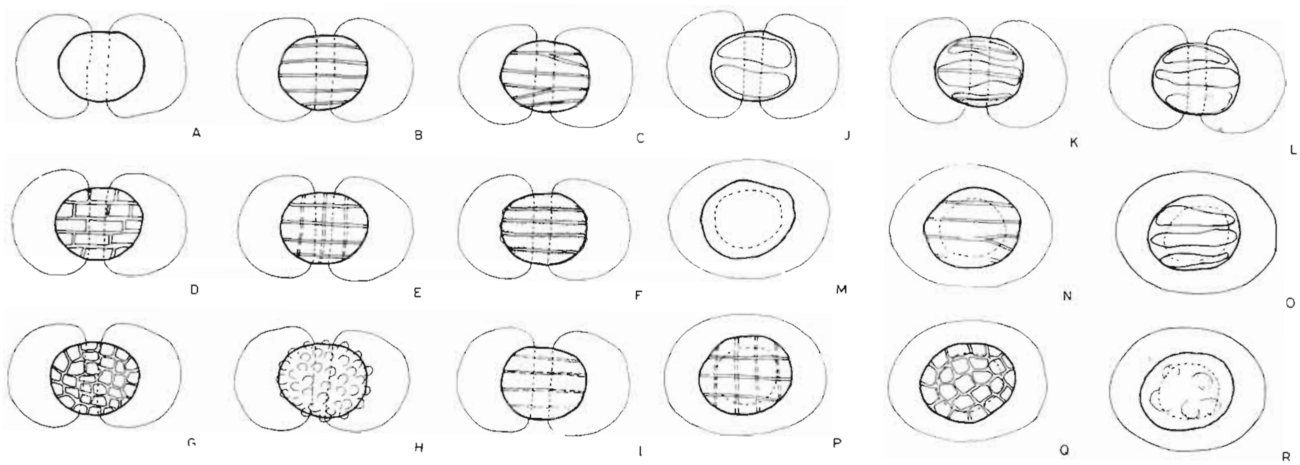
developed while taeniae are tape-worm-like bands having well-developed sexine (Text-fig. 1a, b). These descriptive terms are not mutually homologous. These two populations of pollen are entirely different from each other and, hence, the practice of their being clubed together as "striate pollen" is not acceptable. In view of these derivations, it is proposed here to term the inter-taeniate spaces as *Platea* (Latin-street, pl.-*ae*), and inter-striation space as *Plaga* (Latin-flat surface, tract; pl.-*ae*). The platea is the space irregularly wide along its length between two taeniae, having minimal development of sexine, in which no distinct structure has developed. The plaga is the inter-striation region, having fair development of sexine above the nexine layer exhibiting structure of various kinds (Text-fig. 1c, d). Thus, taeniae delimit the plateae and plagae delimit the striations; the *striations* are homologous to *plateations* and *taeniae* to *plagae*.

During the ontogeny of sporoderm (Taylor, 1982; Taylor *et al.*, 1984), at an advance stage the differentiation of sexine and nexine is relative and also variable in different parts of the pollen body. It is supposed that in the areas of grooves or scars, further development of sexinal part does not occur, leaving thinner areas, probably to provide elasticity to the body. Such situation exists in the case of striations and the plateae. Although both nexine and sexine layers are present in these regions, the latter does not develop the internal structures and remains a least developed homogeneous layer (Text-fig. 1e, f.).

Sequential pattern of evolution

Talchir—The oldest palynofloras of the Indian Gondwana sediments are known from Talchir Formation (Early Permian in age) described by Lele and Makada (1972), Chandra and Lele (1979) and Lele (1984). It has been established that generally simple horizontal grooves (striations) are present at this level in bisaccate pollen only. The striations are simple mostly unbranched and merging at their ends with the body outline (e.g. *Faunipollenites*, Text-fig. 2B). In the younger horizon within the Talchir itself, one more variation is observed where the ends of striations meet with each other at the terminal side of the body forming a circum-striate pattern (e.g. *Circumstriatites*). In this horizon few monosaccate pollen are also recorded which show reticuloid, tuberculoid type of pattern on body (e.g. *Tuberisaccites*, Text-fig. 2R). Thus, it is concluded that simple striate pattern appeared in Talchir which later on showed only a little variation in disaccate pollen The appearance of monosaccate pollen with reticuloid grooves, or islands of sexine to give rise to a tuberculoid mosaic, is independent of the path of disaccate pollen This level is identified as line of appearance of striations—*a starting plane* (Text-fig. 3a).

Karharbari—In the later part of Early Permian (Karharbari Formation), few pollen with slight diversified variation in characters occur, i.e., the number of striations increases and vertical partitions in between these, at places, start appearing. Few bisaccate pollen having reticuloid-type of striations (e.g. *Rhizomaspora*) also make their appearance. Such forms may have their lineage of origin from monosaccate pollen which bear comparable characters of older horizon, i.e., Talchir Formation These variations take place in gradual pace among the pollen of Early Permian time. The divergence



Text-figure 2—Pattern of variations in striations and taeniae: **A.** Non striate bisaccate pollen (*Platysaccus*); **B.** Simple horizontal striations (*Faunipollenites*); **C.** Bifurcation in horizontal striations (*Striatites*); **D.** Brick-work pattern of striations (*Lahirites*); **E.** Striations on both the faces of central body (*Distriatites*); **F.** Flabbiness of sexine in between striations (*Striatites*); **G.** Reticuloid pattern in bisaccate pollen (*Rhizomaspora*); **H.** Tuberculoid pattern (*Tumeripollenites*); **I.** Faint striations (*Crescentipollenites*); **J.** Two prominent taeniae (*Leuckisporites*); **K.** Taeniae which bear striations (*Lunatisporites*); **L.** Taeniae with platea in between them (*Lunatisporites*); **M.** Non-striate monosaccate pollen (*Parasaccites*); **N.** Simple and bifurcated horizontal striations in monosaccate pollen (*Striomonosaccites*); **O.** Striations on both the faces of central body (*Distriomonosaccites*); **P.** Taeniate monosaccate pollen (*Kamthisaccites*); **Q.** Reticuloid pattern in monosaccate pollen (*Barakarites*); and **R.** Tuberculoid pattern in monosaccate pollen (*Tuberisaccites*).

and proliferation in character under study are foreshadowed at the Karharbari level. The most significant event which took place at Karharbari level is the appearance of vertical partitions and then its manifestation into the reticuloid pattern (Text-fig. 3a).

Barakar—Maximum proliferation in the quantity and quality of striations is found among the disaccate and monosaccate pollen grains of Barakar palynofloras. Hence, this level is identified as *Line of maximum proliferation* where the *stabilizing plane* starts, and preponderance of striate pollen is marked in having all kinds of striation patterns—simple, branched, vertical partitions, brick-work and reticuloid (Tiwari, 1965; Bharadwaj & Tripathi, 1981). Beside these, few monosaccate pollen are also recorded for the first time which bear perfect striations on one of the faces of the body (*Striomonosaccites*, Pl. 1, fig. 12), or even on both the sides (*Distriomonosaccites*, Text-fig. 2 O). One more kind of diversification is observed, i.e., the presence of two structured sexinal bands on body, leaving a wide, unstructured part in between. These sexinal bands are described as taeniae, as in *Lueckisporites*. Thus in the true sense of morphography, the bi-taeniate pollen staged at the Barakar level (Text-fig. 3a).

Kulti—In Kulti Formation of Late Permian, further variations in the kind of striations are not seen. However, an increase in the number of vertical partitions has been noted (Kar, 1968). Such an arrangement leads to the close brick-work pattern which appears as an irregular arrangement on periphery (Text-fig. 3a). In any case, the brick-work pattern is not secondary in origin.

Raniganj—In Raniganj Formation (Late Permian), different diversifications take place, both in bisaccate as well as monosaccate pollen (Text-fig. 3b). These are given below:

(i) Flabbiness of plagae (sexinal bands between striations) transgresses towards the taeniate organisation (Pl. 1, fig. 11).

(ii) Beginning of development of irregular platae (space in between two structured sexinal bands); in other words, striations losing their linear nature and stepping towards the plateation (Pl. 1, fig. 8).

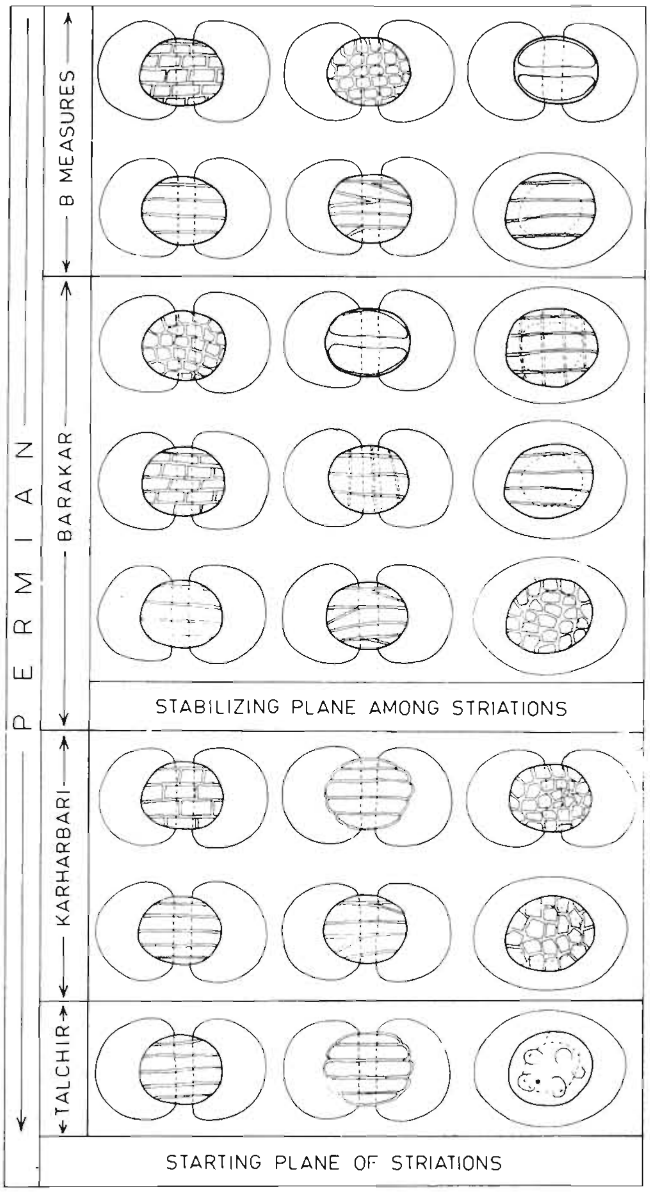
(iii) Existence of faint, incomplete grooves indicating a disappearing phase of striations (Pl. 1, fig. 4).

(iv) Prominent taeniae (sexinal bands) and well-defined platae (irregular unstructured areas in between them) forming taeniate organization (*Lunatisporites, Kamthisaccites*; Pl. 1, figs 10, 13).

(v) Taeniae, which bear striations on them (Pl. 1, fig. 14).

(vi) Tuberculoid pattern developed because of sexinal islands on body (Text-fig. 2R).

Panchet—Early Triassic pollen flora in Panchet

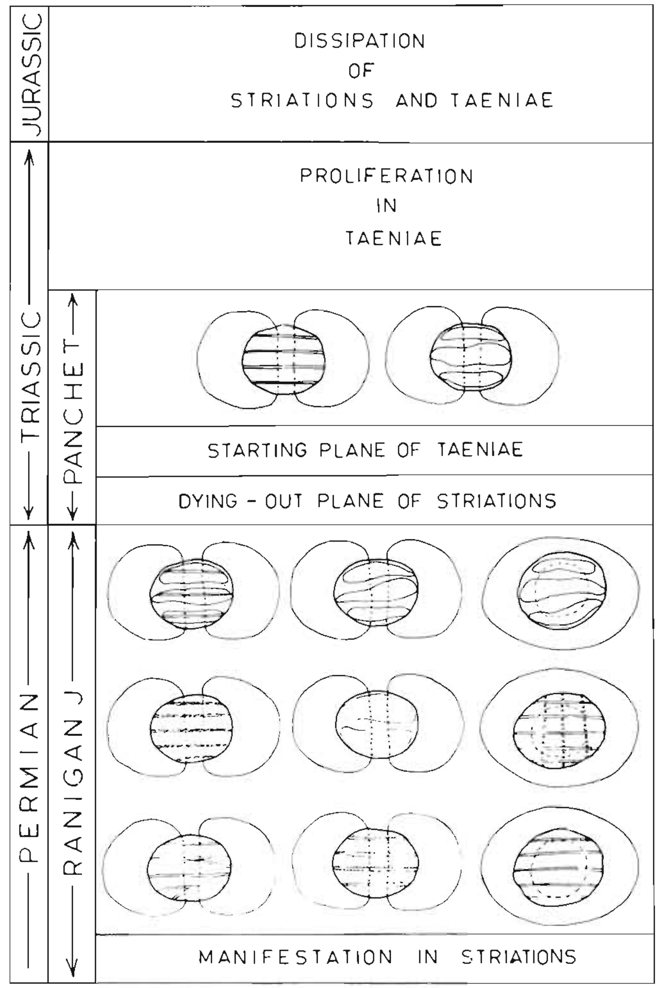


Text-figure 3a

Formation (Maheshwari & Banerji, 1975; Bharadwaj & Tiwari, 1977; Tiwari & Rana, 1980, 1981) opens another chapter in the course of evolution of striations and plateations (Text-fig. 1), as it heralds the era of diversification in nature of taeniae on one hand and declination phase of striations on the other. Therefore, it makes the *Starting plane* of taeniae and *Dying-out plane* for striations (Text-fig. 3b).

Derivations

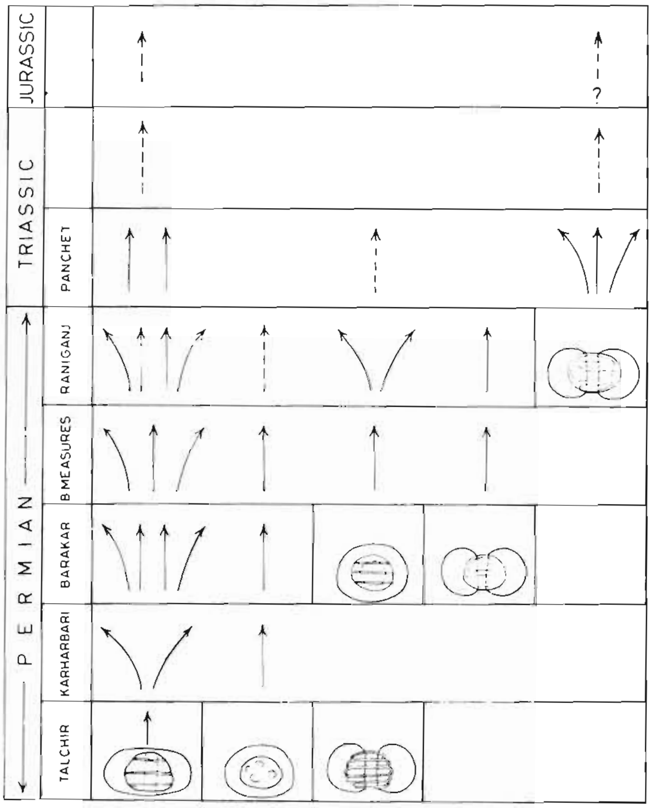
The trends of complexity and paths of variability followed by striations, platae and allied characters (Text-figs 2, 3a, b) in saccate pollen through Gondwana horizons can be summed up (Text-fig. 4) as below:



Text-figure 3b

Text-figure 3 a, b—Relative complexity in nature of striations and taeniae in different palynological assemblages of the Indian Gondwana formations.

1. Few, simple linear horizontal grooves (striations) in bisaccate pollen are recorded within the oldest palynofloras of Early Permian age. Also, bi-taeniate pollen are recorded.
2. Proliferation in quantitative and qualitative nature of striations begins at the level of late Early Permian time (Lower Barakar Palyno-sequence). Such diversification involves increase in number of striations, with bi- or trifurcation, presence of numerous vertical partitions, formation of brick-work, reticuloid pattern and other arrangement.
3. At the level of Late Permian/Early Triassic times, number of vertical partitions between horizontal striations declines. In some cases, striations become faint probably indicating the *dying-out plane* of that character.
4. The multi-taeniate nature scantily appears in the late Late Permian palynofloras but diversifies into several lines of variability in the Early Triassic.



Text-figure 4—Pattern of diversification and proliferation in striations and taeniae through Indian Gondwana formations.

5. Both, the striations and taeniae tend to die out in the Late Triassic, the former precedes the latter. In the Upper Mesozoic almost every line of striation-taeniae character disappears in the saccate pollen.

CLIMATIC RELATIONSHIP

With the accumulation of data for palaeoclimatic inferences in variously related disciplines, viz., lithology, sedimentology and palaeogeography, it is evidenced that the earliest Permian (Talchir) sediments are glacigene in nature. The palynoflora is the simplest and primitive in its diversification which indicates a result of extreme cold climate with low humidity during Early Permian. Such inferences are also supported from the studies conducted by Suttner and Dutta (1986) on mineralogical analysis.

During late Early Permian (Karharbari) the climate ameliorated. Also, an increase in humidity was favourable for producing luxurient vegetation which contributed to the formation of coal. As discussed in preceding pages, at the level in geological sequence, the evolutionary paths of striations initiated several new experiments; the reticuloid pattern, vertical partitions and bifurcation of simple linear grooves made their appearance. This kind of variability seems to be related with the relatively higher humidity and rise in temperature.

With the commencement of late Early Permian time (Lower Barakar), maximum diversification is recorded in the nature of striations, with several lines of manifestations. The acme of qualitative preponderance in striations is exhibited at this level, which persisted throughout the Barakar Formation. Such a state of complexity in striations appears to have a direct relationship with increasing precipitation, temperate climate and moderately warm condition. It is also supported by the studies of Dutta and Suttner (1986) and Tiwari and Tripathi (1988).

During the time of deposition of Kulti Formation (Barren Measures; early Late Permian), the climate had been interpreted to be warm with low to medium humidity (Lele, 1976; Chandra & Chandra, 1988). However, existence of diversified palynoflora does not support dry or arid conditions. The continuity in the complexity of striations from Barakar Formation to Barren Measures can be corroborated with the results of heavy-mineral analysis of these sediments (Kar *et al.*, 1964) which suggests a tropical to subtropical humid climate.

Later part of Late Permian was a warmer period with very high humidity; such a condition is represented through the whole span of Raniganj Formation. However, the decline of temperature and humidity in the upper most Permian is indicated. The reticuloid and brick-work pattern of striations decline during Raniganj. Simple striations with lesser frequency of bifurcations are in prominence. Two new trends have been observed in the nature of these striations at this level (a) vanishing-phase of striations is depicted by the presence of faint grooves on central body, (b) flabbiness of plagae (sexine in between two striations) tending towards taeniate construction.

In Early Triassic time, there are evidences for change in climate, but the desertic or arid conditions were not existing because luxuriant vegetation thrived as implied by the diversified and rich spore-pollen populations. Diminishing trend of striation-complexity and diversification in taeniae characterise the Early Triassic saccate pollen group. The warming up of climate thus appears to be linked with thickening of several strips in the form of taeniae. Recently Suttner and Dutta (1986) on the basis of mineralogical and oxygen isotope studies have inferred that the climate gradually changed to warmer and moderately semi-arid in Upper Panchet with seasonal fluctuations rather than extreme aridity. Abundance of taeniae and their maximum complexity are indicative of severe seasonal fluctuations with drier intervals than those experienced during Late Permian time.

FUNCTIONS

Functions of striations and plateations are still a mystery. Direct attempt to link climate with these characters does not lead to conclusion because similar climatic conditions existed at several different levels of geological period where such characters did not develop. But, if their appearance, dominance and disappearance are taken as events of evolutionary phenomenon in a particular time period, they may have an expression of climate during that span of time.

Appearance, existence and disappearance of striations and taeniae during Permian through Triassic is a global phenomenon. The cause of moisture-content-variability may be attributed to these grooves and furrows, so as to accommodate the shrinkage of exine during the loss of moisture and to save the mother cell from destruction. This factor of harmomegathy might give rise to some similar pattern in exine of pollen grain but the striations and plateations are very regular, well organized and systematic features: the reticuloid pattern, the vertical partitions, the irregularly wide space between thick sexinal strips and an array of other arrangements do not evidence the functionality of these grooves as accommodative safty-valves.

It has also been opined that the striations and the plateae might act as emergency tenuitates for germination (Tiwari, 1982). This appears to be a plausible explanation for their existence because after the shifting of germinal pole, multiple probable sites for germination could prove to be an asset for the cell. However, the striations and plateations are not made up of nexine alone but contain a thin layer of sexine also. Therefore, evidence must be sought for such a proposition. It appears that occurrence of striations and plateations in saccate pollen is nothing but an episode in the course of evolution of organisation with several paths of experimentation in nature for the search of fittest situation during the Permian and Triassic times. In any case they are not without mechanism meaning—they could play a role of exine protector, providing volume compensation, germination gates, or moisture regulators.

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