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RESEARCH ARTICLE

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Paleogene *Ficus* leaves from India and their implications for fig evolution and diversification

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Abstract

Premise: *Ficus* is a scientifically and economically important genus with abundant fossil records from the Paleocene to Pleistocene, but with an intriguing early evolutionary history that remains unresolved. Here, the foliage of three well-preserved figs is described from the early Paleogene succession of the Gurha mine, Rajasthan, India. These fossils provide new morphological data that strengthens our understanding of the past occurrences of *Ficus* and, alongside all validly published records of fossil figs, helps to trace the evolutionary history of figs.

Methods: Fossils were identified and described by comparison with their closest modern analogs using the Nearest Living Relative (NLR) technique. Validated fig records are listed and categorized into six geological time frames. Modern precipitation data for the current distributions of NLRs were downloaded from the Climatic Research Unit Timeseries.

Results: Fossil leaves assigned to three new species *Ficus paleodicranostyla*, *F. paleovariegata*, and *F. paleoauriculata* closely resemble their modern analogs based on leaf morphology. Reliable fossil records were used to hypothesize historical fig distributions and paleodispersal pathways. Precipitation data suggest higher precipitations at the fossil locality during the early Paleogene than at present.

Conclusions: The fossils described herein supplement fig fossil records known from other regions indicating that figs were widely diverse across low latitudes by the early Paleogene. These data support a Eurasian origin for figs, highlight a pivotal role for the Indian subcontinent during the early phase of fig diversification, and depict a perhumid-to-humid climate with high rainfall concordant with paleoclimate evidence from the Gurha mine.

KEYWORDS

climate change, evolution and diversification, figs, Gurha lignite mine, lowland forests, Moraceae

Ficus (Moraceae), is a diverse genus encompassing ~750 species of what are commonly called "figs" and one of the most important woody plant genera. *Ficus* has been further divided into six subgenera: *Pharmacosycea*, *Sycomorus*, *Sycidium*, *Ficus*, *Synoecia* and *Urostigma* (Berg, 1989; Cruaud et al., 2012). Various habits and life forms across a wide-ranging geographical distribution have been observed within the genus (Rohwer, 1993). Because of their habitat-specific growth forms (tall evergreen trees or stranglers in lowland rainforests; deciduous trees in tropical seasonal forests; shrubs with small-sized leaves dominating riparian vegetation; and on rock surfaces as shrubs, ramblers, or climbers), a particular fig species is a strong indicator of the vegetation type, environment and climate it is associated with (Berg, 1989).

Figs, collectively an old Cretaceous element (Rønsted et al., 2005; Zerega et al., 2005; Xu et al., 2011; Cruaud et al., 2012), are highly diversified and notable for displaying high alpha-diversity in lowland tropical rainforests (Corner, 1958; Berg, 1989; Berg and Corner, 2005; Harrison, 2005). Alpha diversity represents the local richness or diversity within a defined area such as a vegetation quadrat or forest (Birks et al., 2016). In the case of figs, the observed high alpha diversity derives from the exceptional efficiency of active pollination that has enabled figs to occupy rare (micro)-niches (Harrison, 2005). The earliest records of figs, known from the middle Cretaceous, are based on superficial leaf form comparisons and are thus doubtful (Manchester, 2014). More secure identifications show that fig diversity developed conspicuously in the Neogene, specifically in the Miocene and onwards (Figure 1; Appendix S1).

Fossils preserved in sedimentary rocks provide an invaluable record of macro-evolutionary patterns, associated processes, biodiversity, and climate through time. Moreover, climate plays an important role in shaping overall plant diversity over large spatial scales (Forster, 1778;

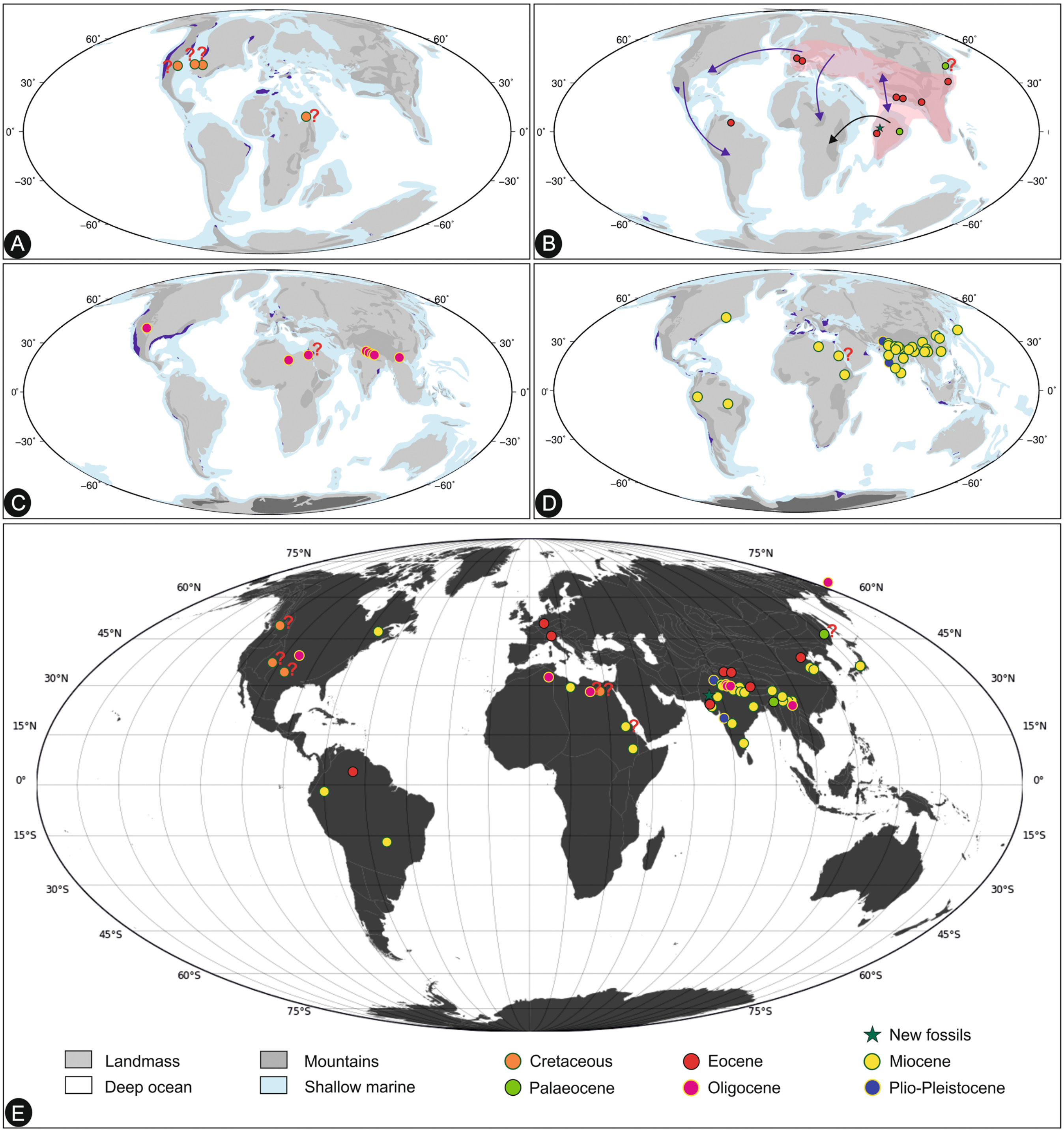

FIGURE 1 Molleweide projection of paleogeographic maps (from Cretaceous to Plio-Pleistocene) showing the fossil records of *Ficus* of different ages: (A) Cretaceous; (B) Paleocene (green dots) and Eocene (red dots) also showing hypothetical ancestral distribution of *Ficus* (pink color, based on the recovered fossil records) along with the hypothetical paleo-dispersal route (for section *Oreosycea*, black arrow and for other subgenera/subsection with blue arrows); (C) Oligocene; (D) Miocene and Plio-Pleistocene; (E) Modern map showing fossil records of *Ficus* documented from Cretaceous to Plio-Plesitocene.

Watson, 1835; Darwin, 1859; Wallace, 1880; Arrhenius, 1921; MacArthur and Wilson, 1967; Hanski, 1999). The early Paleogene was a time when the Indian subcontinent had begun accreting to Asia while continuing northward after being separated from rest of the Gondwanaland continents (Chatterjee and Scotese, 1999), and the fossil record archived in the early Paleogene sediments of the Gurha (Rajasthan) is diverse, rich, and distinctive, and useful for understanding climate-vegetation relationships in deep time (Shukla and Mehrotra, 2018; Shukla et al., 2018). Notably, the vegetation represented by this rich and diverse early Paleogene assemblage is now absent from Rajasthan and restricted to other, more climatologically favorable, areas like the Western Ghats in South India (Prasad et al., 2009).

The present study is based on three new fossil species of *Ficus* from the early Paleogene and deep time occurrences of this genus are particularly valuable for understanding the evolutionary pattern of figs as climate changed through geological time. Here we aim to (1) provide new morphological data to strengthen our understanding of the past occurrences of *Ficus*, (2) achieve a better understanding of the historical biogeography of the pantropical genus *Ficus*, bearing in mind that there is a persistent incongruity between fossil data and existing molecular phylogenetic results, and (3) combine our data with previously known fossils to recognize how climate change has affected this tropical genus.

MATERIALS AND METHODS

The fossil leaves described here were collected from the open cast Gurha lignite mine (East) (27.87398°N, 72.86709°E) situated 22 km northwest of Kolayat in the district of Bikaner (Figure 2A), which lies in the Bikaner-Nagaur Basin of Rajasthan, India. In the Gurha mine, a 38.5 m thick lignite seam (Figure 2B) occurs at a depth of 105 m (Shukla et al., 2014). The mine exposes gray clays, silty clays, sands, lignite, and volcanic ash (Figure 2C). Observed sedimentation began with a significant influx of volcanic ash that is now altered to clay. The lignite forms more or less uniform deposits containing abundant amber and charcoal particles dispersed throughout (Shukla et al., 2014). Lignite-bearing successions occur in an area (70 km long and 30 km wide) associated with the early Paleogene Palana Formation present in the Palana and Kolayat subbasins (Aggarwal et al., 2011; Agnihotri et al., 2020). On the basis of stratigraphic correlation (with the Ranikot beds in Sind, Pakistan), Khosla (1971) and Pareek (1984) assigned the Palana Formation to the Paleocene, and Kulshreshtha et al. (1989) and Kumar et al. (2005) favored a depositional age of ~60 My BP based on recovered palynomorphs and fish fossils. Detailed work on the microbiota of this mine indicates that sedimentation in the mine began in the late Paleocene (light to dark, clay bands) and continued to the early Eocene (light yellow color clay bands) (Figure 2C) (personal communication with Dr. Vandana Prasad, a palynologist at the Birbal Sahni Institute of Palaeosciences [BSIP] in Lucknow, India). The plant fossils described here were collected from light to dark, clay bands overlying the lignite (Figure 2C, D) and thus are assigned here to the late Paleocene to early Eocene.

Many well-preserved fossil leaves, fruits, and insects reported from this mine have been documented by Shukla and Mehrotra (2018). These include leaves of *Aporosa acuminata* (Phyllanthaceae) (Shukla et al., 2016), *Uvaria zeylanica* (Annonaceae) (Shukla and Mehrotra, 2014), *Holigarna grahamii* (Anacardiaceae), *Pterygota alata* (Malvaceae), *Syzygium* spp. (*S. fruticosum* and *S. cumini*) (Myrtaceae), *Gardenia* spp. (*G. lucida* and *G. gummiefra*) (Rubiaceae) (Shukla et al., 2018), and *Dioscorea* sp. (Dioscoreaceae) (Mehrotra and Shukla, 2019). Fruits of *Saraca asoca*, *Cajanus crassus* (Fabaceae) and *Mallotus mollissimus* (Euphorbiaceae) have also been described (Shukla and Mehrotra, 2018) from the Gurha lignite mine. In addition, a fossil of a mayfly nymph that shows similarities with the modern genus *Teloganella* Ulmer of the family Teloganellidae has also been recorded for the first time from this mine (Agnihotri et al., 2020).

The fossil specimens described here were photographed using a Nikon camera P520 (manufactured by NAVTEQ in Chicago, Illinois). Systematic description of the fossil leaves is based on the terminology and nomenclature proposed by Dilcher (1974) and Ellis et al. (2009). The fossil specimens were identified with the help of herbarium sheets available at the Forest Research Institute (FRI), Dehradun, Central National Herbarium (CNH), Howrah and the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/). The type specimens of the described fossil leaves are deposited in the museum of BSIP.

In this study, the occurrence data for three species, i.e., *Ficus auriculata, F. variegata*, and *F. dicranostyla* were extracted from the GBIF database (extracted on July 4, 2021). A total of 118, 289, and 63 occurrence records were downloaded for *F. auriculata, F. variegata*, and *F. dicranostyla*, respectively, from the GBIF portal. Geolocation data based on current biogeographic distributions of *F. auriculata, F. variegata*, and *F. dicranostyla* were marked on Google Earth Pro, and precipitation data (from 1901–2021) were obtained from Climatic Research Unit Timeseries (CRU TSP, Harris et al., 2020) for each species. This precipitation data was plotted using Origin 2019b (OriginLab, software developed by OriginLab Corporation, headquartered in Northampton, Massachusetts, USA) software.

Key leaf morphological characteristics of figs

We studied approximately 430 herbarium sheets (Appendix S2) available at various herbaria (CNH, Howrah; FRI, Dehradun) as well as online (GBIF, https://www.gbif.org/), and noted several distinctive morphological characteristics among the modern leaves

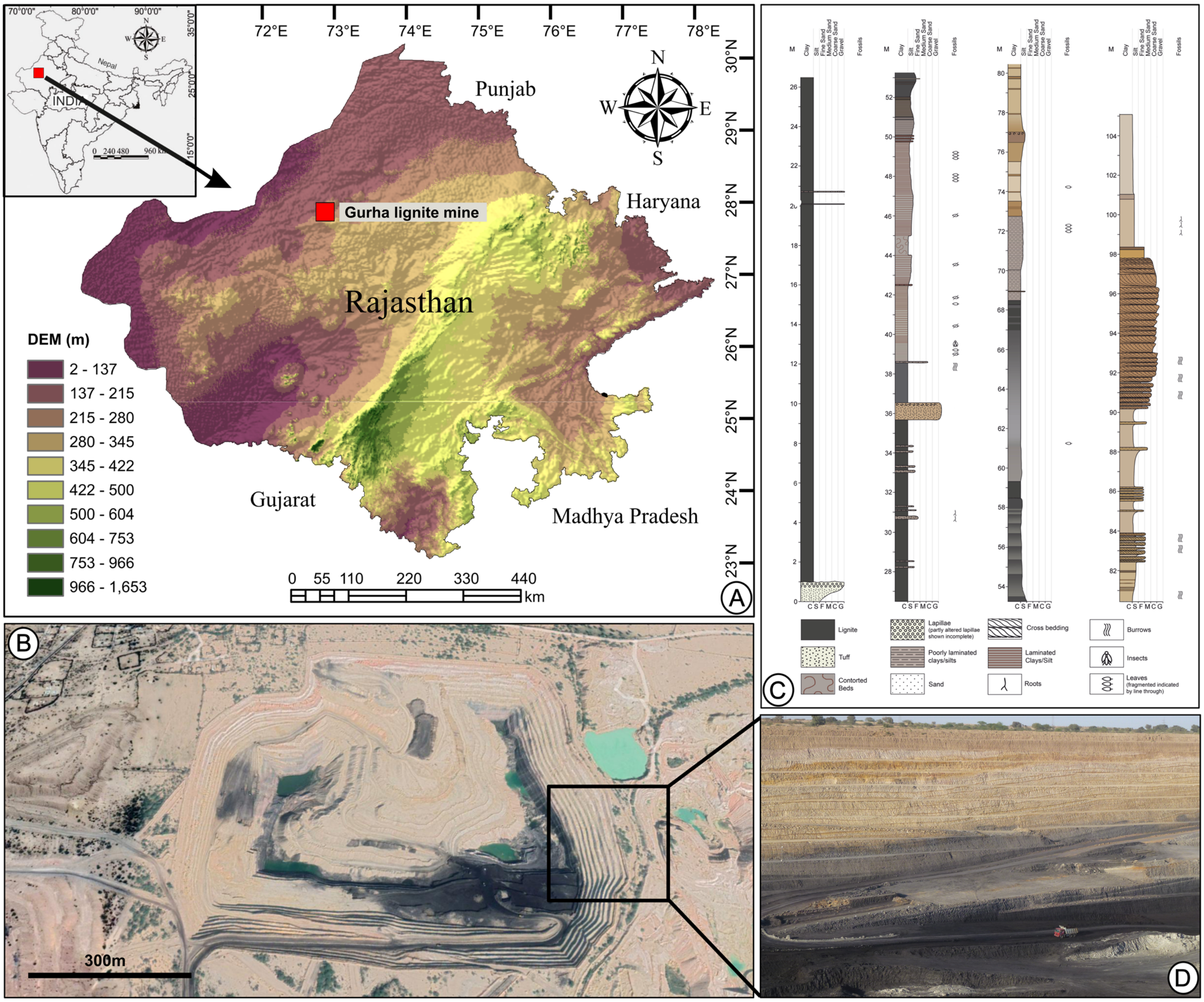

FIGURE 2 (A) Shuttle Radar Topographic Mission (SRTM) is a digital elevation model (DEM) of Rajasthan. The red square shows the location of the Gurha lignite mine (fossil locality). (B) A Google Earth Pro image shows panoramic view of the Gurha lignite mine (C) A detailed lithologic column of the Gurha lignite mine (Shukla et al., 2014) shows the occurrence of plant fossils in the section. (D) An enlarged view shows the detailed litho-stratigraphic sections of mine.

of figs. These include the angle of the basal-most secondaries often being more acute than other secondaries (acute basal secondaries [ABS]; also mentioned by Huang et al., 2018), tertiary veins predominantly percurrent-to-admedially ramified, and quaternaries being dense and irregularly reticulated. Areoles can easily be seen with well-developed free ending venation (FEV) and dichotomous branching. Other features like the basal-most secondaries mostly covering two-thirds of the leaf from the base can be observed among the species of some of the subgenera of *Ficus*. Representative morphological features usually dominant among the species of the subgenera of *Ficus*, i.e., *Pharmacosycea*, *Sycomorus*, *Sycidium*, *Ficus*, *Synoecia*, and *Urostigma* are tabulated (Table 1).

SYSTEMATICS

Order—Rosales

Family—Moraceae

Genus—*Ficus* Tourn. ex. L.

Subgeneus—*Sycomorus*

Section—*Sycomorus*

Species—*Ficus paleoauriculata* Chandra et al., sp. nov. (Figures 3, 4)

Specific diagnosis—Leaf unlobed, asymmetrical in medial symmetry, tooth with second order, pinnate, semicraspedodromous secondaries, <10 pairs; first pair of major secondaries covering two-thirds of the leaf from the base; tertiary vein percurrent; quaternaries densely irregularly reticulated, FEV well developed showing dichotomous branching.

TABLE 1 Comparison among the subgenera of *Ficus* based on morphological characters.

Subgenera	Section	Texture	Shape	Venation	Symmetry	Margin	Agrophic veins	Pairs of 2°	2° spacing	2° angle	Inter-2°	3°	ABS upto Two-third of lamina from Base
Pharmacosycea	*Pharmacosycea*	Char., Cor.	Elliptic	Brochido., EBB.	Sym.	Entire	Absent, Present	>10 (14-22)	Regular, AIP	70°–80° ABS	Prom.	Reti., Per.	Absent
	Oreosycea	Char.	Elliptic, Ovate	Brochido.	Asym., Sym.	Entire	Present, Absent	>8 (8-14)	Irregular	60°–80° ABS	Ab., Prom.	Per.	Absent
Sycomorus	*Sycomorus*	Char., Cor.	Ovate, Obovate, Elliptic	Semicras., Brochido.	Asym., Sym.	Tooth (One, Two order), Entire	Present	<10 (6-9)	AIP, Regular	40°–70°, ABS	Ab.	Per.	Present
	Hemicardia	Char.	Ovate, Elliptic	EBB., Semicras.	Sym., Asym.	Entire, Tooth (One order)	Present, Absent	<10 (5-9)	GIP	50°–70°	Ab.	Per.	Absent
	Adenosperma	Char.	Elliptic	Brochido., EBB.	Sym.	Entire	Present, Absent	>10 (11-14)	AIP, Regular	70°–80°, ABS	Prom.	Per.	Absent
	Bosscheria	Char.	Ovate	Semicras.	Sym.	Entire, Tooth (One order)	Present	>10 (10-12)	AIP	70°–80°, ABS	Ab.	Per.	Present
	Dammaropsis	Char.	Ovate, Obovate, Elliptic	EBB., Brochido.	Sym.	Entire	Absent, Present	>10 (14-20)	Regular, AIP	60°–80°	Prom.	Per.	Absent
	Papuasyce	Char.	Elliptic	Brochido.	Sym.	Entire	Absent	>10 (10-12)	AIP, ADP	70°–90°, ABS	Prom.	Per.	Absent
	Sycocarpus	Char.	Elliptic, Ovate	Semicras., Eucamp., EBB., Brochido	Sym., Asym.	Tooth (One order), Entire	Present, Absent	>10 (10-12)	Irregular, GDP, ADP, AIP	50°–60°	Prom.	Per.	Absent
Urostigma	*Americana*	Char., Cor.	Obovate, Elliptic, Ovate	Brochido.	Sym., Asym.	Entire	Absent, Present	>10 (10-18)	Regular, ADP, GIP, GDP, AIP	60°–80°, ABS	Prom.	Per., Reti.	Absent
	Urostigma	Char.	Obovate, Elliptic, Ovate	Brochido.	Sym.	Entire	Absent, Present	≤10 (9-10)	Irregular, AIP, ADP	70°–80°, ABS	Prom.	Per., Reti.	Absent
	Malvanthera	Char.	Elliptic, Ovate	Brochido., EBB	Sym.	Entire	Absent	>10 (15-22)	GIP, AIP	70°–80°, ABS	Prom.	Ram., Reti.	Absent
	Galoglychia	Char.	Elliptic, Obovate, Ovate	Brochido.	Sym.	Entire	Absent, Present	>7 (7-13)	ADP, AIP, GDP	60°–80°, ABS	Prom.	Ram., Reti., Per.	Absent

(Continues)

TABLE 1 (Continued)

Subgenera	Section	Texture	Shape	Venation	Symmetry	Margin	Agrophic veins	Pairs of 2°	2° spacing	2° angle	Inter-2°	3°	ABS upto Two-third of lamina from Base
Sycidium	*Sycidium*	Char.	Elliptic, Ovate	Semicras., Brochido., EBB.	Asym., Sym.	Tooth (One, Two, Three order), Entire	Present	<7	AIP	60°–70° ABS	Absent, Present	Per.	Present
	Palaeomorphe	Char.	Ovate, Elliptic	Eucamp., EBB., Brochido., Semicras.	Sym., Asym.	Entire, Tooth (One order)	Absent, Present	>7	ADP, AIP, Irregular	80°–90° ABS	Present	Per., Reti.	Present
Synoecia	*Rhizocladus*	Char.	Ovate, Elliptic	Eucamp., EBB., Brochido.	Sym.	Entire	Present, Absent	<7	GIP, AIP	50°–60°, ABS	Present	Per., Reti.	Absent
	Kissosycea	Char.	Elliptic, Ovate	EBB., Brochido.	Sym.	Entire	Present, Absent	<7	AIP, ADP	50°–60°, ABS	Present	Per.	Absent
Ficus	*Ficus*	Char.	Ovate, Elliptic, Obovate	Eucamp., Brochido.	Sym.	Entire, Tooth (One order)	Absent, Present	<7	GIP, Irregular, AIP	50°–60°, ABS	Present, Absent	Per., Reti.	Present
	Eriosycea	Char., Cor.	Ovate, Elliptic, Lobed	Eucamp., Brochido., Semicras.	Sym.	Tooth (One order), Entire	Present, Absent	<10	GIP, AIP	50°–60°, ABS	Present, Absent	Per.	Present

Cor. = Coriaceous; Char. = Chartaceous; Sym. = Symmetric; Asym. = Asymmetric; AIP = Secondaries spacing Abruptly Increasing Proximally; ADP = Secondaries spacing Abruptly decreasing Proximally; GIP = Secondaries spacing Gradually Increasing Proximally; GDP = Secondaries spacing Gradually Decreasing Proximally; ABS = with one pair of Acute Basal Secondaries; EBB = Eucamptodromous venation becoming brochidodromous; Brochido. = Brochidodromous; Semicras. = Semicraspedodromous; Eucamp. = Eucamptodromous; Per. = Percurrent; Ram. = Ramified; Reti. = Reticulate; Ab. = Absent; Prom. = Prominent.

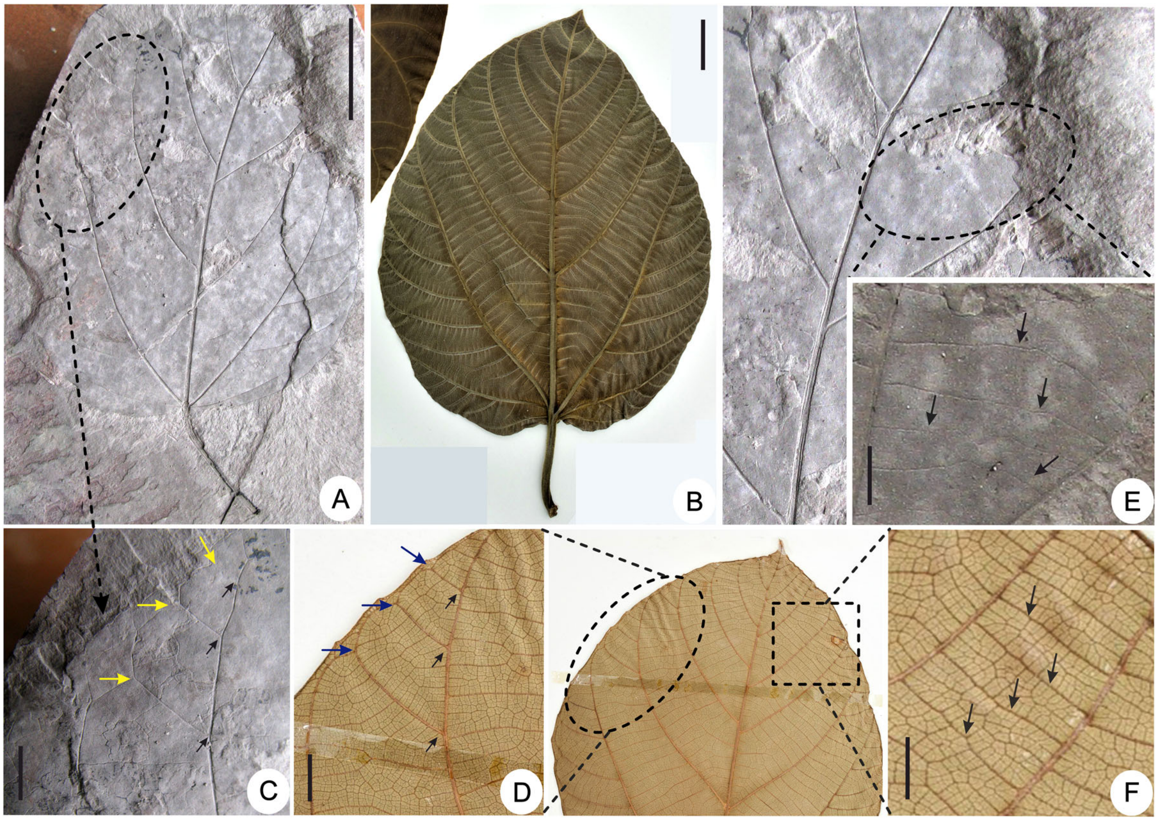

FIGURE 3 (A) A fossil leaf of *Ficus paleoauriculata* Chandra et al., sp. nov., shows the shape size, and venation pattern (specimen no. BSIP No. 42246). (B) A modern leaf of *Ficus auriculata* shows a similar shape, size, and venation pattern as in the fossil (voucher no. USCH0039189). (C) An enlarged portion of the fossil leaf, *Ficus paleoauriculata*, shows semicraspedodromous venation (yellow arrows) with loops near the margin and major secondaries joining superadjacent secondaries at acute angles, shown by black arrows. (D) An enlarged portion of the modern species, *Ficus auriculata* (voucher no. NYBG02512746) shows similar semicraspedodromous venation (blue arrows) with loops near the margin and major secondaries joining superadjacent secondaries at an acute angle (black arrows). (E) A fossil leaf shows percurrent tertiaries (black arrows). (F) A modern leaf of *Ficus auriculata* (voucher no. NYBG02512746) shows similar percurrent tertiaries (black arrow). The scale bar represents 2 cm (A, B); 1 cm for (D); 0.5 cm for (C, G); 0.25 cm for (E).

Holotype—BSIP No. 42246 (Figures 3, 4)

Etymology— The name of the fossil species is based on its modern analog.

Description—Leaf asymmetrical in medial symmetry (broader part 3.4 cm, narrower part 2.8 cm), ovate in shape (Figure 3A), length 9.8 cm up to the broken apex, 6.2 cm wide in the middle portion of the leaf, length-width (L/W) ratio 1.5:1, mesophyll; apex broken, seemingly acute when extended; base obtuse, slightly cordate (Figure 4E); unlobed; petiole attachment marginal, 1.6 mm in thickness, 2.5 cm in length; texture possibly chartaceous; margin toothed (Figure 4C), unlobed; primary vein markedly curved, moderate, 7.3 cm in length, 1.1 mm in thickness, pinnate; first pair of secondaries more acute, extending up to two-thirds of the leaf from the base, opposite to alternate, 0.3–0.6 mm thick, spacing abruptly increasing proximally, semicraspedodromous (Figure 3C), joining superadjacent secondary at acute angle (Figure 3C), decurrent on the primary vein, the angle of divergence acute (37°–63°); intersecondaries absent; minor secondary veins semicraspedodromous; agrophic veins present, simple (Figure 4A); margin toothed, serrate, irregular, order of teeth two (second), sinus shape angular to rounded, straight/straight (st/st), concave/flexuous (cc/fl) (Figure 4C), principal vein present, termination marginal, at the apex of tooth; tertiary veins percurrent (Figure 3E), opposite, sinuous, convex, mostly simple, straight, rarely forked, angle to midvein perpendicular to widely acute, close, angle variability increasing exmedially, angle of origin obtuse-obtuse (OO), acute-right (AR), right-right (RR), epimedial tertiary present, alternate percurrent, perpendicular to wide acute to the midvein; quaternary veins, reticulate, irregular, areoles developed (Figure 4G) showing dichotomous branching.

Leaf identification and comparison

The notable morphological characteristics of the fossil leaf such as its ovate shape, serrate margin, slightly cordate base, pinnate venation, the first pair of major secondaries being more acute, extending to serve a two-thirds portion of leaf together with percurrent tertiary veins suggest its similarity to the modern genera of the following families: Asteraceae

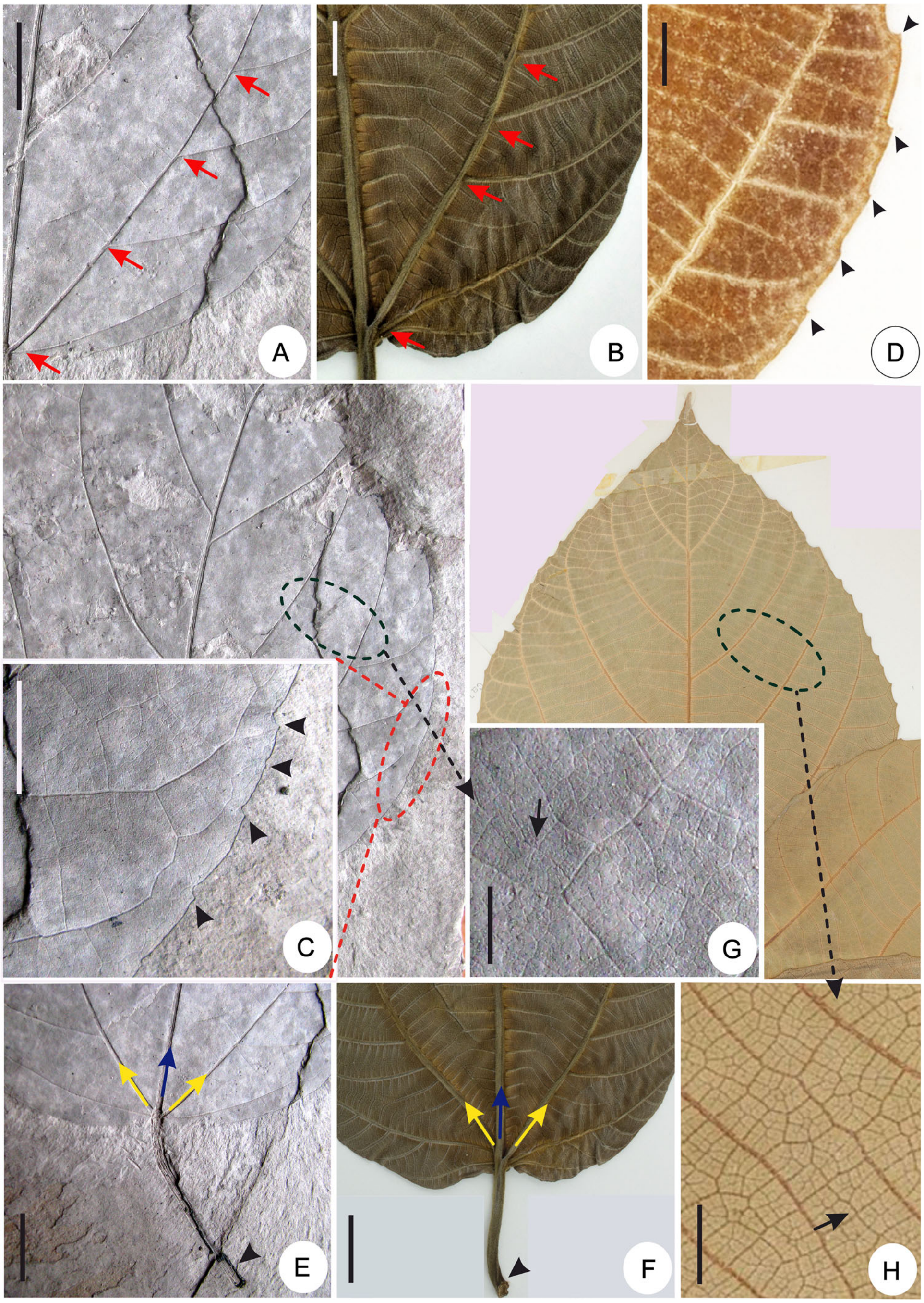

FIGURE 4 (A) An enlarged portion of the fossil, *Ficus paleoauriculata* Chandra et al., sp. nov., shows the angle of origin of major secondaries (red arrows) (specimen no. BSIP No. 42246). (B) An enlarged portion of the modern species, *Ficus auriculata* (voucher no. USCH0039189) shows similar angles of origin of major secondaries (red arrows) as seen in the fossil. (C) This fossil leaf shows a serrated margin with second order teeth marked with black arrows. (D) A modern leaf shows a similar serrated margin with second order teeth marked with black arrows, as seen in the fossil (voucher no. NYBG01368338). (E) The basal portion of the fossil leaf shows the slightly cordate base and angles of origin of the secondaries (yellow arrows) from the primary vein (blue arrow). (F) The basal portion of a modern leaf (voucher no. USCH0039189), shows a similar slightly cordate base and angles of origin of secondaries (yellow arrows) from the primary vein (blue arrow), as in the fossil. (G) A portion of the fossil leaf shows preserved areoles. (H) A portion of the modern leaf shows similar preserved areoles (voucher no. NYBG02512744). Scale bar represents 1 cm (A, B, E); 2 cm for (F); 0.5 cm for (C, D, H); 0.25 cm for (G).

(*Ageratum* L.), Euphorbiaceae (*Tragia* Plum. ex L.), Lamiaceae (*Leonotis* (Pers.) R.Br.), Malvaceae (*Eriolaena* DC., *Grewia* L., *Hibiscus* L.), Moraceae (*Morus* L., *Fatoua* Gaudich., *Broussonetia* L'Hér. ex Vent., *Ficus* Tourn. ex L.), and Verbenaceae (*Lantana* L.). The modern leaves of the malvaceous genera, i.e., *Eriolaena, Grewia*, and *Hibiscus* can easily be differentiated by the presence of a symmetrical lamina and a prominent cordate base with a basal extension in *Eriolaena*, whereas *Grewia* and *Hibiscus* have compound agrophic veins and all these features are absent in the fossil leaf. Furthermore, *Tragia* (Euphorbiaceae) can be ruled out by having third-order teeth and *Lantana* (Verbenaceae) and *Broussonetia* (Moraceae) have only simple teeth (first order) as compared to second-order teeth in the present fossil. Extant leaves of *Ageratum* (Euphorbiaceae) and *Leonotis* (Lamiaceae) do not possess a cordate base as found in the fossil. Further comparison has been made with *Morus*, *Fatoua*, and *Ficus* of the family Moraceae, which show some features similar to our fossil leaf but the presence of a naked basal vein in *Morus* and *Fatoua* differentiate them from the fossil. As a result, the extant species of *Ficus* share more of the characteristic features seen in our fossil, therefore, a thorough comparison was carried out with its six subgenera: *Pharmacosycea*, *Sycomorus*, *Sycidium*, *Ficus*, *Synoecia*, and *Urostigma* (Table 1). Among all the subgenera, species of *Sycomorus*, *Sycidium*, and *Ficus* embrace peculiar characters such as the presence of ABS covering two-thirds of the lamina from the base, as seen in our fossil, therefore, the present fossil leaf was compared to modern leaves of these subgenera.

Firstly, we have compared our fossil leaf with various species of the subgenus *Ficus*. Modern leaves of *F. carica* L., *F. abelii* Miq., *F. iidaiana* Wilson, *F. pustulata* Elm., *F. bruneiensis* Corner, *F. brunneoaurata* Corner, and *F. trivia* Corner can easily be differentiated in having entire margin as compared to the tooth margin in the fossil. Presence of toothed margins in extant leaves of *F. tikoua* Bureau, *F. androchaete* Corner, *F. aurata* (Miq.) Miq., *F. aureocordata* Corner, *F. auricoma* Corner ex C.C. Berg, *F. endospermifolia* Corner, *F. eumorpha* Corner, *F. inaequipetiolata* Merr., *F. setiflora* Stapf, *F. hirta* Vahl, *F. subglabritepala* C.C. Berg, and *F. paramorpha* Corner indicate some similarity to our fossil leaf. However, *F. androchaete*, *F. tikoua*, and *F. aureocordata* differ in having simple teeth, while *F. aurata, F. auricoma, F. endospermifolia*, *F. eumorpha, F. inaequipetiolata, F. hirta*, and *F. paramorpha* have first-order teeth with regular spacing and this is markedly different from the second-order teeth with irregular spacing seen in the fossil leaf. Although *F. subglabritepala* and *F. setiflora* have second-order teeth similar to those of our fossil, they differ in having regular spacing and shorter distances between the teeth. *Ficus carica* is distinct in having a lobed lamina.

The extant species within the subgenus *Sycidium*, i.e., *Ficus complexa* Corner, *F. cyrtophylla* Miquel, *F. elmeri* Merrill, *F. bojeri* Baker, and *F. lateriflora* Vahl, possess ABS covering up to two-thirds of the lamina from the base and toothed margins as found in our fossil, but *F. complexa* and *F. elmeri* have first-order teeth and the spacing between the teeth is predominantly regular, unlike the fossil. Although second-order teeth are seen in some modern leaves of *F. cyrtophylla, F. bojeri*, and *F. lateriflora* similar to our fossil, they differ because of the presence of intersecondaries, regular teeth spacing and their predominantly convex/convex (cv/cv) tooth shapes.

A detailed comparison has been carried out among the species of subgenus *Sycomorous*, namely *Ficus mauritiana* Lam., *F. mucuso* Ficalho, *F. sycomorus* Linnaeus, *F. torrentium* Perrier, *F. trichoclada* Baker, *F. vallis-choudae* Delile., *F. vogeliana* (Miq.) Miq., *F. auriculata* Loureiro, *F. hainanensis* Merrill and Chun, *F. nodosa* Teijsmann and Binnendijk, *F. robusta* Corner, *F. semivestita* Corner, *F. variegata* Blume, *F. minahassae* Teijsmann and De Vriese, *F. pungens* Blume, *F. karthalensis* C.C. Berg, *F. polyphlebia* Baker, *F. sakalavarum* Baker, *F. sur* Forsk, and *F. racemosa* Linnaeus. However, *F. karthalensis, F. polyphlebia*, *F. sakalavarum*, *F. sur*, and *F. racemosa* have entire and wavy margins, while *F. robusta* lacks a toothed margin in contrast to the fossil. The presence of second-order teeth with irregular spacing in modern leaves of *F. semivestita, F. nodosa*, and *F. trichoclada* indicates some similarity with our fossil, yet these species differ in having wide angles of divergence in secondaries and larger teeth. The extant leaves of *F. mauritiana* have crenate teeth, whereas *F. mucuso* differs in having spine teeth and a difference in secondaries curvature. *Ficus vallis-choudae* and *F. torrentium* have only simple teeth, while *F. sycomorus* and *F. vogeliana* have irregular second-order teeth but *F. sycomorus* can be differentiated in having intersecondaries and predominantly cv/cv teeth shapes, whereas *F. vogeliana* is elliptical in shape as compared to the ovate shape of our fossil. Detailed comparisons indicate that the present fossil leaf, *F. paleoauriculata*, shows close affinity to the modern species *F. auriculata* in lamina shape and size, including venation structure and curvature of the secondaries, ABS approaching a two-thirds portion of the lamina from base, and second-order teeth prominently with st/st, cc/fl shapes. However, a few extant leaves of *F. auriculata*, have concave/convex (cc/cv) teeth shape, which is a feature not seen in the present fossil.

Subgeneus—*Sycomorus*

Section—*Sycomorus*

Species—*Ficus paleovariegata* Chandra et al., sp. nov.

Etymology—The name of the fossil species is based on its modern analog.

Specific diagnosis—Leaf unlobed, asymmetrical in medial symmetry; pinnate, simple brochidodromous secondaries, <10 pairs, first pair major secondaries covering two-thirds of the leaf from the base; tertiary veins percurrent; quaternaries densely irregular reticulated, FEV well developed showing dichotomous branching.

Holotype—BSIP No. 42247 (Figures 5, 6)

Description—Leaf complete, asymmetrical in medial symmetry (width of the broader part 4.4 cm, width of the narrower part 4 cm), wide elliptic in shape, length 12 cm, 8.4 cm wide in the middle portion of leaf (Figure 5A), L/W ratio 1.5:1, mesophyll; apex nearly preserved, seemingly acute when extended; lamina asymmetrical in basal symmetry, basal width asymmetrical, obtuse, rounded; lamina unlobed; petiole attachment marginal, 3 mm in width; texture possibly chartaceous; margin entire, erose, unlobed; primary vein markedly curved (Figure 6A), monopodial, stout, 12 cm in length, thickness 3.1 mm, pinnate (Figure 5A); major secondaries first pair covering

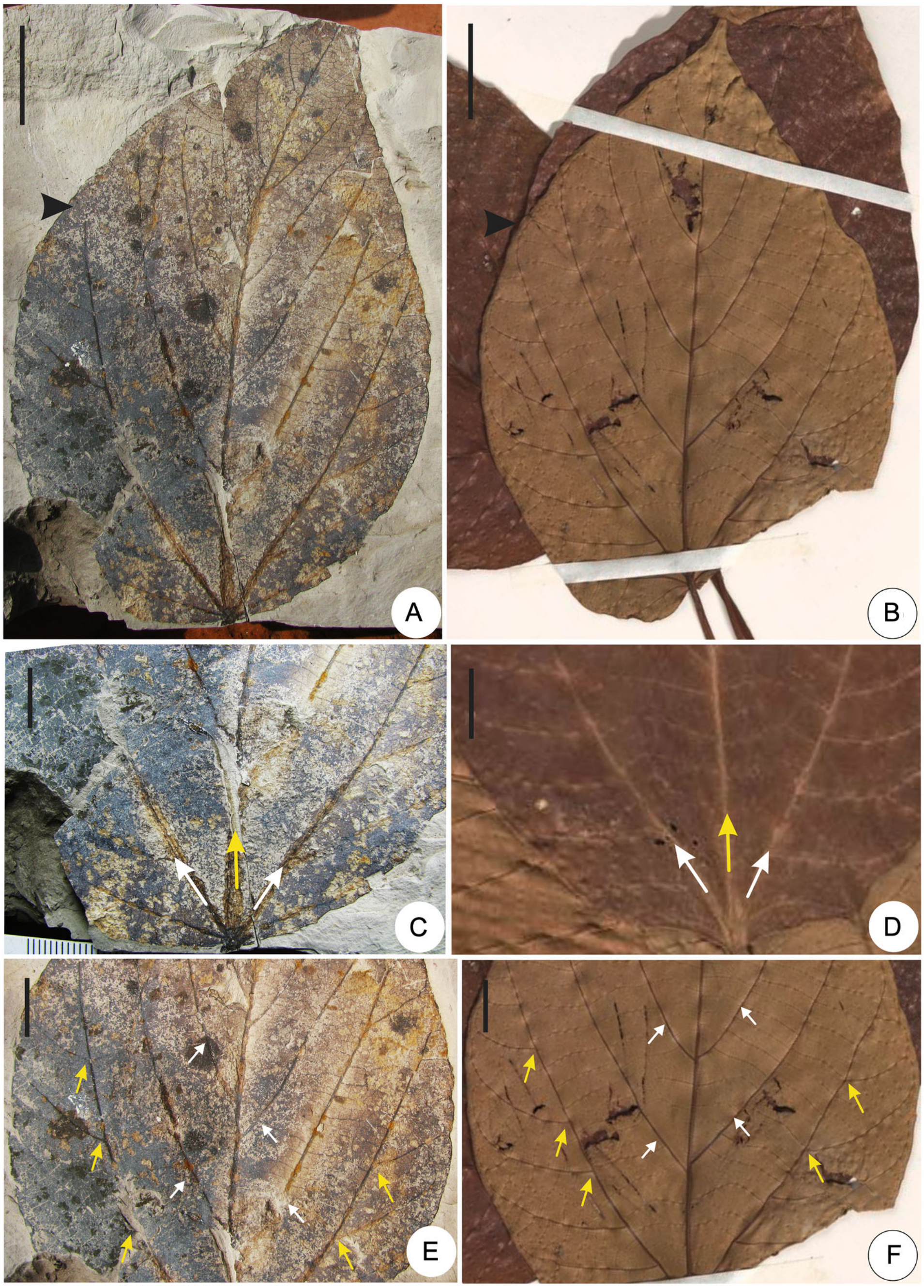

FIGURE 5 (A) A fossil leaf of *Ficus paleovariegata* Chandra et al., sp. nov., shows the shape, size, and venation pattern (specimen no. BSIP No. 42247). (B) A modern leaf of *Ficus variegata* shows a similar shape, size and venation pattern as in the fossil (voucher no. L.1617987). (C) An enlarged basal portion of the fossil leaf shows the angle of origin of the first pair of major secondaries (white arrows) from the primary vein (yellow arrow). (D) An enlarged basal portion of a modern leaf shows a similar angle of origin of the first pair of major secondaries (white arrows) from the primary vein (yellow arrow) (voucher no. L.1617987). (E) A fossil leaf shows the origin and angles of major secondaries (white arrows) and minor secondaries along with brochidodromous venation (yellow arrows). (F) A modern leaf (voucher no. L.1617987) shows a similar origin and angles of major secondaries (white arrows) and minor secondaries, along with brochidodromous venation (yellow arrows). The scale bar represents 2 cm for (A, B); 1 cm for (C–F).

two-thirds of the leaf from the base (Figure 5A), eight pairs present 1.5–0.3 mm thick, mostly alternate, opposite, spacing irregular, simple brochidodromous (loops of secondary veins approaching the margin, Figure 6E), joining superadjacent secondary at acute angle, excurrent on the primary vein; angle to midvein inconsistent, angle of divergence acute (30°–65°); intersecondary veins absent; minor secondary vein simple brochidodromous; agrophic veins present, simple (Figure 5E); tertiary veins percurrent (Figure 6C), opposite, sinuous, mostly simple, straight, recurved, rarely forked, angle to midvein perpendicular to widely acute, close, angle variability increasing exmedially,

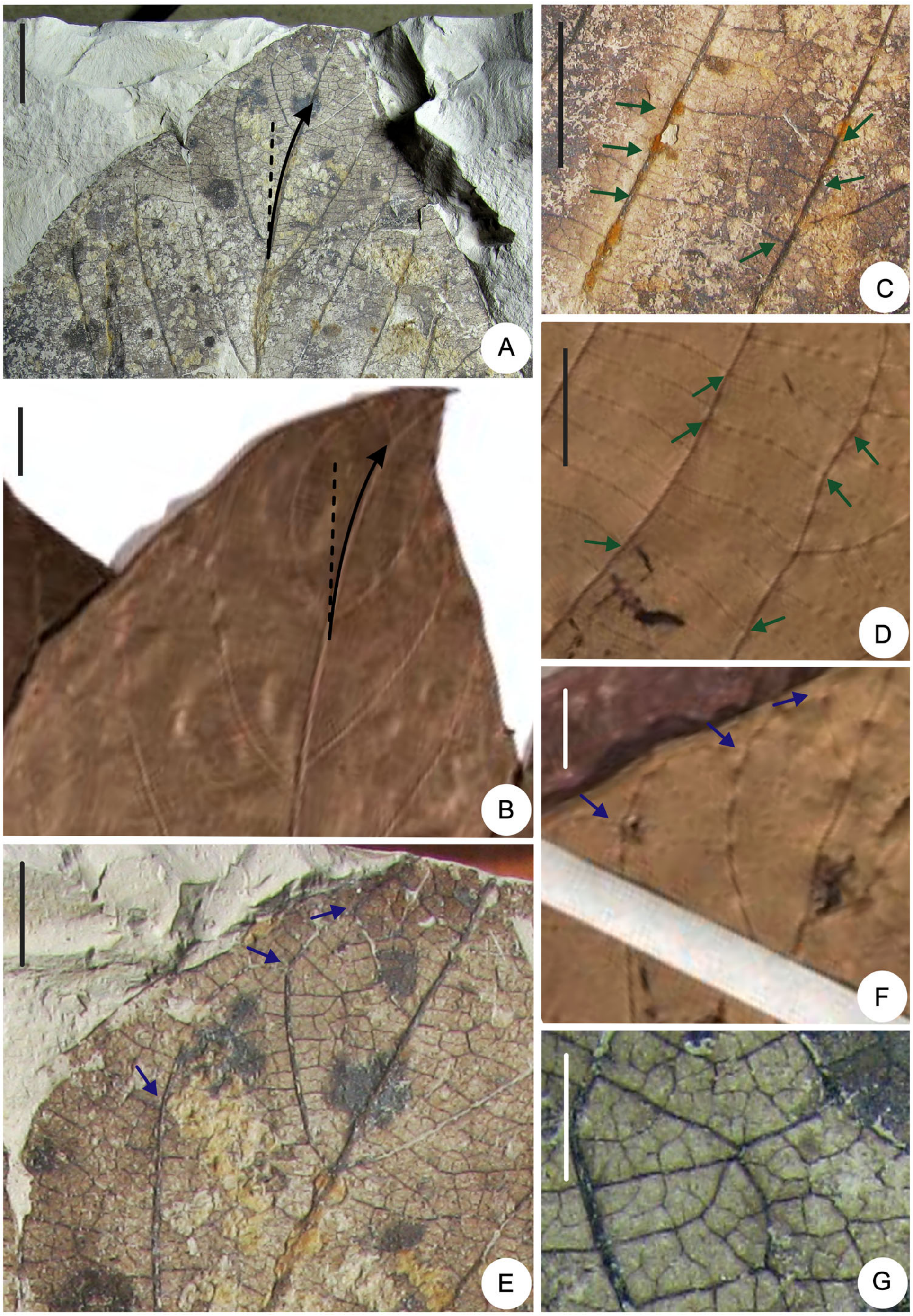

FIGURE 6 (A) A portion of the fossil leaf, *Ficus paleovariegata* Chandra et al., sp. nov., shows the curved primary vein (black arrow) near the apex. (B) A portion of a modern leaf of *Ficus variegata* shows a similar curved primary vein (black arrow) near the apex (voucher no. L0735108). (C) An enlarged portion of the fossil leaf shows percurrent tertiaries (green arrows). (D) An enlarged portion of the modern leaf of *Ficus variegata* (voucher no. L0735108) shows similar percurrent tertiaries (green arrows). (E) An enlarged portion of the fossil leaf, *Ficus paleovariegata*, shows the brochidodromous venation (blue arrows). (F) An enlarged portion of the modern species, *Ficus variegata* (voucher no. L0735108) shows a similar brochidodromous venation (blue arrows) as shown in the fossil. (G) A portion of the fossil leaf shows the preserved areoles. The scale bar represents 1 cm for (A); 0.5 cm for (B–F); 0.25 cm for (G).

angle of origin obtuse-acute (OA), acute-right (AR), right-obtuse (RO), right-right (RR), epimedial tertiary present, opposite percurrent, perpendicular to midvein; quaternary veins, reticulate, irregular; areoles present (Figure 6G), FEVwell developed showing dichotomous branching.

Leaf identification and comparison

The characteristic feature of our fossil is that the first pair of major secondaries are more acute than the others, which indicates its similarity to only a limited number of plant genera, namely *Ageratum* L. (Asteraceae), *Tragia* Plum. ex L., *Mallotus* Lour. (Euphorbiaceae), *Leonotis* (Pers.) R.Br. (Lamiaceae), *Eriolaena* DC., *Grewia* L., *Hibiscus* L. (Malvaceae), *Morus* L., *Fatoua* Gaudich., *Broussonetia* L'Hér. ex Vent., *Ficus* Tourn. ex L., *Artocarpus* Forst. and Forst. (Moraceae), *Lantana* L. (Verbenaceae), and *Ocotea* (Lauraceae). All these genera, except for a few species of *Artocarpus, Ficus*, *Ocotea*, *Mallotus*, and *Hibiscus* can be easily differentiated from our fossil in that they have serrate margins as compared to the entire margin present in the fossil. The modern species of *Artocarpus* differs in lacking basal secondaries that extend to the apical two-thirds portion of the leaf. In addition, the presence of a symmetrical lamina and intersecondaries in extant leaves of *Ocotea* (Lauraceae) rules out the genus as a possible relative of our fossil. Though *Mallotus* has ABS extending apically up to two-thirds of the leaf, it differs in having 5–6 pairs of major secondaries with wider angles of divergence. Further comparison was carried out among the six subgenera of *Ficus* (Moraceae), namely *Pharmacosycea*, *Sycomorus*, *Sycidium*, *Ficus*, *Synoecia*, and *Urostigma*. However, the more acute first pair of major secondaries, reaching up to the apical two-thirds of the lamina and high density of secondaries, as found in our fossil species, are commonly seen only among the extant species of the subgenera *Sycomorus, Sycidium*, and *Ficus*.

A detailed comparison was made, therefore, with various species of the subgenus *Ficus*: *F. iidaiana, F. pyriformis, F. pustulata, F. trivia, F. bruneiensis, F. brunneoaurata, F. androchaete*, and *F. padana* Burm. The extant leaves of *F. pyriformis* and *F. trivia* differ in having intersecondaries and reticulate tertiary veins, while the spacing between the angles of the secondary veins gradually increases basally in *F. iidaiana* and *F. padana*. The modern leaves of *F. bruneiensis, F. brunneoaurata*, and *F. androchaete* are very similar to our fossil, but they can be differentiated in having fewer secondary veins than seen in our fossil, while *F. pustulata* differs in having a narrow elliptic lamina. A thorough examination within the species of the subgenus *Sycidium* reveals that they differ in having wider angles of divergence of their major secondaries.

Leaves of the subgenus *Sycomorus* were examined thoroughly to assess their similarity to our fossil. *Sycomorus* has two subsections; one of them named *Neomorphe* was identified having the most characters similar to those of our fossil. Among the six species of *Ficus* within subsection *Neomorphe*, the modern leaves of *F. auriculata* and *F. semivestita* differ in having serrated margins, while the attachment of major secondaries to the primary vein is deflected in *F. robusta* as compared to excurrent form in the present fossil. Moreover, the secondaries do not reach more than two-thirds along the lamina in *F. nodosa* and *F. semivestita*, as in the fossil. A detailed comparison shows that *F. variegata* encompasses most of the diagnostic morphological characters, namely lamina shape, size, and secondary architecture, similar to those of the present fossil. However, subalternate-to-alternate origins of major secondaries are seen in some modern leaves of *F. variegata*, in contrast to alternate in our fossil.

Subgenus—*Pharmacosycea*

Subsection—*Oreosycea*

Type species—*Ficus paleodicranostyla* Chandra et al., sp. nov.

Specific diagnosis—Leaf unlobed, pinnate; simple brochidodromous secondaries, <10 pairs, angle of the basal most secondaries more acute than other secondaries; tertiary veins percurrent; quaternaries densely irregular reticulated, FEV well developed showing dichotomous branching.

Specific epithet—The name of the fossil species is based on its modern analog.

Repository—Birbal Sahni Institute of Palaeosciences, Lucknow, India

Holotype—BSIP No. 42248 (Figures 7, 8)

Locality—Gurha lignite mine, Bikaner, Rajasthan, India

Horizon and age—Palana Formation, late Paleocene-early Eocene

Description—Leaf medial and basal asymmetry present, narrow ovate in shape (Figure 7A), length 6.8 cm up to the apex, 3.4 cm wide in middle portion of leaf, L/W ratio 2:1, microphyll; apex seemingly acute when extended; base seemingly obtuse, convex; petiole not preserved; texture possibly chartaceous; lamina unlobed; margin entire, sinuous, primary vein 6.8 cm in length, thickness 0.7 mm, pinnate; major secondaries 9 on left and 8 on right half (Figure 7A), 0.2 mm thick, alternate to opposite, simple brochidodromous (loops of secondary vein approaching the margin), spacing irregular, joining super-adjacent secondary at an obtuse angle, excurrent on the primary vein, basalmost secondary more acute than other secondaries; intersecondary veins absent; minor secondary veins simple brochidodromous (Figure 8A, E); agrophic vein present, simple (Figure 7A); tertiary veins percurrent (Figure 8C), mostly opposite, straight, recurved, concave, mostly simple, rarely forked, angle to midvein perpendicular to obtuse, close, angle variability increasing exmedially, angle of origin AR, RR, RO, epimedial tertiary vein present, mostly alternate to opposite percurrent (Figure 8C), proximal course to midvein mostly perpendicular, obtuse, acute; quaternary veins present, irregular reticulate; areoles present (Figure 8G), FEV well developed showing dichotomous branching.

Leaf identification and comparison

The presence of morphological features, such as an ovate shape and simple brochidodromous venation with densely reticulated higher order veins in our fossil species, indicate its similarity to genera within the families Lauraceae, Sapindaceae, and Moraceae. Some characteristic leaf morphology such as hemi-eucamptodromous secondary veins, weakly developed FEV and even sometimes undeveloped quaternaries (Huang et al., 2018) feature

FIGURE 7 (A) A fossil leaf of *Ficus paleodicranostyla* Chandra et al., sp. nov. (specimen no. BSIP no. 42248) shows the shape, size, and venation pattern (B) A modern leaf of *Ficus dicranostyla* (voucher no. BR0000017476447) shows a similar shape, size, and venation pattern as in the fossil. The scale bar represents 1 cm (A) and 0.5 cm (B).

among most of the genera of Lauraceae and these differentiate the family from our fossil, which has simple brochidodromous and well-developed FEV showing dichotomous branching. However, a few genera such as *Neolitsea, Ocotea*, and *Laurus* of the Lauraceae do show some similarities to our fossil but can be separated in that they have different origins of the major secondaries (narrow acute angle) in *Neolitsea*, the presence of intersecondaries in *Ocotea*, and an absence of acute basal secondary veins in *Laurus*. In the modern genus *Acer* (Sapindaceae) FEVs are simple and single branched as compared to dichotomous branching in the fossil, so it differs from the present fossil. In *Artocarpus* (Moraceae), major secondaries terminate in loops at a distance from the margin, which along with the presence of intersecondaries in the modern leaves, differentiates it from the fossil, which has major secondaries looping close to the margin and lacks intersecondaries.

The cumulative leaf architecture of our fossil indicates its similarities to several fig species, so to assign a nearest living relative to our fossil we have examined the six subgenera of *Ficus*, i.e., *Pharmacosycea*, *Sycomorus*, *Sycidium*, *Ficus*, *Synoecia*, and *Urostigma*, emphasizing the presence of certain key phenotypic features that are usually dominant among the species of these subgenera (Table 1). The subgenus *Pharmacosycea* section *Oreosycea* was identified encompassing all the shared morphological features most similar to those of our fossil, while the other section, *Pharmacosycea*, differs by having more than 10 pairs of regularly spaced secondaries.

Oreosycea is categorized into two subsections *Glandulosae* and *Pedunculatae*. An absence of agrophic veins and asymmetry found among the species of subsection *Glandulosae* rule out a close relationship with our present fossil, whereas *Pedunculatae* shares most of the morphological characters. A detailed comparison has also been carried out among the phylogenetically similar Afrotropical species of the subsection *Pedunculatae*, which is composed of four species. The extant leaves of *Ficus ampana* Berg show similarities in shape, but the presence of intersecondaries and lack of an agrophic vein differentiates it from our fossil leaf. *Ficus assimilis* Baker and *Ficus variifolia* Warb differ in having intersecondary veins. A thorough

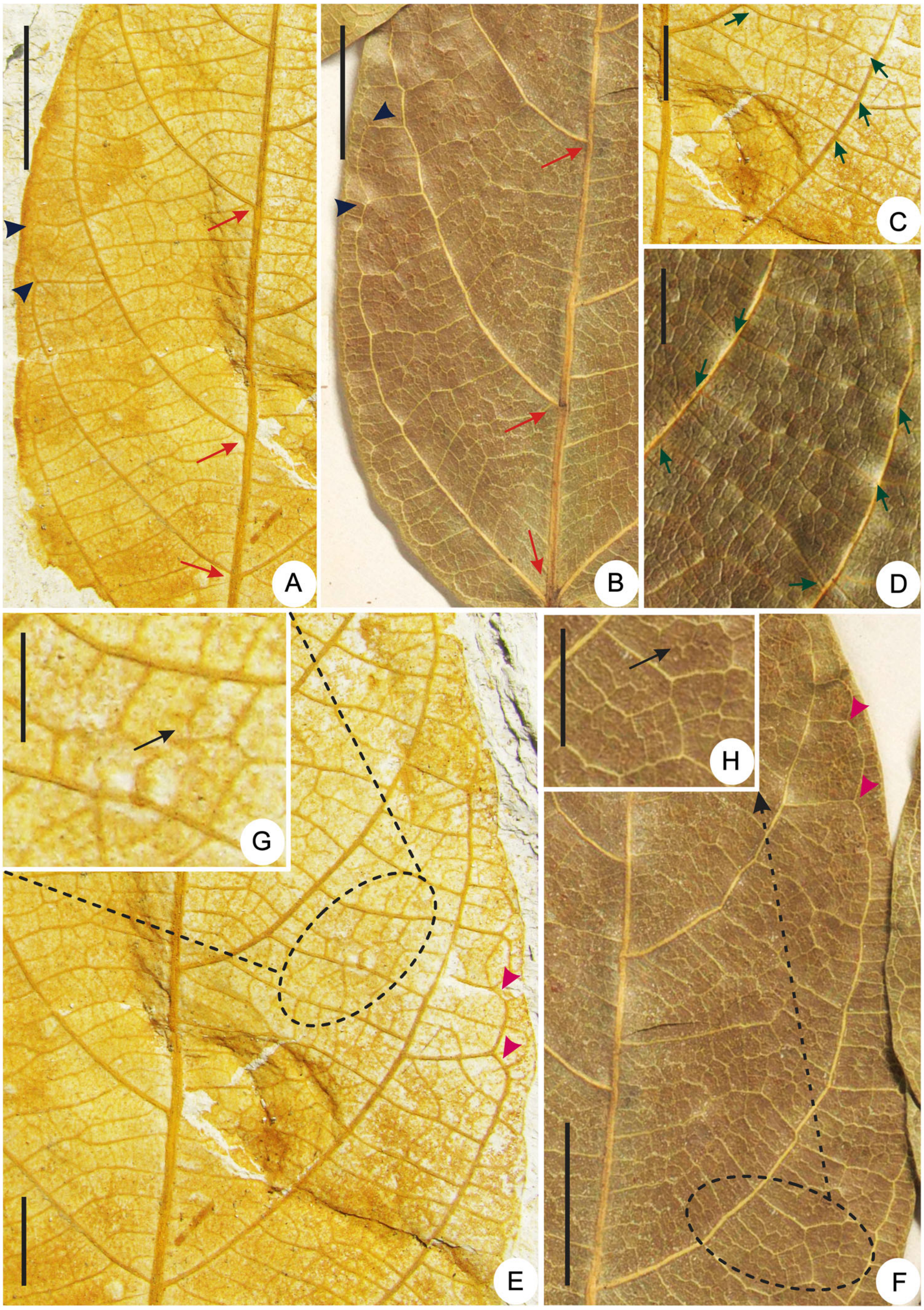

FIGURE 8 (A) An enlarged portion of the fossil, *Ficus paleodicranostyla* Chandra et al., sp. nov., shows the angle of origin of major secondaries, their irregular spacing, excurrent attachment (red arrows) and brochidodromous architecture (black arrows) (specimen no. BSIP no. 42248). (B) An enlarged portion of the modern species, *Ficus dicranostyla*, voucher no. BR0000017476447, shows a similar angle of origin of major secondaries, irregular spacing, excurrent attachment (red arrows) and brochidodromous venation (black arrows) as seen in the fossil. (C) Fossil leaf shows percurrent tertiaries (green arrows) in an enlarged view. (D) A modern leaf of *Ficus dicranostyla* (voucher no. BR0000017476447), shows a similar percurrent tertiaries (green arrows). (E) A fossil leaf shows the brochidodromous venation in the other half of the leaf (pink arrows). (F) A modern leaf (voucher no. BR0000017476447), shows a similar brochidodromous venation in other half of the leaf (pink arrows). (G) A portion of the fossil leaf shows preserved areoles. (H) A portion of the modern leaf (voucher no. BR0000017476447), shows similar preserved areoles. The scale bar represents 1 cm for (A); 0.5 cm for (B–F); 0.25 cm for (G, H).

comparison suggests that *Ficus dicranostyla* Mildbr (Figures 7B, 8B, 8D, 8F, 8H) embraces all the distinct features found in the fossil leaf except that the distance between the first and second pair of secondaries varies slightly as compared to those of the fossil.

Comparison with other fossil fig species

Fossil *Ficus* is well known all over the world from Cenozoic sediments. The Gurha fossils were compared with fig fossils documented from both Southern and Northern Hemispheres

(Srivastava et al., 2011; Huang et al., 2018; Dong et al., 2022), but in all cases they were found to be different. The fossil leaves of *F. arnottiana* (Mahajan and Mahabale, 1973), *F. caricites, F. religiosities* (Trivedi, 1980), *F. glaberrima, F. tomentosa* (Bande and Srivastava, 1988), *F. khariensis* (Lakhanpal and Guleria, 1982), *F. retusoides* (Prasad, 1990; Antal and Awasthi, 1993; Agarwal, 2002), *F. kumarhattiensis, F. kasaulica, F. banogensis, Ficus* sp. A, *Ficus* sp. B, *Ficus* sp. C (Mathur et al., 1996) differ in having reticulate tertiary veins as compared to percurrent tertiaries in both *F. paleovariegata* and *F. paleodicranostyla*. The fossil leaves of *F. benjamina* (Prasad et al., 2002), *F. eomysorensis* (Tripathi et al., 2002), *F. glomerata* (Mahajan and Mahabale, 1973), *F. macrocarpa* (Singh and Prasad, 2008), *F. miocenicus* (Konomatsu and Awasthi, 1999), *F. nepalensis* (Prasad, 1990), *F. oodlabariensis* (Prasad et al., 2004; Prasad, 2006), *F. raptiensis* (Prasad and Awasthi, 1996), *F. palaeoracemosa* (Srivastava et al., 2011), *F. champarense* (Lakhanpal and Awasthi, 1984), and *F. praecurticeps* (Agarwal, 2002) possess an elliptical shape and so can be differentiated from our fossil leaf, *F. dicranostyla*, because it is ovate. However, they do show some resemblance to *F. paleovariegata* in shape, but differ in being symmetrical, except for *F. champarense* and *F. praecurticeps*. *Ficus champarense* is different in having an auriculate base, while *F. praecurticeps* differs in having eucamptodromous venation and intersecondaries. *Ficus precunea* and *F. rumphii* also show some similarities to our fossil leaf *F. paleodicranostyla*, in having an ovate shape, but *F. precunea* differs in having eucamptodromous venation, whereas *F. rumphii* can be ruled out because it possesses an attenuate apex with craspedodromous venation. The new fossils described here also differ in shape, and major secondary venation pattern from the Miocene leaf fossils *F. fujianensis, F. zhangpuensis*, and *Ficus* sp. (from China), which possess elliptic to obovate shapes and prominent intersecondaries (Dong et al., 2022). *Ficus microtrivia* resembles the present fossil species in having ABS across up to two-thirds of the lamina, but differs in secondaries divergence and curvature and obovate shape (Huang et al., 2018). Another Miocene fossil, *F. proreligiosa*, described by Guo (2011) differs in having reticulate tertiaries. Tao (2000) described *Ficus* cf. *auriculata*, which differs from *F. paleoauriculata* in having brochiodromous veins and reticulate tertiaries as well as an entire margin.

Ficus caricites, described by Trivedi (1980), is the only *Ficus* leaf record displaying a tooth margin, but it can be differentiated from our fossil, *F. paleoauriculata*, because of its rounded apex, dentate teeth, and reticulate tertiary venation. As the present Gurha fossil leaves named *F. paleovariegata* Chandra et al., *F. paleodicranostyla* Chandra et al., and *F. paleoauriculata* Chandra et al., differ from the earlier described fossil leaves of *Ficus*, we have designated new specific epithets for them.

All these fossil species of *Ficus* described can easily be distinguished from each other, i.e., *F. paleoauriculata* can easily be distinguished from the other two species (*F. paleovariegata*, *F. paleodicranostyla*) in having toothed margin and semicraspedodromous venation, while the other two species differ from each other in shape and size.

DISCUSSION

Paleobiogeographic history of *Ficus*

Ficus diversity in deep time

Fossils attributed to *Ficus* are widely reported from both hemispheres from the middle-Cretaceous to the Neogene. In this study, we attempt to gather all fossil records and divide them into four time intervals, i.e., the Cretaceous, the Paleocene-Eocene, the Oligocene, and the Miocene-Pliocene (Figure 1; Appendix S1) to determine the deep-time diversity dynamics of *Ficus*. The credibility of many fossils from the Cretaceous has been questioned by Manchester (2014), and previously these uncertain fossil records have not been included to try and elucidate the evolutionary history of the genus (Xu et al., 2011; Cruaud et al., 2012; Pederneiras et al., 2018). Reliable remains of *Ficus* are known from the Paleocene and become more prevalent by the Eocene. There are only two fossil records of *Ficus* known from Paleocene successions, i.e., *F. lucidus* from the Paleocene-Eocene of England and *F. cherrapunjiensis* from the Paleocene of the Indian subcontinent (Meghalaya). By the Eocene, *Ficus* had attained a wide geographical distribution (Appendix S1) presumably favored by Eocene warmth, i.e., the early Eocene Climatic Optimum (Greenwood and Wing, 1995; Zachos et al., 2008; Westerhold et al., 2020). Five leaf impressions of *Ficus* are known from the Eocene in China, including *F. myrtifolia, F. shanwangensis, F. protobenjamia, F. praepumila, Ficus* sp. (Appendix S1 for details), and one from India (*F. kachchhensis*), Vicenza, Italy (*Ficus* sp.), Venezuela (*F. americanafolia*) and Germany (cf. *Ficus* sp. sensu). Four fossil species of Oligocene age (i.e., *Ficus* sp. A, B, and *F. banogensis*) were described by Mathur et al. (1996) from the Shimla highway. Three more species representing *Ficus* have been described from the Oligocene of Colorado (*F. bruesi*), Yunnan (*F. parasemicrordata*) and Libya (*Ficoxylon cretaceum*) (Appendix S1). It is apparent from fossil records (Figure 1; Appendix S1) that by the Miocene *Ficus* was ubiquitous on the Indian subcontinent and South and North America and Africa, apparently favored by the warm climatic conditions in the Middle Miocene Climatic Optimum (Zachos et al., 2008).

Divergence scenarios for *Ficus*

Evidence for the oldest-known Asian tropical rainforest occurs in the early Paleogene sedimentary deposits of India (Prasad et al., 2009). Previous studies have demonstrated that many fossil organisms found on the Indian subcontinent relate closely to those found in Africa, Madagascar, and the Seychelles (these islands are the Cretaceous fragments of the India–Madagascar landmass) (Murphy and Collier, 1997; Bijou and Bossuyt, 2003; Noonan and Chippindale, 2006). Fossils and phylogenetic data suggest that many recent taxa found in southeastern Asia today represent migration either from the Indian subcontinent or through boreotropical distributions (e.g., Bossuyt and Milinkovitch, 2001; Gower et al., 2002; Conti et al., 2002; Corlett, 2007; Macey et al., 2008; Su et al., 2020).

It is recognized that angiosperms mostly diversified during the Cenozoic, however, the hyperdiversity seen in modern rainforests has either resulted from them being a museum of diversity with constant speciation and low extinction (Wallace, 1878; Stebbins, 1974), or a cradle of diversity, referring to more recent and rapid speciation (Richardson et al., 2001; Pennington et al., 2015). Many studies based on phylogenetic analysis reveal that old lineages exhibit a steady accumulation over time, which supports the museum model (Couvreur et al., 2011a, b; Wang et al., 2012). A diversification rate analysis (Bruun-Lund et al., 2018) also suggests a museum model of evolution for *Ficus* with a gradual accumulation of species over time, very low extinction rates, and no significant evolutionary shifts. High dynamic diversification processes seen in modern rainforests have been linked to environmental changes that have taken place since the early Cenozoic, which is the case with *Ficus* (Couvreur et al., 2011b; Xing et al., 2014; Koenen et al., 2015).

Ficus has been divided into six subgenera and 19 sections (Berg and Corner, 2005; Pederneiras et al., 2015; references therein), concentrated in four main geographical areas: (1) Southeast Asia—section *Urostigma*, subsection *Stilpnophyllum* (Endl.) C.C. Berg, subgenera *Sycomorus* Raf., *Terega* Raf., *Synoecia* (Miq.) Miq. and *Ficus*; (2) Australasia—subsection *Malvantherae* (Corner) C.C. Berg and section *Oreosycea* (Miq.) Corner; (3) Africa—section *Platyphyllae* Mildbr. and Burret; and (4) the Neotropics—section *Americana* (Miq.) Corner and section *Pharmacosycea* (Miq.) Griseb. The fossil leaves described here belong to subgenus *Pharmacosycea* (section *Oreosycea*; *F. dicranostyla*) and section *Sycomorus* (*F. variegata*, *F. auriculata*). Although Corner (1958) has placed section *Oreosycea* in the subgenus *Pharmacosycea* (a Neotropical subgenus), molecular phylogenetic evidence (Bruun-Lund et al., 2018) suggests that it is more closely related to the subgenus *Sycomorus*, and the current biogeographical distribution of *Sycomorus* (paleotropical) agrees with these recent studies. The retrieval of remains of *Sycomorus* (subgenera) and *Oreosycea* (section) from the late Paleocene-to-early Eocene succession of the Indian subcontinent paleotropics indicates the early existence of these subgenera on the subcontinent and supports studies showing close affinities of *Oreosycea* (*Pharmacosycea*) and *Sycomorus*. This is further supported by the divergence time of *Sycomorus* and section *Oreosycea* of the subgenus *Pharmacosycea* as 46.69 Ma and 36.77 Ma, respectively (Xu et al., 2011).

Based on the molecular studies, two biogeographical settings were proposed for the origin and further dispersal of *Ficus*. (1) Xu et al. (2011) proposed that the fragmentation of Gondwana led to the diversification of the group, and the Indian subcontinent (including Madagascar) played a significant role in the early evolution of the genus. (2) Cruaud et al. (2012) and Pederneiras et al. (2018) proposed a boreotropical origin for the stem lineages of *Ficus* along the Tethys Seaway (Europe to Southeast Asia) at the beginning of the Cenozoic, with subsequent dispersals to the Americas, Africa, India, Madagascar, and Australia. The Gondwanan origin of the genus suggested by Xu et al. (2011) seems inappropriate and not congruent with the estimated origin of Moraceae in the Late Cretaceous (Zerega et al., 2005; Magallón et al., 2015). These proposed hypotheses should, however, be tested in the light of the new evidence presented here. In the present study, we add to the current knowledge base by reporting three new fossil species of *Ficus* belonging to the section *Sycomorus* and subsection *Oreosycea* (subgenus *Pharmacosycea*).

For the calibration of crown and stem nodes, *Ficus lucidus* Chandler (Collinson, 1989) has been used as the oldest fossil record reported from the Paleocene-Eocene boundary (~56 Ma) of England. Although fossils belonging to *Ficus* have been reported from the uppermost Cretaceous to Plio-Pleistocene horizons (Appendix S1), many of them (mainly the older ones) were discarded (as not belonging to *Ficus*) by Manchester (2014). The genus has been commonly reported from the Eocene onwards from North-to-South America, Europe, and Asia (Figure 1; Appendix S1), and by Miocene time it was widespread in Asia (mainly from India), Africa, the southern part of North America, and South America (Figure 1; Appendix S1). Southeast Asia and the Indian subcontinent were hypothesized to be the ancestral area for the section *Sycomorus* and subsection *Oreosycea* by Xu et al. (2011) and Pederneiras et al. (2018). Based on dispersal-vicariance analysis (DIVA), Xu et al. (2011) estimated that the subgenus *Sycomorus* originated around 58.2 Ma and then diverged to adjacent regions via different possible migratory routes from the Eocene onwards (ca. 46.7 Ma). Pederneiras et al. (2018) reported a 32.6 Ma crown age for *Sycomorus* and 26.1 Ma for *Oreosycea*. According to Xu et al. (2011), the section *Sycomorus* (subgenus *Sycomorus*) and section *Oreosycea* (subgenus *Pharmacosycea*) split at ~58 Ma and then diverged at 46.69 Ma and 36.77 Ma, respectively. The two modern species, i.e., *F. variegata* and *F. auriculata* (section *Sycomorus*, subsection *Neomorphe*) were confined to Southeast Asia, islands of the Pacific and Northeast of Australia, while the other, i.e., *F. dicranostyla* (subgenus *Pharmacosycea*, section *Oreosycea*) was limited to the northwestern margin of Africa. The presence of section *Oreosycea* (subgenus *Pharmacosycea*) on the Indian subcontinent at ~56 Ma suggests it is likely that the various clades of African *Ficus* (section *Oreosycea*) evolved in India then dispersed to Africa in the Paleocene (via the Ladakh-Kohistan arch) (Chatterjee and Bajpai, 2016; Bansal et al., 2022). Here, we report foliage similar to modern leaves of *Sycomorus* and *Oreosycea*, which supports the concept of the Indian subcontinent being the ancestral area for these two lineages.

This study does not comment on the origin of *Ficus* but suggests that Eurasia might be the center of origin and the Indian subcontinent was likely to be an integral part of the processes of diversification suggested by Xu et al. (2011). Contact between the wandering Indian plate and Asia was initiated around 60 Ma, as suggested by recent studies (An et al., 2021; Bian et al., 2021; Guo et al., 2021; Jadoon et al., 2022), therefore, our conjecture is that a robust phylogenetic study, including the present fossils, is now required for a more precise estimation for the origin of *Ficus*.

Deep time climate-diversity association

The northward movement of the Indian subcontinent, since its breakup with the rest of the Gondwanaland continents, had a considerable influence on the vegetation of the Indian raft that was severely affected by changes in latitudinal positions and land-sea configurations. Plant diversity is shaped more strongly in space and time by climate than by any other factor (Harrison et al., 2020). Although the northward moving Indian plate was situated south of the equator in the early Paleocene (Chatterjee and Bajpai, 2017), and the northwestern part of the Indian subcontinent experienced a climate favoring tropical rainforests (Spicer et al., 2017; Shukla et al., 2018; Bhatia et al., 2021), the northward journey across the equator exposed the region to a range of changing conditions (Bhatia et al., 2021). This led to some taxa becoming extinct while a few managed to survive this environmental filter (Prasad et al., 2009; Shukla et al., 2018).

The fossils described here from the early Paleogene succession are significant for the reconstruction of tropical paleovegetation and their relationship to climate. Here, we applied the nearest living relative (NLR) approach (Wolfe, 1995) to reconstruct the paleoclimate. In this approach, the climatic tolerances of the NLRs are assumed to mirror their relics in the earlier geological time. Normally, NLR methods are regarded as being most reliable for Neogene and younger assemblages (Utescher et al., 2014), so we recognize this application is not without risk.

The presence of tropical evergreen taxa (NLRs) in the fossil assemblage recovered from the Gurha lignite mine suggests a tropical humid climate during the period of deposition (Shukla et al., 2014), but today the fossil locality is located in the Thar Desert with xeric (arid) conditions demonstrating a substantial change in the climatic conditions in the area since the time of deposition. The NLRs of megafossils retrieved from the Gurha lignite mine such as *Aporosa acuminata* (Phyllanthaceae) (Shukla et al., 2016), *Uvaria zeylanica* (Annonaceae) (Shukla and Mehrotra, 2014), *Holigarna grahamii* (Anacardiaceae), *Pterygota alata* (Malvaceae), *Syzygium* spp. (*S. fruticosum* and *S. cumini*) (Myrtaceae), *Gardenia* spp. (*G. lucida* and *G. gummiefra*) (Rubiaceae) and fruits of *Saraca asoca*, *Cajanus crassus* (Fabaceae) and *Mallotus mollissimus* (Euphorbiaceae) (Shukla et al., 2018) from the lignite mine show affinities with tropical evergreen taxa growing in wet evergreen forests of the Western Ghats (south India), which today experiences a high annual precipitation (Shukla et al., 2018). Because *Ficus variegata* currently thrives in wet conditions within a precipitation range of 2300–3000 mm (Figures 9, 10), this further indicates that the fossil locality experienced a far wetter climatic

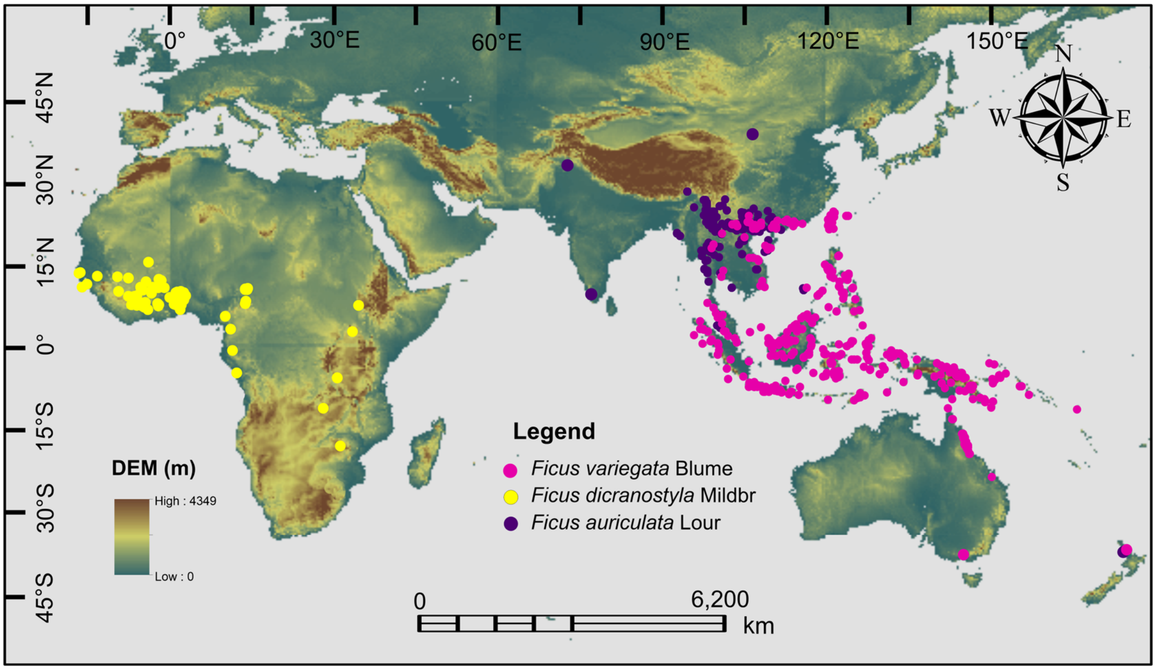

FIGURE 9 The present distribution of *Ficus* spp. (*F. auriculata*, *F. variegata*, and *F. dicranostyla*) (colored dots) plotted on the Shuttle Radar Topographic Mission (SRTM) digital elevation model (DEM).

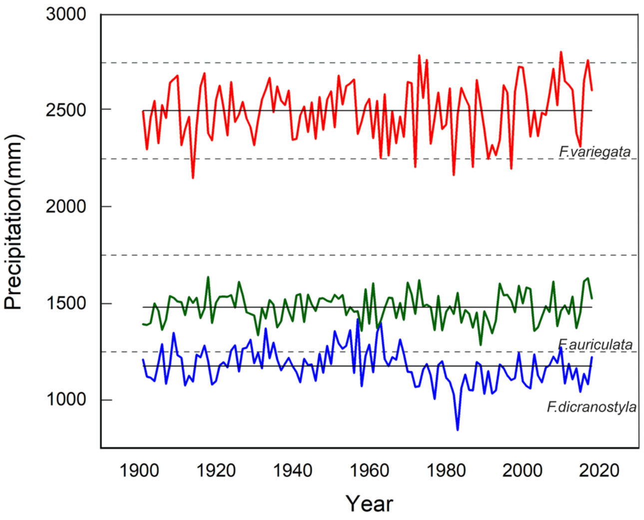

FIGURE 10 A line graph depicting mean annual precipitation (mm) for the three species of *Ficus* (*F. auriculata*, *F. variegata*, and *F. dicranostyla*).

regime in the early Paleogene time as compared to the present day arid conditions prevailing in the area. A quantitative study on leaf fossils from the Gurha lignite mine using the Climate Leaf Analysis Multivariate Program has suggested a humid regime (80% annual relative humidity) and high mean annual precipitation of ~1800 mm, but with a pronounced wet-dry seasonality indicative of a pronounced monsoonal regime (Shukla et al., 2014). This study also estimated a mean annual temperature of ~24°C ± 2.82°C (Shukla et al., 2014). Thus, the climatic conditions during the Paleogene were ideal for thriving tropical ecosystems.

CONCLUSIONS

We have reported three well-preserved impressions of fig foliage from early Paleogene sediments of the Indian subcontinent. Although we do not comment on the origin of *Ficus*, our data clearly demonstrates that the Indian subcontinent was an integral part to the early phase of fig diversification. In this study, we have gathered all the authentic fossil records of *Ficus* and grouped them into six geological ages, signifying that a major diversification of this genus occurred around the Eocene and the Miocene concordant with the Early Eocene Climatic Optimum and Middle Miocene Climatic Optimum, respectively.

The presence of tropical evergreen taxa (NLRs) in the Gurha fossil assemblage suggests a tropical humid climate during the period of deposition, as compared to the present-day arid conditions prevailing in the area, and demonstrates a substantial change in the local climatic conditions since the time of deposition. *Ficus variegata* (modern analog of *Ficus paleovariegata*) currently thrives in the wet conditions experiencing a high precipitation range of ~2500 mm (as shown in Figure 10) and indicates that the fossil locality experienced a far wetter climatic regime in early Paleogene time.

AUTHOR CONTRIBUTIONS

A.S. and K.C. identified the fossil leaves and designed the manuscript. K.C. downloaded the climate data, took the photographs and prepared all the figures included in the manuscript. All the authors contributed equally in writing the manuscript.

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DATA AVAILABILITY STATEMENT

The precipitation data for this study is available in the Figshare Data Repository with https://doi.org/10.6084/m9.figshare.21939986.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Fossil records of the genus *Ficus* from the Cretaceous to present.

APPENDIX S2. Details of Herbarium (voucher numbers) included in comparison and tabulation of the morphological study within the subgenera of *Ficus*.

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