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Variations in Bennettitalean leaves of the Indian Gondwana

NEERU PRAKASH* AND MADHAV KUMAR

Birbal Sahni Institute of Palaeobotany, 53 University Road, Lucknow 226 007, India.
**Corresponding author: neerup_in@yahoo.com*

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ABSTRACT

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The Bennettitales is a group of extinct seed plants characterized by pinnately compound crown of leaves which occur at the top of the stem and resembles cycads. These plants constitute a major portion of the Mesozoic vegetation and have a long geological history. The morphological variations in pinnate leaves exhibit primitive to advanced characters, i.e. simple to pinnately compound leaves with variable shapes, sizes and venation patterns. The inter-relationships among various genera of the group have been traced.

Key-words—Bennettitales, Leaf Morphology, Variations, Mesozoic Gondwana, India.

भारतीय गोंडवाना की बेनेटिटेलीय पत्तियों में विभिन्नता

नीरू प्रकाश एवं माधव कुमार

सारांश

बेनेटिटेल्स एक विलुप्त पादप समूह, जिसके तने के शिखर पर सज्जित किरीट समतुल्य पिच्छाकार पत्तियां साइकेड्स से समानता दर्शाती हैं। ये वनस्पतियां मध्यजीवीकल्प के विशाल भाग को संघटित करती हैं तथा अपने दीर्घ भू-वैज्ञानिक इतिहास को प्रदर्शित करती हैं। इन पिच्छाकार पत्तियों में आकारिकीय विभिन्नताएं आदिरूप तथा उन्नत स्वरूपों अर्थात् परिवर्तनीय रूपों, आकारों एवं शिराविन्यास प्ररूपों को प्रदर्शित करती हैं। इस समूह के विविध वंशों में अंतःसंबंधताओं का अनुरेखण किया गया है।

संकेत-शब्द—बेनेटिटेलीज, पत्ती आकृतिविज्ञान, विभिन्नताएं, मध्यजीवी गोंडवाना, भारत।

INTRODUCTION

The Bennettitales is an extinct group of Mesozoic seed bearing plants that did not persist beyond the Early Cretaceous. The group is characterized by pinnately compound leaves that bore resemblance to cycads and had complex reproductive structures. Thus, they are taxonomically ascribed to the class Cycadopsida or Cycadeopsida (Watson & Sincock, 1992). Traditionally two families are recognized, i.e. Cycadeoidaceae (Bennettitaceae) and Williamsoniaceae (Alvin *et al.*, 1967; Taylor & Taylor, 1993; Stewart & Ruthwell, 1993). These two families are distinguished by their growth habit and structure of reproductive organs. The former had short, herbaceous / stocky trunk whereas, the latter was characterized by the slender profusely branched stems. They were herbaceous midstorey elements of the Mesozoic vegetation. The first Bennettitalean record of leaf, e.g. *Pterophyllum sahnii* was made from South Rewa Basin, while extensive genera and species have been recorded from various Jurassic and Early Cretaceous sedimentary basins of Indian Gondwana (Bose, 1974; Bose & Banerji, 1981; Pant, 1987). The bennettitalean leaves from various sedimentary basins depict morphological variations in foliar characters (Cleal & Thomas, 2001). The similar looking leaves are generally identified by comparing their shapes and mode of attachment on the rachis (Fig. 1). Therefore, the present attempt is aimed to define morphological

distinctions between various records of Indian taxa. A review of their detailed morphology and configuration of the bennettitalean leaves has been revised in detail for better understanding of their taxonomic similarities, dissimilarities and variations.

BENNETTITALEAN LEAF GENERA

Genus—PTILOPHYLLUM Morris

Type species—***Ptilophyllum cutchense*** Morris

(Pl. 1.11, 12; Pl. 2.3)

Ptilophyllum fronds are preserved as impressions, incrustations and petrifactions; common fronds, widely occur in Upper Jurassic to Early Cretaceous deposits of Indian Gondwana (Bose & Kasat, 1972); pinnae linear to slightly sickle shaped, attached on adaxial surface of rachis, closely set or imbricate, mostly attached by entire base, arising at an angle of 50°-70 °, margins mostly straight, acroscopic margin rounded at base, basiscopic margin straight to slightly decurrent, veins more or less parallel, forked or unforked, mostly arising from base and reach up to apex, apex obtuse or acute.

Genus—PTEROPHYLLUM Brongniart

Type species—*Pterophyllum distans* Morris

(Pl. 1.8, 9; Pl. 2.5)

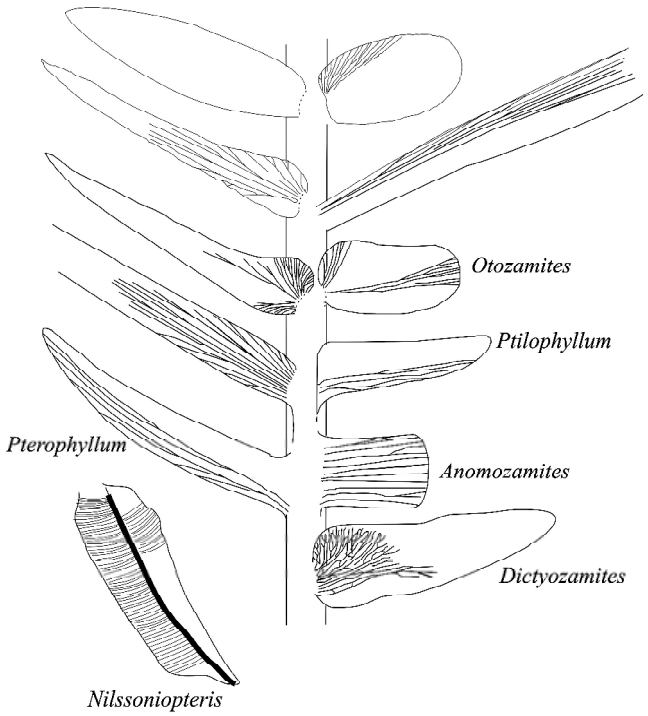

Fig. 1—The pinna morphology used to define Bennettitalean leaves of Indian Gondwana (after Watson & Sincock, 1992).

Characters	*Nilssoniopteris*	*Anomozamites*	*Ctenozamites*	*Pterophyllum*	*Ptilophyllum*	*Otozamites*	*Dictyozamites*
Shape	Linear lanceolate	Rectangular, squarish or somewhat cuneate	Rhomboidal	Linear, mostly longer than broad, straight	Linear-lanceolate, slightly sickle shaped or falcate	Mostly oval, linear-lanceolate	Falcate, lanceolate
Apex	Obtuse	Rounded, notched or wavy	Obtuse	Acute or sub - acute	Obtuse or acute	Rounded or ovate	Sub-acute or obtuse
Attachment of the base with rachis	-	Directly attached by broad base	Attached by decurrent broad base	Directly attached by their broad/decurrent base	Attached laterally by entire un-contracted base	Base asymmetrical, mostly auriculate	Base contracted, symmetrical, asymmetrical and auriculate
Venation Pattern	Simple forked at different levels	Forked at different levels	Veins parallel, simple or forked usually obscure	Mostly parallel forked or unforked	Mostly parallel forked or unforked	Spreading veins	Anastomosing patterns to form areoles

Fig. 2—Variations in Bennettitalean leaves.

Localities / Taxa	Satpura Basin	South Rewa Basin	Kutch Basin	Rajmahal Basin	Mahanadi Basin (Athgarh)	Godavari Basin (Gollapalle–Raghavapuram)	Krishna Basin (Vemavaram–Budavada)	Cauvery Basin (Sivaganga)	Palar Basin	Sriperumbudur Satyavedu Basin	Pranhita Godavari Gangapur
Anomozamites crenata (Mc Clelland) Bose & Banerji	–	–	–	+		–	–	–	–	–	–
Anomozamites hasnapurensis Bose & Banerji	+	–	–	–	–	–	–	–	–	–	–
Anomozamites fissus Feistmantel	–	–	–	+	+	–	–	–	–	–	–
Anomozamites cf. *fissus* Feistmantel	–	–	+	+	–	–	–	–	–	–	–
Anomozamites amarjolense Sharma *et al.*	–	–	–	+	–	–	–	–	–	–	–
Anomozamites haburensis Bose & Banerji	–	–	–	–	–	–	–	+	–	–	–
?*Anomozamites* sp.											–
Nilssoniopteris pannuceus Nathorst	–	–	+		–	–	–	–	–	–	–
Nilssoniopteris variabilis Bose & Banerji	–	–	+		–	–	–	–	–	–	–
Nilssoniopteris sp.	–	–	–	–	+	–	–	–	–	–	–
Pterophyllum princeps Oldham & Morris	+		–	–	–	–	–	–	–	–	–
P. medlicottianum Oldham & Morris	–	–	–	–	–	–	–	–	–	–	+
Pterophyllum distans Morris	–	–	+	–	+	–	+		–	–	–
Pterophyllum kingianum Feistmantel	–	–	–	–	+	–	+	–	–	–	–
Pterophyllum morrisiana Morris	–	–	–	–	–	+	+	+	–	–	–
Pterophyllum footeanum Feistmantel	–	–	–	–	–	–	+	–	–	–	–
Pterophyllum rajmahalense Morris	–	–	–	+	–		–	–	–	–	–
Pterophyllum incisum Sahni & Rao	–	–	–	+	–	–	+	–	–		–
Pterophyllum princeps Oldham & Morris				+							–
Ptilophyllum acutifolium Morris	+	+	+	+	+	+		+	+	–	+
P. cutchense Morris	+	+	+	+	+	+		+	+	+	+
P. distans (Feist.) Jacob & Jacob	–	+	+	–	–	–	–	–	–	–	+
P. horridum Roy	+	–	–	–	–	–	–	–	–	–	+
P. jabalpurense Jacob & Jacob	+	–	–	–	–	–	–	–	–	–	–
P. institacallum Bose	+	–	+	–	–	–	–	–	–	–	–
Ptilophyllum oldhamii Jacob & Jacob	–	–	+	–	+	–	–	–	–	–	–
Ptilophyllum indicum Jacob & Jacob	–	–	+	–	+	–	–	–	–	–	–

(cont.)

Ptilophyllum rerinervis Feistmantel	–	–	–	–	–	–	–	+	–	–	–
Ptilophyllum sakrigaliensis Sah	–	–	+	–	–	–	–	–	–	–	–
Ptilophyllum cf. *amarjolense* Bose	–	–	+	–	–	–	–	–	–	–	–
Ptilophyllum sahnii Gupta & Sharma	–	–	–	+	+	–	–		–	–	–
Ptilophyllum nipanica Vishnu Mittre	–	–	–	+	–	–	–		–	–	–
Ptilophyllum sp.	–	–	+	–	+	–	–	–	–	–	–
Otozamites imbricatus Feistmantel	–	–	+	–	–	–	–			–	–
Otozamites hislopi (Feistmantel) Bose & Kasat	+	–	–	–	–	–	–	–	–	–	–
Otozamites bengalensis Feistmantel	–	–	–	+	–	–	–	–	–	–	–
Otozamitesvenia vemavarensis Bose & Jain	–	–	–	–	–	–	+	–	–	–	–
Otozamites goldlaei Feistmantel	–	–	+	–	–	–	–	–	–	–	–
Otozamites walkamotaensis Bose & Zeba–Bano	–	–	+	–	–	–	–	–	–	–	–
Otozamites kachchhensis Bose & Banerji	–	–	+	–	–	+	–	–	–	–	–
Otozamites sp. cf. *O. kachchhensis* Bose & Banerji	–	–	–	+	–	–	–	–	–	–	–
Otozamites gondwanensis Bose	–	–	–	+	–	–	–	–	–	–	—
Otozamites rerinervis Feistmantel	–	–	–	–	–	–	+	+	+	–	
Otozamites angustatus Feistmantel	+	–	–	–	–	–	–	+	+	+	
Dictyozamites feistmantelli Bose & Zeba–Bano	–	–	–	–	–	–	–	+		–	
Dictyozamites gondwanensis Sukh-Dev & Rajanikanth	–	–	–	–	–	–	–	–	–	–	+
Dictyozamites falcatus (Morris) Medlicott & Blandford	–	–	–	+	–	+	+	+		–	–
Dictyozamites indicus Feistmantel	–	–	–	–	–	–	+	+	–	–	–
Dictyozamites sp.	–	–	+	+	–	–	–	–	–	–	–
Nilssoniopteris pannuceus Bose & Banerji	–	–	+	–	–	–	–	–	–	–	–
Nilssoniopteris variabilis Bose & Banerji	–	–	+	–	–	–	–	–	–	–	–

Fig 3—Distribution of Bennettitalean leaves in Indian Gondwana basins (+ recorded, – not recorded).

PLATE 1

1. *Nilssoniopteris pannuceus* Bose & Banerji, BSIP No. 4/2411c. x 0.5 cm.
2. *Anomozamites amarjolense* Sharma *et al.*, BSIP No. 16695. x 2.8 cm.
3. *Anomozamites* sp. Prakash, BSIP No. 38008, x 1.5 cm.
4. *Ctenozamites kachchhensis* Bose & Banerji, BSIP No.77/2079B. x 1.3 cm.
5. *Ctenozamites kachchhensis* Bose & Banerji, BSIP No.77/2079 B. x 1 cm.
6. *Dictyozamites feistmantelii* Bose & Zeba-Bano, BSIP No. 1/1366. x 1.6 cm.
7. *Dictyozamites indicus* Bose & Zeba-Bano, BSIP No. 78/1268. x 1.3 cm.
8. *Pterophyllum guptai* Bose & Banerji, BSIP No. 35115. x 0.5 cm.
9. *Pterophyllum morrisianum* Oldham, BSIP No. 1492. x 0.4 cm.
10. *Otozamites kachchhensis* Bose & Banerji, BSIP No. 52/2411. x 1.2 cm.
11. *Ptilophyllum cutchense* Morris, BSIP No. 65/2302. x 1 cm.
12. *Ptilophyllum cutchense* Morris, BSIP No. 58/2982. x 0.8 cm.

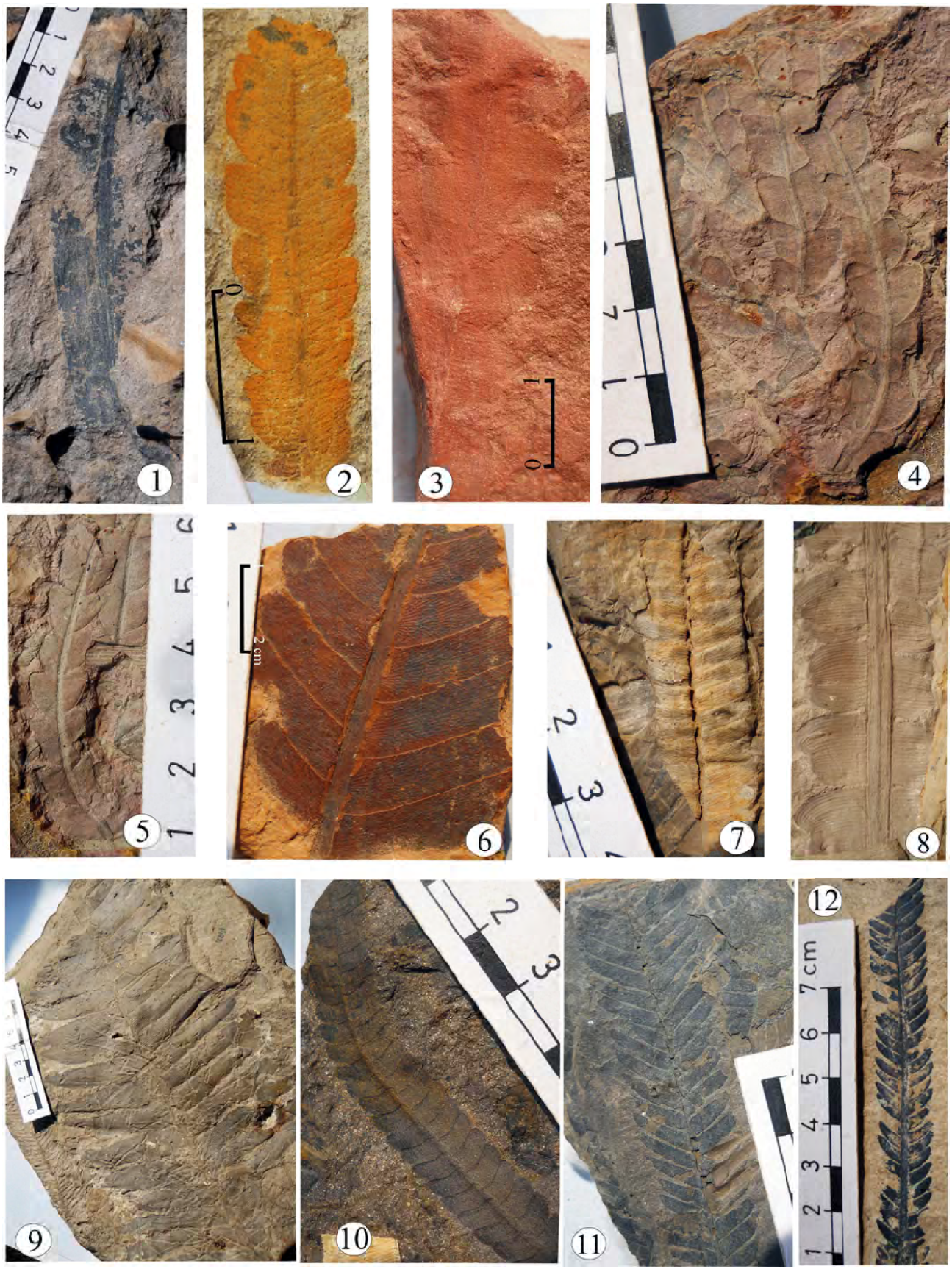

PLATE 1

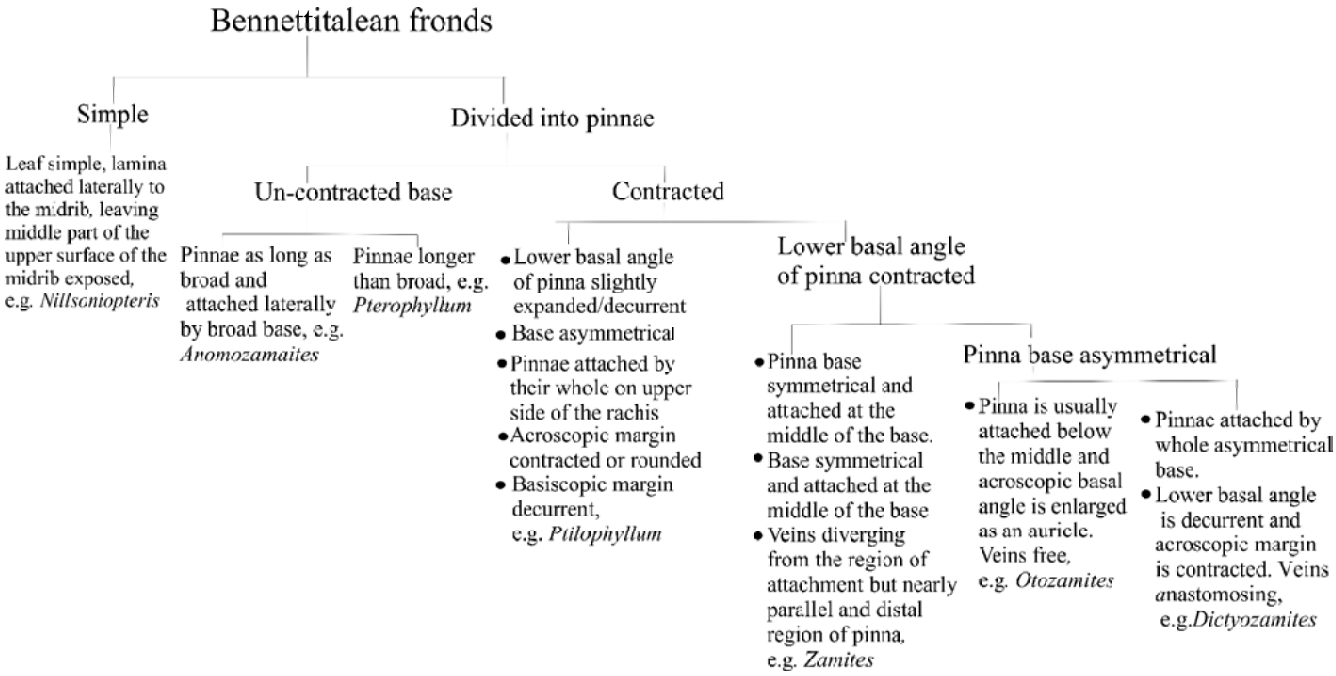

Fig. 4—Morphological characters of Bennettitalean fronds.

Leaves mostly large in size, rachis broad in middle region, characterized by long slender pinnae with parallel margins, pinnae larger than broad, attached laterally by entire un-contracted base, veins mostly parallel forked or unforked.

Genus—NILSSONIOPTERIS Nathorst

Type species—*Nilssoniopteris pannuceus* Bose & Banerji

(Pl. 1.1; Pl. 2.1)

Leaves linear to lanceolate with thin substances of lamina and entire margins, midrib gradually tapers towards apex, sometimes finely striated, lateral veins mostly arise at right angle, simple, straight and parallel, forking at different levels.

Genus—ANOMOZAMITES Schimper

Type species—*Anomozamites fissus* Feistmantel

(Pl. 1.2, 3; Pl. 2.6)

Leaves linear, segmented, segments attached on upper side of rachis by entire base, rectangular in shape, as long as broad, bases of segments joined with each other, apex rounded, notched or wavy, venation simple, veins parallel, arising at almost right angle reaching up to apex.

Genus—CTENOZAMITES Nathorst

Type species—*Ctenozamites kachchhensis* Bose & Banerji, 1984

(Pl. 1.4, 5; Pl. 2.5)

Frond bipinnate, pinnae alternate, arising at an angle of 35°- 45°, pinna rachis smooth or faintly striated, pinnules sub-opposite, attached by broad base, mostly broader than long, more or less contiguous, rhomboidal in shape, veins parallel, simple or forked, usually obscure, sometimes faintly visible, apex obtuse.

Genus—DICTYOZAMITES Oldham & Morris

PLATE 2 →

1. *Nilssoniopteris pannuceus* Bose & Banerji, enlarged showing midrib and lateral veins, BSIP No. 4/2411c. x 3. 5 cm.
2. *Dictyozamites feistmantelii* Bose & Zeba-Bano, Leaf enlarged showing arranged of pinnae on rachis, enlarged basal lobe and reticulate venation pattern, BSIP No. 1/1366. x 9 cm.
3. *Ptilophyllum cutchense* Morris, enlarged showing upper rounded and lower decurrent margin with few parallel or forked veins, BSIP No. 65/2302. x 5.9 cm.
4. *Otozamites kachchhensis* Bose & Banerji, enlarged showing cordate shaped base and venation pattern, BSIP No. 52/2411. x 5 cm.
5. *Ctenozamites kachchhensis* Bose & Banerji, BSIP No.77/2079B. x 3 cm.
6. *Pterophyllum morrisianum* Oldham, enlarged pinnae showing deep dissected laterally joined pinnae attached by broad base, BSIP No 1492. x 1.4 cm.
7. *Anomozamites amarjolenses* Sharma *et al.*, enlarged showing venation pattern and attachment of pinnae by broad base, BSIP No. 16695. x 5 cm.

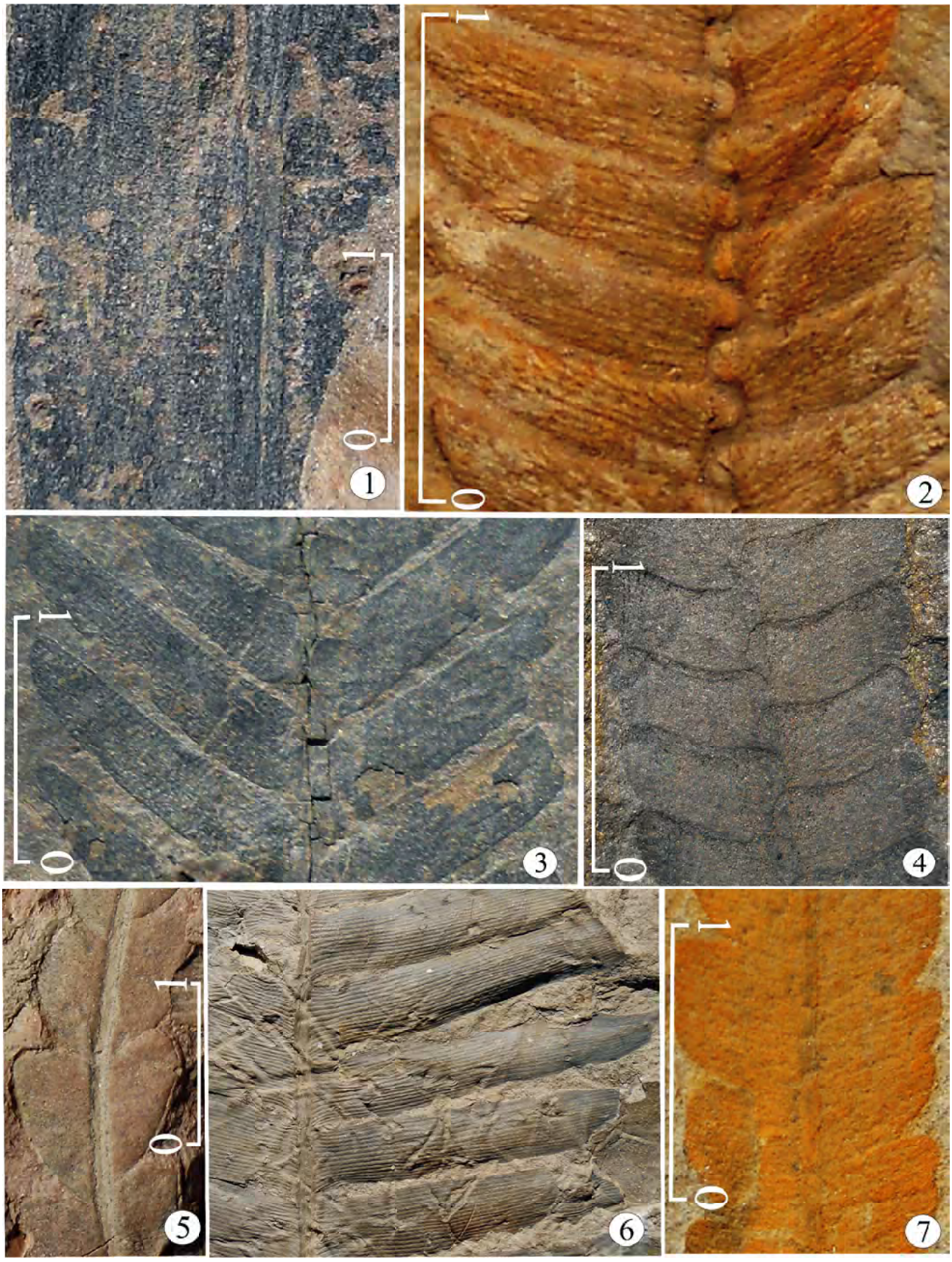

PLATE 2

Type species—*Dictyozamites falcatus* (Morris) Medlicott & Blandford

(Pl. 1.6, 7; Pl. 2.2)

Leaves pinnate, linear, attached on upper surface of rachis, lanceolate, pinnae falcate with entire margins, veins prominent, forking and anastomose to form areoles. The anastomosing pattern of veins distinguish this genus from others, bases contracted, asymmetrical and auriculate, apex sub-acute or obtuse.

Genus—OTOZAMITES Braun

Type species—*Otozamites bengalensis* (Schimper) Feistmantel

(Pl. 1.10; Pl. 2.4)

Leaves pinnate, linear-lanceolate, tapering to a blunt apex, pinnae opposite or subopposite, alternate, attached mostly at 50°–70° angles to rachis and partially concealed by base of lower pinnae, upper basal margin with spreading veins, apex rounded or ovate, base asymmetrical, mostly auriculate.

EVALUATION OF LEAF MORPHOLOGY

Bennettitalean remains were widely distributed in both northern and southern hemispheres during the Mesozoic Era. The Jurassic Period was a paradise for their luxuriant growth. Though *Pterophyllum sahnii* (Lele, 1956) first appeared in Early Triassic but it is found extensively in sedimentary deposits of Jurassic and became extinct by the end of Early Cretaceous. The morphological variations (Fig. 2) from simple to compound leaves are apparent in Mesozoic fossil records of Indian Gondwana basins (Figs 3, 4). The undivided simple leaf of *Nilssoniopteris* is considered as ancestral form (Mamay, 1969; Zimmermann, 1952; Stewart & Ruthwell, 1993; Kenrick & Crane, 1997; Doyle, 1988), while leaflets of compound leaves were developed gradually (Mamay, 1969) by subdivision and suppression of simple laminae (Zimmermann, 1952). These suppressions however dissected inwardly towards midrib and form broad lobes, remain joined at the base. They may or may not reach up to the rachis, e.g. *Anomozamites* and *Ctenozamites.* In *Pterophyllum,* these dissections are drawn even more deeply and reach up to the rachis. Though, they apparently touch each other, they adhere to the rachis by their broad base. In *Ptilophyllum* fronds these longitudinal subdivisions reach to the rachis with the fusion of catadromic and anadromic margins of pinnae at base exhibiting further advanced morphological features. Furthermore advancement is also visible in *Otozamites,* where the pinnae sizes are reduced.

The distinctions are drawn in between leaf lamina where in, two or more veins running from midrib reaching up to the apex, exhibit parallel venation. This is further supported by syngenesis of leaf stele which leads either to forked vein with open to pinnate venation or by anastomizing of steles, i.e. net venation (secondary veins fused to form areoles or reticulate venation), e.g. *Dictyozamites*. The multi-pinnate architecture increases the amount of photosynthetic surface of the leaves which keeps wind loading to a minimum. This is another advance stage of Bennettitalean leaves. Thus, these hallmark changes (simple to compound leaf, parallel to reticulate venation) might have impelled for their survival in warm and drier palaeoclimatic conditions.

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