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Cenozoic *Dalbergia* (Fabaceae) plant fossils from Southwest China: Biogeographic implications and plant-insect interactions

Yishan Zhao [a], Torsten Wappler [b,c], Conrad Labandeira [d], Jian Huang [e], Ai Song [a], Sanping Xie [f], Linbo Jia [g], Weiyudong Deng [b,c,e,**], Tao Su [a,*]

[a] *State Key Laboratory of Oil and Gas Reservoir Geology and Exploitation & Institute of Sedimentary Geology, Chengdu University of Technology, Chengdu 610059, China*
[b] *Department of Natural History, Hessisches Landesmuseum Darmstadt, Darmstadt 64283, Germany*
[c] *Paleontology Section, Institute of Geoscience, Rheinische Friedrich-Wilhelms Universität Bonn, Bonn 53115, Germany*
[d] *Smithsonian Institution, National Museum of Natural History, Washington, DC 20560, United States*
[e] *CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, Yunnan, China*
[f] *Key Laboratory of Mineral Resources in Western China (Gansu Province) and School of Earth Sciences, Lanzhou University, Lanzhou 730000, China*
[g] *CAS Key Laboratory of Biodiversity and Biogeography, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650204, China*

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ABSTRACT

Dalbergia is a pantropical genus of Fabaceae with limited fossil records. In this study we describe diverse and well-preserved *Dalbergia* fossils distributed through Cenozoic (Eocene to Pliocene) strata in Yunnan Province, Southwest China. Comparison with newly collected modern samples from Eurasian forests and herbarium specimens allow accurate identification of our fossil materials, and we demonstrate that Yunnan Province represents an hitherto unrecognised hotspot for the diversification of *Dalbergia*. Our findings also include evidence of the earliest known mining damage reported on *Dalbergia* leaflets, which sheds light on their interactions with various arthropods (*Leucoptera* and other insects) during the early Neogene. As such, our results improve knowledge of *Dalbergia* fossils in East Asia and are crucial for understanding the evolutionary history of analogous mining behavior observed from modern *Dalbergia*.

1. Introduction

Dalbergia L. f. comprises 274 living species disjunctively distributed in pantropical regions (POWO, 2023), mostly in Central and South America, Africa, and Asia (Klitgaard and Lavin, 2005). Growth forms of *Dalbergia* vary from bushes, trees, and climbing lianas, which adapt to diverse habitats, including tropical forests, savannas, and rocky shores (De Carvalho, 1997; Du Puy and Moat, 2002; Mabberley, 2008). Of all extant *Dalbergia*, approximately 28 species are native to China (Chen et al., 2010), and many were treated as economic plants in the history of East Asian countries (Zhao et al., 2020); among them, Huanghuali (*D. odorifera*) is the most famous for spices and furniture making (Huang et al., 2015).

The oldest *Dalbergia* macrofossil is mentioned in the biota overview of the North American Bighorn Basin (early Paleogene, Appendix A2 in Wing et al., 1995), but without detailed morphological descriptions. Fossil leaflets of *Dalbergia* were reported from Eocene floras in China (Liu and Kong, 1978; Qiu, 2010), which remain controversial. Macrofossil records in the forms of pod and leaflet are from the Oligocene to Pliocene of Europe (Hably, 1992; Shakryl, 1992), particularly in Caucasia (e.g., Hungary and Azerbaijan), with convincing figures and descriptions. The Miocene *Dalbergia* pods were documented in the South Himalayas, India (Prasad, 1989; Awasthi, 1992; Khan and Bera, 2014; Prasad et al., 2017) and East China (Li, 2010), but hard to determine based on the blurry pictures. During recent years, numerous *Dalbergia* macrofossils were found from the Eocene to Pliocene of Yunnan (Table 1); some were briefly mentioned in previous studies (Jia et al., 2013; Huang, 2017; Jia, 2018; Cheng et al., 2018). Owing to the scale and diversity of the Fabaceae family, the fossil legumes in Tertiary have not often been studied in detail, and some of the listed *Dalbergia* fossils in the older literature require reevaluation (Herendeen, 1992).

The biogeography of *Dalbergia* is still under debate. Fossil-based

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* Corresponding author.
** Corresponding author at: Department of Natural History, Hessisches Landesmuseum Darmstadt, Darmstadt 64283, Germany.
E-mail addresses: dengweiyudong@xtbg.ac.cn (W. Deng), sutao@cdut.edu.cn (T. Su).

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dispersal routes proposed by Jia et al. (2013) indicated an Afrotropical origin of the *Dalbergia* regardless of the ambiguity in identification. However, Sanger sequencing data-based phylogenetic tree indicated a possible Neotropical origination of modern *Dalbergia* and reconstructed an Oligocene divergence of species distributed in other parts of the world (Vatanparast et al., 2013; Sotuyo et al., 2022).

Additionally, extant plant-insect interactions on *Dalbergia* (hole feeding, margin feeding, skeletonization, and mining) are commonly observed from our collection, and some specific mining damages were also observed from worldwide herbarium specimens (Supplementary materials). As specific host insects and their communities shifted their ranges together from plate movements and environmental changes in geological time (Adroit et al., 2018; Donovan et al., 2020), those leaf miners were possibly involved with the ancient *Dalbergia* dispersal. Current research on the plant-insect interaction of *Dalbergia* lacks fossil evidence. Although some ichnofossil functional feeding groups (FFGs) are documented in historical Fabaceae (Labandeira et al., 2007), most of which were in deep geological age, indistinctly preserved, or without typical modern ecological analog, thus less possible to interpret the evolutionary history of modern plant-insect interactions of their relevant species.

To address the issues, this study introduced all updated *Dalbergia* macrofossils in Yunnan (Table 1; Fig. 1; Fig. S2), including the best-ever fossil pods with clear pedicels and stipes insertion positions. We also reported the earliest plant-insect interactions of the genus, the damage traces on fossil leaves were comparable to modern mining and skeletonization observed from worldwide *Dalbergia* collections.

2. Materials and methods

2.1. Fossil collection and geological backgrounds

Fossil of *Dalbergia* was recorded from the upper Eocene to the Pliocene fossil localities in Yunnan (7 localities, all revealed in Fig. 1; Table 1; Fig. S2), where modern *Dalbergia* still exists in the nearby forests. *Dalbergia*-bearing layers of Maguan County (23°01′N 104°23′E, Wenshan Prefecture) were of late Eocene age (Jia et al., 2021). The Lühe Town (25°14′N 101°44′E, Chuxiong City) and Wenshan City's *Dalbergia* (23°20′N 104°17′E, Wenshan Prefecture) were dated to the early Oligocene via U/Pb zircon (Linnemann et al., 2017; Tian et al., 2021). Nalaipo Village (23°52′N 100°71′E, Jinggu County) was regarded as the lower Sanghaogou Formation, which was early Miocene based on multiple stratigraphic analyses but is controversial owing to the complex sedimentary environments (Zhao et al., 2023). *Dalbergia* from Xiaolongtan town (23°30′N 103°12′E, Kaiyuan City) was of the late Miocene age given from previous geological research (Li et al., 2015). Fossils from Bangmai Village (23°54′N 100°0′E, Lincang City) were placed in the late Miocene based on biostratigraphic and lithostratigraphic correlations (Hu et al., 2009; Xie et al., 2018). Besides leaflets and pods, the *Dalbergioxylon* wood fossils (close to extant *Dalbergia*) from Yuanmou County (25°71′N 101°88′E, Chuxiong Prefecture) were of Pliocene age and represented the youngest record in Yunnan according to Cheng et al. (2018).

Most pod fossils are housed at Lanzhou University, and leaves are stored in Xishuangbanna Tropical Botanical Garden (XTBG) and Kunming Institution of Botany (KIB). Fossils in corresponding institutions were provided by Sanping Xie, Jian Huang, and Linbo Jia, respectively.

2.2. Morphological observation

Details of fossils were obtained under a Leica S8APO stereoscope and photographed with a Nikon D800 digital camera. Modern leaf miners and host plants were photographed using Sony ILCE-7C. Line-drawing reconstructions were based on digital photos assisted with stereoscope observation. ImageJ (v1.53) was applied for measuring parameters, and

Table 1
Records of *Dalbergia* macrofossils from Yunnan (sorting by geological age). The question marks indicate unverifiable fossil records from previous studies.

Fossil localities	Species	Age	Organ	Reference
Yunnan, China (Fig. 1A)				
(1) Maguan, Wenshan	*Dalbergia maguanensis* L.B. Jia et Z.K. Zhou	Late Eocene	Fruit	Jia, 2018 (Fig. S2T)
(2) Lühe, Chuxiong	*Dalbergia* sp. 1	Early Oligocene	Leaflet	Wu et al., 2022 (Fig. S2N)
(3) Dashidong, Wenshan	*Dalbergia* sp. 2	Early Oligocene	Leaflet	Huang, 2017 (Fig. S2M)
(4) Nalaipo, Jinggu	*D. ziwenii* Y.S. Zhao, J. Huang et T. Su sp. nov.	Early Miocene	Fruit, leaflet	This study (Fig. 2: A and B)
(5) Bangmai, Lincang	*D. prehupeana* Hance	Late Miocene	Leaflet	Tao and Chen, 1983
	D. yunnanensis Franch	Late Miocene	Leaflet	Tao and Chen, 1983
	D. sigilata S.X. Guo	Late Miocene	Leaflet	Guo, 2011
	Dalbergia sp. 3	Late Miocene	Leaflet	Jia et al., 2013 (Fig. S2L)
	Dalbergia sp. 4	Late Miocene	Fruit	Jia et al., 2013
	D. cf. *mecsekens*	Late Miocene	Fruit	Jia et al., 2013 (Fig. S2: O—S)
(6) Xiaolongtan, Kaiyuan	*D. lucida* Geng	Late Miocene	Leaflet	WGCPC, 1978 (pp. 105–106)
	Cf. *Dalbergia* sp.	Late Miocene	Leaflet	Guo and Zhou, 1992 (pp. 215–216)
(7) Yuanmou, Honghe	*Dalbergioxylon biseriatensis* Cheng, Wang, Liu, Jin, Mehrotra, Jiang & Li	Pliocene	Wood	Cheng et al., 2018
Other localities (Fig. 1B)				
(8) The United States	*Dalbergia* sp. 5 (?)	Early Paleogene	?	Wing et al., 1995
(9) China (Henan)	*Dalbergia* sp. 6 (?)	Eocene	Leaflet	Liu and Kong, 1978
(10) China (Hainan)	*Dalbergia* sp. 7 (?)	Eocene	Leaflet	Qiu, 2010
(11) Mexico	*Dalbergioxylon*. sp. (?)	Oligocene	Wood	Sotuyo et al., 2022
(12−13) Caucasus	*Dalbergia longicordioides* Kassum	Oligocene	Leaflet	Shakryl, 1992
	D. kryshtofovichii Kassum	Oligocene	Leaflet	Shakryl, 1992
(14) Cuba	*Dalbergia*. sp. 8 (?)	Miocene	?	Berry, 1939
(15–17) Abkhazia	*D. rectinervis* Ettingshausen	Miocene	Leaflet	Shakryl, 1992
	D. sarmatica Kolakovsky	Miocene	Leaflet	Shakryl, 1992
	D. bella Heer	Miocene to Pliocene	Leaflet	Shakryl, 1992
(18) Hungary	*D. mecsekense*	Miocene	Fruit	Hably, 1992
(19) Nepal	*D. miosericea* (?)	Miocene	Leaflet	Prasad, 1989
(20) China (Zhejiang)	*Dalbergia*. sp. 9 (?)	Miocene	Fruit	Li, 2010
(21−22) India	*D. prelatifolia* Khan & Bera (?)	Middle to Late Miocene	Fruit	Khan and Bera, 2014
	D. tanakpurensis (?)	Middle Miocene	Fruit	Prasad et al., 2017
(23) Abkhazia	*D. derrisaecarpa*	Pliocene	Fruit	Shakryl, 1992
(24) Switzerland	*D. bella* Heer	Late Pliocene	Leaflet	Shakryl, 1992

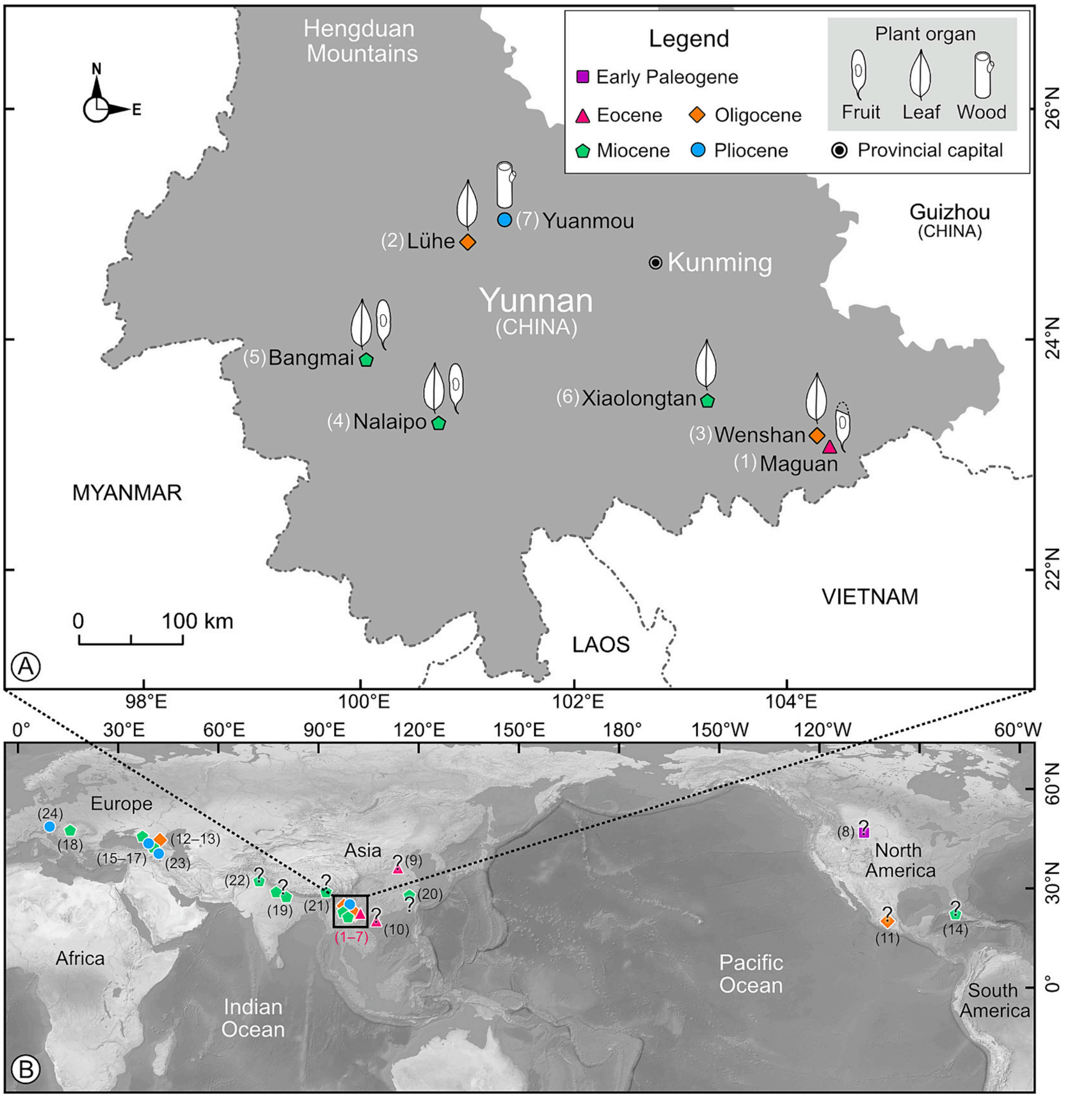

Fig. 1. Global fossils distribution of *Dalbergia*. (A) Fossil localities in Yunnan. (B) Worldwide *Dalbergia* fossils. Numbers matched with the fossil localities in Table 1. The question marks indicate unverifiable fossil records from previous studies. The background world map was modified from Xu (2021).

all the illustrations were performed with Affinity Software Suites (v2.1.1).

Extant plant specimens, including *Dalbergia stipulacea* Roxb. and *D. odorifera* T.C. Chen, *D. rimosa* Roxb., and *D. polyadelpha* Prain were sampled from the Yunnan (XTBG and Jinggu) and stored in the Paleoecology Research Group (XTBG). Cleared leaves of *D. odorifera* were made (Fig. 2: D, F, and K; Fig. S2: B and J) by a quick leaf skeletons method (unpublished) and using Safranin-O for staining. Pods of *D. stipulacea* were dried in an oven and dissected. This study also obtained online herbarium resources, including the virtual herbaria of the Chinese Virtual Herbarium (CVH, https://www.cvh.ac.cn), the Smithsonian National Museum of Natural History (NMNH, e.g., collection of 00001131, 00411764, and 02152677, provided by Ingrid Lin), and the National Herbarium of the Netherlands (NHN, e.g., U0027785, provided by Roxali Bijmoer) for detailed plant morphological comparison, the manager of corresponding museums or institutions authorized all the specimens used in our figures. The morphological description terms of pods refer to Kirkbride et al. (2003), and leaves refer to Ellis et al. (2009).

Plant-insect interaction research applied all our extant sampling of leaf miners from Europe and China; these samples were partly stored in XTBG and Hessen Land Museum of Darmstadt (HLMD). This study also applied some specimens from the above institutions as many of their collections from South America contain similar damage traces. Our descriptions of damage types (DTs) and FFGs were based on Labandeira et al. (2007).

3. Systematics

Order: FABALES Bromhead.
Family: FABACEAE Lindley.
Subfamily: PAPILIONOIDEAE DC.
Tribe: DALBERGIEAE DC.
Genus: *Dalbergia* L. f.
Species: *Dalbergia ziwenii* Y.S. Zhao, J. Huang et T. Su sp. nov.

Diagnosis: Pod flattened, oblong-shaped, and slightly curved. Pedicels straight to slightly curved. Receptacles unobvious. Stipes thickened, slightly curved. Valve with prominent longitudinal veins. Suture lines thickened. Seed chamber shape elliptic, thicker than periphery area, taking up ca. 30% of the valve. Seed reniform, wider at the radicle side. Leaflet ovate-shaped with medially asymmetrical and base basal width and extension symmetrical. Apex angle acute, shape asymmetrical, straight on the left and acuminate on the right, base angle obtuse, shape convex.

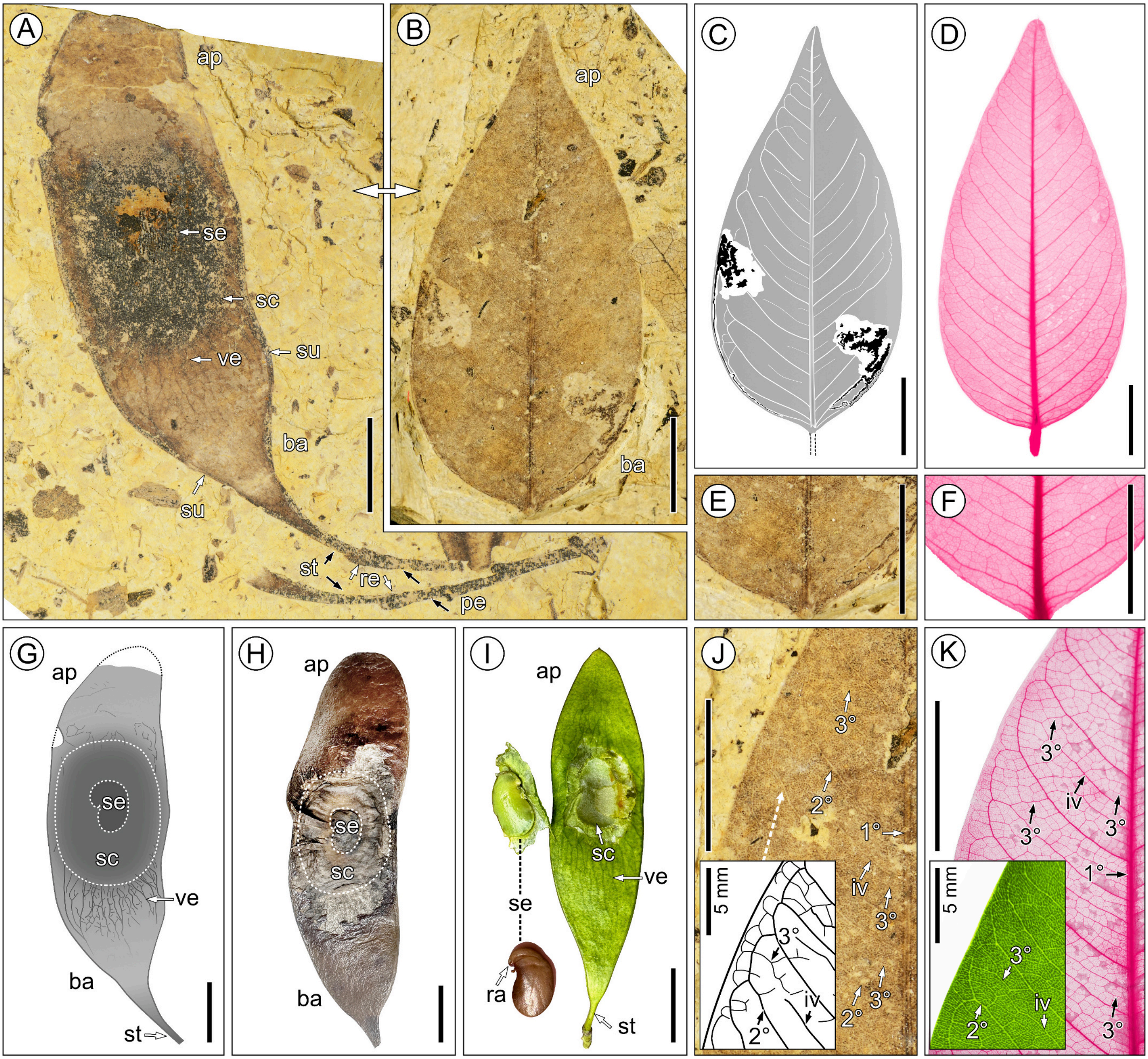

Fig. 2. Macrofossils and extant *Dalbergia* from Yunnan. Abbreviations: ap, apex; ba, base; se, seed; sc, seed chamber; su, suture; st, stipe; pe, pedicel; ra, radicle; re, receptacle; ve, vein; 1°, primary vein; 2°, secondary vein; 3°, tertiary vein; iv, intersecondary vein. (A–B) *Dalbergia ziwenii* Y.S. Zhao, J. Huang et T. Su; NLP-0114 (Picture A) preserved on the same mudstone with NLP-0116 (Picture B). (C) Line drawing of NLP-0116. (D) *D. odorifera* clear leaflet made by this study. (E) Leaf base of picture B. (F) Leaf base of picture D. (G) Reconstruction of the fossil pod (NLP-0114). (H) Pod of *D. stipulacea* Roxb. from XTBG. (I) Pod and seeds of *D. odorifera* from XTBG. (J) Zoom of picture B, line drawing shows the details of venation. (K) Zoom of the clear and untreated leaflets. Scale bars = 10 mm.

Holotype: NLP-0114 (Fig. 2A), NLP-0116 (Fig. 2B).

Etymology: The specific name honors Hang Yanzhi, whose courtesy name is ‘*ziwen*’. He was a 12th-century Chinese botanist who wrote the world’s first book on citrus research.

Type locality: Nalaipo Village, Jinggu County, Yunnan Province, China (23°52′N 100°71′E).

Stratigraphic horizon and age: Lower Sanhaogou Formation, Early Miocene.

Repository: Palaeobotanical Collections of the Qinghai–Tibetan Plateau, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

Description: The fossil taxon consists of associated pod (Fig. 2A) and leaflet (Fig. 2B) preserved together on the same mudstone. Pod arrangement unknown (infructescence incomplete). Pedicels straight to slightly curved, 7–15 mm long (Fig. 2A, “pe” marked). Receptacles unobvious (Fig. 2A, “re” marked). Pod stiped. Stipes thickened, slightly curved, 7 mm long (Fig. 2: A and G, “st” marked). Pod flattened, indehiscent, leathery, with single seed. Pod shape oblong, ca. 65 mm long (incomplete), 21 mm wide (Fig. 2A). Pod bent at both ends, apex shape asymmetrical, convex on the left and straight on the right (Fig. 2: A and G, “ap” marked); base shape asymmetrical, straight on the left and acuminate on the right (Fig. 2: A and G, “ba” marked). Suture lines thickened (Fig. 2A, “su” marked). Valve having reticulate venation, denser in the seed chamber and periphery area, primary longitudinal veins prominent (Fig. 2A, “ve” marked). Seed chamber shape elliptic, thickened, 24 mm long, 18 mm wide, and taking up ca. 30% of the valve (Fig. 2: A and G, “sc” marked). Seed flattened, 8 mm long, 6 mm wide. Seed shape reniform, asymmetrical, wider at the radicle side (Fig. 2G, "se" marked), radicle inflexed (Fig. 2G, "ra" marked).

Leaflet arrangement unknown. Leaflet attachment petiolate, petiole ca. 1 mm long (incomplete, Fig. 2: B and E). Blade marginal. Leaflet size microphyll, 52 mm long, 25 mm wide, L: W ratio 2.1:1 (Fig. 2: B and C). Blade shape ovate with medially asymmetrical and base basal width and extension symmetrical (Fig. 2: B and C). Margin entire. Apex angle acute, shape asymmetrical, straight on the left and acuminate on the right; base angle obtuse, shape convex (Fig. 2: B and C). Primary venation pinnate (Fig. 2: B and C). Major secondaries simple brochidodromous, ca. 21 pairs, spacing irregular, angles to midvein inconsistent, about 35°–47°, attachment basally decurrent (Fig. 2J, "2°" marked). Intersecondaries present, length > 50% of subjacent major secondary, proximal course almost parallel to subjacent major secondary, >1 per intercostal area (Fig. 2J, "iv" marked). Intercostal tertiary veins reticulate (Fig. 2J). Exterior tertiary course looped (Fig. 2J). Quaternary vein irregularly reticulate. Areolation with good development (Fig. S2A), marginal ultimate venation looped.

Order: Lepidoptera Linnaeus, 1758.

Family: Lyonetiidae Stainton, 1854.

Ichnogenus: *Paleoleucoptera* W.Y.D. Deng, Y.S. Zhao et T. Su gen. nov.

Ichnogenus diagnosis: A long and thin mine terminated with a large chamber-like mine. Frass trails dark, continuous, full-filled the initial mine and half-filled in the chamber area. Mine areas are light in color, without distinct reaction rims, and avoid the leaf midvein.

Derivation of name: Fossil mines are similar to a series of extant *Leucoptera* damages (Fig. 4I–K; Fig. 5B). Ichnogenus name use '*paleo*' to distinguish fossil and extant *Leucoptera*.

Material: Two damage scars on NLP-0116 (Fig. 2B) excavated from Nalaipo village, Jinggu County (Precise information described in Chapter 2.1).

Type ichnospecies: *Paleoleucoptera jinggu* W.Y.D. Deng, Y.S. Zhao et T. Su sp. nov.

Etymology: Named after the fossil locality of Jinggu County.

Description: Two mines observed from the *Dalbergia* fossil leaflet (Fig. 2B), each consisting of two distinct regions (here described the lower right one): initiated with a ca. 15 mm long and 0.2–0.5 mm width thin mine (some highly coiled, Fig. 4: F—H, "im" marked), and terminated with a polylobate chamber-like ca. 42 mm^2 broader area, ca. 8 mm in the longest dimension (Fig. 4: G and H, "ch" marked). The initial mines follow typical leaf structures (Fig. 4: F—H, leaf margin or secondary veins), and mining width shows no significant change until connecting to the chamber areas. Two mining scars take ca. 5.2% and 5.6% of leaf size, respectively. Insect frass was continuous and solid, filled in the narrow initial mines, whereafter the frass broadened at the beginning of the chamber area and was absent in the end.

Remark: Modern *Leucoptera* mines are various and some typical damages (e.g., *L. malifoliella*) have representative ichnofossil (Maccracken et al., 2021). Similar *Leucoptera* mining traces to this study are mainly Fabaceae hosts, including *L. laburnella*, *L. erythrinella* (typically host on *Erythrina L.*), and *L. sphenograpta* (typically host on *Dalbergia sissoo* Roxb. from India, Fig. 4I). Our sampling of *Dalbergia rimosa* (Fig. 4: J and K) from Yunnan (Fig. S3I) has also consistent mines caused by undescribed *Leucoptera*, and some could observe one pupa in the chamber area.

4. Discussion

4.1. Morphological comparisons

Abundant different forms (pod, leaflet, and wood) of *Dalbergia* fossils were found in ancient Yunnan (Table 1; Fig. 1; Fig. S2), except for Nalaipo (Fig. 2: A and B) fossils, some previous identification results (Fig. S2: O—S) need reevaluation because of lacking identify

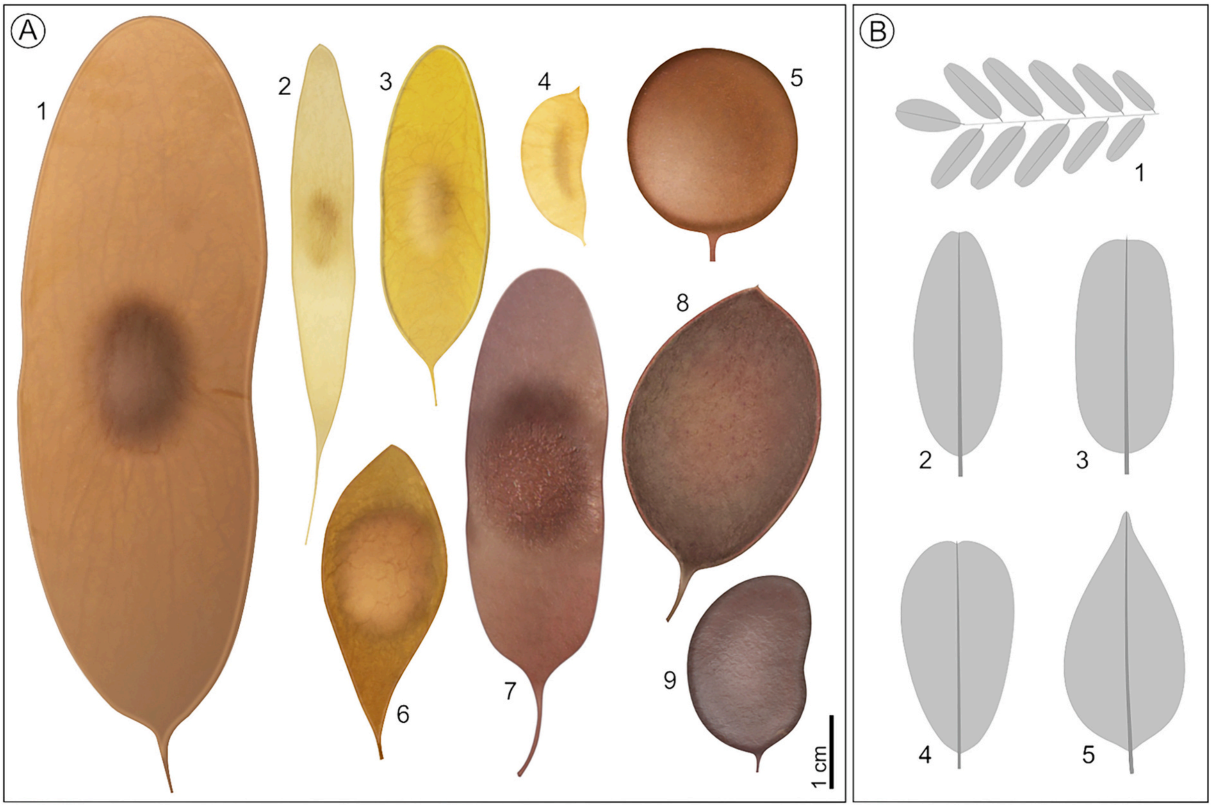

Fig. 3. Illustration of extant *Dalbergia* pods and leaves refers to our samples and collections of NMNH and NHN. (A1) *D. afzeliana* G. Don. (A2) *D. sissoo* Roxb. ex DC. (A3) *D. hostilis* Benth. (A4) *D. thorelii* Gagnep. (A5) *D. riedelii* (Benth.) Sandwith. (A6) *D. melanoxylon* Guill. & Perr. (A7) *D. stipulacea* Roxb. (A8) *D. xylocarpa* O. Lachenaud. (A9) *D. ecastaphyllum* (L.) Taub. (B1) A leaf with leaflets. (B2–B5) Leaflet types, from top left: elliptic, oblong, obovate, and ovate leaflet shape.

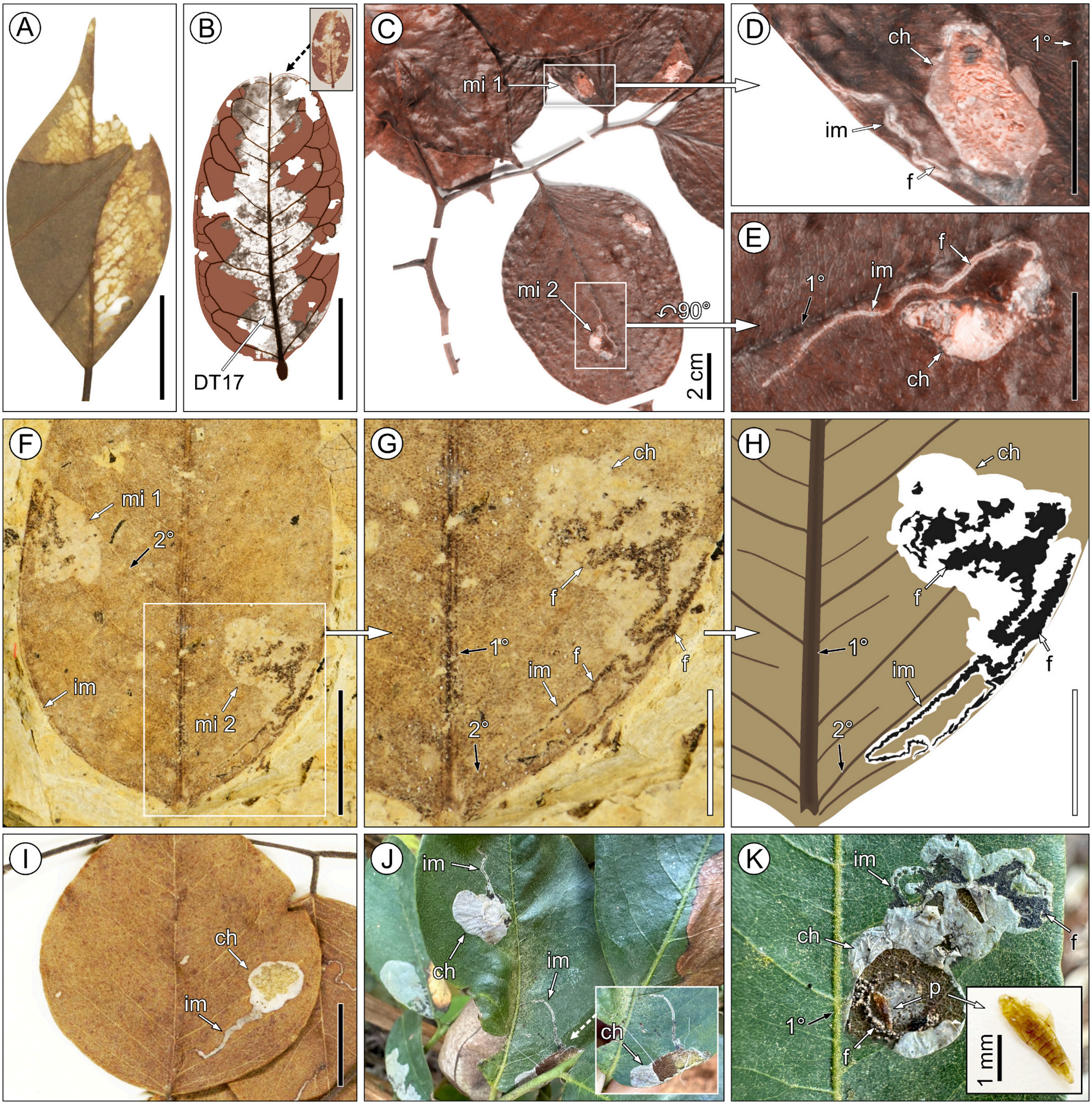

Fig. 4. Plant-insect interactions from fossil and extant *Dalbergia* leaflets. Abbreviations: ch, chamber; im, initial mine; f, frass; mi, mining; 1°, primary vein; 2°, secondary vein; iv, intersecondary vein; p, pupa. (A) Leaflet of *D.* sp. (WAG.1014183). (B) Drawing of *D.* sp. from Huang (2017), Fig. S2M. (C) *D.* sp. from the collection of the NHN, provided by Roxali Bijmoer. (D) Enlargement of picture C, showing the mining 1. (E) Enlargement of picture C, showing the mining 2. (F) Enlargement of Fig. 2B. (G) Enlargement of picture F, showing the mining 2. (H) Drawing of picture G. (I) Similar damage traces on *D. sissoo* Roxb. (WAG.1017532). (J–K) Similar damage traces on *D. rimosa* Roxb. sampled by Yishan Zhao in Binglin Village, Jinggu, Yunnan; Picture K shows the pupa in the chamber. Black scale bar = 10 mm, white scale bar = 5 mm.

characteristics, and others are either not adequately preserved to judge (Fig. S2T), or only have leaflets found from the same formation (Fig. S2: L–N).

Nalaipo pod (NLP-0114; Fig. 2: A and G) contains typical *Dalbergia* features with longitudinally oriented valve venation, dense reticulate venation in seed chamber and periphery area, seed reniform, and radicle inflexed, e.g., *D. odorifera* (Fig. 2I) and *D. rimosa* (Fig. S3B), but with a large seed chamber (ca. 24 × 18 mm, taking up ca. 30% area of the valve) and thicker stipe. The pod of NLP-0114 also resembles *D. stipulacea* (Fig. 2H), while differs in seed chamber proportion, thicker stipe, and the valve has conspicuous longitudinal veins (Fig. 2: A and G, "ve" marked). Usually, pods of *Dalbergia* are distinguished into two types: one obvious winged pod, valve margin thin into a wing around seed and seed chamber (e.g., Fig. 3: A1–A4, and A6–A7), and another unwinged, valve circular, elliptic or reniform, thicker (e.g., Fig. 3: A5, and A8–A9). Compared to the other fossils in this study, the valve of NLP-0114 has an intermediate morphology (Fig. 3: A6–A7) between thinly winged (e.g., Fig. 3: A1–A4) and thick unwinged pods (e.g., Fig. 3:

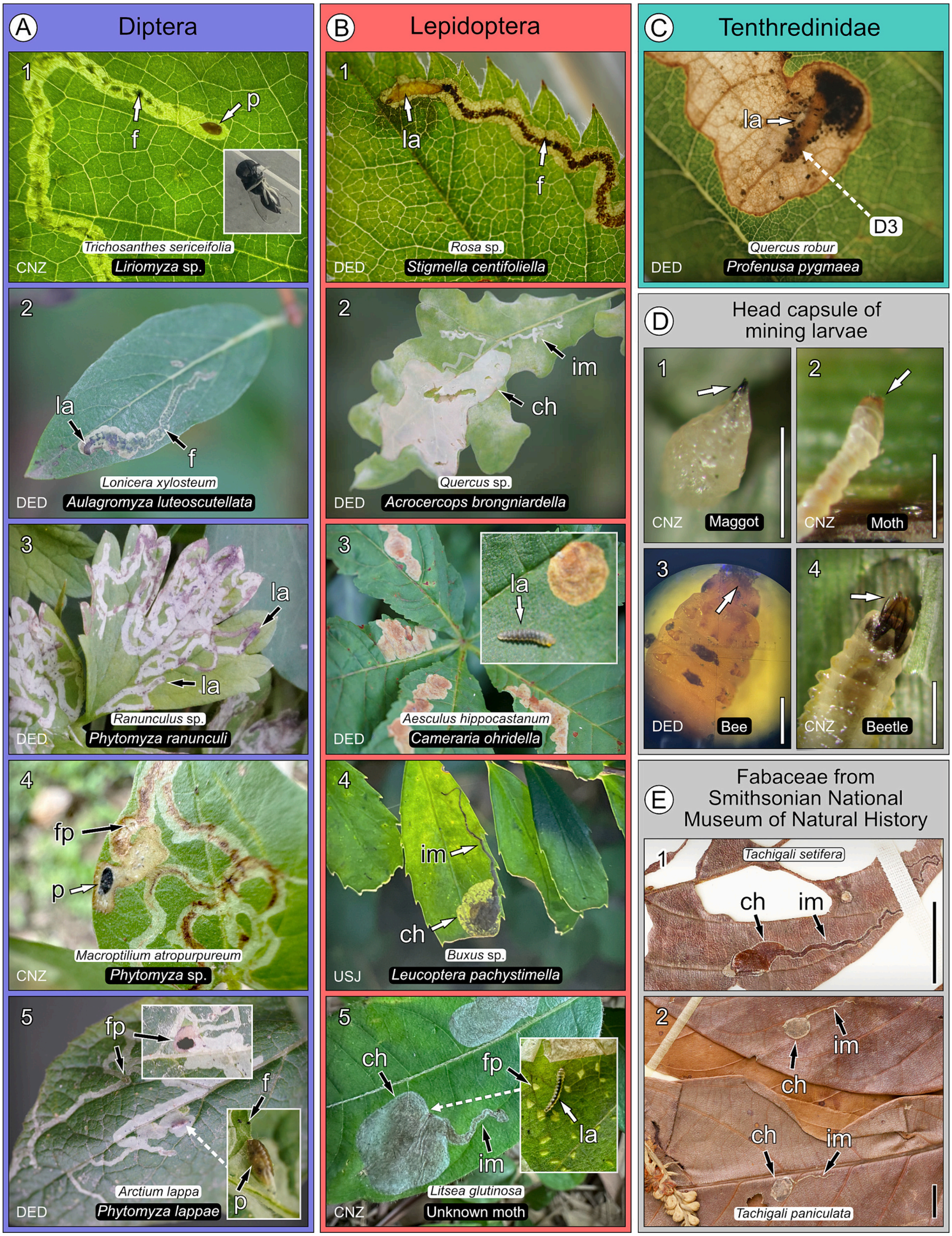

Fig. 5. Comparison of different leaf miners and their damage traces onto the leaves. Abbreviations: la, larva; p, pupa; f, frass; fp, feeding puncture; im, initial mine; ch, chamber. CNZ = Sampled from Yunnan, China, by Yishan Zhao. DED = Sampled from Hessen, Germany, by Weiyudong Deng. USJ = Sampled from the United States, by Jeff Ward. (A1–A5) Pictures show Diptera miners (all Agromyzidae) on shrub plants. (B1–B5) Pictures show Lepidoptera miners (Nepticulidae, Gracillariidae, and Lyonetiidae) on shrub and tree plants. (C) *Profenusa pygmaea* mining *Quercus robur* L. (D1–D4) The head capsules of larvae, picture D3 is the zoom of picture C; the rest are larvae sampled from bamboo leaves (*Gigantochloa* sp., *Dendrocalamus* sp., and *Gigantochloa atroviolacea* Widjaja). Arrows pointed to the head capsules of each larva. (E1–E2) Details of mining damage traces on Smithsonian specimens (provided by Ingrid Lin). White scale bar = 0.5 mm, black scale bar = 10 mm.

A5, and A8–A9). The fossil pods of *D.* cf. *mecsekens* (Fig. S2: O—S, fossil species followed Shakryl, 1992) and *D.* sp. from Bangmai (Jia et al., 2013), and *D. maguanensis* (Fig. S2T; Jia, 2018) from Maguan have identical thinner valves, and all pods (24–40 × 7–12 mm; 23 × 6 mm; and ca. 33 × 11 mm, respectively) are obviously smaller than NLP-0114 (Fig. 2A: ca. 65 × 21 mm).

Extant *Dalbergia* species have pinnately compound leaves (Fig. 3 B1), Leaflets are commonly shaped as elliptical (Fig. 3 B2), oblong (Fig. 3 B3), obovate (Fig. 3 B4), and ovate (Fig. 3 B5). NLP-0116 has an ovate shape (Fig. 2B) common in many extant *Dalbergia*, e.g., *D. monetaria* L. f. (South America), *D. odorifera* (East Asia, Fig. 2D), *D. polyadelpha* (southwestern China, Fig. S3: D—F), and *D. greveana* Baill. (Madagascar, Supplementary figure, Fig. S1X). Venational features of NLP-0116 are common in tropical Asian *Dalbergia* (e.g., *D. assamica* Benth., *D. odorifera*, *D. benthamii* Prain), which major secondaries and tertiaries inapparent, areolation with good development. Of the three listed modern species, size and outlook of NLP-0116 are almost identical to *D. odorifera* (Fig. 3: M and N): both leaflets shape ovate (Fig. 2: B and D), apex shape acuminate, without drip tip (Fig. 2: C and D), base shape convex, come close to rounded (Fig. 2: E and K), with equal major secondaries and angles to midvein (Fig. 2: C and D), intersecondaries resemble (Fig. 2: C—D and J–K, "iv" marked), epimedial tertiaries match pattern of adjacent intercostal tertiaries (Fig. 2: J and K), intercostal tertiaries reticulate and inapparent (Fig. 2: J and K), exterior tertiaries looped (Fig. 2: J and K), areolation with good development. Collections of other 23 genera, including species that are morphologically or molecularly (Sotuyo et al., 2022) close to *Dalbergia*, were also added to the comparison (Supplementary figure; Fig. S1 and S2), characteristics of both *Dalbergia* and NLP-0116 are distinct to them. Based on the fact that NLP-0114 and NLP-0116 were preserved together and leaflets characteristics of other legume fossils from all nearby sites (WGCPC, 1978; Guo and Zhou, 1992; Zhao et al., 2024) are all distinct to *Dalbergia*, this study considers pod and leaflet as the same species (Chapter 3.1).

Other *Dalbergia* leaflets (Table 1, Fig. S2: E–G) identified or mentioned in previous studies (WGCPC, 1978; Tao and Chen, 1983; Guo, 2011; Jia et al., 2013; Huang, 2017; Wu et al., 2022) were slightly different to NLP-0116, and no *Dalbergia* pods were excavated from these fossil sites. Given the complexity of the Fabaceae family and the leaflet shape variation of *Dalbergia* (Fig. 3B), this study listed them without discussing previous identification results.

4.2. Plant-insect interactions

Most previous *Dalbergia* fossils in Yunnan present skeletonization structures (Fig. S2: M and N); after stereoscope examination and line-drawing reconstruction (Fig. 4B), they are assigned DT16 (Fig. S2N) and DT17 (Fig. S2M) regarding the previous definition (Labandeira et al., 2007). The skeletonization takes a small portion on the left side of the leaflet (Fig. S2N) or extensive distribution along the midvein (Fig. 3M), both of which are very common in extant *Dalbergia* (e.g., Fig. 4A; Fig. S3D). As plenty of insects (especially Coleoptera) or even fungi caused similar damage skeletonization traces (Labandeira et al., 2007), the DT16 and DT17 in this study are hard to link with modern insects.

For the typical mining damage traces on the fossil leaflet, we first compared them with our modern leaf miner collections (Fig. 5). Extant arthropod leaf miners are mainly small-size larvae of flies (Agromyzidae), moths (Eriocraniidae, Elachistidae, Gracillaridae, Lyonetiidae, and Nepticulidae), beetles (Chrysomelidae), and bees (Tenthredinidae). Generally, most maggot miners host on shrubs or herbs, produce discontinuous frass (Fig. 5: A1–A5), form irregular and elongated mines, and feeding punctures along the mines are commonly observed in modern and fossil leaves (Fig. 5: A4 and A5, "fp" marked, similar to Winkler et al., 2010). In contrast, many mining moths host on shrubs and tree plants and produce continuous frass, resulting in relatively regular or chamber-like mines, and the feeding punctures are found in the chamber, not in the initial mine (Fig. 5 B5). Only a few of the beetles and bees have mining behaviors larvae, whereas most of their relevant are wood-boring insects (Deng et al., 2022), and among all the leaf miners, their larvae have well-developed and robust head capsules, resulting in wider or chamber-like mines (Fig. 5 B4).

Fossil mining traces in this study show evident different stages: 1) a long, narrow, serpentine trajectory following the leaf margin or secondary veins, full-filled with frass that indicates unidirectional mining behavior in this stage; and 2) a chamber area, indicating the insect started expanding damage area and created a chamber preparing for subsequent feeding and pupa stage. Most Diptera miners, including *Liriomyza* and *Phytomyza* (Fig. 5: A1, and A3–A5), usually do not have an obvious chamber for their pupa stage. Although mines ending in a terminal chamber exist in some *Agromyza* species (https://www.leafmines.co.uk), their frass is usually discontinuous. Also, multiple larvae in the interlace mine and flexible direction of mining behavior are observed in some Diptera families. Lepidoptera moth miners are the highest possibility, as plenty of genera, e.g., *Acrocercops* (Fig. 5 B2), *Leucoptera* (Fig. 5 B4), and *Mompha* (DT176) have analogous feeding behaviors, and all documented species host on Fabaceae from our collection or online database (https://www.leafmines.co.uk). Herbarium collections of some Fabaceae specimens (Fig. 5: E1 and E2) present similar long trajectories but more ovate chamber structures, close to DT 176 (Messel flora, Momphidae, from Labandeira et al., 2007). This study also concerned Chrysomelidae and Tenthredinidae, our modern collections of Eurasia leaf miners (Fig. 5: C and D) show they are irrelevant to these fossil damage traces. Tenthredinidae for example, tribe *Fenusini* larvae produce dotted frass, usually damage a large leaf area, and move around in their mines (Fig. 5C), which are totally opposite to the fossil. Among all the modern leaf miner collections, we consider Lepidoptera miners as possible hosts, but it needs to be further investigated as the lack of larvae found directly from *Dalbergia* leaflets.

In order to obtain accurate plant-insect interactions between *Dalbergia* and specific Lepidoptera, we extended the sampling time and expanded the sampling areas in Yunnan (Fig. S3), and finally found *Leucoptera* sp. pupae in *D. rimosa* damage mines (Fig. 4: J and K; Fig. S3: D, G, and I). The latest samples proved our hypothesis that the chamber was built for the pupa stage and this specific mining behavior of *Leucoptera* on *Dalbergia* was already established in the Miocene.

4.3. Paleoecology implication

The plentiful fossils from Yunnan and Tibet have controversial biogeographical implications as they are located in Southwest China, where the uplift of the Tibetan Plateau profoundly affected regional topography and ecosystems (Lu et al., 2018; Su et al., 2022; Zhu and Tan, 2022). Previous phylogeny interpretations of *Dalbergia* continental and island distribution as the Ocean dispersal (Sotuyo et al., 2022), considering current phylogenetic status and global fossil records (Fig. 1), Yunnan's *Dalbergia* is hard to implicate its origin and relations with other coastal distributed species. But like many other Oligocene plant fossils from Southwest China, extant *Dalbergia* species are still rich in Yunnan (Fig. S3), proving the hypothesis that modern ecological systems in Southwest China were established by the early Oligocene (Wu et al., 2022). The leaf-mining traces on the fossil represent the earliest known plant-insect interaction in this genus, which are caused by Lyonetiidae larva, consistent with our extant *Dalbergia* samples in Yunnan and herbarium specimens sampled from South America. As most host-specific insects may shift their ranges with their communities (Adroit et al., 2018; Donovan et al., 2020), our fossil damage evidence proved that worldwide similar mining plant-insect interactions on extant *Dalbergia* were established in the Miocene and could be highly involved in the *Dalbergia* dispersal. Although complex tectonic activities in Yunnan and incomplete phylogeny research prevent us from concluding a comprehensive biogeography of *Dalbergia*, these new fossils proved both plants and insects of Yunnan were deeply linked with contemporaneous worldwide tropical realms from the late Paleogene to early Neogene.

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CRediT authorship contribution statement

Yishan Zhao: Resources, Investigation, Conceptualization, Writing – review & editing, Writing – original draft. **Torsten Wappler:** Validation, Resources, Methodology, Writing – review & editing. **Conrad Labandeira:** Methodology, Data curation. **Jian Huang:** Resources, Writing – review & editing. **Ai Song:** Resources. **Sanping Xie:** Resources, Writing – review & editing. **Linbo Jia:** Resources, Writing – review & editing. **Weiyudong Deng:** Validation, Resources, Project administration, Data curation, Writing – review & editing, Writing – original draft. **Tao Su:** Validation, Supervision, Resources, Project administration, Funding acquisition, Data curation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no conflict of interest.

Data availability

No data was used for the research described in the article.

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