

## Angiosperms from the Early Cretaceous sediments of India

*Angiospermas de sedimentos do Cretáceo inicial da Índia*

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### Abstract

This study presents the first report of angiosperm macrofossil assemblage from the Early Cretaceous sediments of India, containing a fruit, a spike, a petal, leaves, and an axis from the Krishna Godavari Basin. This assemblage provides clues to angiosperm evolution and ecology during the Early Cretaceous of India. The described enigmatic forms are comparable to fruits of *Trapa*, and palm leaves and spikes of *Potamogeton*. The fossil material also includes ribbon-like leaves with a small axis; fossil remains suggest affinity with the monocotyledon group and support recent morphological and molecular phylogenetic studies to establish the divergence of this group from dicotyledons, during the early Cretaceous. Fossils described in the present study suggest an affinity for an aquatic environment that appears to be ideal for some early angiosperms.

**Keywords:** Angiosperms; Evolution; Early Cretaceous; India.

### Resumo

Este estudo constitui o primeiro relato de assembleia de microfósseis de angiospermas a partir dos sedimentos cretáceos iniciais da Índia. Os restos fósseis de angiospermas são preservados na forma de frutas, espigas, pétalas, folhas e eixos, que exemplificam a ocorrência explícita na bacia de Krishna Godavari. Essa assembleia fornece pistas sobre a evolução e a ecologia das durante os primeiros tempos do Cretáceo na Índia. As formas enigmáticas descritas são bem comparáveis aos frutos de *Trapa*, folhas de palmeira, espiga de *Potamogeton*. O material fóssil também inclui folhas em forma de fita com um pequeno eixo, restos fósseis sugerem afinidade com o grupo das monocotiledôneas, dão crédito aos recentes estudos filogenéticos, morfológicos e moleculares para estabelecer a divergência do grupo em relação às dicotiledôneas, no início do Cretáceo. Os fósseis descritos aqui sugerem uma afinidade por um paleoambiente aquático que parece ser ideal para algumas angiospermas primitivas.

**Palavras-chave:** Angiospermas; Evolução; Cretáceo inicial; Índia.

## INTRODUCTION

Angiosperms are the major group of land plants with more than 300,000 species and are 89.4% among embryophytes (Cronquist, 1981; Crepet, 2000). The sudden appearance of angiosperms during the Early Cretaceous and their further dominance in the later part of the Cretaceous is a Darwin's abominable mystery (Friedman, 2009). The origin and rapid explosion of this plant group changed the face of Earth and provides the structural definition for most terrestrial ecosystems (Crepet, 2000; Graham, 2011). The diversification of this group also assisted in the coevolution of various new organisms in the animal kingdom such as insects (Grimaldi and Engel, 2005). The group also helped to diversify the ferns (Schneider et al., 2004). Although there are still controversies about the origin (Doyle, 2012 and references therein) and ancestry (Doyle, 2006) of this plant group, its timing of appearance is considered as the Early Cretaceous (Hughes, 1994; Bell et al., 2005, 2010; Friis, 2011).

Angiosperms are known from various geographic locations around the world during Early Cretaceous (Hickey and Doyle, 1977; Hill, 1994; Sun et al., 1998; Taylor et al., 2009; Friis, 2011). However, their presence in India during the Early Cretaceous is equivocal. Sahni (1932) described a vesselless fossil wood named *Homoxylo*n from Rajmahal, India and compared it with vesselless angiosperms. Conversely, Bose and Sah (1952) presented the affinity of *Homoxylo*n Sahni within Bennettitales and transferred it to the new genus *Sahnioxylon* Bose and Sah (1952). Long afterward, Sharma (1997) described *Lesqueria* Crane and Dilcher and Banerji (2000) containing a fruiting body under a new genus *Sonajoricarpon* and a flower-like structure from the Rajmahal Formation. Banerji (2000) compared *Sonajoricarpon* with the fruits of extant fabaceous genus *Butea* Roxb. ex Willd (1802). Interestingly, these fossils were also proved to be non-angiosperms and are now considered belonging to the gymnosperms (Srivastava and Krassilov, 2012).

Some fossil remains are described in the present article, which can be comparable with angiosperms from Neocomian-Aptian (Early Cretaceous) sediments of Krishna-Godavari Basin, East Coast of India. The described fossils consist of cf. *Trapa* L. fruits, Palm-like leaves, petals of flower, pentamerous flower-like structure, and some enigmatic leafy axis and ribbon-like leaves.

## GEOLOGICAL SETTING

The Krishna-Godavari Basin is a pericratonic basin that came into existence following rifting along the Eastern continental margin of the Indian Craton during the early Mesozoic (Sastri et al., 1974; Lal et al., 2009) (Figure 1A). Geographically, the basin is located between the Kakinada in the NE and Ongole

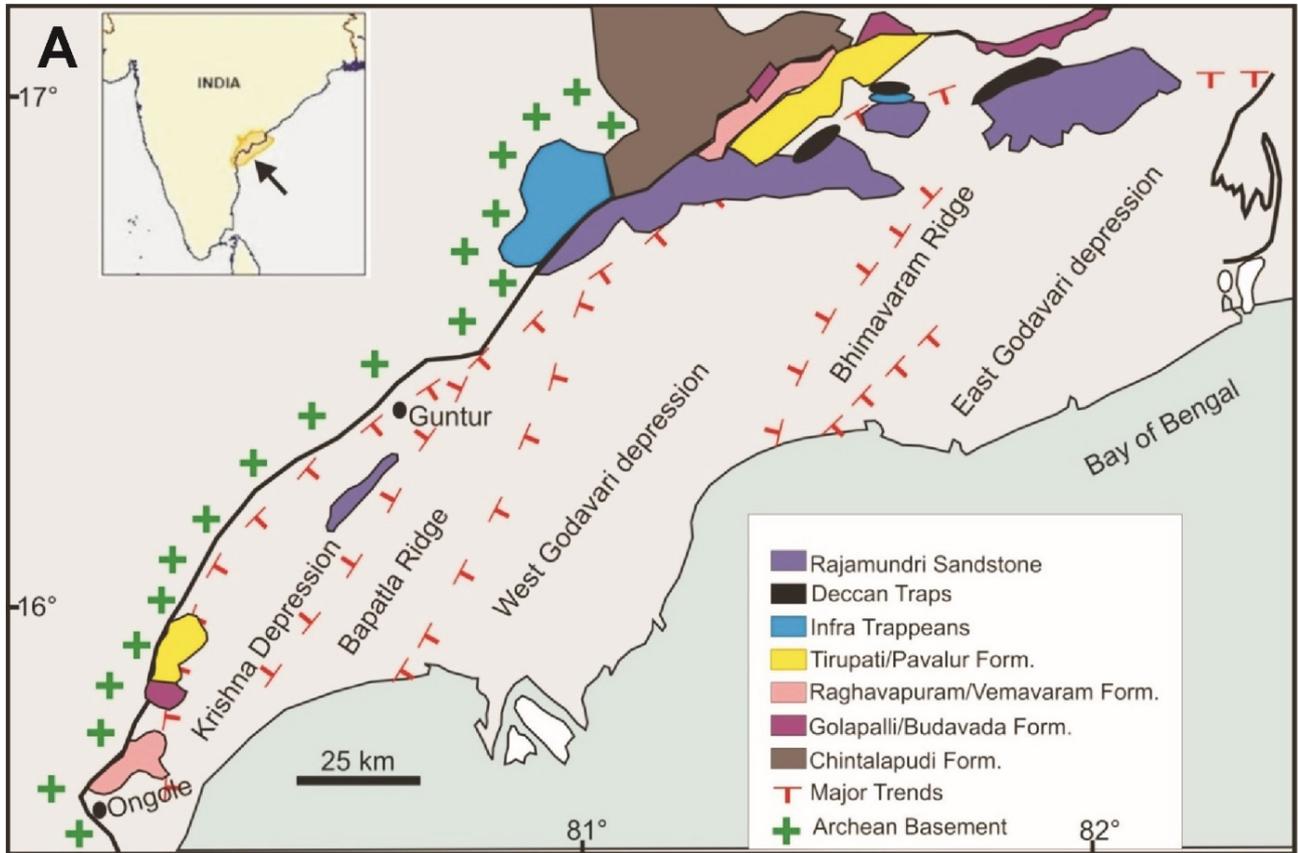
in the SW of Andhra Pradesh (Figure 1B). It is one of the promising petroliferous basins of India. The basin has a half-crescent shape and measures about 15,000 km on land and about 25,000 km of the adjoining offshore regions (Kumar, 1983). This basin was a major intracratonic Gondwanan rift basin until the Early Jurassic period (Rao, 2001), and after the Cretaceous it became a pericratonic rift basin (Biswas et al., 1993). The basement is composed of an Archean igneous and metamorphic complex overlain by Lower Gondwana (Permian) sediments represented by the Chintalapudi Formation (Lakshminarayana and Murti, 1990; Biswas, 1992).

The "Upper Gondwana" sediments are exposed toward the western and northwestern fringes of the basin (Figure 1) and distributed in two depressions named Godavari and Krishna (Sastri et al., 1974; 1981; Kumar, 1986; Venkatachala and Sinha, 1986). Sediments exposed in the Godavari Depression are divided into three litho-units, the Golapalli, Raghavapuram, and Tirupati formations. The Golapalli Formation (16°43'N; 80°55'E), is the oldest and comprises white to pale white and light brown sandstones with siltstone partings. The Raghavapuram Formation (17°02'N; 81°22'E) sandwiches between the Golapalli and Tirupati formations. This formation is characterized by white pale to pinkish earthy shale and dark brown ferruginous claystones, light buff to grayish white, medium grained glauconitic sandstones with rich fossil plant and animal materials (Bhalla, 1969; Baksi, 1968; Prasad and Pundir, 1999; Chinnappa et al., 2014). The Tirupati Formation (16°57'N; 81°17'E) overlying the Raghavapuram Formation is composed of purple red to light brown, medium grained sandstone and lacks plant macrofossils (Prasad and Pundir, 1999).

Sediments exposed in the Krishna Depression were also divided into three litho-units, the Budavada, Vemavaram, and Pavaluru formations. Sedimentary rocks of the Budavada Formation are the oldest in that order and is characterized by sandstones containing fragmented plant remains (Feistmantel, 1879). The Vemavaram Formation, which lies between the Budavada and Pavalur formations and is primarily composed of shales containing carbonaceous matter, has provided many fossil plants (Feistmantel, 1879; Chinnappa et al., 2014). The Pavalur Formation is comprised of medium to coarse grained clays and lateritic sandstones, and it is overlain by the Deccan intertrappeans (Rao, 2001) (Table 1). The lithology of the studied sections is provided in Figure 2.

## MATERIALS AND METHODS

Fossil plants were collected from the mudstone/shale sequence of the Raghavapuram Formation, exposed about 1 km toward the South East of the Ramanujapuram village (17°13'27"N; 81°19'11"E), near Jangareddigudam, West Godavari District, Andhra Pradesh, India (Figure 2). Fossil plants were preserved



**Figure 1.** (A) Geological map of Krishna-Godavari Basin (Source: Chinnappa et al., 2014). (B) Map showing the fossil locality.

as impressions on whitish-yellow colored shale and pale-reddish mudstone/shale. Despite the preservation limitation, most morphological details are still retained, including the venation pattern in maximum number of specimens. Fossil plants were studied under an Olympus SZH 10 stereo dissecting microscope. All the specimens were photographed with a Canon SX 150 IS digital camera using either polarized light or low angle light to reveal surface details. The described material is assigned a BSIP (Birbal Sahni Institute of Palaeosciences) specimen number and lodged with the BSIP fossil repository.

## RESULTS

### Systematic palaeobotany

ANGIOSPERMAE

Class MAGNOLIOPSIDA – DICOTYLEDONS

Order MYRTALES Jussieu ex Brechtold and Jan Svatopluk Presl

Family LYTHRACEAE (formerly in Trapaceae) Saint-Hilaire. Reveal and Chase, 2011

*cf. Trapa sp.*

Figure 8A

**Referred specimen.** BSIP specimen number: 40457

**Locality and age.** Ramanujapuram, Raghavapuram Formation, East Coast of India, Early Cretaceous.

**Description.** Fruits are medium in size with two massive external horns triangular in outline. The fruit is 16 mm in length (including neck), with about 20 mm in width at the surface of the horn. The upper surface of the fruit is depressed with a well-developed neck (Figure 8A). The neck is obtuse in outline, about 5-mm long and 11-mm wide, and does not usually protrude from the upper horns. Apertures are not visible. Corona is lacking. The horns are about 30-mm long, triangular in outline, and usually downward pointed. The arms are gradually attenuating into straight, elongate thin spine-like tips, and are ascending at an angle of 50–60°. The arm ends are not properly preserved. Barbed spines (harpoons) cannot be visible on arms due to poor preservation of arm ends. The fruit body is well-developed, the lower part of the fruit body is obtriangular in outline.

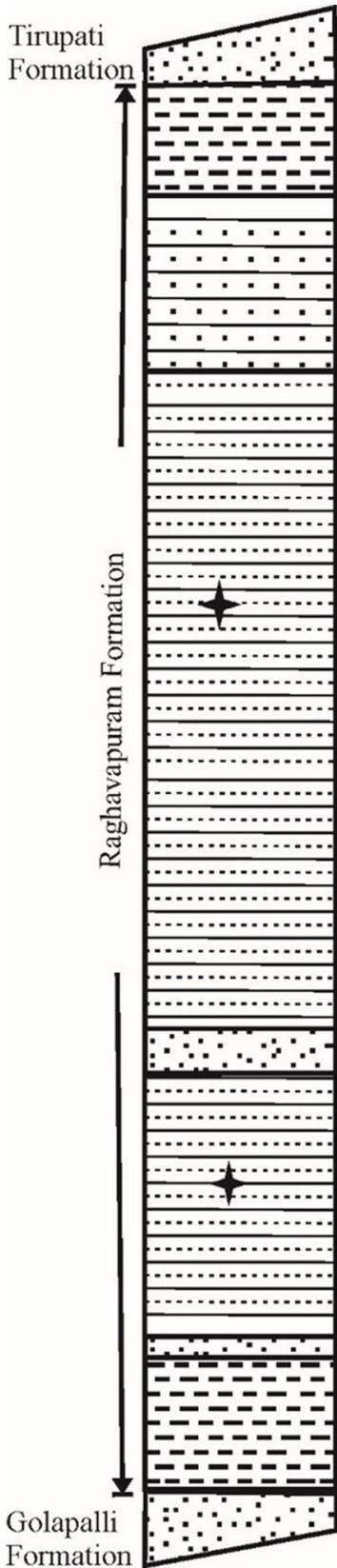
**Comments.** Fruits of *Trapa* Linnaeus (1753) are characterized by two-four strongly recurved to ascending horns (indurated sepals) with thick bases, and the horns bear coarse harpoon-like barbs (Graham, 2013). Fruits of well-developed body with two massive horns with thick bases, ascending at an angle of 50–60°, can be well compared with the *Trapa*. The lack of harpoon-like barbs is due to the preservation limitations rather than their actual absence. The fossils of *Trapa* and *Hemitrapa* Miki are among the most intensively studied and the most easily recognized fossils in the Lythraceae (Graham, 2013). The earliest known fossil related to *Trapa* is fruit impressions described as *Prototrapa* Vassiljev from Early Cretaceous of Australia (Vassiljev, 1967).

Fruit impressions resembling the *Trapa* described in this study are the oldest records of such type in the fossil record to date. *Trapa* is mostly recorded from the Tertiary

**Table 1.** Lithostratigraphy and ages of the various litho-units in the Krishna Godavari Basin.

| Group          | Formation              | Lithology  | Age                             |
|----------------|------------------------|--|---------------------------------|
|                |                        | Recent alluvium  |                                 |
| Tertiary       | Rajahmundry            | Red, feldspathic, ferruginous, laterized, cross-bedded, and conglomeratic sandstone  | Miocene-Pliocene                |
|                | Infra-Inter-Trappean   | Basaltic lava  | Late Cretaceous-Early Paleocene |
|                |                        | Unconformity   |                                 |
| Upper Gondwana | Tirupati/Pavalur       | Purple, red-light, brown sandstones/clay and caleritic sandstones  | Late Cretaceous                 |
|                | Raghavapuram/Vemavaram | White, pale-reddish earthy shales, red ferruginous claystones, light buff-grayish, white glauconitic sandstones/shale containing carbonaceous matter | Early Cretaceous                |
|                |                        | Unconformity   |                                 |
|                | Golapalli/Budavada     | White-pale, white, and light brown sandstones with siltstone partings/sandstones   | Early Cretaceous                |
|                |                        | Unconformity   |                                 |
| Lower Gondwana | Chintalapudi/Kamthi    | Coarse grained feldspathic sandstones, alternating calcareous claystones   | Permian                         |
|                |                        | Unconformity/Fault   |                                 |
| Proterozoic    | Khondalite             | Igneous and metamorphic rocks  | Precambrian                     |

Source: Chinnappa et al., 2014.



**Figure 2.** Lithological succession showing the position of fossiliferous beds.

sequences (Miki, 1959; Kovar-Eder et al., 2005; Wójcicki and Velitzelos, 2007). The horns of the fruits described in the present article can be comparable with the *T. silesiaca* (Wójcicki and Zastawniak, 2002), but differ in size and shape of the body and neck. There are few other reports of fruit impressions related to the Trapaceous species (the term “Trapaceous” is used in a general sense to indicate the fossil fruit relation with the extant *Trapa*) (Vassiljev, 1967; Golovneva, 1991). Fruit impressions of *Prototrapa* Vassiljev from Early Cretaceous of Australia (Vassiljev, 1967) and *Palaeotrapa* Golovneva from Late Cretaceous of Russia (Golovneva, 1991) differ in characteristic shape of the body and horn base. The shape of the body in cf. *Trapa* fruit described in this study is somewhat triangular, and horn base is wide and narrow at the ends; but in *Prototrapa* and *Palaeotrapa*, the body is fusiform and horn base is narrow and long.

Class LILIOPSIDA

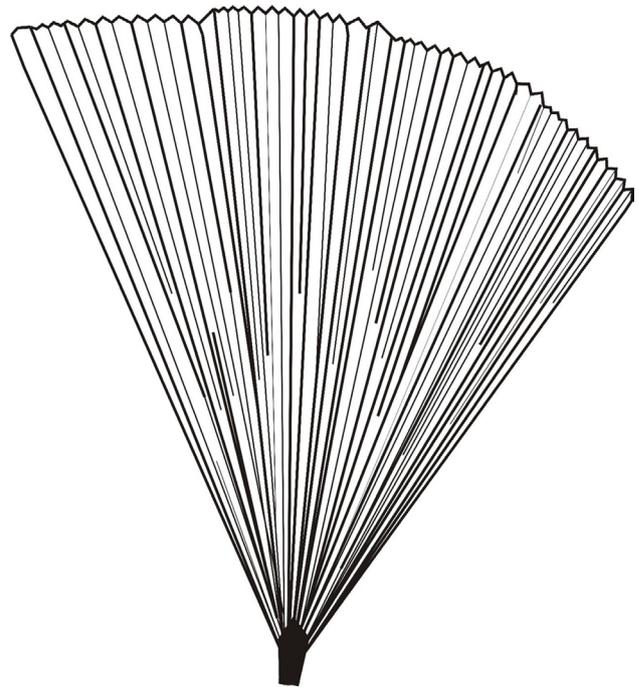
Order ARECALES Juss. ex Brecht. and J. Presl

Family ARECACEAE Bercht. and J. Presl, nom. cons.

cf. *Arecaceae leaf 1*

Figures 3, 8C and 8E

**Referred specimen.** BSIP specimen number: 40458 and 40459.



**Figure 3.** Reconstruction of cf. *Arecaceae leaf 1* (Base of the leaf is based on the BSIP specimen number 40458. Apex of the leaf is based on the BSIP specimen number 40459) (not to scale).

**Locality and age.** Ramanujapuram, Raghavapuram Formation, East Coast of India, Early Cretaceous.

**Description.** Simple palmate leaves with fan shape, preserved lamina length of 80–100 mm and width of about 50–100 mm at widest region. The texture of the lamina is coriaceous. Petiole and hastula were not recovered. Lamina consisting of more than 25 plicate segments (Figures 3, 8B and 8E). Leaflets are symmetrical and diverging from base to apex, 2–4 mm wide, and the length varies. Venation is parallel with indistinct midrib and few faint lateral veins.

**Comments.** Fossil records of palms clearly indicate its quite ancient origin, having been found from the Liassic to modern period, if not from Triassic (Mahabale, 1962). Modern members of *Arecaceae* are diverse and share numerous similarities in form and gross external features, which hinders the comparison of fossil with modern members (Read and Hickey, 1972). Preservation limitations in fossil specimens are another important factor that precludes the matter. Read and Hickey (1972, p. 130) suggested a set of five characters that can either be used in combination or alone to identify fossil palms and palm-like leaves. They also considered all fossil palms and palm-like leaves under the nine genera, namely: *Amesoneuron* Goeppert (1852), *Bactrites* Berry (1924), *Sabalites* Saporta (1865), *Palmacites* Brongniart (1822), *Phoenicites* Brongniart (1828), *Phoenix* Linnaeus (1753), *Sanmiguelia* Brown (1956), *Paloreodoxites* Knowlton (1930), and *Propalmophyllum* Lignier (1895).

The fossil leaves described in this article can be grouped in the *Palmacites* Brongniart (1822), based on the available evidences. The fossil genus *Palmacites* Brongniart (1822) includes “all fossil palm-like leaves adequate for determining original form; lamina with pure palmate lacking a costa or extension of the petiole into the blade” (Read and Hickey, 1972). So far, *Palmacites* is only known from the sediments younger than the Cretaceous, and their reports within the Cretaceous are largely unknown. There are frequent reports of *Palmacites* from Tertiary sequences of India. Leaflets are smaller in the present specimens, but they are comparatively larger in specimens from younger sediments (Singh; Patnaik, 2012; Srivastava et al., 2012). All the younger species of *Palmacites* greatly differ from the present specimens by nature of leaf base and size of leaflets. Similarly, base is very acute and narrow in the present specimens, but it is comparatively wide in the later specimens. The acute and narrow base and V shape of the leaf (Figure 3) can be comparable with the extant *Korthalsia* Blume (1843). However, it is not plausible to make further comparisons at species level either with extant or extinct members because of preservation limitations and the long chronological gap. Any imposed comparison with the relatively younger members is unlikely, and it hinders the knowledge of early forms and their utility in understanding the evolutionary process (Hughes, 1994).

#### *cf. Arecaceae leaf 2*

Figures 4 and 8B

**Referred specimen.** BSIP specimen number: 40460.

**Locality and age.** Ramanujapuram, Raghavapuram Formation, East Coast of India, Early Cretaceous.

**Description.** Simple fan-shaped palmate leaves, preserved lamina length of 80 mm and width of about 50 mm at widest region. The texture of the lamina is coriaceous. Petiole and hastula were not recovered. Lamina is divided into wedge-shaped segments. Leaflets are symmetrical and diverging from base to apex, 2–4 mm wide and the length varies. Venation is parallel with distinct midrib and few faint lateral veins.

**Comments.** The fossil leaf differs from the *cf. palm leaf A* in the lamina segmentation and nature of lamina. At one corner, the lamina shows mark as if the petiole extended to the lamina and developed a primary costa (Figures 4 and 8C). However, careful observation demonstrated that this is due to preservation factors. The present leaf shows some resemblance with *Licula ramsayi* (F. mueller) Domin (1915) in the nature of attachment on the petiole.

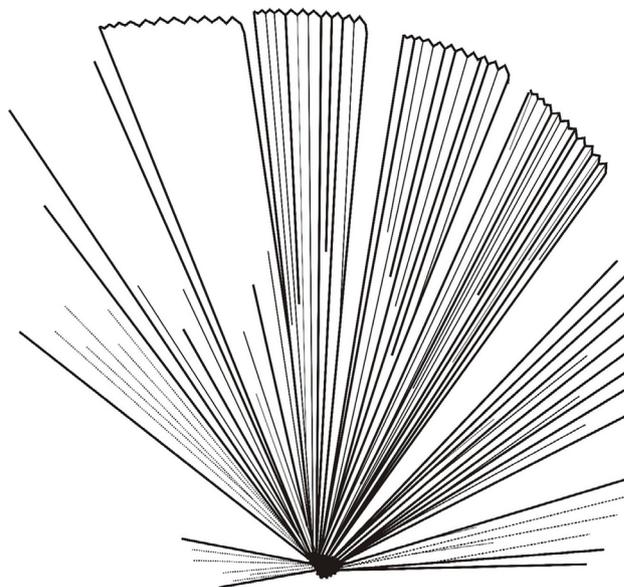
#### *Monocotyledon sp. A*

Figures 5 and 8D

**Referred specimen.** BSIP specimen number: 40461.

**Locality and age.** Ramanujapuram, Raghavapuram Formation, East Coast of India, Early Cretaceous.

**Description.** The specimen is partially preserved with a small axis and five leaves. The surface of the axis is striated and the maximum available size is 40 mm. The leaves are ribbon-like; five leaves can be seen radiating from a



**Figure 4.** Reconstruction of *cf. Arecaceae leaf 2* (not to scale).

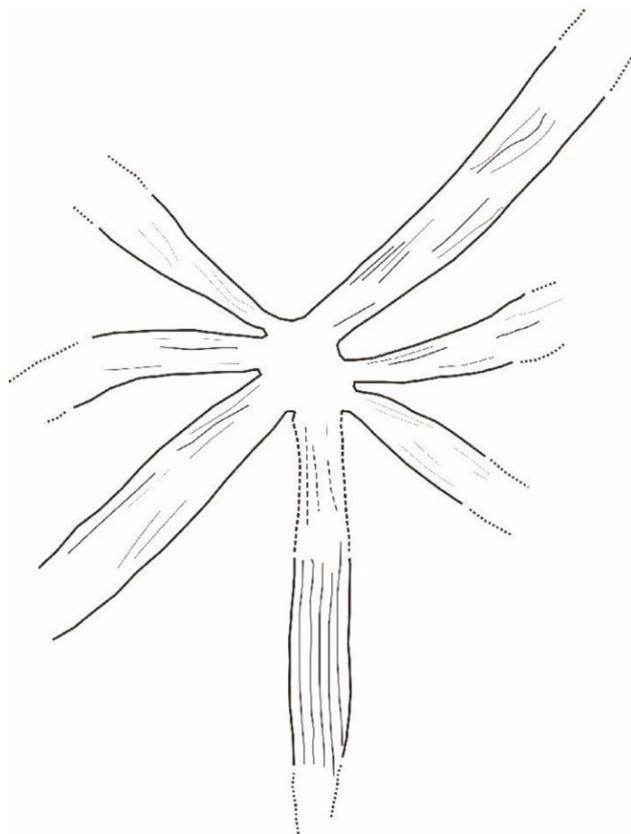
common central point (Figures 5 and 8D). The maximum available size of the leaf is 80-mm long and 10-mm wide. Parallel margins. Apex is unknown. Venation is faintly preserved and parallel.

**Comments.** A single specimen is available with limited characters. Veins preserved as small parallel scars on the leaves at some places, thus indicating parallel venation. Though the specimen is partially preserved, the characteristic shape of the leaves and veins indicates affinity with angiosperms, more specifically with the monocotyledons. Fossil ribbon-like leaves and parallel venation are mostly known from the later part of the Cretaceous, are placed either in extinct *Stratiotes* or sea-grass (van der Ham et al., 2007), and largely differ from present specimens by radiation of the leaves from axis (Figures 5 and 8D). The characteristic features of the leaves indicate that the plant might have dwelled in an aquatic habitat. Among the extant members of the monocotyledons, leaves with similar characters are mostly found in Cyperaceae.

#### *Petals of angiosperm flower*

Figures 6 and 8F

**Referred specimen.** BSIP specimen number: 40462.



**Figure 5.** Monocotyledon sp. 1 showing the ribbon-like leaves and venation marks.

**Locality and age.** Ramanujapuram, Raghavapuram Formation, East Coast of India, Early Cretaceous.

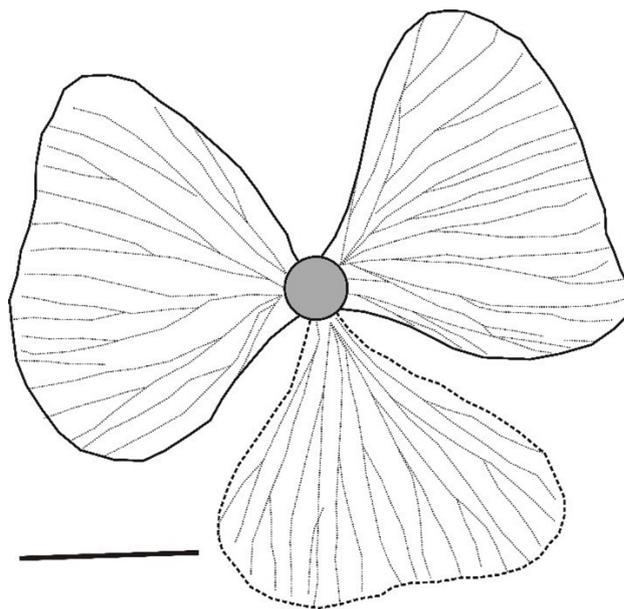
**Description.** Three petals arranged in whorls attached to a central granular structure, which may represent a receptacle, 30-mm long and 34-mm wide at widest region, *i.e.*, apical part gradually narrowing towards the base. The overall shape of each segment is widely elliptical and somewhat triangular (Figures 6 and 8F). Both lateral and apical margins straighten up to slightly wavy. Open dichotomous venation with rare reticulation, thick veins and areoles are not clear.

**Comments.** Isolated petals of fossil flowers are frequent in Cretaceous fossil records and are often mistaken for aquatic ferns such as *Marsilea* Linnaeus (Skog and Dilcher, 1992; Nagalingum, 2007). Petals of the fossil flowers can be distinguished from the *Marsilea* and extinct *Marsileaceaphyllum* Nagalingum (2007) by the variation in size, thickness of the veins, and the irregularly sized, rectangular, or polygonal areoles (Rich et al., 2001). The large size of the segments (petals) and the thick first-order veins suggest the affinity with petals rather than *Marsilea* or *Marsileaceaphyllum*. Two petals were fully preserved and the third one is represented by a most basal part (Figure 8F). Although floral parts confer angiosperm, it is not possible to relate them to any known taxa.

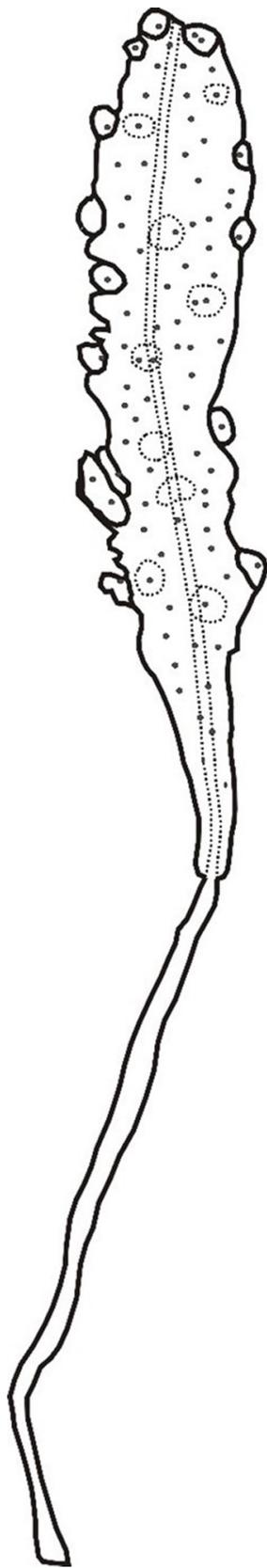
#### *Angiosperm floral Spike*

Figures 7 and 8H

**Referred specimen.** BSIP specimen numbers: 40463 and 40464.



**Figure 6.** Reconstruction of flower showing three petals (scale bar of 15 mm).



**Figure 7.** Angiosperm floral spike showing loosely arranged fruit-like bodies (not to scale).

**Locality and age.** Ramanujapuram, Raghavapuram Formation, East Coast of India, Early Cretaceous.

**Description.** A reproductive axis with stalk and body about 60-mm long. The slender stalk runs throughout the body; a section of about 25-mm long and about 1-mm wide can be seen outside the body. The body, 35-mm long and about 6-mm wide, spindle-shaped, is loosely packed around the central axis. The outer surface of the body is slightly granular (Figure 8H).

**Comments.** This fossil spike, resembling that of *Potamogeton* L., is of special interest mostly due to its close resemblance with cones of Gnetales, primarily of ephedroid affinity (Sun et al., 2001; Rydin and Friis, 2010). Many of the previous fossils described under the genus *Potamogeton* (e.g., Yabe and Endô, 1935; Krassilov, 1982) were later considered as ephedroids (Friis, 2011). The specimens described in this article greatly differ from those previously described as spike-like *Potamogeton* (Krassilov, 1982) and the cones of Gnetales by nature of stalk and body. Cones of extant ephedroids are characterized by the presence of concentric rings of body around the central stalk. The body surface in the described specimens is loosely packed around a central axis and seems to be granular, which can be clearly observed at its outer surface (Figures 7 and 8H). The granular-surface structures around a central axis are highly suggestive of small fruit-like structures. Absence of gnetalean macrofossils from the early Cretaceous or older sediments of the Indian subcontinent also disputes the ephedroid affinity and thereby supports angiosperm affinity, possibly with *Potamogeton*.

*Angiosperm* sp.

Figure 8G

**Referred specimen.** BSIP specimen numbers: 40465 and 40466.

**Locality and age.** Ramanujapuram, Raghavapuram Formation, East Coast of India, Early Cretaceous.

**Description.** A slender axis with whorls of leaves at regular intervals, maximum available size of approximately 40-mm long and 1–2-mm wide. Leaves arranged in whorls around the axis at regular intervals, 5–6 in number (Figure 8G). The leaf about 5-mm long and 3-mm wide at apical part, slightly triangular in shape. Both the lateral and apical margins are straight. Venation not clear, 2–3 parallel veins are visible, running from base to apex.

**Comments.** Plants with slender leafy axis and leaves in whorls at regular intervals on the axis can be found in *Sphenophyllum* Brongniart (1822) and *Equisetum* Linnaeus (1753), belonging to pteridophytes, and *Hydrilla* Richard (1814), belonging to angiosperms. Fossils of this type, in addition to the aforementioned genera, are unknown to the best of the authors' knowledge. The *Sphenophyllum* is an extinct member of Sphenopsids that thrived during Late



**Figure 8.** (A–H) Fossil angiosperm remains A, cf *Trapa* fruit (BSIP 40457). (B) cf. Arecaceae leaf 2 (BSIP 40460). (C and E) cf. Arecaceae leaf 1 (BSIP 40459 and 40458). (D) Monocotyledon sp. 1 (BSIP 40461). (F) Petals of angiosperm flower (BSIP 40462). (G) Angiosperm (BSIP 40465). (H) Angiosperm floral spike (BSIP 40463) (scale bar of 10 mm).

Devonian to Late Permian (Bashforth and Zodrow, 2007). Although, the external shape of the leaf in present specimens resembles those of *Sphenophyllum*, the Early Cretaceous age suggests that its affinity with that taxon is highly improbable, considering that the *Sphenophyllum* had already been extinct by the end of the Permian. Extant *Equisetum* differs in nature of leaves and their fossils are frequently identified based on the ridges and furrows, in addition to axis with well-determined nodes and internodes (Surange, 1966). *Hydrilla* is an extant member of Hydrocharitaceae and is represented by a single species (Cook and Lüönd, 1982). The leaves of *Hydrilla* are characterized by a well-developed midrib, apex is mostly acute, and margins are serrate, thus adequate to compare the present fossil specimen with this genus. Furthermore, molecular phylogenetic studies suggest a recent origin for *Hydrilla* (Chen et al., 2012). Taking this into consideration, it is not possible to compare the present specimens with any known taxa either extant or extinct. However, the available evidence, such as the characteristic nature of the leafy axis, indicates its affinity with angiosperms, which leads the authors to believe it probably represents an extinct lineage within Hydrocharitaceae. More specimens of similar type with better preserved details are needed to confirm its taxonomic position.

## DISCUSSION

Angiosperm macrofossil remains are common in the fossil records of Early Cretaceous sedimentary basins (Taylor et al., 2009). However, little is known about the early presence of this plant group in India, where previous records of fossils placed within the flowering plants were later proved to be Bennettitaleans (Srivastava and Krassilov, 2012). The lack of early angiosperm remains from Early Cretaceous sedimentary basins of India hinders the understanding of the evolutionary history in the Indian subcontinent. In addition, this has historically constrained the authors' understanding of the evolutionary history of the group itself. The present knowledge of angiosperm history in India is solely based on the fossils from Late Cretaceous and cannot be applied to early flowering plants because, by this time, they were markedly different (Crane et al., 2000; Crepet, 2000; Soltis and Soltis, 2004; Friis et al., 2011). The angiosperm fossil assemblage described in this study is the first of its kind to date, and the fossils are mostly described under comparative forms due to the moderately available characters. The assemblage includes the fossil resembling the *Trapa*, *Arecaceae*, *Potamogeton*, ribbon-like leaves, petals of fossil flowers, and an enigmatic leafy axis.

*Trapa* fruits with unquestionable modern affinity are known from Miocene, but fossil reports of this genus from the Cretaceous period are common (Paradkar and Patki, 1987).

Morphological variations in the fossil *Trapa* fruits are great. Besides this well-advanced state of fruits in Miocene, the sporadic reports of the genus in the Late Cretaceous suggest its origin in the Miocene to be highly dubious. Fruits similar to extant *Trapa* described in the present study and also from the Early Cretaceous sediments of Kutch Basin (Rajanikanth and Chinnappa, 2016) suggest this genus might have existed early in the Cretaceous. The progenitors and center of origin of modern forms of *Trapa* still remain an unsettled question, and various opinions are found in the literature (Graham, 2013 and references therein). The *Trapa*-like fruits described in this study closely resemble fossil *Trapa* fruits from the Miocene, as well some extant members, by sharing important characters, such as shape, nature of body, and horn, thus suggesting their close affinity. The present fossil fruits probably represent an ancestral lineage for modern forms, considering that fruit bodies in the Miocene and in modern *Trapa* are comparatively larger; this might be the evolutionary change, as fruit body size has increased since the Early Cretaceous.

*Arecaceae* is an ancient group of angiosperms with a controversial Triassic fossil record, *i.e.*, *Sanmiguelia* (Brown, 1956). However, there are concerns about their affinity with true palms (Read and Hickey, 1972). Pollens of *Spinizonocolpites* Muller (1968) and *Mauritiidites* van Hoeken-Klinkenberg (1964) from Maastrichtian fossil records (van der Hammen and Garcia de Mutis, 1965) indicate an early origin for palms (Harley, 2006), which might have originated during Early Cretaceous, if not before. Reports of advanced forms, such as *Cocos* Linnaeus (1753), from Late Cretaceous sediments of India (Srivastava and Srivastava, 2014), also refer the origin of palms to early Cretaceous or Late Jurassic, which is substantiated by the palm-like leaves reported in this study.

Spike-like structures comparable with *Potamogeton* spike from Early Cretaceous (Krassilov, 1982) were later considered under Gnetales (Friis et al., 2011) based on gross similarities with ephedroid spikes. The described specimen greatly differs from the previously described specimens and from the extant ephedroids. Available evidences corroborate an angiospermous affinity probably with the *Potamogeton* stem lineage rather than with gnetalean (ephedroids). The absence of macrofossils of this latter group in Early Cretaceous sediments of India is also noteworthy.

Petals of flowers provided little information and it is not possible to relate them to any extinct or extant flower, but their presence along with pentamerous flower-like structures are of special interest. Although there are many specimens in the authors' personal collection, with five lobes resembling the pentamerous flower, the poor and asymmetrical preservation of lobes precludes their definite affinity with flowers.

Ribbon-like leaves with parallel venation resembling monocot leaves (Figure 5) support their classification within

the angiosperms, but the exact relation with extant flowering plants is unclear.

Leafy axis with leaves arranged in whorls show a probable angiosperm affinity (see comments under angiosperm sp.). Such whorled leaves are often seen in aquatic taxa, such as *Hydrilla*, and more efforts are needed to recover similar fossils. Except for this leafy axis fossil, all other plant macrofossils reported in this study well establish the existence of angiosperms during the Early Cretaceous in India.

## CONCLUSIONS

The study records the first report of angiosperm macrofossil assemblage from India. The present findings of fossil flowering plant remains with monocots are in close agreement with recent morphological and molecular phylogenetic studies that establish the group divergence from the dicots, early in the Cretaceous (e.g., Bremer, 2000; Soltis and Soltis, 2004; Janssen and Bremer, 2004). The fossils described in the present research show close resemblance to extant aquatic forms, which appears to be an ideal habitat for some early angiosperms. More specimens with well-preserved characters are needed to better establish taxonomical relationships with extant members of angiosperms and to further contribute to the knowledge of their ecological preferences.

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