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Fossil evidence of insect folivory in the eastern Himalayan Neogene Siwalik forests

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ABSTRACT

Fossil leaves from the Siwalik sedimentary rocks of Arunachal Pradesh, eastern Himalaya, evidence a variety of plant-insect interactions that operated during the evolution of monsoon-influenced forests from middle Miocene to lower Pleistocene times. Five principal categories of damage are identified in this study namely leaf mining, hole feeding, skeletonizing, galling and marginal or non-marginal feeding. These traces indicate that insects interacted with the plants for various purposes, including feeding, egg laying and sheltering. Furthermore, these morphotraces tend to suggest similarities in insect interactions with leaves of extant plant species such as *Millettia cineria*, *Canarium bengalense*, *Glochidion gamblei*, *Callicarpa arborea*, *Chonemorpha macrophylla*, *Actinodaphne angustifolia* and others. On the basis of comparison with extant taxa, possible leaf chewers could have belonged to the insect orders Orthoptera, Coleoptera, Lepidoptera and Diptera. Although the morphology of the phytophagous insects associated with the fossil leaves is unknown, present findings reveal that many modern plant-insect relationships were established by the Miocene and continue to the present, shaping both the present day flora and fauna. The study shows an increasing tendency towards folivory (expressed in terms of percentage of leaf damage; 35% in lower Siwalik, 39% in middle Siwalik and 45% in upper Siwalik). This increase in insect activity is unconnected to measurable climate change but was due to biotic change, where there was a competition between insects and plants and insects appear increasingly successful.

1. Introduction

Knowledge of plant-insect interactions is fundamental to understanding the dynamics of present-day terrestrial ecosystems (Gilbert, 1979). Their recognition in the fossil record is essential for the study of co-evolution processes that affected plants and insects throughout geological time (Smart and Hughes, 1973).

Plants and insects are the two most species-rich groups that make up most of the Earth's biodiversity (Wilf and Labandeira, 1999). One of the most valuable contributions of fossil leaves is their uniquely diverse and abundant preservation of insect-feeding damage (Labandeira and Currano, 2013). No other type of fossil preserves such rich, direct evidence of two levels of the food web in a single specimen. Fossil insect damage offers a tremendous opportunity to study plant-insect feeding associations in relation to major environmental stresses and climate change in space and time (Labandeira, 2002, 2006; Labandeira et al., 2002; Wilf et al., 2005, 2006; Currano et al., 2008; Wilf, 2008). These studies also provide valuable information on their associations in the context of co-evolution (Ehrlich and Raven, 1964).

Plant fossils preserve information on many aspects of insect behavior in the form of eaten/chewed leaves, mining activity, gall formations, egg masses over the surface of leaves and burrow damage in stems and seeds etc. (Wappler, 2010; Wappler and Denk, 2011; Knor et al., 2012). On the basis of shape, size and position of damage an insect can be identified up to the taxonomic rank of order (McDonald et al., 2007).

Plant-insect relationships are very common, diversified and well studied in present-day terrestrial ecosystems. Most of them are related to feeding or represent associations between insects and host plants (Southwood, 1973). Such relationships are also known in fossil ecosystems (Opler, 1973; Hickey and Hodges, 1975; Hickey and Doyle, 1977; Scott and Taylor, 1983; Taylor and Scott, 1983; Scott and Paterson, 1984; Scott et al., 1985, 1992; Larew, 1986; Kelber and Geyer, 1989; Zhou and Zhang, 1989; Upchurch and Dilcher, 1990; Chaloner et al., 1991; Labandeira et al., 1994; Grauvogel-Stamm and Kelber, 1996; Ash, 1997; Smith, 1998; Beck and Labandeira, 1998; Wilf et al., 2000; Wappler, 2010; Wappler and Denk, 2011; Knor et al., 2012; Edirisooriya and Dharmagunawardhane, 2013). Some researchers have also attempted to examine changes in herbivore damage over time (Wilf and Labandeira, 1999; Smith, 2000; Wilf et al., 2001) and in

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particular during periods of climate change in the Paleocene and Eocene and found evidence for an increase in herbivory as temperatures increased and a decrease in herbivory as temperatures decreased. This suggests that climate may have played an important role in the evolution of insect-plant associations (Bale et al., 2002). A similar relationship has been identified in modern ecosystems, where decreases in latitude appear to be correlated with increases in temperature and increases in insect feeding damage levels (Coley and Barone, 1996).

Plant fossil assemblages are common in many of India's sedimentary basins. However, in comparison to plant fossils, the record of plant-insect interactions in these outcrops is scarce and inconsistent. Insect activities have been observed in leaf fossils from the Mesozoic (Rao, 1946; Vishnu-Mittre, 1957), the Permian (Chauhan et al., 1985; Srivastava, 1988a,b, 1996, 1998; Pant and Srivastava, 1995; Chandra and Singh, 1996; Banerjee and Bera, 1998) and the Cenozoic (Srivastava and Srivastava, 1998; Srivastava et al., 2000). Earlier workers did not pay much attention to insect related plant damage, and reported such evidences without proper illustrations or descriptions.

In this study, we examine fossil leaves from the lower part (middle-late Miocene: Dafla Formation), middle part (Pliocene: Subansiri Formation) and the upper part (late Pliocene to early Pleistocene: Kimin Formation) of the Siwalik of Arunachal foothills, eastern Himalaya. The quality of preservation in the three Siwalik Formations provides an excellent opportunity for studying plant-insect interactions. Insights into the morphological, behavioral, and physiological adaptations involved in plant-insect interactions are provided by documenting insect-mediated damage, the distribution of feeding guilds, and the presence of specialized damage types. These provide a window into understanding the development of an important part of ecosystem dynamics in sub tropical to tropical Asia over evolutionary timescales. The comparison of herbivory from the three Siwalik floras provides a rare opportunity to detect long-lasting associations (over a period of 13–2.5 Ma) and patterns of change in plant-insect interactions in a strongly monsoonal regime during this period.

2. Materials and methods

The fossil leaves studied here were collected from road-cutting sections of upper (upper Pliocene to lower Pleistocene), middle (Pliocene) and lower (middle to upper Miocene) Siwalik sedimentary strata in Arunachal Pradesh (situated between 26°27′52″ and 29°29′54″ N and 91°29′50″ and 97°24′56″ E), India (Fig. 1). Arunachal Pradesh is the largest northeastern state of India and is bound by the neighbouring countries of China (Tibet) to the north, Bhutan to the west and Myanmar to the east.

Fossil leaves were examined carefully for leaf damage. All the fossil leaves were photographed using a high-resolution digital camera and enlarged images were used for visual examinations. The traces were organized into distinct trace types designated as morphotraces, which were described and separated depending on plant morphotype as well as the size, shape and position on the leaf surface (McDonald et al., 2007). The description of damage patterns was given according to the guide book of "Insect (and other) damage type on compressed plant fossils" of Labandeira et al. (2007). Nearly 350 fossil leaves were collected from Siwalik sediments, but only 138 angiosperm leaves (53 from the lower part, 27 from the middle part and remaining 58 from the upper part of the Siwalik strata) were sufficiently well preserved for this study. Preservation quality is a key determinant in the recognition and classification of herbivore damage. The length and width of each fossil leaf was also measured. Leaf fragments smaller than 1 cm^2 and with a damage area less than 0.1 mm were not considered in the study. All dicotyledonous angiosperm specimens were identified to species level and non-angiosperm plants were not included in the study. Specimens that were not identifiable to the genus level, but were identifiable at the family level, were given a morphotaxon status. For the purposes of this study, a morphotaxon is a designation that is given to a specimen or group of specimens that are morphologically distinct from all other specimens but not yet assignable to a specific taxon. "Unidentified" specimens were usually not identifiable because of poor

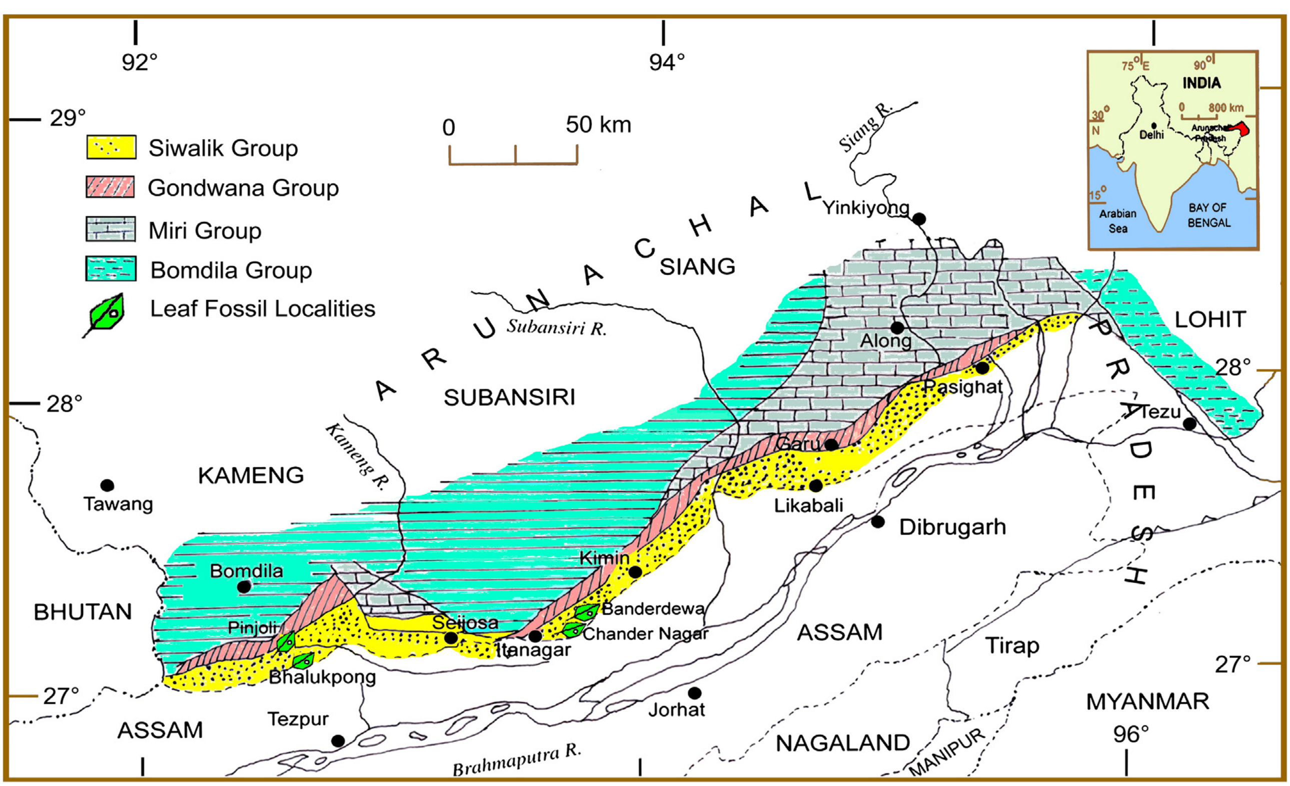

Fig. 1. Geological map of Arunachal foothills (modified after Singh and Tripathi, 1990), line drawing of leaf indicates the fossil locality.