BIOMETRIC RESOLUTION OF *PLICATIPOLLENITES* AND *POTONIEISPORITES* IN THE LOWER GONDWANA SUCCESSION OF INDIA

K. M. LELE & MANOJ SHUKLA

Birbal Sahni Institute of Palaeobotany, Lucknow-226007, India

ABSTRACT

Plicatipollenites and *Potonieisporites* can be distinguished by a new criteria, viz., the " Distal saccus spread ". Accordingly, *Plicatipollenites* belongs to the " Monosaccate group " characterized by " Uniform saccus spread " and *Potonieisporites* to the " Monosaccoid group " having " Differential saccus spread ".

The morphological variation in the two populations has been resolved through a multivariate analysis in time and space, covering the Talchir, Karharbari and Barakar span in five Lower Gondwana basins. Suitable ' norms ' were selected in the two populations for analysing four parameters of variation, viz. (i) Miospore symmetry, (ii) Tetrad mark, (iii) Body infold symmetry, and (iv) Body symmetry.

With the exception of body symmetry parameter, all other variables show direct correlation in their specific trends. The results demonstrate that the Monosaccate group (*Plicatipollenites* population) is characterized by a strong association between radial miospores, trilete/triletoid mark and radial body infold system. The whole group indicates a downward trend in time (regression). Contrarily, the monosaccoid group (*Potonieisporites* population) is characterized by a strong association between bilateral miospores, monolete/monoletoid mark and bilateral infold system. The group indicates evolutionary progression and an upward rise in time.

The evolutionary aspects of the two populations have been discussed. The relative shift in the frequencies of the norms from *Plicatipollenites* to *Potonieisporites* across Talchir to Barakar times provides a means for broad biostratigraphical zonation.

INTRODUCTION

PLICATIPOLLENITES Lele, 1964 and *Potonieisporites* Bharadwaj, 1954 emend. 1964 are among the most characteristic miospore taxa of the Lower Permian succession in India. They are widely distributed in all the major coal basins. Both genera occur abundantly in the Talchir and Karharbari formations and persist in the succeeding Barakar Formation. Records from Barren Measure and Raniganj are very meagre. *Potonieisporites* was originally designated for monolete pollen grains found in the Upper Carboniferous of Saar Basin (West Germany). The pollen of *Lebachia*, which is similar to *Potonieisporites*, also bears a monolete or slightly bent monolete mark (Bharadwaj, 1964a). Subsequently, the taxon has been widely used for Gondwana miospores which often show several modifications of the tetrad mark ranging from monolete to trilete (Potonié & Lele, 1961; Maheshwari, 1967). In the case of *Plicatipollenites* (which was segregated from *Nuskoisporites*), a similar transition from trilete to monolete has commonly been observed (Potonié & Lele, 1961; Lele, 1964, 1974). This variability has led workers to believe that there is some intergradation between *Plicatipollenites* and *Potonieisporites*. Obviously, the identification of border-line specimens has often been quite arbitrary.

While reviewing the Lower Gondwana monosaccates, Lele (1974) elaborated the morphological variation trends between *Plicatipollenites* and *Potonieisporites* and expressed the need to ascertain the morphological relationship of the two genera in space and time through biometric analysis. An objective resolution of the southern *Plicatipollenites-Potonieisporites* complex is further necessitated in view of a similar intergradation known between *Nuskoisporites* and *Potonieisporites* of the northern hemisphere (Nygreen & Bourn, 1967).

It should be remarked that the southern *Plicatipollenites* is distinct from the northern *Nuskoisporites* and in the present analysis the original diagnosis of *Plicatipollenites* (Lele, 1964) is by and large utilized, although this genus is now more precisely understood in the light of biometric data. As to *Potonieisporites* we are not quite sure whether the southern (Gondwana) *Potonieisporites* represents the same morphology as the northern type. Parent plants of *Potonieisporites* are also unknown from the Gondwana. We feel that the original diagnosis of *Potonieisporites* is worthy of consideration because according to that concept the saccus organization of *Potonieisporites* approaches close to that of *Nuskoisporites*. However, in the present treatment we have used the emended diagnosis of *Potonieisporites* (Bharadwaj, 1964) as it answers well the morphographic features of the southern forms in particular. The whole question of *Potonieisporites* taxonomy is obviously a comprehensive problem which can be best resolved by critically studying both northern and southern forms of the genus.

Biometric analysis of *Plicatipollenites-Potonieisporites* complex has been carried out in five different Lower Gondwana basins through the succession ranging from the Talchir to the Lower Barakar Formation. The study was undertaken with the following objectives:

1. To find out some qualitative morphological criteria capable of clearly demarcating *Plicatipollenites* from *Potonieisporites*.

2. To biometrically analyse, in space and time, the variation trends in the whole population plexus and to allocate the variation spread for *Plicatipollenites* and *Potonieisporites* in order to delimit the taxa more precisely.

3. To evaluate the evolutionary implications of the morphological trends in the two lineages.

4. To assess the distribution of *Plicatipollenites* and *Potonieisporites* in time for broad biostratigraphical zonation.

MATERIAL AND METHOD

Material for this study was selected from well-dated sediments of the Talchir, Karharbari and Barakar formations from five coalfields. The Talchir sediments are silt shales while in the younger formations the shales are carbonaceous. The biometric study has provided substantial amount of objective data on the morphographic variations and evolutionary trends of *Plicatipollenites* and *Potonieisporites* both in space and time. Besides, in one basin two complete sections — exposing Talchir to Barakar sequence — were also analysed to examine intra-basinal variations of these taxa.

Details of samples from different coalfields are as follows:

COALFIELD	FORMATIONS	LOCALITY	MATERIAL
Johilla	Upper Karharbari	Ganjra Nala	Lele & Maithy, 1969
	Talchir	Goraia Village	Potonié & Lele, 1961
Jayanti	Lower Barakar	Near Misra Village	
	Talchir	Patharjore Nala	Lele & Makada, 1972
Giridih	Lower Karharbari	Serampur pit	Maithy, 1965
	Talchir	Suknid River	Surange & Lele, 1956
Hutar	Lower Karharbari	Deori Nala	
	Talchir	Deori Nala	
Hutar	Upper Barakar	Koel River	
	Lower Karharbari	Koel River	
	Talchir	Koel River	
North-Karanpura	Lower Barakar	K.B. 21 Drill core	Kar, 1973
	Upper Karhararbi	K.B. 21 Drill core	Kar, 1973
	Lower Karharbari	K.B. 21 Drill core	Kar, 1973

For biometric analysis, a number of variables were selected which are common to *Plicatipollenites* and *Potonieisporites* and which show transition from one to the other genus.

The variables were evaluated quantitatively through measurements under the microscope. Random sampling procedure (as in case of blood counts) consisted of scanning the miospore specimens over the slide along a continuous path (left to right from one edge of the coverslip to other). Hundred specimens, each from the Talchir, Karharbari and Barakar samples of the five coalfields were counted in this manner. In all 600 specimens were counted for the Talchir Formation, 500 for the Karharbari

Formation and 300 for the Barakar Formation. This gives a grand total of 1400 counts (sample size). The data were carefully recorded on predesigned cards and tabulated in a master chart (Table 1). On completion of cards, the data were mathematically worked out for obtaining mean percentage frequencies of selected variables in time and space. The trends of variation were plotted graphically as Time Series. Histograms and scatter diagrams were also prepared to examine and clarify the correlative aspects of variation patterns but these are not presented in the paper.

SACCUS SPREAD — A NEW CRITERIA AND ITS APPLICATION

Plicatipollenites and *Potonieisporites* are well known to differ in their overall spore symmetry and tetrad mark. However,

TABLE 1 — PERCENTAGE DISTRIBUTION OF *PLICATIPOLLENITES* AND *POTONIEISPORITES* NORMS AND THEIR VARIATION CHARACTERS THROUGH TIME IN FIVE LOWER GONDWANA BASINS

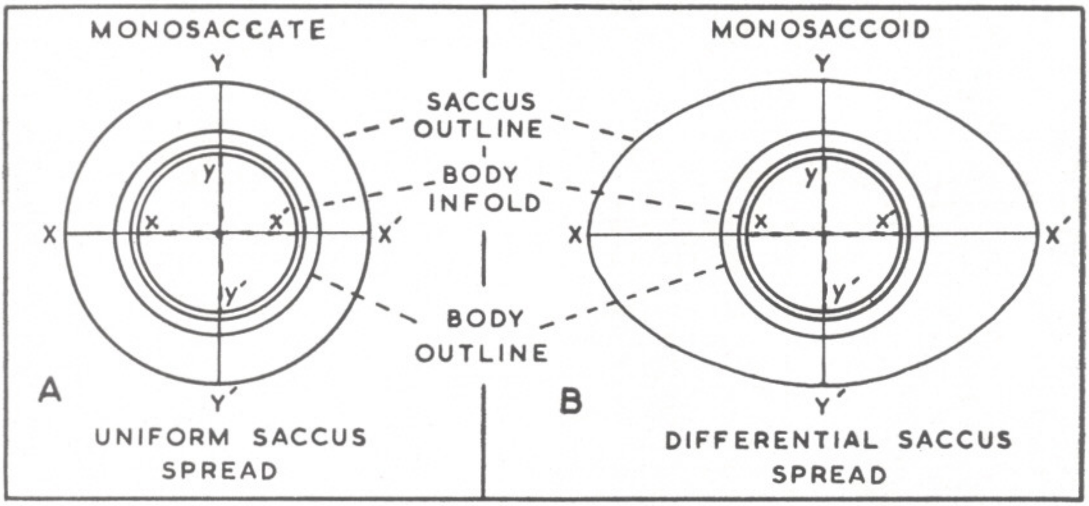
	Norms	Basins / Formations / Tetrad Mark	South Rewa		Jayanti		Giridih		North-Karanpura			Hutar (Deori Nala)		Hutar (Koel River)		
			T	U.K.	T	B	T	L.K.	L.K.	U.K.	B	T	L.K.	T	L.K.	B
			22	18	34	11	21	24	26	23	16	27	24	16	10	2
PLICATIPOLLENITES	A₁	Normal Trilete	5	12	19	7	9	17	12	16	12	15	14	10	10	×
		Triletoid	16	5	14	4	12	6	14	7	4	12	9	6	×	2
		Bilete	1	1	1	×	×	1	×	×	×	×	×	×	×	×
		Monolete	×	×	×	×	×	×	×	×	×	×	1	×	×	×
	A₂		30	20	28	11	27	44	26	26	12	26	32	44	22	8
		Normal Trilete	×	5	3	1	7	9	2	7	×	6	1	8	6	×
		Triletoid	13	1	5	1	7	12	4	5	×	5	8	2	1	×
		Monoletoid	17	13	17	8	10	22	16	12	12	14	21	28	12	8
		Bilete	×	×	×	×	2	×	×	1	×	1	2	×	2	×
		Monolete	×	1	3	1	1	1	4	1	×	×	×	6	×	×
...	...	...	...		...		...		...		...	...	...	...		...
POTONIEISPORITES	B₁		14	24	10	20	15	9	24	20	6	17	13	28	38	12
		Normal Trilete	1	5	×	4	×	1	2	1	2	5	×	4	10	×
		Triletoid	×	2	3	3	×	×	4	1	2	2	3	12	4	×
		Monoletoid	12	9	6	9	12	7	12	13	2	10	7	12	18	6
		Bilete	1	3	×	3	×	1	×	1	×	×	1	×	×	×
		Monolete	×	5	1	1	3	×	6	4	×	×	2	×	6	6
	B₂		15	12	9	18	12	5	8	8	8	18	8	4	16	24
		Normal Trilete	1	1	3	1	1	1	×	2	×	3	×	2	2	×
		Triletoid	2	×	1	4	×	×	2	×	×	×	×	2	4	×
		Monoletoid	9	5	5	7	8	2	6	2	2	12	5	×	6	10
		Bilete	1	×	×	1	×	×	×	1	2	2	×	×	2	4
		Monolete	2	6	×	5	3	2	×	3	4	1	3	×	2	10
	B₃		13	22	13	38	16	12	8	20	56	7	17	6	12	50
		Normal Trilete	×	×	2	4	2	3	×	1	2	×	×	2	×	×
		Triletoid	×	×	2	×	1	×	×	×	×	2	×	×	×	×
		Monoletoid	7	12	3	12	8	4	6	9	22	2	8	4	4	18
		Bilete	1	1	×	8	2	1	×	2	12	1	3	×	2	8
		Monolete	5	9	6	14	3	4	2	8	20	2	6	×	6	24
	B₄		6	4	6	2	9	6	8	3	2	5	6	2	2	4
		Normal Trilete	2	2	×	1	2	3	2	1	2	3	×	×	2	×
		Triletoid	4	2	5	×	7	3	4	2	×	2	5	2	×	4
		Bilete	×	×	1	1	×	×	×	×	×	×	×	×	×	×
		Monolete	×	×	×	×	×	×	2	×	×	×	1	×	×	×

T = Talchir, U.K. = Upper Karharbari, L.K. = Lower Karharbari, B = Barakar.

as both characters are intergrading, they are not helpful in setting clear-cut taxonomic limits between the two genera. From the present extensive study it has been possible to discern one morphographic quality which is mutually exclusive to the *Plicatipollenites* and *Potonieisporites* populations. This criteria is here designated as the 'Distal saccus spread', i.e. the extent of saccus from the body infold system along the two axes of the grain. In our opinion the body infold system is a consistent character of high morphographic-evolutionary significance as it is intimately related to the distal zone of saccus (sexine) separation and also circumscribes what may be the tenuitas or germinal area (Potonié & Lele, 1961; Lele, 1964; Bharadwaj, 1964a, 1974). A striking correlation between the symmetry pattern trends of the body infold and the spore shape has been observed across time. It reflects progressive evolution of the monosaccus (i.e. of the 'Saccus spread' in other words) to attain a nearly bisaccate condition (discussed later, p. 228). We are, therefore, inclined to place considerable emphasis on the distal body infold (rather than the body outline) as a reference line for determining the saccus spread in the genera *Plicatipollenites* and *Potonieisporites*.

Careful observation of hundreds of spores has revealed that in *Plicatipollenites* the saccus generally spreads out from the body infold in a more or less uniform manner along the two axes (Text-fig. 1A). This feature is here recognized as "Uniform saccus spread". Contrarily, in *Potonieisporites* the saccus spreads out in a differential manner along the two axes (Text-fig. 1B). This feature is distinguished as "Differential saccus spread". If we look into the cause, it will be seen that the saccus spread is actually the result of the interplay of two factors: (i) the symmetry of the body infold wherefrom the saccus separates and spreads out, and (ii) the symmetry of the spore (outline). In the present study we have worked out the symmetry of the body infold and the spore in terms of ratios. The difference of these two ratios directly gives the measure or value of the "Saccus spread" (Text-fig. 1).

Although the saccus spread is a continuous variable, it is possible to draw a limit which can define the subjective demarcation of "Uniform saccus spread" from "Differential saccus spread". This saccus spread limit is found to be best set at the zero value. We have found that spores with a



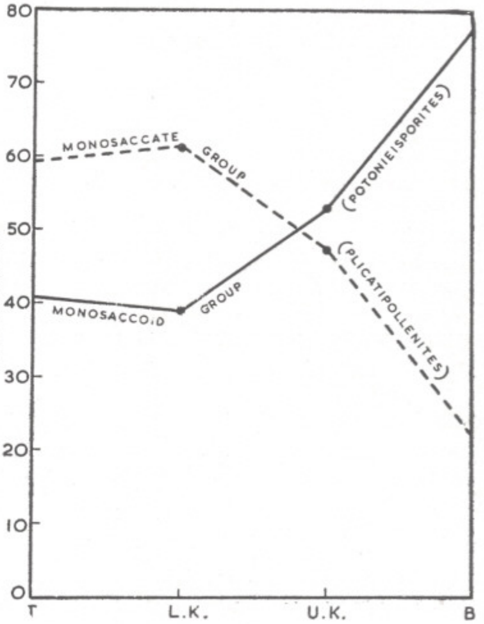
TEXT-FIG. 1 — Elucidation of the criteria of 'Uniform Saccus spread' **(A)** and 'Differential saccus spread' **(B)** which distinguish the Monosaccate and Monosaccoid groups respectively. XX'/YY' = Spore circularity ratio, xx'/yy' = Body infold circularity ratio. The difference of the two ratios gives the saccus spread value.

saccus spread value of zero or below zero (negative) have a more or less uniform saccus spread. Where the saccus spread value exceeds zero, the spore begins to show a differential saccus spread.

Thus, the zero limit of the saccus spread value provides a plausible basis for distinguishing two major groups (Text-fig. 1): (i) the Monosaccate group characterized by " Uniform saccus spread " (value zero or below zero), and (ii) the Monosaccoid group characterized by " Differential saccus spread" (value more than zero). There are two other strong reasons for supporting the two groups.

1. The distribution pattern of the monosaccate and monosaccoid groups in the total population complex (Text-fig. 2) shows clearly that the two groups have very distinct and inverse trends of distribution in time. The monosaccates go downward while the monosaccoids rise upward.

2. The monosaccate group largely conforms with the population represented by *Plicatipollenites* as originally diagnosed by Lele (1964). The new emphasis on saccus spread measurement would further clarify the identification of the taxon. The monosaccoid group largely corresponds to the population represented by *Potonieisporites* as emended by Bharadwaj (1964).



TEXT-FIG. 2 — Distribution trend of Monosaccate and Monosaccoid groups in time. **T** = Talchir stage, **L.K.** = Lower Karharbari stage, **U. K.** = Upper Karharbari stage, **B** = Barakar stage.

We are, therefore, inclined to consider that *Plicatipollenites* and *Potonieisporites* represent two populations. The saccus spread criteria is found to serve as a good basis for differentiating the two genera. From the graph in Text-fig. 2 it can be further observed that the two evolutionary lineages run more or less parallel as far as the Lower Karharbari, during which time there is also a maximum reflection of morphological transitions between the two groups. Segregation and stabilization of morphology appears to have been eventually achieved by the Karharbari-Barakar transition beyond which there is a striking fall in the *Plicatipollenites* population and a concomitant rise in the *Potonieisporites* population. This evidence points out that the monosaccoid organization (by virtue of the differential saccus spread) was more evolved than the monosaccate organization (i.e. uniform saccus spread).

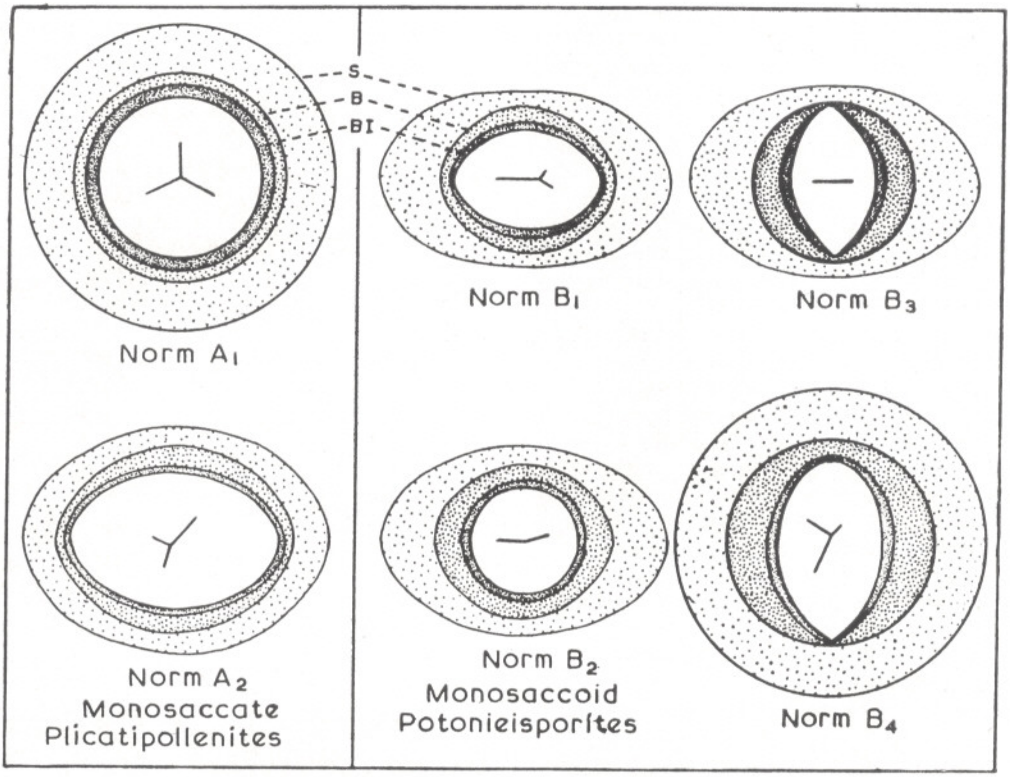
In order to confirm the above contentions, the two populations were critically analysed by biometric methods. For analytical practice and application of qualitative and quantitative values, the populations of *Plicatipollenites* and *Potonieisporites* were further divided into a number of morphographic categories or ' Norms ' which are defined below.

It may be noted that the various norms are based primarily on symmetry rather than on shape pattern, and they can be clearly identified by morphometric criteria set forth. Reasonable allowance in morphometric limits is given so as to reconcile with observational conceptions. The limit between Norm A_2 and Norm B_1 is particularly significant as it also demarcates the monosaccate group (*Plicatipollenites*) from the monosaccoid (*Potonieisporites*). In view of the subtle nature of this limit a diagram (originally made on mm graph) is especially given to ellucidate the morphometric demarcation between Norm A_1 and B_2 (Text-fig. 4).

Plicatipollenites Population

Text-fig. 3

Norm A_1 (Pl. 1, fig. 1) — Characterized by radial symmetry of miospore and uniform saccus spread.



TEXT-FIG. 3 — Norms of *Plicatipollenites* and *Potonieisporites*. **S** = Saccus, **B** = Body, **BI** = Body infold.

Spore circularity ratio 1 ± 0·1.
Saccus spread value 0 ± 0·1.

Norm A_2 (Pl. 1, figs. 2, 3) — Characterized by bilateral symmetry of miospore and uniform saccus spread.
Spore circularity ratio more than 1·1.
Body infold circularity ratio more than 1·1.
Saccus spread value zero or less (negative value).

Potonieisporites Population

Text-fig. 3

Norm B_1 (Pl. 1, fig. 4) — Characterized by bilateral symmetry of miospore and differential saccus spread. Body infold bilateral and horizontally orientated, i.e. its longer axis (x) is parallel to the longer axis of the grain (X).
Spore circularity ratio more than 1·1.
Body infold circularity ratio more than 1·1 *but less than spore circularity ratio. Hence the saccus spread value is always positive.*

Norm B_2 (Pl. 1, fig. 5) — Characterized by bilateral symmetry of miospore and differential saccus spread. Body infold radial.
Spore circularity ratio more than 1·1.
Body infold circularity ratio 1 ± 0·1.
Saccus spread value more than 0·1.

Norm B_3 (Pl. 1, fig. 6) — Characterized by bilateral symmetry of miospore and differential saccus spread. Body infold bilateral and vertically orientated, i.e. its longer axis (x) is at right angles to the longer axis of the grain (X).
Spore circularity ratio more than 1·1.
Body infold circularity ratio less than 0·9.
Saccus spread value more than 0·1.

Norm B_4 (Pl. 1, fig. 7) — Characterized by radial symmetry of miospore and differential saccus spread. Body infold bilateral and vertically orientated as in Norm B_3.

Spore circularity ratio $1 \pm 0{\cdot}1$.

Body infold circularity ratio less than 0·9.

Saccus spread value more than 0·1.

EVALUATION OF VARIABILITY AND EVOLUTIONARY TRENDS

Four morphographic characters, viz., Miospore symmetry; Tetrad mark polymorphism; Body infold symmetry; and Body symmetry, which show continuous variation between the *Plicatipollenites* and *Potonieisporites* populations, were chosen for the multivariate analysis.

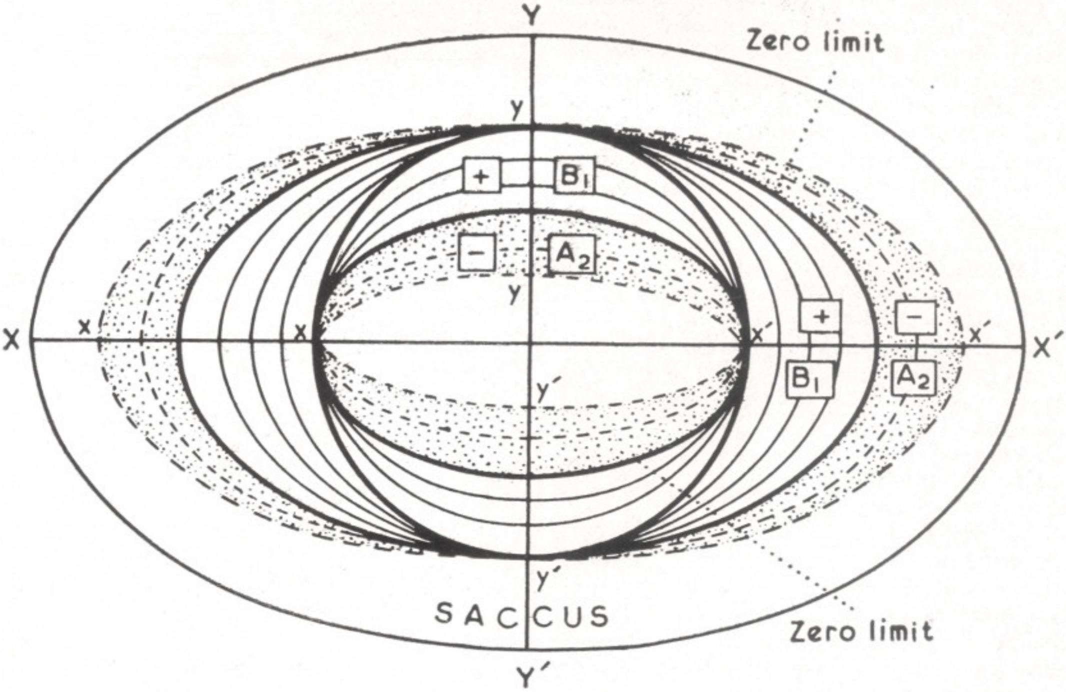
For the evaluation of the variation patterns in time and space and for a reasonable interpretation of the underlying microevolutionary changes, the following simple and practicable procedure was followed.

1. The general trends of the four variables were plotted along the time parameter for the *Plicatipollenites* and *Potonieisporites* populations (without regard to the norms). This general trend is called "Parametral trend" in the following account.

2. Trends of the four variables were plotted for the *Plicatipollenites* and *Potonieisporites* populations at the level of the individual 'Norms'. This is called the 'Norm trend'. By combining one or more Norm Trends, it was possible to evaluate the partial or total trend of a population.

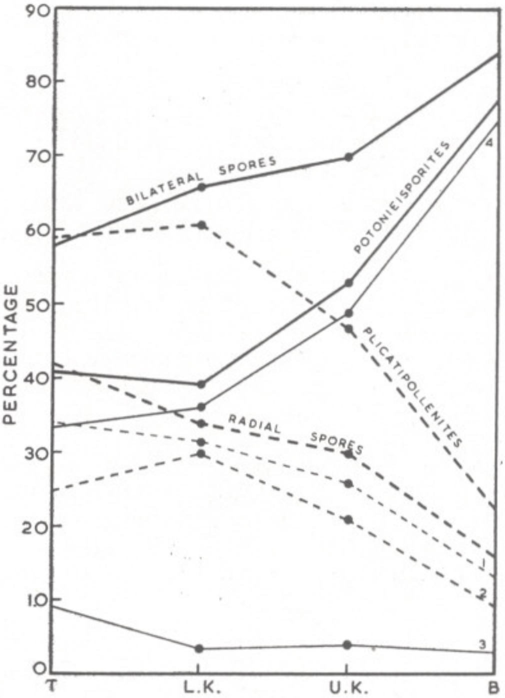
3. Simple graphical method is used for plotting the variation trends in a Time Series. The plots consist of mean percentages of the various Norms in time and space from the five Lower Gondwana basins (Table 1).

4. Interpretation of results is based on correlation between Parametral trends and Norm/Population trends of the four variables. Complementary trends in the four



TEXT-FIG. 4 — Elucidation of morphometric limits between Norm A_2 (*Plicatipollenites*) and Norm B_2 (*Potonieisporites*). The figure was originally drawn on mm graph for accuracy of ratio values. The zero limit represents the two situations (with reference to the two axes) where the saccus spread value is zero. On one side of the zero-limit is the white area where the saccus spread value is positive as characteristic of Norm B_1; on the other side is the stippled area where the saccus spread value is negative as characteristic of Norm A_2. Continuous and dotted oval lines represent situations of body infolds within these areas. XX′ and YY′ are long and short axes of spore. For body infold the corresponding axes are xx′ and yy′.

variables are sorted out to form homogeneous sets characterizing the two populations.



TEXT-FIG. 5 — Distribution trends of miospore symmetry in time. **1,** *Plicatipollenites*, radial (Norm A_1). **2,** *Plicatipollenites*, bilateral (Norm A_2). **3,** *Potonieisporites*, radial (Norm B_4). **4,** *Potonieisporites*, bilateral (Norms, $B_1+B_2+B_3$).

MIOSPORE SYMMETRY

The genera *Plicatipollenites* and *Potonieisporites* include perfectly circular to roundly triangular (radial) and oval (bilateral) spores. The (i) radial, or (ii) bilateral character of the spore symmetry is here determined by the ratio called " Spore circularity ratio". Spore circularity ratio, i.e.

$$\left(\frac{X}{Y}\right) = \frac{\text{Longer axis of spore, i.e. X-axis}}{\text{Axis at right angle to longer axis, i.e. Y-axis}}$$

In perfectly circular and roundly triangular forms (radial) the spore circularity ratio $\left(\frac{X}{Y}\right)$ is 1 because both the axes are identical and equal in length. In oval forms (bilateral) the two axes are unequal and, therefore, distinguishable into a longer axis (X) and a shorter axis (Y) which is at right angles to the X-axis. In actual practice, however, many circular spores appear somewhat subcircular due to oblique compression or other preservation factors. To accommodate such cases and also in view of the microscope resolution error, a reasonable latitude of $\pm 0{\cdot}1$ is allowed to the circularity ratio of radial spores. Spores whose circularity ratio $\left(\frac{X}{Y}\right)$ exceeds 1·1 are evidently considered bilateral. Thus in the variation analysis, the spore symmetry parameter dichotomises into two components, viz. (i) Radial, and (ii) Bilateral. The same holds good for other symmetry parameters (viz., body-infold and body) discussed later.

Evaluation — An assessment of the spore circularity parametral trend shows that the mean spore circularity in the Talchir is 1·16. It increases to 1·24 towards the Karharbari and further rises to 1·3 in the Barakar. In other words it means that bilateral spores have increased in time. This fact is better elucidated by the distribution patterns of radial and bilateral spores; the former shows a downward trend and the latter an upward trend (Text-fig. 5). By further comparison, it will be observed that the trend of *Plicatipollenites* population (Norms A_1 & A_2, individually or combined) closely corresponds with the radial spore-symmetry trend (parametral) while the *Potonieisporites* population trend (Norms B_1 to B_4) is correlatable with the bilateral spore-symmetry trend (parametral). It is also noteworthy that the rise of the *Potonieisporites* population is attributable chiefly to bilateral forms; the radial *Potonieisporites* is minor and shows a declining trend like *Plicatipollenites*.

It is evident from the above analysis that radial symmetry in spores is replaced by bilateral symmetry in course of evolution. This is apparently linked with the successive decline of the whole *Plicatipollenites* population and the progressive proliferation of the *Potonieisporites* population.

TETRAD MARK

Trilete or monolete mark is determined primarily by the tetrad organization: tetrahedral or tetragonal. In the *Plicatipollenites-Potonieisporites* plexus, a considerable intergradation between trilete to monolete has been noticed (Potonié & Lele, 1961; Lele, 1964, 1974; Maheshwari, 1967). A recognizable proportion of specimens do not show any mark at all which may be due to terratological reasons (Wilson, 1965). No definite statistics was so far available on the polymorphism of tetrad mark in the *Plicatipollenites-Potonieisporites* complex.

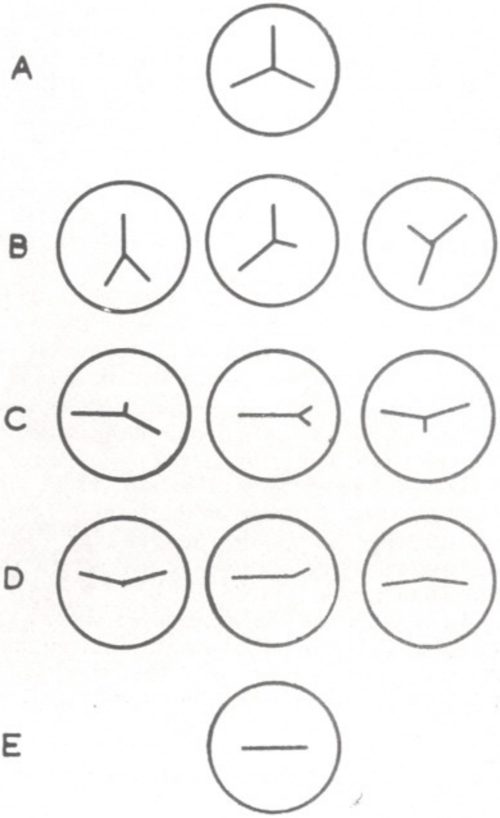
Intermediate stages in tetrad mark development may conceivably result from a gradual shift between tetrahedral and tetragonal tetrad conditions (Staplin *et al.*, 1967; Lele, 1974). It is also known that artificial separation of the tetrahedral tetrad of *Dacrydium taxifolium* yielded monolete to bilete marks on the developing spores (Visscher, 1971). However, it is nearly impossible to test this phenomenon in fossil spores. The best that could be done in the plexus of *Plicatipollenites* and *Potonieisporites* was to decipher the trend of tetrad polymorphism in as much detail as possible so that the two populations could be identified.

In the present study, therefore, it was planned to discriminate the variability of the tetrad mark by as close measurements as possible. For this purpose, the following four main categories of the polymorphic tetrad mark were recognized.

1. *Trilete Mark* (Text-fig. 6A) — Where all the three rays are equal in length and angles between them are also equal.

2. *Triletoid Mark* (Text-fig. 6B) — Where one or more rays of the trilete mark are unequal and/or the inter-ray angles are unequal. Such an asymmetrical mark is called 'Triletoid' as long as the three ray components can be detected and the longer rays or the largest inter-ray angle show no preferential orientation with reference to the X-axis.

3. *Monoletoid Mark* (Text-fig. 6C, D) — A monoletoid mark is one where the longest ray lies nearly parallel to the X-axis of the grain and/or the largest inter-ray angle forms along the X-axis. Sometimes two longer rays may meet at widest angle and tend to lie nearly parallel to the X-axis. The third ray is dwarfed or totally suppressed. In the latter case, the mark is recognized as 'bilete' (Text-fig. 6D). The monoletoid mark is also asymmetrical like the triletoid mark but it is essentially distinguishable by the preferential orientation of its ray components or widest inter-ray angle along the X-axis which links it with the monoletoid tendency.



TEXT-FIG. 6 — Categories of tetrad mark. **A**, Trilete. **B**, Triletoid. **C**, Monoletoid. **D**, Bilete. **E**, Monolete.

The triletoid mark, monoletoid mark and bilete are morphological gradations between the normal trilete and the monolete. In view of the possible bearing of these gradations on the tetrad condition of *Plicatipollenites* or *Potonieisporites* it was felt necessary to critically evaluate these grades in radial and bilateral spores both in space and time.

In the bilateral spores, where the two axes were available for reference, the asymmetrical mark could be further analysed by following scrutiny: (i) longest ray parallel to long axis of grain (X-axis), (ii) longest ray parallel to short axis of grain (Y-axis), (iii) shortest ray parallel to X-axis, (iv) shortest ray parallel to Y-axis, and (v) both rays (in bilete) oblique to axes.

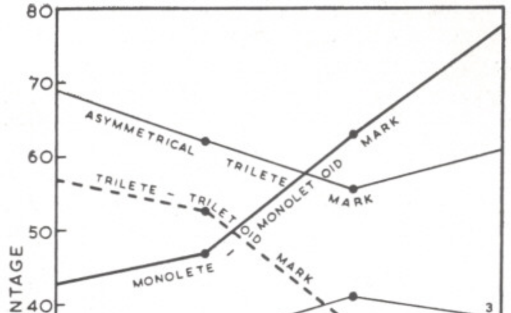
Similarly, the variation of the inter-ray angles was analysed under four heads, viz.

(i) all angles equal, (ii) widest angle along X-axis of grain, (iii) widest angle along Y-axis, and (iv) widest angle oblique to axes.

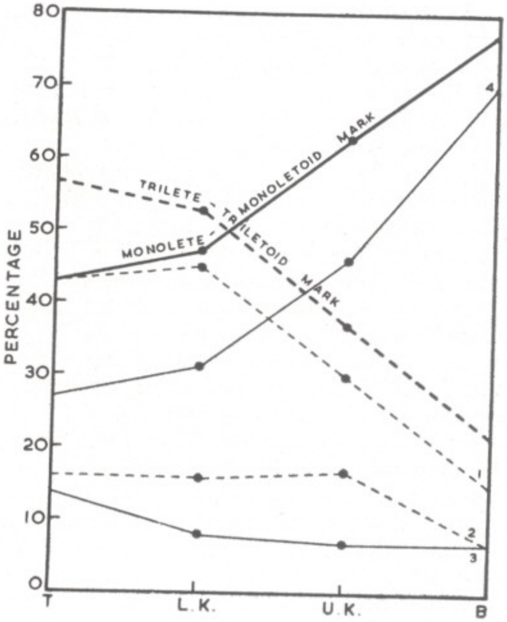
4. *Monolete Mark* (Text-fig. 6E) — Where the tetrad mark is a single straight suture, extending parallel to the longer axis of grain (X-axis), if bilateral.

Evaluation — The parametral variation trend of the tetrad mark reveals (Text-fig. 7) that the normal trilete mark is well represented by 25% spores in the Talchir and the frequency slowly rises up to 27% in the Karharbari; but beyond this, i.e. in the Barakar, there is a rather steep decline (12%) in the incidence of the normal trilete mark. Quite contrary to this, the incidence of normal monolete is rather low in the Talchir (6%) but progressively increases during the Karharbari (18%) and beyond this there is a sharp and rather abrupt rise (27%) in the Barakar. Evidently, the trilete trend is inverse to the monolete trend.

As regards the distribution of the asymmetrical tetrad mark, the results are equally interesting (Text-fig. 7). On the whole the asymmetrical tetrad mark outnumbers the trilete as well as the monolete mark at any time plane. Spores with asymmetrical mark show highest frequency in the Talchir (69%). They suggest a decline during the Karharbari (62-56%) but regain stabilization in the Barakar (61%).



TEXT-FIG. 7 — Distribution trends of tetrad mark categories in time. **1,** Trilete. **2,** Triletoid. **3,** Monoletoid. **4,** Bilete. **5,** Monolete.



TEXT-FIG. 8 — Distribution trends (parametral) of Trilete-triletoid set and Monolete-monoletoid set in time (thick lines) and their correlation with *Plicatipollenites* and *Potonieisporites* trends (Thin lines). **1,** *Plicatipollenites*, trilete-triletoid. **2,** *Plicatipollenites*, monolete-monoletoid. **3,** *Potonieisporites*, trilete-triletoid. **4,** *Potonieisporites*, monolete-monoletoid.

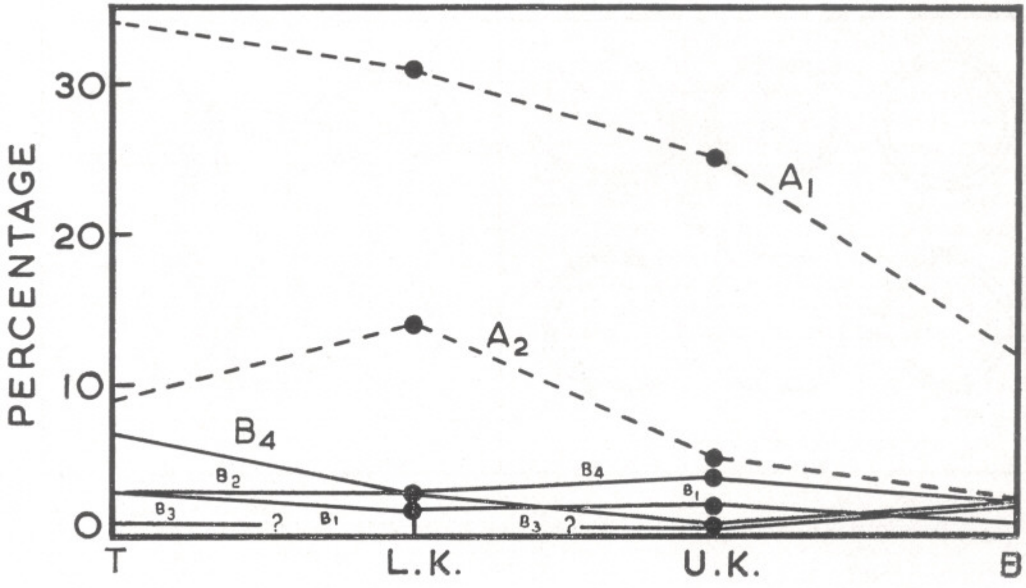
Among the three different categories of the asymmetrical mark, it is observed that triletoid mark registers a progressive decline in time from Talchir onward, and in this behaviour it may be matched with the normal trilete trend. The trilete and triletoid trends can, therefore, be combined to form one set which brings out the downward trend quite clearly (Text-fig. 7). In the same way, the more or less upward trends of the monoletoid mark and the bilete mark can be combined with the normal monolete mark to form another set which brings out a clear upward trend.

By further comparison (Text-fig. 8) it will be clear that the trilete-triletoid trend of the *Plicatipollenites* population is compatible with the trilete-triletoid parametral trend. The dominance of normal trilete and the near absence of monolete in the radial forms of *Plicatipollenites* (Norm A_1) is particularly notable (Text-figs. 9, 10; Table 1). Monoletoid/monolete tendency finds some expression in the bilateral forms of *Plicatipollenites* but on the whole this tendency wanes out in time (Text-fig. 10). On the contrary, the monolete-monoletoid trend of the *Potonieisporites* population is closely complementary to the monolete-monoletoid parametral trend. There is a somewhat time-proportionate shift in the rise of the norms B_1, B_2 and B_3 which indicates progressive establishment of the monolete (Text-fig. 10). Concommitant with this the trilete/triletoid tendency in *Potonieisporites* falls down in time (Text-fig. 9).

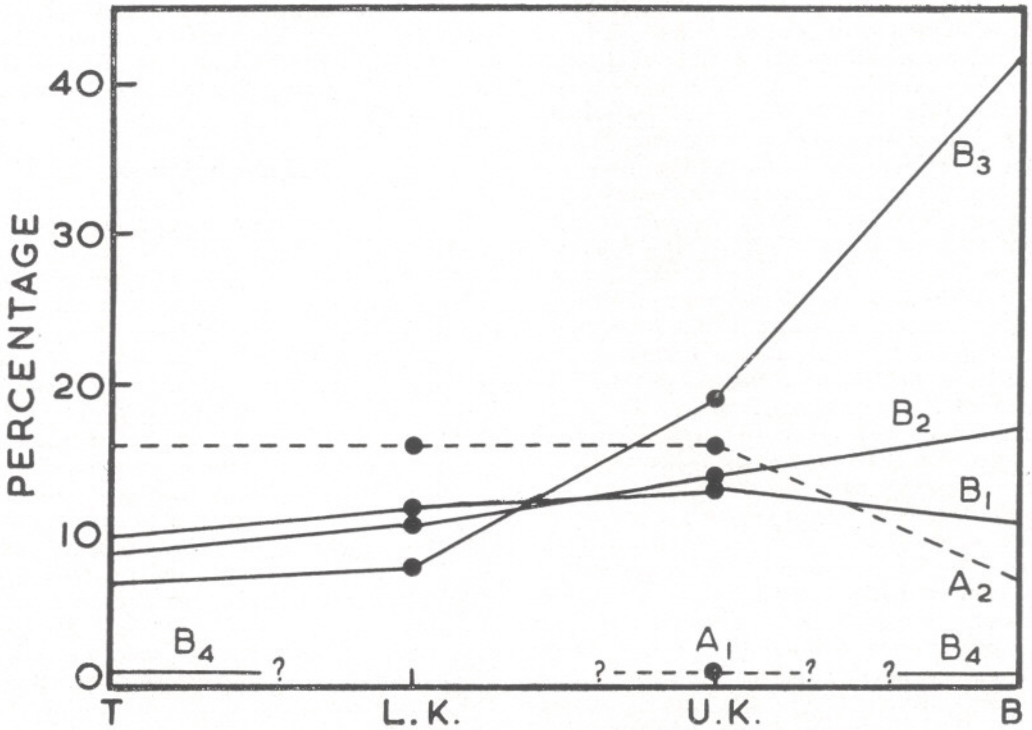
The trends of tetrad polymorphism in the two populations are evidently distinguishable. In *Plicatipollenites* the normal trilete appears to have a crucial role. Any evolutionary modifications toward monolete are apparently not sustained in time by the *Plicatipollenites* population and the whole group eventually suffers a decline. Contrarily, in the progressive *Potonieisporites* populations there is a strong bias for the monolete mark which is ultimately established in time. The present study thus confirms the contention that *Plicatipollenites* is essentially a trilete taxon while *Potonieisporites* is monolete.

BODY INFOLD SYSTEM

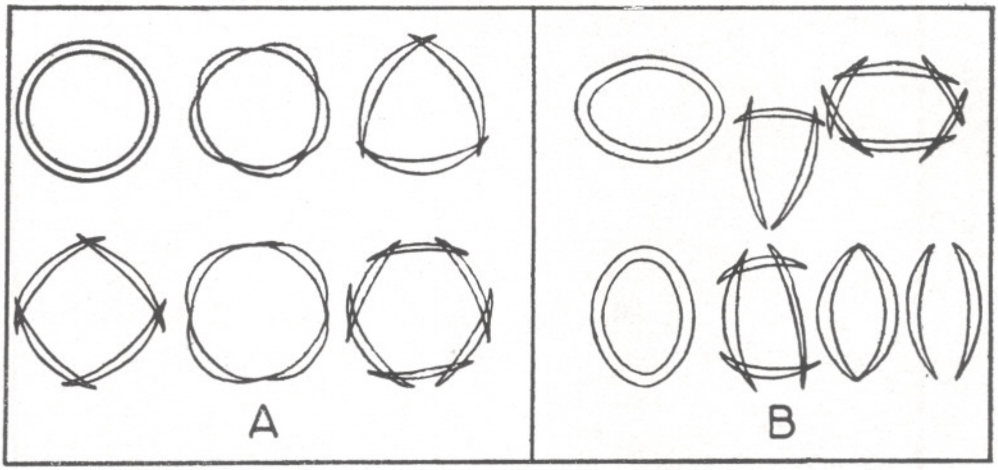
The zone of saccus separation over the distal side of the body is consistently associated, both in *Plicatipollenites* and *Potonieisporites*, with a prominent infolding of the body exine (Lele, 1964). This infold system circumscribes what may be the germinal area or the tenuitas (Potonié & Lele, 1961; Lele, 1964; Bharadwaj, 1964a, 1974). The body infold is radial or bilateral in symmetry and shows various shapes ranging from circular to oval or triangular to polygonal (Text-fig. 11). Further, in a bilateral infold system, the longer axis of the infold may be parallel to the longer or shorter axis of the grain (Text-fig. 12A, B). In the latter case (Text-fig. 12B), the differential saccus spread becomes very conspicuous in the monosaccoid miospores. The saccus along the Y-axis may be further reduced by the development of notches or sinuses along the Y-axis (Text-fig. 12D).



TEXT-FIG. 9 — Distribution trends of trilete triletoid mark in the Norms of *Plicatipollenites* (A_1, A_2) and *Potonieisporites* (B_1, B_2, B_3, B_4) — Norm A_1 has virtually no monolete incidence.

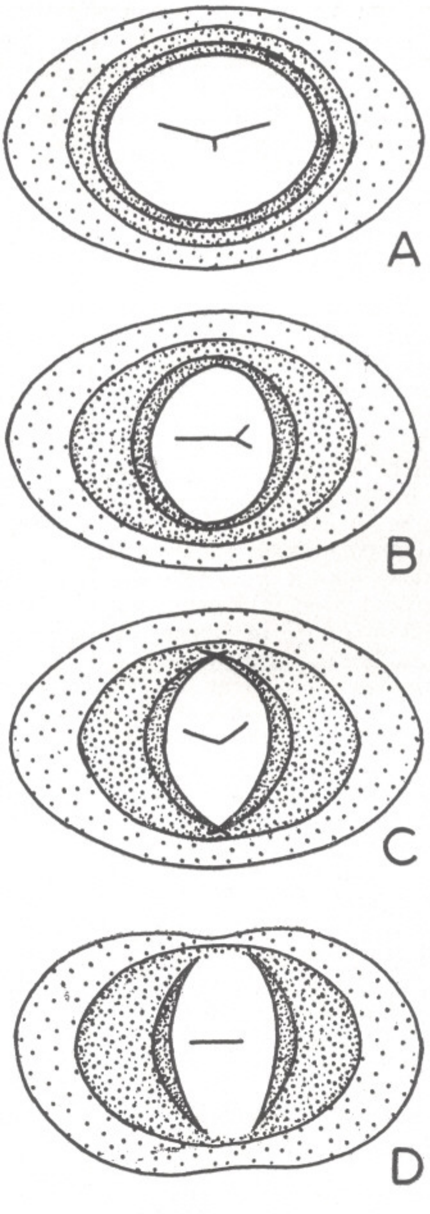


TEXT-FIG. 10 — Distribution trends of Monolete-monoletoid mark in the Norms of *Plicatipollenites* (A_1, A_2) and *Potonieisporites* (B_1, B_2, B_3, B_4).



TEXT-FIG. 11 — Shapes of Radial **(A)** and Bilateral **(B)** body infold systems.

The infold also shows a strong tendency to break up into two bracket-like folds (Text-fig. 12D) oriented parallel to Y-axis of the grain as in the case of some bisaccate taxa (cf. *Limitisporites*). To sum up, the symmetry, orientation and break-up of the



TEXT-FIG. 12 — Orientation and variation of bilateral body infold system (innermost dense stippled ring) in the Monosaccoid group. **A**, Horizontal orientation; infold ± uniform in width. **B**, Vertical orientation; infold gradually narrowing along the vertical axis. **C**, Vertical orientation; infold almost differentiated into two crescent-like vertical components still ± connected at the ends. **D**, Vertical orientation; infold well differentiated into two bracket-like vertical components disconnected from each other at the ends. In the same direction there is an attenuation of the saccus.

body infold system represent evolutionary steps of departure from a monosaccate condition. We are, therefore inclined to recognize the body infold system (distal) as a good reference line to assess the saccus spread and thereby distinguish monosaccate and monosaccoid miospores (defined earlier).

The statistical analysis of the infold symmetry was carried out on the same lines as outlined for the spore symmetry. The ratio is called " Infold circularity ratio ".

Infold circularity ratio, i.e.

$$\frac{X}{Y} = \frac{\text{Extent of infold along longer axis of spore}}{\text{Extent of infold along shorter axis of spore}}$$

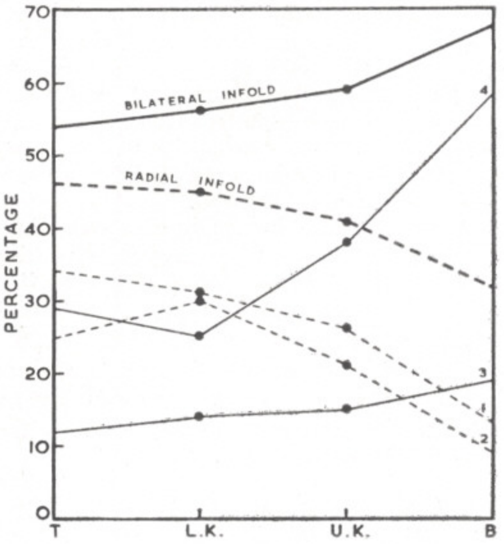
Three categories are recognized on the basis of the above ratio.

	Ratio
1. Vertical bilateral infold ...	$<0{\cdot}9$
2. Radial infold	$1 \pm 0{\cdot}1$
3. Horizontal bilateral infold ...	$>1{\cdot}1$

Marginal allowance of 0·1 is given in the above categories to accommodate preservational affects and microscopic resolution error. The allowances are based on a careful study of the inter-relationship between the body infold and spore symmetry parameters.

Evaluation — Parametral variation trend of the radial body infold symmetry shows (Text-fig. 13) a clear downward trend in time. The highest incidence of radial infold is in the Talchir (46%) but it begins to decline in the Karharbari (45-41%) and ultimately drops down considerably in the Barakar (32%). On the contrary, spores with bilateral infold show an upward trend. In the Talchir the incidence of spores with bilateral infold is 54%. It shows a progressive rise throughout the Karharbari (55-59%) and Barakar times (68%). The biometric data thus indicate that spores with radial and bilateral body infold represent two distinguishable sets with mutually reversed trends.

By further comparison (Text-fig. 13) it will be clear that the declining character of the *Plicatipollenites* population can be closely matched with the radial body infold parametral trend. It is interesting to note that Norm A_2, despite its bilateral infold development, meets the same fate as Norm A_1 which has a radial infold (Text-figs. 13, 14). On the contrary, the rising curve of the *Potonieisporites* population corresponds with the parametral trend of the bilateral



TEXT-FIG. 13 — Distribution trends (parametral) of the body infold symmetry in time and their correlation with *Plicatipollenites* and *Potonieisporites* trends. **1,** Radial infold in *Plicatipollenites*. **2,** Bilateral infold in *Plicatipollenites*. **3,** Radial infold in *Potonieisporites*. **4,** Bilateral infold in *Potonieisporites*.

infold, evidently because the majority of *Potonieisporites* constituents (Norms B_1, B_3 & B_4) have bilateral infold (Text-fig. 13). It is further evident that there is a step-by-step rise in the *Potonieisporites* Norms B_1, B_2 and B_3 in successive time levels (Text-fig. 14) which suggests a time-proportionate evolutionary establishment of the bilateral infold from horizontal to vertical position. A somewhat similar phenomenon is noticed in the Monolete-monoletoid trend (described earlier).

BODY SYMMETRY

Like the body infold system, the central body of the miospore (nexine) may be radial or bilateral in symmetry. In the latter case, the longer axis of the body may be parallel to or at right angles to the X-axis of the grain. The body shows considerable variation in shape patterns which are further affected by a number of factors, e.g. the direction of compression, original curvature and topography of the body, alignment of saccus base, flexibility and thickness of body exine etc. The restoration of the original body from compressed specimens naturally entails a wide analysis of shape variations and compressional features. At any rate, the symmetry of the body can be determined by what is here called the 'Body circularity ratio'.

$$\text{Body circularity ratio} = \frac{\text{Body extent along X-axis of spore}}{\text{Body extent along Y-axis of spore}}$$

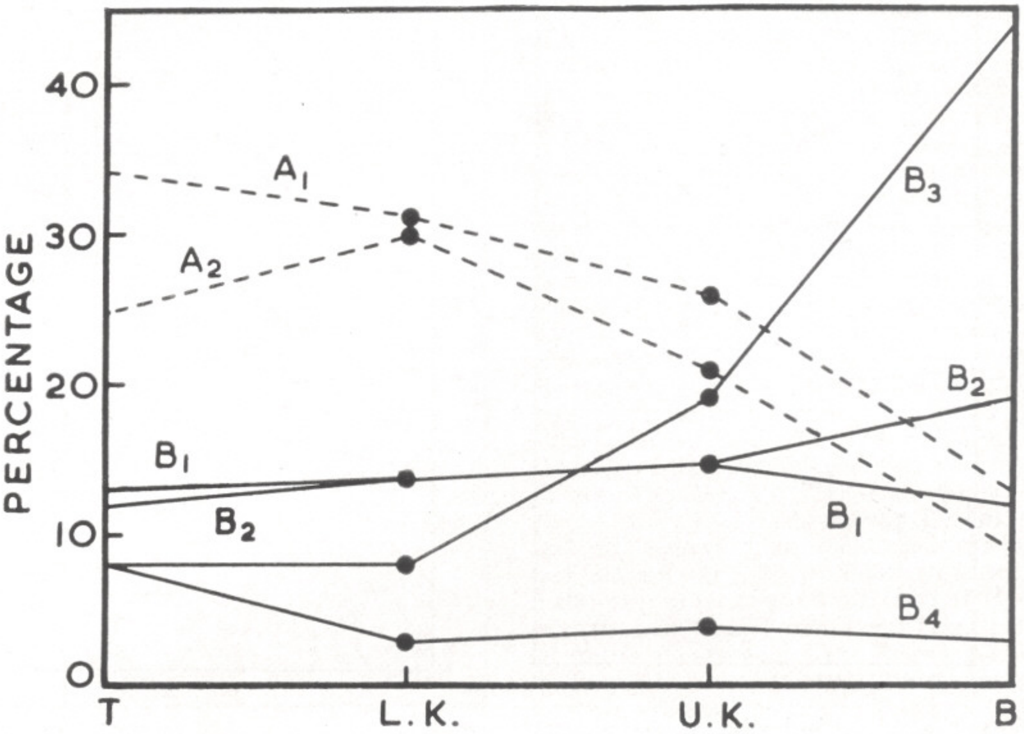
Evaluation — Biometric analysis reveals that the body circularity ratio decreases in time from 1·17 in the Talchir to 1·14 in the Lower Karharbari to 1·11 in the Upper Karharbari to 1·02 in the Barakar. This is due to the fact that spores with radially symmetrical body have gradually increased: 15% in Talchir, 26% in Lower Karharbari, 34% in Upper Karharbari and 32% in Barakar (slight fall) (Text-fig. 15). On the contrary, spores with bilateral body have decreased: 85% in Talchir, 74% in Lower Karharbari, 66% in Upper Karharbari and 68% in Barakar (slight rise).

Although there is an inverse correlation between the radial and bilateral aspects of body symmetry but it is important to observe that the body parameter as such is not compatible in its behaviour with other variation parameters, viz., body infold, spore shape and tetrad mark. In the body parameter, radial symmetry has generally an upward trend while bilateral symmetry has a general downward trend (Text-fig. 15). In all other parameters, however, it is just reverse. Therefore, it is clear that the body symmetry trend is not homogeneous with other variation parameters. There is also a noticeable lack of correlation between the body parametral trend and the *Plicatipollenites* and *Potonieisporites* population trends.

CONCLUSIONS

Resolution of Plicatipollenites & Potonieisporites populations — On taxonomic qualitative grounds the whole miospore complex falls into two clear-cut groups, viz. (i) the monosaccate group that conforms with the *Plicatipollenites* population (Norms A_1 & A_2), and (ii) the monosaccoid group that conforms with the *Potonieisporites* population.

The trends of morphological variation in the two taxa have been biometrically



TEXT-FIG. 14 — Distribution trends of the body infold symmetry in the norms of *Plicatipollenites* (A_1, A_2) and *Potonieisporites* (B_1 to B_4).

analysed and evaluated in the foregoing account. The frequency graphs of the three variation parameters, viz., overall spore shape, body infold and tetrad mark show striking correlation with each other as well as with the *Plicatipollenites* and *Potonieisporites* trends. On this basis it is now possible to segregate two homogeneous sets of morphological criteria which can characterize the *Plicatipollenites* and *Potonieisporites* populations respectively (Text-figs. 16, 17). The main results of correlation lead to the following conclusions:

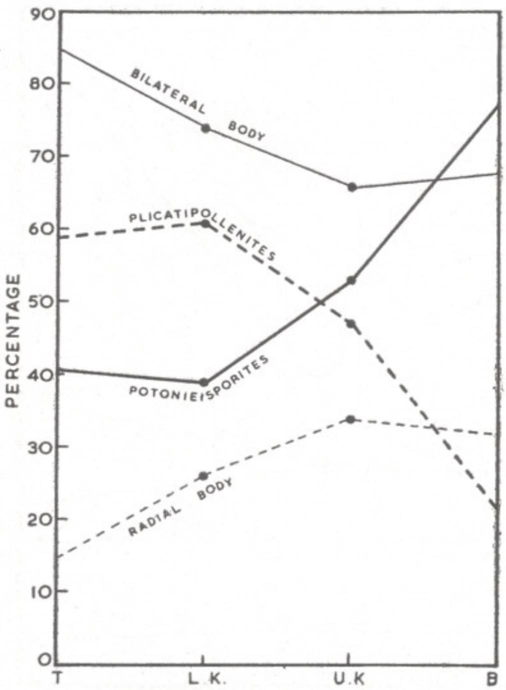
1. Each parametral variation trend reveals two distinct components pertaining to (a) radial and (b) bilateral symmetry respectively.

2. The first component (radial symmetry) is characterized by a strong association between radial spore symmetry, trilete/triletoid mark and radial body infold symmetry. This component has a declining character across time and is regressive in an evolutionary sense. The monosaccate group, represented by *Plicatipollenites* (Norms A_1 & A_2) largely conforms to this component (Text-fig. 16).

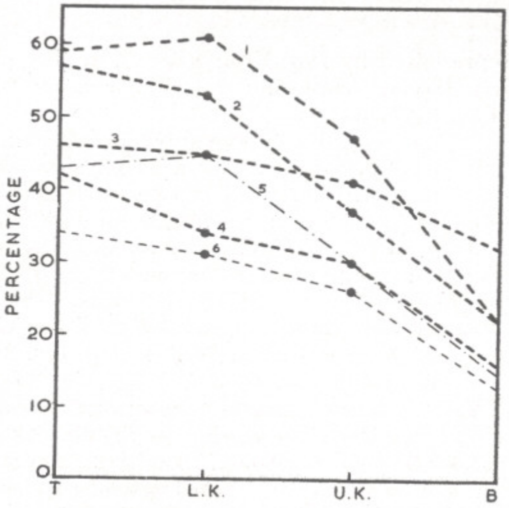
3. The second component (bilateral symmetry) is characterized by a strong association between bilateral spore symmetry, monolete/monoletoid mark and bilateral infold symmetry. This component has a rising character across time and it is progressive in an evolutionary sense. The monosaccoid group, represented by *Potonieisporites* (Norms B_1, B_2, B_3 & B_4) largely conforms to this component (Text-fig. 17).

4. The body symmetry parametral trend shows negative correlation with all other parameters of variation. Body symmetry is, therefore of little or no relevance to the resolution of *Plicatipollenites* or *Potonieisporites* populations.

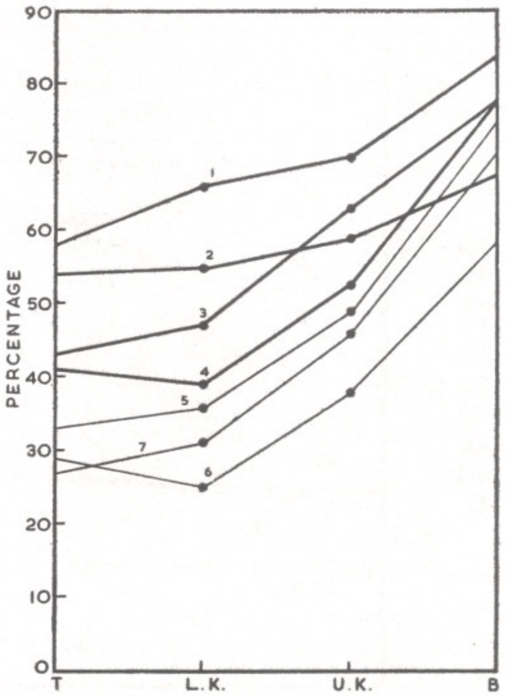
5. The multivariate analysis, confirms the classification of monosaccate and monosaccoid groups, based on the criteria of ' uniform ' and ' differential ' saccus spread. The taxa *Plicatipollenites* and *Potonieis-*



TEXT-FIG. 15 — Distribution trends of body symmetry in time.



TEXT-FIG. 16 — Composite correlation of variation trends in *Plicatipollenites*. Parametral trends of *Plicatipollenites* population **1**; Trilete-triletoid mark **2**; Radial body infold symmetry **3**; Radial spore symmetry **4**; *Plicatipollenites* with trilete-triletoid mark **5**; and radial spore symmetry +radial body infold **6**.



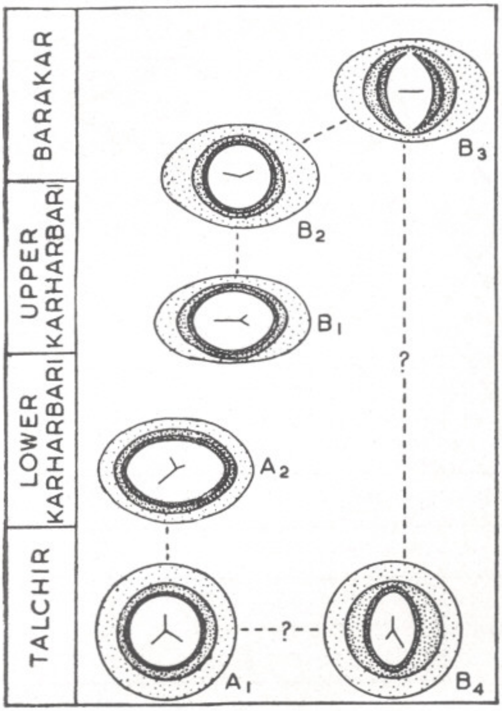
TEXT-FIG. 17 — Composite correlation of variation trends in *Potonieisporites*. Parametral trends of bilateral spore symmetry **1**; Bilateral body infold symmetry **2**; Monolete-monoletoid mark **3**; *Potonieisporites* population **4**; *Potonieisporites* with bilateral spore symmetry **5**; bilateral body infold **6**; and monolete-monoletoid mark **7**.

porites can now be precisely identified through an objective assessment of the saccus spread value.

6. Variation trends for the Talchir, Karharbari and Barakar as obtained separately from different basins are in general agreement with the result of complete successional studies in the Hutar and North Karanpura basins.

Evolutionary Considerations of Population Norms — Considerable evidence has emerged from the biometric analyses on the basis of which it is possible to broadly conceive the course of evolutionary events as reflected by the norms of the *Plicatipollenites* and *Potonieisporites* lineages in time (Text-fig. 18).

In the *Plicatipollenites* population, both the norms (A_1 & A_2) show identical regressive tendency in time. However, among the two, Norm A_1 conforms to the basic monosaccate model in its preference to radial



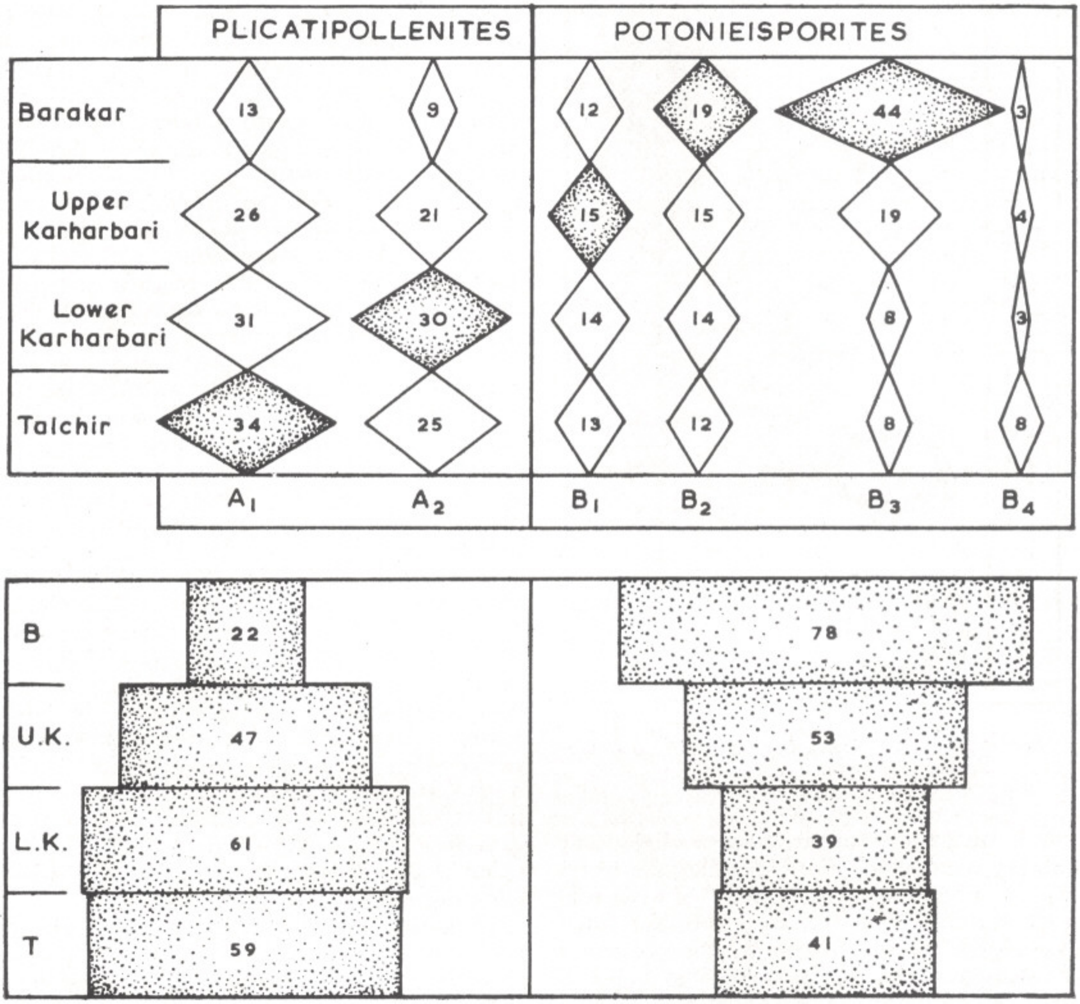
TEXT-FIG. 18 — *Plicatipollenites* and *Potonieisporites* lineages in time.

spore symmetry as well as radial body infold symmetry. Correspondingly, Norm A_1 is predominantly trilete or triletoid without any or very rare expression of a monoletoid mark. Norm A_2 shows an advancement over A_1 in achieving bilateral symmetry for the spore as well as the body infold. Correspondingly, the monolete/monoletoid tendency also finds somewhat better expression. Norm A_2 can, therefore be regarded as an evolutionary progression from Norm A_1. Stratigraphically, Norm A_1 is most abundant in the Talchir time (Text-fig. 19) while Norm A_2 shows its peak in the Lower Karharbari. This lends further support to the evolutionary relationship between the two norms.

In the *Potonieisporites* population Norm B_1 appears at first sight to be close to Norm A_2 of *Plicatipollenites* in gross morphology and variation pattern. However, the basic difference between Norm B_1 and Norm A_2 is set forth by the differential saccus spread in the former and the uniform saccus spread in the latter. The variation trends of the two norms also differ in certain important details. Norm B_1 of *Potonieisporites* shows a definite upward tendency (at least in the Talchir-Karharbari) with regard to its infold symmetry (Text-fig. 14) and monoletoid mark (Text-fig. 10) which links it with the *Potonieisporites* general trend. On the other hand, Norm A_2 of *Plicatipollenites* shows a downward trend which is characteristic of *Plicatipollenites* population. The frequency distribution of the two norms across time also does not show any correlation. Norm B_1 (*Potonieisporites*) has a consistently uniform distribution from the Talchir to the Barakar (12%-15%), the maximum being in the Upper Karharbari. Conversely, Norm A_2 (*Plicatipollenites*) shows relatively very high frequencies (25%-30%), nearly double of Norm B_1, in the Talchir-Lower Karharbari and drops down from the Upper Karharbari onward (21%-8%). From this assessment, we are inclined to believe that Norm B_1 (*Potonieisporites*) represents the point where the divergence of the *Potonieisporites* lineage from the *Plicatipollenites* lineage becomes clearly evident. There is also reason to suggest that this divergence can be linked with the attainment of monosaccoid organization (i.e. differential saccus spread) by the *Potonieisporites* population which gave it a lead over the main *Plicatipollenites* trend that suffered corresponding regression (Text-fig. 2).

Norm B_2 is morphologically a step ahead of Norm B_1. Here the monosaccoid construction of the saccus becomes clear enough with the shift in the body infold symmetry from bilateral to radial. Correspondingly, there is a further advance in the tetrad polymorphism; the monolete/monoletoid trend shows a steady upward rise across time (Text-fig. 10) while the trilete/triletoid tendency is further weakened (Text-fig. 9). Stratigraphically also, Norm B_2 shows a steady increase in its distribution (Text-fig. 19), its peak being in the Barakar.

Norm B_3 is morphologically nearer to Norm B_2 but at the same time it shows a distinct lead in the construction of the body-infold system which has become vertically oval (bilateral). Thus Norm B_3 represents a situation just reversed to that in Norm B_1. Possibly, therefore, Norm B_2 may represent an intermediate evolutionary event between Norm B_1 and B_3. In Norm



TEXT-FIG. 19 — Percentage frequency distribution of *Plicatipollenites* and *Potonieisporites* and their respective norms in time. Number inside the histogram indicates percentage.

B_3 one can notice an approach towards bisaccation of the saccus. The infold system also tends to break up into two semilunar bracket-like infolds which are reminiscent of bisaccates like *Limitisporites* or other Striatiti genera (e.g. *Crescentipollenites*). It is thus evident that Norm B_3 touches the highest level of morphological evolution within the monosaccoid group in the direction of bisaccate organization.

The morphological trends of Norm B_3, though closer to Norm B_2, are unique and most advanced within the *Potonieisporites* population. Here the monolete/monoletoid trend shows a continuous and rapid upward rise across time while the trilete/triletoid tendency has lost itself into insignificance (Text-figs. 9, 10).

In stratigraphical incidence also, Norm B_3 shows a much sharper rise (than say, Norm B_2) and attains its peak in the Barakar (Text-fig. 19). Thus the rise of the *Potonieisporites* population from Talchir upward is to be largely attributed to Norm B_3.

Norm B_4 is somewhat exceptional. In spore symmetry it stands with Norm A_1 of *Plicatipollenites* population while in the infold system it is like Norm B_3 of *Potonieisporites* population. Besides, Norm B_4 shows a generally poor stratigraphical distribution with a downward trend (Text-fig. 19). As to the tetrad mark, the polymorphism tendency has no particular inclination but probably it is comparable to that of *Plicatipollenites* population (Text-figs. 9, 10). Norm B_4 evidently suggests an evolutionary course different from that taken by Norms B_1, B_2 and B_3: here a 'monosaccoid' organization has been attained without losing the radial symmetry of the spore.

To sum up, it can be said that the morphological variations in *Plicatipollenites* and *Potonieisporites* may appear to suggest intergradation as long as the populations are seen along one time plane. However, when they are observed across successive time levels, it becomes evident that the trends of *Plicatipollenites* are not compatible with those of *Potonieisporites*. The *Plicatipollenites* population appears to be rather conservative in having essentially retained the uniform saccus spread and the trilete tetrad mark. The whole group as well as its morphological variation show a progressive decline in time. On the other hand, the *Potonieisporites* population shows a more or less time-proportionate evolution and diversification in form and proliferates through successive time levels. There is a step-by-step establishment of the monolete mark and bilateral spore symmetry. These events are accompanied by a corresponding shift in the orientation of the bilateral infold from horizontal to a vertical position which maximizes the differential saccus spread. The whole series of morphological changes seems to be directed towards evolving a bisaccate condition.

Biostratigraphical Considerations — The usefulness of evolutionary palynology in stratigraphy is now widely acclaimed (Sylvester-Bradley, 1956; Visscher, 1971). The present study is also of a similar nature. The main course of events in the *Plicatipollenites* and *Potonieisporites* populations are now known across the Lower Gondwana time. When these events are examined in terms of the norms, a clear shift can be marked in the frequencies of the two populations in successive time levels (Text-fig. 19). On this basis, therefore it is possible to recognize broad time zones. It is clear from the histogram (Text-fig. 19) that the Talchir and Lower Karharbari together form a broad time zone characterized by the predominance of *Plicatipollenites* (Norms A_1 & A_2). In the Upper Karharbari, *Potonieisporites* begins to take a lead over *Plicatipollenites* and subsequently attains a predominating position in the Barakar (especially Norm B_3). Thus, the Upper Karharbari and Lower Barakar form another broad time zone. The major change has evidently occurred in the Lower and Upper Karharbari transition. For finer biostratigraphical zonation it would be necessary to work out the species content of the various norms. In fact, no complete scheme of Lower Gondwana biozonation can be evolved until several other stratigraphically important and morphologically allied generic groups are also investigated biostratigraphically.

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EXPLANATION OF PLATE

PLATE 1

1. *Plicatipollenites*, Norm A_1 (Talchir Formation, Hutar Coalfield). *Spore circularity ratio* (1·04). *Infold circularity ratio* (1·04). *Saccus spread value* (zero).

2. *Plicatipollenites*, Norm A_2 (Talchir Formation, Hutar Coalfield). *Spore circularity ratio* (1·34). *Infold circularity ratio* (1·54). *Saccus spread value* (−0·2).

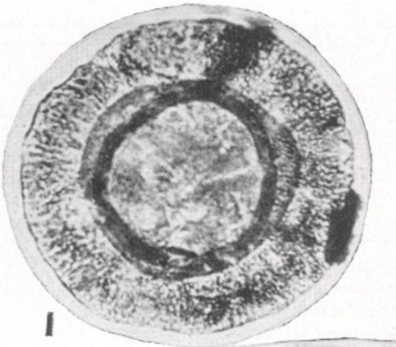
3. *Plicatipollenites* Norm A_2 (Talchir Formation, Hutar Coalfield). *Spore circularity ratio* (1·45). *Infold circularity ratio* (1·45). *Saccus spread value* (zero). The grain falls just on the boundary demarcating 'Monosaccate' and 'Monosaccoid'.

4. *Potonieisporites*, Norm B_1 (Talchir Formation, Johilla Coalfield). *Spore circularity ratio* (1·67). *Infold circularity ratio* (1·33). *Saccus spread value* (0·34).

5. *Potonieisporites*, Norm B_2 (Lower Barakar Formation, Hutar Coalfield). *Spore circularity ratio* (1·57). *Infold circularity ratio* (0·95). *Saccus spread value* (0·62).

6. *Potonieisporites*, Norm B_3 (Lower Barakar Formation, Hutar Coalfield). *Spore circularity ratio* (1·44). *Infold circularity ratio* (0·47). *Saccus spread value* (0·97).

7. *Potonieisporites*, Norm B_4 (Talchir Formation, Johilla Coalfield). *Spore Circularity ratio* (1·02). Infold circularity ratio (0·81). Saccus spread ratio (0·21).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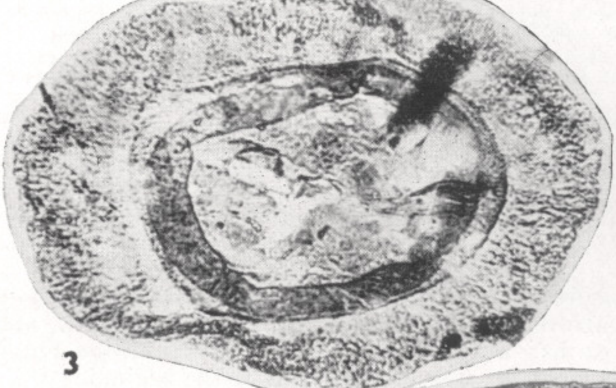
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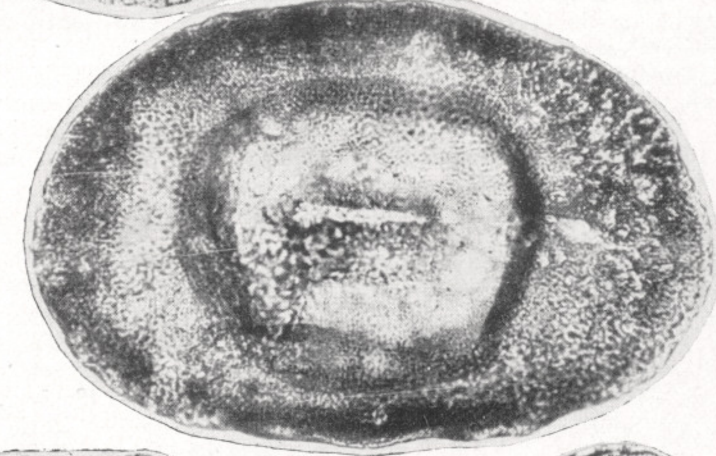
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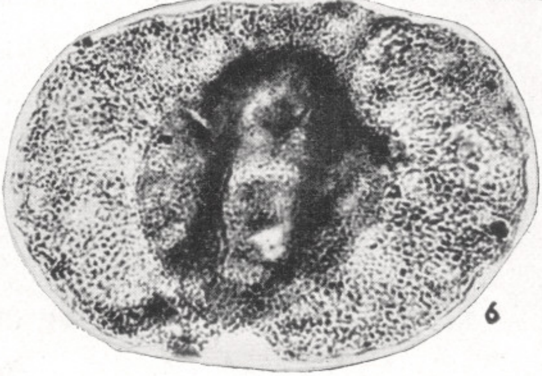
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PLATE 1