

Insect-induced plant galls of India: unresolved questions

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With about 2000 different galls (implies that almost the same number of inducing-insect species exists), the Indian subcontinent displays a rich variety in gall flora. Gall-inducing insects of peninsular India are endemic, whereas those in the temperate Himalayan slopes and in the Indo-Gangetic plains show affinity to Central Asian and European gall-inducing elements. Fossil records indicate that galls existed in India from the late Cenozoic period. Throughout the Indian subcontinent, species richness in gall midges (Diptera: Cecidomyiidae) is almost uniform, inducing different types of galls, including the incredible 'cylinder-piston' gall, which, however, has been recorded only in the natural areas around Coimbatore. In the light of the global pattern, cecidomyiid-induced galls should be the major component in Indian gall flora, although much needs to be known about the identities of midges and the nature of galls they induce. Gall-inducing cynipids (Hymenoptera: Cynipidae) and aphids (Hemiptera: Aphididae) are restricted to the Himalayan slopes, whereas gall-inducing thrips (Thysanoptera) are confined to peninsular India. Against such a confusing but interesting distributional pattern, this review brings into focus several biological, ecological, and evolutionary questions that remain unanswered in the background of what a gall is, how galls are initiated and what factors trigger gall growth, what designs are evident among gall-inducing insects in terms of host dependence, and biogeographical patterns in the distribution of gall-susceptible plants vis-à-vis gall-inducing insects, referring specifically to the gall flora of the Indian subcontinent.

Keywords: Gall-inducing insects, gall-bearing plants, India.

THE ability to induce galls is a specialized behaviour within the broad context of insect (the term 'insect' is used liberally to include mites as well) phytophagy. Between phytophagous insects and their host plants, different types of interactions occur, from insects which depend on plants for nutrition, to those which are exclusive pollen and nectar feeders (e.g. species of Oedemeridae, Coleoptera; several butterflies and bees) and gall inducers. Within the broad context of phytophagy, however, levels of in-

teractions between insects and plants vary immensely. Insects that use plants as their source of food can be specialized feeders using only specific plant species (monophagous; e.g. *Bombyx mori*, Lepidoptera: Bombycidae) or a range of unrelated plants (polyphagous; e.g. *Myzus persicae*, Hemiptera: Aphididae). Most of the pollen and nectar feeders are generalists, whereas gall-inducing insects are specialists and remain tied closely to their food plants. Different propositions explain the origins of insect phytophagy over time¹. The specialized gall-inducing habit among insects is considered to have arisen from leaf-mining Diptera (e.g. Agromyzidae) and Microlepidoptera (e.g. Nepticulidae, Stigmellidae)², which, over time, are purported to have sought 'new' food sources in concealed, and thus, 'protected' environments³; in such a context, we need to recognize the origin of leaf-mining habit from mycophagy. Other proponents⁴ suggest that gall-inducing habit originated from tunnelling Lepidoptera (e.g. Tortricidae) and Coleoptera (e.g. Curculionioidea). What is critical, however, will be to be conscious that gall-inducing insect species, which are scattered among diverse unrelated natural orders, and which induce galls on host-plant species from unrelated families, have arisen many times and through many different evolutionary routes. Physiological differences in the behaviour of the inducing insect and susceptibility level of the plant have also contributed to the variety of galls we see today.

Within the unique and complex vegetation and equally unique and complex faunal composition of India (referring to the land mass presently known as the Indian Republic as 'India' will be inappropriate in a biogeographical context; the whole of former British India [including the present Pakistan, Bangladesh and Myanmar], Sri Lanka, Nepal and Bhutan will need to be factored into the term 'India' for a holistic understanding; therefore, in this article, any reference to the term 'India' will necessarily imply the larger land mass, referred commonly as the Indian subcontinent, which will transcend the present-day political boundaries, because the floral and faunal elements do not recognize human-induced borders)⁵, richness and abundance of galls and inducing insects are no less simple, compared with those from the rest of the world, and their origins date back to several millions of years. At least two definite fossil evidences support the early origins of gall-inducing insect association with flowering plants in India: (i) insect-induced gall impressions (induced by a species

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of Cynipidae(?), Hymenoptera) on the leaves of *Sophora benthamii* (Leguminosaceae) from the late Cenozoic sediments of Mahuadanr Valley (Palamu District, Bihar)⁶ and (ii) gall midge-induced (Diptera: Cecidomyiidae) galls on the fossil leaves of mango (*Eomangiferophyllum damalgiensis*; Anacardiaceae) from the Upper Palaeocene-aged flora of Tura Formation in north-eastern India⁷. In the modern context, close to 2000 different galls (from simple erinoses and leaf-fold/leaf-roll galls to complex 'cylinder-piston', 'sea-urchin'-shaped, and 'fir-cone'-like galls) are known from India. The plant taxa that host such galls range from as many as 90 natural orders (dicotyledons – 84, monocotyledons – 4; gymnosperms – 2) induced by arthropod taxa belonging to Acarina (eriophyid mites), Thysanoptera (thrips), Hemiptera (aphids, psyllids, coccids, whiteflies) and Coleoptera (weevils). Diptera (gall midges, tephritid fruitflies), Lepidoptera (moths) and Hymenoptera (sawflies, chalcids, eulophids, fig-wasps, cynipids) are known in India⁸. If we rely on global patterns of gall-inducing insect abundance and richness, then it is easy to imagine that gall midges should be the most abundant and rich group in India as well. Several gall-inducing thrips⁹ and gall-inducing eriophyid mites¹⁰ along with details of their host plants have been documented. Limited notes on gall-inducing psyllids and their host plants are available^{11,12}. Besides these, several papers on gall midges, gall-inducing aphids, fig-wasps, gall-inducing thrips and gall-inducing psyllids and coccids are also available, but scattered in different journals; valuable information has also been added to the botany of insect-induced galls of India. For information on contributors on gall-inducing insects and galls prior to Mani¹³, refer to Raman and Ananthakrishnan¹⁴, and Raman¹⁵. The key point, however, is that several galls still remain to be discovered in India; systematic descriptions of the insects and comprehensive catalogues of galls are distinctly lacking, and such an inadequacy interferes with making generalizations. However, in the present article, I will be raising a few unanswered questions in the context of Indian galls and inducing insects, keeping Mani's *Plant Galls of India*⁸ as a generic reference point. To ensure a logical flow, I will also be using different models and generalizations developed on galls and inducing insects based on research done elsewhere.

What is a gall?

The current definition of a gall is that it is a cumulative expression of a suite of adaptations achieved by the host plant for accommodating the inducing insect. In principle, a gall provides nutrition and shelter to the inducing insect and, in a few taxa, to its progeny as well. The insect activates a perturbation in growth mechanisms and alters the differentiation processes in the host plant, modifying the plant's architecture to its advantage¹⁶. A gall often achieves

a symmetrical form, which could be either radial or bilateral. Classical definition of a gall⁸ would include any generic, anomalous growth on plants such as those induced by bacteria, fungi, nematodes, and this definition also includes growth induced by arthropods. However, the modern explanation of a gall would exclude plant growths incited by bacteria and fungi, because their actions would normally result in amorphous growths, and therefore should be called tumours, whereas those induced by insects mostly result in symmetrical structures, and therefore should be called galls.

Diverse, unrelated insect natural orders include gall-inducing species. However, the ability to inhibit normal growth and differentiation, and to induce new growth by establishing new polarity points and gradients in their host plants is common to all gall-inducing insects. Not only galls are symmetrical, but also they display novel patterns of differentiation¹⁷. Since insects derive their nutrition from gall tissue, the gall becomes a sink for different nutrients and energy that will be vital for the insect's growth^{16,18}. A majority of gall-inducing insects stimulate the host-plant tissue to develop into galls by their feeding action, whereas species of Hymenoptera trigger gall development via oviposition. Even the vascular tissues can be modified by gall induction, so that they supply nutrients and water subserving the needs of the inducing insect^{19–21}. Some of the gall-inducing gall midges and cynipids show an unusual ability to induce differentiated tissues to revert to a meristematic state and resume cell-division activity^{16,17}.

Insects of the same orders induce galls that will be reasonably similar in shape and structure (e.g. species of *Gynaikothrips* [Thysanoptera: Phleothripidae] induce leaf-fold galls, species of *Aceria* [Acarina: Eriophyidae] induce pouch galls bearing erineal hairs on leaves). However, such a behaviour is not common among gall inducers belonging to more advanced families (e.g. gall midges and cynipids), because a diverse range in morphologies of galls exists even within those induced by different species of the same genus¹⁷. As nutrition is a fundamental reason for the dependence of gall-inducing insects on plants, the insects, either singly or as a group (usually the progeny of the initiating female), through their feeding action, incite differentiation of a special tissue of nutrition, which will be rich in sugars, proteins, and lipids, in addition to a battery of different hydrolysing enzymes^{16,22–24}. Physiology of a gall is broadly similar to that of endosperm or meristematic tissues^{25,26}. Feeding action (viz. insertion of mouthparts and sucking by insects of hemipteroid stock; biting and chewing by insects of coleopteroid stock) and the secreted salivary chemicals are the two principal factors that trigger gall induction. Feeding action inflicts wound and secretion of salivary chemicals alters the subcellular chemistry in host tissues; both of these, when they occur concurrently, stress the host-plant cells. As a neutralizing response to the stress, the plant translocates different metabolites (mainly photo-assimilates) to the site where the insect

feeds. Continued feeding activity by the insect induces the plant to respond, resulting in a gall. Questions have been raised rather regularly, whether the gall is initiated by a microbe (e.g. virus, phytoplasma), and whether the insect in reality, plays a vectorial role transmitting such a microbe. At least two explanations negate such questions rather clearly: (i) rigorous sub-microscopic searches have not revealed the incidence of either microbes or any extra-nuclear nucleic acids in galled cells; (ii) no secondary galls develop (similar to secondary tumours developing in the absence of *Agrobacterium tumefaciens*, Proteobacteria: Rhizobiaceae) when the insect is either killed or removed.

Initiation of galls and factors triggering gall growth

As in all known hypertrophic plant growths, auxins (e.g. indole-acetic acid, IAA) are a key factor in galls as well. An imbalance arising because of the stress induced by the physical action (wounding, sucking) and salivary secretions either triggers new growth because of synthesis of growth promoters or enhances the vulnerability of plant cells to growth promoters that are already present at that site. Such an imbalance results in a 'combined' function of different growth promoters (e.g. auxins and kinins), which activates growth. However, the question 'how symmetry in gall shape, either radial or bilateral, is achieved?' remains unanswered: not only that the 'stimulus' from the insect spreads uniformly, but also that at some point of time, even while including a living insect, growth of the gall ceases. As of now, growth in galls based on the 'auxin' theory is explained with two contrasting hypotheses, one by Hartley²⁷ and another by Miles²⁸, which explain the pathways of IAA synthesis in galls.

The Hartley hypothesis²⁷ builds on the premise that insect-induced galls are similar to any microbe-induced abnormal growth (e.g. tumours induced by *A. tumefaciens*), in that both systems accumulate large quantities of phenolic compounds. Synthesis and accumulation of phenolic compounds is the defence reaction of the host-plant to attack by the invading organism. However, in bacteria-induced tumours, phenolic compounds are implicated to have two other roles: (i) they are indicators of vulnerability levels in host plants; (ii) they neutralize manipulation of the plant consequent to attack by altering gene expression of the host-plant and by changing hormone activity. This understanding opens a window to interpret growth in insect-induced galls. Phenolic compounds abound in gall tissues; moreover, gall tissues also show high activity of phenyl-ammonia lyase, the enzyme that catalyses the first committed step in phenolic biosynthesis. Such events disappear when the inducing insect is either dead because of natural causes or removed under experimental conditions. Since some of the phenolic compounds are well-known growth promoters, it is implicated that phenolic compounds

can promote cell division and gall growth by interacting with existing plant hormones (IAA) and/or IAA-oxidase, which are especially abundant in meristematic tissues (where galls are mostly induced). Nonetheless, the unexplained context here is whether one or more chemical signals, which are specific in a particular 'gall inducer–host plant' situation, operate linking phenolic substances with the 'IAA–IAA-oxidase' complex. Alternatively, what kind of interaction occurs at the plant cell level? Does any kind of 'immune' system work and mediate the interactions?

The Miles hypothesis²⁸ explains that salivary components (e.g. amino acids) are similar in both gall-inducing and other (free-living, but plant-feeding) insects. IAA precursors (e.g. tryptophan) in insect saliva are of negligible quantities compared with those found in plant systems. Moreover, the suggestion that salivary proteinases are utilized to release plant-bound IAA is disputable, because the saliva of gall-inducing insects (e.g. aphids) does not include proteinases. Vigorous uptake of oxygen occurs in the gall tissues; such an uptake coupled with 'wounding' (consequent to feeding action) stimulates plant-bound auxin activity. Use of oxygen in plant tissues under insect attack will be so intense that IAA oxidase activity, which regulates accumulation of IAA, is deprived of oxygen. Such an oxygen-deprivation enhances the synthesis and accumulation of IAA at insect-feeding sites, triggering growth at the involved meristems. Salivary oxidases could be playing a role in the disruption of the IAA-oxidase pathway – a supposition to be established.

The Hartley and Miles hypotheses^{27,28} explain the phenomenon of growth in galls, implicating the role of auxins. Nonetheless, the question 'what specific factor triggers cell enlargement, which works synchronously with cell multiplication, in gall development?' remains unanswered. Several studies implying the role of cytokinins in insect-induced galls are available^{2,29}. Whereas growth promoters (auxins and/or kinins, either individually or in combination) have a definite role in gall growth involving cell enlargement and cell division, the most critical element that has not been alluded to is the precise trigger mechanism involving a single host-plant cell or a small group of cells that receive the direct initial 'stimulus' from the insect. Could that 'stimulus' from the insect be a 'novel' protein³⁰? Notwithstanding the above commentary on Hartley and Miles hypotheses, a comment from Rohfritsch (per. commun.) needs to be factored into gaining an understanding of gall initiation and growth: "The insect does not inject any specific substance into the plant cell. It attacks the plant cell(s) with its chitinous mandibles and salivary secretions, and inflicts a wound. Through wounding, several molecules become active in the attacked plant cell(s), which, in turn activate the cells around it; and such an action results in the gall. The insect's behaviour is genetically determined". As shown in many thoroughly studied gall systems³¹, the earliest and most significant event in gall development is metaplasia; all other sub-cellular

events in gall development occur only after this event^{2,17}. However, what we do not know are the nature and types of subcellular hormone receptors and transporters, and gene switches in that cell, which receive the impact of the stimulus, turn metaplastic, and activate the growth phase involving both cell enlargement and division, and how these work.

Galls present unique patterns of differentiation, which normally do not occur in normal morphogenesis of the involved organ. As explained earlier, a 'gall' is an expression of perturbation of normal morphogenetic events. Several extraordinary examples illustrating altered differentiation pathways resulting in 'novel' expressions are available^{17,25,31}. Within Indian gall flora also, many equally fascinating examples exist such as the cylinder–piston galls on the leaflets of a species of *Acacia* (*A. ferruginea*?) induced by *Contarinia* sp. (= *Lobopteromyia* sp.) (Diptera: Cecidomyiidae)³² (Figure 1 *a* and *b*), sea-urchin-shaped galls induced on the vegetative shoot-apical meristems of *Hopea ponga* (Dipterocarpaceae) by *Mangalorea hopeae* (Hemiptera: Beesoniidae)³³ (Figure 1 *c*), and the fir-cone-like galls induced on the vegetative shoot-apical meristems of *Mangifera indica* (Anacardiaceae) by *Apsylla cistellata* (Hemiptera: Psyllidae)⁸ (Figure 1 *d*). In spite of the galls on *H. ponga* and *M. indica* being induced by hemipteran gravid females, the final gall forms are strikingly different: *H. ponga* galls are woody, nearly spherical, and bear several stiff, spiny appendages between which the larvae live (the term 'larva[e]' is used generically referring to immature stages of all insect orders), whereas those of *M. indica* develop similar to fir cones, with vertically arranged chambers for sheltering and nourishing the larvae. Galls on both *H. ponga* and *M. indica* continue to grow until the progenies of *M. hopeae* and *A. cistellata* emerge, inhabit the locations 'meant' for them, grow, and females disperse to new sites to initiate new galls. Nonetheless, given that the vegetative axillary meristem is the site of infestation for both *M. hopeae* and *A. cistellata* (both Hemiptera), how are both galls strikingly different in their morphology and morphogenesis? Even in rudimentary galls such as those induced by whiteflies (Hemiptera: Aleyrodidae), which are well-known as poor gall-inducers³⁴, several morphogenetic questions remain unanswered. For example, the soft, parenchymatous galls on the leaves of *Achyranthes aspera* (Amarantaceae) induced by *Bemisia tabaci* (Hemiptera: Aleyrodidae)³⁵ are characteristically scarlet-red because of intense accumulation of anthocyanins. Identical pigmentation exists as faint striations on the ungalled bristly bracts. How does the leaf, under the feeding pressure of *B. tabaci*, express the pigmentation, which exists normally only at sites in the same plant, not affected by *B. tabaci*?

We know that plant morphogenesis entails signal-trafficking and crosstalk across all levels of organization to coordinate metabolic and genomic networks³⁶. Inherited genetic traits obviously play a definite role, followed by

that played by correlating morphogenetic factors. Both of these, acting in conjunction, facilitate expression of the phenotype, and in the present context, the gall. Galls offer the best opportunity to reconstruct steps in a modified, but geometrical biological structure that arises solely through the trigger messages received from an alien organism³⁷, viz. the insect. The question here is how logical circuits and signal-activated subsystems work in galls, such as those induced on *Acacia* sp., *H. ponga*, and *M. indica*? We need an articulated step-by-step explanation of the developmental process, which commences from a single metaplastic cell, gets transmitted through subsequent growth promoter-mediated cell expansion, until the commitment of the metaplastic cell and those in its neighbourhood enabling the start of 'novel' cell-cycle patterns and cell multiplication. Although these are similar to those occurring in tumours of primary and secondary origins, the difference is that the processes identified in galls are highly controlled (this phenomenon has been referred to as 'limited

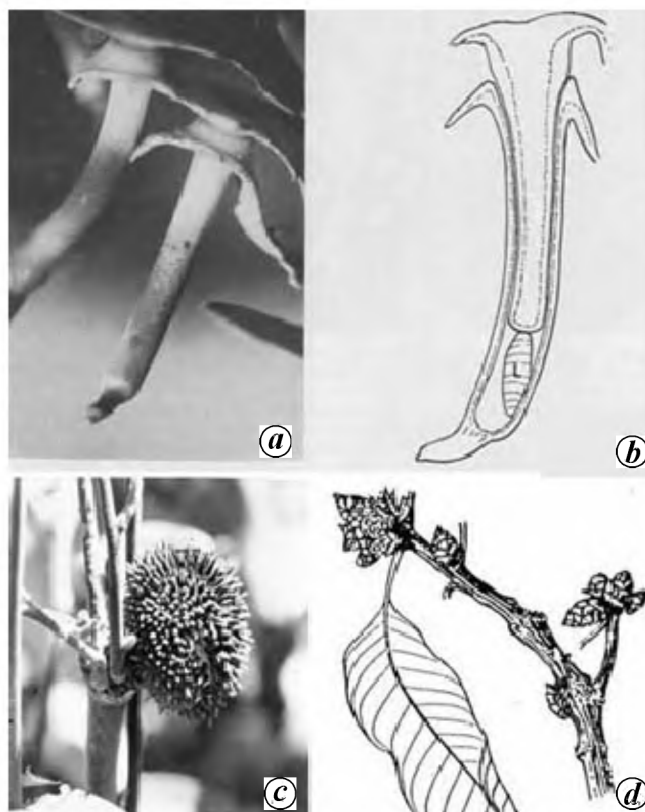


Figure 1. *a*, Cylinder–piston galls on leaflets of *Acacia* sp. (Leguminosaceae) induced by *Contarinia* sp. (= *Lobopteromyia* sp.) (Diptera: Cecidomyiidae). (Modified from Rohfritsch³², with permission from the author.) *b*, Longisectional cartoon of cylinder–piston gall on leaflets of *Acacia* sp. induced by *Contarinia* sp. (= *Lobopteromyia* sp.). L, Larva (modified from Rohfritsch³², with permission from the author.) *c*, Sea-urchin-shaped gall on vegetative axillary meristems of *Hopea ponga* (Dipterocarpaceae) induced by *Mangalorea hopeae* (Hemiptera: Beesoniidae). *d*, Fir-cone-like gall on vegetative axillary meristems of *Mangifera indica* (Anacardiaceae) induced by *Apsylla cistellata* (Hemiptera: Psyllidae). (Reproduced from Mani⁸, with permission from Science Publishers, Inc., New Hampshire, USA.)

neoplasm' by Mani⁵⁷). Moreover, what mechanism facilitates intercellular auxin transport? For each of these, a genomic subsystem obviously exists and mediates. Processes facilitating these steps need be identified in experimentally tested gall models. We know presently that in normal developmental process in plants, meristems control patterns, e.g. phyllotaxy. At a macroscale, in leaf ontogenesis, the first recognizable step is tissue-folding, which not only determines specific overall shoot patterns, but also determines leaf shape. At a fine scale, oriented cell divisions and proteinaceous microtubular cytoskeleton reinforcements control cell divisions and growth directions. Structural specification at each scale is efficient only when pertinent gene activity and mediation occur concurrently in both of the complementary scales of development. In the fir-cone-like galls of *M. indica* and sea-urchin-shaped galls of *H. ponga*, galling incites perturbation through an asynchrony initiated between the macroscale and fine-scale differentiation processes. Whereas we know, with reasonable clarity, that the 'stimulus' from the insect (physical injury [wounding] and salivary chemicals) initiates perturbation, but at what temporal point during gall initiation, does the asynchrony between macroscale and fine scale get activated? The more intriguing question is, in spite of the asynchrony at the two scales, how does the gall achieve symmetry at the conclusion of its growth, which matches precisely with the life-cycle of the inducing insect? What factors trigger the vegetative meristem of *M. indica* to deviate from the normal differentiation pathway in leaf ontogenesis and phyllotaxy, but to differentiate structures similar to microphylls (such as those that occur in lower pteridophytes), which enclose and provide nutrition to the developing insect stages? On the contrary, why does the apical meristem follow a completely different pathway of development in galls of *H. ponga*, compared with that of *M. indica*, involving total suppression of leaf development, but the 'soft' trichomes developing into woody spines? The most obvious in the two compared gall systems is that the gall – in its wholeness – accommodates the progeny that emerges from the initiating female, a trait that is shared by diverse species of Adelgidae (Hemiptera: Aphidoidea) that induce galls on different species of Coniferales in Europe¹⁷.

Hormones modulate complex suites of ecologically relevant traits through differentially modulated signal transductions. Given that changes in the function of one hormone can result in multiple changes in plant traits³⁸, the role of abscisic acid (ABA) is gaining importance in understanding the function of insect-induced gall systems^{39,40}, because of greater levels of ABA detected in gall tissue, and especially those suffering anoxia. However, the precise role of ABA in the regulation of subcellular osmotic stability and/or liability and membrane integrity in galls remains to be established. The specific role of cytokinins, which promote cell division, stimulate

growth, and enhance gall-tissue capacity in becoming nutrient sinks (more specifically that of nitrogen), needs to be interpreted better in galls. Because of regulated growth and also because a large part of the insect life cycle is completed within, galls are useful as ideal laboratory models for both ecologists and evolutionary biologists to creatively interpret, and even manipulate, plant strategies.

Host-plant dependence, monophagism, and taxonomic subtleties

Gall-inducing insects demonstrate a high degree of orientation to specific trophic niches⁴¹. Nearly 90% of them are host specific¹⁷, displaying a high level of fidelity to particular species of plants². More importantly, gall inducers are specific to particular plant organs, i.e. a leaf galler will induce galls on leaves only. However, exceptions such as *Thilakothrips babuli* (Thysanoptera: Phlaeothripidae) occur. *T. babuli* usually induces rosette galls on vegetative shoot meristems of *Acacia leucophloea* (Leguminosaceae)⁴². Rarely, however, *T. babuli* is known to induce galls on floral meristems. Such a shift in the gall-induction site is explained as an adaptive capacity to evade seasonal non-availability of vegetative meristems⁴³.

The level of sensitivity of gall-inducing insects is so high that they can discriminate between 'subtle' differences in host-plant physiology, chemistry, development and phenology, and go for their most preferred organs on specific host plants. The ability of gall inducers to distinguish even between plant hybrids is well documented⁴⁴, although we need to recognize that a few exceptions (e.g. *Dasineura marginemtorquens* [Diptera: Cecidomyiidae], which attacks non-host plants; *Adelges abietis* [Hemiptera: Adelgidae], which oviposits on resistant plants) also exist. Nevertheless, the capacity to remain committed to a single host species is so striking that, in practice, gall insects serve as reliable 'plant taxonomists' and gall-bearing plants serve as useful 'insect taxonomists'^{41,45,46}. The relationship between several species of *Crotonothrips* (Thysanoptera: Phlaeothripidae) and *Memecylon* (Melastomaceae) distributed almost evenly in the dry scrub (southern stretches of the Eastern Ghats) and dry deciduous (eastern slopes of southern Western Ghats) vegetation in peninsular India, illustrates the point mentioned earlier: *C. gallarum*, *C. coorgensis*, *C. dissimilis*, *C. memecylonicus*, and *C. dantahasta* induce galls on *Memecylon* sp., *M. talbotianum*, *M. lawsonii*, *M. lushingtonii*, and *M. edule* respectively, and galls emerging in these interactions range from simple epiphyllous rolls to complex leaf rosettes^{47,48}. No *Crotonothrips* occurs in either the remainder of India or the rest of the Orient. On the contrary, gall induction on leaflets of different species of *Schefflera* (Araliaceae) by diverse species of *Liothrips* (Thysanoptera: Phlaeothripidae) is known not only from cooler and upper slopes (above 1500 m asl) of the Western Ghats, peninsular India^{49,50}, but

also in rain forests of Northeast India (e.g. Thoubal and Chandel districts, Manipur; R. Varatharajan, pers. commun.), Java and Celebes (Indonesia)⁵¹, and the Philippines⁵². Several similar examples are available in Ananthakrishnan⁹ and Mani⁸.

The imperative host dependence underscores the 'ability' of a majority of gall-inducing insects to choose the right host plant and right site at the right time for oviposition initially and feeding subsequently: gravid females of *Trioxa jambolanae* (Hemiptera: Triozidae) oviposit along the lateral sutures of leaves of *Syzygium cumini* (Myrtaceae), displaying extraordinary level of precision; oviposition by *T. jambolanae* coincides with emergence of new leaf flushes after monsoon rains in natural areas near Chennai⁵³. Because the inducing insect (and in some instances, also its progeny) spends a major part of its life cycle within the gall, no chance can be taken by the gall-inducing insect, given that it invariably encounters diverse species of plants in a heterogeneous, natural environment. Gall-inducing insects use tactics that are more sophisticated than their non-gall-inducing relatives by directing their movements towards their preferred host plants and sites. However, the following questions remain: What levels of chemotaxis do they use? Do these insects pick up environmental cues based on vision and/or olfaction? Physiology of receptors is not known among Indian gall-inducing insects, although what we know today is that the number of sensilla distributed along the length of the labium increases with each larval moult, at least in gall-inducing psyllids, e.g. *Phacopteron lentiginosum* (Hemiptera: Phacopteronidae)^{16,54}.

Evolutionary pressure between random search and specific pattern of orientation in host-plant selection by phytophagous insects depends on a delicate balance between (i) cost in time and energy for finding the host, and (ii) difficulty in detecting or processing information from the host plant. Consequently, insects that remain restricted to a single plant species, such as gall inducers, have to search and locate the most 'ideal' host plant within specific temporal constraints. The plant that offers least resistance becomes the host; yet under extremely rare circumstances, gall-inducing insects also invade plants closely related to their most-preferred hosts and survive on them by inducing galls. *Trioxa fletcheri minor* (Hemiptera: Triozidae) is known as a gall inducer on leaves of *Terminalia tomentosa* and *T. arjuna* (Combretaceae), common not only in the temperate foothills of the Himalaya and the Indo-Gangetic plains^{55,56}, but also in the subtropical and deciduous forests in peninsular India⁵⁷. Through karyotyping, populations of *T. f. minor* obtained from both *T. tomentosa* and *T. arjuna* have been established as the same species⁵⁸. *T. f. minor* is also recorded on *T. catappa*, *T. paniculata*, and *T. tomentosa* × *T. arjuna*¹¹. Whereas almost all species of Triozidae – a group that principally includes gall inducers – are restricted to specific host-plant species, the behaviour of *T. f. minor* is exceptional

because it induces galls not only on the leaves of several species of *Terminalia*, but also on flowers⁵⁹ of more than one species of *Terminalia*. Patterns of occurrence of *T. f. minor* in naturally occurring populations of different species of *Terminalia* could be due to poor configuration of the taxonomy of *Terminalia* – which in reality could be either sympatric or geographic races, rather than well-defined species. Alternatively, incidence of *T. f. minor* in naturally occurring populations of *Terminalia* could also be due to evolution of host races in *T. f. minor*, which would isolate themselves as individual species in time. Which of these is true?

In short, what can be easily surmised from the above examples is that a high degree of specialization and diversification is continuing to occur between gall-inducing insects and their host plants. However, much needs to be known in Indian gall flora, whether any specific and/or unique relationships exist between particular groups of insects and particular taxonomic sections of plant taxa. For example, more than a dozen species of cecidomyiids induce different types of galls on leaves of *Mangifera indica*⁸. In the example of '*M. indica* – gall-inducing cecidomyiids', does any pattern of adaptive radiation occur? Given that all these cecidomyiids induce galls on leaves, how do they partition either time or resources to minimize (or avoid) interspecific competition? Continuing with the chosen example of gall midges and *M. indica* interactions, a few more questions become obvious. Given that natural and cultivated populations of *M. indica* above and below the Tropic of Cancer vary in flowering, fruiting and leafing phenologies, does any pattern in terms of the taxonomic groups of infesting cecidomyiid populations and trees exist? How do the cecidomyiids respond to varietal differences of *M. indica*? Do any variations manifest, when gall midges respond to different varieties of *M. indica*? Do gall structure and morphological complexity foreshadow any evolutionary trend? Does the ability to induce complex galls have any bearing on the adaptive advantage to the inducing insect: for example, do complex galls reflect a better 'sink' strength on the one hand, and a better reproductive fitness of the insect on the other? Some work has progressed with *Orseolia oryzae* and *Mayetiola destructor* (Diptera: Cecidomyiidae) in resolving the relationships between the gall midge and their host-plant varieties^{60–62}. However, much more needs to be done in dealing with similar questions in the context of tree species, whose physiology is considerably different from that of the annuals. Answers to these questions should offer insights into the nutritional behaviour of insects and susceptibility (and resistance) responses among subspecific variants within the same species that may be occurring because of geographical distribution and isolation. Moreover, investigations verifying the possible patterns of congruence between insects and plants should reveal 'related' clusters, which have not been detected by techniques used conventionally in taxonomic resolutions.

Biogeographical patterns of galls and gall-inducing insects

At a global scale, gall-inducing capability exists principally within Thysanoptera, Hemiptera, Diptera and Hymenoptera, whereas Lepidoptera and Coleoptera include relatively less number of gall-inducing species. Gall-inducing taxa among all these orders are few and confined to specific families. The Indian gall-inducing insects are no exception to such a pattern. For example, within Diptera (Cecidomyiidae), only 60% of gall midges are typical gall inducers, the remainder are either saprophagous or mycophagous or zoophagous⁶³. A similar situation prevails among other gall-inducing insects; e.g. Adelgidae (Aphidoidea)⁶⁴, Triozidae (Psylloidea)⁶⁵, and Eriococcidae (Coccoidea)⁶⁶. Within Indian Thysanoptera, almost all gall-inducing species occur in Phlaeothripidae, Tubulifera; only *Amphithrips* and *Aneurothrips* are the known gall inducers in Terebrantia⁶⁷. Among the gall-susceptible Indian plants, dicotyledons are the most susceptible hosts for a majority of gall inducing insects. Among gymnosperms, only the species of Coniferales host gall-inducers (random records of insect-induced galls on species of *Gnetum* also exist), and a small minority of monocotyledons bear galls. An exceptional example of a gall on monocotyledons will be the 'silver shoot' induced by species of *Orseolia*⁶⁸, which occurs extensively throughout the tropical regions in the Orient, but hosted by a limited number of species of Poaceae (e.g. *Oryza sativa* and *Cynodon dactylon*). Although galls occur in all natural orders of plants, Leguminosaceae, followed by Moraceae, Lauraceae, Combretaceae, Anacardiaceae, Cucurbitaceae, and Asteraceae bear the greatest numbers of galls in India, whereas the natural orders Fagaceae, Salicaceae, Convolvulaceae, Malvaceae, Capparidaceae, Rosaceae, and Euphorbiaceae that host galls in temperate parts of the world do not host any significant numbers of galls in India⁸.

Distribution of galls in India includes multiple peculiarities, indicating that galls and their inducers are unique to the Indian biogeographical region. Examples such as *Aceria pongamiae* (Acarina: Eriophyidae) that induce pouch galls on the leaves of *Pongamia glabra* (Leguminosaceae) and *T. jambolanae* that induce protruding globular galls on the leaves of *S. cumini* occur throughout India, notwithstanding latitudinal differences⁸, whereas the sea-urchin-shaped galls on *H. ponga* induced by *M. hopeae* occur restricted to the Konkan coast, from Sringeri in the north to Calicut in the south³³. Several other species of gall inducers are characteristically confined to specific biogeographical subregions of India. For example, the aphid-, cynipid-, and sawfly-induced galls occur only in the Himalayan slopes, whereas galls induced by thrips, psyllids and coccids occur only in the warm and humid peninsular India². Several species of non-gall-inducing aphids occur commonly (vegetable pests, such as *Bre-*

vicoryne brassicae, Hemiptera: Aphididae) in peninsular India, whereas no gall-inducing aphid is known in this region. We need to recognize that gall-inducing insects have been transmitted to other parts of the world, because of export of economic produce: for example, *Apsylla cistellata* is becoming a pest in parts of the world, where mango is cultivated (e.g. the Middle East)⁶⁹. According to Mani^{8,57}: "Most galls in the peninsular India are endemic and a considerable proportion of them, especially those in the Deccan, exhibit striking Ethiopian and Mediterranean and even Himalayan affinities ... The West and Northwest Himalaya are rich in endemic galls and have also a high proportion of true European and Middle Asiatic elements and sometimes the galls are identical to those found in Europe". Although the channelling effect of the Himalaya on monsoon currents and the topographic peculiarity of peninsular India explain the oddities in the distribution of gall flora and their inducing organisms⁵, questions such as why gall-inducing sawflies and aphids are confined only to the temperate Himalayan slopes? and why most of the gall-inducing thrips, psyllids and coccids occur only in the subtropical and tropical stretches of peninsular India? remain unanswered. The profundity of these questions deepens, especially when we reckon diverse human-induced changes to vast tracts of land and natural areas in India over several thousands of years into the equation.

Conclusion

Especially in the last two and a half decades, interest in studying galls and their inducers has grown throughout the world: several new species of gall-inducing insects that live on specific host plants have been determined and described⁷⁰; greater volume of information explaining subtle physiological and morphogenetic processes in galls is known than before^{16,71}; unique patterns in the distribution of gall-inducing insects and their host plants have been unveiled, clarifying fascinating details not only on the evolution of insect phytophagy, but also that of the interacting plants and insects^{72,73}. Further to being useful as excellent biological-control agents of weeds⁷⁴, in terms of applied ecology, several of the gall-inducing insects are being currently used as models for studying and interpreting chemical and molecular ecology of insect-plant interactions. However, in India, much needs to be done; for example, processes and patterns of migration and colonization of several gall-inducing insects remain unexplained. For example, in the *M. hopeae*-*H. ponga* interactions³³, what we know are that (i) a young female larva initiates the gall, and (ii) the winged males (which do not induce galls) mate with the females, which remain trapped within the gall. What we do not know are: (i) Is the first progeny all-males only (if yes, how do population trends of an 'all-male' progeny match with gall growth, because the gall

continues to grow)?'; (ii) 'What is the composition of the second and subsequent progenies – all females or mixed?'; (iii) 'How long does the gall continue to grow?', and (iv) 'Do the winged brothers enable dispersal of their apterous sisters, which are meant to initiate new galls, similar to what has been shown in the Australian gall-inducing species of Ericoccidae'?⁶⁷

Keeping the enormous volume of literature that has accumulated in the recent past in view, I have endeavoured to raise some questions that remain unanswered in the overall context of (i) what a gall is, (ii) how galls are initiated and what factors trigger gall growth, (iii) what are the patterns in host dependence, and (iv) biogeographical patterns of galls and gall-inducing insects, particularly referring to examples unique to the Indian subcontinent. I recognize that I have not discussed many finer aspects in the interactions between gall-inducing insects and their host plants, such as (i) tritrophic relationships involving endophytic fungi in galls ('ambrosia' galls) induced by gall midges belonging to Asphondyliini, Alycaulini, Lasiopterini^{75,76}, (ii) interactions among arthropods within gall communities, which include parasitoids, predators, inquiline and casual visitors⁷³, (iii) social behaviour known in several gall-inducing non-hymenopterans^{64,77}, (iv) ability of gall-inducing insects to live on plants that contain strong anti-insect compounds^{33,78}, and (v) emergence and outbreak of alien gall-inducing insect species as pests of commercially important plants^{79,80}. Several other intriguing questions such as 'Why so many different types of galls exist?', 'How can two or more different species of insects induce distinctive galls on the same plant organ?'⁸¹ also remain unanswered. Perhaps the most critical and immediate call in India would be the determination and documentation of gall midges, which should be occurring in a high frequency, similar to what is known in the remainder of the world⁸². Because a remarkable variety of fascinating gall systems induced by different insect species exist in India, I felt compelled to write this article, which I hope will provoke Indian biologists to look for convincing answers. However, we need to reckon with the fact that because of rapid and indiscriminate industrialization in India, we are losing several fascinating biological materials that are special to India, and the galls and their inducing insects are no exception to such a non-recoverable loss.

- Labandeira, C. C., Insect mouthparts: Ascertaining the paleobiology of insect feeding strategies. *Annu. Rev. Entomol.*, 1997, **28**, 153–193.
- Raman, A., Schaefer, C. W. and Withers, T. M. (eds), Galls and gall-inducing arthropods: An overview of their biology, ecology, and evolution. In *Biology, Ecology, and Evolution of Gall-inducing Arthropods*, Science Publishers, Inc., Enfield, New Hampshire, 2005, pp. 1–33.
- Crane, P. R. and Jarzembowski, E. A., Insect leaf miners from the Palaeocene of southern England. *J. Nat. Hist.*, 1980, **14**, 629–636.
- Scott, A. C., Stephenson, J. and Collinson, M. E., The fossil record of leaves with galls. In *Plant Gall – Organisms, Interactions, and Populations* (ed. Williams, M. A. J.), The Systematics Association Special Volume 49, Clarendon Press, Oxford, 1994, pp. 447–470.
- Mani, M. S., Introduction. In *Ecology and Biogeography in India* (ed. Mani, M. S.), Dr Walter Junk Publishers, The Hague, 1974, pp. 1–10.
- Srivastava, A. K. and Srivastava, G. P., Insect gall impression on fossil angiosperm leaf. *Geophytology*, 1998, **26**, 95–97.
- Srivastava, A. K., Abbas, S. R., Mehrotra, R. C. and Srivastava, R., Cecidomyiid leaf galls in Palaeocene leaves from north-eastern India. *Acta Palaeobot.*, 2000, **40**, 43–47.
- Mani, M. S., *Plant Galls of India (Second Edition)*, Science Publishers, Inc., Enfield, New Hampshire, 2000, p. 477.
- Ananthakrishnan, T. N., Thrips galls and gall thrips. *Zool. Surv. India, Tech. Monogr.*, 1978, **1**, 1–69.
- Channabasavanna, G. P., *A Contribution to the Knowledge of Eriophyid Mites (Eriophyoidea: Trombidiformes: Acarina)*, University of Agricultural Sciences, Bangalore, 1966, p. 153.
- Mathur, R. N., *The Psyllidae of the Indian Subcontinent*, Indian Council of Agricultural Research, New Delhi, 1975, p. 429.
- Kandasamy, C., Taxonomy of south Indian psyllids. *Rec. Zool. Surv. India*, 1986, **84**, 1–111.
- Mani, M. S., Zooecidia and cecidozoa from India. *J. R. Asiatic Soc. Bengal (Sci.)*, 1948, **14**, 27–195.
- Raman, A. and Ananthakrishnan, T. N., Recent advances in cecidological research in India. In *Recent Advances in Entomology in India* (ed. Ananthakrishnan, T. N.), S. Viswanathan (Printers & Publishers) Private Limited, Madras, 1981, pp. 67–78.
- Raman, A., Review of *Plant Galls of India* by M. S. Mani (2000; second edition). *Curr. Sci.*, 2001, **79**, 1731–1732.
- Raman, A., Cecidogenetic behaviour of some gall-inducing thrips, psyllids, coccids, and gall midges, and morphogenesis of their galls. *Orient. Insects*, 2003, **37**, 359–413.
- Meyer, J., *Plant Galls and Gall Inducers*, Gebrüder Bornträger, Stuttgart, 1987, p. 291.
- Raman, A. and Abrahamson, W. G., Morphometric relationships and energy allocation in the apical rosette galls of *Solidago altissima* (Asteraceae) induced by *Rhopalomyia solidaginis* (Diptera: Cecidomyiidae). *Environ. Entomol.*, 1995, **24**, 635–639.
- Meyer, J., Irrigation vasculaire dans les galles. *Bull. Soc. Bot. Fr., Mem.*, 1969, 75–97.
- Wool, D., Aloni, R., Ben-Zvi, O. and Wollberg, M., A galling aphid furnishes its home with a built-in pipeline to the host food supply. *Entomol. Exp. Appl.*, 1999, **91**, 183–186.
- Raman, A., Madhavan, S., Florentine, S. K. and Dhileepan, K., Stable-isotope ratio analyses of metabolite mobilization in the shoot galls of *Parthenium hysterophorus* (Asteraceae) induced by *Epiblema strenuana* (Lepidoptera, Tortricidae). *Entomol. Exp. Appl.*, 2006, **119**, 101–107.
- Raman, A. and Ananthakrishnan, T. N., Studies on some thrips (Thysanoptera, Insecta) induced galls. Fine-structure of the nutritive zone. *Proc. Indian Natl. Sci. Acad., Part B*, 1983, **49**, 525–561.
- Mani, T. and Raman, A., Biochemical changes in relation to growth in two leaf gall systems induced by *Trioza jambolanae* and *Microceropsylla longispiculata* (Homoptera: Psylloidea). *Phytophaga* 1994, **6**, 59–64.
- Raman, A., Chemical ecology of gall insect–host plant interactions: Substances that influence the nutrition and resistance of insects and the growth of galls. In *Chemical Ecology of Phytophagous Insects* (eds Ananthakrishnan, T. N. and Raman, A.), Oxford & IBH, New Delhi, 1993, pp. 227–250.
- Meyer, J. and Maresquelle, H.-J., *Anatomie des Galles*, Gebrüder Bornträger, Stuttgart, Germany, 1983, p. 662.

26. Bronner, R., The role of nutritive cells in the nutrition of cynipids and cecidomyiids. In *Biology of Insect-induced Galls* (eds Shorthouse, J. D. and Rohfritsch, O.), Oxford University Press, New York, 1992, pp. 118–140.
27. Hartley, S. E., Are gall insects large rhizobia? *Oikos*, 1999, **84**, 333–342.
28. Miles, P. W., Aphid saliva. *Biol. Rev.*, 1999, **74**, 41–85.
29. Mapes, C. C. and Davies, P. J., Cytokinins in the ball gall of *Solidago altissima* and in the gall-forming larvae of *Eurosta solidaginis*. *New Phytol.*, 2001, **151**, 203–212.
30. Carango, P., McCrea, K. D., Abrahamson, W. G. and Chernin, M. I., Induction of a 58,000 Dalton protein during goldenrod gall formation. *Biochem. Biophys. Res. Commun.*, 1988, **152**, 1348–1358.
31. Rohfritsch, O., Patterns in gall development. In *Biology of Insect-induced Galls* (eds Shorthouse, J. D. and Rohfritsch, O.), Oxford University Press, New York, 1992, pp. 60–86.
32. Rohfritsch, O., Étude d'une galle de *Lobopteromyia* sp. sur *Acacia* (*A. ferruginea* DC?). *Marcellia*, 1971, **37**, 139–149.
33. Raman, A. and Takagi, S., Galls induced on *Hopea ponga* (Dipterocarpaceae) in southern India and their gall-maker belonging to the Beesoniiidae. *Insecta Matsumurana* (N.S.), 1992, **47**, 1–32.
34. Byrne, D., Gall-inducing whiteflies (Hemiptera: Aleyrodidae). In *Biology, Ecology, and Evolution of Gall-inducing Arthropods* (eds Raman, A. et al.), Science Publishers, Inc., Enfield, New Hampshire, 2005, pp. 143–158.
35. Jesudasan, R. W. A. and David, B. V., Histological studies of scarlet red patch induced by the whitefly *Bemisia tabaci* (Gennadius) on under surface of leaf of *Achyrothes aspera* Linn. *J. Bombay Nat. Hist. Soc.*, 1986, **83**, 245–248.
36. Farnsworth, E., Hormones and shifting ecology throughout plant development. *Ecology*, 2004, **85**, 5–15.
37. Maresquelle, H.-J., La morphogenèse dans l'impasse? Reflexions d'un cécidologue. *Bull. Soc. Bot. Fr. (Actual. Botan.)*, 1980–81, **127**, 9–16.
38. Fleming, A. J. (ed.), *Intercellular Communication in Plants*, Blackwell Publishing Limited, Oxford, 2005, p. 280.
39. De Bruyn, L., Vandevyere, I., Jamine, D. and Prinsen, E., Effects of *Lipara lucens* (Diptera: Chloropidae) on its host *Phragmites australis* (Poaceae). In *The Biology of Gall-inducing Arthropods* (eds Csóka, G. et al.), General Technical Report NC 199, North-Central Research Station, USDA, Forest Service, St Paul, Minnesota, 1998, pp. 175–187.
40. Florentine, S. K., Raman, A. and Dhileepan, K., Response of the weed *Parthenium hysterophorus* (Asteraceae) to the stem gall-inducing weevil *Conotrachelus albocinereus* (Coleoptera: Curculionidae). *Entomol. Gener.*, 2002, **26**, 195–206.
41. Raman, A., Nutritional diversity in gall-inducing insects and their evolutionary relationships with flowering plants. *Int. J. Ecol. Environ. Sci.*, 1996, **22**, 133–143.
42. Raman, A. and Ananthakrishnan, T. N., On the developmental morphology of the rosette galls of *Acacia leucophloea* Willd. (Mimosaceae) induced by *Thilakothrips babuli* Ramk. (Thysanoptera: Insecta). *Proc. Indian Acad. Sci.*, 1983, **92**, 343–350.
43. Varadarasan, S. and Ananthakrishnan, T. N., Biological studies on some gall thrips. *Proc. Indian Natl. Sci. Acad., Part B*, 1982, **48**, 35–43.
44. Floate, K. D. and Whitham, T. G., Insects as traits in plant systematics: Their use in discriminating hybrid cottonwoods. *Can. J. Bot.*, 1995, **73**, 1–13.
45. Sýlven, E., Gall midges (Diptera, Cecidomyiidae) as plant taxonomists. *Symb. Bot. Ups.*, 1979, **22**, 62–69.
46. Abrahamson, W. G., Melika, G., Scrafford, R. and Csóka, G., Gall-inducing insects provide insights into plant systematic relationships. *Am. J. Bot.*, 1998, **85**, 1159–1165.
47. Ananthakrishnan, T. N., New gall thrips of the genus *Crotonothrips* (Thysanoptera). *Orient. Insects*, 1976, **10**, 411–419.
48. Raman, A. and Ananthakrishnan, T. N., Cecidogenous *Crotonothrips* (Thysanoptera) and *Memecylon* interactions: Host relations, nutritive tissue, tissue dynamics, and cecidogenetic patterns. *Proc. Indian Acad. Sci.*, 1985, **95**, 103–120.
49. Ananthakrishnan, T. N., Further studies on Indian gall thrips. *Marcellia*, 1972, **37**, 3–20.
50. Krishnamurthy, K. V., Raman, A. and Ananthakrishnan, T. N., On the morphology of the ceratoneon thrips galls of *Schefflera racemosa* Harms. *Marcellia*, 1975, **38**, 179–184.
51. Karny, H., Docters van Leeuwen, W. and Docters van Leeuwen-Reijnvaan, J., Beiträge zur Kenntnis der Gallen von Java. 5. Über die Javanischen Thysanoptero-cecidien und deren Bewohner. *Bull. Jard. Bot. Buitenzorg.*, 1913, **10**, 1–54.
52. Uichanco, H. R., A biological and systematic study of Philippine plant galls. *Philipp. J. Sci.*, 1919, **14**, 527–554.
53. Raman, A., Cecidogenesis of leaf galls of *Syzygium cumini* (L.) Skeels (Myrtaceae) induced by *Trioza jambolanae* Crawford (Homoptera: Psylloidea). *J. Nat. Hist.*, 1991, **25**, 653–663.
54. Raman, A., On the cecidogenesis and nutritive tissues of the leaf galls of *Garuga pinnata* Roxburgh (Burseraceae) induced by *Phacopteron lentiginosum* Buckton (Pauropsyllinae, Psyllidae, Homoptera). *Phytophaga*, 1987, **1**, 141–160.
55. Crawford, D. L., Indian Psyllidae. *Rec. Indian Mus.*, 1912, **7**, 419–437.
56. Mathur, R. N., On the biology of Psyllidae. *Indian For. Rec.*, 1935, **1**, 35–70.
57. Mani, M. S., *Plant Galls of India (First Edition)*, Macmillan India, New Delhi, 1974, p. 323.
58. Raman, A., Singh, R. N. and Maryanska-Nadachowska, A., Biology and karyology of a cecidogenous psyllid, *Trioza fletcheri minor* (Homoptera: Psylloidea) and morphogenesis of galls on the leaves of *Terminalia tomentosa* and *T. arjuna* (Combretaceae). *Insecta Matsumurana* (N.S.), 1997, **53**, 117–134.
59. Sokhi, J. and Kapil, R. N., Morphogenetic changes induced by *Trioza* in flowers of *Terminalia arjuna* – I. Androecium; II. Gynoecium. *Phytomorphology*, 1984, **34**, 117–128; 1985, **35**, 69–82.
60. Behura, S. K., Sahu, S. C., Rajamani, S., Devi, A., Mago, R., Nair, S. and Mohan, M., Differentiation of Asian rice gall midge, *Orseolia oryzae* (Wood-Mason), biotypes by sequence characterized amplified regions (SCARs). *Insect. Mol. Biol.*, 1999, **8**, 391–397.
61. Katiyar, S. K. et al., Biodiversity of Asian rice gall midge (*Orseolia oryzae* Wood Mason) from five countries examined by AFLP analysis. *Genome*, 2000, **43**, 322–332.
62. Harris, M. O., Stuart, J. J., Mohan, M., Nair, S., Lamb, R. J. and Rohfritsch, O., Grasses and gall midges: Plant defense and insect adaptation. *Annu. Rev. Entomol.*, 2003, **48**, 549–577.
63. Skuhravý, M., Skuhravý, V. and Brewer, J. W., Biology of gall midges. In *Biology of Gall Insects* (ed. Ananthakrishnan, T. N.), Oxford & IBH, New Delhi, 1984, pp. 169–222.
64. Wool, D., Gall-inducing aphids: Biology, ecology, and evolution. In *Biology, Ecology, and Evolution of Gall-inducing Arthropods* (eds Raman, A. et al.), Science Publishers, Inc., Enfield, New Hampshire, 2005, pp. 73–142.
65. Burckhardt, D., Biology, ecology, and evolution of gall-inducing psyllids (Hemiptera: Psylloidea). In *Biology, Ecology, and Evolution of Gall-inducing Arthropods* (eds Raman, A. et al.), Science Publishers, Inc., Enfield, New Hampshire, 2005, pp. 143–158.
66. Gullan, P., Miller, D. R. and Cook, L. C., Gall-inducing scale insects (Hemiptera: Sternorrhyncha: Coccoidea). In *Biology, Ecology, and Evolution of Gall-inducing Arthropods* (eds Raman, A. et al.), Science Publishers, Inc., Enfield, New Hampshire, 2005, pp. 159–230.
67. Ananthakrishnan, T. N. and Raman, A., *Thrips and Gall Dynamics*, Oxford & IBH, New Delhi, 1989, p. 120.
68. Grover, P., Cecidomyiid larvae and host-plant interaction. In *Dynamics of Insect-Plant Interaction* (eds Ananthakrishnan, T. N. and Raman, A.), Oxford & IBH, New Delhi, 1988, pp. 177–200.

69. <http://www.hort.purdue.edu/newcrop/morton/index.html> (viewed on 19 July 2006).
70. Gagné, R. J., *The Plant-feeding Gall Midges of North America*, Cornell University Press, Ithaca, 1989, p. 356.
71. Shorthouse, J. D. and Rohfritsch, O. (eds), *Biology of Insect-Induced Galls*, Oxford University Press, New York, 1992, p. 285.
72. Abrahamson, W. G. and Weis, A. E., *Evolutionary Ecology Across Three Trophic Levels: Goldenrods, Gallmakers, and Natural Enemies*, Princeton University Press, Princeton, 1997, p. 456.
73. Raman, A., Schaefer, C. W. and Withers, T. M. (eds), *Biology, Ecology, and Evolution of Gall-inducing Arthropods*, Science Publishers, Inc., Enfield, New Hampshire, 2005, 2 vols, p. 817.
74. Muniappan, R. and McFadyen, R., Gall-inducing arthropods used in biological control of weeds. In *Biology, Ecology, and Evolution of Gall-inducing Arthropods* (eds Raman, A. et al.), Science Publishers, Inc., Enfield, New Hampshire, 2005, pp. 709–730.
75. Yukawa, J. and Rohfritsch, O., Biology and ecology of gall-inducing Cecidomyiidae. In *Biology, Ecology, and Evolution of Gall-inducing Arthropods* (eds Raman, A. et al.), Science Publishers, Inc., Enfield, New Hampshire, 2005, pp. 273–304.
76. Roskam, H. C., Phylogeny of gall midges (Cecidomyiidae). In *Biology, Ecology, and Evolution of Gall-inducing Arthropods* (eds Raman, A. et al.), Science Publishers, Inc., Enfield, New Hampshire, 2005, pp. 205–320.
77. Mound, L. A. and Morris, D. C., Gall-inducing thrips: An evolutionary perspective. In *Biology, Ecology, and Evolution of Gall-inducing Arthropods* (eds Raman, A. et al.), Science Publishers, Inc., Enfield, New Hampshire, 2005, pp. 59–72.
78. Balakrishna, P. and Raman, A., Cecidogenesis of the leaf roll galls of *Strychnos nux-vomica* induced by the plant louse species, *Diaphorina truncata* (Homoptera: Psylloidea). *Entomol. Gener.*, 1992, **17**, 285–292.
79. Faizal, M. H., Prathapan, K. D., Anith, K. N., Mary, C. A., Lekha, M. and Rini, C. R., *Erythrina* gall wasp *Quadrastichus erythrinae*, yet another invasive pest new to India. *Curr. Sci.*, 2006, **90**, 1061–1062.
80. Jacob, J. P., Outbreak of gall-inducing *Leptocybe invasa* (Hymenoptera: Eulophidae) in *Eucalyptus* plantations in India. *Entomon.*, 2007, communicated.
81. Shorthouse, J. D., Wool, D. and Raman, A., Gall-inducing insects – nature’s most sophisticated herbivores. *Basic Appl. Ecol.*, 2005, **6**, 407–411.
82. Skuhrová, M., Species richness of gal midges (Diptera: Cecidomyiidae) in the main biogeographical regions of the world. *Acta Soc. Zool. Bohem.*, 2006, **69**, 327–372.

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