Plant–insect interaction patterns in the late Neogene palaeoforest of Chotanagpur Plateau, eastern India

How to cite:

For guidance on citations see FAQs.

© 2022 Elsevier B.V. All rights reserved.

https://creativecommons.org/licenses/by-nc-nd/4.0/

Version: Accepted Manuscript

Link(s) to article on publisher’s website:
http://dx.doi.org/doi:10.1016/j.revpalbo.2022.104633

Copyright and Moral Rights for the articles on this site are retained by the individual authors and/or other copyright owners. For more information on Open Research Online's data policy on reuse of materials please consult the policies page.

oro.open.ac.uk
Plant–insect interaction patterns in the late Neogene palaeoforest of Chotanagpur Plateau, eastern India

Manoshi Hazra, Robert A. Spicer, Taposhi Hazra, Subhankar Kumar Sarkar, Teresa E.V. Spicer, Subir Bera, Mahasin Ali Khan

PII: S0034-6667(22)00031-8
DOI: https://doi.org/10.1016/j.revpalbo.2022.104633
Reference: PALBO 104633

To appear in: *Review of Palaeobotany and Palynology*

Received date: 23 October 2021
Revised date: 11 February 2022
Accepted date: 16 February 2022


This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

© 2022 Published by Elsevier B.V.
Plant-insect interaction patterns in the late Neogene palaeoforest of Chotanagpur Plateau, eastern India

Manoshi Hazra¹, Robert A. Spicer² ³, Taposhi Hazra¹, Subhankar Kumar Sarkar⁴, Teresa E. V. Spicer², Subir Bera⁵ and Mahasin Ali Khan¹*

¹Palaeobotany-Palynology Laboratory, Department of Botany, Sidho-Kanho-Birsha University, Ranchi Road, Purulia-723104, India

²CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Mengla 666303, P.R. China

³School of Environment, Earth and Ecosystem Sciences, The Open University, Milton Keynes, MK7 6AA, UK.

⁴Entomology Laboratory, Department of Zoology, University of Kalyani, Kalyani, Nadia, West Bengal-741235, India

⁵Centre of Advanced Study, Department of Botany, University of Calcutta, 35, B.C. Road, Kolkata-700019, India

*Corresponding author

E-mail: khan.mahasinali@gmail.com
Abstract

Plants and insects are essential components of terrestrial ecosystems and insect herbivory is the most important type of biotic interaction in these ecosystems alongside the role of insects as pollinators. Insect damaged fossil leaves are the only direct sources of documenting the historical effect of folivorous arthropods on once living foliar tissue. The present study focuses on the patterns of plant-insect association for the Pliocene locality of the Chotanagpur Plateau, Jharkhand, eastern India. Out of 1500 fossil angiosperm leaves that were studied, 1080 leaves (72%) were damaged. About 37 damage types (DTs) representing six functional feeding groups (FFGs) were identified, i.e., galling (50.74%), margin feeding (23.24%), hole feeding (17.04%), skeletonization (1.94%), mining (2.22%), surface feeding (3.33%) and others (1.49%). Galling is the prevalent form of damage here. The host plant taxa bearing the damage types belonged to Fabaceae, Malvaceae, Anacardiaceae, Moraceae, Rhamnaceae, Rubiaceae, Myrtaceae, etc. On the basis of comparison with extant taxa, possible culprits could have belonged to the insect orders Orthoptera, Coleoptera, Lepidoptera, Diptera, Hemiptera, and Hymenoptera. The evidence of numerous body fossils of Lepidoptera (caterpillar), Diptera (gall midge), and Hemiptera from our studied sedimentary section provides direct clues to the plant-insect interaction. It seems the tropical, predominantly humid, Pliocene climate favored large-scale herbivory in the palaeoforest of Jharkhand, eastern India.

Keywords: Fossil leaves; Insect damage; Jharkhand; Neogene; Palaeoclimate; Palaeoecology

1. Introduction
Plants and insects occupy a wide range of niches, from those of hot deserts to those of the arctic zone, and interaction between them is ubiquitous (Coenye and Vandamme, 2003; Behmer and Joern, 2008; Calatayud et al., 2018). Three common types of interactions occur mutualistic, antagonistic, and commensalistic. Among these, antagonistic relationships include phytophagy by insects where one counterpart benefits and the other is harmed (Calatayud et al., 2018). Plant fossils preserve information on many aspects of such insect behaviour in the form of feeding, mining, galling, oviposition, etc. (Wappler, 2010; Wappler and Denk, 2011; Knor et al., 2013). The study of plant-insect interactions provides important information about the ecology of feeding behaviour and the interrelation between the host plant and the producer insect (Wappler et al., 2012).

The study of Cenozoic insect herbivory is particularly important as it allows us to understand how climate change has affected ecosystems at basic trophic levels on the evolutionary pathway to the modern condition, and how things may continue to change under future warming. Of particular interest are the Pliocene, mid-Miocene, and Eocene because these can be regarded as possible analogues for future climate conditions as atmospheric CO₂ continues to rise.

Numerous studies have been conducted worldwide on Cenozoic insect herbivory and it provides a window into the evolution of many insect and plant interactions that make up our modern ecosystems. Some of the important localities in the world depicting plant-insect association during the Cenozoic include the Bighorn Basin of Wyoming (PETM boundary; Currano et al., 2008), Eocene flora of Laguna del Hunco, Argentina (Wilf et al., 2005), Oligocene (27–28 Ma) leaf localities in the Chilga Basin, northwest Ethiopia (Currano et al., 2011), Miocene deposit at Bílina Mine Most Basin, Czech Republic (Knor et al., 2012), the Late Pliocene Longmen Flora, Yunnan, China (Su et al., 2013) and Pleistocene deposits of Bernasso, France (Adroit et al., 2016).
Reports of plant-insect interaction are mainly from the Siwaliks, a Neogene succession deposited in the Himalayan foredeep now undergoing rapid uplift (Lavé and Avouac, 2000). These include the Miocene Dafla Formation, the Pliocene Subansiri Formation, the Plio-Pleistocene Kimin Formation of Arunachal Siwalik Himalaya, and the Miocene Gish Clay Formation of Darjeeling sub-Himalaya (Khan et al., 2014a, 2015). The damage types in the leaf fossils of Siwalik Himalaya include five Functional Feeding Groups (FFGs): hole feeding, margin feeding, mining, galling, and skeletonization, showing that a variety of plant-insect interactions were present in the Siwalik monsoon-influenced forests during the middle Miocene times.

The Pliocene climate of the Indian subcontinent was characterized by a strong monsoon within a generally year-round humid regime and diversification of native vegetation, which in turn led to increased biotic interaction between angiosperms and arthropods (Khan et al., 2014a, b). Patterns of leaf damage by foliar herbivores have been documented previously in India (Banerji, 2004; Srivastava and Agnihotri, 2011; Srivastava and Srivastava, 2016) but there are very few records from Pliocene localities of eastern India (Khan et al., 2014b). The present census study is undertaken with the aim of investigating different types of FFGs produced by insects on impressions of angiosperm fossil leaves from the Pliocene, Rajdanda Formation, Chotanagpur Plateau, eastern India.

2. Materials and methods

During palaeobotanical fieldwork conducted in 2018, 2019, 2020, 2021, and 2022 a large number of compression and impression leaf fossils were recovered from river-cutting sections of the latest Neogene (Pliocene: Rajdanda Formation) sediments in Mahuadanr Valley (23.3965°N, 84.1066°E; altitude 353 m a.s.l.) of Jharkhand, Chotanagpur Plateau, eastern India (Fig. 1). The fossil leaves were examined carefully for in vivo insect damage.
All the specimens were photographed using a high-resolution digital camera. For the recognition, identification, and description of the folivory damage patterns, the initials DT (Damage Type) and the corresponding number for the different types were used, according to the guide book “Guide to Insect (and Other) Damage Types on Compressed Plant Fossils” by Labandeira et al., (2007).

Nearly 1500 fossil leaves were collected from the Pliocene sediments, of which 1080 angiosperm leaves were sufficiently well-preserved for this study (Fig. S1). All analyses presented here are based on quantitative data (the herbivorized leaf area) and qualitative data (the number of Functional Feeding Groups, FFGs; Damage Types, DTs observed) for recovered damaged leaf specimens. The damage types in the leaf fossils include six Functional Feeding Groups (FFGs): hole feeding, margin feeding, surface feeding, mining, galling, and skeletonization (Plates I, II, III, IV, V, VII). Modern angiosperm leaves bearing such damages were also collected from near the fossil site for comparative study (Plate VII; Fig. S1). Line drawings of the leaf remain to have the various damage types and insects to depict the palaeoenvironmental reconstruction of the ancient forest were made using Corel Draw ver. 20 (Fig. 2). All the fossil specimens are housed in the Palaeobotany-Palynology Laboratory, Department of Botany, Sidho-Kanho-Birsha University, Purulia, India (SKBUH).

3. Geologic setting of the fossil locality

The fossil locality, Rajdanda Formation, Mahuadanr Valley (23.3965°N, 84.1066°E), Jharkhand, lies on the left bank of Birha River and is exposed over a length of 2.6 km and is 1.5 km wide (Fig. 1). The section reaches a maximum thickness of 5 m within which the dominant lithology is shale and sandstone. The structural dip of the unit varies from 2-5° towards the northwest. The shale layer is composed of silty clay to clay-sized grains. "Paper
shales’ with fine millimeter-scale laminations also occur. Lenses of yellowish-brown sandstones are intercalated between the shale layers. The fossil leaves, representing mostly dicotyledonous angiosperm leaf impressions and compressions, are well preserved in the upper 2.5 m of the shale unit. The presence of authigenic pyrite occurring within the fossiliferous shale layers, and the overall sedimentary package, indicates a low oxygen floodplain lake environment (Kumar et al., 2000; Bajpai et al., 2001). Previous palaeobotanical studies from the Rajdanda Formation have reported a rich and diverse assemblage of fossil specimens including leaves and fruits (Bande and Srivastava, 1990; Srivastava and Bande, 1992; Srivastava et al., 1990; Singh and Prasad, 2007, 2008, 2009a, b, 2010; Hazra et al. 2020; Hazra et al. 2021a, b, c).

Previous workers (Prakash et al., 1987; Srivastava and Bande, 1992; Guleria, 1992; Srivastava et al., 1992; Singh and Prasad, 2010; Singh and Chauhan, 2008) have assigned the age of the Rajdanda Formation to the ‘late Cenozoic’ (Pliocene) based on megafossil records and palynological analysis. The district resource map as published by the Geological Survey of India of Palamau, Jharkhand, also assigns a Pliocene age to the Rajdanda Formation.

4. Results

4.1. Categories of folivory

Of the 1080 specimens studied in the present study, the 37 damage types (DTs) mostly fall within six FFGs: Galling, margin feeding, hole feeding, skeletonisation, mining, and surface feeding (Tables 1, 2). Galling constituted (50.74%) of all damage type occurrences, followed by margin feeding (23.24%), hole feeding (17.04%), surface feeding (3.33%), leaf-mining (2.22%), and skeletonization (1.94%). Just 10% of leaves had two damage types and damage types more than two were found only on a few specimens (2.89%).
Margin feeding (Plate I)

In margin feeding, the insect makes shallow to deep excisions wherein the tissues may be removed from the leaf margin to the apex of the leaf (Gangwere, 1966; Heinrich, 1979; Heinrich and Collins, 1983; Labandeira et al., 2007; Vesilenko, 2007; Schachat, et al., 2014; Hazra et al., 2021b).

Margin feeding DTs in this investigation are represented as DT 12: semi-circular, shallow to deep excisions along the leaf margin that measure 8–15 mm in width and are 10–16 mm deep (Plate I 3, 4, 5, 9, 10); DT 13: excisions removing the leaf apex that are 8–32 mm deep (Plate I 2); DT 14: Margin feeding traces that reach the midvein, measure 10–26 mm in width and are 8–75 mm deep (Plate I 1, 2, 7, 8); DT 81: cuspate shaped excisions with diameters of ~1.8 mm (Plate I 6).

Host plants: Galactia sp., Rhamnus sp., Rutaceae, Ficus sp. (Moraceae), Malvaceae, Fabaceae, Rubiaceae, Anacardiaceae

Inferred culprits: Lepidopteran caterpillars, Coleoptera

Hole feeding (Plate II)

Hole feeding is the consumption of the entire thickness of a leaf blade that is circumferentially enveloped by unaltered leaf tissue (Heinrich, 1979; Heinrich and Collins, 1983; Labandeira et al., 2007; Schachat, et al., 2014; Hazra et al., 2021b). In fossils, the colour of the removed area mimics the surrounding rock but is different from that of the leaf blade. Hole feeding DTs are generally defined by a combination of hole size and shape, whereas damage from more complex modes of hole feeding is defined by shape.

Hole feeding DTs in this investigation are represented as DT 2: Circular and ellipsoidal holes measure 2–11 mm in diameter (Plate II 1, 2, 4, 8, 11); DT 3: polylobate holes range between 0.8–12 mm diameter (Plate II 3, 5, 6, 7); DT 5: polylobate holes range
between 10–12 mm diameter (Plate II 9); DT 8: rectilinear hole with length: width ratio = 2:1 (Plate II 10).

Host plants: *Rhamnus* sp. (Rhamnaceae), *Albizia* sp., *Galactia* sp. (Fabaceae), Rutaceae, Fabaceae, Combretaceae, Anacardiaceae

Inferred culprits: Lepidopteran caterpillars, Coleoptera

**Skeletonization** (Plate III)

In the skeletonized area, the interveinal tissue is generally removed between the vein meshwork (Ranney et al., 1992; Gu et al., 2008; Beenen and Roques, 2010; Feng et al., 2014). Therefore, the colour of the skeletonized area is the same as that of the surrounding rock. Locally, even minor portions of the secondary and subsidiary veins are removed, exposing the midvein, and, lateral veins. It is hard to differentiate skeletonization from natural decomposition, especially in fossil leaves. If the remains of the fossil leaf are still intact and the tissue is missing only in a few areas, then it is a skeleton trace fossil.

Skeletonization DTs in this investigation are represented as DT 16: irregularly shaped skeletonization patches with no reaction rims (Plate III 2, 3, 8); DT 19: rectangular skeletonized area (Plate III 7); DT 297: feeding traces scattered across the surface of the lamina avoiding only main veins and exhibits elongated (1–2 cm long) skeletonization, divided into a series of many chain-like holes (Plate III 6); DT 24: ovoidal shaped skeletonization adjacent to 1° or 2° veins (Plate III 4, 5); DT 21: skeletonization where there is maximum removal of the finest venation (Plate III 1).

Host plants: *Abroma* sp. (Malvaceae), *Mangifera* (Anacardiaceae)

Inferred culprit: Coleoptera

Surface feeding (Plate IV)
Unlike skeletonization, the interveinal tissue of surface feeding is generally not removed between the vein meshwork (Donovan et al., 2018; Fiene et al., 2013; Adati and Matsuda, 1993). Surface feeding is different from skeletonization in the colour of the damaged area. In skeletonization, the colour of the damaged area is the same as that of the surrounding rock. However, in surface feeding, the colour of the surface area is different from that of the remaining tissues and the surrounding rock.

Surface feeding DTs in this investigation are represented as DT 29: polylobate surface abrasions with poorly developed reaction rims (Plate IV 1, 2, 4, 5, 7, 8); DT 82: polylobate window feeding, ~ symmetrical about 1° or 2° vein (Plate IV 3, 6, 9).

Host plants: Fabaceae, Indeterminate dicot leaf remains
Inferred culprits: Diptera, Coleoptera

Galling (Plate V)

Galls (Cecidia) are cells, tissues, or plant organs modified by hypertrophy and/or hyperplasia induced by parasitic or pathogenic organisms (Stephenson and Scott, 1992). They are circular to ellipsoidal in shape and are surrounded by protective and commonly hardened or woody tissue.

Galling DTs in this investigation were represented as DT 34: circular galls on 2° veins, measure 0.8–2.0 mm in diameter (Plate V 1, 3); DT 33: circular galls on 1° vein, measure 1.5–2.0 mm in diameter (Plate V, 4); DT 32: circular to ellipsoidal; avoiding major veins (Plate V 6, 11, 12); DT 85: elongate, elliptical, striated; on mid-vein (Plate V 4, 9); DT 80: small, hemispherical; thoroughly carbonized, diameters ~ 0.1 - 1.0 mm, 1° and 2° veins avoided (Plate V 7, 13); DT 145: spheroidal, large central chamber surrounded by a thick wall and second tissue layer, outermost layer thin (Plate V 5, 8, 14); DT 52: circular, with
fusianized tissue in radiating partitions (Plate V 10); DT 144: multiloculate, dark inner core, surrounding smooth surface and circular margins, often fused (Plate V 15). In addition, we also assigned distinctive galls to another six galling Damage Types (DTs) such as DT 32, DT 80, DT 83, DT 85, DT 120, and DT 144 (Hazra et al., 2021c).

Host plants: *Hylodesmum* sp. (Fabaceae), *Albizia* (Fabaceae), *Mangifera* sp. (Anacardiaceae), *Adina* sp. (Rubiaceae), *Syzizium* sp., *Psidium* sp. (Myrtaceae), *Rhamnus* sp. *Zizyphus* sp. (Rhamnaceae), *Ficus* sp. (Moraceae), *Galactia* sp. (Fabaceae), Malvaceae, Lauraceae, Combretaceae and Dipterocarpaceae

Inferred culprits: Gall midge (Diptera), leafhopper (Hemiptera), Aphid (Hemiptera), Psyllid (Hemiptera), *Ophion* (Hymenoptera), *Psylla* (Hemiptera).

*Leaf mining* (Plate VI)

Leaf mining is the remaining trace that larva produces as it feeds within host–plant leaf tissue, typically in a serpentine or blotch-like fashion but without eliciting a noticeable plant response (Opler, 1982; Crane and Jarzembowski, 1980; Donovan et al., 2014; Jud and Sohn, 2016). Often in a fossil, the colour of mining is usually much darker than that of the leaf blade, and the mining is slender and sinuous.

Leaf mining DTs in this investigation are represented as DT 42: It is a linear mine 45–52 mm long with expanding width, irregular margin, and no frass (Plate VI 1 and 2); DT 92: It is medium in length, undulatory mine located on 1° or 2° veins; pellets in center-half to full mine width (Plate VI 3 and 4); DT 65: The mine is long, serpentine in shape and rapidly expanding, the terminus is blotch-like with a width of 8 mm and originates between two secondary veins close to the leaf margin (Plate VI 5 and 6); DT 111: It is serpentine in shape with thick frass that lies between 2° veins having a terminal bulb-like chamber (Plate VI 7).
DT 109: is a short, thin and threadlike mine, frass probably solid; all significant veins avoided (Plate VI 8).

Host plants: *Rhamnus* sp. (Rhamnaceae), *Ficus* sp. (Moraceae), Sterculiaceae

Inferred culprits: Diptera, Hymenoptera

*Other damage types*

The other damages include some evidence of piercing and sucking, together with a few fungal spots on fossil leaves comprise only a small percentage of all damage (1.49%). Sucking traces caused by insects such as aphids, leafhoppers, bugs, and scales feed on the sap from plants by piercing the epidermal layer of the plant and sucking the plant sap from the cells resulting in spotting or stippling patterns on leaves (Wari et al., 2021).

Host plants: *Galactia* sp. (Fabaceae), *Ficus* sp. (Moraceae)

Inferred culprits: Lepidoptera, Diptera, Fungi

4.2. *Damage composition in different plant families*

931 damaged leaf specimens belong to eleven host plant families (Table 1). Among them, the Fabaceae family was found to be the maximum herbivorized taxa (20.83%) followed by Anacardiaceae (10.65%), Moraceae (10.09%), Dipetrocarpaceae (8.42%), Rhamnaceae (8.15%), Combretaceae (7.41%), Malvaceae (7.41%), Rubiaceae (5.65%), Apocynaceae (3.15%), Lauraceae (2.5%) and Myrtaceae being the least (1.94%). However, 149 (13.8%) damaged leaf specimens couldn't be diagnosed at the family level (Table 1).

4.3. *Evidence of fossil phytophagous insects from the fossil locality (Plate VIII)*
Although evidence of predatory marks on fossil leaf remains provides a unique window into ecological and evolutionary associations of the past, the finding of both damage types on leaf remains and the responsible phytophagous insects offers particularly valuable insights into those interactions and can confirm the origins of DTs that otherwise just have to be inferred. A large number of phytophagous insects have been recovered from the latest Neogene (Pliocene: Rajdanda Formation) sediments (Fig. 3) that are candidates for producing the different DTs on the fossil leaves in that same assemblage (Plate VIII). 43 fossil insect specimens belong to five insect orders as Coleoptera, Diptera, Hemiptera, Hymenoptera, and Lepidoptera (Fig. 3). Among them, Lepidoptera was found to be the maximum (32.56%) followed by Hemiptera (23.26%), Diptera (11.63%), Coleoptera (6.97%), and Hymenoptera being the least (4.65%). However, 9 (20.93%) insect specimens couldn't be identified (Fig. 3). Recently, we reported the first fossil evidence of leaf-feeding caterpillars, along with their characteristic feeding patterns, on the surface of Galactia (Fabaceae) leaf remains, providing a rare direct insight into past plant-insect interaction (Hazra et al., 2021b). In addition, different types of gall-inducing insects including leafhoppers or planthoppers (Hemiptera), the egg of an aphid or a psyllid (Hemiptera), a wingless adult aphid (Hemiptera), a lateral view of a gall midge (Diptera) and a mature larva of a gall midge (Diptera) were reported by Hazra et al. (2021c). We have also recovered some Coleoptera larva (grub) (Plate VIII7, 8). Hazra et al. (2020) also reported for the first time from India the in-situ occurrence of a gall midge (Insecta, Diptera, Cecidomyiidae) as well its pupal exuviae on the abaxial cuticular surface of fossilized leaf cuticle fragments of Fabaceae leaves (cf. Albizia). Shukla et al. (2000) also reported resin-embedded gall inducer fossil insects such as Psylla (Hemiptera), Ophion (Hymenoptera), a chrysalis (Lepidoptera), and the mandibles of ants (Hymenoptera) from the same fossil locality.
4.4. Modern forest types and insects

Jharkhand is a biodiversity-rich state and is known as 'the land of the forest'. Important vegetation in this region mainly comprises moist to dry deciduous forests. *Shorea* and *Bambusa* are the major components. At and around the fossil localities the principal modern constituents of the tropical moist to dry deciduous forest are *Acacia*, *Adina*, *Aegle*, *Ailanthus*, *Alangium*, *Albizia*, *Alstonia*, *Anogeissus*, *Antidesma*, *Arotocarpus*, *Azadirachta*, *Bauhinia*, *Bombax*, *Boswellia*, *Bridelia*, *Buchanania*, *Butea*, *Careya*, *Casearia*, *Cassia*, *Chloroxylon*, *Dalbergia*, *Diospyros*, *Dipterocarpus*, *Elaeocarpus*, *Ficus*, *Litsea*, *Pongamia*, *Schima*, *Gmelina*, *Sterculia*, *Michelia*, *Amoora*, *Lagerstroemia*, *Syzygium*, *Elaeocarpus*, and *Musa* (FSI, 2019).

Besides floral components, Jharkhand also possesses a rich faunal heritage. Insects belonging to orders Collembola, Thysanura, Hemiptera, Odonata, Hymenoptera, Isoptera, Orthoptera, Diptera, Coleoptera, Lepidoptera are common (Sanyal et al., 2014; Kumar and Siakia, 2020).

5. Discussion

5.1. Host-insect interaction patterns

The six functional feeding groups (FFGs) (galling, margin feeding, hole feeding, skeletonization, mining, and surface feeding) vary in abundance with high host specificity in some of the FFGs, but in the Pliocene Jharkhand assemblage galling (50.74%) is the most common and skeletonization (1.94%) being the least common.

Galls are structures composed of plant tissue within which the insect feeds, and they involve active differentiation and growth of plant tissue, which provides enhanced nutrition, a favourable microclimate, and protection from natural enemies for the inducer (Mani, 1973; Stone and Schönrogge, 2003). This functional feeding group occurs as anomalous
protuberances on the surface of the leaves, with a characteristic reaction rim. In fossil specimens, the galls have a dark brownish hue. All the galls are circular in shape and occur on 1°, 2°, and 3° veins. Possible gall producers belong to the insect orders Orthoptera, Coleoptera, Lepidoptera, Copepoda, Nematoda, and Rotifera (Mani, 1973; Knor et al., 2013). Hemipterans, Hymenopterans, and Dipterans are the most important gall makers (Fig. 4; Knor et al., 2013). The high richness of galling DTs on a broad spectrum of host lineages—such as Fabaceae, Malvaceae, Anacardiaceae, Combretaceae, Moraceae, Rhamnaceae, Sterculiaceae, Rubiaceae, and Myrtaceae—suggests that host-specific associations were a common feature in the palaeoforest of Jharkhand. Components of host plant include leaf quantity and quality such as leaf size, the position of leaf, nutritional and defensive chemistry (carbon, nitrogen, and defensive metabolites), physical barriers, and phonological changes that directly affect potential and achieved herbivory (Faeth, 1985; Agrawal, and Fishbein, 2006; Ali and Agrawal, 2012; Curran, and Jacobs, 2021). The high galling DT richness found here is ecologically consistent with the high richness of galls found in the canopy of modern tropical rainforests (Julião et al., 2014). The upper canopy and emergent trees mimic some of the ambient conditions observed in xeric environments where galling is particularly prevalent. These similarities include intense solar radiation, higher leaf temperatures, and high vapor-pressure deficit (Julião et al., 2014). Where trees are particularly tall and tree height-induced sclerophyll exists in the upper canopy galling is particularly intense, such as we see in the Pliocene Forest. We infer that the Jharkhand Pliocene forests in an otherwise humid climate contained a high proportion of exceptionally tall trees with sclerophyllous, gall-rich, crowns.

Margin feeding and hole feeding together account for 40.28% of the damaged leaves. Most hole feeding types are made by leaf-chewing insects, such as Orthopterans, Lepidopterans, and Hemipterans (Fig. 4) (Carvalho et al., 2014). However, most margin leaf-
chewers are Orthopterans, Hymenopterans, and Lepidopterans (Fig. 4) (Carvalho et al., 2014). External foliage feeding is a common form of herbivory in Cenozoic fossil leaves and in the Jharkhand, specimens bearing margin feeding, the excisions are circular to semicircular in shape and extend from leaf margin to primary vein.

Surface feeding or window feeding represents 3.33% of all damaged leaves. Here, the surface feeding is characterized by a circular to ellipsoidal shape with no reaction rim. Coleopterans are the common surface feeders in leaves (Fig. 4) and we infer this was also the case in the Jharkhand Pliocene forests. During surface feeding, the beetles (Coleoptera) perform symmetrical, usually alternating series of bites to the right and to the left of the longitudinal body axis. In most species, individual incisions merge into a single hole that usually does not reach the leaf margin. They start a small hole first and then enlarge it lengthwise and sidewise. During feeding the beetles advance slowly onto the damaged area. The incision is only part-through, from several millimeters to 2 cm long and 1–3 mm wide, with rough margins. It runs along with the leaf, not crossing any veins. (Bienkowski, 2010) (Plates IV, VII 6).

Skeletonizations occur when the trace maker consumes interveinal tissues of leaves composed of softer cells, leaving some vein-like network and can be caused by holometabolous insects that have distinct larval and adult stages, e.g., Coleoptera, Hymenoptera, Diptera, and Lepidoptera (Fig. 4; Bernays and Janzen, 1988). The skeletonized area in the specimens is variously shaped (rectangular to circular) where broad swaths of interveinal tissues are absent. The skeletonizations are located adjacent to primary or secondary veins. Beetles, particularly coccinellid and scarab beetles, feed on soft plant tissue but do not chew through veins and thereby make skeletonized areas on the leaf (Plates III, VII 5, 7).

Insect leaf mines are linear or blotch-like excavations produced by certain specialized larvae that feed in the leaf mesophyll or epidermis leaving the outer cell layers intact. Mines
are made by four orders of living insects: Hemiptera, Diptera, Hymenoptera, and Lepidoptera (Fig. 4; Crane and Jarzembowski, 1980; Winkler et al., 2010; Labandeira et al., 1994). Leaf mining comprised only 2.22% of all damaged leaves in the Jharkhand samples. The types of leaf mine shapes could be classified as linear, blotch, serpentine. Linear mines occur when the leaf-mining larvae keep feeding forward and have subtypes such as serpentine, spiral, and branched (Kato, 1984). When the leaf miners have several feeding directions, blotch occurs. The sub-types of blotches include circular, oval, rectangular, tentiform, amoeba shape, etc. The “linear-blotch mines” (Hering, 2013; Kang, 1996; Csóka, 2002), may be due to a change in feeding habitats in different larval stages (Hering, 2013). In our fossil specimens, the linear and serpentine type of mines is the most common ones. The leaf-mining diversity found in the Pliocene of Jharkhand suggests niche differentiation of leaf-mining insects seeking favourable microhabitats on host plant leaves.

5.2. Comparison of insect herbivory on leaves from different Neogene floras in Asia

Neogene fossil records in Asia reveal an exceptionally rich flora and fauna, allowing the direct investigation of the evolutionary history of Asian paleoherbivory. Climatic changes during the Neogene have likely had a direct influence on the plant-insect interaction in Asia (Patnaik and Prasad, 2016). The comparison of plant–insect interaction between different locations in Asia (Table 3) during the Neogene is important to understand how the patterns of herbivory have changed through time under different climatic regimes. The Neogene fossil record on insect herbivory of Asia is mostly represented in the Miocene and Pliocene localities of India and China (Table 3; Fig. 5a, b). The comparison of damage frequency versus different types of FFGs has been done from the Pliocene locality of Jharkhand (our study) and Longmen flora of Yongping, western Yunnan (Su et al., 2015) and represented on a box plot (Fig. 6; Table S2).
The Miocene localities from where traces of plant-insect interaction have been reported include Toupi Formation, Fotan Group, and Bangmai Formation, China (Ma et al., 2020; Dong et al., 2018; Zhang et al., 2018; Wang et al., 2021), Gish Clay Formation (Khan et al., 2015) and Dafla Formation (Khan et al., 2014b) of India. The percentage of leaf damage was highest in the Gish Clay Formation, Darjeeling (38%) followed by the Dafla Formation, Arunachal Pradesh (35%), the Fotan Group, Zhangpu County, China (34.1%), the Bangmai Formation, Yunnan Province, China (21%) and the Toupi Formation, Guangchang, China (20.33%). Different categories of endophytic and exophytic functional feeding groups, identified as hole feeding, margin feeding, surface feeding, skeletonization, mining, and galling existed in the Miocene palaeoforests of Asia. Among these, external foliage feeding is the most common form of herbivory. The important angiosperm host plants are Liquidambar sp., Woodfordia sp., Callicarpa sp., Albizia sp., Persea sp., Lagerstroemia sp., Shorea sp., Artocarpus sp., Millettia cineria, Anogeissus acuminata, Albizia gamblei, Actinodaphne sp., Terminalia tomentosa, Glochidion gamblei, Actinodaphne angustifolia, Chonia morpha macrophylla, and Canarium bengalense. The occurrence of such plant taxa indicates a humid broadleaved tropical to subtropical evergreen forest and a large number of plant species and damage richness in the Miocene localities of Asia imply high insect species richness. The various damage types as seen in the fossil leaves suggest that trophically diverse insect herbivore fauna inhabited in the Asian palaeoforest during the Miocene.

The Pliocene localities showing evidence of plant-insect interaction include the Subansiri Formation Siwaliks, eastern India (Khan et al., 2014b), the Kimin Formation, Siwaliks, eastern India (Khan et al., 2014b), the Rajdanda Formation (present study), eastern India, the Mangbang Formation, Yunnan Province, China (Jingyu et al., 2015), and the Sanying Formation (Su et al., 2015), China. The important host taxa-bearing insect damage include Quercus preguyavaefolia, Rhodoleia tengchongensis, Terminalia sp., Millettia sp.,
Glochidion sp., Actinodaphnae sp., Dysoxylum sp., Chonemorpha sp., Fabaceae, and Moraceae. As compared to all the Neogene localities in Asia, especially in Southeast Asia, the present study from the Pliocene Rajdanda Formation, Jharkhand shows the highest percentage of leaf damage (75%) and highest damage diversity with galling representing the most common form of herbivory (Hazra et al., 2021). Galling is also one of the most prevalent forms of herbivory in the Subansiri Formation of Arunachal Pradesh (Khan et al., 2014b).

Hence, from this comparative study, we can say that percentage of leaf damage increased from Miocene (~30%) to Pliocene (~56%) with a corresponding increase in angiosperm diversity and insect richness (Fig. 5b). The increased herbivory is mainly dependent on two factors 1) insect metabolism, which generally is directly dependent on climate conditions (Archibald et al., 2010; Woods and Hill, 2004); and 2) plant metabolism, which determines the quality and quantity of nutrients, which in turn also depends on climate and soil type (Ahmad and Prasad, 2011; Dusenge et al., 2019; Drew, 1992). Therefore, the increased insect herbivory in the Pliocene of Asia was inevitably due to the suitable climatic conditions favouring both plant and insect metabolism.

5.3. Palaeoclimatic interpretation

There are many factors that contribute to the plant-herbivore interactions. Generally, they are shaped by the mixture of climatic components like temperature, carbon dioxide, precipitation (Zvereva and Kozlov, 2006; Loughnan and Williams, 2019), and environmental conditions related to elevational gradients (Adroit et al., 2018; Sohn et al., 2019; Sam et al., 2020). Regional variations in climatic factors are the major drivers of the global diversification of damage frequencies (DFs) and damage types (DTs) (Adams et al., 2010, 2011), as they directly influence both plants and herbivores in an ecosystem (Bale et al.,
Climatic factors shape the global patterns of herbivore quantity, consumption, and diversity (Tylianakis et al., 2008), so plant-animal interaction studies can be useful as indicators of climate change (Wilf and Labandeira, 1999; Currano et al., 2008; Westerhold et al., 2020; Labandeira and Li, 2021).

The Pliocene is a critical period for understanding the origin and evolution of modern biota (Montanari et al., 2013), and the Pliocene fossil locality of Jharkhand is an ideal setting to study the relationship between low latitude climate and biodiversity under conditions warmer than today, but with a similar palaeogeographic configuration. Crucially, it is prior to human degradation of terrestrial ecosystems.

The Jharkhand palaeoforest was dominated by thermophillic angiosperm taxa (Puri and Mishra, 1982; Srivastava and Bande, 1992, Srivastava et al., 1990; Singh and Prasad 2007, 2008, 2009a, b; 2010; Singh and Chauhan 2008; Hazra et al., 2021a, b). They exhibiting insect-induced folivory experienced a warm humid climate during the time of deposition and overall, the palaeoforest resembles a modern tropical forest in terms of palaeoclimate, physiognomy, floristics, and plant-insect interaction. A defining feature of the palaeoforest is the high number and frequency of specialized interactions, particularly the abundant galls. A recent quantitative determination using CLAMP (Climate Leaf Analysis Multivariate Program; http://clamp.ibcas.ac.cn) of the Pliocene climate of the Chotanagpur plateau (Hazra et al., 2020) based on recovered fossil leaf architectural signatures revealed a weakly monsoonal tropical warm humid climate (Hazra et al., 2020). The CLAMP analysis indicated a mean annual temperature (MAT) of 21.9 °C ± 2.3 °C; a cold month mean temperature (CMMT) of 16.7 °C ± 3.5 °C, a warm month mean temperature (WMMT) of 26.9 °C ± 2.9 °C and growing season precipitation (GSP) of 201.2 ± 64.3 cm. The average annual relative humidity was 71.2%. Notably, the dry season was wetter than today, hence the weaker monsoon signature.
Herbivory rates have generally been reported as being higher in the tropics than in temperate latitudes and more favourable conditions in the tropics allow the insects to feed constantly compared to conditions at higher latitudes. Consequently, the rate of leaf area loss to herbivory tends to be greater in warmer than in cooler environments (Coley and Aide, 1991; Coley and Barone, 1996). This is in conformity with the climate estimation of the Chotanagpur Plateau, eastern India, and the intensity of the feeding damage pattern. However, the high galling DT richness can be explained by the more xeric environment and consequent leaf sclerophyll in the upper canopy of the tropical palaeoforest of Jharkhand.

In addition to the Jharkhand locality, evidence of plant-insect associations has also been found in the Siwalik (middle Miocene-early Pleistocene) leaf assemblages of Arunachal Pradesh and the Darjeeling foothills, eastern Himalaya (Khan et al., 2014b, 2015). Khan et al., (2015) compared insect herbivory in the Darjeeling lower Siwalik flora to those of three Arunachal Siwalik floras (lower, middle and upper Siwalik floras) and found a similar range of FFGs and DTs observed among all four fossil floras (Table 3). CLAMP analyses also suggested that all the Siwalik fossil assemblages attest to warm (tropical) humid climates with a monsoon signature. The CLAMP retrodictions for the Darjeeling and Arunachal Siwalik assemblages are, within uncertainty, identical as regards temperature, humidity and enthalpy estimates (Table 3; Khan et al., 2015)

The climatic parameters of all the localities of eastern India, including Jharkhand, yielded similar temperature, precipitation, and humidity conditions (Table 3), and similar herbivory patterns were observed in the monsoon-influenced forests of eastern India as a whole. This is also consistent with the modern-day climate variability in eastern India. As the patterns of damage type diversity and agent host specificity closely resemble those of the present day, the present study demonstrates that modern plant-insect interactions of the types
preserved in the fossil record were indistinguishable from those of the present in similar climatic conditions just prior to human modification of ecosystems.

6. Conclusion

1. This is the first detailed census of the presence of diverse phytophagous insect activity on fossil angiosperm leaves of the Pliocene flora of Chotanagpur plateau, eastern India. The exceptional quality of preservation of fossils as well as traces of feeding activity shows that the observed specimens were not transported long distances from the habitat area to the depositional area. The preservation of details in the leaves and interactions suggest that rapid deposition took place.

2. The diversity of functional feeding groups presented adds to those already described for other Pliocene localities of India. The functional feeding groups in this study include galling, margin feeding, hole feeding, skeletonization, mining and surface feeding. The damage types found here indicate a high level of herbivorous activity, according to the number of leaf specimens analyzed here and the percentage of damage in each category. Galling is the prevalent form of herbivory here.

3. Evidence of folivory traces on fossil angiosperm leaves is quite a common phenomenon but finding both damage and phytophagous insects likely to have caused the damage are quite rare. The present study provides a direct clue to the biotic interactions that existed between 5.3 and 2.9 million years ago in eastern India.

Acknowledgments

TH, MH and MAK gratefully acknowledge the Department of Botany, Sidho-Kanho-Birsha University for providing infrastructural facilities to accomplish this work. RAS and TEVS were supported by NERC/NSFC BETR Project NE/P013805/1. SKS acknowledges the
Department of Zoology, University of Kalyani, India. SB acknowledges the Centre of Advanced Study (Phase-VII), Department of Botany, University of Calcutta for providing necessary facilities.

References


Fiene, J., Kalns, L., Nansen, C., Bernal, J., Harris, M., Sword, G.A., 2013. Foraging on individual leaves by an intracellular feeding insect is not associated with leaf biomechanical properties or leaf orientation. PloS one, 8(11), p. e80911.


Hazra, T., Hazra, M., Kumar, S., Mahato, S., Bera, M., Bera S., Khan M.A. 2021c. First fossil evidence of Palaeocarya (Engelhardioideae: Juglandaceae) from India and its biogeographical implications. J. Syst. Evol. 59(6), 1307–1320.


India State of Forest Report 2019. Forest Survey of India (Ministry of Environment Forest and Climate Change) Kaulagarh road, P.O. IPE Dehradun – 248195, Uttarakhand. India.


30


the Upper Eocene Florissant Formation, Colorado. Geological Society of America, Boulder, Colorado, USA.


Table caption

Table 1: Insect damage composition in different plant families of the Jharkhand Pliocene flora

Table 2. The quantitative data of each insect damage type (DT)
Table 3. A comparison of insect herbivory on angiosperm leaf assemblages from the different fossil localities of Asia studied to date. (MAT= mean annual temperature; WMMT= warm month mean temperature, CMMT=cold month mean temperature).

**Figure and Plate Captions**

**Fig. 1.** Map of Latehar District, Jharkhand, eastern India, showing the fossil locality near Mahuadanr.

**Fig. 2.** Palaeoenvironmental reconstruction of the ancient forest showed various damage types during the Pliocene on the Chotanagpur Plateau, eastern India, Jharkhand.

**Fig. 3.** Percentage of fossil phytophagous insects from the fossil locality

**Fig. 4.** Inferred relationships between functional feeding groups and insect orders

**Fig. 5.** (a). Comparison of the percentages of damaged leaves from various Miocene and Pliocene floras of Asia; (b). Comparisons of the percentage of Miocene and Pliocene leaf damage. Abbreviations: Toupi Formation, Miocene (TF M); Fotan Group, Miocene (FG M); Bangmai Formation, Miocene (PG M); Gish Clay Formation, Miocene (GC F M); Dafla Formation, Miocene (DF M); Subansiri Formation, Pliocene (Su F P); Kimin Formation, Pliocene (KF P); Mangbang Formation, Pliocene (MF P); Sanying Formation, Pliocene (SaF P); Rajdanda Formation, Pliocene (RF P)

**Fig. 6.** Box-plot of the frequency of damage in the Pliocene locality of Jharkhand (our study; blue box) and Longmen flora of Yongping, western Yunnan (Su et al., 2015; orange box). Here, external foliage feeding includes hole feeding, margin feeding, surface feeding, and skeletonization.

**Plate I.** Margin feeding traces on angiosperm leaves from the Neogene of sediments of Jharkhand. (1–2) Excision of the leaf blade extending to the mid-vein (DT14); (2) excisions
removing the leaf apex (DT 13); (3–5) isolated, circular, excision of a leaf margin (DT12); 
(6) circular arc of leaf-margin excision (DT81); (7–8) margin feeding traces that reach the 
mid-vein (DT14); (9–10) semicircular, shallow to deep excisions along the leaf margin 
(DT12). Scale bars= 1 cm

**Plate II.** Leaf fossils bearing hole feeding from the latest Neogene sediments of Jharkhand. 
(1–2) Circular, elliptical, and polylobate holes (DT 2); (3) polylobate holes range between 
0.8–12 mm diameter (DT 3); (4) circular and ellipsoidal holes (DT 2); (5–7) polylobate holes 
range between 0.8–12 mm diameter (DT 3); (8) circular, elliptical, and polylobate holes (DT 
2); (9) polylobate holes range between 10–12 mm diameter (DT 5); (10) rectilinear hole with 
length: width ratio= 2:1 (DT 8); (11) circular and ellipsoidal holes (DT 2). Scale bar = 1 cm

**Plate III.** Skeletonization on selected fossil leaves from the Rajdanda formation. (1) 
Skeletonization where there is maximum removal of the finest venation (DT 21); (2–3) 
irregularly shaped skeletonization patches with no reaction rims (DT 16); (4–5) ovoidal 
shaped skeletonization adjacent to 1° or 2° veins (DT 24); (6) traces of elongated 
skeletonization (DT 297); (7) rectangular skeletonized area (DT 19); (8) irregularly 
skeletonization without reaction rims (DT 16). Scale bar = 0.5 cm

**Plate IV.** Surface feeding and galling on fossil leaves from the Rajdanda formation. (1) 
removal or abrasion of surface tissues with a weak reaction rim (DT 29); (2) polylobate 
surface abrasions with poorly developed reaction rims (DT 29); (3) polylobate window 
feeding, ~ symmetrical about 1° or 2° vein (DT 82); (4) polylobate surface abrasions with 
poorly developed reaction rims (DT 29); (5) polylobate surface abrasions with poorly 
developed reaction rims (DT 29); (6) polylobate window feeding, ~ symmetrical about 1° or 
2° vein (DT 82); (7–8) removal or abrasion of surface tissues with a weak reaction rim (DT 
29); (9) polylobate window feeding, ~ symmetrical about 1° or 2° vein (DT 82). Scale bar = 
0.5 cm
Plate V. Galling on fossil leaves from the Rajdanda formation. (1) Circular gall on 2° veins (DT 34); (2) circular gall on 1° veins (DT 33); (3) circular gall on 2° veins (DT 34); (4) elongate, elliptical, striated; on mid-vein (DT 85); (5) spheroidal, large central chamber surrounded by thick wall and second tissue layer, outermost layer thin (DT 145); (6) circular to ellipsoidal; avoiding major veins (DT 32); (7) small, hemispherical; thoroughly carbonized, diameters ~ 0.1 - 1.0 mm, 1° and 2° veins avoided (DT 80); (8) spheroidal, large central chamber surrounded by thick wall and second tissue layer, outermost layer thin (DT 145); (9) elongate, elliptical, striated; on mid-vein (DT 85); (10) circular, with fusanized tissue in radiating partitions (DT 52); (11, 12) circular to ellipsoidal; avoiding major veins (DT 32); (13) small, hemispherical; thoroughly carbonized; diameters ~ 0.1 - 1.0 mm, 1° and 2° veins avoided (DT 80); (14) spheroidal; large central chamber surrounded by thick wall and second tissue layer; outermost layer thin (DT 145); (15) multiloculate, dark inner core, surrounding smooth surface and circular margins, often fused (DT 144). Scale bar = 0.5 cm

Plate VI. Fossil leaf mines from the Neogene of sediments of Jharkhand. (1) Linear mine with expanding width, irregular margin, and no frass (DT 42); (2) close-up of linear mine (1); (3) medium length, undulatory mine located on 1° or 2° veins; pellets in center-half to full mine width (DT 92); (4) close-up of mine; (5) mine initially long, serpentine and rapidly expanding, terminus blotch-like occupies (DT 65); (6) close-up of long mine (5); (7) serpentine with thick frass that lies within 2° vein having a terminal bulb-like chamber (DT 111); (8) short, thin and threadlike mine avoiding significant veins (DT 109). Scale bar = 1 cm for (1–3) and 0.5 cm for (4) Plate VII. Modern leaves showing various damage patterns collected from the surrounding area of the fossil locality

Plate VIII. Insect remains from the Pliocene sediments from Jharkhand, eastern India. (1–6) Caterpillars; (7–8) Coleoptera larva (grub); (9) probable remains of Diptera; (10) an
unidentified insect remain; (11) probable remains of a caterpillar; (12) an unidentified remain of an insect pupal chamber or exuviae; (13) probable remains of a leafhopper (Hemiptera); (14) mature larva of gall midge; (15) an unidentified insect remain; (16) egg of a psyllid (Hemiptera); (17) an adult gall midge (lateral view); (18) a wingless adult aphid (Hemiptera); (19) egg of an aphid (Hemiptera); (20) pupal exuviae of a gall midge; (21) lateral view of a gall midge. Scale bar: 5 mm for (1–18) and 1 mm for (19–20).

**Supplementary Material Captions**

**Fig. S1.** Modern leaves having galls collected from the adjacent area of the fossil locality

**Table S1.** A dataset of recovered fossil leaf specimens with their characteristic damage patterns

**Table S2.** A dataset of the frequency of damage types for box-plot.
<table>
<thead>
<tr>
<th>Family</th>
<th>Number of damaged leaves</th>
<th>Percentage of damage (%)</th>
<th>Damage area (mm²)</th>
<th>Functional feeding groups (FFGs)</th>
<th>Damage Types (DTs)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fabaceae</td>
<td>225</td>
<td>20.83</td>
<td>2139.53</td>
<td>8 2 10 3 2 9 3 2 4 2 16</td>
<td></td>
</tr>
<tr>
<td>Anacardiaceae</td>
<td>115</td>
<td>10.65</td>
<td>1963.42</td>
<td>1 1 83 1 2 1 1 5 2 8</td>
<td></td>
</tr>
<tr>
<td>Dipterocarpaceae</td>
<td>91</td>
<td>8.42</td>
<td>799.31</td>
<td>1 7 38 1 9 3 2 1 1 1 7</td>
<td></td>
</tr>
<tr>
<td>Combretaceae</td>
<td>80</td>
<td>7.41</td>
<td>795.14</td>
<td>1 3 50 1 1 1 3 1 1 1 14</td>
<td></td>
</tr>
<tr>
<td>Malvaceae</td>
<td>80</td>
<td>7.41</td>
<td>715.91</td>
<td>4 28 3 4 1 1 0 1 1 2 12</td>
<td></td>
</tr>
<tr>
<td>Moraceae</td>
<td>109</td>
<td>10.09</td>
<td>1044.02</td>
<td>7 20 1 6 3 1 1 1 9</td>
<td></td>
</tr>
<tr>
<td>Rubiaceae</td>
<td>61</td>
<td>5.65</td>
<td>632.08</td>
<td>5 34 2 1 0 0 0 1 13</td>
<td></td>
</tr>
<tr>
<td>Rhamnaceae</td>
<td>88</td>
<td>8.15</td>
<td>863.89</td>
<td>5 48 3 3 1 1 1 1 1 10</td>
<td></td>
</tr>
<tr>
<td>Apocynaceae</td>
<td>34</td>
<td>3.15</td>
<td>401.37</td>
<td>5 15 9 1 2 1 1 1 12</td>
<td></td>
</tr>
<tr>
<td>Moraceae</td>
<td>21</td>
<td>1.94</td>
<td>120.32</td>
<td>8 4 3 2 1 1 2 16</td>
<td></td>
</tr>
<tr>
<td>Lauraceae</td>
<td>27</td>
<td>2.3</td>
<td>340.39</td>
<td>6 14 3 3 0 0 1 11</td>
<td></td>
</tr>
<tr>
<td>Unidentified</td>
<td>149</td>
<td>12.8</td>
<td>1378.81</td>
<td>2 3 51 6 1 5 0 8 1 19</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>1080</td>
<td>100</td>
<td>11354.19</td>
<td>184 54 25 14 21 3 6 16 37</td>
<td></td>
</tr>
<tr>
<td>Functional Feeding Groups (FFGs)</td>
<td>Damaged types (DTs)</td>
<td>Total DTs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>---------------------------------</td>
<td>--------------------</td>
<td>-----------</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hole feeding</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>DT 01 DT 02 DT 03 DT 04 DT 05 DT 08</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>7 66 52 29 53 9</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Margin feeding</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>DT 12 DT 13 DT 14 DT 15 DT 81</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>117 98 44 11 15</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf mining</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>DT 41 DT 42 DT 43 DT 65 DT10 DT11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 5 2 4 6 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Skeletonization</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>DT16 DT19 DT21 DT24 DT61 DT413</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3 2 2 3 2 10</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface feeding</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>DT29 DT31 DT82</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6 8 11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galling</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>DT33 DT34 DT11 DT32 DT11 DT8</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>97 81 68 95 10 13</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>DT 83 DT 14 DT 52 DT 14 DT 14</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>8 3 9 4</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Unrecognizable</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>6 23 303</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2 24</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>19</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>46 657</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Palaeoflora in Asia</td>
<td>Age and Formation</td>
<td>No. of fossil leaf specimens examined</td>
<td>Leaf damage (%)</td>
<td>Most prevalent form of damage type</td>
<td>Dominant herbivorized plant taxa</td>
</tr>
<tr>
<td>---------------------</td>
<td>-------------------</td>
<td>---------------------------------------</td>
<td>-----------------</td>
<td>-----------------------------------</td>
<td>--------------------------------</td>
</tr>
<tr>
<td>Toupi Basin, Guangchang, Jiangxi, China</td>
<td>Early-middle Miocene (Toupi Formation)</td>
<td>123</td>
<td>20.33</td>
<td>Mining</td>
<td>Smilax Quercus</td>
</tr>
<tr>
<td>Zhangpu County, Fujian Province, SE China</td>
<td>Middle Miocene (Fotan Group)</td>
<td>138</td>
<td>34.1</td>
<td>Margin feeding</td>
<td>Liquidambar</td>
</tr>
<tr>
<td>Lincang, Yunnan Province, southwest China</td>
<td>Miocene (Bangmai Formation)</td>
<td>233</td>
<td>21</td>
<td>Hole feeding</td>
<td>Fagaceae, Leguminosae, Juglandaceae</td>
</tr>
<tr>
<td>Darjeeling, India</td>
<td>Middle Miocene (Gish Clay Formation); Lower Siwalik</td>
<td>137</td>
<td>38</td>
<td>Margin feeding</td>
<td>Shorea, Woodfordia, Callicarpa</td>
</tr>
<tr>
<td>Location</td>
<td>Geologic Location</td>
<td>Age Range</td>
<td>Tissue/Feeding Type</td>
<td>Taxa Details</td>
<td>MAT ± SD</td>
</tr>
<tr>
<td>--------------------------------</td>
<td>-----------------------------------------------------------------------------------</td>
<td>--------------</td>
<td>---------------------</td>
<td>---------------------------------------------------</td>
<td>----------</td>
</tr>
<tr>
<td>Arunachal Pradesh, India</td>
<td>Middle-upper Miocene (Dafla Formation); Lower Siwalik</td>
<td>150</td>
<td>Margin feeding</td>
<td>Callicarpa, Cinnamomum, Anogeissus</td>
<td>25.3 ± 2.8</td>
</tr>
<tr>
<td>Arunachal Pradesh, India</td>
<td>Pliocene (Subansiri Formation), Middle Siwalik</td>
<td>70</td>
<td>Margin feeding</td>
<td>Terminalia, Millettia, Glochidion</td>
<td>23.7 ± 2.8</td>
</tr>
<tr>
<td>Arunachal Pradesh, India</td>
<td>Late Pliocene –Early Pleistocene (Kimin Formation), Upper Siwalik</td>
<td>130</td>
<td>Galling</td>
<td>Actinodaphne, Dysoxylum, Chonemorpha</td>
<td>25.4 ± 2.8</td>
</tr>
<tr>
<td>Tengchong County, Yunnan</td>
<td>Upper Pliocene (Mangbang Formation)</td>
<td>21</td>
<td>Hole feeding</td>
<td>Rhodoleia</td>
<td>16.3–20.8</td>
</tr>
<tr>
<td>Longmen Flora, Yongping County of</td>
<td>Late Pliocene (Sanying Formation)</td>
<td>1028</td>
<td>Margin feeding and hole feeding</td>
<td>Quercus preguyavaefolia, Quercus</td>
<td>17.4 ± 1.3</td>
</tr>
<tr>
<td>Location</td>
<td>Age</td>
<td>Fauna</td>
<td>Genus</td>
<td>Holocene Range</td>
<td>Notes</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>-------------</td>
<td>---------</td>
<td>------------------------</td>
<td>----------------</td>
<td>------------------------</td>
</tr>
<tr>
<td>western Yunnan Province, China</td>
<td>n)</td>
<td></td>
<td>guyavaefolia</td>
<td>8.9±2.6</td>
<td></td>
</tr>
<tr>
<td>Jharkhand, India</td>
<td>Pliocene</td>
<td>1500</td>
<td>Galling</td>
<td></td>
<td>MAT=21.9± 2.8</td>
</tr>
<tr>
<td>(Rajdanda Formation)</td>
<td>72</td>
<td></td>
<td>Fabaceae, Moraceae</td>
<td>WMMT=26.9± 3.4</td>
<td>CMMT=16.7± 4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>This study</td>
</tr>
</tbody>
</table>
The authors declare that they have no competing interests.
Highlights

- Comprehensive census of insect folivory in the Pliocene Chotanagpur Plateau forests
- Six principal categories of damage identified, with galling predominating
- Records of fossil phytophagous insects co-occur in the fossil locality
- Insect activity similar to modern ecosystems on the Chotanagpur Plateau