Review of Palaeobotany and Palynology 298 (2022) 104589

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

# New discovery of rare insect damage in the Pliocene of India reinforces the biogeographic history of Eurasian ecosystems

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## ARTICLE INFO

*Article history:*
Received 17 October 2021
Received in revised form 8 December 2021
Accepted 14 December 2021
Available online 17 December 2021

*Keywords:*
*Abroma*
Chotanagpur plateau
Fossil leaves
Paleoenvironment
Pliocene
Skeletonization

## ABSTRACT

Plant–insect interactions in the fossil record are, as yet, sparsely known and understudied. Here, we document evidence of a new type of insect skeletonization on *Abroma augustum* (L.) L. f. (Malvaceae) leaf remains from the latest Neogene (Pliocene) sediments of Chotanagpur plateau, Jharkhand, eastern India. This unique skeletonization feeding trace attributable to herbivorous insects occurs all over the surfaces of our recovered Pliocene leaf remains. In the skeletonized area, the interveinal tissues are completely removed leaving behind only the tough leaf veins. This type of insect feeding behaviour is documented for the first time on Indian Cenozoic leaf remains. Based on published data, as well as our survey of modern forests adjacent to the fossil locality, we suggest that probable damage inducers of this skeletonization on *Abroma* Jacq. fossil leaves might be Chrysomelid (Coleopteran) beetles. This finding also reveals that specific insect feeding damage, such as the one presented here, can reveal similarity of environments despite the difference of plant species observed. Such results strengthen the importance of using plant–insect interactions on leaves as a complementary proxy to others revealing paleoenvironmental conditions.

## 1. Introduction

Insect-feeding damage on plants provides insights into plant–insect interactions and has the potential for documenting the effects of extant, and ancient, environmental temporal and spatial gradients in respect of insect herbivory and the evolutionary diversification of the insect groups through geological time (Wilson, 1992; Wilf and Labandeira, 1999; Labandeira, 2002; Schoonhoven et al., 2005; Currano et al., 2008, 2010; Krassilov, 2008; Adams et al., 2010; Sohn et al., 2017). Feeding or chewing damage, perhaps the most widely recognised type of insect injury to plants, can take many forms such as hole feeding, margin feeding, surface feeding, galling, mining, skeletonization and so on. Leaf chewing adult insects have mouthparts with two opposing mandibles, or jaws, (Labandeira, 1997) and several insect orders have such chewing mouthparts, including beetles (Coleoptera), caterpillars (Lepidoptera), grasshoppers (Orthoptera), and termites (Isoptera).

Like other foliar feeding damages, one specific interaction between an insect and its host plant is leaf skeletonization. Leaf skeletonization is a type of surface feeding damage generally caused by leaf beetles (Coleoptera), but rarely caused by other insect groups such as Hymenoptera, Diptera and Lepidoptera (Hering, 1951). The insects feed by removing the soft and tender epidermal tissue leaving behind tough leaf veins. The skeletonized area can be reticulate or striate andgenerally depends on the venation pattern of the leaves of the host plant. However, in many cases, the insects do no not feed over the whole lamina, but leave areas of incomplete skeletonization in which a substantial amount of the lamina tissue remains intact (Sohn et al., 2017). This distinguishes insect induced skeletonisation from that produced from post mortem microbial decay, which tends to affect the whole lamina.

The history of plant–insect associations can be dated back to the Early Devonian (Labandeira, 2006, 2007; Labandeira and Currano, 2013; Feng et al., 2014). There are various records of insect-mediated damage preserved in diverse megafossil remains (Straus, 1977; Crane and Jarzembowski, 1980; Lang, 1997; Srivastava, 1987, 1998, 2007; Srivastava and Srivastava, 1998, 2010, 2016; Srivastava et al., 2000; Srivastava and Agnihotri, 2011; Labandeira, 2002; Banerji, 2004; Krassilov, 2008; Singh and Prasad, 2010; Winkler et al., 2010; Carvalho et al., 2014; Ding and Labandeira, 2014; Feng et al., 2014;

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https://doi.org/10.1016/j.revpalbo.2021.104589
0034-6667/

Khan et al., 2014, 2015; Ghosh et al., 2015; Sohn et al., 2017; Sohn et al., 2018; Zhang et al., 2018; Adroit et al., 2020; Hazra et al., 2020a; Giraldo et al., 2021). Such records provide a primary source of information on the evolutionary history of plant–insect association and the patterns of tissue consumption through geological time (Labandeira, 2013; Labandeira and Currano, 2013; Feng et al., 2014). Feng et al. (2014) reported the earliest evidence of insect-mediated skeletonization on leaves of *Dictyophyllum nathorstii* Zeiller, from the Late Triassic Yipinglang flora of south-western China. Leaf skeletonizations have also been reported from K-Pg boundary of Great Plains, USA (Donovan et al., 2014), but skeletonization is scarcely documented on Cenozoic angiosperm leaves (Labandeira, 2006, 2007; Vasilenko, 2006; Feng et al., 2014; Adroit et al., 2020).

Here, we report well-preserved and rare insect-mediated skeletonizations on *Abroma augustum* (L.) L. f. (Malvaceae) leaf remains from the Pliocene sediments of Jharkhand, eastern India. In the fossil record, only Adroit et al. (2020), and that was on *Parrotia* (Hamamelidaceae) leaves from the Pliocene sediments of Willershausen, Germany and the Miocene sediments of Shanwang formation of China. In this context, our discovery on a different host plant (*Abroma*) is therefore of significance and is documented for the first time on Indian fossil leaves.

## 2. Materials and methods

The fossil leaf remains displaying skeletonization were collected from an outcrop of latest Neogene (Rajdanda Formation) sediments exposed on the left bank of the Birha River in Mahuadanr Valley (23.3965°N, 84.1066°E; 353 m asl), Jharkhand, eastern India (Fig. 1). The outcrop exposes mostly shale (arenaceous and clayey) and sandstone, while the studied fossil leaves are preserved as impressions and compressions in greyish blue mudstones and light-brown diatomite. Earlier workers (Prakash et al., 1987; Srivastava and Bande, 1992; Hazra et al., 2020a) have considered the age of the Rajdanda Formation to be 'late Tertiary' (Pliocene), but till date no absolute (radiometric) dating has been carried out.

The fossil leaf specimens (Plates I, II, III); Figs. S1, S2, S3) required little preparation before photography as leaves that were not fully exposed in the initial fracture were simply revealed by careful removal of the overlying matrix using fine needles, scalpels and brushes. Macroscopic images of fossil leaf specimens (Plate I, II, III; Figs. S1, S2, S3) were photographed using a digital camera (Canon Power Shot A720IS). After photography, the photographs were edited only for contrast using image editing software Adobe Photoshop CS ver 7. The line drawings for accompanying figures and photographs were made using Corel

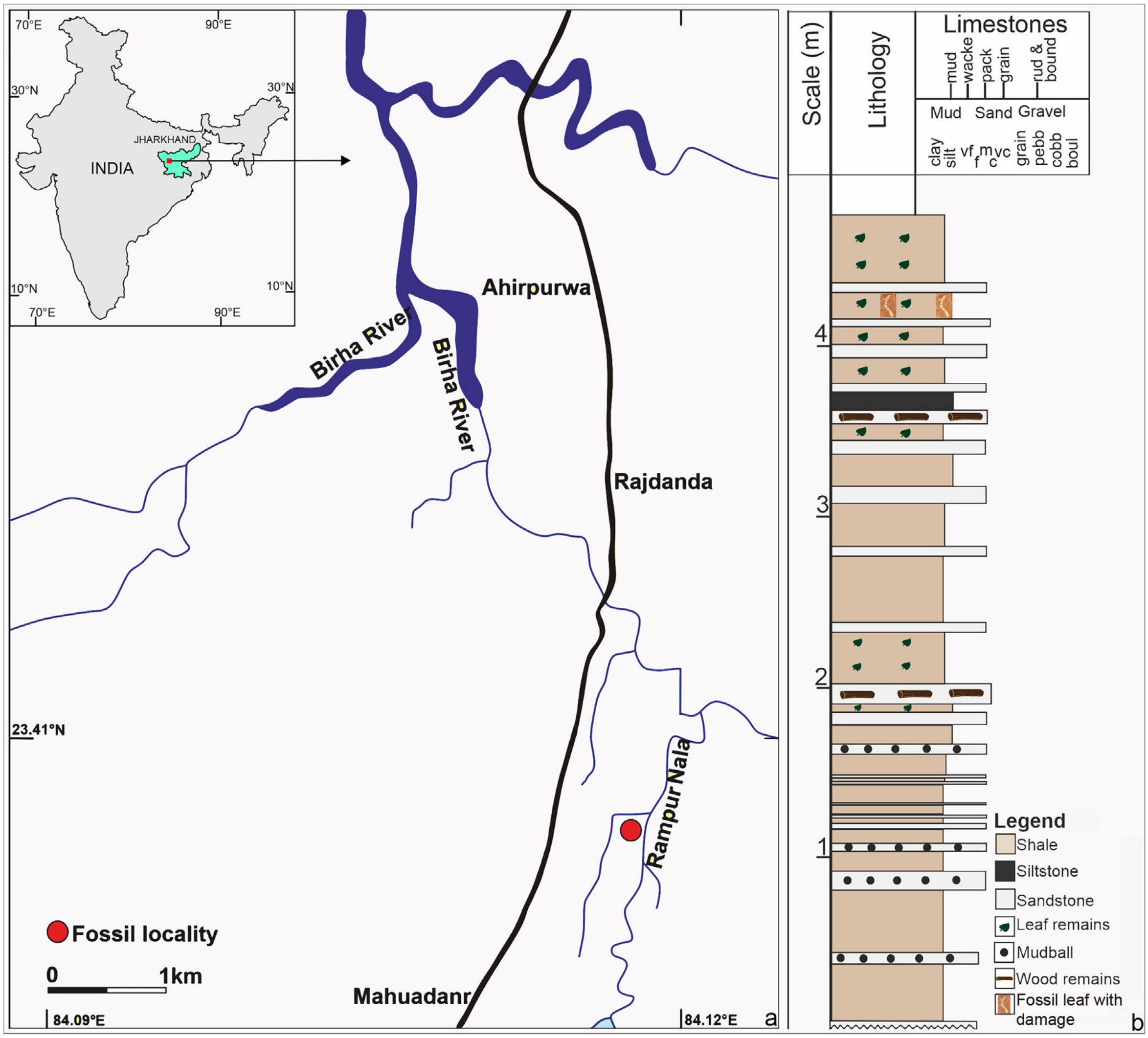

**Fig. 1.** (a) Geological map of Mahuadanr, Latehar district, Jharkhand (a part of the district resource map of Palamu district, Bihar published under the direction of Director General, Geological Survey of India, Kolkata), along with the fossil locality map; (b) generalised lithological section made using SedLog 3. 0 software showing litho-units with a composite graphic log of 3 m of exposed sedimentary section.

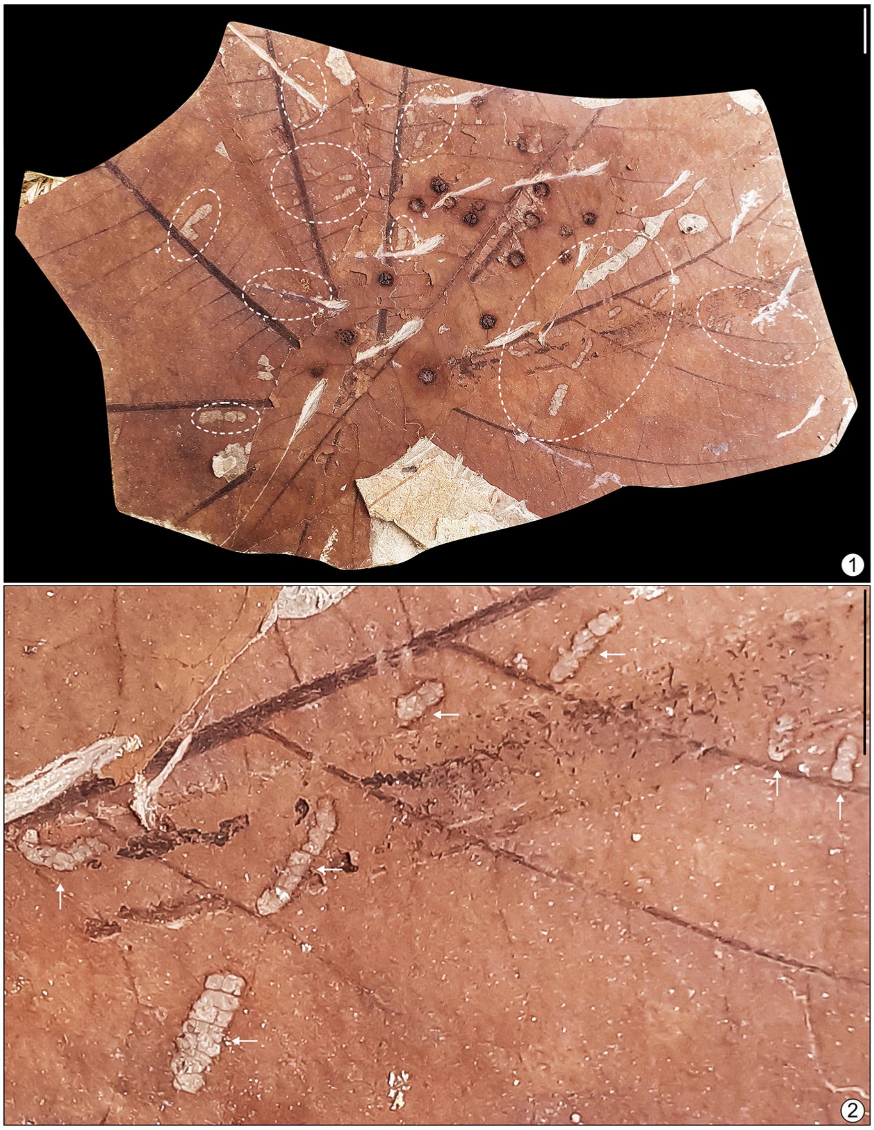

**Plate I.** Traces of skeletonization on the lamina surface of specimen SKBUH/PPL/JH/136A. (1) elongated to curvilinear skeletonization scattered all over the surface of the lamina; (2) Enlargement of A (arrows indicate insect mediated skeletonization). Scale bar = 1 cm.

Draw ver. 21 (Fig. 2; Fig. S1). We also surveyed the forests adjacent to the fossil exposures looking for similar feeding traces on modern leaves and photographed all the collected skeletonized modern leaves (Plate IV). The rational for doing this is that previous work has shown local floral and climatic similarities between the Pliocene and the modern (Hazra et al., 2020b). We followed the Labandeira et al. (2007) guide for identifying and classifying plant–insect interactions in the fossil. Morphological descriptions of fossil leaf specimens follow the terminology and nomenclature proposed by Dilcher (1974) and Ellis et al. (2009). The eleven fossil leaf specimens (SKBUH/PPL/JH/136A; SKBUH/PPL/JH/136B; SKBUH/PPL/JH/137; SKBUH/PPL/JH/138A; SKBUH/PPL/JH/138B; SKBUH/PPL/JH/139; SKBUH/PPL/JH/155; SKBUH/PPL/JH/156; SKBUH/PPL/JH/157; SKBUH/PPL/JH/158; SKBUH/PPL/JH/165) are housed in the Museum of the Palaeobotany and Palynology Laboratory, Department of Botany, Sidho-Kanho-Birsha University (SKBUH), Purulia.

## 3. Results

We have collected eight leaf specimens with skeletonization feeding traces from the Pliocene sediments of Jharkhand, eastern India. We also reconstructed an insect-mediated damaged leaf remain of *Abroma* (Fig. 3). The feeding trace recorded in this study did not match any of the fossil DTs described by Labandeira et al. (2007). The skeletonization DTs in this investigation are represented as damage type DT297 of Adroit et al. (2020).

### *3.1. Damage type (Plates I, II, III; Fig. 2; Fig. S1)*

The feeding trace is scattered across the surface of the lamina avoiding only main veins and exhibits elongated to curvilinear skeletonization subdivided in a row of many holes resembling a chain. This elongated to curvilinear structure is approximately 1–2 cm long. Each hole is usually rectangular with rounded corners, ~2 mm length. The number of holes per chain varies from 2 to 15. However, most traces bear 4–10 holes per chain. The lines separating individual holes are very thin, commonly inconspicuous or sometimes missing. The margin of the trace is dark, thick and distinct. This dark scar is due to reaction tissue being produced in the leaf lamina after being attacked by feeding insect (Schoonhoven et al., *2005*). *This dark scar makes it possible to* distinguish it as a herbivory trace made by an insect during the leaf's lifespan as distinct from a detritivorous trace made after abscission (Labandeira, 2002;

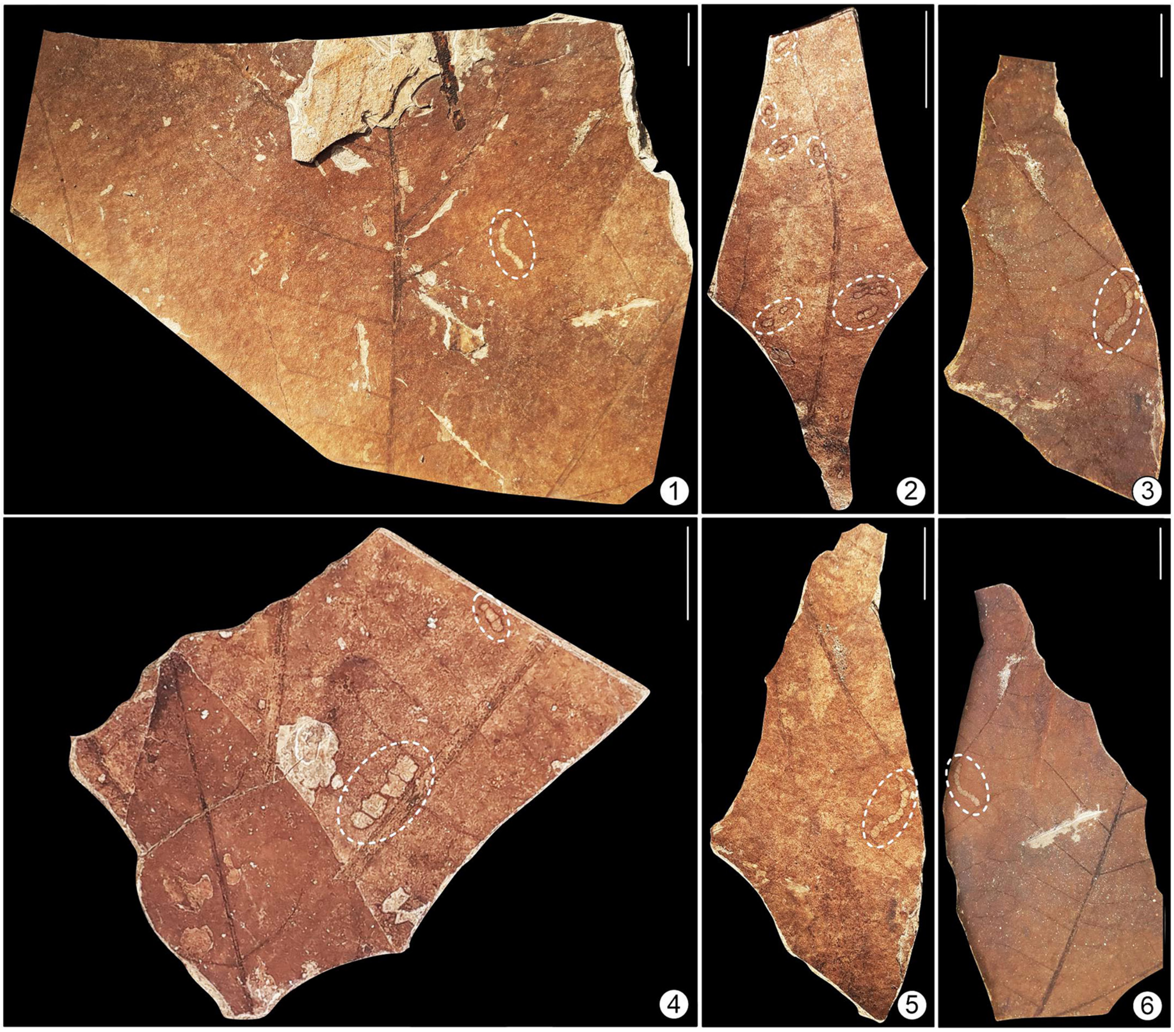

**Plate II.** (1–6) Fossil specimens of *Abroma* showing skeletonization on the lamina surface (marked in white oval). (1, 3, 5 and 6) curvilinear skeletonization divided in a row of many holes resembling a chain (SKBUH/PPL/JH/139; SKBUH/PPL/JH/156; SKBUH/PPL/JH/158 and SKBUH/PPL/JH/165); (2 and 4) linear skeletonization scattered on the lamina surface with row of many holes (SKBUH/PPL/JH/155; SKBUH/PPL/JH/157) Scale bar = 1 cm.

Labandeira et al., 2007). Following the Adroit et al. (2020) protocol, we measured almost all the DT297 occurrences in terms of length, width and surface area, and counted the number of holes for each occurrence (Table S1). Some damages that could be identified as DT297 have been excluded from these measurements because the preservation was not good enough to be certain about the various dimensions. Overall, the size of DT297 can vary significantly in terms of surface area and length. The smallest damage is ca. 3.4 mm$^2$, while the largest ones reach ca. 25.4 mm$^2$. However, these raw measurements do not take into account the leaf surface area, because it was not always possible to measure that due to leaf fragmentation and partial preservation. The width is uniform along the length of each damage occurrence and quite similar among the different DT297 instances observed. All detailed measurements can be found in the spreadsheet Table S1.

### 3.2. Host

*Abroma augustum* (L.) L. f. (Family: Malvaceae) (Plate I; Figs. S2, S3)

Leaf symmetrical, lamina well-preserved, complete, mesophyllous, palmately lobed (five lobed), length 10–15 cm; width 10–14 cm; broadly ovate shape; odd-lobed acute apex, base cordate, margin slightly dentate; petiole well preserved, 4–10 cm; primary venation suprabasal actinodromous i.e., seven veins diverging radially from a single point; secondary venation brochidodromous, moderately curved near the margin, irregularly spaced; angle of divergence acute; tertiary venation percurrent, sometimes branched, oblique in relation to primary veins, predominantly alternate and distant; quaternary veins very faint.

Remarks: The large size, lobed laminae, acute apices, cordate bases, suprabasal actinodromous venation with seven primary veins arising from a single point are the important characters of the fossil leaf. The above-mentioned combination of characters shows close resemblance to modern leaves of *Gossypium herbaceum* L., *Sterculia colorata* Roxb., *Pterygota mildbraedii* Engl. and *Abroma augustum* (L.) L. f. However, the detailed morphological study of the leaves of the above-mentioned species indicates a strong affinity of the fossil leaves to the leaf of extant *A. augustum* in shape, size and venation pattern.

*Abroma* Jacq. is a monotypic genus, with the sole species being *A. augustum, which is* widely distributed in tropical Asia, South and eastern Africa, and Australia (Gupta et al., 2011; POWO, 2019). It is found both in the wild and is cultivated, throughout the hot and moist regions of India from the Punjab and Uttar Pradesh eastwards to Arunachal Pradesh, Assam, Meghalaya and Tripura, ascending to 1200 m, and southwards in peninsular India. It is also cultivated for medicine as well as an ornamental. This taxon is also very common in the forests of the Chotanagpur region (Wood, 1902).

**Plate III.** Enlargement of traces of skeletonization. (1–2) curved skeletonization; (3–9) elongated skeletonization. Scale bar = 1 cm.

## 4. Discussions

Skeletonization is a distinctive kind of insect feeding behaviour in which an insect feeds on the whole thickness of the leaf including both the upper and lower epidermis, while the tough veins remain intact, so that the skeleton of the leaf is preserved. Feeding on tough veins often results in considerable wear and tear of the mandibles of many insect species and thereby, insects leave the tough veins (Crepet and Friis, 1987). Thus, the feeding behaviour of leaf skeletonising insects is quite different from those that cause external foliage, such as hole or margin feeding (Feng et al., 2014). Not only the feeding behaviour, but leaf nitrogen levels are also regarded as an important determinant of

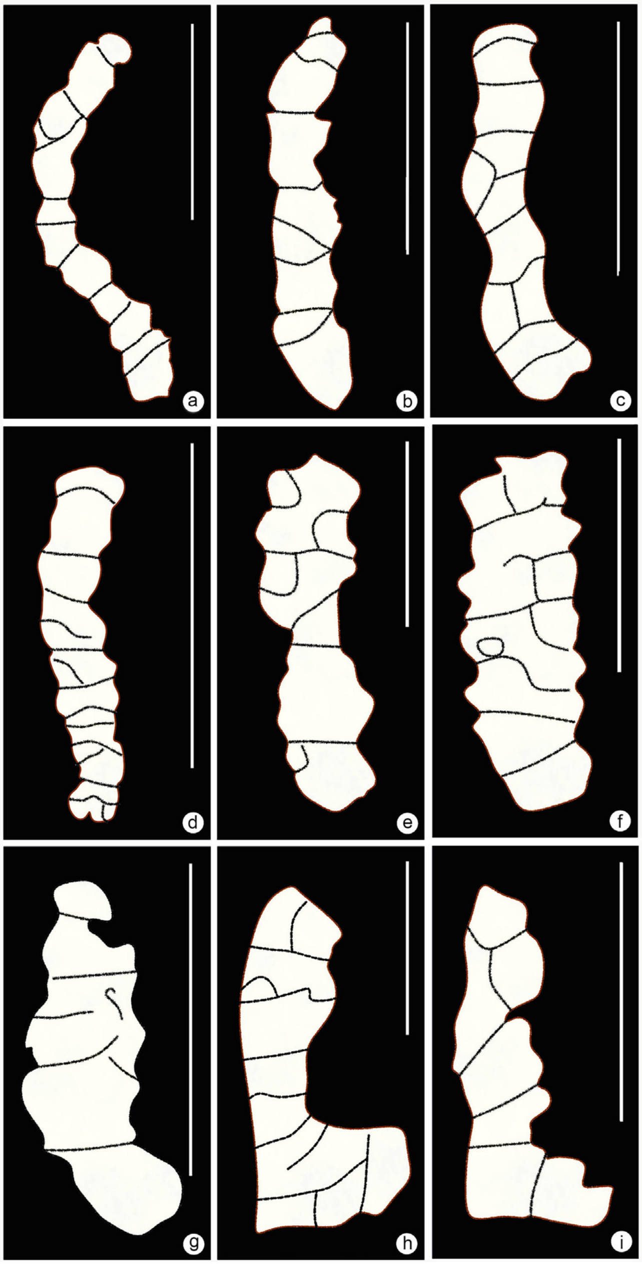

**Fig. 2.** Line drawing of various types of elongated to curvilinear skeletonization feeding traces. Scale bar = 1 cm.

leaf quality for herbivorous insects (Sinclair and Hughes, 2010; Feng et al., 2014). The preference of insects to feed on particular plant tissues can either be enhanced by phagostimulants or reduced by anti-herbivore defences such by reducing the digestibility and nutrient content (Theis and Lerdau, 2003; Feng et al., 2014). Different insects prefer to target different portions of the leaf lamina according to the physical and chemical properties of the plant tissues (Schoonhoven et al., 2005). However, skeletonization tends to be generated mainly by holometabolous insects belonging to Coleoptera (Bernays and Janzen, 1988), even if some members of Hymenoptera, Diptera and Lepidoptera can also skeletonize leaves (Bernays and Janzen, 1988).

Our study documents, for the first-time, the evidence of the rare damage type DT297 on the surface of fossil leaf remains of *Abroma* recovered from the Pliocene sediments of Jharkhand, eastern India. Our discovery of fossil skeletonised *Abroma* leaves provides direct evidence of the continuous relationship between plants and herbivorous insects since Pliocene. It is evident from our specimens that the interveinal tissues were selectively targeted, and the larger vascular bundles were conspicuously avoided, probably because of their coarse texture and low nutritive values. The evidence of the feeding pattern on our fossil leaves takes the form of traces characterised by elongate to curvilinear skeletonization in a row of several holes scattered randomly on the surface of lamina, either between or over the veins, and sometimes follows a linear pattern.

This rare DT297 damage type was noticed for the first time in the fossil record by Straus (1977) on the fossil leaves of *Parrotia* from the German Willershausen (Pliocene) locality (Fig. 4). Recently, Adroit et al. (2020) discovered this specific type of skeletonization on other *Parrotia* leaves in both the fossil record (China) and modern forests (Iran). The damage measurements made in this study present DT297 damage that is, on average, significantly larger and longer (ca. 11.8 mm$^2$ of surface area; 8.2 mm length; 1.3 mm large) than the ones previously measured on *Parrotia* leaves (ca. 4.1mm$^2$ of surface area, 5.42 mm of length, 0.62 of large) (Adroit et al., 2020). However, such direct comparison is not fair because for our fossil specimens, the leaf blade could not be measured due to their partial preservation and fragmentation during recovery. It means that our DT297 measurements cannot be related directly to leaf area. Finally, these new observations add to the previous ones and allow us to further refine the description of DT297.

We have extensively surveyed the modern tropical forests adjacent to the fossil exposures to compare our fossil skeletonization leaf feeding traces with those in extant vegetation. We have noticed the existence of similar types of feeding traces on modern leaves from different angiosperm taxa namely, *Zizyphus* sp. (Rhamnaceae), *Desmodium* sp. (Fabaceae), *Tilia* sp. (Malvaceae), *Shorea* sp. (Dipterocarpaceae), and *Solanum* sp. (Solanaceae) (Plate IV). In addition, various authors have reported similar types of skeletonization damage patterns in different modern angiosperm taxa, namely *Lantana* (Verbenaceae), Fabaceae, *Cistus* sp. (Cistaceae), *Ziziphus mauritiana* (Rhamnaceae) (Świętojańska et al., 2014). Świętojańska et al. (2014) reported a similar type of skeletonization pattern to that seen in our fossil specimens on various *Cistus* leaves. So, based on the above-mentioned published data, as well as our survey in the modern forests adjacent to the fossil locality, we suggest that probable damage inducers of our skeletonization on *Abroma* fossil leaves might be Coleopteran beetles, especially Chrysomelid beetles that cause morphologically similar damage traces on modern leaves of several angiosperm taxa. Our interpretation fits with that of Straus (1977) who suggested the damage type DT297 on *Parrotia* fossil leaves from Willershausen (3 Ma, Germany) could have been produced by *Chrysomelidae* larvae. In addition, such assumptions have been restated by Adroit et al., (2020) who also observed DT297 on *Parrotia* fossil leaves in Shanwang (15 Ma, China) and on their modern analogues *P. persica* (Hyrcanian forest, Iran) and *P. subaequalis* (Yixing forest, China). In the same vein, our comparative study of leaf-feeding skeletonization caused by Coleopteran beetles on modern leaves shows they are similar to the feeding patterns seen in our fossil leaves of *Abroma,* suggesting no marked change in leaf-feeding strategies of this type of herbivorous insect since the Pliocene. Our recent finding also suggests that the same damage inducers (Coleopteran beetles) were active in the monsoon-influenced Pliocene evergreen forest of the Chotanagpur plateau, eastern India. This is consistent with the occurrence of some fossil Coleoptera larva (Grub) from the fossil locality (Fig. S4).

It is interesting to note that at present on the Chotanagpur plateau, these rare skeletonization feeding traces are not found to be associated with the host genus *Abroma*, but they are still found to be associated with another taxon (*Tilia*) of the same host family Malvaceae (Plate IV). So, based on modern and present fossil evidence, it seems that in the eastern Indian area Chrysomelid beetles have not changed their host preference at the family level since the Pliocene. Our observations are similar to the ones made by Adroit et al. (2020) on the

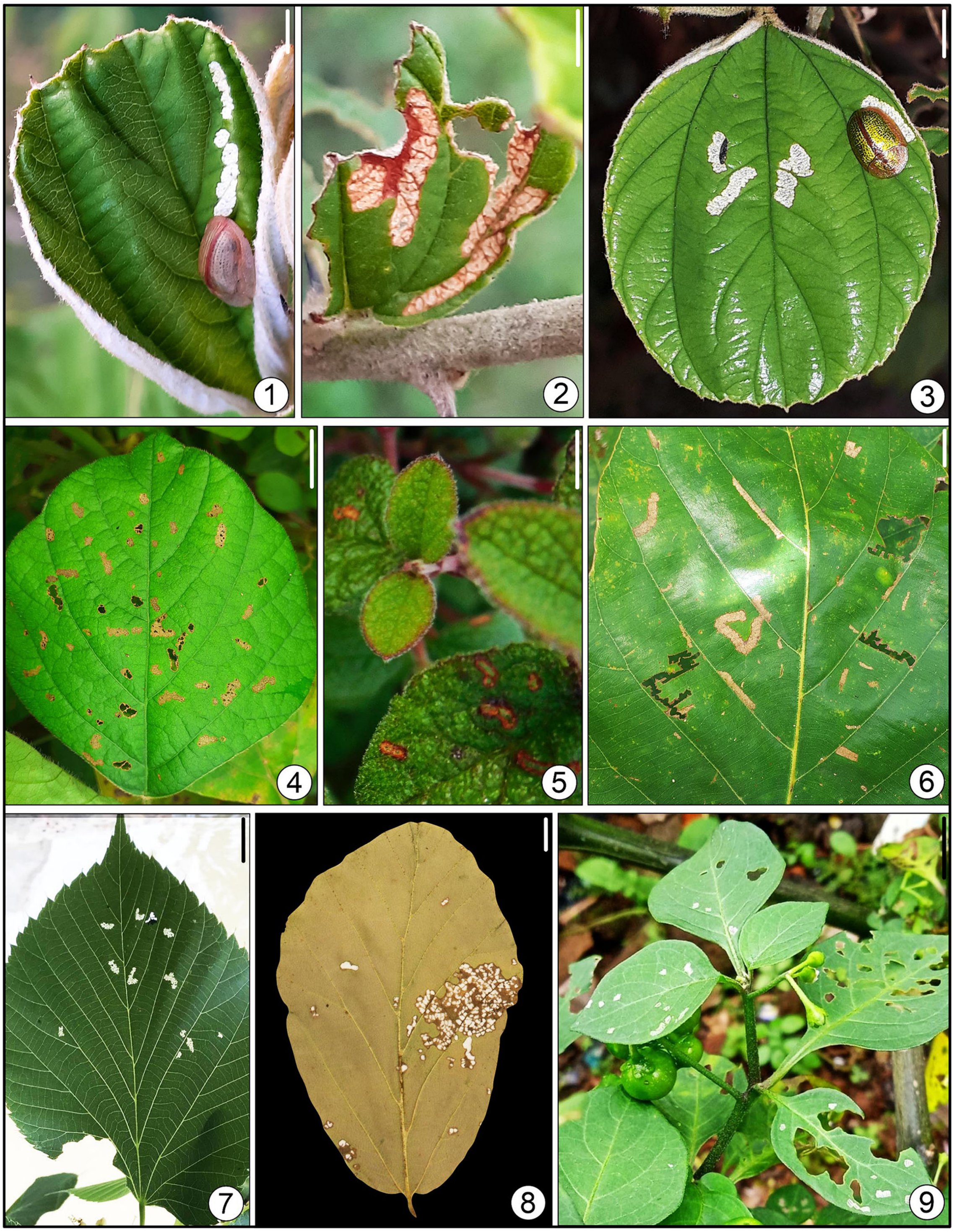

**Plate IV.** Skeletonization on modern angiosperm leaves inflicted by Coleoptera. (1–3) skeletonization on leaves of *Zizyphus* induced by the Tortoise beetle *Cassida*; (4) skeletonization on leaf of *Desmodium* sp.; (5) elongated rectilinear skeletonization on a leaf of *Cistus* sp.; (6) elongated to curvilinear skeletonization on a leaf of *Shorea* sp., (7) skeletonization on a leaf of *Tilia* sp.; (8) elongated to curvilinear skeletonization on a leaf of *Parrotia* sp.; (9) skeletonization on leaves of *Solanum* sp. Scale bar = 1 cm.

Hamamelidaceae and support the assumption that DT297 could be intimately related to a specific plant family in a geographic area. However, our results are not consistent with a previous assumption that an exclusive relationship between *Parrotia* and the damage type DT297 might exist. Nevertheless, such specific insect feeding DT297 could relate of similar chemical and/or nutrient quality of these plant taxa (*Parrotia*, *Tilia* and *Abroma*) for the insect, and then could suggest close ecological niche of these plants in their respective geographic areas and times. Specific and specialised insect damages such as the one observed in our study, could reveal similarities between two paleoecosystems that description of plant species alone may not highlight (Adroit et al., 2021).

At least, in our case, there are no obvious changes in leaf architecture, such as differences in vein density, that might indicate why there might have been a switch in host preference at the genus level and this suggests external environmental factors may have played a role. Since Pliocene time in this part of eastern India published qualitative

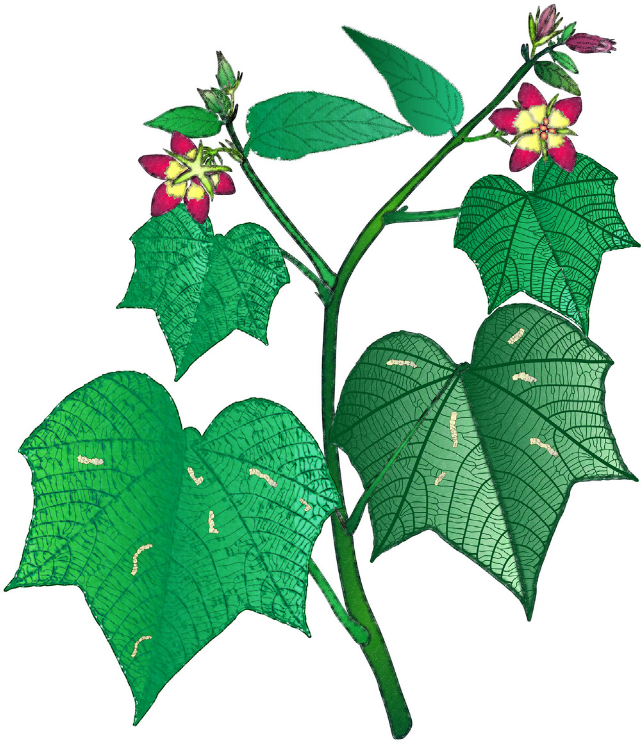

**Fig. 3.** Hypothetical reconstruction of insect-mediated skeletonized *Abroma* leaf.

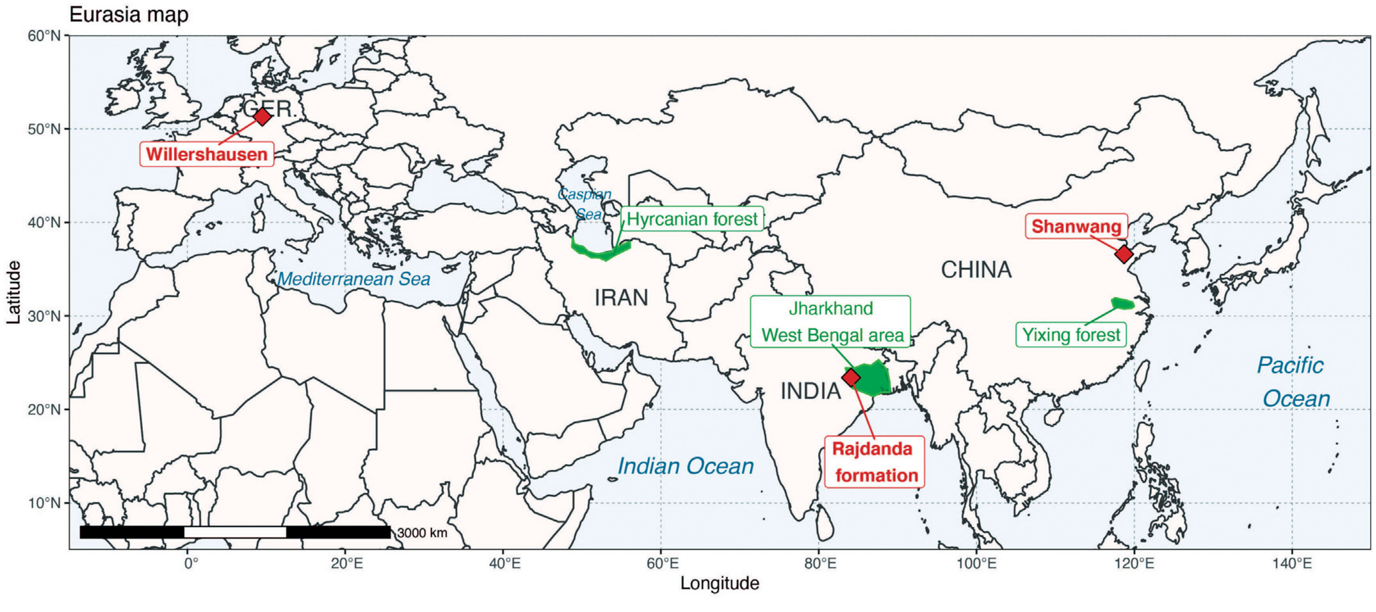

**Fig. 4.** Map of the Eurasian continent showing where the damage type DT297 has been observed on fossil leaves (red dots) and modern leaves (green zones).

(Singh and Prasad, 2007, 2008, 2009a, 2009b, 2009c; Hazra et al., 2021) and quantitative climatic data (Hazra et al., 2020b) suggest that during Pliocene time the monsoon in the Jharkhand area of eastern India was slightly weaker than now, with a wetter dry season.

## Declaration of Competing Interest

The authors declare that they have no competing interests.

## Acknowledgments

TH, MH and MAK gratefully acknowledge the Department of Botany, Sidho-Kanho-Birsha University for providing infrastructural facilities to accomplish this work. BA acknowledges Department of Botany, Sidho-Kanho-Birsha University for its kind invitation in order to contribute to that present manuscript. RAS and TEVS were supported by NERC/NSFC BETR Project NE/P013805/1. SB acknowledges the Centre of

Advanced Study (Phase-VII), Department of Botany, University of Calcutta for providing necessary facilities.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2021.104589.

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