Plant Insect-Interactions in Jurassic Fossil Flora from Sri Lanka

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Abstract- Early Jurassic fossil plants from sedimentary rocks of Tabbowa, Sri Lanka show a variety of evidence for plant-insect interactions indicative of a terrestrial habitat prevailed in the Gondwanaland. The observed interactions are skelitonizing, blotch and galls, ovipositions or coprolites, leaf mines and leaf chewing. These traces indicate that insects had associated the plants for various purposes, such as feeding, ovipositioning and sheltering for insect larvae etc. Further, these morphotraces tend to pin point some similarities of plant- insect interactions among extant plant species such as *Piper betle* and *Musa sp.* local plants of Sri Lanka. Although the taxonomic morphology of the phytophagous insects associated with fossil samples are unknown, present findings reveal that observed plant-insect relationships existed during early Jurassic period and continued up to present, having a role in the co-evolution of present day flora and fauna.

Index Terms- Early Jurassic Plants, Insect Interactions, Tabbowa Sri Lanka, Terrestrial habitat,

1. INTRODUCTION

The study of plant insect interactions provides valuable information on their associations and co-evolution. Wide range of plant insect interactions in present ecosystems have received great attention from the commercial activities associated with the food production [1] &[9] Plant-insect associations have been existing for over 300 million years from the Gondwana period and continued up to the present [20]. Plants and insects are the two most species-rich groups that make up the greatest part of the Earth's biodiversity [21].

Earliest evidence of insect-plant association in fossil flora is known from the Lower Devonian period [12] & [5]. Plant fossils have preserved 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. [13], [14], [15], [16] & [8]. The trace fossils indicate the type of insect that made the damage at least to order according to the shape, size and position of the damage [7].

Plant-insect interactions have not been reported so far in Sri Lanka based on plant fossil data. Therefore, results of this study can serve as the basis for further comparisons and correlations with other scientific disciplines to enhance the understanding of Jurassic palaeo- environments in the Gondwanaland, particularly in relation to Indian biota.

II OBJECTIVES

The objective of this paper is to present the evidence of insect plant interactions observed in plant fossils found in the Jurassic sedimentary rocks of Tabbowa, Sri Lanka. It is also intended to examine some of morphological, behavioral, and physiological adaptations that have evolved as a result of these interactions.

III METHODOLOGY

The materials presented in this paper consist of fragmented leaves of *Ptilophyllum, Glossopteris, Taeniopteris, Otozamites, Zamites and Cladophlebis spps.* Each fossil leaf was examined carefully for leaf damage. All were photographed using a high-resolution digital camera and enlarged images were used for visual examinations. The traces were organized into distinct trace types as morpho-traces, which were described and separated depending on plant morphotype as well as the size, shape and position on the leaf surface [7]. The description of excisions patterns were given according to the guide book of "Insect (and other) damage type on compressed plant fossils" of Labandeira (2007). The length and width of each leaf was also measured and the leaves with damage area less than 0.1 mm were not considered.

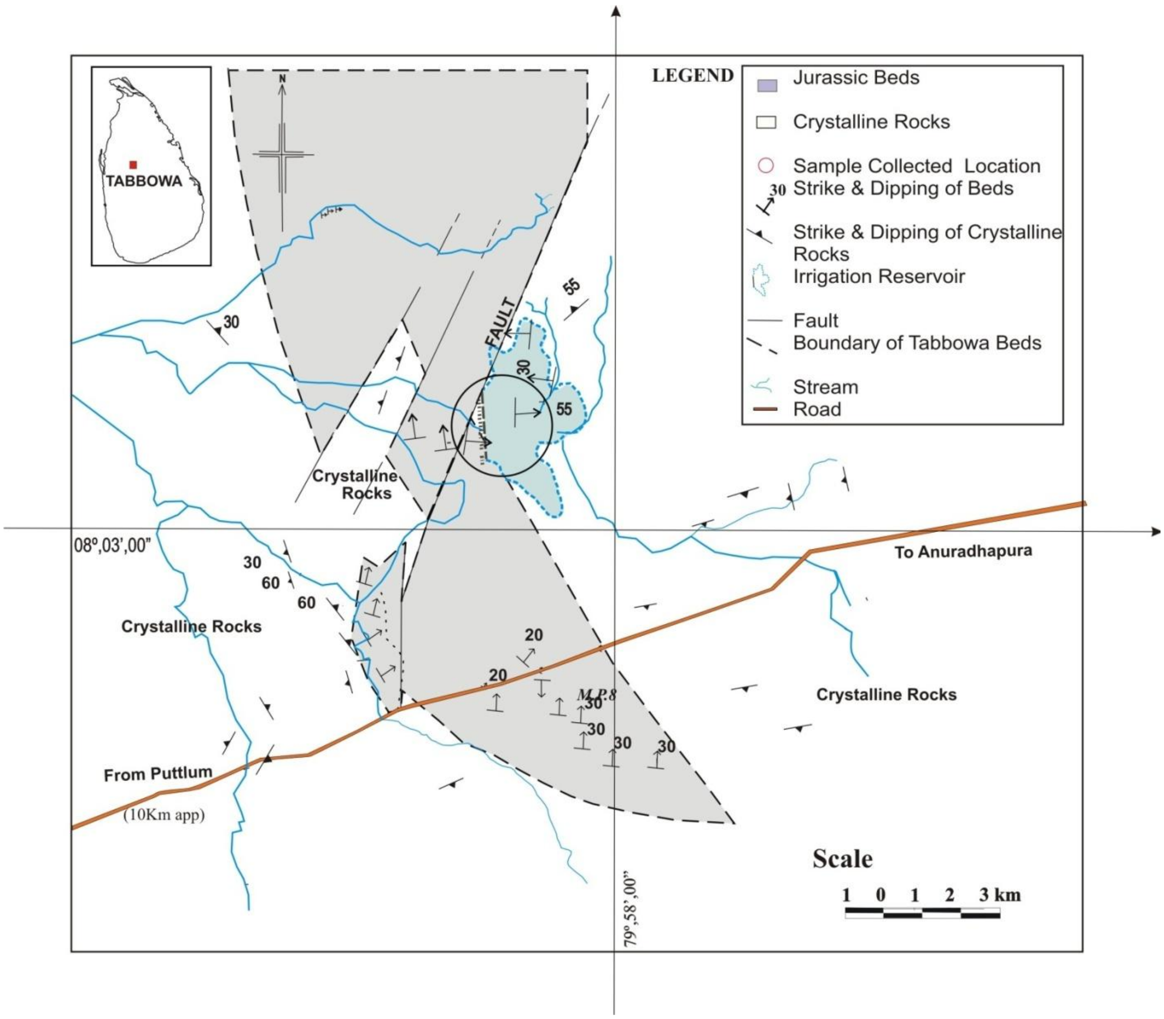


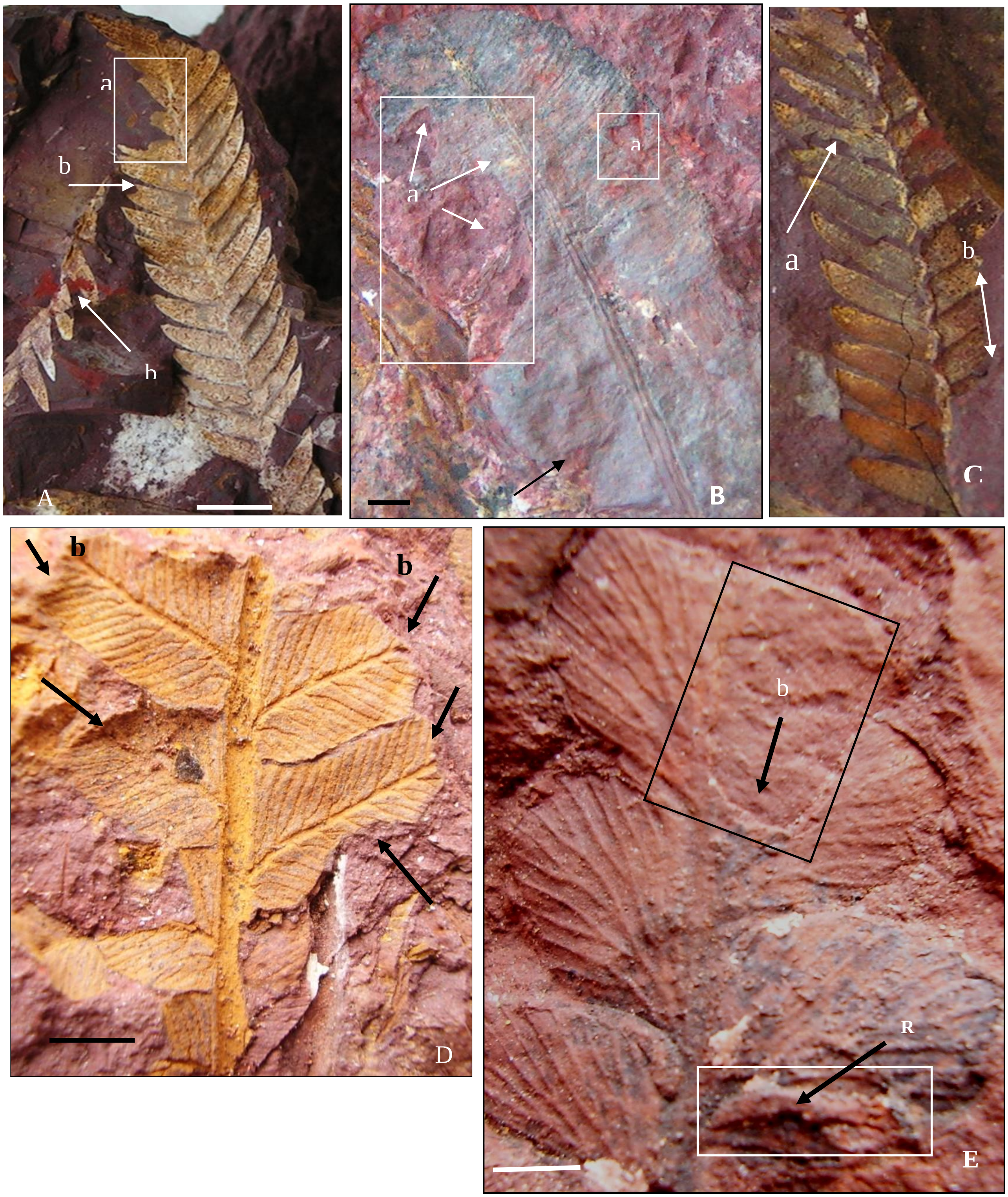
Figure 1 Location and the Geology of the Study Area. (Modified After Wayland 1925)

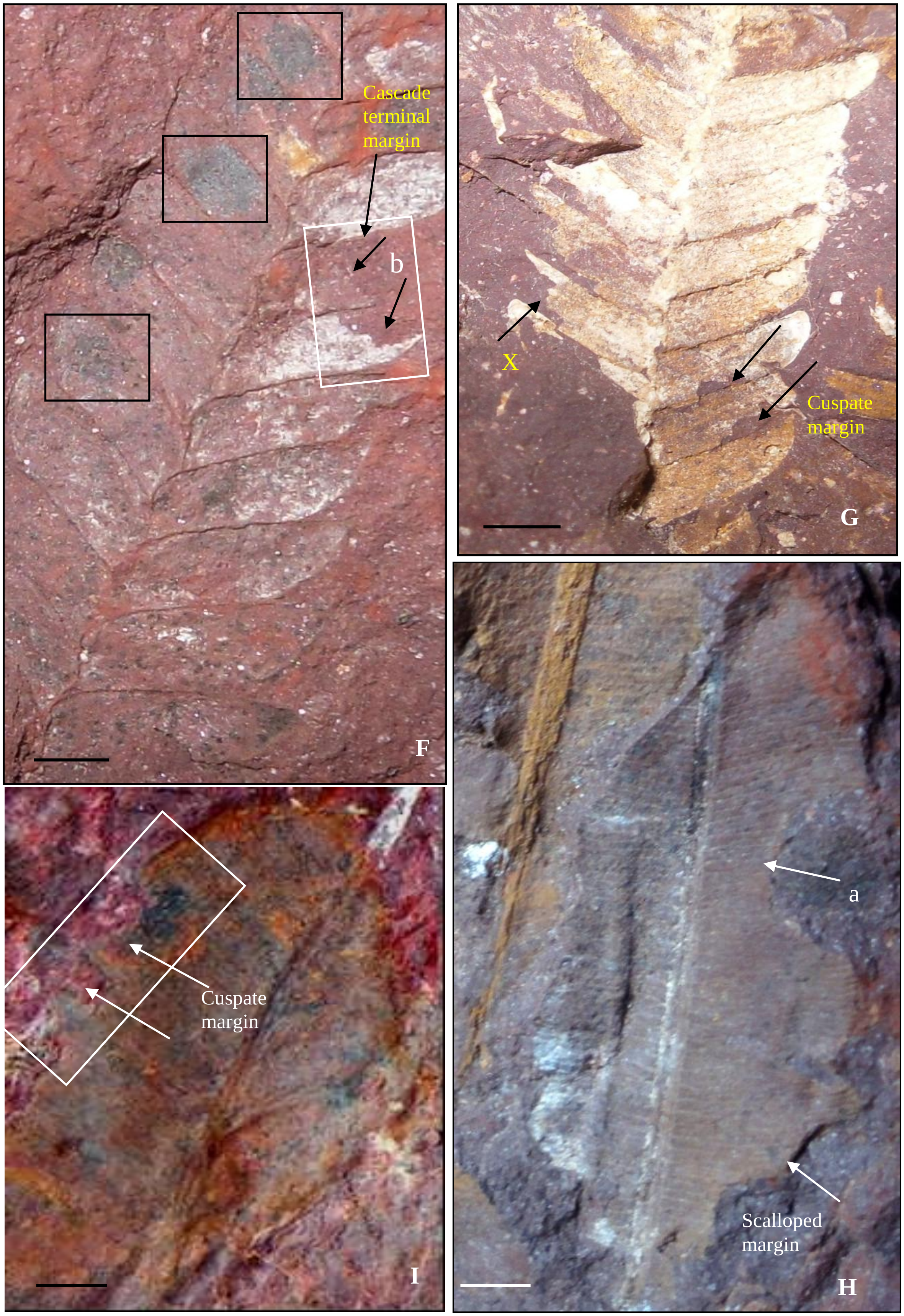
IV GEOLOGICAL BACKGROUND

The Jurassic beds in Tabbowa, Sri Lanka are spread over an area of few tense of square kilometers forming a slightly elevated flat terrain. The beds are confined to a faulted basin within the Precambrian crystalline basement rocks; mainly granitic gneiss. The beds consist of a series of sandstone, feldspathic sandstone, siltstone and mudstone with occasional thin bands of nodular limestone (Fig.1). The sediments vary in color from light gray, dark brown to purplish red while texture varying from fine to coarse grains. The rocks are well bedded, and jointed with variable strike and dips. This variation of the dips may be due to faulting within the basin and consequent tilting [2]. Evidence of faulting is clear in the gneissic rocks that are surrounding the Tabbowa beds. Plant fossils are present only in the Mudstone and siltstone beds.

V. FINDINGS

1




Cascade terminal margin
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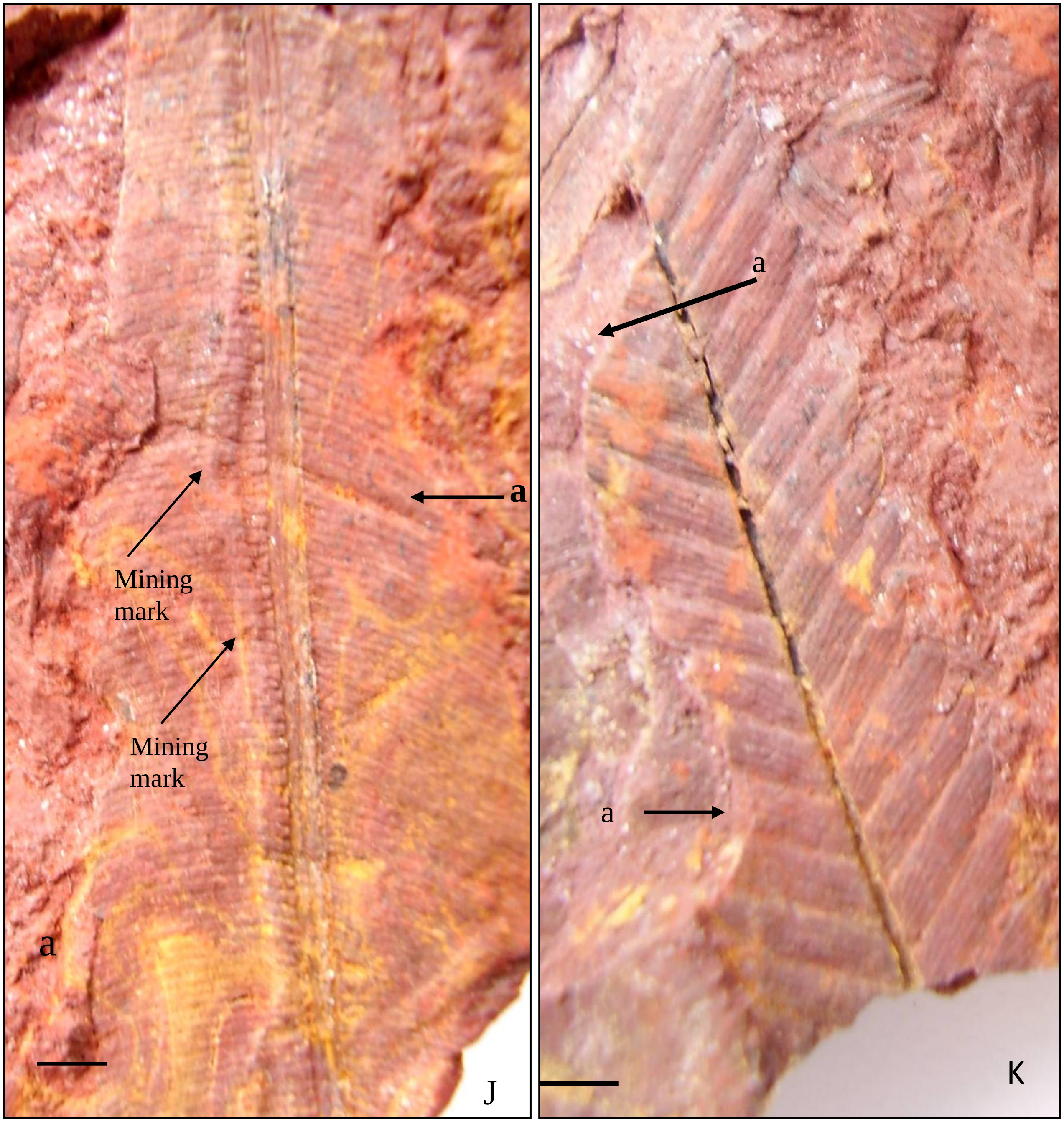

Figure 2 (Scale bar =1mm) **Specimens are showing different leaf feeding Traces as following**

1. **Terminal marginal feeding traces** (**A, C & G**) *Ptilophyllum* sp.- shallow to deeper circular excision of pinnule apex including lateral veins and midrib, (**E**) *Otozamites beanii* & (**D**) *Cladophlebis* sp: perfect, centered, deeper, circular excision of pinnule apex towards the base including midrib and lateral veins., (**F**) *Otozamites* sp. showing cascade excision of pinnule lamina.

2. **Continuous marginal feeding**: (**B**) *Glossopteris* sp.- shallow to deeper, circular excisions including lateral veins towards a mid rib (**H**) *Taeniopteris* sp. circular shallow to deep excision of margin including lateral veins (**J,K**) *Taeniopteris* sp.,*Zamites*- Shallow excision along the leaf margin.

3. **Discontinuous marginal feeding:** (**I**) *Glossopteris* sp. two or more marginal excision separated by short segments (cuspules) of pinnule margin (**D & L**) *Cladophlebis* and *Ptilophyllum* sp. excision of pinnule apex with midrib and primary veins.

a- Marginal feeding traces, b - Terminal feeding traces

2

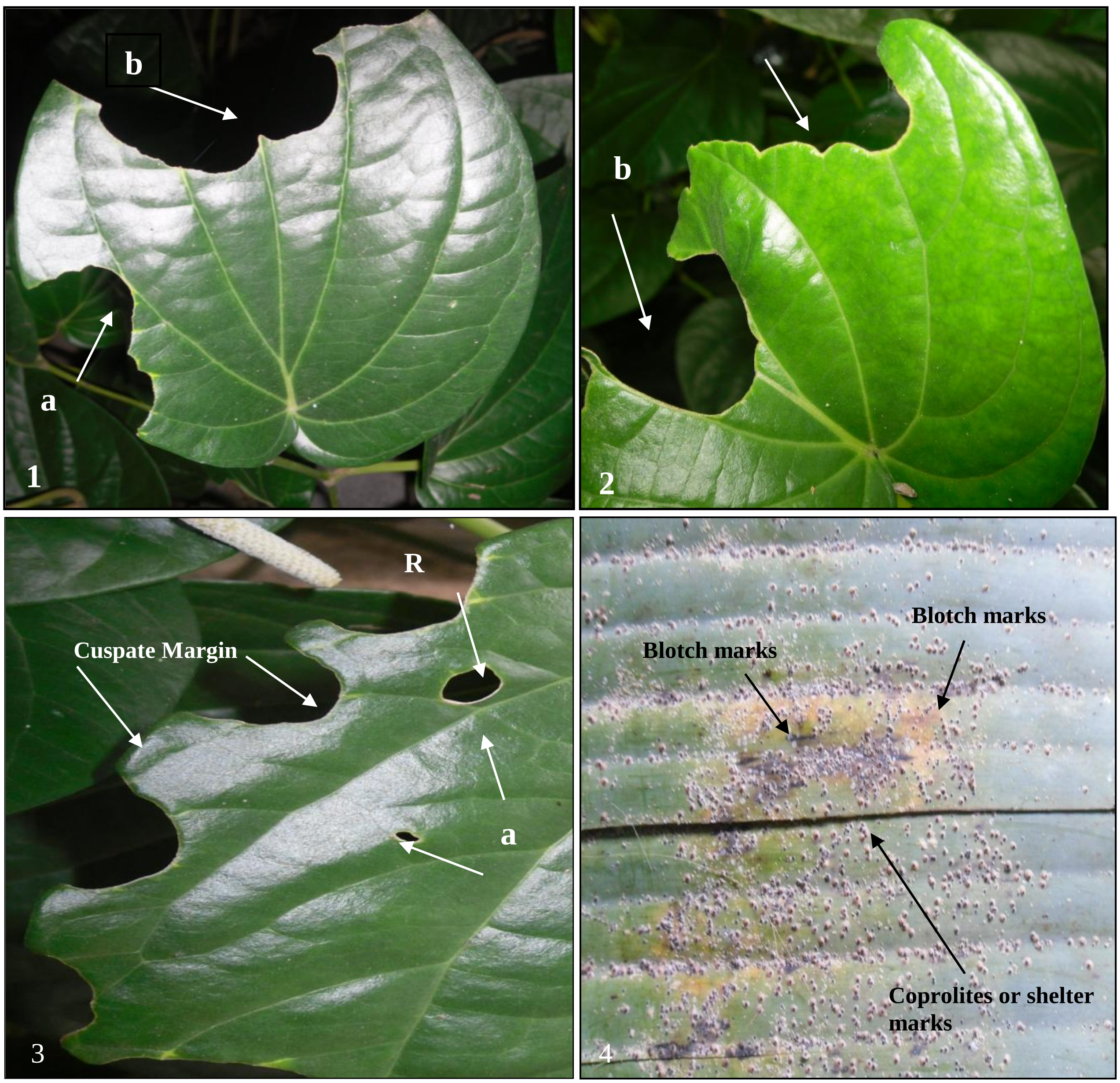

Figure 3 Existing (Live Specimens- *Piper betle*) **Evidences For General Feeding Traces: (**Scale x1): **Specimen 1**.- Shallow to deeper circular shaped excision of pinnule apex including primary veins and midrib, **Specimen 2**.: Shallow to deeper, circular excisions of lamina including primary veins, towards a mid rib, margin cuspate (a), Perfect, centered, circular shaped, deep excision

of pinnule apex towards the base including mid rib and primary veins (b). **Specimen 3 -** Two or more serial cuspate margin excision consisting of cuspules separated by short segments of leaf margin (Cuspate margin). **Specimen 4** showing a blotch marks on the *Mesua* sp. surface and insects sheltering marks or coprolites marks.

3

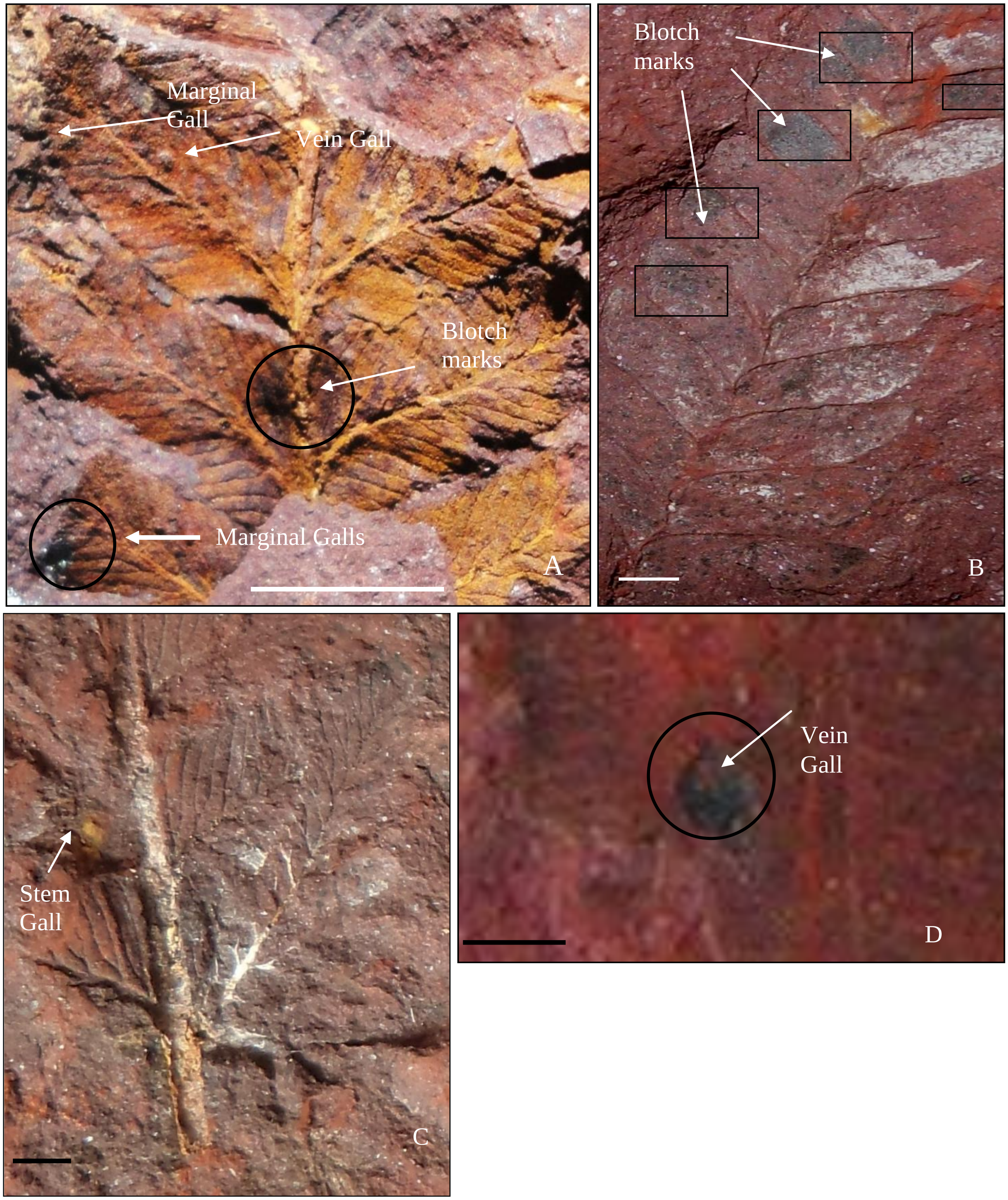

Figure 4 : Evidence for varity of insect Galls and Blotching marks. (Scale bar = 5mm) **(A)** *Cladophlebis* shows galls and blotching marks of insects (**B**) *Otozamites* shows blotching marks of insects or eggs laid by insects (some eggs are perhaps infested by fungus). (**C**) Stem gall of *Cladophlebis* sp. and (**D**) Close up image of vein gall of *Taeniopteris* sp.

4.

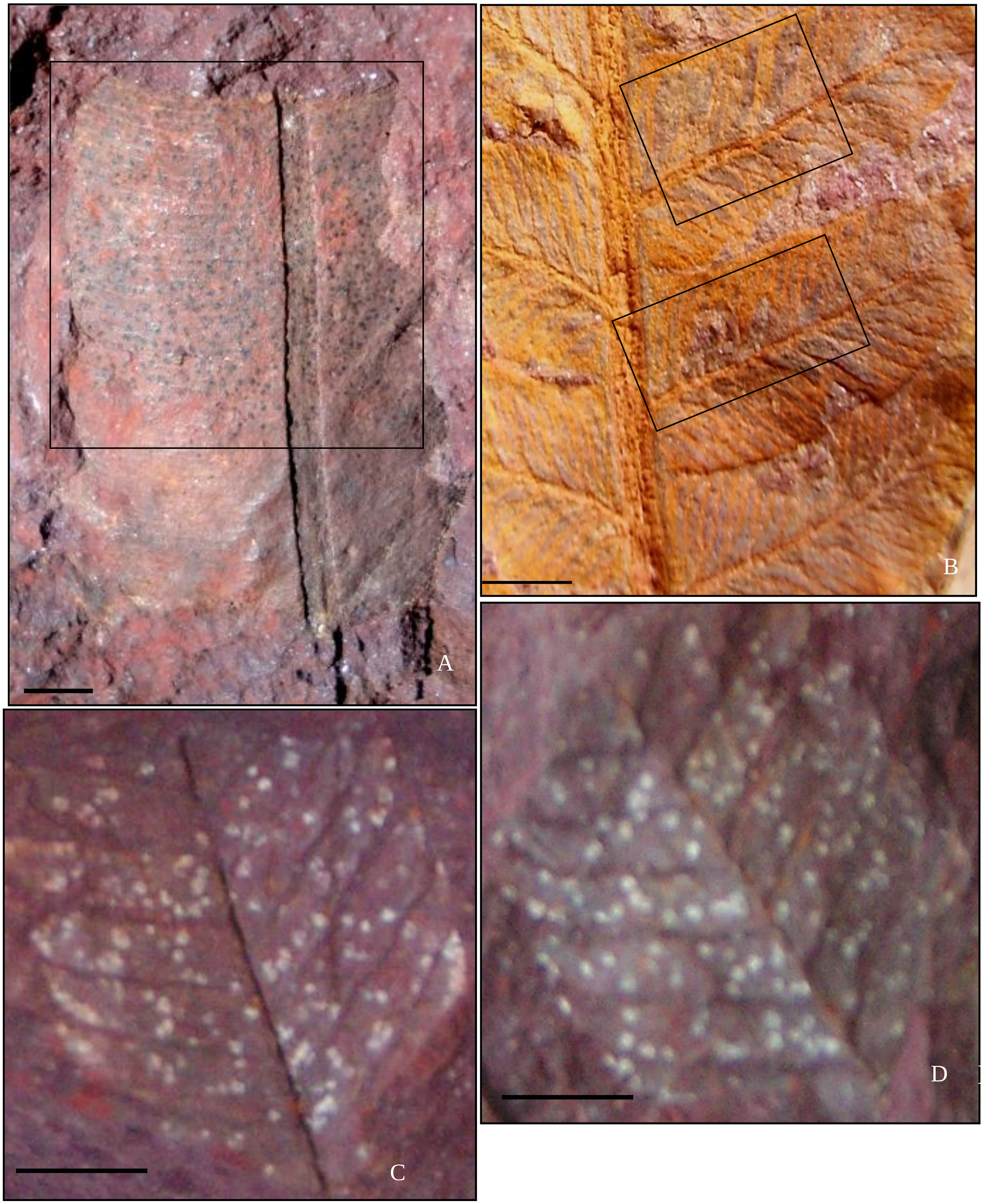

Figure 5 Coprolite (Insect Droppings) or Substratum for Oviposition or Insects used as Shelter (Scale bar = 1mm) (**A**) *Taeniopteris* sp., *(***B**) *Cladophlebis* sp. and. **(C,D part and counterpart)** *Otozamites* spp. show leaf lamina used as a substratum for oviposition or used as shelter for insects or may be insect droppings. Specimen B, could be seed bearing structure on lateral veins.

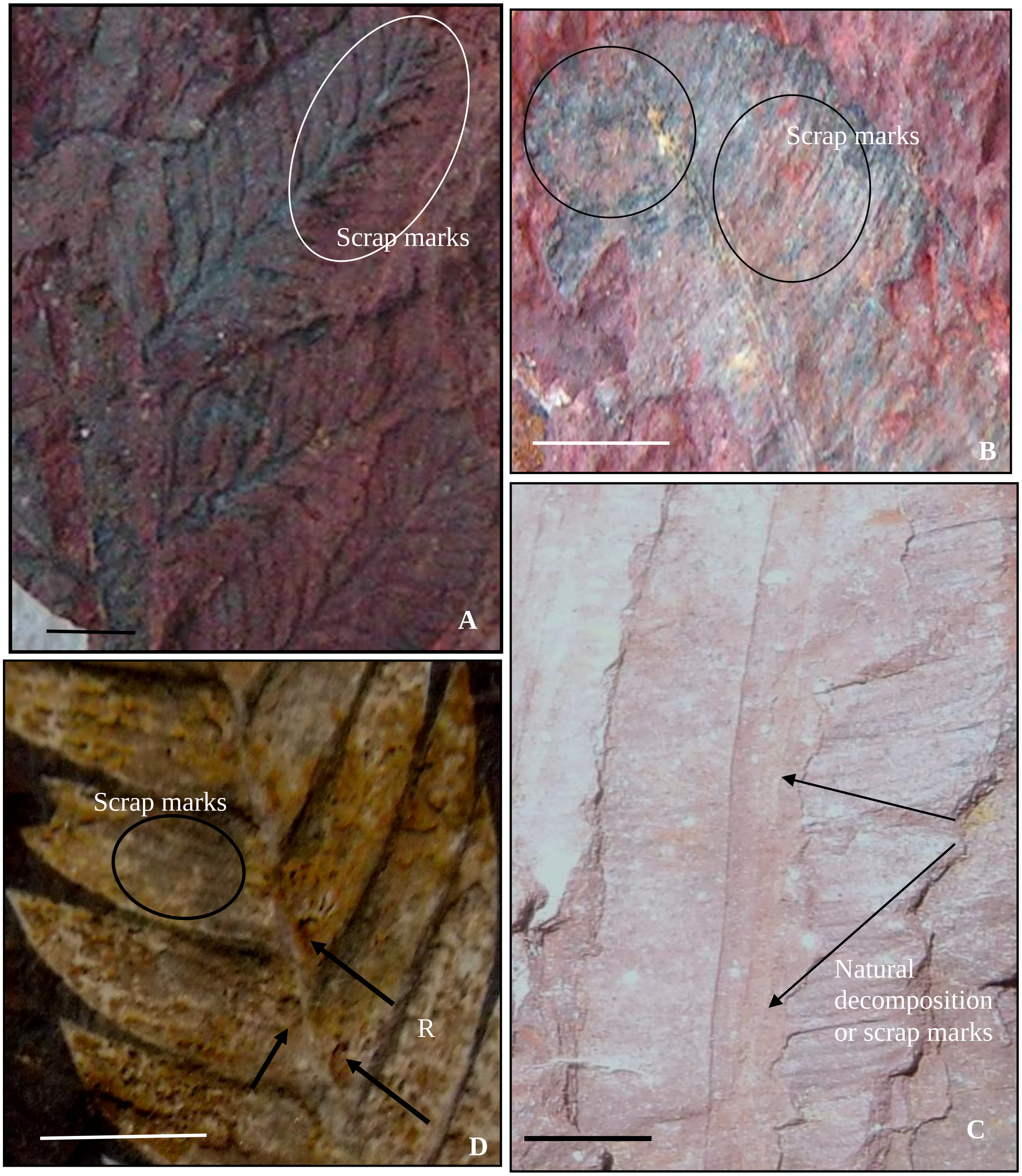

Figure 6 Skeletonizing or decomposition of leaves (scale bar = 5mm): Evidence of external foliage feeding of an insect on soft tissues of the leaf surface of *Cladophlebis & Glossopteris* spp. (A & B). Reaction rim (R) of *Ptilophyllum* sp. (D). Natural decomposition or scrap marks on soft tissues of *Taeniopteris* sp. (C).

VI. DISCUSSION

Fossil Leaf Data

Fossil leaves from Tabbowa are fragmentary and isolated clues and impressions. The majority of the studied leaves are Gymnosperms and Pteridophyts. The leaves are preserved as mudstone compressions of lack of cuticles. Complete leave impressions are rare in those specimens. The fossil leaves show a wide range of damage in all plant species. The intensity of damage varies from species to species.

Insect Trace data

Three main categories of damage were identified as marginal and non-marginal leaf feeding, skeletonizing, galls and mines. In addition, some of the features are similar to ovipositing or mating marks or lamina used for a shelter of insects. No insect body parts or wings were found in association with the present specimens and therefore, the taxonomic morphology of these phytophagous insects is unknown.

General feeding/chewing marks on leaves (Fig. 3, 1-4) provide general, micro palaeontological evidences of plant insect interaction [9]. Three kinds of chewing marks were identified for feeding on leaf margins as discontinuous, continuous, and terminal feeding marks. In addition, non-marginal traces referred as bullet hole marks [7] on leaf lamina were also noted. Sizes as well as the shape of the leaf damages are variable and circular, scallop or cuspate, oblong or elliptical shapes were noted. Leaf feeding, chewing marks are identified from the present study are given below.

As shown in Figure 2, specimens, well preserved pinnate leaves of *Ptilophyllum zeylanica* (A, C & G), *Cladophlebis* (D), *Otozamites* (E,F),*Glossopteris* (B & I), *Taeniopteris* (H,J), *Zamites* (K), clearly show feeding /chewing traces on leaf margins as well as on lamina. Specimen B,C,G and I show discontinuous marginal feeding traces as scalloped (B-a & G) and cuspate marginal edges (C-a), while other (A, D, E,F,H, & K specimens show continuous marginal feeding edges.

*Ptilophyllum (*A-b*)* a deeply reduced leaf apex with bite marks on apical region. The damage is isolated and the trace starts from the apex, then deeper towards the base. Some of the excisions are cascade pattern starting from apical region towards the leaf base including midrib, primary veins, and associated tissues.

Comparing with modern analogues *Piper betle* and *Mesua* (Fig.3, 1-4), *Glossopteris* sp. (B) and *Cladophlebis* sp. (D) leaf margins are significantly damaged and corrugated by insect biting at several places along the margin. The lamina was chewed but the bite marks do not reach the mid rib. It shows different sizes of scallop shaped (Fig.3, 2-a) shallow to deep (B-a) removal of a leaf margin extending towards the mid rib including lateral veins (Fig.3,1-b). The depth of a large excision (B-a) is 0.6 mm and the length along the margin is 1.2 mm. Isolated feeding traces on leaf surface could also be identified. Specimen *Ptilophyllum* (C, G); and *Glossopteris* sp. (I); Show semi circular, excision of leaf margin. Some of these circular shaped excisions are separated by short segments (Fig.3,3-a) resulting in a discontinuous leaf margin (cuspate margin) and others are named as scalloped margins [6].

Some of these biting marks show darker outlines (Fig.3, 3-R) or thicken ridge (Fig.2, E-R) wound reactions, that indicate the tissues around the damages were dried up and nibbled during the life time of the plant [4, 18]. Some of the margins (G-x) do not show any browning line that suggesting pinna was no longer alive when it was eaten [19]. In some of the specimens B *Glossopteris,* E: *Otozamites*, D: *Cladophlebis*, a pinnule was damaged on one side of the margin including lateral veins. The browning is obvious along the trace due to a wound reactions or remains of the lateral veins [17].

Terminal feeding traces **-**Well-preserved impressions of pinnate leaves of Fig 2, *Ptilophyllum* (A-b & C), *Cladophlebis* (D) *Otozamites* (E, F,J) show unusual form of feeding traces in apical region. Feeding has removed, apex, mid rib and associated tissues with lateral veins. The leaf appears as a clipped terminus midrib (Fig.2, C-b) and circular or sub-circular shaped isolated excision on a leaf apex extends inwardly. Length directed towards the base is about 2.0 mm and width is about 1.0 mm.

Leaf mines**:** Leaf mine is an insect larvae feed inside the tissues of the two lamina, (parenchyma or epidermis tissues) of the leaf creating a distinctive channel. The adult insects lay their eggs inside the tissue where the emerging larvae can feed and continue to develop [3].The morpho-traces on *Taeniopteris* (Fig.2, J) is the only specimen that shows a thick linear mine which runs parallel to the mid vein. This channel starts from the left side of base at the mid vein and end up at the apical region. Width of the channel is about 3.3 mm, and length is about 16.1 mm. There is a small curvature at the middle portion of the channel.

Galls, Oviposition and blotch marks*:* Galls (Cecidia) are formed by extensive growth of the plant tissue due to a feeding insects, compared with the existing plant specimen (Fig. 3- 4), for an ovipositing insects reaction or for protection [18]. *Taeniopteris* sp. leaf impression (Fig.4, D) shows a small < 3.0 mm size, simple spot gall, positioned on the surface of the laminar between primary veins. Leaf impression of *Cladophlebis* sp. (Fig 4, C) shows small cone gall on the main rachis at the base of the primary midrib. The size of the gall is small < 3 .0 mm in diameter; nature of the wall of gall is rough with single exit pore at the central of the gall.

Another observation noted small circular thickening of 0.2 mm - 0.3mm in diameter on a leaf sheath of *Cladophlebis* (Fig 4, A). They have scattered near the midrib, leaf margin especially in leaf apex, which are well prominent. Some of them submerged in the leaf sheath. This scars resemble galls or trace fossils of insect eggs but can be ovoid bodies or depressions filled with sediments, ready to detach. According to some of the interpretations of scars, it appears to be acceptable because they represent ovules in fertile leaves or they correspond to the trace fossil eggs, the specimen witnesses an insect plant host interaction.

In *Cladophlebis* (Fig. 4, A) and *Otozamites* (Fig.4, B) show reddish, black and white stains similar to blotch marks of insects at the leaf bases and leaf apices. These stains may have been caused by the larvae leaving fecal material when they were in the mines or on lamina. Leaf lamina seems to have been used as a substratum for shelter.

Coprolites or shelter marks: Evidence for coprolites or shelter marks was noted on O*tozamites* leaves (Fig.5, C & D**),** two of the specimens show small circular white markings arranged all over the adaxial and abaxial surfaces. One of the *Taeniopteris (*Fig.5,A) and (Fig 3, 4) leaves show black spotted appearance on the lamina surface without specific orientation along the mid rib and lateral veins. *Cladophlebis* (Fig.5, B) shows thickening lateral veins on the surface of lamina and along the midrib. These can be either due to the insects laying their eggs along the veins, or sedimentary deposition.

Skeletonizing: Skeleton feeding of leaf (Fig.6, A-D) is defined as scraping out the leaf tissue by insects [7]. It is difficult to separate skeleton feeding and natural decomposition especially for fossil leaves. If the remaining of the fossil leaf is still intact and the tissue is missing only in few areas, then it is a skeleton trace fossil [11]. The Skelitonized tissue-missing areas are elongated, rectangular, or irregular in shape. Removal of inter-venal tissue on the surface of leaf is observed in *Cladophlebis sp, Glossopteris,* and *Ptilophyllum* sp. and *Taeniopteris* (Fig. 6, A-D).

Well developed defensive reaction rim/ ridge (Fig 6.D) can be seen around a bullet hole wounds on *Otozamites and Ptilophyllum, (*Fig. 6 C, D). This indicates that the damage has occurred while the leaf was alive and plant as attempted to harden the tissue forming a ridge to prevent further feeding by the insect [4,19].

VII. CONCLUSION

The findings of the present study provide evidence for presence of leaf feeding and dwelling insects as a part of the ecosystem of the Jurassic in Sri Lanka. Most of the leaves have a specific pattern of feeding. A comparison with the extant taxa (*Piper betle*), leaf chewers can be of the insect orders Orthoptera that make bite holes in the margin and, the Coleoptera which is known to scoop out the edges of leaf margin at intervals. Comparing with extant leaves, galls may have been produced by gall mites, Lepidoptera and Diptera. Skeleton feeding by Coleoptera on extant species is known to scrap the surface of the leaves, sparing only the network of veins. Although fossilized samples of insects have not yet been found in the Tabbowa beds of Sri Lanka, the above orders must have been a common species during Jurassic of Sri Lanka. We consider that these observations and findings would provide pioneering evidence for Jurassic fauna from Sri Lanka.

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