First fossil evidence of Connaraceae R. Br. from Indian Cenozoic and its phytogeographical significance

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Fossil leaflet impression described here as a new species *Rourea miocaudata* sp. nov., showing close resemblance with the modern leaflets of *Rourea caudata* Planch. (Connaraceae R. Br.), has been recorded from the lower part of the Siwalik sediments (Dafla Formation, middle–upper Miocene) exposed at the road-cutting section of Pinjoli area in West Kameng district, Arunachal Pradesh. The important morphological characters of the fossil are its narrow elliptic leaflet, cuneate base, long caudate apex, entire margin, eucamptodromous to brochidodromous secondary veins, presence of intersecondary veins, percurrent and reticulate tertiary veins and orthogonally reticulate quaternary veins. This is the first authentic record of the occurrence of leaflet comparable to *R. caudata* of Connaraceae from the Cenozoic sediments of India and abroad. At present *R. caudata* does not grow in India and is restricted only in southeast Asia especially in China and Myanmar. This taxon probably migrated to these southeast Asian regions after lower Siwalik sedimentation (middle–upper Miocene) due to climatic change caused by post-Miocene orogenic movement of the Himalaya. The recovery of this species and other earlier-described evergreen taxa from the same formation, suggests the existence of a tropical, warm and humid climatic conditions during the depositional period.

1. Introduction

Connaraceae R. Br., are mostly evergreen or deciduous woody climbers and pantropical (mainly southern hemisphere) in distribution, with species occurring in both the Old and the New World. Members of the family can be found in lowland rain forest or forest patches in savannas (Heywood *et al.* 2007). Cronquist (1981) placed Connaraceae in the Rosales and Takhtajan (1997) placed it in the Connarales. The APG II (2003) and APG III (2009) and Reveal (2012) place the family in order Oxalidales, next to the Oxalidaceae, Brunelliaceae, Cephalotaceae, Cunoniaceae, and Elaeocarpaceae. Phylogenetic studies showed that Connaraceae are sister to Oxalidaceae (Nandi *et al.* 1998). These

two families share the presence of heterostyly, benzoquinone rapanone, and extegmic seeds (Nandi *et al.* 1998, though Connaraceae are mainly a woody family of 17 genera and Oxalidaceae mainly herbaceous. The genus *Rourea* Aubl. consists of about 50 species distributed pantropically. The extant species, *R. caudata* Planch., with which fossil shows resemblance, is a common climber found on the trees in the open mountain forest of China and Myanmar (Brandis 1971; Mabberley 1997).

West Kameng district (lying between the longitude of 92°24'4.0026'E and latitude of 27°16'14.2428'N) is surrounded by Tibet region of China in the north, Bhutan in the west, Tawang district and east Kameng district of Arunachal Pradesh in the northwest and east respectively and the southern

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boundary of adjoining Sonitpur district of Assam. Among the Siwalik fossiliferous localities of Arunachal Pradesh, this district has been proved as an important site recording a variety of angiospermous leaves of *Bambusa* (Poaceae); *Amesoneuron* (Arecaceae); *Fissistigma bicolor* (Anonaceae); *Calophyllum* (Calophyllaceae); *Shorea ridleyana* (Dipterocarpaceae); *Dysoxylum costulatum* (Meliaceae); *Breynia rhamnoides* (Euphorbiaceae); *Randia wallichii* (Rubiaceae); *Memecylon* (Melastomaceae); *Litsea glabrata*, *Actinodaphne malabarica*, *Cinnamomum bejolghota* (Lauraceae); *Millettia macrostachya* (Fabaceae); *Salacia beddomei* (Celastraceae); *Tabernaemontana coronaria* (Apocynaceae); *Terminalia catappa*, *Terminalia chebula*, and *Combretum chinense* (Combretaceae) (Joshi *et al.* 2003; Joshi and Mehrotra 2007; Khan and Bera 2007; Khan *et al.* 2008; Srivastava and Mehrotra 2009; Khan and Bera 2014a; Khan *et al.* 2015). Recently during a palaeobotanical excursion, a large number of well-preserved fossil leaves have been collected by the present authors from the road cutting sections along Bhalukpong to Pinjoli area. A thorough study of the recovered fossil leaflet enabled us to identify the fossil counterpart of modern south-east Asian element *Rouea caudata* of Connaraceae which is being described here. The fossil leaflet is described here for the first time from the Cenozoic sediments of India and abroad. The present paper also discusses its phytogeographical and palaeoclimatic significance.

2. Materials and methods

2.1 Geological setting

The Siwalik sediments are lying along the foothills of Arunachal Pradesh and sub-divided into lower Siwalik (Dafla Formation, middle–upper Miocene), middle Siwalik (Subansiri Formation; Pliocene)

and upper Siwalik (Kimin Formation, upper Pliocene to lower Pleistocene) exposed in reverse stratigraphic order brought out by the reverse faults (Kumar 1997; Joshi *et al.* 2003). The Main Boundary Fault (MBF) demarcates the northern limit of the Dafla Formation from the overlying Lower Gondwana rocks (table 1). The present fossil leaflet was collected from the lower Siwalik sediments exposed at the road-cutting section of Pinjoli area about 18 km east of Bhalukpong (near culvert no. 48/1) in West Kameng district (figure 1). Earlier, we reported few leaf and fruit remains from this fossil site (Khan and Bera 2007, 2010, 2014a, b; Khan *et al.* 2008, 2015). The lower Siwalik (middle to upper Miocene) sediments consist of well-indurated medium to fine grained, generally well-sorted sandstones, subordinate to micaceous sandstones, bluish nodular shale containing lenses/fragments of woody materials and small lenses of lignitic coal. The shale fraction locally contains plant fossils including compressed and impressed leaf remains. Recently on the basis of magnetostratigraphic data, Chirouze *et al.* (2012) proposed that the Siwalik Formation in Kameng section of Arunachal Pradesh was deposited between 13 and 2.5 Ma. The transition between the lower and middle Siwaliks is dated at about 10.5 Ma and the middle to upper Siwaliks transition is dated at 2.6 Ma.

2.2 Morphological study

The photographs showing structural details of fossil leaflet and their nearest living relative were taken using an incident light compound microscope (Stemi SV 11, Zeiss), a transmitted light compound microscope with photographic attachment (Zeiss Axioskop 40). This fossil leaflet has been compared with the herbarium specimens kept at Central National Herbarium (CNH), Sibpur, Howrah. The terminologies adopted by Dilcher (1974) have

Table 1. Generalised lithotectonic sequence in the West Kameng district, Arunachal Pradesh (after Joshi *et al.* 2003).

North		
Gondwana Group		Carbonaceous shale, sandstone and coal
	Main Boundary Faults.....	
Lower Siwalik (Dafla Formation)		Well indurated sandstone, shale and siltstone with plant fossils
	Thrust.....	
Middle Siwalik (Subansiri Formation)		Weakly indurated sandstone, shale and siltstone with plant fossils
	Thrust.....	
Upper Siwalik (Kimin Formation)		Sand rock and claystone/shale with plant fossil's fossil wood
	Main Frontal Fault.....	
Assam Alluvium/Quaternary deposits		
South

Figure 1. Location of the study area in West Kameng district, Arunachal Pradesh and a geological setting of the area around Pinjoli.

been followed for description of leaflet. The holotype specimen (CUH/PPL/P/82) is preserved in the Herbarium cum Museum of the Department of Botany, University of Calcutta (CUH).

3. Systematic description

Kingdom: Plantae
 Phylum: Tracheophyta
 Class: Magnoliopsida
 Order: Oxalidales Bercht. & J. Presl
 Family: Connaraceae R. Br.
 Genus: *Rourea* Aubl.
 Species: *Rourea miocaudata* Khan and Bera sp. nov. (figure 2a, c, e and g)
 Holotype: CUH/PPL/P/82 (figure 2a)

Repository: Fossil specimen is kept at the Herbarium cum Museum of the Department of Botany, University of Calcutta (CUH).

Type locality: Road-cutting section, east of Pinjoli area of West Kameng district.

Type horizon: Lower Siwalik sediments (Dafla Formation, middle to upper Miocene).

Etymology: The specific name is derived by adding the prefix 'mio' to the modern comparable specific epithet *caudata*.

Material: One well preserved, complete leaflet impression.

Diagnosis: Narrow elliptic; maximum length 8 cm, width 3.5 cm; base equilateral, cuneate; apex long caudate with obtuse tip; margin entire; texture chartaceous; venation eucamptodromous to brochidodromous; secondary veins alternate with

Figure 2. *Roureia caudata* leaflets. (a) Fossil leaflet of *Roureia miocaudata* Khan and Bera, sp. nov. showing apex, base, shape, petiole (marked by black arrow), size and venation pattern (eucamptodromous venation pattern marked by yellow arrows). (b) Modern leaflet of *Roureia caudata* Planch. showing similar apex, base, shape, petiole (marked by black arrow), size and venation pattern (eucamptodromous venation pattern marked by yellow arrows). (c) Enlarged portion of the fossil leaflet showing median primary vein (marked by yellow arrow), secondary vein (marked by red arrow), intersecondary vein (marked by blue arrow), tertiary vein (marked by green arrow) and quaternary vein (marked by white arrow). (d) Enlarged portion of the modern leaflet of *Roureia caudata* showing similar median primary vein (marked by yellow arrow), secondary vein (marked by red arrow), intersecondary vein (marked by blue arrow), tertiary vein (marked by green arrow) and quaternary vein (marked by white arrow). (e) Enlarged apical portion of the fossil leaflet showing long caudate apex (purple arrow), curved secondary vein (marked by red arrow) and brochidodromous venation pattern (marked by blue arrows). (f) Enlarged apical portion of the modern leaflet of *Roureia caudata* showing similar nature of apex (purple arrow), secondary vein (marked by red arrow) and venation pattern (marked by blue arrow). (g) Enlarged portion of the fossil leaflet showing tertiary vein (marked by green arrow) and quaternary vein (marked by white arrow). (h) Enlarged portion of the modern leaflet showing tertiary vein (marked by green arrow) and quaternary vein (marked by white arrow) (scale bar = 1 cm).

acute angle of divergence, joined to superadjacent secondary at a nearly obtuse angle; intersecondary veins present; tertiary veins AO, orthogonal reticulate and percurrent.

Macromorphology: Leaflet symmetrical, narrow elliptic; maximum length 8 cm, width 3.5 cm; base cuneate, equilateral; apex long caudate with obtuse tip; margin entire; texture chartaceous; petiole 0.3 cm long, normal; venation pinnate, eucamptodromous to brochidodromous; primary vein (1°) single, prominent, stout, almost straight; secondary veins (2°) six visible, anastomosing near margin, 0.5–1.2 cm apart, usually alternate, angle of divergence acute (about 50° – 60°), moderate, thick, uniformly curved up and joined to superadjacent secondary at a nearly obtuse angle, usually unbranched; intersecondary veins present, simple, abundant; tertiary veins (3°) fine, angle of origin usually AO, predominantly orthogonal reticulate, occasional percurrent, almost straight, sometimes branched, oblique in relation to midvein, predominantly alternate and close; quaternary veins (4°) fine, orthogonal reticulate.

4. Discussion

4.1 Comparison

The most characteristic features of the present fossil leaflet are narrow elliptic shape, long caudate apex with obtuse tip, cuneate base, entire margin, eucamptodromous to brochidodromous venation, alternate and acute angle of divergence of secondaries, presence of intersecondary veins and AO, orthogonal reticulate, predominantly alternate tertiaries. These features collectively indicate its affinity with the modern leaflets of family Connaraceae. In order to compare and find the nearest generic affinity of the present fossil leaflet, six available modern genera of Connaraceae were examined (table 2; figure 3a–f). These modern genera are *Agelaea* Sol. ex Planch., *Ellipanthus* Hook.f., *Connarus* L., *Rourea* Aubl., *Cnestis* Juss. and *Roureopsis* Planch. Both *Agelaea* (C. N. Herbarium Sheet No. 00497) and *Ellipanthus* (C. N. Herbarium Sheet No. 01131) differ in having acute-acuminate apex and obtuse base as compared to the long caudate apex and cuneate base in our fossil specimen. *Connarus* (C. N. Herbarium Sheet No. 5147) differs in being larger in size. It also differs from our Siwalik fossil in having a narrow ovate shape. *Cnestis* (C. N. Herbarium Sheet No. 6713) has a rounded-obtuse apex and a cordate base differentiating it from our fossil specimen. On the other hand, *Roureopsis* (C. N. Herbarium Sheet No. 101207) differs from the fossil specimen by

Table 2. Comparative morphological chart of the available modern leaflets among genera in Connaraceae.

Genera	Leaflet morphological characters									
	Apex	Base	Margin	Size	Shape	Balance	Angle of divergence of secondary veins			
							Venation pattern	Inter-secondary veins	Tertiary veins	
<i>Rourea</i>	Caudate, attenuate	Cuneate	Entire	Microphyll	Narrow elliptic, lanceolate	Symmetrical	Eucamptodromous, brochidodromous	Moderate acute	Present	Predominantly orthogonal reticulate, occasional percurrent
<i>Cnestis</i>	Round, obtuse	Oblique, cordate	Entire	Microphyll	Elliptic	Symmetrical; asymmetrical	Brochidodromous	Moderate acute	Present	Orthogonal reticulate
<i>Connarus</i>	Acute, acuminate	Obtuse, cuneate	Entire	Mesophyll	Narrow ovate	Symmetrical	Eucamptodromous	Wide to moderate acute	Present	Percurrent
<i>Agelaea</i>	Acute, acuminate	Obtuse	Entire	Microphyll	Elliptic	Asymmetrical	Eucamptodromous, brochidodromous	Moderate acute	Present	Predominantly orthogonal reticulate, occasional percurrent
<i>Roureopsis</i>	Acute, tip bifurcated	Obtuse	Entire	Microphyll	Ovate, elliptic	Asymmetrical	Eucamptodromous, brochidodromous	Moderate acute	Present	Percurrent
<i>Ellipanthus</i>	Acute, acuminate	Obtuse	Entire	Mesophyll	Narrow ovate	Symmetrical	Brochidodromous	Moderate acute	Present	Percurrent and reticulate

Figure 3. Modern leaflets among genera in Connaraceae. (a) Leaflet of *Ellipanthus*. (b) Leaflet of *Rourea*. (c) Leaflet of *Connarus*. (d) Leaflet of *Roureopsis*. (e) Leaflet of *Agelaea*. (f) Leaflet of *Cnestis* (scale bar = 1 cm).

having an asymmetrical shape, acute apex with bifurcated tip and obtuse base. Our fossil leaflet possesses a symmetrical shape, caudate apex and cuneate base.

The above-mentioned diagnostic features of the present fossil leaflet indicate close resemblance of the fossil leaflet to the modern genus *Rourea* Aubl. The herbarium sheets of all the available species of

this genus have been studied in order to find out its exact affinity and it is found that only three species of *Rourea*, viz., *R. minor* (Gaertner) Leenhouts; *R. microphylla* (Hooker and Arnott) Planch. and *R. caudata* Planch. come close to the fossil specimen. In *R. minor* (C. N. Herbarium Sheet No. 00494) leaflet blade apex is acute to shortly acuminate, whereas in the fossil specimen it is long caudate. On the other hand, in *R. microphylla*, apex is acuminate and base is not equilateral in contrast to cuneate, equilateral base and caudate apex in the fossil leaflet. *R. microphylla* (C. N. Herbarium Sheet No. 76573) also differs in being smaller in size. On the basis of leaf morphology (size, shape, nature of apex and base, texture and venation pattern), *R. caudata* (C. N. Herbarium Sheet No. 6532) shows the closest resemblance to the fossil specimen (figure 2a–h).

As far as the authors are aware, there is no record of fossil leaflets of this genus, *Rourea* from the Cenozoic sediments of India. One fossil leaflet resembling the genus *Rourea* has been reported so far from the Siwalik sediments of western Nepal

(Prasad and Pandey 2008). This is *R. palaeorugosa* (Prasad and Pandey) comparable to modern *R. rugosa* Planch. from the lower part of the Siwalik (middle Miocene) sediments of Surai Khola, western Nepal. *R. palaeorugosa* attains mucronate apex and obtuse base as compared to long caudate apex with obtuse tip and cuneate base in the present fossil leaflet. As the present fossil leaflet is distinct from the only known fossil leaflet, it has been described under a new specific name, *Rourea miocaudata* sp. nov.

4.2 Phytogeography

Rourea are lianas or scandent or shrubs, sometimes trees and consist of about 50 species distributed pantropically, but mainly in tropical regions of Africa, America, Oceania and southeast Asia. The extant species, *R. caudata* Planch. is a common woody climber found on the trees in the open mountain forest of China (Guangdong, Guangxi and Yunnan) and Myanmar (Brandis 1971; Mabberley 1997). It is interesting to note that *R. caudata*

Figure 4. Modern distribution and fossil locality of studied taxon *Rourea caudata*.

does not occur at present in India and this taxon is now confined to the tropical evergreen forest of SE Asian regions (China and Myanmar) where the conditions are more suitable for its luxuriant growth (figure 4). The vegetation is widely distributed in open mountain forest below 800 m, more commonly below 600 m.a.s.l. These places are wet and hot all year round and the soils are thick, fertile, organic and water-retaining. Climatic parameters of this vegetation type are mean annual temperature 22°–26°C; mean month coldest temperature 18°C and total annual rainfall >2000 mm (Xiwen and Walker 1996).

During the Neogene (20–10 Ma), land connections were well established between Indian plate and mainland masses of southeast Asia (Smith and Briden 1979) causing possible migration of some tropical plants from southeast Asia to the Indian subcontinent and *vice-versa* (Takhtajan 1969; Bande and Prakash 1986). A number of taxa such as *Hopea*, *Dipterocarpus* (Dipterocarpaceae), *Dalbergia*, *Albizia* (Fabaceae), *Protospermum* (Sterculiaceae), *Litsea* (Lauraceae), etc., are known to be migrated from southeast Asia to India and taxa like *Garcinia* (Clusiaceae), *Sterculia* (Sterculiaceae), *Cinnamomum* (Lauraceae), *Gluta* (Anacardiaceae), *Grewia* (Tiliaceae), etc., are believed to be migrated from India to southeast Asia after the land connections between these two land masses were established during the Neogene (Bande and Prakash 1986). So far, the present fossil is not reported from both the Palaeogene and Neogene of southeast Asia (Bande and Prakash 1986; Mehrotra *et al.* 2005) and its present occurrence from the Neogene of India suggests a probable migration of this taxon from Indian landmass to SE Asian regions due to climatic change caused by post-Miocene orogenic movement of the Himalaya.

4.3 Palaeoclimate

The ‘nearest living relative’ approach is a widely employed tool to reconstruct paleoclimate of an area. This approach presupposes that fossil plants and their modern relatives share similar physiological requirements for climate. The earlier recovered fossils from Daffa Formation are referable to modern *Bambusa* (Poaceae); *Amesoneuron* (Arecaceae); Thelypteridaceae, *Fissistigma bicolor* (Anonaceae); *Calophyllum* (Calophyllaceae); *Shorea assamica*, *Shorea ridleyana* (Dipterocarpaceae); *Dysoxylum costulatum* (Meliaceae), *Breynia rhamnoides* (Euphorbiaceae); *Mastertia assamica*, *Acacia catechuoides* (Fabaceae); *Randia wallichii* (Rubiaceae); *Memecylon* (Melastomaceae); *Litsea glabrata*, *Actinodaphne malabarica*, *Cinnamomum bejolghota* (Lauraceae); *Millettia macrostachya* (Fabaceae); *Salacia beddomei* (Celastraceae); *Tabernaemontana*

coronaria (Apocynaceae); *Terminalia chebula*, *Combretum chinense* (Combretaceae), collectively indicative of a tropical humid environment (Joshi and Mehrotra 2003, 2007; Khan and Bera 2007, 2010, 2014a, b; Khan *et al.* 2008, 2015; Srivastava and Mehrotra 2009). So, the present day distribution of comparable modern taxa of recovered fossil specimen and other earlier-reported specimens from the same formation suggests the existence of a tropical, warm and humid climatic condition during the depositional period (middle to upper Miocene). For the reconstruction of palaeoclimate, quantitative study was also made on the lower Siwalik flora of eastern Himalaya (Khan *et al.* 2014). For quantitative study CLAMP (Climate Leaf Analysis Multivariate Program) analysis was used and suggested a MAT (mean annual temperature) 25.3°–25.4°C ± 2.8°C, a CMMT (cold month mean temperature) 17.9°–21.3°C ± 4°C and a WMMT (warm month mean temperature) of 27.8°–28.3°C ± 3.3°C and a week monsoonal climate with GSP (growing season precipitation) of 174–242 cm ± 92 cm during the Miocene (Khan *et al.* 2014). The physiognomic features such as optimal size, entire margin, and drip tip of the fossil leaflet also indicate tropical humid climate with plenty of rainfall supporting luxuriant evergreen forests in the area during Siwalik sedimentation.

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