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Palaeogene plant fossils of Manipur and their palaeoecological significance

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ABSTRACT

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The paper describes for the first time some Palaeogene plant fossils from Manipur, Northeast India. The fossils were recovered from the late Eocene and early Oligocene sediments in the vicinity of the boundary of the Disang and Barail Groups of rocks of the Imphal Valley and its adjoining areas. All the fossils belong to Angiosperms and represent monocots and dicots. The assemblage consists of mainly dicotyledonous leaves, two types of palm leaves, a fruiting shoot, a leguminous fruit and a bark. The fossil leaves show a rich morphological diversity and indicate the existence of warm and humid tropical vegetation at the time of deposition.

Key-words—Plant fossils, Angiosperms, Late Eocene-Early Oligocene, Imphal Valley, India.

सारांश

मणिपुर के कुछ पेलियोजीन पादप पादपाश्म तथा उनका पुरापारिस्थितिक महत्त्व

जे.एस. गुलेरिया, आर.के. हेमन्ता सिंह, आर.सी. मेहरोत्रा, आई. सोयबम एवं राजकुमार किशोर

इस शोध-पत्र में पूर्वोत्तर भारत के मणिपुर से प्राप्त कुछ पेलियोजीन पादप पादपाश्मों को प्रथम बार वर्णित किया गया है। इम्फाल घाटी तथा इसके आस-पास की चट्टानों के दिसांग एवं बैरल समूहों के सीमांत क्षेत्रों के उपरि ईओसीन तथा निम्न ओलिगोसीन अवसादों से इन जीवाश्मों को खोजा गया है। सभी जीवाश्म आवृतबीजियों से संबंधित हैं तथा ये एकबीजपत्री एवं द्विबीजपत्री निरूपित करते हैं। इस समुच्चय में मुख्य रूप से द्विबीजपत्री पत्तियाँ, दो प्रकार की ताड़ की पत्तियाँ, फलन प्ररोह तथा एक छाल सम्मिलित हैं। ये जीवाश्म आकार-वर्गिकी पत्रीय विविधता की प्रचुर उपस्थिति तथा निक्षेपण के समय उष्ण एवं आर्द्र उष्णकटिबंधीय वनस्पतिजात की विद्यमानता प्रदर्शित करते हैं।

संकेत शब्द—पादप पादपाश्म, आवृतबीजियों, उपरि ईओसीन-निम्न ओलिगोसीन, इम्फाल घाटी, भारत।

INTRODUCTION

TERTIARY plant megafossils of Northeast India (Assam, Arunachal Pradesh, Meghalaya, Mizoram, Nagaland and Tripura) are well documented except for Manipur (Guleria, 1992; Mehrotra, 2000a,b; Mehrotra & Mandaokar, 2000, 2002; Mehrotra & Bhattacharyya, 2002; Mehrotra *et al.*, 2003, 2004; Mandaokar *et al.*, 2004). The only known record from Manipur is a fossil wood, *Glutoxylon* from the ?Quaternary (Recent/ Sub Recent) sediments of Manipur (Ghosh, 1958). However, detailed investigations on plant megafossils of Manipur have not been attempted till date. In order to fill this gap, the authors investigated a small assemblage of Tertiary plant remains from the Imphal Valley of Manipur and its peripheral areas. The objective of the study is to build up the floral history of this part of northeast India.

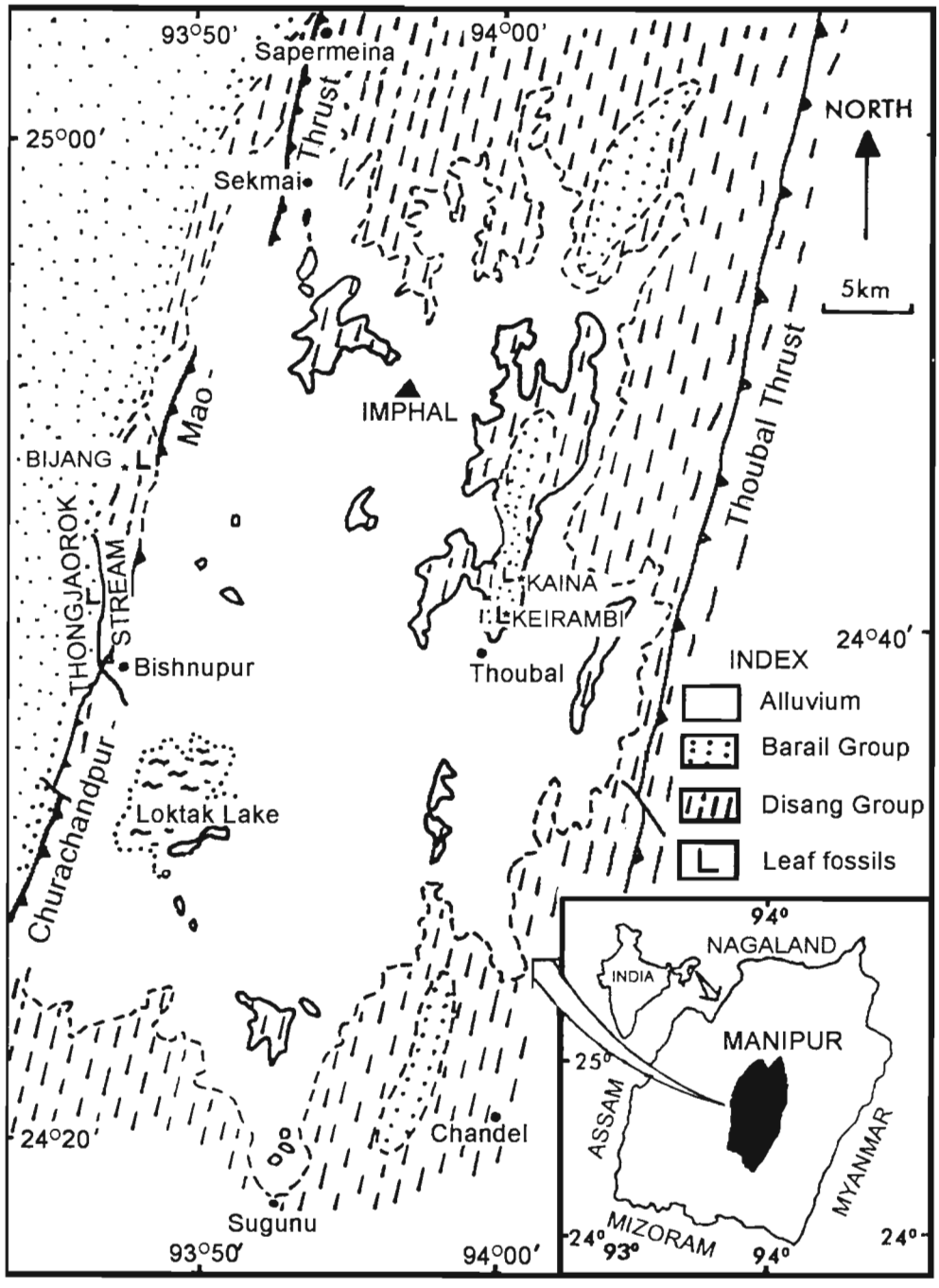

Fig. 1—Geological Map of the Imphal Valley showing plant fossil localities. Darkened portion in the index map represents the portion of the Imphal Valley.

GEOLOGICAL SETTING

The state of Manipur is situated in the north-eastern part of India and is bounded by Myanmar on the east, Nagaland on the north, Assam on the west and Mizoram on the south and southwest (Fig. 1). The Manipur Hills, which form an integral part of the Indo-Myanmar Ranges (IMR) of Northeast India, have been evolved as an accretionary prism due to subduction of the Indian plate below the Myanmar plate during the Alpine-Himalayan tectogenesis (Desikachar, 1974; Acharyya *et al.*, 1986; Mitchell, 1993). As a result, almost all the lithounits present in the region lean one over the other in the form of an imbricate thrust system where older lithounits lie above the younger ones (Soibam, 1998, 2001). Thus, the oldest group of rocks, the Metamorphic Complex (Brunnschweiler, 1966) lies on the extreme eastern part of the state while the Ophiolite Melange Zone comprising the Ophiolite suite and its associated sediments such as chert, limestone, shale and sandstone of the late Cretaceous age occupies the eastern part of the state. The Disang and Barail sediments of Palaeogene age occupy the major central part and constitute the principal lithounits of the state while the Neogene Surma and Tipam sediments lie on the western and south-western part of the state. The lithounits of the state are, therefore, more or less exclusively made up of Tertiary and Cretaceous sediments with minor igneous and metamorphic rocks, of which principally the flysch sediments of Disang and Barail constitute nearly 60-70% of the state's total area. All these lithounits can be represented in a generalised stratigraphic sequence in the form of a table (Fig. 3). The structural and tectonic trend of the lithounits is NNE-SSW where the lithounits dip at moderate to high angles towards east to west.

The Imphal Valley, which is believed to have evolved as a tectonic basin in the later phase of IMR tectogenesis (Soibam, 1998), lies in the central part of Manipur extending approximately between 24°14' N and 25°00' N latitudes and 93°48' E and 94°07' E longitudes and at a mean elevation of about 782 m above mean sea level (Fig. 1).

The valley is an intramontane depression within the IMR of Northeast India bounded in the east by Thoubal Thrust and Churachandpur-Mao Thrust in the west. It is virtually a flat land filled with sediments of fluvio-lacustrine origin principally consisting of dark clay, silt and sand deposits in

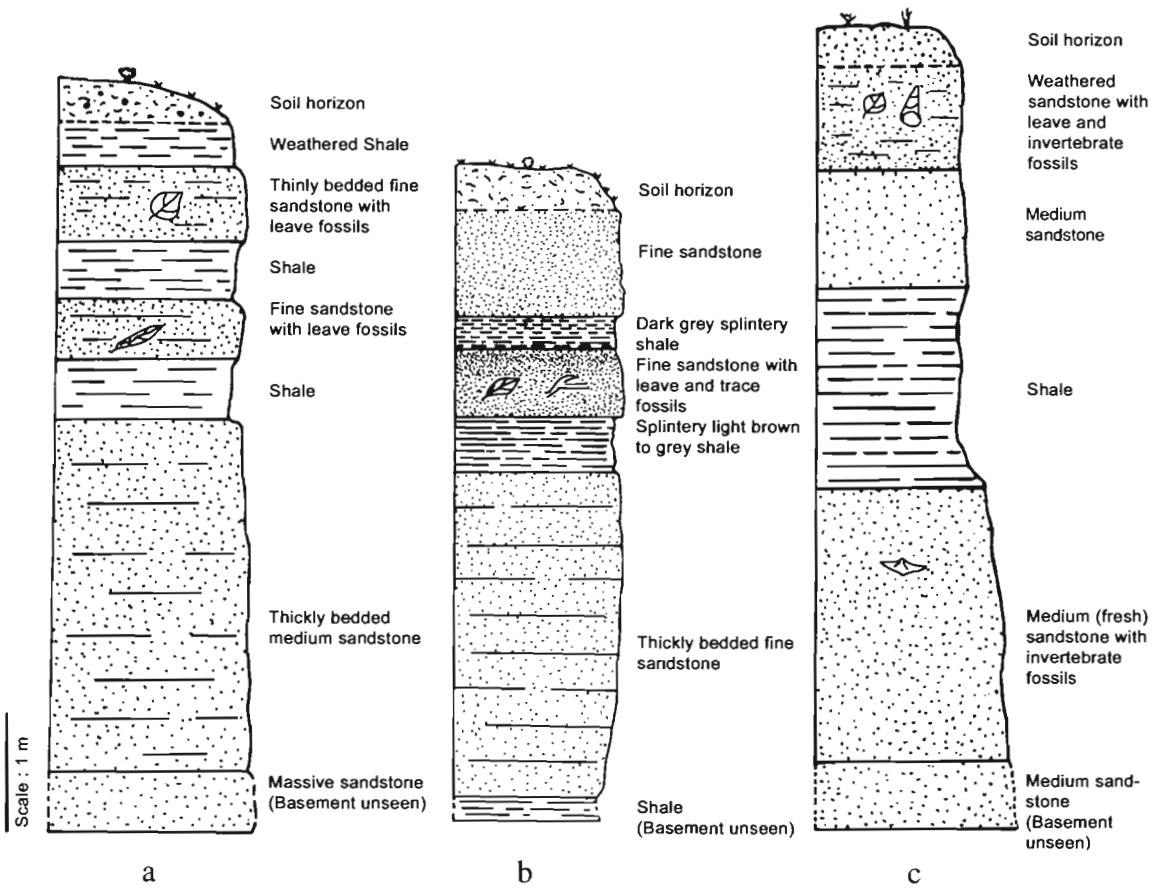

Fig. 2—Lithologs showing the fossil leaf horizons. a. Bijang, b, Kaina and c, Keirambi

Lithounits and age	Description of rocks
Alluvium (Quaternary – Pleistocene)	Dark grey to black clay, silt and sandy fluvio-lacustrine deposits of Imphal Valley. Fluvial alluviums in the Barak Valley area of (?)Older Western plains.
	Clay, sand, gravel, pebble, boulder deposits of the foothills and older river terraces.
----------	-Unconformity ----------
Tipam (Miocene)	Mottled clay, mottled sandy clay, sandy shale, clayey shale and sandstone
	Greenish to blue, moderate to coarse ferruginous sandstones with sandy shale, clay. Often brown to orange due to weathering. Molasse type of deposits.
Surma (Mio. to Up. Oligocene)	Shale, sandy shale, siltstone, ferruginous sandstone, massive to false bedded ferruginous sandstone.
	Alternations of sandstones and shales with more argillaceous horizons in the middle and minor conglomerate. Transitional character from flysch to molasse sediments.
----------	-Unconformity ----------
Barail (Oligo. to Up. Eocene)	Massive to thickly bedded sandstone. Alternation of shale and sandstone with carbonaceous matters. Intercalation of bedded sandstone with shales. Flysch sediments of turbidite character showing littoral characters.
Disang (Eocene to Up. Cretaceous)	Dark grey to black, splintery shales and intercalation of shales, siltstones and sandstones showing occasionally rhythmite and sub-littoral characters.
----------	-Unconformity ----------
Ophiolite Mélange Zone (Lr. Eo. to Up. Creta.)	Basic and ultrabasic intrusives, extrusives of peridotite, gabbro, serpentinite composition. Associated sediments are mainly pelagic, such as cherts, limestones, shales, etc.
----------	-Unconformity ----------
Metamorphic Complex (Pre-Mesozoic or Older)	Low to medium grade metamorphic rocks of various composition - phyllitic schists, quartzites, micaceous quartzite, quartz-chlorite-mica-schists and marble.
----------	(?) Unconformity ----------
Basement Complex	Unseen. (?) Early Mesozoic rocks or Precambrian rocks

Fig. 3 - Generalised Stratigraphic Succession of Manipur (after Soibam, 1998).

the central part and cobbly to bouldery deposits in the piedmont regions. A number of isolated, small to considerably large hills and hillocks do occur within the valley protruding above the flat alluvium. These are principally made up of Upper Disang shales which are generally dark grey in colour but often red to reddish brown due to weathering, splintery in character and consist of occasional to considerable silty and fine sandy bands sometimes giving rise to rhythmite character.

The Lower Barail sediments, which are mainly found in the western foothills as well as outliers (forming cap of the Disang) in the eastern part of the valley, show generally interbedded nature characterised by thinly bedded sandstones, shales with bedded sandstone, sandy and silty shales and shales displaying typical turbidite characters at places (Evans, 1932; Dayal & Daura, 1966; Daura & Debadhikari, 1968; Soibam, 1998). The sandstones are generally fine to medium grained and light grey to light brown in colour. The contact between the Disang and Barail is a gradational lithoboundary, except in some places of western foothills where it is tectonic. Such a gradational contact indicates a gradual change from dominantly argillaceous deep marine to a dominantly arenaceous shallow marine depositional environment. Presence of invertebrate fossils such as bivalves, gastropods and crustaceans which have been assigned late Eocene age (Kachhara *et al.*, 1998) and trace fossils such as *Thalassinoides*, *Skolithos* and *Chondrites* indicating shallow marine depositional environment (Hemanta Singh, 2005), besides the plant fossils reported here, further strengthens the change in the depositional environment.

Lithologs prepared for the important sections at Bijang, Kaina and Keirambi (Fig. 2) have a nearly identical interbedded shale and sand character where plant fossils are associated with fine sandstone beds alternating with shales. Sections at Bijang (24°46'53"N; 93°46'53"E) and Kaina (24°40'41"N; 94°01'26"E) that are separated by about 26 km normal to the regional strike, show similarity in lithocharaters and fossil leaves may serve as a marker horizon for the Upper Disang and Lower Barail lithoboundary. The Keirambi hillock (24°39'31"N; 94°00'11"E) is along the strike continuation of the Kaina hill at a distance of about 2 km south. This locality contains invertebrate and leaf fossils similar to those of Kaina Hill. So, the age of fossil leaves of the two sections (Bijang and Kaina) may be late Eocene while the fruiting shoots at Thongjaorok Stream section (24°37'41"N; 93°44'48"E) found well within the interbedded sand-shale Laishong Formation of Barail Group may be of the early Oligocene age.

MATERIAL AND METHODS

A number of small to large leaves, fruit bearing shoots, bark and leguminous fruit remains were collected by two of the authors (Hemanta and Rajkumar Kishor) from different localities, namely, Bijang, Kaina, Keirambi and Thongjaorok Stream sections of Bishnupur foothills of the Imphal Valley and its peripheral regions (Fig. 1). In general the material is fragmentary and sometimes not well preserved. The specimens are in the form of impressions comprising mainly leaves.

The collection largely consists of leaf remains which were studied in detail for their morphological structures. The terminology in describing these leaves, has been followed as proposed by Hickey (1973) and Dilcher (1974). Identification has been based on the morphology and the venation of fossil leaves and wherever possible, attempts have been made to relate the fossils to extant taxa. In view of the poor preservation and fragmentary nature of the material, the fossils have been described under the artificial system of nomenclature. All the specimens and photographs are preserved at the repository of the Birbal Sahni Institute of Palaeobotany (BSIP), Lucknow.

SYSTEMATICS

MONOCOTYLEDONS

Family—ARECACEAE

Genus—PHOENICITES Brongniart, 1828

PHOENICITES INDICA sp. nov.

(Pl. 1.1-2)

The description is based on a single well preserved impression specimen.

Description—Leaf pinnate, three incomplete leaflets seen on one side of the rachis, two of them showing attachment with rachis; leaflets narrower at the point of attachment, apex of leaflets broken; rachis 4.5 cm long, 1.0 cm thick, pinnae or leaflets 4.0-8.5 cm long, 1.0-2.5 cm wide, appearing reduplicate type, thick, coriaceous; venation pinnate, decurrent, midvein distinct, strong and uniform, angle of divergence narrow acute, about 5-7 secondaries running parallel on either side of midvein, equidistant, spines absent on the leaflet and rachis; occurrence of small gall like structures seen on secondary veins of middle leaflet.

Holotype—Specimen No. BSIP 39203.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The important features are: thick coriaceous pinnate leaf, pinnae joined to strong rachis by their entire narrow bases, venation pinnate, decurrent, strong midvein and secondaries running parallel to midvein on either side. All these characters indicate that the fossil belongs to a pinnate-leaved palm or feather palm.

In view of the fragmentary nature of the palm leaf it is difficult to trace its natural affinity with living genera, as such reduplicate type of pinnate leaves are found in a number of palms (Tomlinson, 1990, p. 224). Leaf remains of pinnate-leaved palms have been assigned to the genus *Phoenicites* Brongniart,

1828 (Read & Hickey, 1972). Consequently, the present fossil has been placed under this genus. A number of fossil palm leaves, both pinnate and palmate types are known from India and a list of 17 records is given by Guleria and Mehrotra (1999, p. 77). While listing these, two more records reported by Mahabale and Rao (1968) skipped their mention in the list. No formal name has been given to them and they have simply been reported as Specimen B 47/63 and B 61/63. Specimen B 47/63 has been compared with the leaflets of *Cocos*. Since then five more palm leaves have been reported. These are: *Amesoneuron sahnii*, from the early Miocene of Kasauli, Himachal Pradesh (Guleria *et al.*, 2000); *A. lakhanpalii* and *A. deccanensis* from the late Palaeocene of Garo Hills, Megahalaya (Mehrotra, 2000a); *Palmacites* sp. from the Oligocene of Tirap District, Arunachal Pradesh (Mehrotra & Mandaokar, 2000); and leaf fragments assigned to *Nypa fruticans* from the Oligocene of Assam (Mehrotra *et al.*, 2003). Amongst these, there are about half a dozen records which can be compared with the present fossil.

The ?*Sabalites* sp. (Bose & Sah, 1964) and *Phoenicites lakhanpalii* (Guleria & Mehrotra, 1999), both represent unsegmented pinnate leaves and are not comparable with the present fossil. *Zalaccites jaintiensis* (Barman & Daura, 1970) shows some resemblance with the present fossil although leaflets in *Zalaccites* seem fused or very closely placed (Barman & Daura, 1970, p. 64, fig.1) as compared to the present specimen which shows distinctly separate leaflets. A fossil specimen showing resemblance with the pinnate leaf of *Phoenix* spp. has been reported by Mahabale (1966, p. 216, pl. 1, fig. 6) as *Palmophyllum mohgaonense*. It is based on the basal part of the leaf exhibiting spines on the axis or rachis and thus is not comparable with the present fossil. A pinnate leaf reported by Mahabale and Rao (1973, pl. 2, fig. 32) from the Rajahmundry Sandstones of Bommuru, Andhra Pradesh, is without any description and represented by a very poor photograph. Hence, it is not possible to compare this specimen with the present fossil due to lack of details. Isolated palm fragments were reported by Lakhanpal (1964) without any description from Nangwalbibra of Garo Hills, Meghalaya. He referred them to the genus *Phoenicites* and assumed their affinity with the leaflets of *Phoenix* without depicting or mentioning diagnostic features of a *Phoenix* leaflet. The fragments, indeed belong to palm, however, the specimens being fragmentary, it is not possible to say with certainty whether they belong to a pinnate or palmate leaf. Such types of fragments have been assigned to the genus *Amesoneuron* (Read & Hickey, 1972). Obviously, the present specimen which represents an undoubtedly pinnate leaf, is not comparable with Lakhanpal's specimen. Such leaves as reported by Lakhanpal (1964) have lately been described from Nangwalbibra under the genus *Amesoneuron* (Mehrotra, 2000a). As the present specimen differs from the known fossil palm leaves, it is given a new specific name *Phoenicites indica* sp. nov.

Genus—AMESONEURON (Goeppert) Read & Hickey, 1972

AMESONEURON MANIPURENSIS sp. nov.

(Pl. 1.3-4)

The description is based on four well preserved leaf fragments, representing both the dorsal and ventral sides of lamina.

Description—Leaf fragments vary in size, seemingly plicate, preserved length 5.5 cm to 9.0 cm, width 1.3 to 3.5 cm, strap-shaped, thick chartaceous to coriaceous, apex and base not preserved, margin entire without any spines or teeth; midvein prominent, stout, running almost straight, sunken in one specimen and raised in another representing the two sides of lamina, two orders of secondaries closely placed, 1-2 mm apart, equidistant, running parallelly straight, moderately thick; further details obscure. Minute, oval and smooth raised surfaces or protuberances arranged in a linear sequence are seen on the surface of lamina (Pl. 1.3-4) mostly on secondary veins indicating the occurrence of leaf galls.

Holotype—Specimen No. BSIP 39204A.

Paratype—Specimen Nos. BSIP 39205-39207.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The thick strap-shaped, plicate leaf fragments exhibiting a distinct midvein and lower orders of parallel veins indicate that the specimens are fragments of palm leaf/leaves. Three main types of lamina are seen in palms, namely, palmate, costapalmate and pinnate (Tomlinson, 1990). The available specimens are too fragmentary to decipher clearly the kind of palm lamina they represent, i.e., the original leaf form. Such fossil leaf remains (segments or fragments) have been assigned to an artificial genus *Amesoneuron* (Goeppert) Read and Hickey, 1972.

PLATE 1 →

1. *Phoenicites indica* sp. nov.– a fossil leaf showing rachis and attached pinnae. x 1; specimen no. BSIP 39203.
2. The same specimen enlarged to show parallel venation. x 2.
3, 4. *Amesoneuron manipurensis* sp. nov.– plicate strap-shaped leaf fragment showing distinct mid-rib, parallel venation and raised gall like structures. x 1& 2 respectively; specimen no. BSIP 39204A.
5. *Dicotylophyllum kainai* sp. nov.– a fossil leaf showing size, shape, pinnate venation and a hook-shaped trace mark. x 1; specimen no. BSIP 39208.
6. *D. undulatum* sp. nov.– a fossil leaf showing size, shape and venation pattern. x 1; specimen no. BSIP 39209.
7. *D. intramarginalivenoides* sp. nov. – a fossil leaf fragment showing venation pattern. x 1; specimen no. BSIP 39210A.
8, 9. The same specimen enlarged to show venation pattern and intramarginal vein. x 3.

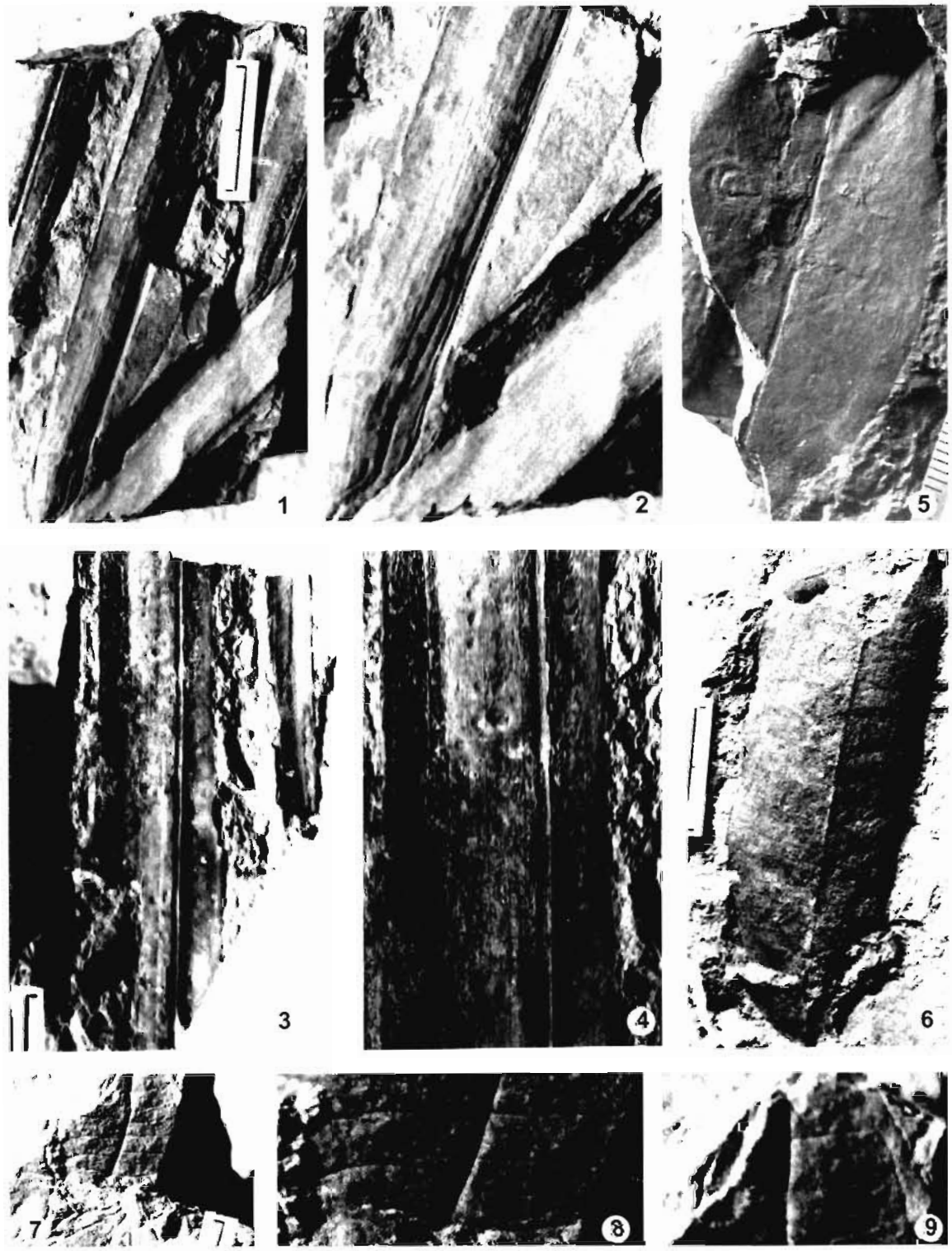

PLATE 1

Among the known Indian records of fossil palm leaves (see p. 66 of the present paper), the present specimens show near resemblance with *Amesoneuron deccanensis* (Guleria & Mehrotra, 1999; Mehrotra, 2000a). However, the occurrence of raised, oval and smooth, gall-like structures arranged in linear order on the lamina differentiate the present specimens from *A. deccanensis*; hence a new name, *A. manipurensis* sp. nov., is assigned to the present fossils.

The authors take this opportunity to review the *Amesoneuron* spp., viz., *Amesoneuron lakhanpalii* and *A. deccanensis* reported from the Garo Hills, Meghalaya. In view of the close similarity observed in their morphological characters, the authors have merged the former species into the latter (*A. decannensis* Guleria & Mehrotra, 1999), the earlier described species.

Type species—*Amesoneuron deccanensis* Guleria & Mehrotra (1999), Palaeobotanist, 47, pp. 78-79, pl. 1, figs 5-7.

Synonyms

2000a *A. deccanensis* Mehrotra, p. 236, pl. 3.2
2000a *A. lakhanpalii* Mehrotra, pp. 234, 236, pl. 3.1, 3.3

DICOTYLEDONS

Genus—DICOTYLOPHYLLUM Saporta, 1894

DICOTYLOPHYLLUM KAINAI sp. nov.

(Pl. 1.5)

The description is based on a single specimen.

Description—Leaf appearing symmetrical, preserved length of lamina about 5.0 cm, width about 3.0 cm, appearing elliptical in shape; apex and base broken; margin entire; texture thick, chartaceous; venation pinnate, eucamptodromous; primary vein moderately thick, more or less straight; secondaries poorly preserved, only two visible in one half of the leaf; 2.8 cm apart, uniformly curved and turning upward towards margin, angle of divergence 45°; a hook-type trail or trace mark seen on the upper part of the leaf.

Holotype—Specimen No. BSIP 39208.

Occurrence—Upper Disang; Kaina, Imphal Valley, Manipur; late Eocene.

Remarks—The thick chartaceous lamina with distinct midrib and eucamptodromous venation indicates that the fossil is a dicotyledonous leaf. Occurrence of a trace mark on the surface of the leaf indicates some kind of animal activity. The fragmentary nature of the fossil makes it difficult to compare it with leaves of any extant plant. Therefore, the fossil is assigned to a form genus *Dicotylophyllum* Saporta, 1894. Since it differs from the known fossil dicotyledonous leaves and species of *Dicotylophyllum* known from various parts of India (Guleria & Mehrotra, 1999, pp. 68, 71; Mehrotra & Mandaokar, 2000), a new name *Dicotylophyllum kainai* is assigned to it. The specific name is after the fossil locality Kaina, from where the fossil was collected.

DICOTYLOPHYLLUM UNDULATUM sp. nov.

(Pl. 1.6)

The description is based on a single leaf impression.

Description—Leaf symmetrical, narrow, oblong; preserved lamina length 8.2 cm, maximum width about 3 cm; apex broken; base appearing obtuse, normal; margin entire but undulating; texture chartaceous; petiole not preserved; venation pinnate appearing craspedodromous; primary vein moderately thick to stout, slightly curved; secondary veins faintly preserved, more than 10 pairs visible, alternate, 3-5 mm apart, angle of divergence wide acute (65°-75°), straight, unbranched, moderately thick; higher order venation not visible.

Holotype—Specimen No. BSIP 39209.

Occurrence—Upper Disang; Kaina, Imphal Valley, Manipur; late Eocene.

Remarks—The long leaf with entire undulating margins depicting pinnate craspedodromous venation shows that the fossil is a dicotyledonous leaf and thus represents the form genus *Dicotylophyllum* Saporta. In the absence of apex and base, it is difficult to compare it with leaves of extant genera. The specimen, however, differs from all the known fossil dicotyledonous leaves (Guleria & Mehrotra, 1999; Mehrotra & Mandaokar, 2000) from India. Hence, a new specific name, *Dicotylophyllum undulatum* sp. nov., is assigned to it. The specific name indicates characteristic shape of its margin.

PLATE 2 →

1. *Dicotylophyllum lakhanpalii* sp. nov.– a fossil leaf showing size, shape and venation pattern. x 1; specimen no. BSIP 39210B.
2, 7. *D. asymmetricum* sp. nov.– a fossil leaf showing size, shape and venation pattern. x 1 & 2 respectively; specimen no. BSIP 39211.
3, 8. *D. palaeoellipticum* sp. nov. –leaf fragments showing venation pattern . x 1; specimen nos. BSIP 39213 and BSIP 39212 (Holotype) respectively.
4. *D. eopulvinatum* sp. nov.– a fossil leaf showing size, shape and pinnate venation. x 1; specimen no. BSIP 39210C.
5. *D. evansii* sp. nov.– a fossil leaf showing size, shape and venation pattern. x 1; specimen no. BSIP 39210D.
6. A part of *D. evansii* enlarged to show venation and trace mark. x 2.
9, 10. Two specimens of fruiting shoots showing central axis and attached fruit-like bodies. x 1; specimen nos. BSIP 39214 and BSIP 39215 respectively.
11. *Leguminocarpon kainai* sp. nov.– a part of a legume pod. x 1, specimen no. BSIP 39216A.

PLATE 2

DICOTYLOPHYLLUM INTRAMARGINALIVENOIDES sp. nov.

(Pl. 1.7-9)

The description is based on a single fragmentary leaf impression.

Description—Leaf symmetrical, seemingly elliptic; preserved lamina length 2.1 cm, maximum width 1.7 cm; apex and base broken; margin entire; texture chartaceous; venation pinnate brochidodromous; primary vein moderately thick, markedly curved; secondary veins about eight pairs visible, alternate to sub-opposite, 2-3 mm apart, angle of divergence more or less right angle, straight to uniformly curved, parallel to each other, moderately thick; intramarginal vein present; intersecondary veins present, simple; tertiary veins not preserved; a number of dot-like features seen on the surface of lamina.

Holotype—Specimen No. BSIP 39210A.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The pinnate brochidodromous venation forming a distinct intramarginal vein clearly shows that the fossil is a dicotyledonous leaf. The most characteristic feature of the fossil is the presence of the intramarginal vein. This character is confined to the leaves of some genera belonging to a few families such as Anarcardiaceae, Apocynaceae, Clusiaceae, Euphorbiaceae, Melastomataceae, Moraceae, Myristicaceae, Myrtaceae, Rutaceae and Sapotaceae. Due to the fragmentary nature of the fossil, it is difficult to compare it with the leaves of any modern genera. The fossil being a dicot leaf, is described here as *Dicotylophyllum intramarginali-venoides* sp. nov.

DICOTYLOPHYLLUM LAKHANPALII sp. nov.

(Pl. 2.1)

The study is based on a single fragmentary leaf impression.

Description—Leaf appearing asymmetrical, probably elliptical in shape; preserved length of lamina 3.5 cm, maximum width 3.5 cm near the middle; apex and base broken; margin entire; texture chartaceous; venation pinnate; primary vein moderately thick, markedly curved; secondary veins faintly preserved, 2-3 incomplete veins seen, about 1.5-2 mm apart, angle of divergence wide acute (65°-70°), straight, unbranched, parallel to each other, moderately thick; tertiary veins not preserved.

Holotype—Specimen No. BSIP 39210B.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The above mentioned characters indicate that the fossil is a dicotyledonous leaf. The lack of apex and base and the obscure venation make its comparison difficult with leaves of any modern genera. The specimen, being different from the known dicot leaves (Guleria & Mehrotra, 1999; Mehrotra & Mandaokar, 2000), is given a new name, *Dicotylophyllum lakhanpalii* sp. nov., the specific name is after one of the senior Indian Palaeobotanists, Dr R.N. Lakhanpal who initiated work on Tertiary fossil leaves of Northeast India.

DICOTYLOPHYLLUM ASYMMETRICUM sp. nov.

(Pl. 2.2, 2.7)

The description is based on a solitary specimen.

Description—Leaflet appearing asymmetrical, elliptic; preserved length of lamina 3.5 cm, maximum width about 2 cm in the middle; apex broken but may be obtuse; base slightly asymmetrical, acute, normal; margin entire, texture chartaceous; venation eucamptodromous; primary vein moderately thick to stout, straight; secondary veins about 5 in number, alternate to sub-opposite, about 5-8 mm apart, angle of divergence moderately acute (45°-55°), uniformly curved, unbranched, moderately thick; intersecondary veins not clearly visible; finer veins not preserved.

Holotype—Specimen No. BSIP39211.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The small size, acute asymmetrical base, pinnate venation and apparently sessile nature of the specimen indicate that the fossil most probably represents a leaflet of a dicotyledonous plant. The specimen differs from the known

PLATE 3 →

1. A bark impression–showing striations on its surface. x 1; specimen no. BSIP 39220.
2. *D. acrodromoides* sp. nov. – a fossil leaf showing shape, size and venation pattern. x 1; specimen no. BSIP 39210E.
3. The same specimen enlarged to show typical acrodromous venation. x 3.
4, 5. *D. bijangense* sp. nov.– a fossil leaf showing shape, size and pinnate venation. x 1 & 2 respectively; specimen no. BSIP 39210F.
6. *D. calophylloides* sp. nov.– a fossil leaf showing very closely placed secondary veins. x 1; specimen no. BSIP 39204B.
7. *D. oblongum* sp. nov.– a fossil leaf showing oblong shape and pinnate venation. x 1; specimen no. BSIP 39210G.
8. *D. cordifoliatum* sp. nov.– a fossil leaf showing shape and type of venation. x 1; specimen no. BSIP 39218.
9. *D. alstonioides* sp. nov.– a fossil leaf showing *Alstonia* type of venation. x 1; specimen no. BSIP 39219.
10, 11. *D. lateovatum* sp. nov. – a fossil leaf showing pinnate venation and wide ovate base. x 1& 3 respectively; specimen no. BSIP 39217B.
12. *D. thoubalense* sp. nov.– a fossil leaf showing shape, size and venation pattern. x 1; specimen no. BSIP 39216B.

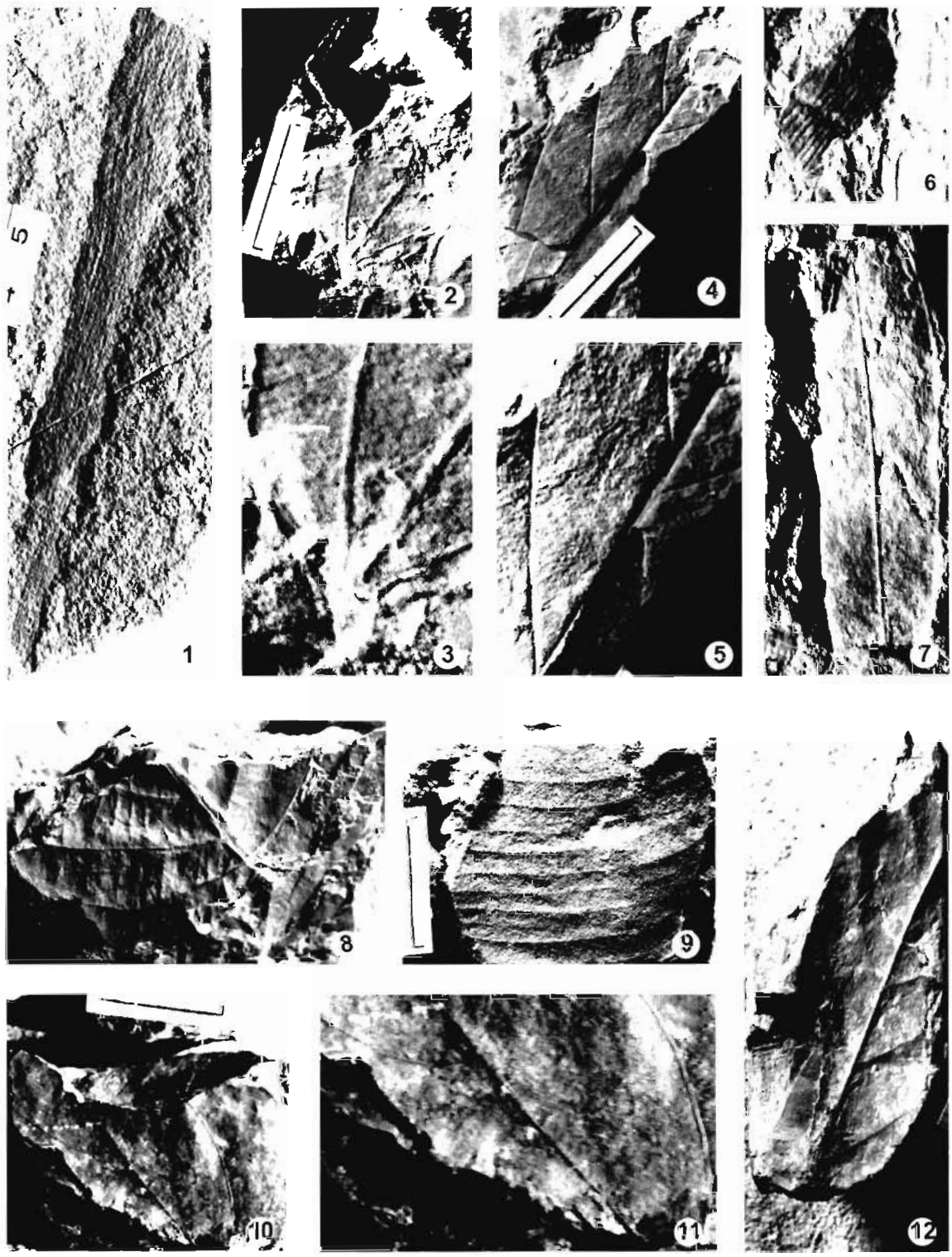

PLATE 3

dicotyledonous leaves (Guleria & Mehrotra, 1999; Mehrotra & Mandaokar, 2000), hence a new specific name, *Dicotylophyllum asymmetricum* sp. nov., is assigned to it.

DICOTYLOPHYLLUM PALAEOELLIPTICUM sp. nov.

(Pl. 2.3,8)

The description is based on two poorly preserved leaf impressions, one representing the ventral side of upper half and the other representing the dorsal side of the lower half of a leaf.

Description—Leaf appearing symmetrical, preserved lamina length about 4.2-6.5 cm, maximum width in the middle portion about 2.1-4.0 cm, narrow elliptic to elliptic; apex broken, seemingly acute; base appearing acute, normal; margin entire, straight in the middle part; texture chartaceous; primary vein raised in specimen no. 39213 and depressed in specimen no. 39212, representing ventral and dorsal sides of lamina, moderately thick, straight; secondary veins seemingly pinnate type.

Holotype—Specimen No. BSIP 39212.

Paratype—Specimen No. BSIP 39213.

Occurrence—Upper Disang; Kaina, Imphal Valley, Manipur; late Eocene.

Remarks—The characters depicted by the leaf impressions indicate that they belong to a dicot plant. Despite poor preservation, the specimens are important in the sense that they show diversity in the leaf-forms in the present collection. Since the leaves belong to a dicot and are morphologically different from the known fossil leaves (Guleria & Mehrotra, 1999; Mehrotra & Mandaokar, 2000), they are assigned to a new species, *Dicotylophyllum palaeoellipticum* sp. nov.

DICOTYLOPHYLLUM EOPULVINATUM sp. nov.

(Pl. 2.4)

The study is based on a single fragmentary leaf impression.

Description—Leaf seemingly symmetrical, probably elliptic; preserved lamina length 3.5 cm, maximum width 1.7 cm; apex broken; base symmetrical, acute, normal; margin entire; texture chartaceous; petiole pulvinate, broken; venation obscure; primary vein moderately thick, straight; secondary veins not preserved.

Holotype—Specimen No. BSIP 39210C.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The size, shape and general morphology of the leaf show that it is a dicotyledonous leaf. As it represents a different kind of leaf in the present assemblage and also differs from the known dicot leaves, it is named as *Dicotylophyllum eopulvinatum* sp. nov. The specific name refers to the pulvinate nature of the petiole of the leaf.

DICOTYLOPHYLLUM EVANSII sp. nov.

(Pl. 2.5,6)

The description is based on a single fragmentary leaf impression.

Description—Leaf seemingly symmetrical, appearing elliptic; preserved lamina length 4.5 cm, preserved width 2 cm (estimated width 2.6 cm); apex appearing acute, normal; base broken; margin entire, markedly curved; texture chartaceous; venation eucamptodromous; primary vein moderately thick, straight; secondary veins five pairs (visible), alternate to sub-opposite, 5-12 mm apart, angle of divergence moderately acute (45°-55°), uniformly curved, moderately thick; intersecondary veins indistinct; tertiary veins not preserved; trace fossils or trail marks observed on the surface of lamina depicting traces of organic activity most probably produced by some larvae.

Holotype—Specimen No. BSIP 39210D.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The pinnate eucamptodromous venation of the fossil at once indicates that it is a dicotyledonous leaf. The markedly curved entire margin with five pairs of alternate to sub-opposite secondaries differentiate the present specimen from the known fossil dicot leaves (Guleria *et al.*, 1999; Mehrotra & Mandaokar, 2000). Hence, it is assigned a new species, *Dicotylophyllum evansii* sp. nov. The specific name is after the late P. Evans, who worked on the geology and compiled the data on the geological succession of this region in a comprehensive manner.

DICOTYLOPHYLLUM ACRODROMOIDES sp. nov.

(Pl. 3.2,3)

The description is based on a single leaf impression representing only the basal half of the leaf.

Description—Leaf symmetrical, probably narrow ovate in shape; preserved lamina length about 2 cm, maximum width 2.1 cm; apex broken; base symmetrical, acute, normal; margin entire; texture thick chartaceous; venation acrodromous, basal; mid-vein thick, straight, lateral primaries two, moderately thick, arising at narrow acute angle (30°), arising from the base, curved; secondary veins moderately thick, closely placed (1-1.5 mm apart), straight (those arising from the midvein) to uniformly curved (those arising from the lateral primaries), unbranched, moderately thick; tertiary veins not preserved.

Holotype—Specimen No. BSIP 39210E.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The most characteristic feature of the fossil is basal acrodromous venation and entire margin. Such types of trinerved leaves are found in a number of dicot families (Lakhanpal & Guleria, 1981, pp. 358-359) including Lauraceae. Since the fossil is represented by only one specimen and its

upper half is also missing, it is difficult to compare it with the leaves of extant genera with certainty. Nevertheless, the fossil tends to show affinity with *Cinnamomum* leaves of the family Lauraceae. In view of its typical venation, the fossil is named as *Dicotylophyllum acrodromoides* sp. nov.

DICOTYLOPHYLLUM BIJANGENSE sp. nov.

(Pl. 3.4,5)

The description is based on a single fragmentary leaf impression.

Description—Leaf incomplete, seemingly symmetrical, probably narrow ovate, preserved lamina length 4 cm, preserved width 1.7 cm (estimated width 3.2 cm); apex and base broken; margin entire; texture chartaceous; venation appearing eucamptodromous; primary vein moderately thick, straight; three secondary veins distinctly visible on one half of the preserved lamina, one secondary vein seen on the other half, alternate, about 2 cm apart, angle of divergence narrow acute (35-45°), uniformly curved, moderately thick; intersecondary veins absent; tertiary veins percurrent, angle of origin RR, fine, closely placed (2-4 mm apart), straight to retroflexed, predominantly alternate, simple, oblique in relation to primary vein.

Holotype—Specimen No. BSIP 39210F.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—In view of the eucamptodromous and alternate venation seen in the fossil, it can safely be said that the fossil represents a dicot leaf. However, the fragmentary nature of the specimen makes it difficult to compare the fossil with leaf of any modern genus satisfactorily. On account of its distinct form and morphology, the fossil is assigned to a new species and named as *Dicotylophyllum bijangense*. The specific name is after the fossil locality, Bijang, from where the fossil was collected.

DICOTYLOPHYLLUM CALOPHYLLOIDES sp. nov.

(Pl. 3.6)

The study is based on a single fragmentary leaf impression.

Description—Leaf, elliptic ? in shape; preserved length of lamina 0.5 cm, preserved width 1.5 cm; apex and base not known; margin incomplete, unpreserved; texture thick, chartaceous; venation pinnate, appearing craspedodromous; primary vein stout, straight; secondary veins nine pairs visible, alternate to sub-opposite, very closely placed, 0.5-1 mm apart, angle of divergence more or less at right angle, straight, unbranched, parallel to each other, thick; finer venation not preserved.

Holotype—Specimen No. BSIP 39204B.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The single diagnostic feature of the fossil is the very closely placed secondaries, running almost at right angle towards the margin, which makes it possible to identify the specimen. This kind of typical venation is seen in the modern leaves of the genus *Calophyllum* belonging to the family Clusiaceae (Pascal & Ramesh, 1987, pl.26, figs 66, 67). Although a number of fossil leaves of *Calophyllum* are known from India and adjoining region (Awasthi & Prasad, 1990; Awasthi & Srivastava, 1992) yet the fragmentary nature of the present fossil makes it difficult to compare it with the known fossil leaves. Thus, it is described as *Dicotylophyllum calophylloides* sp. nov.

DICOTYLOPHYLLUM OBLONGUM sp. nov.

(Pl. 3.7)

The study is based on a single fragmentary leaf impression.

Description—Leaf appearing symmetrical, narrow oblong; preserved length of lamina 6 cm, maximum width 1.8 cm; apex and base broken; margin entire; texture chartaceous; venation pinnate, seemingly eucamptodromous; primary vein moderately thick, markedly curved; secondary veins seen at the basal preserved part, angle of divergence moderately acute; further details not present; gall-like feature seen as small depression in the apical part of the leaf.

Holotype—Specimen No. BSIP 39210G.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The pinnate eucamptodromous type of venation indicates that the fossil is a dicot leaf. Further details are obscure. It is difficult to speculate on the natural affinities of the specimen until better specimens are found. The fossil is being reported as *Dicotylophyllum oblongum* sp. nov., the specific name refers to its oblong shape.

DICOTYLOPHYLLUM CORDIFOLIATUM sp. nov.

(Pl. 3.8)

The description is based on a single impression representing the lower half of the leaf.

Description—Leaf incomplete, seemingly symmetrical, appearing narrow ovate, preserved lamina length 3.0 cm, width 3.5 cm; apex broken; base cordate; petiole thick, seemingly woody, pulvinate; margin entire; texture thick chartaceous; venation pinnate, eucamptodromous, primary vein thick, three pairs of secondaries seen, arrangement opposite to alternate, angle of divergence acute, about 50°-60°, secondaries uniformly curved, moderately thick; intersecondaries not seen; tertiaries percurrent, unbranched, opposite to alternate, obliquely arranged in relation to mid-vein; higher order venation not seen.

Holotype—Specimen No. BSIP 39218.

Occurrence—Upper Disang; Bijang, Imphal Valley, Manipur; late Eocene.

Remarks—The most characteristic features of the fossil are - seemingly symmetrical shape, entire margin, cordate base, thick and seemingly stout petiole, pinnate eucamptodromous venation and obliquely arranged percurrent tertiaries. These characters are seen in the leaves of a number of extant genera. Among them the fossil shows apparent resemblance to the leaves of *Terminalia* spp. The resemblance, however, can only be confirmed on getting better and bigger specimens. Since the fossil is undoubtedly a dicotyledonous leaf and its affinities not yet ascertained, it is named as *Dicotylophyllum cordifoliatum* sp. nov. on account of its difference from the known fossil dicot leaves (Guleria & Mehrotra, 1999; Mehrotra & Mandaokar, 2000).

DICOTYLOPHYLLUM ALSTONIOIDES sp. nov.

(Pl. 3.9)

The description is based on a single fragmentary leaf impression.

Description—Leaf oblanceolate-elliptic? in shape; preserved lamina length and width about 3.5 cm; apex and base broken; margin broken; texture thick, chartaceous; venation appearing pinnate; primary vein not preserved; nine secondaries visible extending from centre to very close to the margin, 3-5 mm apart, angle of divergence appearing at right angle (80°-90°), uniformly curved, unbranched, moderately thick; solitary intersecondary vein observed at one place, incomplete; finer venation not preserved.

Holotype—Specimen No. BSIP 39219.

Occurrence—Upper Disang; Kaina, Imphal Valley, Manipur; late Eocene.

Remarks—Taking into consideration the type of venation, spacing between the secondaries and the width of lamina, the fossil shows apparent resemblance to the leaves of the genus *Alstonia* of the family Apocynaceae. Fossil leaves of *Alstonia* have been reported from Bihar, West Bengal, Assam and Arunachal Pradesh (see Mehrotra & Mandaokar, 2000). Due to the fragmentary nature of the present specimen which represents only a part of the leaf, it can not be compared convincingly either with the extant leaves of *Alstonia* spp. or with the fossil species. Consequently, the present fossil is designated as *Dicotylophyllum alstonioides* sp. nov.

DICOTYLOPHYLLUM LATEOVATUM sp. nov.

(Pl. 3.10-11)

The description is based on a single fragmentary leaf impression representing the lower half of a leaf.

Description—Leaf ?symmetrical, shape not clear but appearing ovate; preserved length of lamina about 4 cm, preserved width 3.5 cm; apex and margin broken; base appears wide ovate; texture chartaceous; venation pinnate, probably eucamptodromous; primary vein moderately thick, straight; secondary veins 2 pairs visible, alternate, about 2.5 cm apart, angle of divergence narrow acute (40°-45°), uniformly curved, moderately thick; intersecondary veins not observed; tertiary veins percurrent, angle of origin usually RR, fine, closely placed (2-6 mm apart), straight, predominantly alternate, simple, horizontal to oblique in relation to primary vein.

Holotype—Specimen No. BSIP 39217B.

Occurrence—Upper Disang; Kaina, Imphal Valley, Manipur; late Eocene.

Remarks—The characteristic pinnate venation indicates that the fossil is a dicot leaf. It differs not only from all the specimens in the present assemblage but also from the known fossil dicot leaves (Guleria & Mehrotra, 1999; Mehrotra & Mandaokar, 2000). Since it represents a different morphotype, it is described as *Dicotylophyllum lateovatum* sp. nov., the specific name is after its wide ovate base.

DICOTYLOPHYLLUM THOUBALENSE sp. nov.

(Pl. 3.12)

The study is based on a single fragmentary leaf impression.

Description—Leaf symmetrical, narrow elliptic; preserved lamina length 4.5 cm, preserved width 1.8 cm (estimated width 2 cm); apex and base broken; margin entire; texture chartaceous; venation pinnate, most probably eucamptodromous; primary vein moderately thick, straight; secondary veins 4 pairs visible, sub-opposite, 6-14 mm apart, angle of divergence narrow acute (30°-45°), straight, unbranched, moderately thick; intersecondary veins not seen; tertiary veins not preserved.

Holotype—Specimen No. BSIP 39216B.

Occurrence—Upper Disang; Kaina, Imphal Valley, Manipur; late Eocene.

Remarks—The characters exhibited by the fossil indicate that it is a dicotyledonous leaf. Since it differs from the known fossil dicot leaves (Guleria & Mehrotra, 1999; Mehrotra & Mandaokar, 2000), it is given a new name, *Dicotylophyllum thoubalense* sp. nov. The specific name is after the well known place Thoubal which is situated very close to the fossil locality.

Fruiting shoots

(Pl. 2.9-10)

The study is based on three well preserved detached shoots bearing fruiting bodies and giving the appearance of spike-like structures.

Description—Fruiting shoots–maximum length 9 cm, maximum width about 5 mm; many fruiting bodies present on either side of the axis; fruiting bodies oval shaped, appearing sessile, closely placed, opposite to sub-opposite, each fruit 5 mm in length and 1-2 mm in width.

Figured Specimens—Specimen Nos BSIP 39214-39215.

Occurrence—Lower Barail; Thongjaorok stream section, Imphal Valley, Manipur; early Oligocene.

Remarks—It is difficult to comment on the affinities of the fruiting axes in the absence of any cuticles or attached leaves on the fruiting shoots. However, it is important to record such specimens which are rarely preserved.

Genus—LEGUMINOCARPON Goeppert, 1855

LEGUMINOCARPON KAINAI sp. nov.

(Pl. 2.11)

The study is based on two fruit impressions.

Description—Specimens represent broken part of pod, preserved length 1.5-5.5 cm, width 1.6-1.8 cm, strap-shaped, margins thick, almost parallel to each other, texture coriaceous. No mark or impression of seed visible in available part of the specimens.

Holotype—Specimen No. BSIP 39216A.

Paratype—Specimen No. BSIP 39217A.

Occurrence—Upper Disang; Kaina, Imphal Valley, Manipur; late Eocene.

Remarks—The fossil looks like part of a legume pod. Leguminous fruits have been described under an artificial/ organ genus *Leguminocarpon* Goeppert, 1855. A number of legume pods have been reported from various parts of India (see Mehrotra & Mandaokar, 2002) but the present specimens differ from them in shape and size and accordingly have been placed under a new species, *Leguminocarpon kainai* sp. nov.

Bark

(Pl. 3.1)

Description—Specimen slightly wavy, preserved length 11.0 cm, width varying from 0.5 to 1.3 cm; texture thick coriaceous, parallel striations seen on the surface.

Figured Specimen—Specimen No. BSIP 39220.

Occurrence—Upper Disang; Keirambi, Imphal Valley, Manipur; late Eocene.

Remarks—It is evident from the features of the fossil that it represents an impression of the bark of a woody plant. Bark portions rarely get preserved.

DISCUSSION

The present study provides a brief account of the Tertiary plant megafossils of the Imphal Valley and its adjoining areas (Manipur State) and gives a glimpse of their rich diversity. It has revealed the occurrence of two types of palm leaves, sixteen types of dicotyledonous leaves, one type of fruiting axis, a leguminous pod and a bark impression in the present assemblage from the Disang (late Eocene) and Barail (early Oligocene) sediments. Numerically the assemblage is dominated by dicotyledonous leaves showing a rich morphological diversity. The morphological variations depicted by the leaves show a wide range, such as symmetrical to asymmetrical leaves; narrow oblong elliptic to narrow ovate forms; normal, entire, straight to undulate margins; acute, obtuse, ovate to cordate bases; craspedodromous, eucamptodromous, brochidodromous to acrodromous venations; and presence of intramarginal veins, etc.

The morphology of leaves provides an additional tool to reconstruct the prevailing climatic conditions. Sinnott and Bailey (1915) and Bailey and Sinnott (1916) were the pioneers who studied the correlation between leaf morphology and climate. They pointed out that entire margined leaves and leaflets are predominantly found in arctic, alpine, xeric and tropical rainforest environments. The percentage decreases to near equality in the upland tropics and subtropical forests, while the leaves of temperate forests are mainly non-entire, i.e., with serrate/dentate margins. Further leaf size can also be correlated with temperature and humidity. For instance, in a hot arid climate (higher temperature and lower humidity) the leaves are smaller in size (Axelrod & Bailey, 1969; Ginvish, 1984). Similarly, Dilcher (1973) also showed that leaf size decreases with the decreasing moisture. In recent years a number of leaf workers such as Wolfe (1995), Wilf *et al.* (1998), Wiemann *et al.* (1998) and Burnham *et al.* (2001) have also considered leaf size and leaf margin as the most important predictors of climate (temperature and precipitation). Leaves of dry and desertic areas are generally small, thick and succulent, whereas entire margined leaves with intramarginal veins are found more typically in tropical areas. The morphological analysis of the dicot leaves of the present assemblage shows 100 percent entire margined, mainly chartaceous (non-succulent) and large leaves, which leads to the conclusion that the assemblage indicates the existence of a moist tropical environment at the time of deposition of the leaves.

As far as taxonomy is concerned only a few specimens could be compared with Recent genera due to fragmentary nature of the material. The occurrence of leaves grossly comparable to *Calophyllum* (*Dicotylophyllum calophylloides*), *Cinnamomum* (*D. acrodromoides*), *Alstonia* (*D. alstonioides*) and *Terminalia* (*D. cordifoliatum*) also substantiates the prevalence of moist tropical conditions in Manipur during the late Eocene-early Oligocene times since all these plants are denizens of moist tropical forests. They further indicate the richness of woody elements in the region.

The palms are generally associated with a humid tropical environment barring a few exceptions like *Phoenix* (a palm of drier region); *Chamaerops* and *Trachycarpus* – the palms of cooler or temperate region (Corner, 1966, p. 352). The rest are most abundant in the moisture laden coastal tropical regions of the world. Many of the palms are rain forest species. The two types of palm leaves/leaflets reported in the paper belong to neither *Phoenix* nor *Chamaerops* as evident from (i) the reduplicate nature of *Phoenicites indica* and (ii) the associated

dicotyledonous taxa represented by entire margined leaves further suggest the existence of typical tropical vegetation. Consequently the two palm leaves may belong to two different types of tropical palms.

The presence of galls or cecidia on some leaves indicates interaction between the leaves and other organisms such as, bacteria, viruses, fungi or animals. The galls are pathologically developed structures (swellings or outgrowths) representing reaction of the plant to a wide variety of parasitic organisms (Mani, 2000). The occurrence of trace marks representing leaf mines on *Dicotylophyllum kainai* and *D. evansii* provides further evidence of interaction between the plants and animals. Leaf mines are blotch-like or linear excavation made by insect larvae in leaf tissue and represent insect-plant interaction (Strong *et al.*, 1984). The numerous dotted structures seen on the lamina of *Dicotylophyllum intramarginalivenoides* (Pl. 1.7-9) most probably depict aphid infestation. High humidity and hot days are conducive for aphid infestation (see pages 307-316 in Joshi & Viraktamuth, 2004; fig. on p. 272). The galls, leaf mines and aphid infestation all provide evidence of plant-animal interaction and dependence of animals on plants.

The absence of twigs, seeds and aquatic elements in the assemblage coupled with fragmentary nature of the leaves suggests the allochthonous nature of the plant material which must had been brought to the site of deposition by river or current action.

The present study has given a hint about the richness of the past vegetation of Manipur. Future work on plant megafossils will provide a comprehensive picture of the Tertiary flora of the state.

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