



Revision of Early Cretaceous angiosperm remains from the Rajmahal Basin, India, with notes on the palaeoecology of the *Pentoxylon* plant

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ABSTRACT

In India, potential sources of angiosperm macrofossils are the intertrappean cherts of Rajmahal Hills, palynologically and radiometrically dated as Barremian–Aptian. However, our revision of the previously reported flower-like and fruit-like fossils from the Rajmahal Formation does not confirm their angiosperm affinities. Instead they are related to bennettitalean and pentoxylean gymnosperms. At the same time, the underground storage organs and supposed feeding marks on *Carnoconites* seeds revealed in the course of this study suggest angiosperm-like habits in the Indian *Pentoxylon* plant.

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1. Introduction

In wrestling with the problem of angiosperm origins, when and where questions are the most challenging, because they require not only adequate coverage of potential stratigraphic and geographic ranges, but also periodic reassessment of available paleobotanical data. The chronology of angiosperm origin is based primarily on palynological records. However, angiospermoid pollen grains of dubious, and most probably non-angiospermous affinities are known from the Early Permian (Tripathi, 1997; Zavalova and Gomankov, 2009) onwards. For the Mesozoic pollen morphotypes of this sort, a conventional assignment to angiosperms has yet to be confirmed by reliable *in situ* records (or rejected on the basis of *ex situ* nucellar pollen chamber records, documenting a gymnospermous pollination mode).

The geographic coverage of the advent of angiosperms by macrofossil records is so far sporadic, coming mostly from late Early Cretaceous deposits in North Atlantic coastal areas. A recent revision of relatively well-dated mid-Cretaceous sequences of the USA and Portugal indicates that angiosperm meso- and macrofossil

records are not older than Early Albian (Heimhofer et al., 2005, 2007; Hochuli et al., 2006). In the Lake Baikal area, Mongolia and China, age assignments of lacustrine shales with early angiosperms has shifted from Jurassic or Early Cretaceous 'Neocomian' to Aptian and Albian (e.g. Nichols et al., 2006). In addition, some alleged angiosperm fossils from these regions and the Middle East have been reassigned to gnetophytes (Krassilov et al., 2004).

Although a Gondwanan origin of flowering plants is a fairly popular hypothesis, the early history of this group is poorly represented over the larger part of Gondwana. For such countries as India with abundant fossil plant localities, evidence for early angiosperms is surprisingly meagre. All relevant finds come from Early Cretaceous deposits in the Rajmahal Hills (Fig. 1), discovered in 1860s and a source of important paleobotanical discoveries ever since.

In the Rajmahal Basin, fossil plants are represented by both petrified and impression/compression material coming from intertrappean deposits of the Rajmahal Formation, the geological age of which ranges from Berriasian to Aptian on palynological evidence (Tripathi, 2008). Tiwari and Tripathi (1995) reported *Clavatipollenites* and *Retimonocolpites* from the uppermost lower intertrappean Rajmahal deposits, radiometrically dated as 117 Ma, Aptian.

The macroflora of Rajmahal is essentially gymnospermous, with a subordinate fern component of marattiaceous, osmundaceous, and matoniaceous alliances. It is dominated by diverse bennettites

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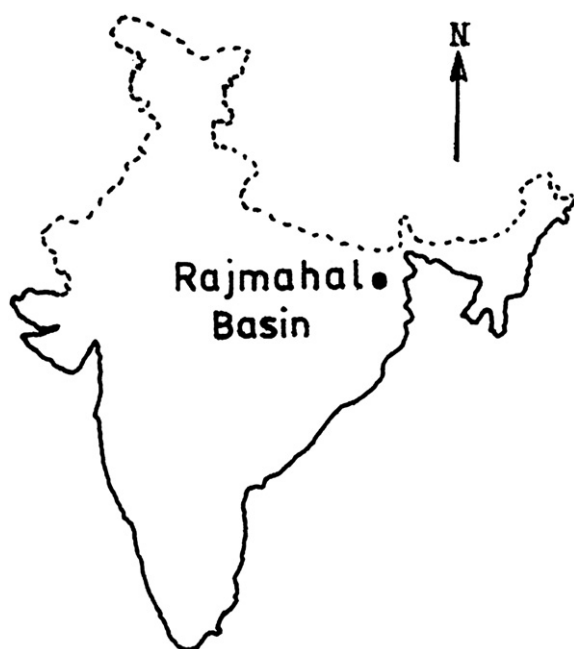


Fig. 1. Location of fossiliferous intertrappean deposits of Rajmahal Hills.

with leaf and fructification morphotypes known, with few exceptions, from European Jurassic and early Cretaceous 'Wealden-type' assemblages. In contrast, the conifers represented by seed/pollen cone material are mostly assigned to endemic genera of Podocarpaceae (Vishnu-Mitre, 1957; Banerji and Ghosh, 2006). The pentoxyleans, a Gondwanan group of Mesozoic gymnosperms with fleshy, fruit-like seed cones are fairly common in the Rajmahal Formation of the Nipania locality and elsewhere (Srivastava, 1946; Sahni, 1948; Bose et al., 1985).

The presence of angiosperms in Rajmahal Hill localities is unfortunately based on low reliability records. The vessel-less wood *Homoxylon rajmahalense* and *H. andrusii*, once thought to be angiospermous (Sahni, 1932), was reassigned to *Sahnioxylon* of putative bennettitalean affinity (Bose and Sah, 1954). There are three alleged fructification records assigned to angiosperms. Sharma (1997) described from the Amarjola locality fructification material resembling *Lesqueria*, a mid-Cretaceous infructescence from Kansas (Crane and Dilcher, 1984). Banerji (2000) described from the Sonajori locality an impression of a flower-like structure (unnamed) and a fruit-like body assigned to a new genus *Sonajoricarpon*. This was reconstructed as a pod with numerous seeds and compared with fruits of an extant fabaceous genus *Butea*. Banerji cautiously noted, however, that affinities of *Sonajoricarpon* to the Fabaceae or any other family of extant angiosperms remain uncertain.

2. Revision of angiosperm-like fossils

2.1. *Lesqueria*-like fossil from Amarjola

Sharma's (1997) *Lesqueria*-like fructification is a hemispherical structure on a short pedicel, covered with scale-like appendages. The Amarjola locality is exceptionally rich in bennettitalean remains (Bose, 1953a, 1953b, 1953c, 1968), including fructifications of *Amarjolia* (Bose et al., 1984) and several species of *Williamsonia* (Bose, 1968) with gynoecial structures of basically the same type as the *Lesqueria*-like fossil. Sharma (1997, p. 308) admitted that "the present specimen resembles in shape, size and plan of construction the bennettitalean seed-bearing fructification *Williamsonia* Carr.",

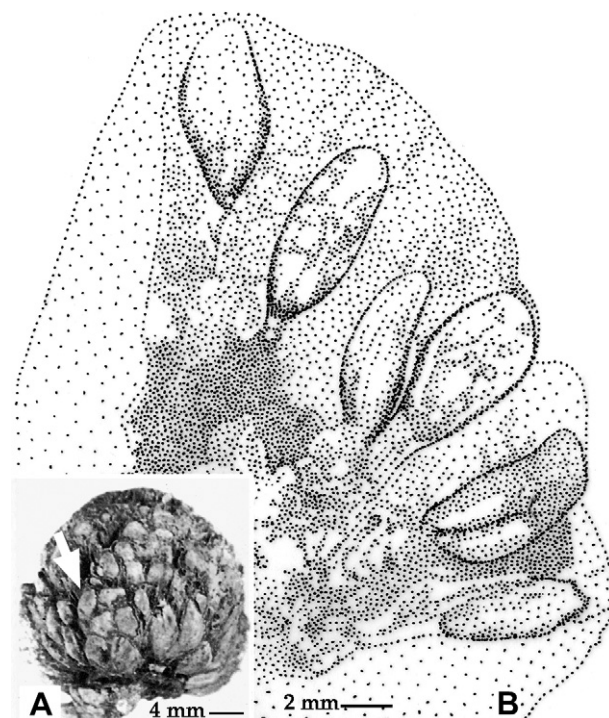


Fig. 2. *Lesqueria*-like fructification (Sharma, 1997), specimen no. BD101/RajA, Amarjola, Rajmahal Hills. A, receptacle with peltate scales (arrow), reproduced from Sharma (1997, fig. 1A). B, longitudinal section showing scales and stalked seeds, redrawn from Sharma (1997, fig. 1D).

but in his opinion the appendages represent follicles rather than orthotropous seeds and/or interseminal scales typical of bennettitalean fruiting structures. However the scaly appendages of the *Lesqueria*-like receptacle appear peltate like bennettitalean interseminal scales, while the elongate casts interpreted as empty locules of longitudinally sectioned follicles more likely represent stalked ovules adhering to interseminal scales. Our interpretation of these structures is given in Fig. 2.

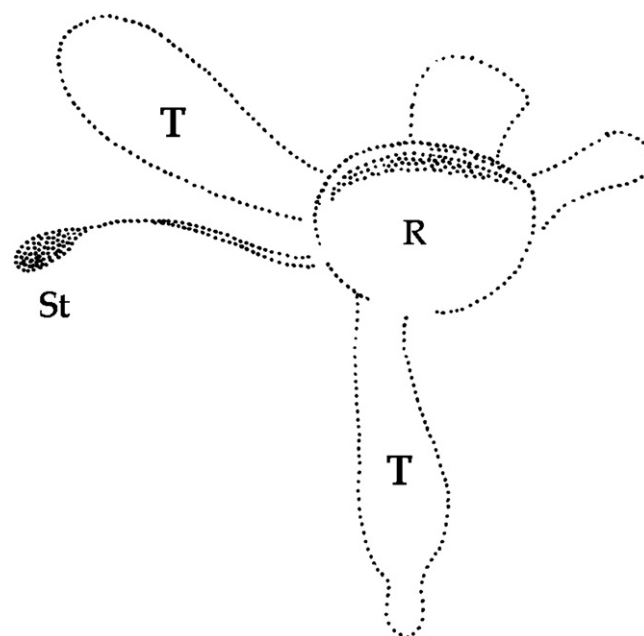


Fig. 3. Flower-like structure (Banerji, 2000), specimen BSIP no. 27233, Sonajori, Rajmahal Hills: reconstruction redrawn from Banerji (2000, fig. 6); St, stamen, T, tepal.

2.2. Flower-like structure from Sonajori

Banerji (2000) illustrated an elliptical body 2 mm long and a few vaguely marked structures supposedly radiating from it in the manner of perianth lobes. Her line-drawing also depicts stamen-like appendages attached between the lobes. It is redrawn in Fig. 3 with the omission of a “stamen” where no appendage was detected. The fossil is preserved on a slab of chert with many variously orientated seed casts and molds, most of which represent *Carnoconites*, the fruiting organs of *Pentoxylon* plant.

Carnoconites is a compact cone borne on a long pedicel and has closely packed seeds that are spirally arranged on a slender axis (Srivastava, 1946; Sahni, 1948; Bose et al., 1985). The seed coat consists of a hard sclerotesta composed of thick-walled stone cells and fleshy sarcotesta of thin-walled polygonal cells. Detached seeds on the Sonajori slab dimensionally correspond to *C. compactus*

Srivastava. Only stone shells are preserved, but vague impressions of sarcotesta are discernible on the cutting surface.

What has been described as a flower-like structure occurs among seed casts representing a heterogeneous assemblage in which a well-marked elliptical body 2 mm long in the middle (but not exactly in the centre) is recognizable as a stone cast of *Carnoconites* seed (Sc in Fig. 4). Thick-walled stone cells are discernible over the dark area in the micropylar part of it. Of the surrounding impressions interpreted by Banerji as perianth lobes, one is a longitudinally ridged axial structure (P in Fig. 4) showing corrugate surface markings as on the pedicels of *Carnoconites* cones amply illustrated by Sahni (1948, figs. 39 and 40) and elsewhere. It is conspicuously different from the rounded-ovate bodies (S on Fig. 3) that are irregularly clustered on the top of the pedicel. These bodies are identical to detached seeds, one of which is seen adjacent to the cluster. They are embedded at different levels, leaving

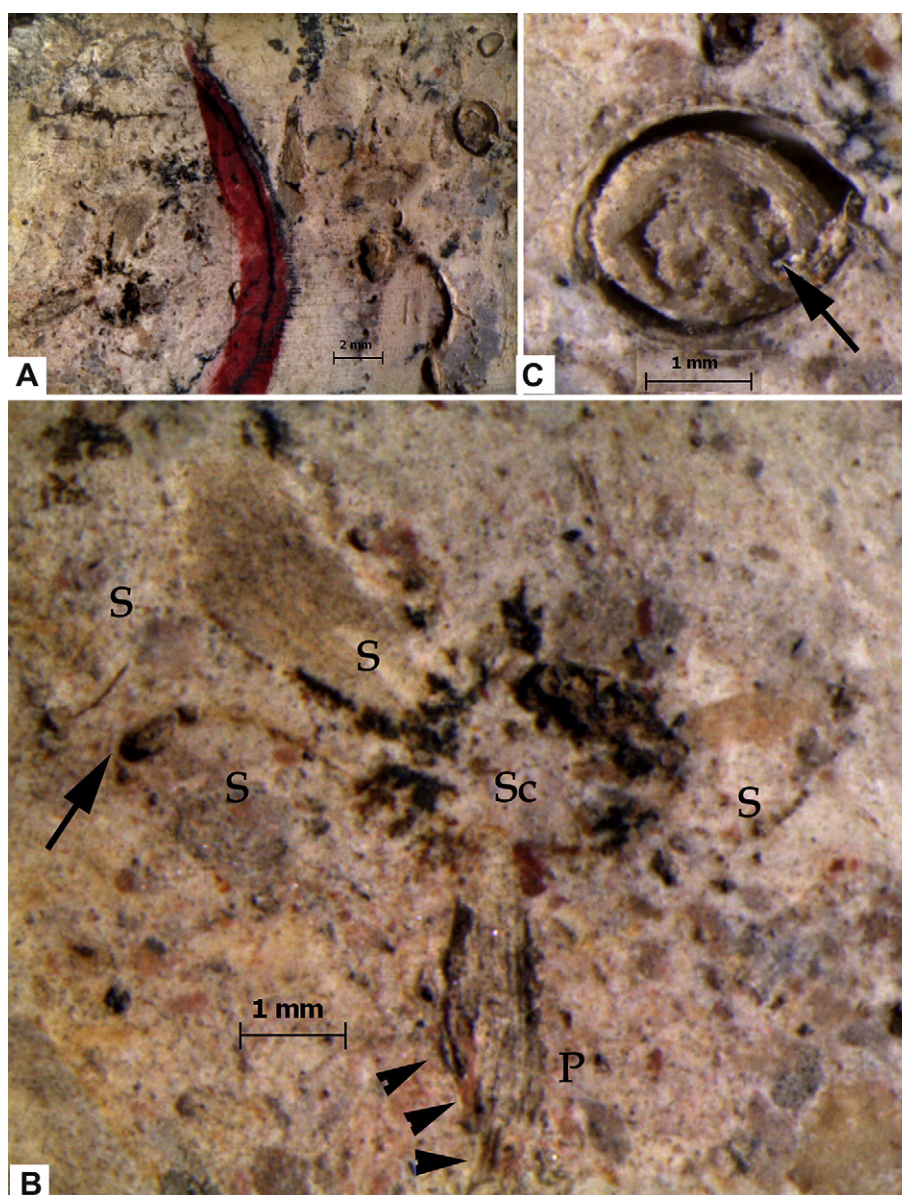


Fig. 4. Flower-like structure (Banerji, 2000), specimen BSIP no. 27233, Sonajori, Rajmahal Hills. A, flower-like structure, bottom left, among scattered casts of *Carnoconites* seeds. B, flower-like structure here interpreted as disintegrated *Carnoconites* cone; P, pedicel, S, seed impression representing outer coat (sarcotesta), Sc stone shell (sclerotesta); arrow on a splinter of sclerotesta figured as anther of a stamen in Fig. 3; arrowheads on a series of cutting scars across the petiole. C, stone shell showing a pair of punctures, probably a bite mark (arrow).

shadowy outlines alone or vaguely impressed, nearly smooth, showing files of thin-walled cells as in fleshy sarcotesta of *Carnioconites* seeds (e.g., Srivastava, 1946, fig. 65). Fragments of thick stone shells are here and there imprinted upon the outer seed coat. One such piece of stone shell over an arching outline of sarcotesta (arrow in Fig. 4) was interpreted in Banerji (2000, fig. 6) as a staminate structure.

We conclude, that the “flower-like structure” represents a basal part of disintegrated *Carnoconites* with a pedicel, a complete stone shell above it, and a few spirally disposed fleshy seeds outlined on the grinded surface. Fragments of sclerotesta are deeper impressed upon the fleshy layer. Detached seed casts of the same kind are scattered all over the cutting surface.

2.3. *Sonajoricarpon*, a fruit-like structure from Sonajori

Sonajoricarpon rajmahalensis Banerji (2000, p. 782) is based on a rough cast of a globose body in an irregularly split block of chert. A

linear knobby structure extends out of the globose body and forks at a short distance from it. The cast surface appears scaly and fibrous. One side of the split shows an irregularly rounded outline, with a few thick, longitudinally ridged, leafy appendages (Fig. 5C). A rhomboid leaf scar at the periphery exhibits two distinct marks of vascular bundles (arrow in Fig. 5C). On the counterpart, the laminar appendages are seen to be folded around the cast. A well-marked series of ovate scars surrounded by concentric ridges of fibrous tissue over the periphery of the cast were interpreted as seeds, but these more likely represent scars of endogenously borne appendages, presumably adventitious roots (arrowheads in Fig. 5A and enlarged in Fig. 5B).

We therefore suggest that *Sonajoricarpon* is a tuberose stem base wrapped in swollen leaf bases. The linear fibrous structure appears flexible with a knobby surface representing a branching rhizome. Such structures are described in Bose et al. (1985) as long slender shoots of *Pentoxylon*. The leaf scars of the cast are as on *Pentoxylon* shoots illustrated by Srivastava (1946), Sahni (1948),

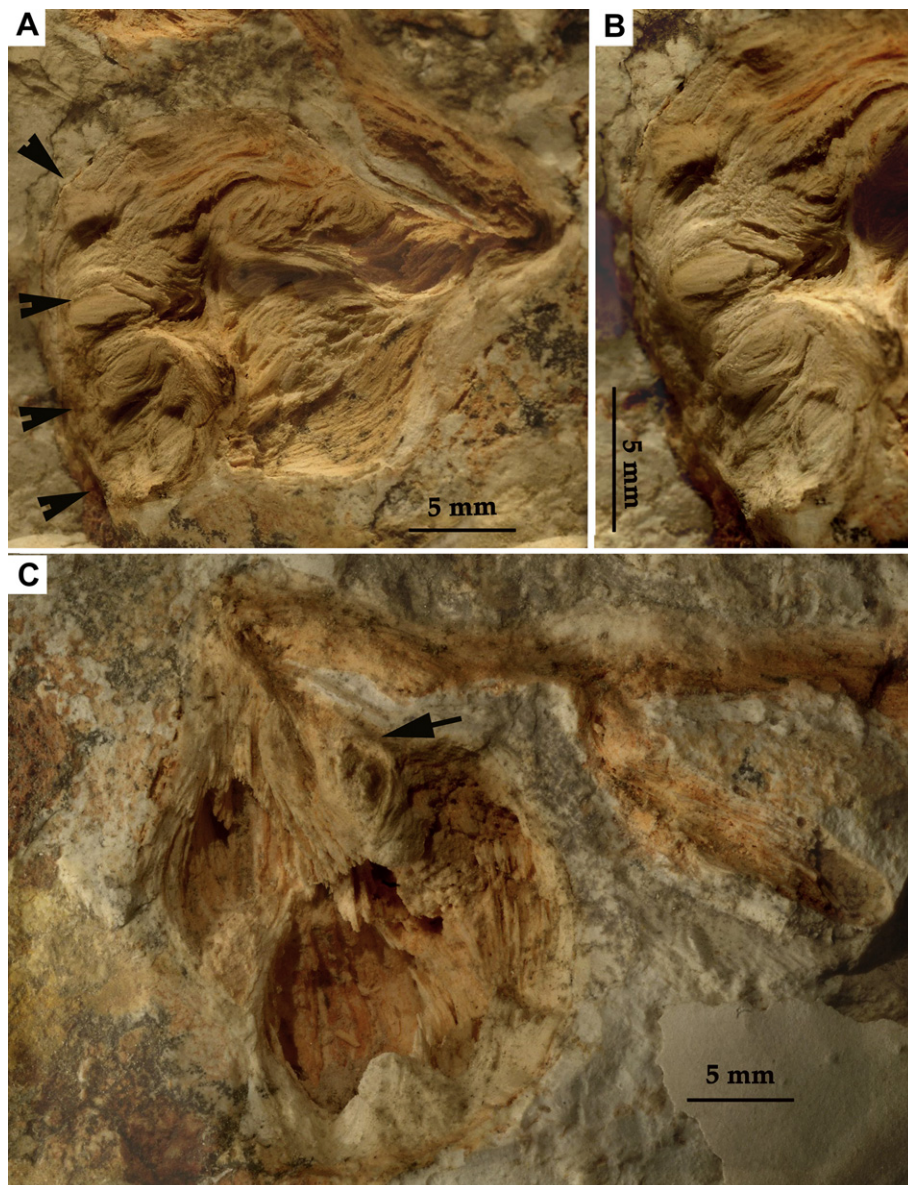


Fig. 5. Specimen BSIP no. 27234, Sonajori, Rajmahal Hills, described as *Sonajoricarpon* (Banerji, 2000), representing a tuberose stem base with a branching rhizome spreading from it. A, C, part and counterpart showing swollen leaf bases, arrow on a rhombic leaf scar, arrowheads on peripheral scars of adventitious roots. B, root scars enlarged.

Howe and Cantrill (2001) and others. Srivastava (1946) described an axis with dense rhombic leaf scars, wrapped in scale leaves, but this interpretation was questioned by Bose et al. (1985) who noted that scale leaves are unknown in *Pentoxylon* and that the wrapping structures more probably represented leaf bases.

3. Discussion

Our revision fails to confirm angiosperm macrofossils in Rajmahal Basin. The *Lesqueria*-like structure from Amarjola (Sharma, 1997) probably represents a bennettitalean receptacle, whereas the flower-like structure from Sonajori (Banerji, 2000) can be interpreted as a fragmentary *Carnoconites*, the seed-cone of *Pentoxylon* plant. *Sonajoricarpon* from the same locality (Banerji, 2000) is a swollen stem base rather than a fruit. It might belong to *Pentoxylon*, but better preserved material is needed for a definite conclusion. A few observations made during this study of angiosperm-like fossils seem to be of some interest for interpreting the palaeoecology of the *Pentoxylon* plant.

3.1. Feeding marks on *Carnoconites*?

Carnoconites is a fleshy, fruit-like cone that invites speculations on frugivory. Bose et al. (1985) cautioned against frugivory being taken for granted without compelling evidence. However they mentioned frequent finds of *Carnoconites* seed stones deprived of their fleshy coat. Such stone shells occur on the chert slab with the flower-like fossil re-interpreted here as a crumpled *Carnoconites*. The pedicel is not torn or broken off, but obliquely abscised with a series of scars cutting across the hypodermal fibers (arrowheads in Fig. 4B). In seeds clustered on the top of the pedicel and scattered around it, hard stone shells are exposed to varying degrees and some are crushed, with splinters imprinted upon the fleshy coat. One seed shows the nucellus shrunk away from the stone shell and separated from it by a distinct gap (Fig. 4C). A conical depression at the chalazal end marks a hypostase. Near the micropylar end there are two conspicuous punctures scarcely corresponding to any seed structure, but obviously representing damage probably inflicted by tooth cusps cutting through fleshy coat. Such bite marks might have been left by the protruding front teeth of a small tuatara-like lizard (*Sphenodontia*). Notably, various present-day reptiles feed on fruits of *Annona* and other members of the angiosperm family *Annonaceae* that resemble *Carnoconites* in their external morphology (reviewed in Kessler, 1993).

3.2. Geophytic habit in *pentoxyleans*?

Sonajoricarpon is here interpreted as an underground storage organ wrapped in swollen leaf bases, and attached to a branching rhizome. It suggests an incipient geophytic habit in Mesozoic plants, presumably in *pentoxyleans* that are reconstructed as low stature plants with slender above-ground stems forming dense thickets (Bose et al., 1985). Such habits predominantly occur in perennial plants of seasonally dry climates. Geophytes might have evolved under such climatic conditions. Notably, stem tubers are encountered in early angiosperms from variegated deposits of the Far East (Krassilov and Volynets, 2008).

4. Conclusion

The quest for the first angiosperm is based on a notion of angiosperm plants occasionally entering Mesozoic-type fern–gymnosperm communities and, therefore, leaving a sporadic fossil record. Indeed, angiosperm-like features sporadically appeared in Mesozoic and even Permian seed plants (Krassilov, 1997). But new

plant groups are more likely to have appeared in new plant communities rather than as occasional intruders (Krassilov and Volynets, 2008). An alleged solitary record of a new plant group in the midst of a well-established plant community seldom withstands critical evaluation.

The Early Cretaceous flora of Rajmahal Hills has potential in the search for early angiosperms in peninsular India. However, the angiosperm-like macrofossils that have been reported hitherto from the Rajmahal Formation do not provide hard evidence of early angiosperms. At the same time, they are of certain interest as evidence of predominantly angiosperm habits, such as a geophyte life form or zoochorous dissemination, appearing in non-angiospermous groups of Mesozoic plants. Was the angiosperm advent in Gondwana retarded because their prospective ecological niches were occupied by *pentoxyleans*? To address this question with more evidence at hand, more has to be learned about the enigmatic fossils from the Rajmahal Hills.

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