Lagerstroemia L. from the middle Miocene Siwalik deposits, northern India: Implication for Cenozoic range shifts of the genus and the family Lythraceae

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Fossil leaves of *Lagerstroemia* (Lythraceae) are described from the Siwalik deposits (middle Miocene) of Kathgodam, Uttarakhand, India. The fossil records of the Lythraceae indicate its worldwide distribution in the Cenozoic. The family had its widest distribution during the Miocene but became less widespread during the Pliocene, followed by range expansion during the Quaternary. The present leaf fossil, along with the previous fossil records of *Lagerstroemia*, indicates that the genus followed the same pattern of expansion and retraction as the entire family Lythraceae suggesting that both the genus and the family adapted in similar ways. The fossil plant assemblage from the Lower Siwalik deposits indicates warm and humid climate with plenty of rainfall in the region during the depositional period.

1. Introduction

The family Lythraceae consists of ~31 genera and 600 species distributed mainly in tropical and subtropical areas of the Old World (18 genera) and New World (13 genera) (figure 1), and includes four small, previously independent families, i.e., Duabangaceae, Punicaceae, Sonneratiaceae, and Trapaceae (Graham *et al.* 2005). The Lythraceae has been placed in the order Myrtales with closely allied family Onagraceae based on the morphological, anatomical, embryological, and molecular studies (Dahlgren and Thorne 1984; Johnson and Briggs 1984; Conti *et al.* 1997; Sytsma *et al.* 2004). On the basis of molecular data it was suggested that the Lythraceae diverged from the Onagraceae at 93 Ma, i.e., in the early Late Cretaceous (Sytsma *et al.* 2004); however, the oldest fossil records of the family (pollen grains) are from the early Campanian (81–82 Ma) of Wyoming, USA (Grimsson *et al.* 2011).

Lagerstroemia (crape myrtle) is a genus of ~53–56 species of deciduous and evergreen trees and shrubs native to the Indian subcontinent, south-east Asia, northern Australia, and parts of Oceania (figure 1) (Mabberley 1997; Graham 2013). The genus mainly grows in lowland swamps and montane and secondary forests (Graham 2013). *Lagerstroemia*, along with other taxa such as *Sonneratia* L.f., *Duabanga* Buch.-Ham. and *Trapa* L. form a subclade of one of the two major clades of the family Lythraceae (Graham *et al.* 2005; Morris 2007). The genus is economically very important as it is used as timber, fuel, and fodder and is also used in making drugs for diabetes (Judy *et al.* 2003).

In the present communication a new fossil leaf of *Lagerstroemia* is described from the Siwalik sediments of northern India (figure 2). The evolutionary history, expansion, and phytogeography of the genus and its family in the geological context are also discussed.

Keywords. Miocene; northern India; palaeoclimate; phytogeography; Siwalik.

Figure 1. World map showing fossil as well as modern distribution of the family Lythraceae (after Graham *et al.* 2005; Graham 2013) and modern distribution of *Lagerstroemia* (after Mabberley 1997).

Figure 2. (a) Map of India showing the fossil locality (red solid rectangle). (b) High resolution map showing the fossil locality (marked with yellow spot).

Figure 3. Geological map of the fossil locality (Ranga Rao *et al.* 1979).

2. Materials and methods

For better understanding of the floristics and palaeoclimate of Kathgodam Siwalik, an excursion was undertaken by one of us (RG), who collected a few fossil leaves from the yellowish grey mudstone exposed along the Gola River near Kathgodam, Nainital District of Uttarakhand (figure 2). The geology of the area has been given by Middlemiss (1890), Heim and Gansser (1939), Tiwari and Mehdi (1964), Fuchs and Sinha (1974) and Ranga Rao *et al.* (1979). According to them, the Siwaliks are exposed in this area all along the main boundary thrust in the southwest and are overridden by the Krol Group rocks (Fuchs and Sinha 1974). The Siwalik beds in the aforesaid area are found

running in a northeast direction (figure 3). The area is characterized by the middle Miocene Lower Siwalik deposits (Ranga Rao *et al.* 1979). These deposits are made up of alternating layers of medium-grained sandstones and mudstones and an age between 10.8 and 18.3 Ma was assigned to them on the basis of palaeomagnetic investigations in the Pakistan Siwalik (Gaur 1987). According to Tandon (1976), the Lower Siwalik of Kumaon Himalaya probably indicates a fluvial and deltaic environment.

After cleaning the surface of the leaves, the fossils were photographed under low angled sunlight using a 10 megapixel digital camera (Canon SX 110). The terminology used in describing the fossil leaf is based on Hickey (1973), Dilcher (1974) and

Ellis *et al.* (2009). The leaf fossils were identified at the Central National Herbarium (CNH), Howrah, the Forest Research Institute (FRI), Dehradun, and the Birbal Sahni Institute of Palaeobotany, Lucknow after comparing them with herbarium material of the extant plants. The fossil specimens are deposited in the museum of the Birbal Sahni Institute of Palaeobotany, Lucknow. The accepted fossil records of Lythraceae and *Lagerstroemia* as provided by Graham (2013) are discussed in view of the new fossil.

3. Systematic description

Family: Lythraceae J. St.-Hil.

Genus: *Lagerstroemia* L.

Species: *Lagerstroemia himalayaensis*, Srivastava, Gaur et Mehrotra, sp. nov. (figure 4A, B, D, E)

Holotype: Specimen no. BSIP 40116.

Paratype: Specimen no. BSIP 40117.

Horizon: Lower Siwalik.

Locality: Gola River near Kathgodam, Nainital District of Uttarakhand.

Age: Middle Miocene.

Material: Two well preserved specimens.

Etymology: After the Himalaya.

Description: Leaf simple, symmetrical, mesophyll, elliptic to narrow elliptic; preserved lamina length and width 6.1×3.1 cm and 7×3 cm; apex acuminate with round tip; base acute; margin entire, slightly wavy; texture supposedly chartaceous; petiole not preserved; venation pinnate, eucamptodromous to brochidodromous; primary vein stout, almost straight; nine pairs of secondary veins, 0.5–0.9 cm apart, predominantly alternate, angle of divergence moderate to wide acute (49° – 69°), uniformly curved and running parallel to each other up to the margin, sometimes turning sharply upwards near the margin to form loops with the adjacent secondaries at the upper part of lamina, moderately thick; intersecondary veins present, 1 or 2 in number; tertiary veins percurrent, simple, rarely forked, recurved, oblique in relation to midvein, angle of origin predominantly acute-obtuse (AO); marginal ultimate venation looped.

Affinities: The characteristic features of the fossil leaves, specifically the elliptic to narrow elliptic shape, eucamptodromous to brochidodromous venation, moderate to wide acute angle of divergence of secondary veins, percurrent and recurved oblique tertiary veins suggest their close affinity with *Lagerstroemia* of the family Lythraceae. A large number of taxa of many tropical and subtropical families like Anacardiaceae, Annonaceae,

Combretaceae, Euphorbiaceae, Moraceae, Myrtaceae, Polygalaceae, Phyllanthaceae, Rutaceae, Sapindaceae, Sapotaceae, and Simaroubaceae were studied and compared with the present fossil. *Anacardium occidentale*, *Parishia maingayi*, and *Taxicodandron acuminatum* of the Anacardiaceae, *Alphonsea lutea*, *Oxymitra fornicata* of the Annonaceae, *Combretum decandrum*, *Illigera khasiana*, *Terminalia chebula* of the Combretaceae, *Hancea penangensis* of the Euphorbiaceae, and *Artocarpus integrifolia* and *Ficus pumila* of the Moraceae show most resemblance but the presence of character combinations such as an attenuate apex, eucamptodromous venation and reticulate tertiaries differentiates the fossil. *Pimenta dioica* of the Myrtaceae has obtuse base and brochidodromous venation while in *Psidium guineense* secondary veins are moderately acute and the venation is eucamptodromous, which distinguishes them from the present fossil.

Various taxa of the Lythraceae such as *Ammannia baccifera* L., *Lagerstroemia* spp, *Lawsonia alba* Lamk., *Lythrum salicaria* L., *Punica granatum* L., *Rotala indica* and *Woodfordia fruticosa* (L.) Kurz have been compared with the present fossil. In *Ammannia baccifera*, *Lythrum salicaria*, and *Woodfordia fruticosa*, the venation is brochidodromous. In *Lawsonia alba* and *Rotala indica*, the leaves are smaller (nanophyll) in size, while in *Punica granatum*, the apex is acute and venation is only reticulate. In the present fossil, the apex is acuminate and venation is eucamptodromous to brochidodromous. Among the *Lagerstroemia* species such as *L. calyculata* Kurz, *L. floribunda* Jack, *L. hypoleuca* Kurz, *L. indica* Linn., *L. minuticarpa* Debb. ex Kanjilal, *L. parviflora* Roxb., *L. speciosa* (L.) Pers., *L. tomentosa* Presl, *L. turbinata* Koehne, *L. venusta* Wall. ex Clarke, and *L. villosa* Wall. ex Kurz, it has been inferred that the present fossil is similar to *L. parviflora* (figure 4C, F) (herbarium sheet nos. CNH 8629, 10513; FRI:21817 and *L. speciosa* (herbarium sheet no. FRI 41562). A large number of herbarium sheets of *L. indica*, *L. tomentosa* and *L. villosa* were examined. In these species, the apex is attenuate to mucronate and the base is obtuse to round, unlike in our fossil. The presence of simple to forked percurrent and reticulate tertiaries in *L. hypoleuca* and *L. turbinata* differentiate them from the present fossil. Leaves of *L. floribunda* are bigger in size ($\sim 16.5 \times 4.8$ cm) than our fossil (length and width 6.1×3.1 cm and 7×3 cm), though size is a variable feature. In *L. minuticarpa*, the adjacent secondary veins are not running parallel to each other as in the fossil, while *L. venusta* differs from the fossil in eucamptodromous venation and having attenuate apex.

Figure 4. (A) and (B) Fossil leaves of *Lagerstroemia himalayaensis* sp. nov. (specimen nos. BSIP 40116, 40117) showing shape, size and venation pattern. (C) Modern leaf of *L. parviflora* showing similar shape, size and venation pattern as in the fossil. (D) Enlarged portion of the fossil leaf showing primary vein (white arrow), secondary veins (yellow arrows), intersecondary vein (red arrow) and percurrent tertiary veins (pink arrows). (E) Enlarged apical portion of the fossil leaf showing brochidodromous venation (yellow arrow). (F) Enlarged portion of *L. parviflora* showing similar primary vein (white arrow), secondary veins (yellow arrows), intersecondary vein (red arrow) and percurrent tertiary veins (pink arrows) (Bar = 1 cm unless otherwise mentioned).

As far as the fossil leaf records of *Lagerstroemia* are concerned, they are known mainly from India and Japan. *Lagerstroemia patellii*, Lakhanpal and

Guleria (1981) reported from the lower Eocene sediments of Kachchh, differs from the present fossil in having a cuneate base. Two species, namely

Table 1. Comparative chart of the known fossil leaves of *Lagerstroemia*.

Fossil species	Modern comparable forms	Lamina				Venation pattern	Distance between two secondary veins (cm)	Angle of divergence of 2° veins	Inter-secondary veins	Tertiary veins
		Apex	Base	Thickness	Size	Shape				
<i>Lagerstroemia patelii</i> Lakhnupal and Guleria (1981) (NS=1)	<i>L. speciosa</i>	NP	Cuneate	Chartaceous	Mesophyll	Narrow elliptic	1–2	Moderate–wide acute	Present	NP
<i>L. imamurae</i> Tanai and Uemura (1991) (NS=1)	<i>L. indica</i> and <i>L. speciosa</i>	Round	Acute	Coriaceous	Microphyll	Oblong	NG	Moderate–wide acute	Present	Percurrent
<i>L. siwalika</i> Prasad (1994b) (NS=2)	<i>L. lanceolata</i>	NP	NP	Chartaceous	Nanophyll	Narrow elliptic	0.6–1.4	Moderate acute	Present	Percurrent
<i>L. siwalika</i> Prasad (Agarwal 2002) (NS=1)	<i>L. lanceolata</i>	NP	Acute	Chartaceous	Mesophyll	Narrow elliptic	0.6–1	Acute	Present	Percurrent
<i>L. jamraniensis</i> Prasad et al. (2004) (NS=2)	<i>L. speciosa</i>	Acute	Acute	Coriaceous	Mesophyll	Narrow elliptic	1–1.6	Moderate acute	Present	Percurrent
<i>L. mioparviflora</i> Dwivedi et al. (2006) (NS=2)	<i>L. parviflora</i>	Acute	Acute	Chartaceous	Microphyll	Narrow elliptic	0.4–1.2	Moderate acute	Present	Percurrent
<i>L. comicrocarpa</i> Dwivedi et al. (2006) (NS=2)	<i>L. microcarpa</i>	Acute	Acute	Chartaceous	Microphyll	Narrow elliptic	0.3–0.8	Moderate acute	Present	Percurrent
<i>L. himalayaensis</i> sp. nov. (NS=2)	<i>L. parviflora</i> and <i>L. speciosa</i>	Acuminate	Acute	Chartaceous	Microphyll	Elliptic–narrow elliptic	0.5–0.9	Moderate–wide acute	Present	Percurrent

NP= not preserved; NG= not given; NS= No. of specimens studied.

L. siwalika (Prasad 1994b) and *L. jamraniensis* (Prasad *et al.* 2004) were reported from the Siwalik sediments of Nepal and northern India. Later, *L. siwalika* Prasad was again reported from the Miocene sediments of the Neyveli Lignite mine (Agarwal 2002). These fossils have pinnate craspedodromous to brochidodromous venation in contrast to the present fossil, where it is eucamptodromous to brochidodromous. Dwivedi *et al.* (2006) reported two species, viz., *L. mioparviflora* and *L. eomicrocarpa* from the Siwalik of Nepal. Both these fossils have only eucamptodromous venation and the angle of divergence of secondary veins is moderate acute, whereas it is moderate to wide acute in the present fossil. Another fossil *L. imamurae* Tanai and Uemura (1991) was reported from the Oligocene sediments of Japan, but it is different in being oblong in shape. A comprehensive chart of the character by character comparison of the aforesaid fossils is provided in table 1. Under these circumstances, the present leaf fossil has been assigned to a new species, *Lagerstroemia himalayaensis* Srivastava, Gaur et Mehrotra, sp. nov. The modern comparable species, i.e., *L. parviflora* is distributed on the foothills of the western Himalayas and throughout the Deccan Plateau, while *L. speciosa* is found from Assam to Malacca abundantly, on the hills of the Deccan Peninsula and in Sri Lanka (Hooker 1879).

4. Discussion

4.1 Origin, diversification, modern distribution, fossil records and range shift of the family Lythraceae

The modern distribution and fossil records of Lythraceae are very interesting because nowadays

the family is restricted only to tropical and sub-tropical areas, while its fossils have been reported from almost all parts of the globe (figure 1). They have been reported from the Late Cretaceous of USA and Mexico; Deccan Intertrappean beds (late Maastrichtian–Danian) of central India; Paleocene sediments of France and North America; Eocene sediments of North America, Europe, Libya, and south Asia; Oligocene sediments of North America, Europe, Siberia, and Japan; Miocene sediments of North America including Alaska and Canada, Europe, Denmark, south and southeast Asia, Russia, and China; Pliocene sediments of North America including Canada, Europe and China; Quaternary sediments of Panama, Colombia, Brazil, USA, Europe, and south and southeast Asia (Graham 2013). The family expanded after the Eocene, reached its peak during the Miocene (figure 5) and then declined significantly in the Pliocene as the climate deteriorated (Zachos *et al.* 2001) and now the family is not found in high latitudes such as Alaska, northern Canada, Greenland, and Siberia (figure 1).

Based on the molecular data, Graham *et al.* (2005) suggested an Old World lauracesian origin of the family but the oldest fossil records (*Lythrum* and *Peplis* pollen) from Wyoming, USA indicate that the family was already established by the early Campanian (Late Cretaceous) in the New World Laurasia (Grimsson *et al.* 2011). The oldest megafossil record is a seed of *Decodon* described from the late Campanian (Late Cretaceous) of Mexico (Rodríguez-de la Rosa *et al.* 1998), again suggesting an early diversification of the family in the New World during the Campanian (~70.6–83.5 Ma). Besides the fossil records mentioned above, the next oldest record is from India in the form of a flower (*Sahnianthus*) and

Figure 5. Graph showing number of fossil records of both *Lagerstroemia* and Lythraceae in the geologic past.

Table 2. Fossil assemblage of Lower Siwalik (middle Miocene) of Kathgodam.

Fossil taxa	Modern comparable species	Forest types	References
Monocotyledons			
Marantaceae			
<i>Alpinia siwalica</i> Prasad et al.	<i>A. buteocarpa</i> Poepp.	Evergreen	Prasad et al. (2004)
<i>Clinogyne ovatus</i> Awasthi et Prasad	<i>C. grandis</i> Benth. et Hk.	Moist deciduous	Prasad et al. (2004)
Poaceae			
<i>Bambusa siwalika</i> Awasthi et Prasad	<i>B. tulda</i> Roxb.	Moist deciduous	Prasad et al. (2004)
Dicotyledons			
Achariaceae			
<i>Gynocardia miodorata</i> Prasad et al.	<i>G. odorata</i> R. Br.	Evergreen	Prasad et al. (2004)
<i>Hydnocarpus palaeokurzii</i> Prasad	<i>H. kurzii</i> (King) Wrab	Evergreen	Prasad (1994a)
Anacardiaceae			
<i>Holarrhena nainitalensis</i> Prasad et al.	<i>H. antidysentrica</i> Wall.	Mixed deciduous	Prasad et al. (2004)
Annonaceae			
<i>Cananga tertiara</i> Prasad et al.	<i>C. odorata</i> Hk. f. et Thoms.	Evergreen	Prasad (1994a)
<i>Saccopetalum pretomentosum</i> Prasad et al.	<i>S. tomentosum</i> Hk. f. et Thoms.	Moist deciduous	Prasad et al. (2004)
<i>Uvaria siwalika</i> Prasad	<i>U. hamiltonii</i> Hk. f.	Evergreen to moist deciduous	Prasad (1994a)
Apocynaceae			
<i>Wrightia siwalika</i> Prasad	<i>W. tinctoria</i> R. Br.	Moist deciduous	Prasad (1994a)
Bixaceae			
<i>Bixa kathgodamensis</i> Prasad et al.	<i>B. orellana</i> L.	Evergreen	Prasad et al. (2004)
Capparidaceae			
<i>Capparis palaeomicrantha</i> Prasad et al.	<i>C. micrantha</i> DC.	Evergreen	Prasad et al. (2004)
Calophyllaceae			
<i>Calophyllum suraikholaensis</i> Awasthi et Prasad	<i>C. polyanthum</i> Wall.	Evergreen	Prasad et al. (2004)
<i>Mesua tertiara</i> Lakhanpal	<i>M. ferrea</i> L.	Evergreen	Prasad (1994a)
Clusiaceae			
<i>Garcinia eocambogia</i> Prasad	<i>G. cambogia</i> Roxb.	Evergreen	Prasad (1994a)
Combretaceae			
<i>Terminalia miobelerica</i> Prasad et al.	<i>T. belerica</i> Roxb.	Evergreen to moist deciduous	Prasad (1994a)
Dipterocarpaceae			
<i>Dipterocarpus siwalicus</i> Lakhanpal et Guleria	<i>D. tuberculatus</i> Roxb.	Evergreen to moist deciduous	Prasad (1994a)
<i>Hopea kathgodamensis</i> Prasad	<i>H. micrantha</i> Hk. f.	Evergreen	Prasad (1994c)
<i>Shorea miocenica</i> Antal et Prasad	<i>S. buchananii</i> Fischer	Evergreen	Prasad et al. (2004)
Ebenaceae			
<i>Diospyros kathgodamensis</i> Prasad	<i>D. cacharensis</i> Naithani	Evergreen	Prasad (1994a)
<i>D. palaeobenum</i> Prasad	<i>D. ebenum</i> Kurz.	Evergreen	Prasad (1994c)
<i>D. nainitalensis</i> Prasad et al.	<i>D. chloroxylon</i> Roxb.	Moist deciduous	Prasad et al. (2004)
<i>D. palaeoeriantha</i> Prasad et al.	<i>D. eriantha</i> (Champ.) Benth.	Evergreen to moist deciduous	Prasad et al. (2004)
Euphorbiaceae			
<i>Homonoia mioriparia</i> Antal et Prasad	<i>H. riparia</i> Lour.	Moist deciduous	Prasad et al. (2004)
<i>Mallotus venkatachalai</i> Prasad	<i>M. cochinchinensis</i> Lour. and <i>M. repandus</i> Muell.	Evergreen to moist deciduous	Prasad (1994c)
Fabaceae			
<i>Acacia eosericata</i> Prasad	<i>A. sericata</i> A. Cun ex Benth.	Mixed deciduous	Prasad (1994a)
<i>Albizia siwalika</i> Prasad	<i>A. lebbek</i> Benth.	Evergreen to moist deciduous	Prasad (1994a)
<i>Cassia siwalika</i> Prasad	<i>C. tora</i> L.	Mixed deciduous	Prasad (1994a)
<i>Cynometra palaeoiripa</i> Prasad et al.	<i>C. iripa</i> Kotel	Moist deciduous	Prasad et al. (2004)
<i>Derris prakashii</i> Prasad et al.	<i>D. trifoliata</i> Lour.	Evergreen	Prasad et al. (2004)
<i>Dialium palaeoindum</i> Prasad	<i>D. indum</i> L.	Evergreen	Prasad (1994a)

Table 2. (Continued.)

Fossil taxa	Modern comparable species	Forest types	References
<i>Millettia kathgodamensis</i> Prasad <i>et al.</i>	<i>Callerya atropurpurea</i> (Wall.) Schot (syn. <i>Millettia atropurpurea</i> Benth.)	Evergreen	Prasad <i>et al.</i> (2004)
<i>M. palaeoracemosa</i> Awasthi and Prasad	<i>M. racemosa</i> Benth.	Moist deciduous	Prasad (1994a)
<i>M. siwalica</i> Prasad	<i>M. ovalifolia</i> Kurz	Moist deciduous	Prasad (1994c)
<i>Ormosia robustoides</i> Prasad	<i>O. robusta</i> Wight.	Evergreen	Prasad <i>et al.</i> (2004)
<i>Pongamia kathgodamensis</i> Prasad	<i>P. glabra</i> Vent.	Evergreen to moist deciduous	Prasad (1994c)
<i>Samanea siwalica</i> Prasad <i>et al.</i>	<i>S. saman</i> Merrill	Evergreen	Prasad (1994a)
Lauraceae			
<i>Michilus miocenica</i> Prasad	<i>M. odoratissima</i> Nees.	Evergreen to moist deciduous	Prasad (1994c)
Lythraceae			
<i>Lagerstroemia jamraniensis</i> Prasad <i>et al.</i>	<i>L. speciosa</i> Pers.	Moist deciduous	Prasad <i>et al.</i> (2004)
<i>Lagerstroemia patelii</i> Lakhanpal et Guleria	<i>L. flors-reginae</i> Retz.	Evergreen to moist deciduous	Prasad (1994a)
Malvaceae			
<i>Grewia kathgodamensis</i> Prasad <i>et al.</i>	<i>G. laurifolia</i> Hk.	Evergreen	Prasad <i>et al.</i> (2004)
<i>Pachira palaeomalabarica</i> Prasad <i>et al.</i>	<i>P. sessilis</i> Benth.	Evergreen	Prasad <i>et al.</i> (2004)
<i>Sterculia kathgodamense</i> Prasad	<i>S. coccinea</i> Jack	Evergreen	Prasad (1994a)
Meliaceae			
<i>Chukrasia miocenica</i> Prasad	<i>C. tubularis</i> Adr. Juss.	Moist deciduous	Prasad (1994c)
<i>Dysoxylum mioklanderii</i> Prasad	<i>D. kalanderi</i> F. Muell.	Evergreen	Prasad (1994c)
<i>Toona siwalica</i> Awasthi et Lakhanpal	<i>T. ciliata</i> Roxb.	Evergreen to moist deciduous	Prasad (1994a)
<i>Trichilia miocenica</i> Prasad	<i>T. glabra</i> Vell.	Moist deciduous	Prasad (1994a)
Moraceae			
<i>Ficus oodlabariensis</i> Antal et Awasthi	<i>F. benjamina</i> L.	Evergreen	Prasad <i>et al.</i> (2004)
<i>Ficus precunea</i> Lakhanpal	<i>F. cunea</i> Ham.	Mixed deciduous	Prasad <i>et al.</i> (2004)
Myrsinaceae			
<i>Ardisia palaeosimplicifolia</i> Prasad	<i>A. simplicifolia</i> Walp.	Evergreen to moist deciduous	Prasad (1994a)
Phyllanthaceae			
<i>Glochidion miocenica</i> Prasad	<i>G. chlorophaes</i> Baill.	Evergreen	Prasad (1994a)
<i>Phyllanthus mioreticulatus</i> Prasad <i>et al.</i>	<i>P. reticulatus</i> Poir.	Evergreen	Prasad <i>et al.</i> (2004)
<i>P. siwalica</i> Prasad	<i>P. gracilips</i> Muell. Arg.	Evergreen	Prasad (1994a)
Rhamnaceae			
<i>Zizyphus kathgodamensis</i> Prasad	<i>Z. xylopyrus</i> Wild.	Mixed deciduous	Prasad (1994a)
<i>Z. miocenicus</i> Prasad <i>et al.</i>	<i>Z. jujuba</i> Lam.	Mixed deciduous	Prasad (1994a)
Rosaceae			
<i>Parinari kathgodamensis</i> Prasad	<i>P. excelsa</i> Sabine.	Evergreen	Prasad (1994a)
Rubiaceae			
<i>Gardenia nainitalensis</i> Prasad	<i>G. jasminoides</i> Retz.	Evergreen	Prasad (1994a)
<i>Morinda palaeotinctoria</i> Prasad	<i>M. tinctoria</i> Roxb.	Evergreen	Prasad (1994a)
Rutaceae			
<i>Acronychia siwalica</i> Prasad	<i>A. baueri</i> Schott.	Evergreen to moist deciduous	Prasad (1994c)
<i>Geijera siwalica</i> Prasad	<i>G. laurifolia</i> Hk.	Evergreen	Prasad (1994c)
Sapindaceae			
<i>Cupania moicenica</i> Prasad <i>et al.</i>	<i>C. jackiana</i> Heirn.	Evergreen	Prasad <i>et al.</i> (2004)
<i>Euphoria siwalica</i> Prasad	<i>E. didyma</i> Blanco.	Evergreen	Prasad (1994a)
Sapotaceae			
<i>Sarcosperma mioarboratum</i> Prasad <i>et al.</i>	<i>S. arboretum</i> Benth.	Evergreen	Prasad <i>et al.</i> (2004)
Theaceae			
<i>Uncobia palaeospinosa</i> Prasad	<i>Stewartia</i> L.	Mixed deciduous	Prasad (1994a)

its associated fruit (*Enigmocarpon*) discovered from the Deccan Intertrappean beds of central India (Sahni and Rode 1937; Sahni 1943; Shukla 1944, 1958; Chitale and Kate 1977) considered as late Maastrichtian–Danian in age (~61.7–65 Ma). On the basis of these records it can be inferred that the family was widely distributed on both the northern and southern hemispheres by the Late Cretaceous (~65.6–99.6 Ma) (Venkatesan et al. 1993; Shukla et al. 1997; Salis and Saksena 1998).

4.2 Fossil records of *Lagerstroemia*

The fossil records of *Lagerstroemia* are represented in the form of wood, leaf, and pollen which are restricted to south and southeast Asia, China, and Japan. In south Asia, the fossils are recorded in the form of leaves and wood from the Eocene, Miocene, and Mio–Pliocene sediments of India and Nepal (Prakash and Tripathi 1970; Awasthi 1981; Lakhanpal and Guleria 1981; Lakhanpal et al. 1981; Srivastava and Bande 1992; Antal and Awasthi 1993; Prasad 1994b; Agarwal 2002; Prasad et al. 2004; Dwivedi et al. 2006). Similarly, the genus was recorded as pollen and wood from the Neogene sediments of southeast Asia (Prakash 1965a, b; Prakash 1972; Kramer 1974; Prakash and Bande 1980; Du 1988; Guleria 1989; Watanasak 1990; Songtham et al. 2005). Fossils of the genus have also been reported from the Oligocene and Neogene sediments of Japan (Tanai and Uemura 1991; Miyoshi et al. 1999; Fujiki et al. 2001; Momohara et al. 2006; Choi et al. 2010). Its pollen and wood are also known from the Miocene and Pliocene of eastern and southwestern China (Cheng et al. 2007; Liu et al. 2008). Among all these fossil records, the oldest is from the Eocene sediments of Gujarat (Lakhanpal and Guleria 1981), India suggesting a probable Gondwanic origin of the genus. The aforesaid fossil records of *Lagerstroemia*, at least in south and southeast Asia, suggest that the genus might have migrated from India to southeast Asia after the complete suturing of the Indian and Eurasian plates. Like *Lagerstroemia*, many other taxa such as *Mangifera* and *Semecarpus* of the Anacardiaceae (Mehrotra et al. 1998; Srivastava and Mehrotra 2012; Chatterjee et al. 2013), *Alphonsea* of the Annonaceae (Srivastava and Mehrotra 2013a), *Sterculia* of the Malvaceae (Srivastava and Mehrotra 2013b) and Dipterocarpaceae (Dutta et al. 2011) might have migrated from India to southeast Asia. Their migration supports the ‘Out of India’ hypothesis (Bossuyt and Milinkovitch 2001).

4.3 Expansion and retraction of Lythraceae and *Lagerstroemia* during the Cenozoic

A cursory look at the known fossil records of Lythraceae and *Lagerstroemia* (figure 5) indicates a pattern of expansion and retraction which showed a maximum peak in the Miocene but dropped abruptly in the Pliocene due to the deterioration in the climatic conditions (Zachos et al. 2001). Both the family and the genus show the same pattern of expansion and retraction suggesting that they had a similar behaviour for adaptation during the Cenozoic. The similar behaviour pattern in adaptation might be because of the ecological niche conservatism (ENC). The ENC, therefore, is defined as the tendency of a species (or clades) to hold their ecological traits over a period of time (Peterson et al. 1999) and this phenomenon is observed not only at regional level but on a global scale as well (Crisp et al. 2009).

4.4 Palaeoclimate analysis of the fossil locality

A large number of fossil taxa have been reported from the Siwalik (middle Miocene) of Kathgodam (table 2). The presence of typical megathermal pantropical families like Annonaceae, Bombacaceae, Combretaceae, and Clusiaceae indicates a warm condition with plenty of rainfall. The dominance of evergreen and moist deciduous taxa, along with the mixed deciduous taxa (figure 6) indicates seasonality in the rainfall. The abundance of legumes (table 2) further supports this view. Palaeosol record from northwest Himalaya and quantitative palaeoclimate reconstruction based on pollen assemblage from south India also suggested that during the middle Miocene a monsoonal type of climate was

Figure 6. A pie diagram showing distribution of evergreen and deciduous taxa in the fossil assemblage of the studied interval of Lower Siwalik deposits at Kathgodam.

present in India (Ganjoo and Shaker 2007; Reuter *et al.* 2012).

5. Conclusions

Lagerstroemia (Lythraceae) fossil leaf is described from the middle Miocene (Lower Siwalik) sediments of Kathgodam, Uttarakhand, India. The family Lythraceae had worldwide distribution in the Cenozoic in contrast to modern day tropical to subtropical areas of the world. The present leaf fossil, along with the previous known fossil records of *Lagerstroemia*, indicates that the genus followed the same pattern of geographic expansion and retraction as the entire family Lythraceae. The plant fossil assemblage from the Lower Siwalik deposits indicates warm and humid climate with seasonality in rainfall in the region during the depositional period.

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