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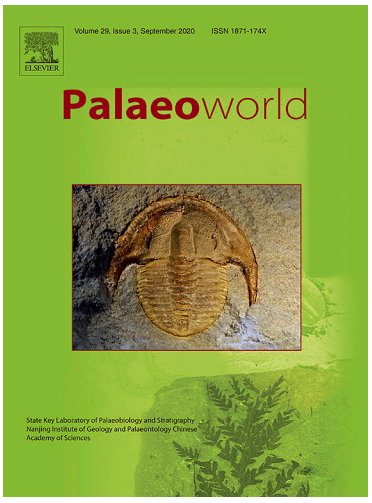

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Galling: the prevalent form of insect folivory in the latest Neogene monsoon-influenced tropical forests of the Chotanagpur Plateau, eastern India

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Abstract

Indian Cenozoic deposits contain well-preserved diverse angiosperm leaf assemblages, but galling, a common form of angiosperm leaf damage in modern tropical forests, has not been well-documented. Here we report insect herbivory on diverse angiosperm fossil leaf specimens from Pliocene (Rajdanda Formation) sediments of the Chotanagpur Plateau, eastern India, revealing that galling was the most common form of folivory in the latest Neogene monsoon-adapted tropical forests of eastern India. Diverse well-preserved galls are described on the basis of their size, shape and position on the host angiosperm leaf remains. Nine gall damage types (DT 32, DT 33, DT 34, DT 80, DT 83, DT 85, DT 110, DT 120, and DT 144) are identified. They are compared with extant galls and the probable gall inducers making morphologically similar galls on related host tropical plant species of *Ficus*, *Mangifera*, *Albizia*, *Galactia*, *Ziziphus*, *Hylodesmum*, *Adina*, and *Psidium*. The gall producers belong to the insect orders Orthoptera, Hemiptera, Hymenoptera, Coleoptera, Lepidoptera, and

Diptera (Cecidomyiidae). Although the detailed morphology of the phytophagous insects associated with the recovered fossil leaves is unknown, our findings indicate that many modern plant-insect relationships were likely established by the Pliocene. The reconstructed warm, humid Pliocene climate with a weak monsoon seasonality was conducive to extensive galling activity during this time.

Keywords: Fossil galls; fossil leaves; Jharkhand; latest Neogene; palaeoecology; plant-insect interaction

1. Introduction

Galls (Cecidia) are cells, tissues, or plant organs modified by hypertrophy and/or hyperplasia induced by parasitic or pathogenic organisms (Stephenson and Scott, 1992), the product of the interaction between the inducer and the 'host' plant (Raman, 1988). Galling, or cecidogeny, is one of the nine major categories of insect damage (other ones are external foliage feeding, piercing and sucking, leaf-mining, seed predation, boring, palynovory, nectarivory, and ovipositioning), or physical interaction with plants (Labandeira et al., 2007), on roots, stems, leaves, flower buds and flowers, or on fruits. Gall induction by insects causes decline in photosynthetic and transpiration efficiencies, stomatal conductance, and water potential (Flinn et al., 1990; Larson, 1998), thus leaving the host plant stressed (Raman, 1994; Abrahamson et al., 1998; Florentine et al., 2001). Gall inducing insects are found among all orders of herbivorous insects, among which the aphids and psyllids (suborder Sternorrhyncha) form the majority of galls (Fernandes et al., 2012).

The first occurrence of terrestrial fossil galling was reported in a liverwort host from the Middle Devonian of New York State with an unknown arthropod inducer (Labandeira et al., 2014). Gall records increased substantially during the Pennsylvanian (Late Carboniferous) in Euramerica, hosted by *Psaronius* tree ferns (Labandeira and Phillips, 1996) and calamitalean horsetails (Van Amerom and Josten, 1973; Kelber, 1988). Permian leaf galls mostly occurred on glossopterid hosts (Adami-Rodrigues et al., 2004; Prevec et al., 2009; McLoughlin, 2011), after which there was a global decline of plant-insect interactions due to the Permian–Triassic ecological crisis (Labandeira et al., 2018). Galling re-appeared, attributable to several insect lineages (Larew, 1992), in middle–late Triassic floras throughout Pangaea (Anderson et al., 2007; Krassilov and Karasev, 2009; Anderson and Anderson, 2018).

Galling types became more common after the angiosperm radiation during Late Cretaceous and a concomitant rise in insect diversity (Scott et al., 1994; Labandeira, 2006; Krassilov, 2008). Gall studies are generally limited. Scott et al. (1994) reported twenty-five different types of gall from the Cretaceous, Paleogene, and Neogene localities and identified probable gall inducers. Buzek et al. (1992) and Diéguez et al. (1996) described Miocene fossil galls from Spain and Bilina mine (Czech Republic) respectively, while Straus (1977) described upper Pliocene gall impression from the Harz Mountain, Germany.

A large number of Cenozoic plant fossil assemblages are known from India, but previous works have mostly paid attention to insect-related plant damage (Srivastava et al., 2000; Khan et al., 2014, 2015); the evidence of galling is scattered and inconsistent. Galling has been observed in Indian leaf fossils from the Triassic (Ghosh et al., 2015), lower Cretaceous (Banerji, 2004), Palaeocene (Srivastava et al., 2000), Miocene (Khan et al., 2014, 2015), Pliocene (Singh and Prasad, 2010; Hazra et al., 2020a), and Pleistocene (Khan et al., 2014). Srivastava and Srivastava (1998) reported a gall impression probably induced by members of the Cynipidae (?) and Hymenoptera on *Sophora* leaves (Fabaceae family) from the latest Neogene (Pliocene) sediments of Jharkhand, eastern India. Srivastava et al. (2000) also reported some Cecidomyiid galls on upper Palaeocene *Mangifera* leaf remains from Northeast India, while Khan et al. (2014, 2015) reported evidence of this type of insect folivory in Siwalik fossil assemblages (Miocene–Pleistocene) of the eastern Himalaya.

We report here gall types on uppermost Neogene (Pliocene) fossil leaves from the Chotanagpur Plateau, eastern India, and identify the gall inducers by comparing the fossil galls with those found on leaves of the extant nearest living relatives of the fossil leaves. The abundance of fossil galls recorded here is useful for understanding the dynamics of associations between angiosperm plants and their dependent insect herbivores during Pliocene; the diversity of galling reported here in the Pliocene palaeoforest of Chotanagpur Plateau is significant for interpreting the prevailing palaeoclimate.

2. Materials and methods

During our field work in 2018–2020, 249 samples of compression and impression leaf fossils with well-preserved and diverse gall types 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 (Figs. 1, 2). The criteria we use for recognizing galls are given in Table S1; in general, galls are characterized typically by circular to ellipsoidal, often darkened areas on leaf laminae, sometimes displayed as rings where the gall has fallen away. Figs. 3–8 and S1–S6 illustrate examples of what we identify as galls, with equivalent modern counterparts. The fossil leaves were examined carefully for damage caused by insect interactions, and those with diverse galls were photographed using a high-resolution digital camera. For the recognition and identification, and description of the folivory damage pattern, the initials DT (Damage Type) and the corresponding number of types were used, following the scheme of Labandeira et al. (2007).

Nearly 700 fossil leaves were collected from the Pliocene sediments, including 400 angiosperm leaves for this study. Different types of insect herbivory (hole feeding: 7.29%; margin feeding: 8.96%; skeletonization: 3.27%; and leaf mining: 11.33%) were found, but galling was particularly common (Table S2; Fig. 9A). Detailed descriptions of other damage types, namely feeding, skeletonization, and leaf mining, is in preparation and will be published in a separate paper. The length, width and diameter of each fossil leaf gall were measured. We have also collected modern angiosperm leaves having diverse gall types from forests adjacent to the fossil exposures. The plant species hosting the fossil galls were identified and compared with the extant species with known gall-inducers as modern analogues (Table S1; Figs. 3–8, S1–S6). Line drawings of some significant fossil galls were made using Corel Draw ver. 20 (Fig. 8). Galling occurrences are summarized in Figs. 9, 10. The fossil leaf specimens are housed in the Museum of the Palaeobotany and Palynology laboratory, Department of Botany, Sidho-Kanho-Birsha University (SKBUH), Purulia.

3. Geologic setting of the fossil locality

The uppermost Neogene sediments of the Rajdanda Formation (Puri and Mishra, 1982), Mahuadanr Valley (23.3965°N, 84.1066°E), Jharkhand, are exposed along the left bank of Birha River in an area of 2.6 km long and about 1.5 km wide (Fig. 1). The studied section reaches a maximum thickness of 5 m, about 100 m along the left bank of the Rampur Nala, a tributary of the Birha River, comprising mainly

shales intercalated with sandstone layers, structurally dipping towards the northwest. The colour of the more clay-rich shale varies from grey to black, whereas the more silty part of the shale is light brown.

Yellowish brown sandstones occur as lenses, embedded with rounded mudballs coated with sand grains (Fig. 2). The upper 2.5 m of the shale unit is highly fossiliferous with mostly dicotyledonous angiosperm leaf impressions and compressions, fruit remains, flowers, fossil fish and bird remains. Carbonized wood fragments occur within the interbedded yellowish sandstone lenses (Fig. 2). The well-preserved fossil plant and animal remains suggest reducing conditions at the time of deposition. The presence of authigenic pyrite occurring within the fossiliferous shale layers indicates a poorly oxygenated lacustrine environment, disturbed by fluvial incursions during flood events (Kumar et al., 2000; Bajpai et al., 2001).

Previous workers (Prakash et al., 1987; Guleria, 1992; Srivastava and Bande, 1992; Srivastava et al., 1992; Singh and Chauhan, 2008; Singh and Prasad, 2010) have determined the age of the Rajdanda Formation as 'late Cenozoic' (Pliocene) based on megafossil records and palynological analysis. A Pliocene age was assigned to these deposits based on the presence of fossil *Sindora* wood (Guleria, 1992), same as in the district resource map of Palamau, Jharkhand, published by the Geological Survey of India.

4. Results

4.1. Galling damage types

Fossil leaf specimens were examined for gall insect damage using the criteria outlined in the "*Guide to Insect (and Other) damage types on compressed plant fossils*" (Labandeira et al., 2007). Distinctive galls are assigned to nine galling damage types (DTs) such as DT 32, DT 33, DT 34, DT 80, DT 83, DT 85, DT 110, DT 120, and DT 144 (Figs. 3–8, S1–S6), observed in our fossil leaves assignable to diverse angiosperm families namely: Fabaceae, Malvaceae, Moraceae, Anacardiaceae, Rhamnaceae, Combretaceae, Dipterocarpaceae, and Rubiaceae. The Fabaceae leaves show the highest amount of galling (32.49%), consistent with previous reports of Chotanagpur plateau, eastern India (Singh and Prasad, 2007, 2009, 2010; Hazra et al., 2020a, 2020b, 2021, in press), followed by Moraceae (12.82%) and Malvaceae (10.34%) (Fig. 10).

Identifications of plant-insect relationship were based on comparison to extant taxa featured in identification keys in Plant Galls of India by Mani (1992), as shown in Table S1 which lists the characteristics of the observed fossil galls and their inducers. On this basis, insects belonging to orders Diptera, Thysanoptera, Hemiptera, Lepidoptera, Hymenoptera, Coleoptera, Homoptera are the probable gall causers in the studied samples (Fig. 11). The most common galling DTs are DT 32, DT 33, and DT 34, with nearly forty-eight leaves among the studied samples showing such damage. The percentage of leaves exhibiting DT 32 (Fig. 9B; 61.24%) exceeds the other types of galling. The insects belonging to the order Diptera are common inducers for almost all of the galling damage types studied here.

Single fossil leaf specimens sometimes host several gall types (Figs. 3, 4, S1, S2, S4–S6) but leaves with only one galling damage type are the most common (64.69%), whereas leaves with two types of damage make up 28.41% of all leaves, and those more than two types only 6.9% (Fig. 9C). Few insect body parts were found in association with the specimens documented here (Fig. 11), but lacking taxonomically diagnostic features. The galls DT 32 and DT 34 are most abundant within the Chotanagpur Pliocene flora. They occur on multiple hosts, and in some cases of high densities on the single leaf surface. The more distinctive gall type DT 110, has unique features in its shape and size, inner gall tissue development, wall thickness, and the responses of the host foliar tissue to gall presence. This gall also tends to occur on only one host plant, usually *Mangifera*.

The identified Pliocene gall types are diverse as in modern plants (Figs. 6, 7). One leaf impression (Fig. 6E) shows a population of small (0.04–0.09 cm) simple spot galls distributed across the whole surface of the laminar between the secondary veins. Similar types of galls are found on the modern leaves of *Albizia* (Fig. 6E) and *Galactia* (Fig. 6O) belonging to the family Fabaceae. Some leaf impressions (Fig. 6M) show small cone galls on the lamina surface adjacent to primary veins. Galls on some fossil leaf specimens are clustered near the primary veins (Fig. S2N), secondary veins (Figs. 3E, S1G), tertiary veins (Figs. 3B, S1A, S2I), leaf margins (Fig. 5H), and especially towards leaf apices (Fig. 3D, K, O).

4.2. Evidence of gall producing fossil insects

A few phytophagous insects have been recovered from the sediments in the Chotanagpur Plateau, eastern India (Fig. 11). Hazra et al. (2020a) reported an *in situ*

phytophagous insect and pupal exuviae of Cecidomyiidae on the abaxial cuticular surface of fossilized leaf cuticle fragments representing Fabaceae leaves (cf. *Albizia*) (Fig. 11A, B). Cecidomyiidae is known to be a very primitive family within the order Diptera, which are plant feeders and induce galls on a variety of flowering plants (Wigglesworth, 1946). Here we show evidence of gall-inducing insects, including leafhoppers or plant hoppers (Hemiptera; Fig. 11E, F), the egg of an aphid or a psyllid (Hemiptera; Fig. 11C, G), a wingless adult aphid (Hemiptera; Fig. 11D), a lateral view of a gall midge (Diptera; Fig. 11J), and a mature larva of a gall midge (Fig. 11I). Shukla et al. (2000) reported resin-embedded fossil insects from the study area, including *Psylla* (Hemiptera), with many phloem feeders that induce galls on their host plant (Pollard, 1973; Walling, 2000), *Ophion* (Hymenoptera), a chrysalis (Lepidoptera), and the mandibles of ants. Such *in situ* occurrences of potential gall inducers from the fossil assemblage here provide clues to the extensive gall development in the Pliocene forest of Jharkhand.

5. Discussion

The impact of galls on forest ecology can be complex (Williams and Whitham, 1986; Karban and Myers, 1989; Silva et al., 1996; Cuevas-Reyes et al., 2006). In general, most of the gall inducers exhibit a close affinity to particular host plants and specific organs (like leaves) (Fernandes, 1990; Floate et al., 1996; Wright and Samways, 1998; Shorthouse et al., 2005). Their diversity is influenced by plant species richness, density, composition, architecture and plant ontogeny (Gonçalves-Alvim and Fernandes, 2001; Cuevas-Reyes et al., 2004; Fonseca et al., 2006; Espírito-Santo et al., 2007).

The different gall morphologies, including gall size, location on the plant host, wall thickness, and number and location of larval chambers, are used to determine the type of inducing insect responsible (Sylvén, 1979; Raman, 1996; Abrahamson et al., 1998; Stone and Schönrogge, 2003). Gall morphotypes can be considered as surrogates for the inducing insect taxa due to their unique morphology and high host plant and plant-organ specificity (Dreger-Jauffret, 1992; Floate et al., 1996; Price et al., 1998; Cuevas-Reyes et al., 2004). Gall type diversity is likely related to the physiological difference in the behaviour of the inducing insects and the susceptibility of the plants. Smaller galls tend to be favoured over larger galls as it is easier for the insect to complete inducing its gall within a single growing season; large galls are

destroyed more easily under conditions of biological pressure (Stone and Schönrogge, 2003).

Although we do not yet have a comprehensive inventory of plant/insect interactions and climate change throughout the Pliocene, we see a strong relationship between the extent and diversity of insect damage under different Pliocene climates. Pliocene localities with documented plant-insect interactions also include the late Pliocene fossil Willershausen Lagerstatten, Germany (Adroit et al., 2018), and the late Pliocene fossils of Berga, Germany (Adroit et al., 2018), showing the importance of temperature in mediating insect activity and the extent of insect damage on leaves.

Globally, gall diversity and abundance peak at middle latitudes in warm, semi-arid to arid environments (Blanche and Ludwig, 2001; Carneiro et al., 2005). Climatic conditions leading to sclerophyllous (evergreen, thick-leaved) vegetation is associated with high gall species diversity (Fernandes and Price, 1988, 1991; Ribeiro and Basset, 2007). In tropical rainforest ecosystems sclerophylly increases vertically due to increasingly greater transpiration stress brought about by more intense irradiance and higher wind speeds affecting the upper canopy; so, gall diversity and abundance tend to be greatest in the upper canopy of tall tropical forests (Ribeiro and Basset, 2007). This may also indicate the upper canopy is likely rich in members of the Fabaceae because this family hosted the most galls. The chances of gall survivorship increase higher in the canopy because leaf mortality by fungal attack, parasitism, or chewing is greatest in the forest understorey (Ribeiro and Basset, 2007).

The frequency of fossil galls documented here, summarized in Figs. 9, 10, indicates high levels of plant-arthropod interactions in the Pliocene monsoon-influenced tropical forests of Chotanagpur Plateau, eastern India. Based on similarities in gall form, size, shape and position on the fossil leaves of host plants compared to similar gall characteristics in extant vegetation, the responsible fossil gall-inducers were inferred.

Our results also support the plant family size hypothesis, which states that the diversity of galling insects should be greater among the host plant families with the highest numbers of species (Araújo et al., 2011, 2019; Santos-Silva and Araujo, 2020). A high number of species within a family creates a greater availability of niches available for galling (Mendonça, 2007). This pattern was strongly influenced by Fabaceae, which showed the greatest species richness, in terms of host plants of galls in the Pliocene forest of Chotanagpur Plateau.

The high diversity of galling in the Pliocene tropical forests of Jharkhand is considered to be related with the diversity of potential host plants (Fernandes and Price, 1991). Although most extant galls can be related to their inducers, few fossil galls preserve their perpetrators. Our recent finding of *in-situ* phytophagous insects such as a gall midge and its pupal exuviae (Fig. 11A, B), of the Cecidomyiidae, on galled fossilized leaf cuticle fragments of Fabaceae leaves (cf. *Albizia*), confirms the presence of such gall-inducers during Pliocene (Hazra et al., 2020a). We found fossil insects belonging to Hemiptera present in the study material; Diptera also occurred in the Pliocene Jharkhand forests together with Hemiptera, Hymenoptera and Lepidoptera as evidenced by their remains preserved in resin (Shukla et al., 2000).

We notice that galls are more abundant than any other form of insect herbivory (mining, various types of feeding etc.) in the studied sediments, probably because the Pliocene Chotanagpur Plateau hosted tropical forests most similar to late successional forests of today where the richness of gall inducing insects is also highest (Leroy and Roiron, 1996; Adroit et al., 2016). Such forests would have supported a high upper canopy where leaf sclerophylly may have increased the galling activity.

We suggest that the Pliocene climatic factors played a major influential role in plant-insect interaction. As it is found that high temperature, high pCO_2 and low precipitation favours the prevalence of galling (Crowley, 1991; Fernandes and Price, 1992; Stults et al., 2011), we infer that the large amount of galling observed in the Chotanagpur palaeo-forest is likely associated with the warm climate of the Pliocene in the region.

Hazra et al. (2020b) used the Climate Leaf Analysis Multivariate Program (CLAMP) on 80 different morphotypes of fossil leaves from the same location, resulting in a mean annual temperature of ~22°C, which is some 3°C cooler than today; the warm month mean is interpreted to be about 6°C cooler than now at ~27°C, but the cold month mean the same as today. These temperature differences could well be due to within-canopy evapo-transpirational cooling (Spicer et al., 2011). Because insects are poikilothermic, and their metabolism is dependent on the environment (Meglitsch, 1972), the relatively warm cold month would not limit insect activity. CLAMP analysis also suggested that the Chotanagpur Pliocene fossil assemblage experienced a weak monsoon climate with a year-round growth high rainfall (Hazra et al., 2020b). A recent modelling study for the evolution of East Asian monsoon by

Farnsworth et al. (2019) also suggest a significant drop in monsoon intensity (rainfall seasonality) during the late Pliocene. The year-round high humidity during Pliocene in the region probably explains why leaf sclerophylly and galling was mostly confined in the upper canopy.

6. Conclusions

Our investigation of leaf damage types shows galling as the most common form of herbivory in the latest Neogene (Pliocene) tropical forests of Chotanagpur Plateau, eastern India. This, combined with our prior palaeoclimate reconstruction, suggests a humid tropical palaeo-forest with trees tall enough to induce considerable leaf sclerophylly in the upper parts of the canopy, which is likely to have favoured galling on the basis of the modern analogue. Some well-preserved phytophagous insects have been recovered from the same fossil leaf assemblage, important for better understanding the ancient plant-insect interactions that govern the dynamics of extensive galling in the Chotanagpur Pliocene forest. Combination of morphological and geochemical studies on the gall fossils is suggested to provide essential information for understanding coevolutionary relationships between terrestrial higher plants and insects, at geologic time scale, as well as macroevolutionary patterns in plant-insect associations.

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Figure captions

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

Fig. 2. Sedimentological log of the study section constructed using SedLog 3.0.

Fig. 3. Occurrence of galls on fossil leaf remains recovered from the Pliocene sediments of Jharkhand, eastern India. Circular to ellipsoidal galls avoiding major veins (DT 32) (A–H, J–P; in white boxes); circular to ellipsoidal galls on secondary veins (DT 34) (C, D, L, green boxes; K in a black box); circular to ellipsoidal galls on primary vein (DT 33) (I, white box). Scale bar = 5 mm.

Fig. 4. Galls are ellipsoidal to spherical, dark, thoroughly filled with thickened carbonized material, diameters 1–3 mm (DT 80) (A–P, in white boxes). Scale bar = 5 mm.

Fig. 5. Fossil leaves with elongate, elliptical to lenticular thickenings, a striated surface centred lengthwise on the midvein (DT 85) (A–C, in yellow boxes); galls ellipsoidal to spherical, dark, thoroughly filled with thickened carbonized material, diameters 1–3 mm (DT 80) (D, black box; E, F, yellow boxes; G, white box); galls on tertiary veins, ovoidal-circular; central chamber sharply separated from thick carbonized rim (DT 110) (H, white box); circular to ellipsoidal galls avoiding major veins (DT 32) (I, black box). Scale bar = 5 mm.

Fig. 6. Galls on selected plants from the Pliocene sediments of Jharkhand, eastern India. (A) Cecidomyid galls on a fossil leaflet of *Hylodesmum* sp. (Fabaceae). (B) Structurally similar galls on a modern leaflet of *Hylodesmum* sp. (C) Ellipsoidal galls are attached on secondary veins of *Adina* sp. (Rubiaceae). (D) Structurally similar galls on a modern leaf of *Adina* sp. (E) Leaflet of *Albizia* sp. (Fabaceae) with cecidomyid galls. (F) Structurally similar galls on a modern leaflet of *Albizia* sp. (G) Ellipsoidal galls attached on secondary veins of *Psidium* sp. (Myrtaceae). (H) Structurally similar galls on modern leaf of *Psidium* sp. (I) Fossil leaf of *Ficus* (Moraceae) bearing ellipsoidal to spherical, dark, thoroughly filled with thickened carbonized material. (J) Similar type of galls on a modern leaf of *Ficus* sp. (K) Circular to ellipsoidal galls on a fossil leaf of *Ziziphus* sp. (Rhamnaceae). (L) Modern

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leaf of *Ziziphus* sp. showing similar type of galls. (M) Fossil leaf of *Ficus* sp. (Moraceae) bearing ellipsoidal to spherical, dark, thoroughly filled with thickened carbonized materials. (N) Similar galls on a modern leaf of *Ficus* sp. (O) Circular to ellipsoidal galls on a leaflet of *Galactia* sp. (Fabaceae). (P) Modern leaflet of *Galactia* showing similar type of galls. Scale bar = 5 mm.

Fig. 7. (A) *Mangifera* leaf bearing circular to ellipsoidal galls scattered on the lamina. (B) Structurally similar galls on a modern leaf of *Mangifera* sp. (C) Counterpart of (A). (D) Enlarged view of (A). (E) Enlarged view of (B). (F) *Mangifera* leaf gall characterised by central chambers, indicated by plug of dark and fusainized central tissue it its outer margin showing an irregular surface. (G) Similar gall produced by *Colletotrichum gloeosporioides* on a modern leaf of *Mangifera* sp. (H) Close-up view of (F). (I) Enlargement of (G). Scale bar = 5 mm.

Fig. 8. Line drawing of a fossil leaf bearing various galling damage types recovered from the Pliocene sediments of eastern India. Scale bar = 5 mm.

Fig. 9. Histograms showing galling occurrences in the Rajdanda Formation leaf assemblage. (A) Percentage of leaves exhibiting the different types of insect herbivory. (B) Percentage of leaves displaying different damage types of galling. (C) Percentage of single leaves showing multiple gall types.

Fig. 10. (A) Frequency of leaves having diverse galls of the host plant taxa. (B) Frequency of different types of galling on host plant taxa. Abbreviations: F**,** Fabaceae; A, Anacardiaceae; D, Dipterocarpaceae; C, Combretaceae; Ma, Malvaceae; Mo, Moraceae; Ru, Rubiaceae; Rh, Rhamnaceae; UT, unidentified taxa.

Fig. 11. (A) Fossil gall midge (Diptera, Cecidomyiidae). (B) Pupal exuviae of a gall midge. (C) Egg of a psyllid (Hemiptera). (D) A wingless aphid (Hemiptera). (E) Probable remains of a leafhopper (Hemiptera). (F) Probable remains of a leafhopper (Hemiptera). (G) Egg of an aphid (Hemiptera). (H) An unidentified insect remain. (I) A mature larva of gall midge. (J) Lateral view of a gall midge. Scale bar: 1 mm for (A, B); 5 mm for (C–J).