Evolutionary reproductive biologies in the Mesozoic plants of India

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The reproductive biologies in the Mesozoic plants are dealt with taking into consideration form and function of the reproductive organs. The Mesozoic flora inherited homospory, heterospory, pollen and seed formation from their Palaeozoic ancestors. Most of the Palaeozoic forms vanished by the close of Permian due to change of environment. The Triassic Period nursed the leftovers from the Permian as well as putforth new elements like *Lepidopteris, Dicroidium* and allied genera of Peltaspermaceae, Corystospermaceae and members of Caytoniaceae in which the seeds were protected in cupules. Thus the development of cupule in these genera changed the course of plant evolution. Later, with the amelioration of climate the cycads grew to prominence with exposed seeds, and subsequently they were overtaken by the rise of more advanced conifers. Meanwhile this flora also produced 'flower-like' structures in the cycadeoides and 'fruit-like' structures in Caytoniales and Pentoxyleae by providing fleshy growth around the seeds. The hot, arid conditions again reoccurred towards the close of Early Cretaceous. At this time the angiosperms appeared with enclosed seeds, heralding another change in the course of plant evolution.

Key-words—Reproductive biologies, Evolution, Mesozoic plants.

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सारॉंश

भारत के मध्यजीवी पौधों में जननांगीय विकास

सुख-देव

जननांगों के आकार एवं कार्य को ध्यान में रखते हुए मध्यजीवी पौधों के जननांगों का वैकासीय अध्ययन किया गया है। मध्यजीवी वनस्पतिजात को, समबीजाणु, विषमबीजाणु, परागकण एवं बीज बनने की प्रक्रिया अपने पूर्वज पुराजीवी वनस्पतिजात से उपलब्ध हुए हैं। वातावरण में परिवर्तन के कारण अधिकतर पुराजीवी प्ररूप परमी कल्प के समाप्त होने तक विलुप्त हो गये। शेष बचे प्ररूप त्रिसंघी कल्प में विकसित हुए तथा पेल्टास्पर्मेसी, कोराइस्टोस्पर्मेसी तथा केटोनिएसी से सम्बद्ध प्रजातियाँ तथा **लेपिडॉप्टेरिस** एवं **डाइक्रोइडियम** नामक नये वर्गकों की उत्पत्ति हुई। इन सभी प्रजातियों में प्यालिका के विकास से पादप-विकास में एक महत्वपूर्ण परिवर्तन हुआ। बाद में जलवायु में सुधार होने के कारण साइकेड पादप-समूह की बाहुल्यता हो गई जिनमें कि बीज नग्न थे। इनके बाद अधिक विकसित कोनिफ़रों की उत्पत्ति हुई। इसी बीच इस वनस्पतिजात से साइकेडों में 'पुष्प-सदृश' संरचनाओं तथा केटोनिएल्स एवं पेंटॉक्सीली में 'फल-सदृश' संरचनाओं का विकास हुआ। प्रारम्भिक क्रीटेशी के समाप्त होते-होते गर्म तथा शुष्क परिस्थितियाँ पुनः लौट आईं। इसी समय आवृतबीजीयों की उत्पत्ति हुई जिनमें कि बीज एक आवरण से ढ़के हुए रहते हैं।

THE Mesozoic Era in the beginning not only nursed the scanty vanishing leftovers from the Permian, but also successfully gave rise to various plant groups, such as new pteridosperms, cycads, cycadeoides, ginkgos and conifers which reigned supreme on land alongwith Caytoniales and Pentoxyleae. The origin, development and radiation of angiosperms also took place in the upper part of this Era. The evolutionary aspects in the reproductive biologies of Mesozoic plants exhibit prominent successful selective characters inherited from the Palaeozoic flora. Reference to Palaeozoic forms is made in order to understand the Mesozoic reproductive biologies. Some important ones are discussed below.

The pioneer land plants, e.g., *Rhynia, Horneophyton, Cooksonia, Baragwanathia* and many others invaded the land from the sea and surmounted several hurdles to make land their

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permanent abode. The early plants being delicate were easily perishable and hence were rarely preserved. Whereas the spores being made of resistant sporopollenin had better chances of preservation, therefore, they are commonly encountered in the dispersed condition in rocks. Moreover, the spores are unique structures for the preservation of the progeny of plant communities. These early spores had marine ancestory, therefore they preferred moist conditions for their terrestrial life.

The second most significant adventive and selective development was heterospory in the land flora in the later Devonian time in certain plants. *Lepidodendron, Sigillaria, Bothrodendron* and species of *Selaginellites* are the best examples in the development of heterospory, though homospory is still continuing in Psilotaceae, Lycopodiaceae, Equisetaceae and all ferns excepting Hydropterideae. Heterospory laid foundation for cross-fertilization and it was a step towards the seed formation.

Heterospory was established firmly in the Carboniferous. It was followed by reduction in the number of megaspores and increase in their size in a megasporangium, thus supplying nourishment for the surviving megaspores—two megaspores in *Stauropteris burntislandica*, a pteropsid, and a single megaspore in *Lepidocarpon*. The megasporangium was protected by overgrowths of bracts as found in *Miadesmia membranacea*—a Carboniferous lycopod. Thus a 'seed-like' habit was initiated, paving a way for the 'true seed' development.

In the dispersed megaspores the wall was quite thick. But as the megaspore was protected by nucellus and integument during the course of time the purpose of thick wall became unnecessary. A pteridosperm seed *Stephanospermum elongatum* is the thickest known, 18-35 μm (Hall, 1954). In the present plants the seed coat thickness is 10 μm in *Dioon edule*, 4.6 μm in *Abies balsamea*, 3 μm in *Pinus sylvestris*, 2.7 μm in *Sequoia sempervirens*, 1.3 μm in *Welwitschia*, and in angiosperms wall thickening is not very significant (Mehra, 1974).

In spore evolution from spore to pollen, the germination in the spores was through a trilete/monolete suture on the proximal surface in the pteridophytes. Several prepollen in many of the early gymnosperms retained this mode. Later, the dehiscence mark shifted to the soft distal surface of pollen in most of the gymnosperms. A pollen tube developed from this sulcus. Primarily it was haustorial in function and also carried male gametes. Whereas the angiosperms developed colpi and pores for the germination of pollen tubes on the stigma of carpel.

THE MESOZOIC ERA

Phase I : Protecting seeds in the cupule

Towards the close of the Palaeozoic Era due to changes in climate and environment towards hot and arid conditions most of the forms of this Era died out, leaving behind some ramnants. In response to the prevailing conditions the Triassic Period putforth new elements, namely *Lepidopteris, Dicroidium* and allied genera belonging to Peltaspermaceae and Corystospermaceae in the Gondwanaland and *Thinnfeldia* in the northern countries . Along with these genera ferns, glossopterids and horse-tails in lesser number and smaller size, cycads, ginkgos and conifers also constituted part of the flora.

Peltaspermaceae and Corystospermaceae

Text-figure 1A-H

Leaves *Lepidopteris* and *Dicroidium* belonging to Peltaspermaceae and Corystospermaceae are found in the Triassic sediments of India, but only few species of pollen-bearing organs *Pteruchus* of *Dicroidium* of the latter family have been discovered so far (Srivastava, 1987).

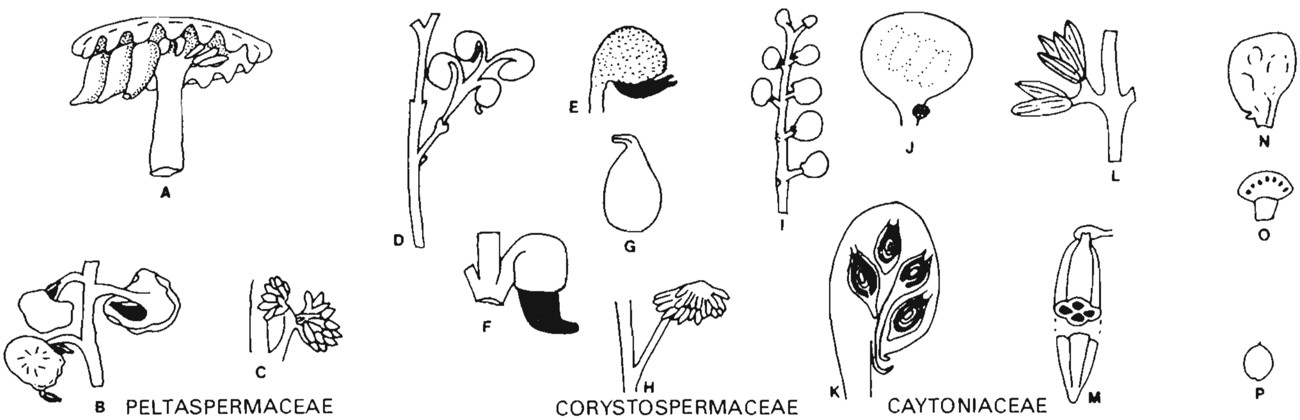
The seeds in *Lepidopteris* were small, borne singly in cupule with a characteristic curved micropylar beak and pinnately arranged on the stalk (fertile frond). Seeds in *Dicroidium* (genus *Umkomasia*) also had long curved bifid micropylar beak of the cupule which had stomata on both the surfaces. Seeds were also borne singly in the cupule.

The pollen-bearing organ *Antevsia* of Peltaspermaceae had 4-12 pollen sacs on the ultimate branches of bipinnate sporophyll. Pollen sacs were photosynthetic on the dorsal surface and had a longitudinal dehiscence line on ventral surface. Pollen grains were circular with a single longitudinal furrow. Pollen-bearing organ *Pteruchus* of *Dicroidium* had a central axis, bearing short lateral branches in one plane. Each branch terminated in a peltate head having more than 30 sporangia on the underside. Dehiscence was by a longitudinal slit. Pollen grains had two large lateral bladders.

Remarks—Pinnate nature of fertile leaves (stalk) and their photosynthetic character signify their primitive frond character.

Caytoniaceae

Text-figure 1I-M



Text-figure 1—Peltaspermaceae : **A.** Reconstruction of seed-bearing organ *Peltaspermum rotula*, disc with three cupulate-seeds, × 1.5; **B,** Part of *P. thomasii*, × 1.5; **C,** Part of pollen-bearing organ *Antevsia zeilleri*, × 1. Corystospermaceae : **D,** Part of *Unkomasia macleanii* seed-bearing organ, × 1; **E,** *Pilophorospermum granulatum* cupulate-seed, × 3; **F,** *Pilophorospermum* sp. cupulate-seed, × 3; **G,** Seed, × 4; **H,** Part of *Pteruchus stormbergensis* pollen-bearing organ, × 1.5. Caytoniaceae : **I,** *Caytonia nathorstii* fruit-bearing rachis, × 1.5; **J,** *C. sewardii* fruit, × 3; **K,** L.S. of *Caytonia* fruit; **L,** Part of *Caytonanthus arberi* pollen-bearing organ, × 2; **M,** Reconstruction of *C. arberi* before dehiscence, × 10. (A, C, based on Harris; B, D-H, Thomas).

Seeds were borne in fruit-like structures or cupules which enclose variable number of seeds covered by juicy pulp. Fruits were borne on a dorsiventral rachis (megasporophyll, primitive character). A flange was present towards one side of fruit close to rachis which had about the same number of ridges as the seeds inside. Only *Caytonia* seeds are discovered in the Chawad River sediments in Kutch (Bose & Banerji, 1984).

Pollen-bearing organ *Caytonanthus* is a 4-lobed synangium, borne terminally on branches of a dorsiventral rachis. Pollen grains had two lateral bladders.

Affinity—Caytoniaceae once created a great stir regarding the origin of angiosperms.

1. Flange of the fruit was earlier considered a kind of stigma where pollen grains germinated—an angiosperm character. But later it was discovered that actually the pollen reached each seed through a separate passage in a drop mechanism as in many living gymnosperms.
2. *Caytonanthus* was considered an angiosperm stamen, but it was radial in symmetry lacking filament and connectives in contrast to angiosperms.

Remarks—The aforementioned three families, viz., Peltaspermaceae, Corystospermaceae and Caytoniaceae did not have favourable mechanism of pollination. The first two families had curved micropyles while in Caytoniaceae the pollen were sucked in through different passages. These mechanisms were devised to protect seeds from hot air reaching directly inside the cupules. As the environmental conditions worsened, *Lepidopteris*, *Dicroidium* and allied genera of Peltaspermaceae and Corystospermaceae vanished by the end of Triassic. In Caytoniaceae juicy pulp around the seeds was provided, which was possibly meant for protecting them from arid environment. Caytoniaceae had rather tough leaves and also poor pollination mechanism, so members of this family did not flourish well and died out by Early Cretaceous.

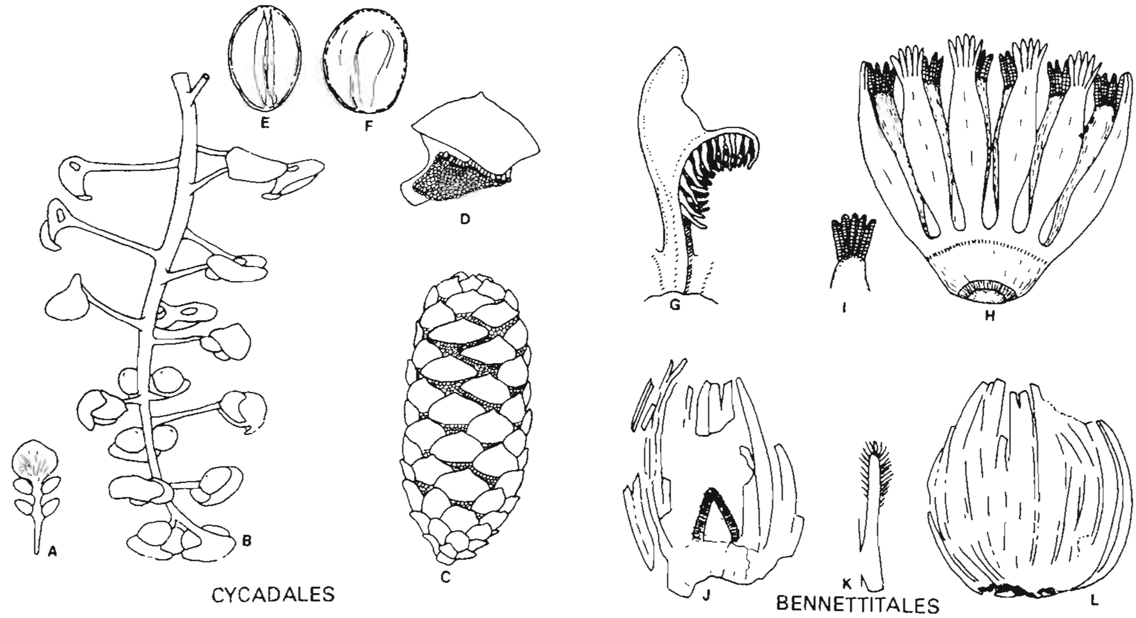
Phase II : Exposing the seeds

Cycadales

Text-figure 2A-F

As the environment became favourable for plant growth, the cycads having large trunks and cones with naked seeds gained prominence. They were abundant in the Jurassic with world-wide distribution; presently they are restricted to Central America, South Africa, Eastern Asia and Australia. They are represented by 10 genera having about 65 species. In gymnosperms, cycads were the first to have cones. Cycad leaves like *Morrisia, Cycadites* and *Taeniopteris* are commonly found in the Mesozoic rocks of India, but their reproductive organs are yet not recovered.

One of the most informative and well known association is of *Nilssonia* leaves, *Beania* seeds and *Androstrobus* pollen organs occurring together in the Middle Jurassic sediments of the Yorkshire coast in England. *Beania gracilis* is a loose cone up to 10 cm long. It bears spirally borne appendages having two seeds on inner side. The largest seed is 16 × 13 mm. Another plant *Beania mamayi* occurring in the Yorkshire Coast sediments had bifid



Text-figure 2—Cycadales : **A**, *Palaeocycas integer* sporangiophore with seeds, × 1/12; **B**, lose 'seed-cone' *Beania gracilis*, × approx. 1/2; **C**, Microsporangiate cone—*Androstrobus manis*, × approx. 1; **D**, Microsporophyll of *A. manis*; **E, F**, pollen grains of *A. manis*, × 400. Bennettitales : **G**, Microsporophyll of *Weltrichia santalensis*; **H**, Reconstruction of *Weltrichia harrisiana* 'male flower'; **I**, Apical part of microsporophyll; **J**, 'Female flower' *Williamsonia kakadbhitensis*, receptacle part slightly modified, × 1/2; **K**, Bract hairy towards apical portion × 1/2; **L**, *W. kakadbhitensis*, × 1/2. (A, based on Florin; B-F, Harris; G, Sitholey & Bose; H-L, Bose & Benerji).

sporangiophores. *Androstrobus manis*, a male cone is about 5 × 2 cm. It bears numerous spirally borne sporophylls, each of which had several cylindrical sporangia containing monosulcate oval pollen grains, typically 36 × 26 μm.

Florin reconstructed a plant *Palaeocycas integer* from the Upper Triassic rocks of Sweden, which bears simple leaves—*Bjuvia simplex* and female sporangiophores—*Palaeocycas integer* terminally on the stem. The sporophylls had probably seeds on the sides of lower portion as in modern *Cycas*, a primitive character still continues today.

Remarks—Though the cycads were abundant in Jurassic-Early Cretaceous in xerophytic habitat, their slow growth, manoxylic stems, large terminal cones and lax female cones later proved as to be drawbacks in comparison to the more advanced conifers. Therefore, the cycads declined, their reproductive biology failed to compete with the vigorously advancing conifers.

Bennettitales (Cycadeoidales)

Text-figure 2G-L

The order is characterized by 'flower-like' structures which appeared for the first time in gymnosperms. The flowers were hermaphrodite or unisexual, protected by numerous bracts. Ovules were stalked, scattered over a receptacle amongst interseminal scales. Micropyles were projected through the loose shield formed by interseminal scales. Pollen-bearing organs were arranged in a whorl. They were free or united, entire or pinnate, having numerous microsporangia borne usually in capsules. Presence of syndetocheilic stomata is also a significant character. Stems, leaves and 'flowers' are commonly found in the Jurassic-Cretaceous rocks of India.

Williamsonia sewardiana is reconstruction of the plant from the Lower Cretaceous of Rajmahal Hills. A lateral branch of 2 m tall slender stem terminates in a female flower having interseminal scales and few seeds. Leaves belong to *Ptilophyllum cutchense*. Male, female and bisexual flowers have also been found (Bose, 1966, 1974; Bose & Banerji, 1984).

Affinity—The flower of Bennettitales shows some similarity in its general organization with the *Magnolia* flower (angiosperm) as its microsporophylls surround the receptacle at its base. The group has been considered as an ancestor of angiosperms. But the bennettitalean flower is quite different in having stalked seeds and interseminal scales from that of *Magnolia* flower.

However, it is quite noteworthy that the bennettitalean flower deviated from the general plan of similarity from the fossil and living cycads. Probably these flowers amused the dinosaurs. However, the flowers were insect pollinated (Crepet, 1974; Taylor, 1982).

Ginkgoales

Text-figure 4A

The ginkgolean remains in the Mesozoic rocks in India are meagerly represented. However, the group had a glorious past with many genera and species spread world over during Jurassic-Early Cretaceous. The group dwindled sharply and is survived by *Ginkgo biloba* only. The terminal seeds and motile sperms of *G. biloba* are features of great antiquity.

Seeds of *Ginkgo* have been described by Zeba-Bano *et al.* (1979) from Pathargama from Lower Cretaceous of Rajmahal Hills. The seeds had an outer fleshy and inner stony layer. The fossil female strobilus differs from *G. biloba* in the absence of seed 'collar' and smaller size of the seeds.

Pentoxyleae

Text-figure 3A-E

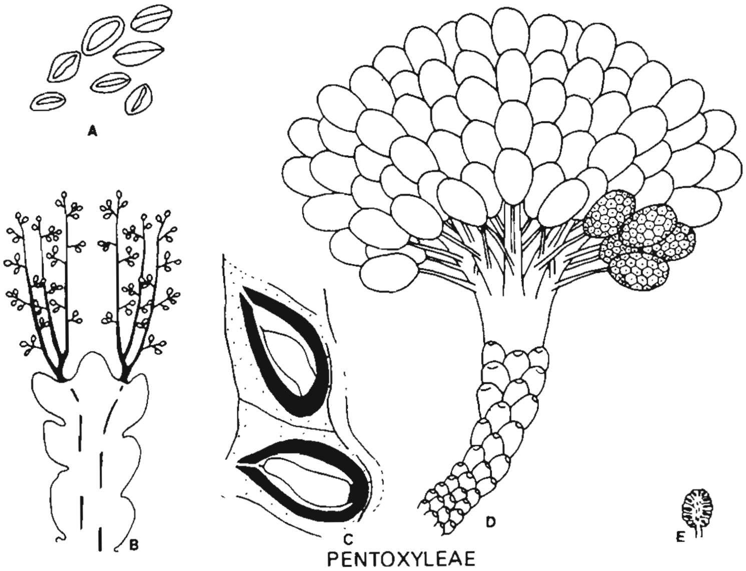
In Pentoxyleae the female cones *Carnoconites* consisted of sessile seeds with inner stony layer of integument and outer fleshy layer by which they were closely united together looking like stalked mulberries. Male flower—*Sahnia* had sporangiophores borne on raised collar-like margin of receptacle with simple pollen sacs. Pollen grains were boat-shaped, monocolpate, 25-26 × 10-25 μm with smooth exine.

Affinity—Sporangiophores of male flower in Pentoxyleae apparently look like the bennettitalean ones, but their detail structure is altogether different from the latter female flower in lacking interseminal scales and stalked seeds. Stomatal structure and leaf-trace anatomy of the Pentoxyleae resemble cycads but the former lacks cycadean encircling girdles. Pentoxylon has pycnoxylic wood like conifers. Polystelic stem of Pentoxyleae resembles Medullosacean woods of *Medullosa* and *Rhexoxylon*, but differs in having stachysporous reproductive organs. Meeuse (1961) considers Pentoxyleae as the possible ancestor of angiosperms.

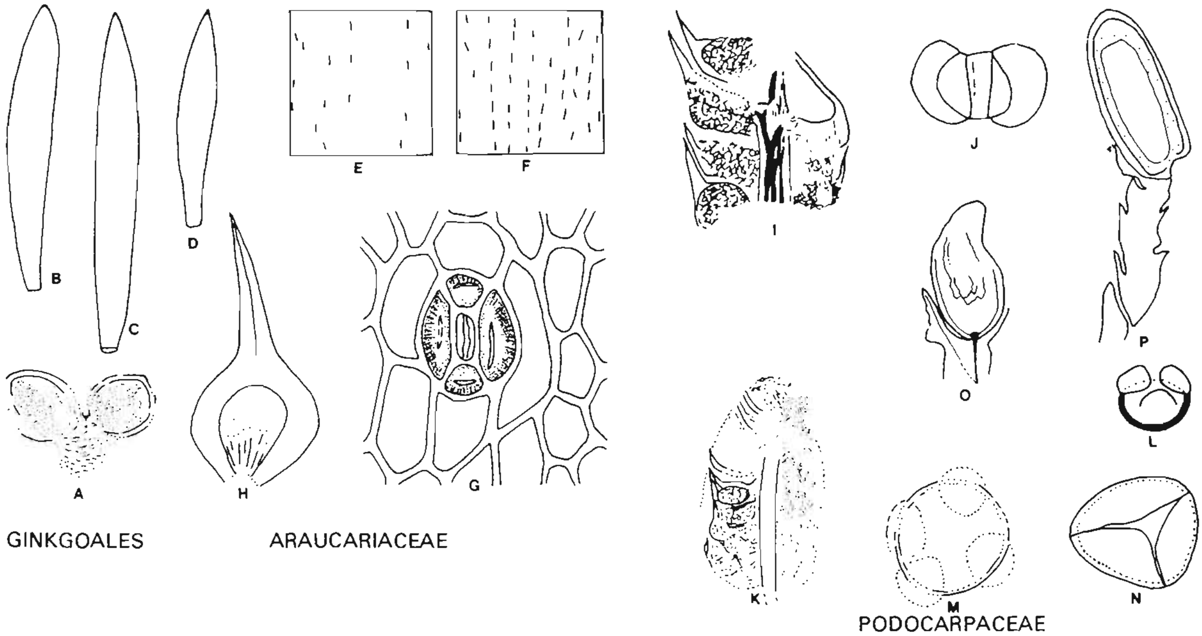
Remarks—In the adventive and selective character experimentation, Pentoxyleae offers the best example of synthesis of characters from various plant groups. It combines characters of Medullosaceae, Bennettitales, Cycadales and Coniferales as mentioned above, but unfortunately this combination of characters did not prove stable and hence Pentoxyleae did not flourish for long. Pentoxyleae probably remained a small localized group in the Early Cretaceous. This group is known only from a few countries—India, New Zealand and Australia.

Coniferales

Text-figure 4B-F



Text-figure 3—Pentoxyleae : **A,** Pollen grains of *Sahnia nipaniensis*, × 150; **B,** Reconstruction of *Sahnia nipaniensis* flower; **C,** *Carnoconites compactus* showing two seeds with inner stony (black) and outer flesly (dotted) layers of integument, × 5; **D,** Reconstruction of *C. compactus* borne on short shoot; **E,** L.S. of *C. compactus*, × 1/2. (A, based on Vishnu-Mittre; B-D, Bose, Pal & Harris; E, Sahni).



Text-figure 4—Ginkgoales : **A**, Strobilus with two seeds, × 2. Araucariaceae : **B-D**, Leaves of *Araucaria indica*, × 1; **E,F**, Distribution and orientation of stomata in 1 sq mm of ?upper and ?lower surfaces of leaves; **G**, Stoma and epidermal cells of leaf, × 250; **H**, Seed-scale, × 1. Podocarpaceae : **I**, Part of microstrobilus *Podostrobus rajmahalensis*, × 13.5; **J**, *in situ* pollen grain, × 265; **K**, *P. sahnii*, × 7 5; **L-N**, *in situ* pollen grains, × 250(L), × 425(M, N); **O**, *Mehtaia rajmahalensis*, seed with bract-scale and vascular supply, × 14; **P**, *Sitholeya rajmahalense*, apical inverted ovule with fertile bract, × 6.5. (A, based on Zeba-Bano *et al.*; B-H, Sukh-Dev & Zeba-Bano; I-N, Rao & Bose; O, P, Vishnu-Mittre).

During Mesozoic time, members of Araucariaceae and Podocarpaceae were abundant in India. The conifers exhibit comparatively a greater economy in the production of cones than the less advanced fossil and living cycads. Further, the cones in conifers are spread over large areas on the tree-branches rather than being borne terminally on the stems in cycads. These features possibly improved the pollination process, favouring the dominance of conifers over the cyads.

ARAUCARIACEAE

Text-figure 4B-H

In the Mesozoic rocks of India Araucariaceae is represented by detached leaves, leafy-twigs, female cones, detached seed-scales and petrified woods.

Bose and Jain (1964) referred to an incomplete megastrobilus of Araucariaceae on the basis of its compact nature, spirally borne non-ligulate megasporophylls having a single seed embeded medianly.

Sukh-Dev and Zeba-Bano (1978) instituted *Araucaria indica* plant, based on cuticular similarity of seed-scales *Araucaria indica* Bose & Maheshwari with the leaves of *Desmiophyllum indicum* Sahni in the distribution and structure of stomatal apparatus. Further, both these organs are found in close association in Bansa, Chandia, Jabalpur, Sehora, etc. in the Jabalpur Formation, Madhya Pradesh. Florin (1937) had already stated that in structure and distribution of stomata the *Desmiophyllum* leaves indeed belong to the living genus *Araucaria*.

PODOCARPACEAE

Text-figure 4I-P

Male and female cones of Podocarpaceae are reported from Rajmahal Hills, Bihar.

Podostrobus sahnii (Vishnu-Mittre) Rao & Bose 1971 is a cone, 7 × 3.5 mm in size, bears closely and spirally arranged sporophylls on a slender axis which in turn produce a broadly ovoid sporangium on their lower surface. Distal part of sporophyll is turned upwards, attenuated and overlap the upper sporophylls. Sporangium contains numerous, 2-4 saccate (mostly 2-3 saccate) pollen grains.

Podostrobus rajmahalensis (Rao) Rao & Bose 1971 is about of the same size as *P. sahnii* except the sporangium containing bisaccate pollen grains.

Female cones, compact or lax, are also reported from Rajmahal Hills (Vishnu-Mittre, 1959) in which the single seeded scales are much reduced or absent and bear terminally erect or inverted ovules. They are known as *Nipaniostrobus, Nipanioruha, Mehtaia* and *Sitholeya*.

Phase III : Enclosing seeds in the carpel

Angiosperms

Text-figure 5A-F

The angiosperms are a dominant and most widely distributed plant group in the modern flora which is more advançed in having enclosed ovules or seeds in an ovary in contrast to the naked seeded gymnosperms. More than 200,000 to 300,000 species are described according to the type of classification one follows. At times ferns, pteridosperms, cycadeoides, Caytoniales, conifers, Gnetales, glossopterids and Pentoxyleae have been considered as the possible ancestors of angiosperms keeping in view character similarities of various plant parts, viz., stem, leaf, perianth, cupule, carpel, anther, flower, etc.

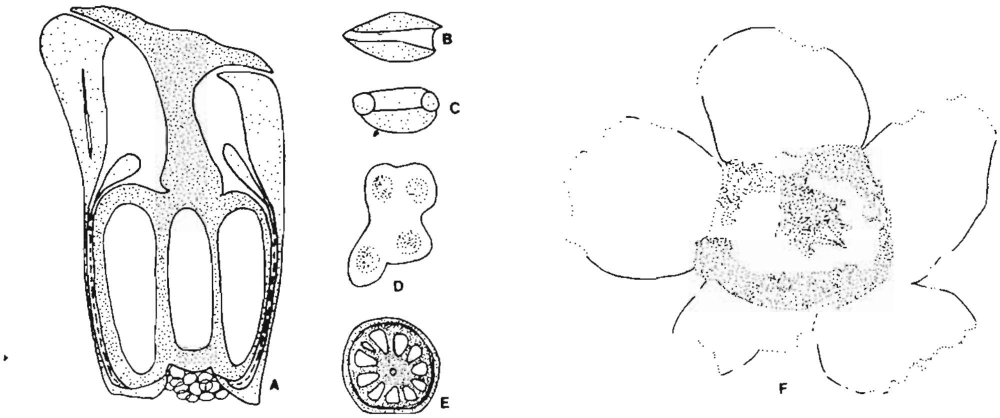
The gymnosperms of the Mesozoic Era were wind pollinated excepting Bennettitales which were partially pollinated by beetles (Crepet, 1972; Taylor, 1982). Before the close of Mesozoic, flower loving insects (anthophilous)—Coleoptera, Diptera, Hymenoptera and Lepidoptera had appeared. Therefore, a shift of wind pollination mechanism of gymnosperms over to insect pollination in angiosperms accelerated the pace of diversity of angiospermous flower in order to attract more insects.

Clavatipollenites is considered to be a primitive angiospermous pollen (Hughes, 1976; Doyle, 1978). It has a monosulcate aperture comparable to those of Cycadales, Ginkgoales, Bennettitales and Pentoxyleae. Therefore, the study of Early Cretaceous monosulcate type of pollen may reveal characters of the early angiosperm pollen.

ORIGIN OF ANGIOSPERMS

The Early Cretaceous (Aptian-Albian) *Weichselia-Onychiopsis-Gleichenia* Assemblage Zone 10 (Sukh-Dev, 1987) exhibited dry conditions by the presence of red beds at the top sediments in the Jabalpur Formation at Bansa, Jabalpur, Jatamao, Morand River in Madhya Pradesh, Rajmahal Hills in Bihar, and Himmatnagar in Gujarat. *Matonidium, Phlebopteris, Gleichenia* and *Weichselia* ferns with small thick, leathery leaves, recurved margins and sunken stomata occurred alongwith the decline of cycadophytes and conifers, coinciding with the successive erruptions of lava flows in the Rajmahal Hills area in Bihar. The hot and adverse environmental conditions once again subjected the existing plants to stress conditions and in response they quickly developed defensive mechanisms to protect their reproductive organs with the result several new forms appeared (as had earlier happened in the Early Triassic time). So a synthesis of already tested successful characters alongwith the development of new characters the coming up angiospermous group evolved rapidly. The following angiospermous characters are worthy to be considered for the evolution of angiosperms.

1. Carpel of angiosperms is a modified *Caytonia* cupule which had stigma-like structure and variable number of seeds.
2. Whorled arrangement of androecium in angiosperms is a derivation of similar arrangement occurring in Bennettitales and Pentoxyleae.
3. Fruit formation in angiosperms is a character of Caytoniaceae and Pentoxyleae where juicy growth or pulp was present around the seeds.



Text-figure 5—Angiosperms : **A,** L.S.—*Sahnipushpam shuklai* flower (semi-diagramatic), × 10; **B, C,** Pollen grains, dorsal and lateral views, × 500; **D,** T. S. anther having pollen grains, × 50; **E,** T. S. -ovary showing 11 loculii, × 5; **F,** Perianth of Siwalik angiosperm flower. (A-E, based on Prakash & Jain; F, Awasthi, Prasad & Antal).

4. Stamens possibly evolved from *Caytonanthus* (Caytoniales) which had bilateral symmetry of synangia in their early stages of development (Krassilov, 1977) like the bilateral angiosperm anthers and from *Williamsoniella* microsporophylls (Bennettitales) which are near to foliar angiosperm stamens.
5. Perianth in angiosperms probably developed from the bracts of the bennettitalean flowers which were protective in function. Later, the perianth differentiated into Calyx (protective) and Corolla (decorative and facilitating pollination).
6. Reticulate venation pattern of angiosperm leaves is borrowed from *Sagenopteris* leaves of Caytoniaceae.
7. Introduction of new character like double fertilization in angiosperms for the formation of endosperm is a new innovation of their own.

Consolidation of the earlier characters and innovation of new ones in due course of time proved very useful in the world-wide radiation of angiosperms from Early Cretaceous onwards to the present time. Thus the angiosperms have a polyphyletic origin. The arid environment in the Indo-European Palaeofloristic Province extending from Europe to India and South China to Japan supported xerophytic floras (Sukh-Dev 1987, Assemblage Zone 10) during Aptian-Albian. The structurally preserved angiosperm flowers with inferior ovary reported by Friis and Skarby (1981) from the Upper Cretaceous sediments of southern Sweden exhibiting rugged appearance possibly testify the prevalence of arid environment. The Indian angiospermous flower *Sahnipushpam* from the Deccan Intertrappean (Late Cretaceous of Eocene) from Madhya Pradesh and Maharashtra had a large, umbrella-shaped over-shadowing stigma and apically enlarged lysigenous perianth to provide shade and cut heat for the developing ovules or seeds and pollen grains in the ovary and stamen respectively (Text-figure 5A). These characters seem to have appeared in response to hot, dry atmosphere prevailing there due to intermittent lava flows. The structure of the *Sahnipushpam* flower from the Deccan Intertrappean and the asymmetrical perianth leaves of the flower from Siwalik sediments, Nepal (Awasthi *et al.*, 1990) also denote primitive angiospermous characters.

Recently, Tiwari and Tripathi (1990) reported angiospermous pollen from the Lower Cretaceous subsurface samples from the Rajmahal Hills. Further palynological investigations of the Lower Cretaceous sediments are the pressing need of the time to decipher early angiospermous characters.

CONCLUSIONS

In the course of evolutionary development in the reproductive biologies of Mesozoic plants in India, only significant characters from pteridosperms to cycads, cycadeoides, ginkgos, Pentoxyleae, conifers, ultimately leading to the origin of angiosperms are mentioned below:

The Mesozoic Era inherited an impoverished Palaeozoic flora characterized by homospory, heterospory, pollen and seed formations.

In response to the prevailing hot, arid environmental conditions in Early Triassic new forms—*Lepidopteris, Dicroidium* and allied genera of Peltaspermaceae, Corystospermaceae and members of Caytoniaceae appeared with their seeds covered in cupules. The seeds in Caytoniaceae were further provided with fleshy growth forming 'fruit-like' structures. *Lepidopteris, Dicroidium* and allied genera vanished by the end of Triassic Period. Members of Caytoniaceae continued to thrive up to Early Cretaceous.

As the climatic conditions improved for plant growth, the cycads gained prominence. They developed cones for the first time in the history of gymnosperms. The cones in cycads were terminal and large.

With the advent of Jurassic Period cycadeoides originated which resembled cycads in general habit but developed 'flower-like' reproductive organs.

Soon the conifers radiated to dominate the less advanced cycads and cycadeoides. They had small, compact cones spread over larger areas on the stem-branches.

In Early Cretaceous, a new small group Pentoxyleae combined the characters from Medullosaceae, cycads, cycadeoides, conifers and formed mulbery-like globose to elongate fleshy female cones and 'flower-like' male structures.

Towards the late Early Cretaceous (Aptian-Albian) a new group of angiospermous plants appeared with a unique carpel which covered and saved the ovules and seeds from drying up and produced true flowers and fruits. The angiosperms developed double fertilization for the formation of endosperm. The angiospermous pollen grains developed colpi or pores for their germination on the stigma of carpel. Several angiosperm characters have lineage with Caytoniaceae, Bennettitales and Pentoxyleae.

The Mesozoic Era seems to have influenced the course of plant evolution twice in response to the hot, arid environment prevailing during the Early Triassic, and Early Cretaceous times; the latter led to the rise of angiosperms.

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