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Insect herbivory in Gondwana plants

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ABSTRACT

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Plant–insect interaction is dominant in the extant flora and it is estimated that more than one million species of insects directly or indirectly survive on plants. In comparison, such association is limited in extinct flora, mainly due to problem in identifying structural features associated with the insect wronged plant fossils. Concerted efforts and comparative structures observed in extant flora have unfolded the mystery of insect herbivory in fossil plants. The study has helped to understand the feeding pattern and evolutionary features of insects during different time intervals and provide significant evidence to comprehend the co–evolution of plant and insect in the geologic past. Herbivorous insect wings discovered from different Gondwana successions of India belong to families and genera of Homoptera, Heteroptera, Mecoptera, Coleoptera and Blattoidea. The remains of Coleoptera and Mecoptera in all probability represent the earliest record in fossil flora. Insect herbivory is well recognized in Indian flora in the form of insect galls, chewing and eaten marks of leaf margin, disfigurement of lamina, egg–like pouches, trailing marks, mining activity, etc. The available records demonstrate the presence of well knit coalition of insect–plant interaction in Indian Gondwana successions.

Diverse type of insect herbivory recovered in the Gondwana flora of India implies that insects used the plants for various purposes such as feeding, shelter and laying eggs for their development/ survival and the process has thus helped in the development and evolution of insects in consortium with plants.

Key–words—Insect–plant interaction, Herbivory, Evolution, Feeding pattern, Gondwana, India.

गोंडवाना पादपों में शाकभक्षी कीट

अश्विनी कुमार श्रीवास्तव एवं रश्मि श्रीवास्तव

सारांश

विद्यमान वनस्पति–जगत में पादप–कीट पारस्परिक –क्रिया प्रभावी है और यह अनुमानित किया जाता है कि कीटों की दस लाख से अधिक जातियाँ प्रत्यक्ष अथवा परोक्षरूप से पादपों पर निर्भर करती हैं। कीटों द्वारा अपकृत पादप जीवाश्मों में संरचनात्मक लक्षण पहचानना कठिन होने के कारण विलुप्त वनस्पतियों में ऐसा साहचर्य निरूपित करना कठिन एवं सीमित है। वर्तमान में वनस्पति–समूह में किए गए संयुक्त प्रयास एवं तुलनात्मक संरचनाओं ने जीवाश्म पादपों में शाकभक्षी कीट के सहचर्य के रहस्योद्घाटन कर दिए हैं। अध्ययन ने भिन्न–भिन्न अंतरालों के मध्य कीटों के भरण प्ररूप और विकासात्मक लक्षणों को समझने में सहायता की है तथा भू–गर्भीय अध्ययन अतीत में पादप व कीट के सह–विकास की ज्ञान के लिए महत्वपूर्ण प्रमाण प्रदान करता है। भारत के विभिन्न गोंडवाना अनुक्रमों से खोजे गए शाकाहारी कीट पंख होमोप्टेरा, हेटेरोप्टेरा, मिकोप्टेरा, कोलियोप्टेरा एवं ब्लैटौएडिया के कुटुबों व वंश के हैं। समस्त संभाव्यों में कोलियोप्टेरा व मिकोप्टेरा के अवशेष जीवाश्म वनस्पति–जगत में प्रारंभिकतम् अभिलेख निरूपित करते हैं। भारतीय वनस्पति–जगत में शाकभक्षी कीट, कीट पिट्टिकाओं, पर्ण पार्श्व के चबाने व खाए हुए चिह्नों, स्तरिका के विरूपण, अंडा–सदृश कोष्ठों, विमुख चिह्नों, खनन गतिविधि इत्यादि के रूप में भली–भाँति मान्य है। प्रस्तुत अभिलेख भारतीय गोंडवाना अनुक्रमों में कीट–पादप पारस्परिक–क्रिया के सम्मिलन की विद्यमानता प्रदर्शित करते हैं।

भारत की गोंडवाना वनस्पति–समूह में प्राप्त हुए विविध प्रकार के शाकभक्षी कीट यह स्पष्ट करते हैं कि कीटों ने अपने विकास/उत्तरजीविता हेतु भरण, आश्रय एवं अंडे देने जैसे विविध उद्देश्यों की पूर्ति हेतु पादपों को प्रयुक्त किया। इस प्रक्रम में पौधों ने कीटों के विकास एवं क्रमिक विकास में सहायता की है।

सूचक शब्द—कीट–पादप पारस्परिक–क्रिया, शाकभक्षी, विकास, भरण प्ररूप, गोंडवाना, भारत।

INTRODUCTION

IN recent years, considerable work has been carried out on insect–plant relationship in fossil flora and the study has helped to understand the feeding pattern and evolutionary features of insects during different time spans. Northern flora has extensively been studied to examine the different types of fossil flora for insect herbivory, i.e. external foliage feeding, piercing and sucking, boring, leaf mining, oviposition mark, galling, tunnelling, seed predation, etc. (Labandeira, 2002, 2006). In comparison, the southern flora has restricted testimony but recent discoveries of Glossopteris flora in India, Brazil, Argentina, South Africa, Antarctica and Australia have provided positive and firm evidences of insect herbivory to understand the insect–plant interaction in Gondwana flora of India (Srivastava & Agnihotri, 2011), Argentina (Gallego *et al.,* 2014), Africa (Prevec *et al.,* 2009), Australia (McLoughlin, 2011a, b; McLoughlin *et al.,* 2013), Antarctica (Slater *et al,.* 2014) and Brazil (Adami *et al.,* 2004).

Different geological successions of Permian, i.e. Talchir, Karharbari, Barakar, Raniganj, Kamthi; Triassic and Early Cretaceous sequences respectively of Indian Gondwana show the presence of well preserved record of insect herbivory in the Glossopteris, Dicroidium and Ptilophyllum floras. The Talchir Formation represents the flora immediately after the glaciation phase (Chandra *et al.,* 1992). Well known assemblages recovered from the Late Talchir shows the presence of insect and insect activities (Dutt, 1977; Chandra & Singh, 1996). Later, in the Karharbari Formation, the coaliferous bed, as such is devoid of insect related fossils but the documentation of Slater *et al*. (2014) indicates the presence of leaf damage and gall like structure in a fossil axis reported by Maithy (1965). The flora of the Barakar Formation immediately after the Karharbari Formation contains a variety of insect wing fossils and different types of insect herbivory in plant fossil assemblages of Glossopteris flora (Srivastava, 1987, 1988, 1996, 1998, 2007; Srivastava & Srivastava, 2010; Srivastava & Agnihotri, 2011). The flora also shows the presence of different types of insect wings along with the insect activities. Equivalent Mamal flora of Kashmir also indicates the presence of insect wing and insect gall–like structure in fossil assemblages (Bana, 1964; Verma, 1967; Pant & Srivastava, 1995). The Late Permian Raniganj and Kamthi floras show the presence of insect damaged leaves, galls, oviposition marks and coprolite–like structure (Chauhan *et al.,* 1985; Banerjee & Bera, 1998; Slater *et al*., 2014). Late Permian flora of Maitur Formation (Pal *et al.,* 2010) has also been found to contain insect nibbled leaf margin (Slater *et al.,* 2014). Early Cretaceous flora of Rajmahal contains distinct evidence of insect herbivory (Banerji, 2004; Srivastava & Krassilov, 2012). First definite record of insect herbivory along with insect wings (Srivastava, 1987) recorded from the Lower Barakar Formation of Raniganj Coalfield are exemplified (Pl. 1).

PHYTOPHAGOUS INSECTS

Phytophagous insects in Indian Gondwana sequence are known by the wings of different groups, e.g. Blattoidea, Homoptera, Mecoptera and Coleoptera. In all likeness, detritivorous role in the flora was performed by blattoids, whereas, insects of other groups were mainly responsible for herbivorous activity (Labandeira, 2006; Srivastava, 1998; Srivastava & Srivastava, 2010; Srivastava & Agnihotri, 2011).

Hislop (1861) for the first time discovered the insect wing–like structure as covers of blattidae from Upper Gondwana Kota–Maleri beds. The sediments also contain the fragments of insect (Rao & Shah, 1959). Feistmantel (1880) reported insect wing–like structure from the Talchir Formation. Later, well preserved complete blattoid insect wing, *Gondwanoblatta reticulata* from Risin spur, Kashmir was described by Handlirsch (1906). Bana (1964) and Verma (1967) reported other blattoid wings *Prognoblatina columbina* and *Kashmiroblatta marahaomensis* from the Mamal Formation, Kashmir. *Rajharablatta laskarii* was recorded by Dutt (1977) from the Talchir Formation and hind wing belonging to the ancient cockroach family, Archimylacridae was described by Srivastava (1988) from the Barakar Formation, Raniganj Coalfield. Faint impression of cockroach body fossil is reported from Mamal Formation of Kashmir (Kapoor *et al*., 1993). Wings of *Triassoblata natalensis* and *Aisoblatta* sp. were recorded by Pant and Srivastava (1995) from the same formation. Srivastava (1988, 1996) described well preserved insect wings of Homoptera: *Prosbolecicada* cf. *P. gondwanica* Pinto, *Prosbole* cf. *P. iratiensis* Pinto; Mecoptera: *Asiachorista beuburgae* Pinto, *Petromantis* cf.

PLATE 1

(Reproduced from Srivastava, 1987) →

1–3. Insect wings showing the venation pattern. Fig. 1 shows the coastal, radial, median, cubital and anal veins. Specimen Nos. BSIP 36147, 36227 and 36228. x 4.25.

4. *Glossopteris* leaf showing distorted and damaged part of lamina. Specimen No. BSIP: 36229. x 1.25.

5. Leaf lamina enlarged to show the pattern of distortion and nibbling. Specimen No. BSIP 36229. x 3.25.

6. *Glossopteris* leaf showing two rows of minute ovoid–shaped structures along the midrib. Specimen No. BSIP 36230. x 1.25.

7. Enlarged portion of leaf showing regular distribution of ovoid structures along the midrib. Specimen no. BSIP 36230. x 8.25.

8. Part of *Glossopteris* leaf showing disfigurement of lamina and irregular shaped outgrowth over the surface. Specimen No. BSIP 36231. x 2.25.

9. Probable insect damaged stem showing helicoidal–shaped structures, distributed all over the surface. Specimen No. BSIP 36232. x 1.75.

10. Stem surface enlarged to show the distribution and organizational pattern of helicoidal structures. Specimen No. BSIP 36232. x 8.25.

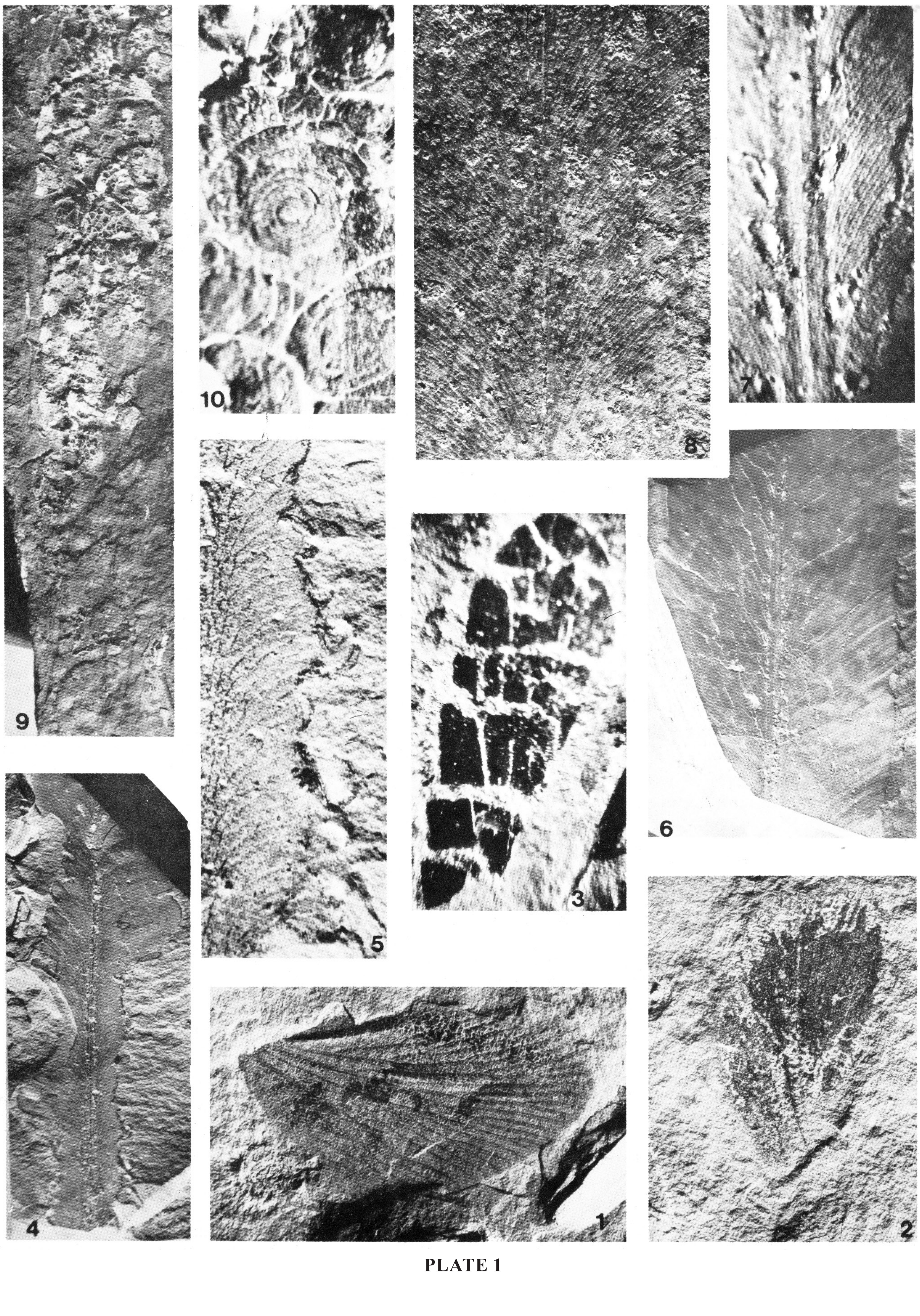

PLATE 1

P. evansi and Coleoptera: *Kaltanicupes* sp. from the Barakar Formation, Raniganj Coalfield. Chandra and Singh (1996) reported unnamed insect wing from the Talchir Formation, Talchir Coalfield. Apart from the insect wings there are many records of vertical and horizontal burrows and faecal pellets which are assigned to trailing behaviour and faecal pellets of insect origin (Kar & Chaudhury, 1981; Maulik & Chaudhury, 1983; De, 1990; Srivastava *et al.,* 1996, 2009, 2010).

INSECT HERBIVORY

It is ironical that the plant fossils of Indian Gondwana are exclusively preserved as impressions and compressions except for permineralized wood specimens. In view of such preservation, insect herbivory in Gondwana flora is visualized only on external morphological features of the plant fossils. These are mainly characterized by different types of foliage feeding structure, galls, regular or irregular occurrence of egg pouches and randomly distributed oviposition marks over the surface of leaf lamina. Scott and Taylor (1983), Kevan *et al.* (1975), Srivastava (1988), Labandeira and Sepkosi (1993) and others have discussed the distinguishing features of insect herbivory in fossil flora and emphasized that evidently there should be a biological response in fossil plant as against the insect damage. Labandeira (1998a, b, 2002) identified certain criteria to recognize the insect damage in plant fossils. Primarily there should be a reaction tissue in the form of callous on traumatic region, normally visible as thickened margin of insect chewed or eaten leaves. Presence of necrotic tissues, veinal stringers and contiguous cuspules is another criterion to recognize the insect damage. Evaluating apparent similarity of host–plant association in extinct and extant floras help to mark the herbivory in fossil plants. There are a variety of functional feeding groups present in the Gondwana flora of India. They may be classified as (i) external foliage feeding, categorized as hole, margin, cuspate excision, trench, and surface feeding (ii) galling (iii) egg pouches and oviposition mark, truly not a feeding damage but egg–laying process makes significant damage (Labandeira *et al*., 2007; Krassilov & Rasnitsyn, 2008).

External Foliage Feeding Structure—External foliage includes marginal feeding pattern characterized by thickened margin of leaf, possibly due to presence of callous tissues formed as a reaction along the damaged margin. Chauhan *et al.* (1985) for the first time recorded the insect damaged leaves of *Glossopteris* and *Belemnopteris* collected from the Raniganj Formation of the Raniganj Coalfield and presence of coprolites over the surface of leaf cuticle recovered from the leaves of *Belemnopteris*. Well preserved *Glossopteris*–leaves showing wavy, nibbled margin with characteristic thickness indicate the incidence of insect eaten or chewed margin of leaves (Srivastava, 1988; Srivastava & Agnihotri, 2011).

Crescent–shaped thickened cuspate margin is another very common feeding structure especially found in apical portion of *Glossopteris* and *Noeggerathiopsis* leaf margins recorded from the Early Permian Barakar Formation of Raniganj Coalfield (Srivastava, 1996).

Some of the leaves in Gondwana flora show deeply cut upper layer of the leaf having faint impression of venation pattern indicative of trench feeding structure (Srivastava & Agnihotri, 2011).

Hole feeding structure is represented by differently shaped small to large size holes irregularly distributed over the surface of leaves. Hole is normally surrounded by thick tissues but devoid of leaf lamina (Srivastava & Agnihotri, 2011).

Leaf lamina of *Glossopteris, Noeggerathiopsis* have been found to contain singular or serpentine structure in between the midrib and margin of leaves. The damaged leaves show faint impression of veins, whereas, other parts have normal structure. These features are attributed to surface feeding of insect (Labandeira & Phillips, 1996; Srivastava & Agnihotri, 2011).

Slater *et al.* (2014) have observed probable presence of external foliage damage and other types of insect herbivory in Indian Gondwana floral assemblages described by various workers right from the year 1828–30 (Brongniart) to 2010 (Pal *et al*., 2010). The attempt is creditable but it is better if fossils are examined physically before coming to any conclusion.

Insect gall—Galling is a direct evidence of insect herbivory and it is well demarcated in Gondwana flora. Srivastava (1987), Pant and Srivastava (1995) and Banerjee and Bera (1998) reported gall over the surface of *Glossopteris*–leaves. Such galls have mainly been attributed to gall produced by homopterous insects. Gall impression over the leaf surface of *Nipanioruha, Ptilophyllum* and *Nipaniophyllum* are found to be related to Diptera Group of insects (Vishnu–Mittre, 1957; Banerji, 2004).

Insect egg pouch and oviposition mark—Many leaves of *Glossopteris* recovered from Barakar Formation of Raniganj Coalfield have been found to contain distinct circular, elliptical to ovoid two rows of egg pouches situated along the midrib (Srivastava, 1996; Srivastava & Agnihotri, 2011). Grauvogel–Stamn and Kelber (1996) have recorded similar structures over the leaf surface of *Taeniopteris angustifolia* and they have compared these features with the egg marks of insect.

There are a number of specimens of *Glossopteris* and *Noeggerathiopsis* possessing randomly distributed oviposition marks in groups or in isolation over the surface of leaves. The oviposition marks are significantly present along the veins and they are very small less than a mm, normally rounded, elliptic, sometimes elongate. Oviposition marks are closely similar to the marks found in the *Glossopteris*–leaves of South Africa (Prevec *et al*., 2009). Recently, oviposition marks have been found to be very common in Gondwana flora of India but there is a need to recognize them with attention and care in the fossil flora (Srivastava & Agnihotri, 2011).

DISCUSSION

Absence of well defined plant fossils during the early part of Permian and the glaciation phenomenon before Permian hamper our endeavour to identify the commencement of insect–plant interaction in Indian Gondwana (Surange, 1975; Srivastava, 1987). The earliest association with insect in the flora is known in the early Permian flora of the late Talchir Formation by insect wings of blattoid,? homopteran and predation marks over seeds/ axis (Chandra & Singh, 1996; Srivastava, 1998). Slater *et al*. (2014) observed some leaves and axis possessing galls, piercement scars and oviposition marks in the plant fossil assemblage of early Permian Karharbari Formation. However, it is very difficult to correlate these marks with those of insect activity because the structure which Slater *et al*. (2014) believed to represent insect gall over the surface of *Cyclodendron*–axis originally described by Maithy (1965) as presence of leaf scars of lycopsid was interpreted as the irregular mark of mineral concretion (Srivastava & Chandra, 1992).

The flora of Barakar Formation mainly recorded from Raniganj Coalfield (Pl. 1) represents almost all the types of insect herbivory, e.g. different kind of feeding traces: leaf margin, cuspate, trench, surface and hole, insect egg set, galls, mining and oviposition marks (Srivastava & Srivastava, 2010; Srivastava & Agnihotri, 2011). Well preserved insect wings belonging to blattoids, homoptera, mecoptera and coleopteran groups of insect are also known. Feeding marks are very much comparable with the feeding structures produced by modern insects e.g. leaf hoppers, grass hoppers, beetles, bugs and aphids. Similarly, some of the galls recovered from the Late Permian flora of Raniganj Formation are also referred to the galls produced by homopteran insects (Banerjee & Bera, 1998). Oviposition marks are very much comparable with the similar marks produced by Odonata and Orthoptera groups of insects (Laaß and Hoff 2015).

There is an apparent loss of insect–plant interaction in the Gondwana flora after the early Permian Barakar Formation. This is because of the arid condition that prevailed during the Barren Measures Formation (after Barakar) when most of the elements of Glossopteris flora trounced due to adverse condition. Severity of climatic condition also affected the insect population and like the flora they also suffered transience. The plants recovered successfully during the late Permian Raniganj/ Kamthi Formation but apparently only gall–like structure is known in these floras. Limited record in onward flora of Triassic–early Cretaceous of Gondwana (Srivastava & Krassilov, 2012) further suggests the declination of insect population which is probably the result of the occurrence of mass extinction during the Permian/ Triassic Period (Carvalho *et al*., 2014).

Insect diversified with the diversification of plants during the Devonian and the Carboniferous times (Scott & Taylor, 1983; Labandeira, 2007, 2012; Labandeira *et al*., 2013). Pollinivory was perhaps also established by the end of Carboniferous (Chaloner *et al*., 1991). In fact, Carboniferous was the period of insect evolution in all its totality, e.g. they acquired new morphological changes, developed new strategies to acquire food and their reproductive behaviour also changed to adopt in new coal swamp flora of Cordaitales, Equisetales and Calamitales (Labandeira, 2001, 2002; Labandeira & Phillips, 2001, 2002). Such a diversification led to establish many groups and orders of the insects including changes in ancient Palaeodictyoptera Group and herbivory became well established phenomenon in the Carboniferous (Carpenter 1971; Labandeira & Phillips 1996). The presence of ovipostion marks have been referred to orthoptera, odonata, homoptera, coleoptera and ovipositors have also been assigned to fossil group Palaeodictyopteroid and Hypoperlida (Labandeira, 2002; Béthoux *et al*., 2004; Carvalho *et al*., 2014). Laaß and Hoff (2015) reported the earliest occurrence of ovipostion marks in the late Carboniferous flora of Germany and discussed the nature and behaviour of modern insects *via* à *vis* fossil insects and observed that Gondwana oviposition marks are very much similar with the egg sets of some modern damselflies.

The study of evolutionary features of mouth parts during different time intervals indicates an early mandible feature during the late Carboniferous which at later stage (? Permian) provided full opportunity for chewing and piercing of plant, e.g. by hexapods and myriapods (Labandeira, 2002). During Permian, significant evolutionary changes occurred when real holometaboly developed and insects were organized under different families of homoptera, heteroptera and coleoptera. Improvement of mandibulate structure help insect to interact frequently with plant. Records of lepidopteran insects are not known during the late Cretaceous and the early Permian but well developed insect chewed or eaten leaves certainly suggest the presence of caterpillar–like insect during the Permian which may or may not be ancestral of true Lepidoptera (Srivastava, 1996; Carvalho *et al*., 2014). Later insect suffered loss during Permian/ Triassic transition (Labandeira, 2002). During the late Triassic and the early Jurassic, there were significant radiation of Diptera insects and by Late Cretaceous ally of modern insects came into existence with the origin and evolution of angiosperms (Krassilov, 2007). In India, further radiation of herbivory in different forms are observed in the onward bennettitalean gymnospermic flora of Jurassic/ Cretaceous and angiospermic flora of Deccan Intertrappean sediments of central India and advanced herbivory is recorded from the Tertiary flora of Kerala, Jharkhand, Assam and Arunachal Pradesh (Srivastava & Krassilov, 2012; Khan *et al*., 2014).

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