Evidence of triplinerved cinnamon from the Siwalik (middle Miocene) sediments of Darjeeling foothill and its biogeographic implication: Asian perspective

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Abstract

*Cinnamomum* Schaeffer (avocado family Lauraceae), commonly known as a cinnamon tree, is a highly diverse, economically important evergreen element of tropical and sub-tropical regions of the world. In the present work, we have recovered six compressed leaf remains similar to modern leaves of *Cinnamomum* from the lower part of the Siwalik strata (middle Miocene) of Darjeeling foothills, eastern Himalaya. The recovered fossil specimens are characterized by an elliptic to the ovate lamina, acute to short acuminate apex, round to acute base, and basal as well as suprabasal acrodromous type of primary venation. Based on preserved architectural features, Siwalik fossil leaves are confidently placed under the genus *Cinnamomum*. However, the recovered Siwalik specimens cannot be traced up to the species level due to a lack of satisfactory macromorphological features (especially tertiary veins) and epidermal anatomy and are designated here as morphotypes. The evidence of current Siwalik specimens and earlier-reported fossil species similar to thermophilic *Cinnamomum* in appreciable number from other Siwalik localities (Darjeeling, Uttarakhand, and Nepal) suggests that *Cinnamomum* was a common Siwalik element and the existence of tropical, warm and humid climatic conditions during the Siwalik sedimentation. This finding also represents an important source of data for understanding the evolution, diversification, and paleobiogeographic history of *Cinnamomum* from an Asian perspective in deep time.

Introduction

The genus *Cinnamomum* Schaeffer comprising of near about 250–350 species is characterized by a varied geographical distribution and wide-ranging ecological preferences (Rohwer 1993; Mabberley 2008; Choudhury et al. 2013; Huang et al. 2016; Tanrattana et al. 2019). Presently, it occurs in tropical to subtropical evergreen broad-leaved forests, montane forests of south and central America, Asia, Africa, and Australia (Schnell 1987; Lorea-Hernández 1996; Tanrattana et al. 2019). It is also common in the tropical and sub-tropical vegetation of Himalayas (up to 2000 m) (Schnell 1987; Lorea-Hernández 1996; Tanrattana et al. 2019). The main centre of diversity of *Cinnamomum* species is tropical Asia (Lorea-Hernández 1996; Geethakumary et al. 2021). *Cinnamomum* belonging to the tribe Cinnamomeae is a well-known source of the cinnamon of commerce (Farrell 1985; Loi 1996). The members of this genus have long been familiar with their economic importance such as the sources of camphor, spices, phytomedicines, and high-quality wood (Wijesekera et al. 1975; Farrell 1985; Loi 1996; Ravindran et al. 2003).

Cinnamomum are monophyletic and strongly suggests that the Cinnamomum group consists of three clades: sect. Camphora, sect. Cinnamomum and the neotropical species respectively.

In India, forty-five species (forty-three species and two varieties) of Cinnamomum are documented and are mostly distributed in the lush vegetation of the north-eastern Himalayan regions and the Western Ghats (Geethakumary et al. 2021). Among them, twenty-four species are endemic with thirteen exclusively in the Western Ghats. Kerala (Peninsular India) is now considered a hotspot area for Cinnamomum (Geethakumary et al. 2021). Cinnamomum exhibits various foliar morphologies like elliptic to obovate leaf shape forms, triplinerved and pinni-nerved venation patterns, and acute, round or attenuate apices (Lorea-Hernández 1996; Ho and Hung 2011; Wuu-Kuang 2011).

Cinnamomum was cosmopolitan in distribution during the geological past (Table 1; Johnson 2002; Coiffard et al. 2008; Cantrill et al. 2011; He et al. 2013; Dao et al. 2013; Shi et al. 2014). Cinnamomum has abundant and extensive fossil records during the Cretaceous period in both the northern and southern hemispheres (von Ettingshausen 1883,1887a, b, 1891; Berry 1929; Guo 1979; Lozinsky et al. 1984; Crabtree 1987; van Boskirk 1998; Johnson 2002; Coiffard et al. 2008). It was reported from the Late Cretaceous sediments of Asia (Berry 1929; Guo 1979), Europe (Coiffard et al. 2008), North America (Berry 1929; Lozinsky et al. 1984; Crabtree 1987; van Boskirk 1998; Johnson 2002), and Australasia (von Ettingshausen 1883; Pole 1992; Cantrill et al. 2011). However, it reached its peak in the early Cenozoic (Eocene) in the U.S.A. and during the Miocene in Europe (Berry 1916). The earliest record of Cinnamomum species C. paluxyense Ball was reported from the Lower Cretaceous (middle Albian) of Paluxy sands, Texas (Ball 1937).
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<td><em>Cinnamomum tamala</em></td>
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<td>Kashmir, India</td>
<td>Late Quaternary (Pleistocene)</td>
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<td>C. sp. cf. Lauraceae</td>
<td><em>C. malabatrum</em> (Burm. f.) Blume</td>
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<td><em>Cinnamomum</em> sp.</td>
<td><em>C. tamala</em> Nees</td>
<td>Darjelling, India</td>
<td>Pliocene</td>
<td>Pathak, 1969</td>
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<td>C. cf. <em>burmannii</em></td>
<td><em>C. burmannii</em></td>
<td>Tengchong, Yunnan Province, China,</td>
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<td>C. cf. <em>camphora</em></td>
<td><em>C. camphoa</em></td>
<td>Tengchong, Yunnan Province, China,</td>
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<td>C. cf. <em>subavenium</em></td>
<td><em>Cinnamomum</em> sp.</td>
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<td><em>Cinnamomum</em> sp.</td>
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<td><em>Cinnamomum</em> sp.</td>
<td><em>Cinnamomum</em> sp.</td>
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<td><em>Cinnamomum</em> sp.</td>
<td>Lincang, China</td>
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<td><em>C. oguniense</em></td>
<td><em>Cinnamomum</em> sp.</td>
<td>Kaiyuan, China</td>
<td>Late Miocene</td>
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<td><em>C. scheuchzeri</em></td>
<td><em>Cinnamomum</em> sp.</td>
<td>Xundian/Lincang, China</td>
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<td><em>Cinnamomum</em> sp.2</td>
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<td><em>C. bejolghota</em></td>
<td>Eastern Zhejiang, China</td>
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<td><em>Cinnamomum</em> sp.</td>
<td><em>Cinnamomum</em> sp.</td>
<td>Kerala, India</td>
<td>Miocene</td>
<td>Awasthi and Srivastava, 1992</td>
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<td><em>C. nepalensis</em></td>
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<td>Uttarakhand, India</td>
<td>Miocene</td>
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<td><em>C. miotavoyanum</em></td>
<td><em>C. tavoyanum</em> Meisn.</td>
<td>Uttarakhand, India</td>
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<td>Shashi et al., 2008</td>
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<td><em>C. palaeotamala</em></td>
<td><em>C. tamala</em> Nees</td>
<td>Nepal</td>
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<td>Konomatsu and Awasthi, 1996</td>
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<td><em>C. glandulifera</em></td>
<td><em>Cinnamomum</em> sp.</td>
<td>Jinchuan, Kaiyuan, China</td>
<td>Miocene</td>
<td>Tao and Du, 1982; Li, 1989</td>
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<td><em>C. mioinuctum</em></td>
<td><em>C. inuctum</em></td>
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<td><em>C. nepalensis</em></td>
<td><em>C. caudatum</em></td>
<td>Nepal</td>
<td>Middle Miocene</td>
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<td><em>C. palaeobejolghota</em></td>
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<td><em>Cinnamomum</em> sp. Morphotype-I</td>
<td><em>Cinnamomum</em> sp.</td>
<td>Darjeeling, India</td>
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<td><em>Cinnamomum</em> sp. Morphotype-II</td>
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<td><em>C. miokachchhensis</em></td>
<td><em>Cinnamomum</em> sp.</td>
<td>Gujrat, India</td>
<td>Early Miocene</td>
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<td><em>Cinnamomum</em> sp.</td>
<td><em>Cinnamomum</em> sp.</td>
<td>Jinchuan, China</td>
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<td><em>Cinnamomum</em> sp.</td>
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<td><em>Cinnamomum eokachchhensis</em></td>
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In Asia, *Cinnamomum* is recorded in India, Nepal, and China (Table 1). To date, ten leaf fossil species similar to *Cinnamomum* are documented from the Cenozoic sediments of India (Puri 1948; Pathak 1969; Lakhanpal and Guleria 1981, 1982; Antal and Awasthi 1993; Shashi et al. 2008; Khan and Bera 2014). However, only six reliable fossil records of *Cinnamomum* are known so far from the Siwalik sediments of India (Table 1). From this perspective, the six-leaf specimens of *Cinnamomum* from one locality i.e., from
the Siwalik (middle Miocene) sediments of Darjeeling sub-Himalaya is noteworthy. The aims of the present study are to 1) report and describe two morphotypes of fossil *Cinnamomum* leaf remains and 2) review comprehensively the fossil history of this economically important lauraceous genus in Asia and suggest its hypothetical migratory routes.

**Materials And Methods**

**Fossil locality and geological setting**

The six fossil leaf specimens similar to modern leaves of *Cinnamomum* are recovered during fieldwork undertaken in the year 2022 (February and April) from the river cutting section belonging to the lower part of Siwalik strata (Gish Clay Formation: middle Miocene) exposed along the Balason River near Dudhia in the Darjeeling district (latitude 26°81'50" N, longitude 88°14'26" E), West Bengal, eastern India (Fig. 1). The studied section is characterized by very fine to fine-grained sandstones, laminated siltstones, and thinly laminated to massive, greenish-grey mudstones with occasional marl beds, locally interbedded with carbonaceous shales. The geological setting, as well as the lithostratigraphic succession of the Siwalik Group of the Darjeeling foothills, was critically analyzed by Ganguly and Rao (1970), Acharyya (1994) and recently by Taral et al. (2017).

**Sample preparation and photography**

We have collected the fossil leaf specimens (Fig. 2, 3) by fracturing the hardy consolidated Siwalik rocks with a hammer and a shovel. Some preparation is needed before photography as some morphological traits (especially apex and basal parts) of our fossil specimens are not well-exposed in the initial fracture of sedimentary strata. The leaf specimens are revealed by careful removal of the overlying sedimentary matrix using fine needles, scalpels, and brushes. We examine critically them under a dissecting microscope and photographed them using a digital camera (Canon EOS 1500D) (Fig. 2, 3). In addition, the leaf architecture is studied with a Stereo zoom microscope. The photographs of the recovered specimens and comparable modern leaves are drawn using CorelDraw 21 software for detailed venation patterns. Their identification is made by comparison with modern angiosperm trinerved leaves having acrodromous primary veins collected from the forests adjacent to our fossil locality, as well as with herbarium sheets of angiosperm leaves bearing similar venation patterns using digital herbarium catalogues namely, Kew herbarium catalogue (https://apps.kew.org/herbcat/gotoCiteUs.do), Florida Plant Atlas (http://florida.plantatlas.usf.edu/) and global biodiversity information facility (https://www.gbif.org/en/citation-guidelines) (Table S1; Fig. 4, 5).

**Terminology and repository**

The terms used here to describe leaf architecture follow Ellis et al. (2009). The fossil specimens (SKBUH/PPL/DJ-BA/133, SKBUH/PPL/DJ-BA/134, SKBUH/PPL/DJ-BA/135, SKBUH/PPL/DJ-BA/136, SKBUH/PPL/DJ-BA/137, ...
Results

Based on the preserved morphological features (size, shape, and acrodromous type of primary venation, trinerved), our recovered six fossil leaf specimens (Fig. 2, 3) are confidently placed under the genus *Cinnamomum*. However, due to the lack of sufficient diagnostic macro (tertiary veins) and micromorphological features (epidermal anatomy), it is awkward to assign our Siwalik specimens to a particular species under *Cinnamomum*. From this point of view, we cannot narrow their identification up to a specific level and here, tentatively describe our specimens under morphotypes (morphotype-I and morphotype-II).

Here, we focus only on detailed macromorphological features of the present fossil specimens. The most significant diagnostic feature of the Siwalik specimens is acrodromous (basal and suprabasal) primary venation having three perfect primaries running in convergent arches towards the leaf apex. So, we compare our fossil specimens with those modern angiosperm leaves which have trinerved acrodromous venation patterns. On critical examination, we found that our Siwalik specimens resemble modern leaves of eight taxa of different families such as *Smilax glauca* Mart. (Smilacaceae), *Cocculus laurifolius* DC. (Menispermaceae), *Rhodomyrtus tomentosa* (Aiton) Hassk. (Myrtaeceae), *Melastoma malabathricum* L. (Melastomataceae), *Ziziphus mauritiana* Lam. (Rhamnaceae), *Sarcococca coriacea* (Hook.) Sweet (Buxaceae), *Strychnos bredemeyeri* (Schult.) Sprague & Sandwith (Loganiaceae) and different genera of Lauraceae (Fig. 4). Leaves of *S. glauca* differ from our specimens in having a broadly ovate, large lamina with a convex base, and an obtuse to sub-acute apex, in contrast, our specimens possess acute-round base and acute-sub-acuminate apex. Among the various species of *Cocculus*, only *C. laurifolius* shows similarity with our Siwalik fossil specimens, but it differs in having a weakly wavy margin and narrow width lamina. In addition, *C. laurifolius* has more acute lateral primary veins than our specimens. Leaves of *S. coriacea* differ in having a large acuminate apex and a perfectly straight midvein than our specimens. In *Z. mauritiana*, the margin of the lamina is slightly serrated. On the other hand, *S. bredemeyeri* differs in having an attenuate leaf apex. In *R. tomentosa*, the leaf apex is obtuse in contrast to the acute-sub-acuminate leaf apex in our Siwalik leaf specimens. The modern leaves of *M. malabathricum* differ in the angle of primary lateral veins. So, based on the macromorphological features (size, the shape of the leaf blade, nature of apex and base, types of venation pattern), our Siwalik fossil specimens show the closest resemblance to the extant genera of Lauraceae (Fig. 4).

Within the family Lauraceae, leaves having acrodromous perfect triplinerved venation patterns occur in seven genera such as *Cryptocarya* R.Br., *Lindera* Adans., *Neocinnamomum* H. Liu, *Neolitsea* Merr., *Caryodaphnopsis* Airy Shaw, *Iteadaphne* Blume, and *Cinnamomum* Schaeffer. In *Iteadaphne*, *Lindera* and *Neolitsea*, leaves exhibit a long acuminate apex. The modern leaves of *Neocinnamomum* possess a caudate tip. On the other hand, *Cryptocarya* and *Caryodaphnopsis* differ in shape and venation pattern. So, our Siwalik specimens most closely resemble modern leaves of *Cinnamomum*. We also compare our
Siwalik specimens with modern leaves of different species of *Cinnamomum* but we observe that there is a great variation in the size and shapes of modern leaves of *Cinnamomum* (Fig. 5) and even in the point of origin of primary veins. Although the ternate venation is very common in all the species of *Cinnamomum*. In addition, due to the presence of thick cuticles in our present fossil specimens, we cannot study the higher venation order. Therefore, it is rather difficult to reach up to a specific level merely on the basis of the limited morphological characters of our Siwalik specimens. Thus, we describe the Darjeeling lower Siwalik leaf specimens preferably as *Cinnamomum* sp.

To date, there are eleven fossil species from India, three from Nepal, and sixteen fossil species from China (Table 1, Fig. 6). We compare our fossil specimens with only available fossil species of Asia. The morphological characters of them are listed in Table-S2.

**Discussion**

**Biogeographical implications from an Asian perspective**

Plant macrofossils give us valuable information about the past geographical distribution of many angiosperms (Tiffney and Manchester, 2001). The fossil record of *Cinnamomum* is rich in Asia and is found in sediments from Eocene to Quaternary (Table 1; Fig. 7a, b; 8). So, our fossil evidence from the Siwalik (middle Miocene) sediments of Darjeeling and earlier fossil record (Eocene-Pliocene) of *Cinnamomum* from Asia are essential for understanding their evolutionary and biogeographical history in deep time. There are plenty of leaf fossils attributed to *Cinnamomum* reported from Cenozoic sediments of Asia, specifically from India and China (Table 1; Fig. 7c, 8). *Cinnamomum* fossils are reported mostly from the Neogene sediments, only three from Palaeogene (two from China and one from India). Lakhanpal and Guleria (1981) described *C. eokachchhensis* as similar to modern triplinerved leaves of *Cinnamomum* from the Eocene sediments of the lignite mine of Kachchh district of Gujarat, western India. The other three Palaeogene *Cinnamomum* are reported from the two Oligocene of China (EGCFC 1978; Tao 2000; Shi et al. 2014) and the other one was reported from Ha Long Oligocene flora of Vietnam (Huang et al. 2022). Among Neogene fossil evidence, *Cinnamomum* leaf fossils are mainly described from the Miocene sediments (Table 1; Fig. 7b). Nine *Cinnamomum* leaf species (*Cinnamomum* sp, *C. naitoanum*, *C. oguniense*, *C. scheuchzeri*, *C. versutifolium*, *Cinnamomum* sp.1, *Cinnamomum* sp. 2, *C. cf. bejolghota*, *C. glandulifera*) are reported from China (Tao and Du 1982; Zhou 1985; Li and Li 1999; Xing 2010; Guo 2011; He et al. 2013), four species (*Cinnamomum* sp., *C. nepalensis*, *C. miotavoyanum*, *C. bejolghota*) from India (Awasthi and Srivastava 1992; Shashi et al. 2008; Khan and Bera 2014) and three species (*C. palaeotamala*, *C. mioinuctum*, *C. nepalensis*) are reported from the lower part of the Siwalik sediments of Nepal (Prasad 1990; Konomatsu and Awasthi 1996; Prasad and Pandey 2008). Two species are reported from Miocene-Pliocene Siwalik strata of India, *Cinnamomum* sp. described by Antal and Awasthi (1993) from the Miocene-Pliocene Siwalik sedimentary strata of Darjeeling and other species *C. palaeotamala* similar to modern leaves of *C. tamala* Nees reported by Lakhanpal and Awasthi (1984) from the Siwalik sediments of Miocene-Pliocene strata of Bihar. Five leaf fossil species similar to *Cinnamomum* are reported from the Pliocene sediments of China. *Cinnamomum*
sp. described by Liu et al. (2002) is reported from Yuanmou, *C. cf. subavenium* and *C. tuantianensis* described by Wu (2010) from Tengchong, *C. cf. burmannii* and *C. cf. camphora* described by Dao et al. (2013) from the Tuantian flora of Tengchong, Yunnan Province. Additionally, Pathak (1969) reported *Cinnamomum* sp. similar to modern *C. tamala* Nees. from the Pliocene sediments of Darjeeling. Only two *Cinnamomum* leaf remains are recorded from the Quaternary (Pleistocene) sediments of India (Puri 1948; Kumaran et al. 2012). Puri (1948) reported *Cinnamomum* species from the Pleistocene sediments of Kashmir and Kumaran at al. (2012) reported other species from the Pleistocene sediments of Konkan, Maharashtra, western India.

So, the above-mentioned earlier records of *Cinnamomum* suggest that this genus was a common forest element during the Neogene (Miocene) as well as in the Siwalik forests of India and Nepal. In Miocene, the seasonal, monsoonal climate became warmer and more moisture because of the Himalayan upliftment (Morley 2000). *Cinnamomum* reached a peak of its geographic distribution becoming the dominant group in the Miocene forests of Asia. However, increasing aridity and seasonality in the late Miocene and Pliocene (Morley 2000) might have led to its gradual disappearance. This hypothesis is in conformity with the less fossil evidence of *Cinnamomum* during the post-Miocene period (Puri 1948; Pathak 1969; Wu 2010; Kumaran et al. 2012; Dao et al. 2013) (Fig. 9).

The earliest fossil record of *Cinnamomum* is from the Eocene sediments of India (Lakhanpal and Guleria, 1981) and numerous post-Eocene cinnamon fossil species are reported from China, India, and Nepal. In this context, we suggest a possible migration of *Cinnamomum* from the Indian landmass to mainland masses of Southeast Asia (especially China) after the land connection between the two landmasses was established and supports the “Out-of-India” hypothesis (Fig. 9). Then, *Cinnamomum* might have moved to other parts of India, China, and Nepal where conditions were more suitable for its lush growth. The detailed scenarios for the phytogeography of *Cinnamomum* in the Asian perspective still require further reliable macrofossil evidence.

**Palaeoclimatic implications**

The family Lauraceae is among the largest and floristically most important woody plant families. In India, this family is mainly distributed in tropical zones (Brandis 1971; Geethakumary et al. 2021). The earlier reported fossil specimens of Lauraceae from India and our fossil specimens described here indicate that a warm and humid tropical to subtropical climate appeared within the area during the time of deposition. Detailed mega floristic studies from the Indian Cenozoic sediments (Mehrotra et al. 2005; Prasad 2008; Khan et al. 2014) also indicated a similar conclusion on climate. The present fossil evidence of economically important lauraceous taxon *Cinnamomum*, suggests that *Cinnamomum* existed in the Siwalik sediments (middle Miocene) of Darjeeling foothills, eastern Himalaya. Earlier workers also
reported *Cinnamomum* fossil leaves as well as other fossil leaves similar to thermophilic lauraceous taxa such as *Actinodaphne angustifolia* (Blume) Nees, *Persea* sp., *Persea villosa* (Roxb.) Kosterm, *Michilus* sp., *Litsea polyantha* Juss. and *Persea gamblei* King ex Hook. f. (Pathak 1969; Antal and Awasthi 1993; Khan and Bera 2016) from the Siwalik sediments of the same locality. So, the current and earlier evidence of cinnamon leaf remains collectively indicate a warm and humid tropical climate. This hypothesis is also reliable with earlier published qualitative and quantitative climate data based on plant megafossils from Darjeeling foothills (Antal and Awasthi 1993; Antal and Prasad 1995, 1996A, B, C, 1997; 1998; Khan and Bera 2014, 2016; Khan et al. 2014, 2015; More et al. 2018; Bhatia et al. 2022).

**Taxonomic Treatment**

Order: Laurales Juss. ex Bercht. & J. Presl

Family: Lauraceae Juss.

Genus: *Cinnamomum* Schaeff.

Morphotype-I (Fig. 2)

Materials: Four-leaf specimens (Fig. 2a, e), two of them incomplete (Fig. 2c, d)

Specimens examined: SKBUH/PPL/ DJ-BA /133 (Fig. 2A): SKBUH/PPL/ DJ-BA /135 (Fig. 2c): SKBUH/PPL/ DJ-BA /136 (Fig. 2d): SKBUH/PPL/ DJ-BA /211 (Fig. 2e)

Description: Leaf simple, symmetrical, well-preserved; blade a microphyll-III type; preserved maximum blade length (BL) 4.7 cm, preserved maximum blade width (BW) 1.8 cm; elliptic to narrow ovate in shape; widest place of lamina (WPL/L) (length of widest place to base/total length) 1.74; apex acute or seemingly sub-acuminate; base acute; margin entire; texture coriaceous; venation suprabasal acrodromous, perfect; primary vein (1º) three, consisting of primary mid vein and two lateral primary veins; midvein almost straight, thick 0.2 cm wide; two lateral primaries opposite with decurrent attachment to the midvein, originating at an angle of divergence of 20º from the midvein, running upwards the leaf; few major secondary veins (2º) seen, faint, running approximately at right angles (forming ripples) to acute angles, sometimes branched, emerging from the median primary and joining the two laterals, also arising from the outer side of the two lateral primaries at acute angles moving upward and forming fine intramarginal veins; tertiary vein (3º) faint, percurrent, present between primaries; areoles and veinlets not seen.

Morphotype-II (Fig. 3)

Materials: Two, almost complete (Fig. 3a, b)

Specimen examined: SKBUH/PPL/ DJ-BA /134 (Fig. 3a): SKBUH/PPL/ DJ-BA /212 (Fig. 3b)

Description: Leaf simple, almost symmetrical, well-preserved; blade microphyll-III type; preserved maximum blade length (BL) 4.5 cm, preserved maximum blade width (BW) 2.4 cm; ovate in shape; widest
place of the lamina (WPL/L) (length of widest place to base/total length) 0.48 cm; apex acute; base round; margin entire; texture coriaceous; venation basal acrodromous, perfect; primary veins (1º) three, mid primary vein slightly curved, lateral primary veins opposite with decurrent attachment to the midvein, the acute angle of divergence of lateral primaries 45–50º, running upwards towards the apex; major secondary and high order veins not clearly seen due to the presence of thick cuticle on the surface of our specimens.

Collectors: Sumana Mahato and Mahasin Ali Khan

Horizon and age: Gish Clay Formation (middle Miocene)

Locality: River cutting section of Balason River (26° 81’ 50”N; 88° 14’ 26”E; elevation: 2361 m a.s.l), Darjeeling district, West Bengal.

Declarations

Acknowledgments

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Conflict of Interest

The authors declare that they have no conflict of interest.

Ethical statement

No specific permits were required for the described field studies. The sampling sites are not protected in any way and the field studies did not involve endangered or protected species.

Author contributions

All authors contributed to the study’s conception and design. Material preparation, data collection, and analysis were performed by Sumana Mahato and Mahasin Ali Khan. The first draft of the manuscript was written by Sumana Mahato and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

References


**Figures**

![Geological map of Himalaya showing different tectonic units (modified from Kumar 1988)](image)

**Fig. 1**

Geological map of Himalaya showing different tectonic units (modified from Kumar 1988) (star indicates the fossil locality) (TT: Tethyan Thrust; MCT: Main Central Thrust; MBT: Main Boundary Thrust; HFF: Himalayan Frontal Fault).
Figure 2

Fossil leaves of *Cinnamomum* sp. (morphotype-I) and modern leaf of *Cinnamomum* (a) a fossil leaf specimen of *Cinnamomum* sp. (Morphotype I: SKBUH/PPL/DJ-BA/133) showing an acute base and an acute apex, elliptic shape shaped lamina and suprabasal acrodromous primary venation pattern; (b) line drawing of fossil specimen SKBUH/PPL/DJ-BA/133; (c, d) two fossil leaf specimens of morphotype I: SKBUH/PPL/DJ-BA/135, SKBUH/PPL/DJ-BA/136 ) showing the percurrent type of tertiary veins; (e) A
fossil leaf of *Cinnamomum* sp. (Morphotype I: SKBUH/PPL/DJ-BA/211) showing an acute base (green arrow), an acute apex (yellow arrow), primary vein (red arrow), lateral primary veins (pink arrow) and tertiary veins (black arrow); (f) line drawing of fossil specimen SKBUH/PPL/DJ-BA/211 showing similar characters; (g) modern leaf of *C. zeylanicum* Blume showing an acute base (green arrow), an acute apex (yellow arrow), primary vein (red arrow), lateral primary veins (pink arrow) and tertiary veins (black arrow) Scale bar = 1 cm.
Figure 3

Fossil leaves of *Cinnamomum* sp. (morphotype-II) and modern leaf of *Cinnamomum* (a, b) fossils leaf specimens of *Cinnamomum* sp. (Morphotype II: SKBUH/PPL/DJ-BA/134, SKBUH/PPL/DJ-BA/211) showing a round base, an acute apex, ovate shaped lamina and basal acrodromous primary venation pattern; (c) a modern leaf of *Cinnamomum verum* J. Presl showing similar shape, size, nature of apex and base and venation pattern; (d) an enlarged view of fossil leaf specimen SKBUH/PPL/DJ-BA/211.
showing acute apex; (e) an enlarged view of modern leaf specimen showing acute apex; (f) line drawings of morphotype-II (SKBUH/PPL/DJ-BA/134, SKBUH/PPL/DJ-BA/211) Scale bar = 1 cm.

Figure 4

Line drawings of modern members of diverse angiosperm families and modern genera of family Lauraceae having trinerved acrodromous venation pattern Scale bar = 2 cm except for (c), (g) and (f) Scale bar =1 cm.
Figure 5

A twig of *Cinnamomum verum* J. Presl showing the various foliar morphologies (https://www.gbif.org/occurrence/3034594545)
Figure 6

Line drawings of available fossil species of *Cinnamomum* from Asia Scale bar = 1 cm.
Figure 7

(a, b) Bar diagram showing the diversity of fossil *Cinnamomum* in different geological periods and Epochs; (c) bar diagram showing the percentage of fossil *Cinnamomum* in different geographical areas.
Figure 8

Map showing the past distribution of fossil species of *Cinnamomum*
Figure 9

Hypothetical migratory routes of *Cinnamomum* in Asian perspectives. The arrows and circles indicate the possible migratory directions and fossil records of *Cinnamomum* respectively.

Supplementary Files
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- TableS1.docx
- TableS2.docx