
Patterns of evolution of Gondwana floras and origin of angiosperms

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Evolution is the montage of patterns and micro-patterns of organism's lineages woven in an array of harmonized system through time. The gaps, or overlappings, in patterns appear to exist in this composite picture because of the lack of interconnecting information, or due to our view-point to look at the available information. The only character which defines angiosperms, exclusively and discretely, is the double fertilization; it cannot be found in fossil state. The conclusion that the flowering plants suddenly upsurged in the Late Cretaceous is based on negative evidences of non-finding of such fossils which must match with the extant forms. The Gondwanaland had been the land of environmental stresses and the Permo-Triassic boundary had witnessed major evolutionary shifts in plant life. The micro-patterns, controlled by genetic material, had manifested in the pollen morphology which are recorded in the Late Permian pollen. The molecular data also indicate a long pre-Cretaceous history for angiosperms. This period much before the breaking and drifting of the continents of the Gondwanaland had witnessed the divergence in patterns which record the initiation of the origin of flowering plants, because the monophyletic origin cannot support their several first-appearances on 'rafting' islands in isolation.

Key-words—Palynology, Evolution, Angiosperms, Gondwana floras.

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सारांश

आवृतबीजी पौधों की उत्पत्ति एवं गोंडवाना वनस्पतिजातों के उद्भव का स्वरूप

राम शंकर तिवारी

जीव विकास विभिन्न भूवैज्ञानिक कालों में विकसित जीवित प्राणियों की श्रृंखला के स्वरूपों एवं सूक्ष्मस्वरूपों की पारस्परिक प्रतिक्रिया का परिणाम है। वैकसिक स्वरूप के सम्बन्ध में यदि कोई रिक्त स्थान अथवा एक दूसरे के ऊपर प्रतिबिम्बित जानकारी है तो वह हमारी सम्पूर्ण सम्बद्ध जानकारी में किसी कमी अथवा उपलब्ध जानकारी के प्रति हमारे दृष्टिकोण के कारण ही है। द्वि-निषेचन ही एक ऐसा लक्षण है जो आवृतबीजी पौधों को परिभाषित करता है लेकिन यह अशिमत अवस्था में नहीं पाया जाता। यह मानना कि आवृतबीजी सपुष्पी पौधों की अनंतिम क्रीटेशियस काल में अचानक उत्पत्ति हुई ऐसा अशिमत पौधों के न मिलने के कारण है जो कि हमारी वर्तमान जानकारी को पूर्णता प्रदान कर सके तथा वर्तमान पौधों से तुलनीय हो। गोंडवानाभूमि ने कई पर्यावरणीय परिवर्तनों का अनुभव किया है तथा परमी-त्रिसंघी सीमा पर पौधों में महत्वपूर्ण विकासीय परिवर्तन हुए हैं। आनुवंशिक पदार्थ द्वारा नियंत्रित सूक्ष्म स्वरूप परागकण आकारिकी के रूप में प्रकट हुए हैं जो कि अनंतिम परमियन कालीन परागकणों में परिरक्षित हैं। आणविक आँकड़े भी आवृतबीजीयों का पूर्व क्रीटेशियस कालीन इतिहास प्रदर्शित करते हैं। गोंडवाना भूमि के विघटन एवं महाद्वीपों के एक दूसरे से पृथक होने से काफी पहले इस काल में पौधों के विभिन्न स्वरूपों के प्रमाण मिले हैं जो कि सपुष्पी पौधों के उद्भव के विषय में महत्वपूर्ण जानकारी प्रदान करते हैं क्योंकि एक जातिवृत्तीय उद्भव अलग-अलग द्वीपों पर प्रथम उद्भव की पुष्टि नहीं करता।

THE only character which exclusively and discretely defines angiosperms is the eight-cell stage of female gametophyte associated with double fertilization.

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The other defining features of this group of plants either overlap with other groups or are absent in certain taxa within the group angiosperm itself. No evidence of double fertilization can be held from fossil records, hence the search for an ideal ancestor

of angiosperms is an exercise in futility. However, this landmark character-state attained by female gametophyte is definitive for the monophyletic evolution of the flowering plants.

The evolution is the process which can be demonstrated by the series of arrangements of repeated or corresponding morphological expressions in organisms through time. Such arrangement when boldly manifested may be termed as *pattern*. Less expressive motifs are thus *sub-patterns* and one or only a few character-states expressed as signatures in a group are *micro-patterns*. Thus, evolution is the montage of patterns, sub-patterns and micro-patterns of lineages of characters woven in an array of organized system through time. The eight-nucleate stage and double fertilization make a micro-pattern which unifies the otherwise highly diversified extant taxa of angiosperms and supports monophyletic origin of the group.

Taphonomic hazards prompt that plant microfossils can be utilized more purposefully than the megafossils in determining the earliest divergence of angiosperms. The astronomical number of pollen produced, the high resistivity of sporopollenin and the preservation of finest exine characters make these organs most suitable determinant of plant relationship. The palaeogeographic set-up and the time levels of micro-pattern-deviation are crucial parameters for initiating any discussion on the origin of angiosperms.

PRE-CRETACEOUS ORIGIN

The Late Cretaceous radiation of angiosperms is generally treated as an "established fact". So also, it appears that some form-similarity with angiosperms existed in a few plant organs, viz., *Karkonia* group, *Gnetophytes-Ephedripites-Classopollis* and other pollen groups from the Early Cretaceous (Hughes, 1994; Tiwari & Tripathi, 1995). The pre-Cretaceous scenario has been the victim of odd scepticism because some fossils although possess apparent form-similarity with angiosperms do not exhibit point-to-point matching with the characters of extant angiosperms. And expectations of such a matching had been a blockade which hinders our thinking in other directions; for example, in the initial stage of origin and evolution of a micro-pattern, a derived character-

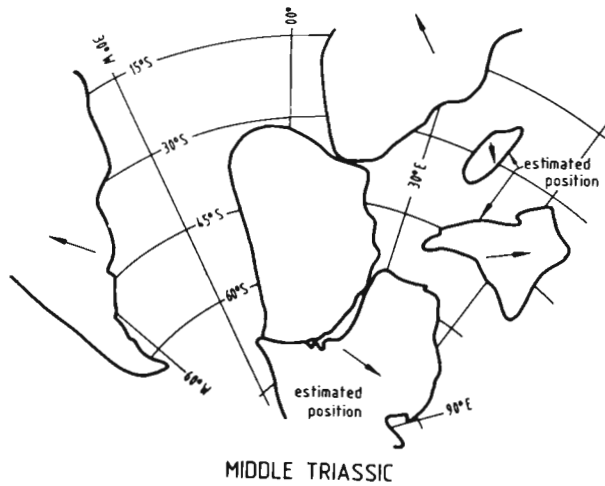
state may be manifested only in one character. Hence, the "absence" of pre-Cretaceous angiosperm records is not a reality but an interpretative fallacy because atleast some character-states of angiospermous relationship are definitely present in pre-Cretaceous period (e.g., in *Glossopteris*, *Peltasperms*, *Corystosperms*, *Sanmiguelia*, *Caytonia*, *Williamsonia*, *Pentoxyleae*, *Cornetipollis*, *Playfordiaspora* and several other colpate, costate pollen with structured exine).

The rarity or absence of angiosperm megafossils in the pre-Cretaceous era is explained away by the theory of their upland origin (Axelrod, 1952). It could be possible that angiosperms have originated and initially evolved on the upland but it is not acceptable, in view of our present understanding, that no chance of fossilization was available on uplands. The dispersal of plant organs particularly seeds, fruits, leaves, pollen—by wind, water and animals, covering wider spatial extent and reaching on to the lowland waterbodies cannot be ruled out. Moreover, even on upland, there exist stet montane lakes and depressions which accumulate sediments. Several sequences of Quaternary sedimentaries in Himalaya recovered from dried or live lakes are the examples of such a situation. Obviously, the theory of non-availability of an environment for fossilization of angiosperms because of their upland origin is negative as well as escapist to the same degree as much as it has been proposed to disprove that angiosperms were non-existent in the pre-Cretaceous Period. Therefore, both the concepts are non-acceptable.

PALAEOGEOGRAPHY

According to the so-far-accepted models of palaeogeography the break-up of eastern Gondwanaland started in late Early Cretaceous Baramian-Aptian time. During Early Aptian the Indian Plate, along with Madagascar Plate, had moved quite some distance away from the Australia-Antarctica duo (Smith *et al.*, 1992).

Based on the 'high-confidence' data that angiosperms suddenly proliferated and radiated in the Late Cretaceous — after Aptian/Albian, it may be concluded that the origin of this group must have occurred when the eastern Gondwanaland was in-



Text-figure 1—Position of India as a separate "island" during Middle Triassic (according to Lee, 1993); however, conventionally it is accepted that the Indian Plate began to separate during Late Early Cretaceous. If Lee's model is accepted, the angiosperms appear to have originated during Late Permian when Gondwanaland was intact.

tact. This, however, not necessarily implies here that the group originated on the Gondwanaland.

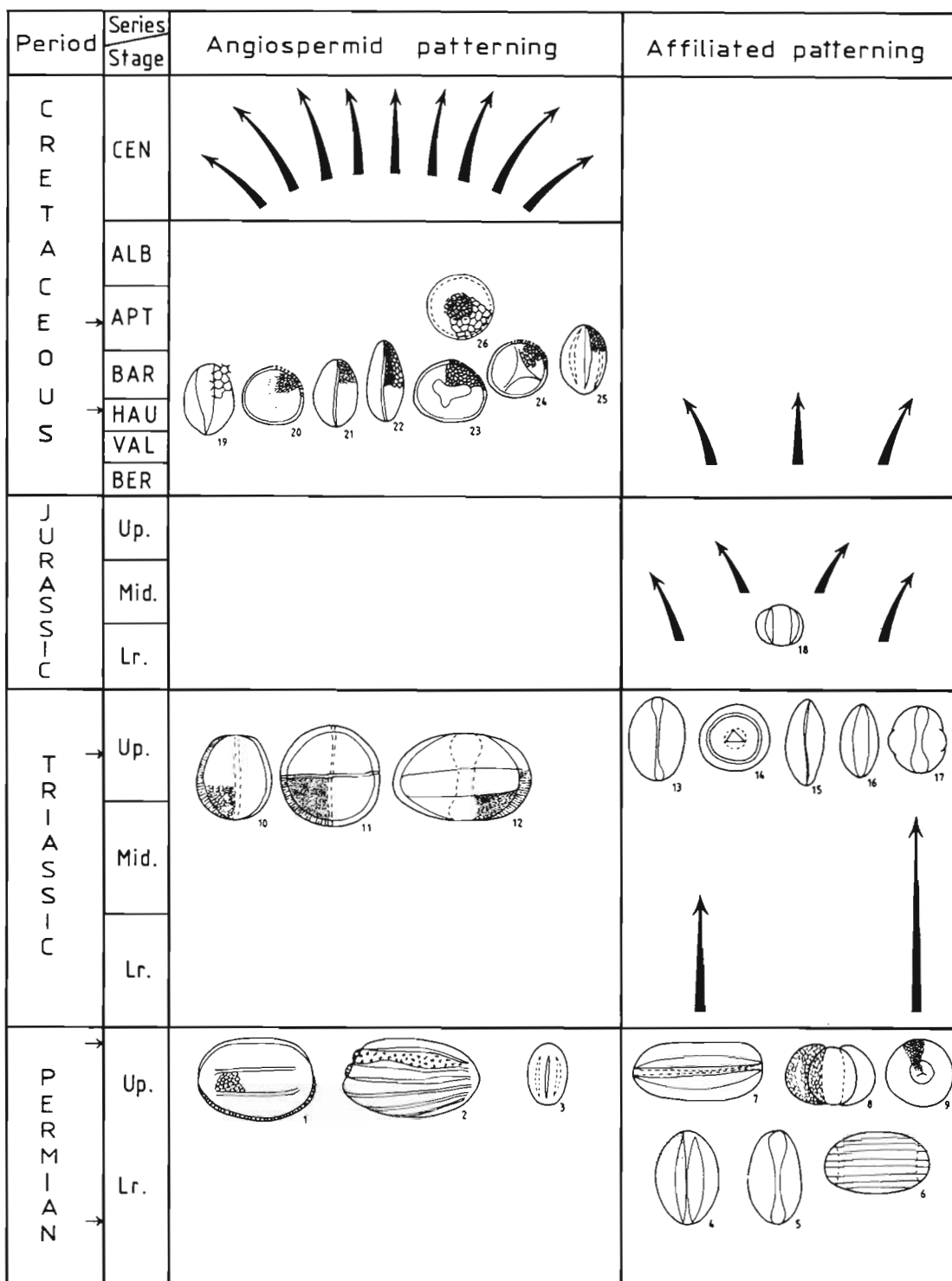
Recently, Lee (1993) has proposed a hypothesis that if the Earth's core were off-set at a particular

position relative to the Earth's geocentre then a mathematical relationship exists between major physiographical and tectonic features. Based on this model, he (Lee, 1993, pp. 525-527) has given palaeogeographic maps from Middle Ordovician to Upper Cretaceous, which suggest that Indian Plate began its long movement toward the Northern Hemisphere during Upper Permian. By the time of Middle Triassic, India was an isolated continent (Text-figure 1). However, Antarctica and Australia remained in contact with each other till Early Tertiary. With reference to the model of Lee (1993) and the fossil records of micro-patterns indicating early angiosperms it may be concluded that angiosperms originated when India was 'rafting' as an isolated continent and Antarctica-Australia made one single landmass separated from other continents.

Although Lee's hypothesis awaits criticism from the profounders of the established models of palaeogeography, there creeps in an implication if this empirically tested hypothesis gets a ground. Have the angiosperms originated on 'rafting' continents independently on widely apart landmasses (Lee's

Text-figure 2—Various pollen organizations through Gondwana Sequence—from Permian to Early Cretaceous, exhibiting expression of angiosperm pattern of exine structure of the main stream along with pollen with affiliated patterning of characters in side stream. **1.** *Daminites* Tripathi (in press) : showing polysulcate nature, columellate tectate sexine and thinning of sexine at lateral ends. **2.** *Cornetipollis* Pocock & Vasanthy 1988 : furrows and ribs on the surface and foveo-reticulate exine structure. **3.** *Pretricolpitenites* Danzi-Corsin & Laveine 1963 : one functional and two abortive colpi. **4.** *Kingiacolpites* Tiwari & Moiz 1971 : single biconvex sulcus associated with folds, exine indistinctly infrapunctate. **5.** *Ginkgocycadophytus* Samoilovich 1953 : one dumb bell-shaped sulcus and granulose to spinose sculpture. **6.** *Welwitschitites* Bolchowitina 1953 : longitudinally striate nonsaccate pollen, striation with cross connections, exine structured. **7.** *Praecolpites* Bharadwaj & Srivastava 1969 : sulcus associated with folds, infrastructured exine. **8.** *Protoeusaccites* Tiwari, Vijaya & Ram-Awatar 1995 : bisaccate pollen showing intermediate stage between Proto- and Eusaccate condition of sacci. The central hollow cavity is seen in the saccus. **9.** *Playfordiaspora* Maheshwari & Banerji emend. Vijaya 1995 : a monosaccate pollen with trilete mark on central body and eusaccate nature of sacci, separation of single layered, reticulate sexinal layer from nexine. **10.** *Brachysaccus* Mädler 1964 : a bisaccate pollen showing infrabaculate nature of sexinal elements in the sacci. **11.** *Staurosaccites* Dolby in Dolby & Balme 1976 : bisaccate pollen with transverse polar cleft, saccus finely columellate showing infrabaculate nature on the periphery. **12.** *Infernopollenites* Scheuring 1970 : bisaccate taeniate pollen showing infrabaculate nature of sexinal elements in the sacci at periphery. **13.** *Cycadopites* Wodehouse ex Wilson & Webster 1964 : pollen monosulcate, sulcus narrow in the middle, exine psilate to scabrate. **14.** *Classopollis* Pflug emend. Pocock & Jansonius 1961 : pollen having trilete mark on one face and polar thinning on the other, exine with girdling thinning; exine structure advanced type multilayered with columellate nexine. **15.** *Ginkgoretictina* Malawkina 1953 : monosulcate pollen, sulcus linear, narrow, exine infragranulose. **16.** *Monosulcites* Erdtman ex Couper 1953 : monosulcate pollen, sulcus narrow with pointed ends, exine granulose. **17.** *Ashmoripollis* Helby 1987 : bisaccate pollen with restricted saccus development. **18.** Small nonstriate bisaccate pollen, having the sulcus as main character. **19.** *Retimonocolpites* Pierce 1961 : monosulcate pollen, coarsely reticulate sexine loosely connected with nexine. **20.** *Clavatipollenites* Couper 1958 : monosulcate pollen showing tectate-columellate microreticulate sexine. **21.** *Retimonocolpites* Pierce 1961 emend. Jobasz & Goczam 1985 : monosulcate pollen showing tectate-columellate, microreticulate sexine. **22.** *Liliacidites* Couper 1953 : monosulcate pollen with reticulate sexine, reticulations decreasing in size towards lateral ends. **23.** aff. *Clavatipollenites* sp. 1 in Walker & Walker 1984 : specimen illustrated by Tripathi & Tiwari 1991, pl. 1, figs 6-9, trichotomosulcate pollen, semitectate sexine. **24.** *Asteropollis* Hedlund & Norris 1968 : trichotomosulcate pollen with tectate columellate sexine. **25.** *Tricolpites* Cookson 1947 ex Couper 1953 emend. Jarzen & Dettmann 1989 : tricolpate pollen with tectate columellate sexine. **26.** *Afropollis* Doyle, Jardine & Doerenkemp 1982 : columellate-tectate sexine loosely attached to nexinal body.

The solid arrows indicate continuity/diversification trends. The signatures of angiosperm characters are recorded at various levels and ultimately they get established at Early Cretaceous. The Jurassic record is meager yet the bisaccate pollen had attained a true sulcate character-state.



Text-figure 2

model)? Was there any micro-pattern of angiosper- Gondwanaland at the Permo-Triassic time (the so far
 mous characters already existing on the unified established model)?

GONDWANALAND

Right from the Late Carboniferous up to Late Cretaceous the life on the Gondwanaland had undergone several intermittent events of severe stresses. By the Late Carboniferous, the Pangea was formed due to the collision of Gondwana with Laurasia. The glaciation which was at its maximum during this time generated strain to cause the origin of Glossopteris flora (Vijaya, 1995a), which got established by the time of Early Permian when the ice-spread shrank and the climate ameliorated. Another major Period of stress was the Permo-Triassic transition when regression followed transgression with an event of mass extinction in the marine life. However, the life on land did not extinct to a great extent but substantially high turnover occurred in plant species and an evolutionary shift had taken place which subsequently gave rise to a new flora. The Late Triassic period on Gondwana also witnessed similar situation but of lesser degree. Thereafter the evolutionary trends do not suggest a catastrophe till Late Jurassic where floras made shifting trend in evolutionary patterns which got established in Early Cretaceous (Tiwari, 1994).

The origin and spread of various floras during Early Permian through Middle Jurassic were more or less similar on all over the Gondwanaland. This was so because the palaeogeography of the Supercontinent was similar during this period.

The incoming of micro-pattern of angiospermid characters in pollen wall at the Late Permian time is an episode of much significance which synchronizes with the evolutionary shift terminating the great Glossopteris flora (Text-figure 2). The origin of angiosperms on Gondwanaland is favoured in view of the intensive stress during glaciation and subsequent changes in evolutionary paths in plant lineages. The angiosperms could not have originated several times independently on isolated rafting island-continent. Thus monophyletic origin on the united Gondwanaland is the only probability of initiation of angiosperm micro-patterns.

SIGNATURES OF MICRO-PATTERNS

1. In their short communication, Martin *et al.* (1989) have reported molecular evidence suggesting that angiosperm ancestors underwent diversification more than 300 Ma. The authors have determined nucleotide for full size complementary DNA for a slowly evolving glycolytic enzyme (GAPDH) and on the basis of comparative study they concluded that angiosperms have a long pre-Cretaceous history and the Permo-Triassic time could have been their radiation period. However, Doyle and Donoghue (1993) consider this as highly inconsistent with fossil record. This is true if we look from the preconceived notion that distinctive angiosperms appeared at Late Lower Cretaceous level, but many of the micro-patterns could have come in the Pre-Cretaceous pollen which are reflected in DNA sequence. Moreover, the propositions of Martin *et al.* (1989) are complimentary to the theory put forth by Lee (1993) discussed above.
2. The structure of the pollen wall is controlled by the genetic programming present in the early sporocyte. The columellate-tectate structure of the exine in angiosperms appears to have been evolved from the infragranulose structure. Thus the infrapunctate-infragranulose character-state is the primitive to columellate-tectate state but the former makes a stock of micropattern if associated with monocolpate organization of pollen. The continuity of database linking infragranulose to columellate-tectate exine needs reinterpretation; we have not been able to identify the columellate-tectate character in all cases because of its variability.
3. The Upper Permian record of *Cornetipollis* Pocock & Vasanthy 1988 from Talcher Coalfield, Orissa and *Daminites* Tripathi 1995 from Rajmahal Basin, India by Tripathi (1995) strengthens the view that tectate-reticulate columellate character-state was initiated at the end Permian level. The inception of this character further suggests that micro-patterning of angiospermid character in pollen was an effective process during the pre-Cretaceous Period. This is further collated with the DNA sequencing which provides such signatures.

EVOLUTION AND POLLEN-SPECIFICITY

Megafossils

In the plant organs found as megafossils several 'symptoms' of angiospermous affinities have been recognized from time to time, and exhaustive discussions have been put forth in the past (Axelrod, 1952; Cronquist, 1968; Takhtajan, 1969; Doyle, 1978; Doyle & Crane, 1985; Donoghue, 1986, 1993; Hughes, 1976, 1994; and other references).

The reticulate venation of *Glossopteris* leaf (Melville, 1962, 1983), the bitegmic ovule of *Dictyopteridium* (Retallack & Dilcher, 1981), the pollen organs of corystosperms (Townrow, 1962), the 'flower' of Bennettitales and fructifications of Pentoxyleae (Sahni, 1948; Vishnu-Mittre, 1953) are some of the well known examples which reflect an image of angiospermid patterns in characters, and theories about the origin of angiosperms from these or certain other plant groups have been proposed from time and again.

The cladistic analysis which attempts to reconstruct the branching pattern of phylogeny based on distribution of shared derived characters, has recently been applied to the problem of origin and evolution of angiosperms (Hennig, 1966; Doyle & Donoghue, 1986, 1993). The theories of origin based on purely comparative morphology of groups mentioned above, are being tested on the objectively structured clades and their nesting. Accordingly it has been suggested that angiosperms belong to the sister group of Bennettitales, Pentoxyleae and Gnetales and this clade is related to Caytoniales and glossopterids (Doyle & Donoghue, 1986). The cladistic analysis has, thus, been able to show the possible relationship amongst the lines of evolution in the angiosperm phylogeny.

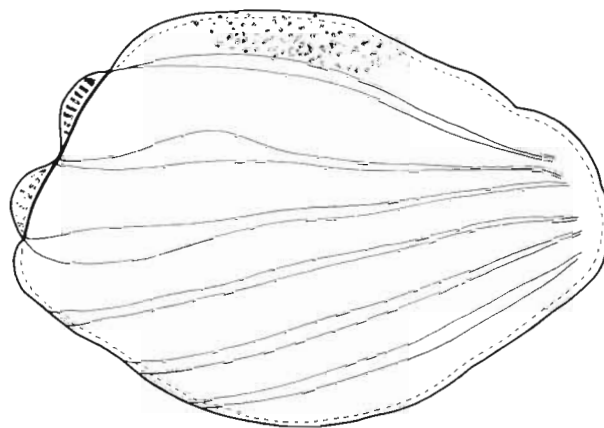
Pollen-specific element

As indicated earlier, pollen are more potential organs for considering the origin of micro-patterns and their nesting through time. Although most of the genes that are expressed in the developing pollen grains are also expressed in sporophytic tissues of the plant, yet some of the genes are pollen-specific and are expressed only in pollen and not in other parts of the plant (Willing *et al.*, 1988; Mascarenhas, 1992).

Such finding may prompt the proposition that the small amount of genetic element necessary for pollen-specificity is very significant and might be manifesting the characters in pollen wall. In case of angiosperm pollen the tectate-columellate structure and its variants make the basis of differentiation of this group from other seed plants. The micro-patterning based on this expression of gene—irrespective of development or non-development of angiosperm characters in other organs of plants—is the key for tracing the origin of the group. The infragranulose, the single layered infra-reticulate and columellate-tectate structures and colpate organization belong to the chain of characters qualified for angiosperms.

POLLEN IN PERMIAN GONDWANA

The Permian palynoassemblages in Gondwana Sequence are dominated by bisaccate pollen, among which striate are in majority (Tiwari & Tripathi, 1992). The glossopterids are supposed to have produced striate bisaccate pollen, and Retallack and Dilcher (1981) consider the sacchi as adaptation for germination rather than of phylogenetic consequence and hence the saccate pollen may represent the pre-micro-pattern for angiospermoid micro-pattern. Besides, monocolpate grains with a proximal trilete mark have also been reported from *Lithangium* Pant



CORNETIPOLLIS

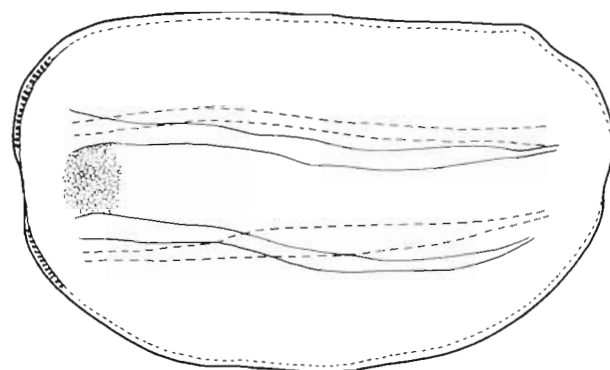
Text-figure 3—Line drawing of a specimen of *Cornetipollis* Pocock & Vasanthi 1988 showing ribs and furrows on the body, foveoreticulate exine pattern in surface view and infrabaculate nature of sexine in optical view (Size 110 μm along the longer axis; Late Permian, Talchir Coalfield, Orissa, India).

& Nautiyal (Gould & Delevoryas, 1977; McLoughlin, 1992). *Lithangium* is an isolated pollen sac thought to be allied with glossopterids.

The saccate pollen of Permian Gondwana are proto-saccate, but a transition state to eusaccatism has been recently reported in *Protoeusaccites* by Tiwari *et al.* (1995). Similarly *Playfordiaspora* Maheshwari & Banerji 1975 has been determined to be eusaccate with only one layered infrareticulate sexine (Vijaya, 1995b). This state imitates columellate structure with a cavity between sexine and nexine.

These lines of trends represent expressions of characters attempting to be angiospermoid. Most important of the forms of such trends is the genus *Cornetipollis* Pocock & Vasanthy 1988 recently discovered in the Upper Permian of India (Text-figure 3). *Cornetipollis* is a costate pollen with distinct nexine and foveo-reticulate structure in the sexine. The columellate-tectate nature of structure is clearly evidenced. Another pollen *Daminites*— polycolpate intrabaculate with thick endexine, in the Late Permian of Rajmahal Basin, is considered to possess angiospermoid character (Tripathi, 1995; fig. 4; pls 1, 2). All such micro-patterning occurred at the close of the Permian and beginning of the Triassic. The P/Tr boundary witnessed a great event of stress and an evolutionary shift in floras—as rigorously evidenced by palynofossils (Tiwari, 1994; Tiwari & Vijaya, 1994).

The occurrence of several taxa of monocolpate (generally referred to as *Ginkgocycadophytus*, *Cycadopitys*, *Kingiacolpites*, etc.) and non-saccate striate/polycolpate (*Vittatina*, *Gnetaceapollenites*, *Ephedripites*, *Welwitschiapitys*, *Decussatisporites*, etc.) pollen in the Permian sequence points out that germinal apertures and infragranulose structure of exine in certain cases have started differentiating in the direction of angiospermoid main-stream character-states (Text-figure 2). The *in situ* records of these



DAMINITES

Text-figure 4—Line drawing of a specimen of *Daminites* Tripathi (in press) showing "polycolpate" nature of body and inframicoreticulate nature of sexine in surface view, infrabaculate nature in optical view and thinning of sexine at lateral ends (Size ca. 125 µm; Late Permian, Rajmahal Basin, Bihar, India).

pollen are not known, yet sub-patterning for a great journey toward angiosperm evolution has started at this level of time.

Pollen in Triassic-Lower Cretaceous Gondwana

The Triassic sequence has more of taeniate bisaccate pollen, consistently replacing striate bisaccates. The Jurassic and Lower Cretaceous saccate pollen group is dominated by non-striate pollen with reduced sacci. In Early Triassic, the genus *Praecolpatites* Bharadwaj & Srivastava 1969, although incipiently infrapunctate exhibit primary mode of colpi which could be precursor of angiosperm stock. Besides, several monocolpate pollen are reported to be present in the Triassic-Jurassic span of time. The columelloid structure has been noted in Carnian-Norian *Brachysaccus*, *Minutosaccus* and *Staurosaccus* (Vijaya & Tiwari, 1992). These taxa find their place in the main stream character-state channel for

PLATE 1

1. *Daminites* Tripathi (in Press). A "polycolpate" pollen from Late Permian, Rajmahal Basin, India, X 750.
2. Portion of the specimen in fig. 1 enlarged to show the infrareticulate sexine structure in surface view (bold arrow) and infrabaculate sexine in optical view (thin arrow), X 1500.
3. *Brachysaccus* Mädlar 1964. Nonstriate bisaccate pollen, X 750.
4. Portion of a specimen of *Brachysaccus* enlarged to show the inframicoreticulate pattern of sexine in surface view (bold arrow) and infrabaculate in optical view (thin arrow), X 1000.
5. Portion of the specimen in fig. 6 enlarged to show the foveoreticulate exine structure, X 1500.
6. *Cornetipollis* Pocock & Vasanthy 1988. From Late Permian, Talcher Coalfield, Orissa, India, X 500.
7. aff. *Clavatipollenites* sp. in Tripathi & Tiwari 1991. From Early Cretaceous (Aptian) intertrappean beds of Rajmahal Basin, India, X 500.
- 8, 9. Portion of the specimen in fig. 7 enlarged to show the exine structure in optical view (fig. 8) and surface view (fig. 9), X 1500.

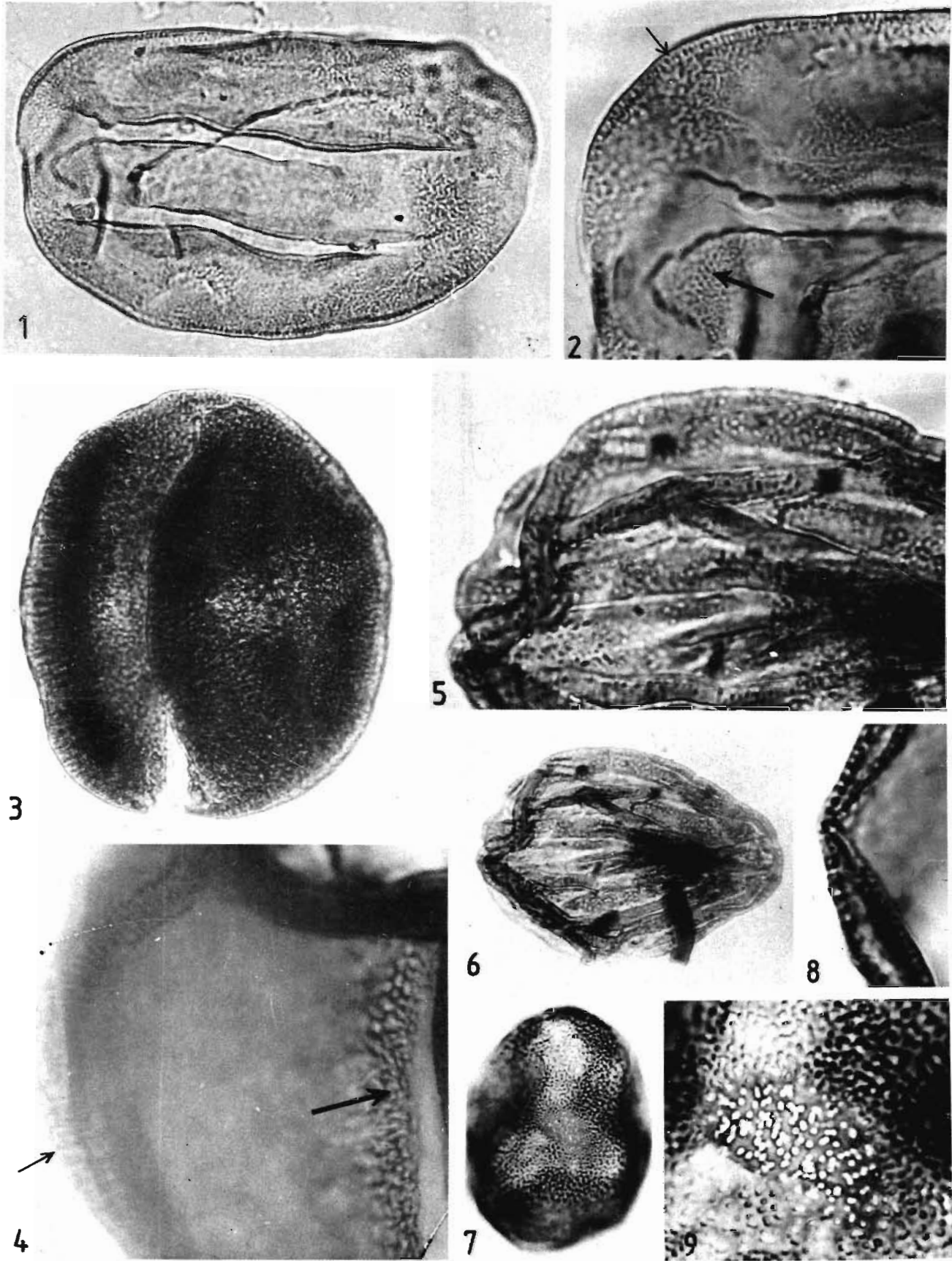
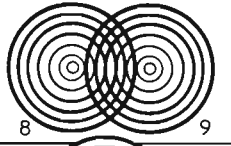
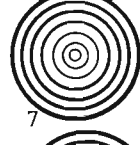
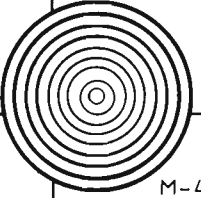
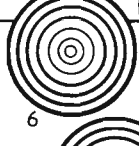
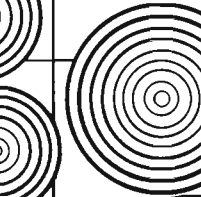

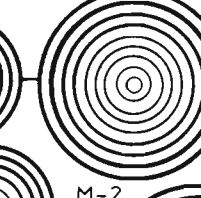
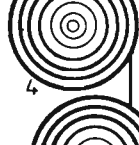
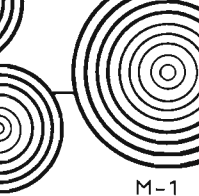

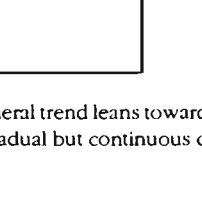
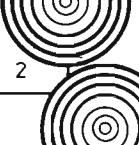
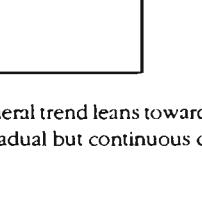
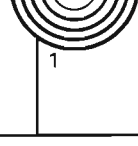
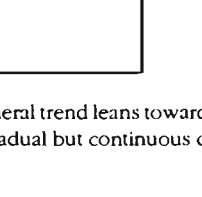


PLATE 1

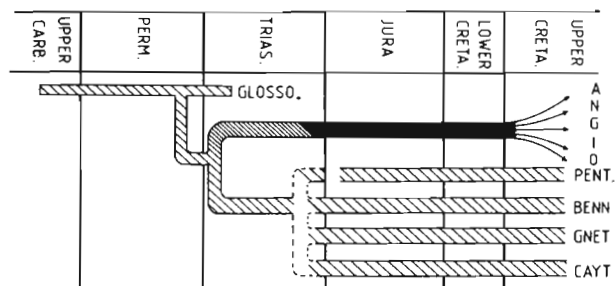
PERIOD	STRESS ZONES & SETTING-IN OF CHANGES	ANGIOSPERMID MICRO-PATTERN	MAIN-STREAM ANGIOSPERM PATTERNS	ALLIED PATTERNS
LATE CRETACEOUS	ANGIOSPERM DIVERSIFICATION	PROLIFIC ANGIOSPERM		
EARLY CRETACEOUS	ESTABLISHMENT OF ANGIOSPERM PATTERNS VISIBLE ANGIOSPERM MAIN PATTERN	TRICOLPITES STELLATOPOLLIS LILIACIDITES CLAVATIPOLLENITES RETIMONOCOLPITES BENNETTITALES - PENTOXYLAE DIVERSE		
JURASSIC	IV STRESS ZONE SETTING-IN OF CRETACEOUS FLORA	CLASSOPOLLIS. COLPATE POLLEN		
TRIASSIC	III STRESS ZONE EVOLUTIONARY SHIFT II STRESS ZONE	PENTOXYLAE BENNETTITALES STAUROSACCITES BRACHYSACCUS INFERNOPOLLENITES CORYSTOSPERMS NON-STRIATE BISACCATE POLLEN MONOCOLPATE COSTATE, GNETALES		
PERMIAN	EVOLUTIONARY SHIFT ANGIOSPERMID MICRO-PATTERNING ESTABLISHED I STRESS ZONE	CORNETIPOLLIS DAMINITES PLAYFORDIASPORA PROTOEUSACCITES COSTATE POLLEN COLPATE POLLEN GLOSSOPTERIS LEAF DICTYOPTERIDIUM		
CARBONIFEROUS	ORIGIN OF GLOSSOPTERIS ANGIOSPERMID MICRO-PATTERNING			
				
				

Text-figure 5—The setting-in of angiospermid character-states in micro (91-9) and mega-fossils (M-1 to M-4). The general trend leans towards main stream angiosperm pattern along the path of time. The various stress-zones have been the causal factors for gradual but continuous change. The circles represent the path of evolutionary shifts and continuity of angiospermid signatures through time.

angiospermization of patterns (Text-figure 6). The Jurassic *Classopollis* group and ultimately Lower Cretaceous angiospermid pollen (Tripathi, 1993; Tiwari & Tripathi, 1995) usher into a state where angiosperms become prominently 'visible'. The bisaccate pollen in Jurassic are regarded as comprising only a slightly modified version of the monosulcate.

DISCUSSION AND CONCLUSIONS

Towards the end of Carboniferous Period, on the Gondwanaland, the micropattern of angiosperm-like leaf was expressed in the *Glossopteris* plant. In some of the pollen-producing organs of *Glossopteris*, monocolpate character in the pollen was also manifested. With these initial micro-patterns, the



Text-figure 6—Relational aspect of *Glossopteris* "root" with angiosperm and other groups of plant. Diagram partially based on available data on cladistics. The closer oblique line on angiosperm stalk indicate differentiation in characters and solid black suggests the period of character establishment on the Gondwanaland which suddenly diversify during Late Cretaceous.

origin of angiosperm was set in. The proliferation of *Glossopteris* flora through the Permian on the Gondwanaland was unidirectional, in as much as no evolutionary shift is on record during this span of period.

At the end of Permian, a major evolutionary shift was initiated. Attempts towards achieving angiospermoid character in *Protoeusaccites*—with half alveolate fill sacchi, and more so in *Playfordiaspora*—single layered reticulate-tectate ectexine detached from endexine, were made. The taxa *Cornetipollis*, *Daminites* and *Praecolpatites* also contributed in making the angiospermoid micro-pattern at the P/Tr boundary. This micro-patterning in pollen morphology at the end of the *Glossopteris*—stock was more definitive and assertive of establishing the lineage of angiosperm group (Text-figure 2).

During Middle and Late Triassic the evolutionary shift did not take place in plants till the end of Triassic. The micro-patterns supportively established in the plant megafossils—Bennettitales and *Pentoxylon*, which flourished in Early Cretaceous. The diversified population of monocolpate, costate, striate non-saccate pollen in the Triassic-Jurassic sequence is the reflection of angiospermous patterning. The pollen and the flower-bearing plants of Mesozoic Period do not require to exhibit typical characters of modern angiosperms, as one adamantly expects, and they are nothing but micro-patterns of angiospermous population.

Early Cretaceous witnessed the separation and drifting of land masses in the Gondwanaland which in all probability had well established angiosperm

patterns of certain characters at Permo/Triassic time and appear to be visible only in the Hauterivian time. The Early Cretaceous evidences are apparently rare but definite in pollen morphology. The Aptian-Albian was the "take-off" pad, as we see it.

The question—When did angiosperms originate?—does not require much of a direct answer. The origin of *Glossopteris* at Late Carboniferous initiated "angiospermy" in leaf and some pattern in pollen. The terminal phase of *Glossopteris*, i.e., at the end Permian, established their origin in varied ways. The other questions are equally important—why there are no definitive angiosperms in pre-Cretaceous Period and why did they suddenly upsurge in the Upper Cretaceous? The upland origin and hence non-preservation of their organs is no answer to this question. At least pollen get preserved in all conditions except highly alkaline milieu. It is opined here that the angiosperm organs including pollen have been preserved and studied but have not been ascertained to be so, because one "wants" to see typical characters of the extant forms in the fossils, which one will never get. The existing data is rich enough but only the angle of looking at them has to be changed. All micro-patterns, i.e., the signatures of angiosperm character-states, must be taken as the evidences for the existence of angiospermous lineages during pre-Cretaceous Period (Text-figure 5).

It is, therefore, concluded that the great *Glossopteris* was the base stock of angiosperms, which group arose during Permian, and branched off into other groups, such as Pentoxylales, Bennettitales, Gnetales and Cytoniales in the Early Triassic which persisted during rest of the period. The other stock of angiospermic traits continued subduedly till Early Cretaceous in several forms of micropatterns not necessarily matching with typical living angiosperms, and then diversified subsequently. The rate of evolution was at low pace during most of the Triassic and no major shift occurred except at the end Triassic and mid Jurassic. The Upper Jurassic flora and that of the Lower Cretaceous had a continuity of quality. The DNA studies also support a long pre-Cretaceous history of angiosperms and the similarities of forms in pollen at several levels of morphology continues to support such propositions.

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