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Abstract

Galls are modified, invariably symmetrical, naturally developing plant structures that arise because of messages from certain specialist insects, mostly from the Thysanoptera, Hemiptera, Diptera, and Hymenoptera, and in a lesser frequency from the Lepidoptera and Coleoptera. Several species of the Eriophyoidea (Acari) induce galls and wherever appropriate, we have considered examples from the Eriophyoidea as well, generically referred under the term “insects.” The insects live within them, deriving nourishment and shelter. When these insects attack plant tissues, osmotic stress alters the electrical properties of the plant-cell plasma membranes and impacts on indole-acetic acid synthesis and activity, which, in turn, affects the H+ transport. Insect action stimulates parts of host-cell wall to break down and the degenerated wall materials in the cytoplasm act as elicitors. In such contexts the susceptible plants use flexible strategies to mitigate stress, which generally manifest as galls. Inherited traits also play a role in providing specific shapes to the gall, which is coordinated by the innate correlating morphogenetic factors that operate normally in the plant. The gall-inducing Diptera (Cecidomyiidae), Hemiptera (Stennorrhyncha), and Hymenoptera (Cynipidae) induce galls of highly defined and exquisite shapes. Almost all of these insects are known for their specificity to plants. The gall-inducing insects, unlike many of their free-living relatives, discriminate between plants and choose from them. Selection of a particular plant by a gall-inducing insect is not a matter of chance, given that the insect encounters varied plant taxa in the natural environment. The gall-inducing insects preferentially feed on specific plant organs, or parts of these, and on specific plant species. One recent explanation is that the gall-inducing insects prefer certain plants or parts of those plants, because they need the lipidic materials, e.g., sterols, available in those plant parts, which the insects utilize for building hormones critically necessary for their metamorphosis. Because of the sedentary nature of the juvenile stages of the inducing insect, the gravid females endowed with specialized sensory structures play a key role in selecting the site precisely for oviposition and thus for the progeny. Although a majority of gall-inducing insects are restricted to specific plant taxa, some of them, as we presently know, are indicated to be capable of inducing galls on plant species closely related to their most-preferred hosts, thus demonstrating some level of oligophagy. A few species of Asphondylia and Schizomyiina (Cecidomyiidae) are presently indicated as polyphagous. Clearly demonstrated host shifts and adaptive radiation in some of the European and North-American gall-inducing Tephritidae populations explain the evolution of sympatric host races, more because of changes either in the preference of feeding and/or oviposition sites or by acquiring “new” physiological adaptations to new plants or through assortative mating. Differences in the temporally regulated flowering and leafing phenologies in the susceptible plants possibly play a role in isolating gall-inducing insect populations, which enable divergence and diversification via genetic drift. The general understanding, as of now, is that host shifts and radiation in gall-inducing insects are more complex than what is known in their non-gall-inducing allies. Such a complexity is attributed to intricate relationships of gall-inducing insects with plants and the dispersal of gall-inducing insects through different biogeographical realms, mainly influenced by the abundance and variety of plant species. The gall-inducing insects, as a highly evolved group, present a stunning diversity, yet share the distinct capacity to redirect developmental programs of plants by generating galls. Propagation of the progeny manifests more prominently in the hemipteroids and Acari, whereas this behavior is not that prominent in the more-derived gall-inducing groups, such as the Cecidomyiidae and Cynipidae, wherein the gall as a facility is better used for the nutrition and development of the immature stages of the inducing insect taxon. The gall-inducing insects are easy to monitor because of the distinct presence of galls, offering an advantage in extending in investigations about the eco-physiology of several other economically important, non-gall-inducing insects.
gall-inducing insects could be termed as ecosystem engineers in the sense that they manipulate plant architecture to create novel habitats. Their impacts on plants will continue to be scrutinized, especially in regions where gall-inducing insects have been introduced and released from their natural enemies, thus potently threatening various other plants, including the economically relevant ones.

**Key words:** adaptations, commensalism, distribution, exploitation, mutualism

Among the diverse plant-feeding insects, only a few induce specialized, enclosing structures referred as galls. Galls are the modified, invariably symmetrical, naturally developing plant structures that arise because of messages from the inducing insects (Mani 1964, Raman 2011a). The great antiquity of galls may be taken as evidence that gall-inducing insects (some examples from gall-inducing Eriophyoida are also considered in this article as “insects”), in particular, continually exploit their host plants, despite the numerous mechanisms by which plants can deter insect feeding. Galls arise as an extension of the host-plant phenotype (Weis et al. 1988; Chen et al. 2015). The inducing insects, mostly the larval stages, live in them for a period of time deriving nourishment and shelter. That the morphology and physiology of the plant influence the biology and ecology of the inducing insect is well established (Shorthouse and Rohfritsch 1992, Raman et al. 2005a), as shown in different species of Cynipidae (Hymenoptera) that induce galls on diverse species of *Quercus* (Fagaceae) (Stone and Cook 1998) and *Rosa* (Rosaceae) (Shorthouse 2010). The message is that plant architecture influences the oviposition behavior of the Cynipidae (Abrahamson et al. 1998, Csóka et al. 2005, Shorthouse et al. 2005). Because of their concealed habitat (also referred as embedded habit), the gall-inducing insects generally show special traits when viewed against the behavior of non-gall-inducing (free-living) insects, particularly in their nutritional physiology and population dynamics (Raman et al. 2005b, Raman 2016, Sharma and Raman 2017).

The origin of gall-inducing habit among insects is not clearly resolved. Although nearly 50% of the known insects are plant feeders (Adler and Footitt 2009), only a small proportion of them induce galls. The capacity to induce galls does not manifest uniformly throughout the Insecta. This capacity manifests predominantly in the Thysanoptera, Hemiptera, Diptera, and Hymenoptera, and in a lesser frequency, in the Lepidoptera and Coleoptera. *Circa 65%* of the world’s gall-inducing insects occur in the Cecidomyiidae (Diptera) in both temperate and tropical regions, followed by the Cynipidae (Hymenoptera), the estimated second richest and most diverse group in North America and Europe (*Espírito Santo and Fernandes 2007*). Gall-inducing habit, as apparent in the Thysanoptera, Hemiptera, Diptera, and Hymenoptera, does not present any definite pattern. For example, in the Psyllidae (Hemiptera), many Triozoidae and Aphalaridae induce galls, whereas only a few taxa of the Psyllidae, Phacopteronidae, and Coccoidea induce galls (*Burckhardt 2005, Raman 2012*). The gall-inducing habit is considered to have evolved independently and multiple times in the Insecta, which has been confirmed in the Coccoidea (Hemiptera) (Cook and Gullan 2004). Gall-inducing capacity generally presents as a defining characteristic of a family, such as the Cecidomyiidae (Diptera) (Roskam 2005, Yokawa and Rohfritsch 2003) and the Cynipidae (Hymenoptera) (Askew 1984, Csóka et al. 2005) or of a tribe, such as the Ophelimini (Hymenoptera: Eulophidae) (La Salle 2005). While considering gall-inducing capacity at the order level, a majority of gall-inducing Hemiptera occur in the Sternorrhyncha. However, occasional reports claiming gall induction in the Auchenorrhyncha exist too. For example, *Aphelaenus nigriceps* (Matsumura) (Hemiptera: Aphrodiridae) is claimed to be inducing roll galls on the leaves of *Prunus speciosa* (Koidz.) Ingram, *P. xyedoensis* (Matsumura), and *Prunus pendula* Miq. cv. *pendula* (Rosaceae) (Sugiura and Yamazaki 2003) and *Cicadulina bipunctata* (Melichar) (Hemiptera: Cicadellidae) as a gall-inducing agent on various species of Poaceae (*e.g.*, *Zea mays* Linn., *Oryza sativa* Linn., and species of *Triticum*) (*Matsukura et al. 2010*). Remarks on galls induced by species of Cercopoidae and Membracoidea are available (Meyer 1987). *Copioidea* and *Paracopioidea* (Hemiptera: Tingidae) are the two alleged gall-inducing taxa (*Werner 2001*) on species of *Teucrium* and *Clerodendrum* (both Lamiaceae) (*Schaefer 2005*). The most recent addition to galls induced by Auchenorrhyncha is *Scenengates viridis* (Vilbaste) (Hemiptera: Cicadellidae) on *Alhagi mauroorum* Fisch. (Fagaceae) (*Rakitov and Appel 2012*). Young instars of *S. viridis* induce tender leaves of *A. mauroorum* to fold along the midrib; subsequent development of *S. viridis* occurs within tightly folded leaves, which grow as thickened, pod-like structures and are indicated as galls. Gravid females insert eggs beneath the inner epidermis of the gall. The ovipositing adults remain within the galls, as an effort to protect the brood. The walls of folded leaves, which include eggs are approximately three times thicker than the leaves uninfested by *S. viridis*.

The abnormalities induced by Auchenorrhyncha, claimed as galls, involve low-level alterations, such as curls and wrinkles on leaves and flowers. More importantly a majority of these is nonspecific to particular plant species (*Murphy 1989*), whereas the gall-inducing Cynipidae, Cecidomyiidae, Psylloidea, Coccoidea, and Phlaeothripidae are specific to one plant species. The debatable point is whether the Auchenorrhyncha induce “true” galls as the Sternorrhyncha do. However, the published articles that speak of galls induced by Auchenorrhyncha offer scope to explore the evolution of gall-inducing behavior in the hemipteroids. Whether the greater abundance of gall-inducing taxa in the Sternorrhyncha than in the Auchenorrhyncha has resulted as a direct consequence of their specialized feeding habits remains to be answered. We know today that a majority of Auchenorrhyncha feed on phloem, similar to adult Sternorrhyncha, but we also know that the species of Cercopoidae and Cacidoidea feed on xylem. Most of the Cicadellidae are phloem feeders, but the Cicadellinae and its allies are xylem feeders. Species of Typhlocybinae (Cicadellidae) feed from individual cells, and that behavior appears distinct. Does the behavior of feeding on parenchyma by the early immature stages and feeding on phloem by the older immature stages and adults of Sternorrhyncha define and delineate gall induction by them? We need to recognize here that at least among the gall-inducing Psylloidea (*e.g.*, Triozidae, Aphalaridae) and Coccoidea (Beesonidae), several examples have demonstrated that younger instars (the first, second, and third stage instars of the Psylloidea and the first and second stage instars of the Beesonidae (Coccoidea) feed on parenchyma, whereas the older instars shift to phloem (*Raman and Takagi 1992, Sharma et al. 2014, 2015a*), probably seeking better-quality nutrients, such as proteins.

**Gall Initiation, Growth, and Development**

Articulate differentiation processes in plant organs regulate growth and development of galls. Among the well-explored examples of

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insect-induced galls, distinct variations in differentiation and in final gall shapes occur (see Dreger-Jauffret and Shorthouse 1992 for several examples). An elegant developmental mechanism occurs in the galls arising on the leaves of *Pistacia palestina* Boiss. (Anacardiaceae) induced by *Geoica wertheimae* Brown, P.A. & Blackman (Hemiptera: Aphidoidea) in Israel, wherein new phloem elements differentiate close to the inner surface of the gall enabling *G. wertheimae* populations living within to feed simultaneously and continuously through the Palestinian summer (Wool et al. 1999). Rohfritsch (1988a) has clarified the food-supply mechanism in the galls on *Galium mollugo* Linn. (Rubiaceae) induced by *Geocrypta galli* Löw (Diptera: Cecidomyiidae).

That the mandibles of gall-inducing arthropods play a key role by discharging chitin, which acts as an elicitor is well demonstrated (Bronner et al. 1989). During early phases of feeding, i.e., <24 h, the chitinous chelicerae of *Aceria cladophthirus* Nalepa (Eriophyidae) perforate the epidermal cell walls of *Solanum dulcamara* Linn. (Solanaceae). Around these perforations, the epidermal cells react by accumulating callose. Within the first hour of *A. cladophthirus*’s feeding action, the nuclei of the injured cells enlarge and appear optically empty, but with a concurrent and gradual loss of DNA — diagnosed as chromatin dispersion — in these cells. Various other subcellular changes, such as vacuolar alkalinization increasing to >8 pH, eventuate in the epidermal cells of plants attacked by different species of gall-inducing Eriophyidae within the first 24 h of attack (Westphal 1982). The surrounding cells differentiate into nutritive cells on which *A. cladophthirus* feed. Chitosan, a polymer of β-1,4-linked glucosamine residues, with a strong affinity for DNA, manifests in the nuclei of the perforated cells within 60 min of attack by *A. cladophthirus*. We need to recall that a high affinity between chitosan and DNA is an established phenomenon in the interactions between 185 plants and pathogenic fungi (see el-Ghaouth et al. 1992).

Wounding of plant tissues inflicted by either feeding (as in the Cecidomyiidae) or ovipositing (as in the Cynipidae) action results in a rapid alteration of the subcellular environment, leaving the target plant cells in a state of chemical shock. This shock evokes the osmotic changes in attacked cells, resulting in the earliest recognizable stage in gall induction, usually in the first 24 h of attack. Wounded cells as well as a few neighboring cells get activated, which include hypertrophied nuclei and nucleoli, further to many other subcellular modifications, such as intensified modified plastids. The cytoplasm increases in volume with a simultaneous reduction in vacuole size as normally would occur in intensely dividing young, normal cells (Meyer and Maresquelle 1983) (Fig. 1). The resulting metabolic changes triggered by alterations in the vacuolar pH — expressed as novel chemicals — diffuse from these dedifferentiated (also referred as metaplasied) cell(s) into the immediate neighborhood, but never throughout either the involved plant organ or the entire plant (Raman 2011b, Rohfritsch 2011). When the chemical shock is of low intensity, the plant responds with certain chemical and molecular factors (details are currently unknown), which diffuse from the dedifferentiated cell(s), triggering gall growth. However, when the shock is of high intensity, the cells under the direct impact of the insect (e.g., *Dasineura marginentorquens* (Bremi), Diptera: Cecidomyiidae; *Daktulosphaira vitifoliae* (Fitch), Hemiptera: Phylloxeridae) die, rejecting the insect and thus protecting plant tissue (Ollerstam et al. 2002, Raman et al. 2009a). For a neat explanation of subcellular resistance response to gall-inducing Adelgidae (Sternorrhyncha: Aphidoidea) read Rohfritsch (1976, 1988b).

Insects feed on the gall tissue continuously for specific periods, i.e., throughout their developmental phase, and this behavior

Fig. 1. Time-related subcellular changes (cross-sectional views, transmission electron microscopy) in the fifth and sixth layers in the gall induced by *Daktulosphaira vitifoliae* (Hemiptera: Phylloxeridae) on the leaf of *Vitis vinifera* by *V. labrusca* cv. Weiße Amerikaner (*Vitacea*). (A) The earliest recognizable response (3–6 h) to feeding by the immatures of *D. vitifoliae*. Dividing parenchyma cells (ϕ) are metaplastic, differentiating into nutritive cells with enlarged nuclei and numerous, small, scattered vacuoles. The adjacent parenchyma cells include polyphenolic materials (pp) distorted chloroplasts (chl). The “↑” points to the upper epidermis. (B) Cells not under the direct feeding impact lying adjacent to the fed cells include thin and hyaline cytoplasm, polyphenolic materials (pp) in the tonoplast; cell walls are thickened (arrow) with electron-dense material deposited at cell junctions (24–48 h). (C) Parenchyma cells adjoining nutritive cells with coagulated cytoplasm, highly fragmented endoplasmic reticular strands, and abundant polyphenolic materials (48–72 h) (scale bar = 10 μm). (Source: Raman, A., Beiderbeck, R., and Herth, W., 2009, *Botanica Helvetica*, 119: 31 — 39).
is unique among the known gall-inducing insect groups. Osmotic-change-related stress builds up when these specialist insects attack plant cells, which stimulates a train of events in the immediate environment of plant cells, including alterations in gas exchange and synthesis of growth promoters. Osmotic stress alters electrical properties of the plasma membrane and impacts on indole-acetic acid synthesis and activity, which, in turn, alters H^+-transport. Feeding action by the insect stimulates parts of host-cell wall to degenerate, and the degenerated wall materials in the cytoplasm usually act as elicitors. Gall-hosting plants employ varied strategies to neutralize the stress that arise subsequent to gall induction. Although the neutralizing strategies seem to be a part of the genetic constitution of plants, their responses are mediated by novel molecular changes, which vary with the kind of insect involved. In the context of gall induction, susceptible plants generally use a flexible, short-term strategy to respond to stress (Schultz et al. 2013). Inherited traits also play a role in providing a specific shape to the induced gall, coordinated by the innate correlating morphogenetic factors that operate normally in the plant. The sequence of steps in the process of induction of a gall is summarized in Fig. 2.

A general model of gall development involves newly initiated and activated features (steps) that can be seen as follows: 1) induction, 2) growth involving cell enlargement, cell division, and special tissue differentiation, and 3) aging and senescence. Each of these steps is distinct in its physiology, although the steps tend to overlap. Several papers have explored the role of plant-growth regulators, such as auxins and cytokinins, which explain the second step, viz., growth. Artificial injection of auxins produces gall-like structures (Schäffer 1968). Several experiments have indicated the role of auxin precursors in the inducing insects (see Hori 1992). Use of instrumentation, such as gas chromatography–mass spectrometry lately, has offered clear and definitive incidence of auxin material in inducing insects (Tooker and De Moraes 2011). These details clarify that the inducing inhabitants of galls (the larvae) are a source of auxins. Toward this end, Yamaguchi et al.’s work (2012) on Pontania–Salix gall sheds significant light.

In brief, insect-induced galls are inimitable, controlled manifestations, when fully mature. Each gall type on a particular species of the plant is unique, because the inducing insect essentially controls its morphology, driving the inherent plant-growth mechanisms to differentiate and grow into a gall in specific patterns; however, what needs to be recognized here is that the galls induced by the same species appear nearly the same in terms of exomorphic features as opposed to galls induced by different species (Tokuda et al. 2008, Raman 2011a). Secondly, the incidence of an articulated tissue of nutrition, amply endowed with different minerals and other nutritious materials such as proteins, lipids, and sugars in cells adjacent to the feeding larva characterizes plant galls of insect origin (Bronner 1992). Third, the insects that induce galls are generally highly selective of and specific to certain plants, reiterating their monophagous behavior.

**Does a Defined Pattern of Specificity Occur?**

**Galls on Gymnosperms and Dicotyledons**

Close to 15,000 vascular plant species — ranging from Pinales (Pinophyta) to Angiosperms — throughout the world, are recorded as hosts of gall-inducing insects (Raman et al. 2005a, Espírito-Santo and Fernandes, 2007). Species of Fabaceae, Moraceae, Lauraceae, Combretaceae, and Anacardiaceae host the highest numbers of gall-inducing insects in the Indian subcontinent (Mani 2000, Raman 2007a), whereas Asteraceae, Euphorbiaceae, Fagaceae, Pinaceae, Rosaceae, and Salicaceae host high numbers in Europe (Houard 1908–1909, Buhr 1965) and North America (Felt 1940). Leaves are the most susceptible plant organs for gall development, although galls on shoot axes, roots, vegetative, and floral meristems too are known, but in less frequency (Dreger-Jauffret and Shorthouse 1992). The richness and specificity of gall-inducing insects can be understood from the following example. The Anacardiaceae of the Indian subcontinent hosts *circa* 50 gall-inducing species belonging to the Cecidomyiidae (Diptera) and Psylloidea (Hemiptera) (Raman et al. 2009b). *Holigarna arnotiana* Wall. ex Hook. f. and *Semecarpus anacardiun* Linn. (Semecarpeae), *Lannea coronandlica* (Hout.) Merr. and *Spondias pinnata* (Linn. f.) Kurz. (= *S. mangiferae*, Spondiadeae), *Buchanania lanzan* Spreng. (Anacardieae), *Pistacio khinjuk* Stocks, and *Rhus semialata* Murray (Rhoeae) host one species of either the Cecidomyiidae or the Psyllioidea. The populous *Mangifera indica* Linn. with its wide range of subspecies and cultivated varieties alone hosts 24 species of Cecidomyiidae (11 of *Procontarinia*, one each of *Lasioptera* and *Dasineura*, two of *Gephyraulus*, one of *Oligostrophus*, and eight unnamed *Cecidomyiidae*) in addition to four species of *Psyllioidea* (one of *Apsylla* (Aphalaridae) and three of *Calophya* (Calophyidae)), which induce galls of characteristic morphologies. It is predicted that because of the effective utilization of *M. indica*, which is available abundantly throughout the extensive landscape of the Indian subcontinent, within a single host–plant taxon, speciation in the *Procontarinia* complex has progressed impressively. A striking phenomenon apparent in the gall-inducing behavior of

**Fig. 2. Schematic sequence of events in gall induction.**
the Cecidomyiidae and Psyllioidea living on *M. indica* is the absence of radiation from leaves either to other organs of *M. indica* or to other Anacardiaceae. This absence suggests that neither the feeding behavior nor the larval salivary physiology of these species (e.g., *Procontarinia*) has changed over time. The reason for such a conservative behavior could either be the lack of resistance-breaking genes in the *M. indica*-associated gall-inducing Cecidomyiidae and Psyllioidea or the abundance of populations of *M. indica* with fresh foliage available almost throughout the year. A provisional reconstruction of the relationships among the extant *M. indica*-infesting gall-inducing Cecidomyiidae reveals that an extremely modest level of radiation in the leaf-gall-inducing species has occurred from those species that induce structurally simple galls to those that induce structurally complex galls (see Figs. 3–8 in Raman et al. 2009b). Because *M. indica* is an evergreen, polyaxial species, with new leaf flushes available almost throughout the year, and thus offering an uninterrupted nutrition, the radiation and diversification of the Cecidomyiidae could have been confined to *M. indica*. In addition, the diverse, geographically localized varieties of *M. indica* with different types of secondary chemicals (e.g., xanthones and flavanols) may also impose a selection pressure on the radiation of the Cecidomyiidae; for instance, mangiferin, the principal secondary xanthoneoid in *M. indica*, possibly acts as an attractant to the Cecidomyiidae and *Apsylla cistellata* and has, consequently, restricted their diversification. The *M. indica*-infesting Cecidomyiidae may have progressed conservatively specializing along the host–plant lines, because of the need for precise timing and for minimizing competitive interactions with other parasitic, predatory, and inquilinous arthropods, from the time of original host colonization.

**Galls on Fungi, Grasses, and Lichens**

Abnormal plant structures, casually indicated as galls, have been reported on some macrofungi (Basidiomycota). Interest in “galls” on macrofungi was intense in the early decades of the 1900s (Thomas 1924). Compared with the numbers of gall-inducing insects living on dicotyledons, those that occur on nonvascular plants, fungi, and monocotyledons are few and far between. *Mycocecis ovalis* Edwards (Diptera: Cecidomyiidae) is indicated to induce tiny, blackish, blister-like swellings on the stroma of *Tomentella ferruginea* (Pers.) Pat. (Basidiomycota: Agaricomycetes: Thelephoraceae) (Edwards 1922). The thickened hyphal mat on the stroma of *T. ferruginea* arising due to *M. ovalis* attack is labeled as gall tissue and the “swellings” on the stroma as silk-fiber canopies from larval secretions (Evans 1970). Conspicuous, irregular growths on the stroma of *Peniophora cinerea* (Pers.) Cooke (Basidiomycota: Agaricomycetes: Peniophoraceae) induced by *Brachyneurina peniophorae* Harris (Diptera: Cecidomyiidae) (Harris and Evans 1979) and growths on *Ganoderma planatum* (Pers.) Pat. (Basidiomycota: Polyporales: Ganodermataceae) induced by *Agathomyia wankouwiczi* (Schnabl.) (Diptera: Platyzinidae) (Ševěk 2006) are indicated as galls. Spooner (2010) provides a summary of the supposed galls on different Agaricomycetes induced by Cecidomyiidae. Pertinent it would be to recall here that circa 30% of the known Cecidomyiidae are mycophagous (Skuharová et al. 1984). Within this guild, species belonging to the Lestreminae, Asphondylinae, and Porricordylinae are mycophagous, although they are also associated with gall induction. The galls induced by the taxa belonging to these subfamilies are generically referred to as “ambrosia galls” (Batra and Lichtwardt 1963, Rohfritsch 2008). Among the lower-vascular plants, notes on “galls” arising on the fronds of an unidentified Filicophyta by a species of Thripidae (determined as a species of *Physothrips* by Docters van Leeuwen 1938) and *Athyrium filix-femina* (Linn.) Roth (Pteridophyta: Filicinaceae) by *Craspedochaeta* (Anthomyiidae) *sig-nata* (Brischke) (Diptera: Anthomyiidae) (Thomas 1924) are available. The “galls” on the fronds of *Elaphoglossum moranii* Mickel (Pteridophyta: Lomariopsidaceae) induced by *Jersonithrips gal-ligenus* Retana-Salazar & Nishida (Tubulifera: Phlaeothripidae) in Costa Rica is known (Retana-Salazar and Nishida 2007).

Catalogues of insect-induced plant galls (Trotter and Cecconi 1902, Houard 1908–1909, Docters van Leeuwen–Reijnvaan and Docters van Leeuwen 1926, Felt 1940, Mani 2000, Gagné and Jaschhof 2014) suggest that circa 90% of them occur on dicotyledons, a handful on monocotyledons, and still fewer on Poaceae. A remarkable example of a “gall” on Poaceae is that, referred as “silver shoot”, induced by *Orseolia oryzae* Wood-Mason (Diptera: Cecidomyiidae) in South Asia (Gagné 2004) (Fig. 3) and *Orseolia oryzae* Harris & Gagné in Africa (Harris and Gagné 1982) on *O. sativa* and *Oryza barthi* A. Chev. (Poaceae), respectively (Raman 2011b). *O. oryzae* in South-east and South Asia has received considerable attention in the last few years, principally because of its damage potential to highly important *O. sativa* (Poaceae) (Krishnaiah 2004, Rajamani et al. 2004). Extensive studies are currently ongoing in determining various dimensions of resistance and susceptibility of different varieties of *O. sativa* and identified biotypes of *O. oryzae* using molecular markers. In many of the tested varieties of *O. sativa* in India, resistance is controlled by a single dominant gene, whereas...
infestation by “O. oryzae biotype 4” on O. sativa var. Phalguni is infrequent, because of the “Gm2” gene, which is inherited as a single recessive gene resisting the Cecidomyiidae (Bentur et al. 2004). In O. sativa var., Phalguni’s resistance to “O. oryzae biotype 4” is inducible by prior infestation using an avirulent biotype (Bentur et al. 2004). At least four species of the Cecidomyiidae induce galls on Phragmites australis (Cav.) Trin. ex Steud. (= P. communis) (Poaceae) in Central Europe (Skuhravá and Skuhravý 1992). A few Northern-European Chloropidae (Diptera) induce galls on species of Poaceae (e.g., Lipara lucens Meig (P. australis) (De Bruyn 2005).

The galls on P. australis induced by Girandula inclusa Frauenfeld (Diptera: Cecidomyiidae) (Rohfritsch 1975) present unique structural details, which differ strongly from the developmental patterns known in the best-explained gall systems (Rohfritsch 1992). In such a context, the questions “why galls on monocotyledons are so few?” and “are those indicated as galls on monocotyledons are true galls?” need close scrutiny and resolution, because, for example, O. oryzae is not specific to O. oryzae only, but induces galls similar to those on O. sativa on Paspalum genninum (Forssk.) Stapt., Paspalum flavidum (Retz.) A. Camus, and Cyperdon dactylon (Linn.) Pers. as well in India (Sain and Kalode 2004).

Established examples of gall-inducing Cecidomyiidae (Diptera), Sternorrhyncha (Hemiptera), and Hymenoptera (Raman et al. 2005a) demonstrate that these are highly selective of plants. Galls are structures that develop on plants displaying well-defined tissue organization in response to either feeding as in the Tubulifera (Thysanoptera), Sternorrhyncha, and Cecidomyiidae or oviposition as in the Cynipidae (see Figs. 21 and 22 in Raman 2011a) and the Eulophidae and Braconidae. However, the usual use of the term “gall” to plant abnormalities induced by nematodes, fungi, and bacteria needs thorough scrutiny. Similarly, the purported galls on monocotyledons, and on grasses in particular, also require re-appraisal.

Selection of the Host Plant

Selection of Optimal Host–Plant Species

From the knowledge accrued thus far (Trotter and Cecconi 1902, Felt 1940, Mani 2000, Gagné and Jaschoff 2014), we can say with some confidence, that the gall-inducing insects, unlike many of their free-living relatives, discriminate between and select specific plants. Selection of a particular plant by a gall-inducing insect is not a matter of chance, given that the insect encounters diverse plant taxa in a natural, heterogeneous environment. What needs to be factored here is that the gall-inducing insects preferentially feed on specific plant organs, or parts of, and of specific plant species. Because of the sedentary nature of the juvenile stages of gall-inducing insects, most vitally, the gravid females play a key role in selecting the potential plant site precisely for oviposition (Raman 1991, Hilker et al. 2008). A striking trait among gall-inducing insects is their ability to select the “right” plants and more especially “right” sites for oviposition. The earliest, definitive remark on the tightness of relationships between gall-inducing insects and plants, implying a strong level of fidelity of gall-inducing insects, came from Edvard Sylven (1979) of the Swedish Museum of Natural History, who articulated this point drawing from various Cecidomyiidae. Sylven, based on distinct morphological traits of the gall-inducing Cecidomyiidae and the hosting plant taxa, remarks (page 62): “Evidently many gall midge species show a high degree of host specificity and might therefore be considered as strongly specialized plant taxonomists”.

As is true of some free-living plant-feeding insects, species choice by gall-inducing insects is an active process. We are imperfectly able to explain how these specialist insects precisely select plants from a wide range of plants available to them. In high probability, the insects respond to biotic factors such as plant chemistry, which, in turn, are influenced by various abiotic factors such as temperature and relative humidity. The manner in which Daphnephila (Diptera: Cecidomyiidae) remains tied to species of Machilus (Laureae) in Taiwan (Tokuda et al. 2008) and a majority of the Cynipoidea remains tied to specific species of Quercus (Fagaceae) in Europe (Cióka et al. 2005) offer insights into this question. Host–plant relationships of several gall-inducing Cynipoidea interacting with different species of Quercus in North America show a strong level of fidelity of the Cynipoidea to specific species of Quercus (Abrahamson et al. 2003). When leaf tissues of the chosen plants were tested for levels of condensed and hydrolyzable tannins, total phenols, lignin, cellulose, hemicellulose, nitrogen, and carbon, every tested species of Quercus included varying levels of these compounds, except carbon. The highly specific associations between plant chemistry and the Cynipidae in question are critical for host-plant selection by the gravid female and for larval performance. Evaluating the quantity and quality of total nonstructural carbohydrates (TNC), δ13C and δ15N isotope ratios, amino acids, and fatty acids in the leaves of Eucalyptus macrocarphoca M. F. M. ex Benth. (Myrtaceae) infested by an unnamed species of gall-inducing Glycaspis (Synglycaspis), Sharma et al. (2015b) have shown that the TNC levels were high in the Glycaspis (Synglycaspis)-infested leaves of E. macrocarphoca. Total mass of amino acids and fatty acids was the lowest in galling E. macrocarphoca leaves, although the δ13C values were high, whereas the δ15N values were not significantly different in infested and uninfested leaves.

Selection of Optimal Plant Organs and Tissues

Physical characteristics of the plant (e.g., phyllotaxy and growth pattern) are equally vital in plant selection by gall-inducing insects. Plant phenology and quality (also referred as plant vigor) are essential factors in plant selection (How et al. 1993). Plant chemistry is yet another critical factor. Evaluating gall induction by Taxomya taxi (Inchb.) (Diptera: Cecidomyiidae) on the vegetative buds of Taxus baccata Linn. (Pinales: Taxaceae), Lovett (1980–1981) elucidated the timing of the synthesis of steroids (e.g., ponasterone–A and ecysterone and, alternatively, a ∆[5,7] bond in their nuclei) by T. baccata, which correlated positively with the infestation periods of T. taxi. The other equally fascinating but unexplained question is how some of these gall-inducing insects have evolved to live and feed on specific plants, which are known for their strong anti-insect compounds: for example, Diaphorina truncata C. (Hemiptera: Psyllidae) feed, survive, and perpetuate their progeny in the roll galls they induce on the leaves of Strychnos nux-vomica Linn. (Loganiaceae), which abundantly include aggressive secondary-metabolic compounds, such as strychnine (Balakrishna and Raman 1992).

Sensory Mechanisms Involved in the Selection of Plant Part

The other unique trait of these specialist insects is site selection. For example, Asphondylia pongamiae Felt and Bruggmannia byroni– maia Maia & Couri (Diptera: Cecidomyiidae) induce galls in the flowers of Milletia pinnata (Linn.) Panigrahi (Fabaceae) (Felt 1921) and Byrsamina sericea DC. (Malpighiaceae) (Guimarães et al. 2014), respectively. Evidences are currently forthcoming indicating that olfaction plays a more definite role than any other sensory perception among gall-inducing insects. The range of sensilla that
exist on the early, immature stages of gall-inducing Psylloidea reinforces the vitality of olfaction. In the unnamed species of Glycaspis (Synglycaspis), which induces pouched galls on the leaves of E. macrorhyncha, a range of sensilla on both gravid females and first-stage immatures occur (Sharma et al. 2015a). In this instance, the adult females of Glycaspis (Synglycaspis) selectively oviposit on the young foliage of E. macrorhyncha, although other related species of Eucalyptus, such as Eucalyptus dives and Eucalyptus rossi are available plentifully in close proximity (circa <5 m radius). Galls arise on the leaves of E. macrorhyncha by the feeding action of the neonate instars of Glycaspis (Synglycaspis) sp. Adult females of this species of Glycaspis (Synglycaspis) bear long filiform sensilla, each of which includes eight flagellomeres, a scape, and a pedicel. The terminal segment of the antenna of adult females includes a pair of 12-μm- and 85-μm-long unequal terminal setae, and they bear ~23-μm-long trichoid sensilla distributed all over and a rhinaria on each flagellar segment 2, 4, 6, and 7 in subapical positions. The adult-female terminalia are densely sculpted with several scale-like spinules, each endowed with a ~180 μm and ~6 μm long spines. The rhinaria occurring near the apices of flagellomeres on the antennae of adult Glycaspis (Synglycaspis) serve as chemoreceptors in selecting E. macrorhyncha precisely in a heterogeneous natural environment. The terminal segment of the antenna of the first-stage immatures of Glycaspis (Synglycaspis) includes two unequal terminal setae. Trichoid sensilla occur close to the apex of each segment. In the immatures, the apical antennal bristles are unequal, which too serve the instar in olfactory function. The four pairs of sensilla at the labial tips of immatures and adults of Glycaspis (Synglycaspis) enable plant-surface exploration and discrimination.

**Exemplary Dispersal Mechanisms in Gall-Inducing Insects and Their Adaptive Significance**

Although dispersal in gall-inducing insects normally involves either the adult or early juvenile stages, occasionally the gall itself disperses, thus enabling movement of the included insect over a distance. Neuroterus saltatorius Edwards (Cynipoidea: Cynipidae) induces two distinct generations of galls on Quercus (Fagaceae) in western North America, alternating between a sessile, spring generation and a summer generation of galls that separate from leaves before dropping to ground, where they “jump” for certain number of days (Rosenthal and Koehler 1971). The jumping behavior results from high-efficiency energy conversion by the larva within the gall, which generates the kinetic energy enabling the gall to jump through a transfer of fluid momentum in the larval body. This dispersal allows the larvae of N. saltatorius to seek spaces within leaf litter in which they can “safely” complete their growth and development remaining in the gall (Manier and Deamer 2014, Prior and Hulcr 2016); however, what needs to be noted is that a high proportion of these larvae usually are parasitized (Russo 2006). Many galls induced by the Cynipidae are known to dehisce from their host plants, but N. saltatorius is one of the few, which augments dispersal through jumping movements of galls, when separated from its host. Another equally fascinating example is the gall induced by Didymomyia tiliae (Bremi (= Oligostrophus réamurianus)) (Diptera: Cecidomyiidae) on the leaves of Tilia × europaea Linn. (= Tilia cordata [Malvaceae]) in Western Europe. The fully mature gall will separate itself and lift from the leaf as such, because of changes in atmospheric humidity, which influence metabolic changes in the gall and in the supporting leaf. Due to locked-up air within the gall, it drifts with the wind for some distance horizontally and then land on the soil thus enabling dispersal of the inhabiting D. tiliae (Rohfritsch 1967). For elegant photographs of this material, see http://www.bladmineerders.nl/gal-len/diptera/didymomyia/tiliae/tiliae.htm created and managed by Willem N. Ellis. Other unusual examples of mobile galls include a Curculionidae (Coleoptera)-induced “jumping” gall and a “portable” gall carried by a Tortricidae (Lepidoptera) (Dreger-Jauffret and Shorthouse 1992). The inducing insect need not always occupy the gall. For example, the foudresses of diverse species of Eriosoma (Aphidoidea: Aphididae: Eriosomatinae) on Ubnus (Ullmaceae) (Akimoto 1989) and Adelgidae (Aphidoidea) (Rohfritsch 1990, Sopow et al. 2003) on different Pinaceae initiate galls at some distance away from the site where they feed. A similar, but subtly different behavior occurs in the galls induced on the shoot meristems of M. indica (Anacardiaceae) by A. cistellata Buckton (Psylloidea: Aphalaridae), wherein the gall foundress induces the gall to develop by transforming a shoot bud, at least 1–2 cm away from her location on the adjacent leaf blade. The neonate foundress of A. cistellata crawls to occupy the spaces in the newly modified bud, which grows into a gall; thereafter, the
foundress never moves from her original site (Raman et al. 2009b, 
Raman 2016). It is curious that similar behaviors manifest in two
different insect groups, viz., Aphidoidea and Psyllidoidea. Just as
gall inducers do not necessarily occupy the gall, not all occupants
are necessarily capable of stimulating growth of galls. Among the
gall-inducing Aphidoidea, a colony usually consists of a single geno-
type in which a clonal division of labor exists (Dixon 1998). The
gall-inducing foundress alone is capable of gall induction, whereas
her clonal offspring are adapted to feed and develop within the gall
before exiting to effect dispersal of the clonal genotype to newer
sites on susceptible plants outside the natal gall. Although a gall-
inducing female and her offspring would appear to represent a single
clonal genotype, the integrity of the aphid clone could be compromis-
ied through inter-gall migration of aphids between galls. Thus,
the nutritional benefits otherwise accruing to a single genotype may
in fact be exploited by alien invaders of the gall (Abbot et al. 2001,
Miller, unpublished data, Table 1). Identical behavior occurs among
gall-inducing Eriophyoidae (Arachnida: Acari) (Oldfield 2005) and
Phlaeothripidae (Thysanoptera: Tubulifera) (Ananthakrishnan and

Origins of Gall Induction, Host–Plant Shifts,
and Adaptive Radiation

Historical Plant Interactions With Gall-inducing Insects
and the Messages They Relay

Kuster (1930) suggested that gall-inducing insects have evolved
to induce galls for the sole purpose of deriving the best nutrition,
wheras evolutionary ecologists, such as Price et al. (1987) reiter-
ate that the benefits of gall induction extend beyond obtaining
nutrition. de Ponti (1982) indicated that at some point of histori-
tical time, insects indiscriminately fed on plants, since plants lacked
appropriate defenses; some of those plants attacked by insects,
with the passage of time, acquired the capacity to “resist” insect-
feeding pressure through the evolution of novel metabolic pathways
and thus building new, chemical-defense capacities. Gall-inducing
habit has evolved independently in various groups of insects (Gagné
1984). Evidences of leaf-mining habit are available in certain groups
of plant-feeding insects (e.g., Agromyzidae, Diptera) from the Eocene (Dempewolf 2005). Dempewolf (2005) suggests that the
Agromyzidae larvae preferred confined plant sites from the Upper
Cretaceous — the period when flowering plants were diversifying
and establishing. Progressive integration of the capacity of insects
to exploit plants, and their level of either resistance or susceptibility has
to have evolved into gall-inducing habit (Scott et al. 1994). This
explanation impresses as a strong possibility, when we superimpose
monophagous plant-selection behavior and evolution of multiple
adaptive strategies in extant insects (Roskam 1992, 2005). Fossil
evidences from the Tertiary support this proposition (Mohn 1960,
Gagné 1968). However, the Cecidomyiidae possibly arose during the
Oligocene-Eocene epochs (Skuhrová 2006). The discovery of
Holometabola-induced galls on the fronds of Psaronius (Filicopsida:
Marattiales) from the Carboniferous (Labandeira and Phillips 1996)
continually challenges the premise that gall-inducing strategy originated
concurrently with the diversification of angiosperms (Labandeira
galls, especially on the leaves of seed plants, were not only diverse,
but also abundant in the Permian. Because the presence of insects
is deemed a critical prerequisite in gall induction (Schafer 2005),
Schachat and Labandeira (2015) suggest that in insects of the small-
body size, hemipteroid lineages, such as the extinct Protopsylidiidae
(Hemiptera) and Lophionureidae (Thripida), gall-inducing habit
originated in the Permian. Plant damage, insect-body fossils, and the
paleoclimate record collectively support the ecological expansion of
gall induction particularly in leaves of seed plants from the Early
through to the late Permian.

Although a majority of gall-inducing insects are restricted
to specific plant species (Abrahamson et al. 1998, Raman et al.
2005a), some of them have been reported to be capable of induc-
galls on plant species closely related to their best-preferred hosts
(Raman 1996, 2007a; Gagné 2004). Some of the Cecidomyiidae are
shown to be narrowly oligophagous (e.g., gall-inducing Propodispos
longifila Gagné living on Jatropha gossypiifolia Linn., Jatropha excisa Griseb., Jatropha clavuligera Müll. Arg., and Jatropha curas
Linn. [Euphorbiaceae] in Peru, Bolivia, and Paraguay; Gagné
2004, Dhileepan et al. 2017). A few species of Asphondyliina and
Schizomyiina are presently indicated as polyphagous (Uchci et al.
between species in the gall-inducing Tephritidae populations of
North America and Europe have been explained by the evolution of
symptomatic host races — more due to changes either in the prefer-
ence in feeding and oviposition sites or by acquiring “new” physiologi-
cal adaptations to new host plants or through assortative mating
(Abrahamson and Weis 1997, Korneyev et al. 2005). Differences in
the temporally regulated flowering and leafing phenologies in sus-
ceptible plants possibly play a role in isolating gall-inducing insect
populations, thus enabling divergence and diversification via genetic
drift (Stone et al. 2002). The general understanding, as of now, is
that host shifts and radiation in gall-inducing insects are more com-
plex than what is known in free-living insects. Such complexity is
attributed to 1) complex relationships of gall-inducing insects with
host plants and 2) the dispersal of gall-inducing insects through differ-
ent biogeographical realms, mainly influenced by the abundance and
variety of plant species.

In the Tenthredinidae (Hymenoptera), sibling species live on
sibling plant species: many of them induce galls on various spe-
cies of Salix (Salicaceae) and a few on different species of Populus
(Salicaceae) in Europe (Kopelke 1999). Gall-inducing habit in the
Tenthredinidae originated from the free-living Nematinae,
first evolving into those that could either fold or roll leaves (e.g.,
Phyllocolpa), subsequently into species that induced galls on leaves
(e.g., Pontana), and finally into species that induced galls on stems

Table 1. Results of 70 trials in which Tamalia aphids were marked with tracking powder to trace movement between galls

<table>
<thead>
<tr>
<th>Distance from natal gall to recipient gall (cm)</th>
<th>1–10</th>
<th>11–20</th>
<th>21–30</th>
<th>31–40</th>
<th>41–50</th>
</tr>
</thead>
<tbody>
<tr>
<td>Galls inspected</td>
<td>152</td>
<td>54</td>
<td>46</td>
<td>34</td>
<td>27</td>
</tr>
<tr>
<td>Number with marked animals</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

*With a laboratory pipettor about 100 µl of fluorescent insect-tracking powder were injected into a gall designated the “natal gall”. After monitoring for 1–2 wk, the natal gall and all of the neighboring galls on the same branch tip of Arctostaphylos viscosa (Ericaceae) (“recipient galls”) within 0.5-m walking distance were collected and contents examined under an ultraviolet lamp. Minimum walking distance was estimated (to the nearest 1 cm) between natal galls and all recipient galls. Mean distance of dispersal was 3.3 cm (± 2.8 cm SD); none of the marked animals was recovered at a distance greater than 10 cm.*
(e.g., Eunora) (Nyman et al. 2000). These Tenthredinidae taxa living on different species of Salix indicate that the newly diversified Tenthredinidae genera invade new adaptive zones, possibly exploring new diets. At least some species of large genera of gall-inducing insects are capable of colonizing diverse plant species and invading new plant organs, indicating shifts into varied ecological niches and adaptive zones (Price 1996, 2005; Miller 2005; Roininen et al. 2005). The Nematanthidae are implicated to have undergone host shifts between unrelated species of Salix (Nyman et al. 2000, 2006), in contrast to the strong patterns of gall-inducing insect–plant co-evolution demonstrated in Ficus–Agaoniidae (Ronsted et al. 2005) and Thysanoptera–Acacia (McLeish et al. 2007a) interactions: insect spread being mediated by the abundance and richness of plant species.

Host–Plant Specific Radiation

The Beesoniidae (Coccoidea) that include taxa with uncommon behaviors illustrate how the abundance and variety of host–plant species in different biogeographical regions can influence radiation. Among the described species of Beesoniidae, Beesonia dip- terocarpi Green and Beesonia shoreae Takagi are associated with Diptercarpus tuberculatus Roxb and Shorea curtisi Dyer, ex King (both Dipterocarpaceae), respectively, in tropical Asia (Myanmar [Burma] and Singapore), whereas Beesonia napiformis (Kuwana) and Beesonia brevipes Takagi are always associated with various species of Quercus, Castanopsis, Lithocarpus (Fagaceae) in temperate Asia (China, Japan, and higher elevations of Nepal). The Fagaceae-associated B. napiformis and B. brevipes occur as free-living, non-gall-inducing taxa. Other species of tropical Beesoniidae, viz., Gallacoccus secundus Beardsley, Gallacoccus anthonyae Beardsley, Gallacoccus spinigallula Takagi, Gallacoccus heckrothii Takagi, Gallacoccus longisetosus Takagi, Hosaka, & Okuda, Mangalore hopeae Takagi, Echinogala pastulata Takagi, and Danumococcus parashoreae Takagi & Hodgson are associated with particular species of Hopea, Shorea, and Parashorea (Diptercarpaceae) in tropical southern and south-eastern Asia (Takagi 1987, 1995, 2001; Gullan et al. 2005). Based on the predominant disposition of the Beesoniidae to Dipterocarpaceae in tropical Asia, Takagi (2007) proposes that the Beesoniidae have primarily evolved with Dipterocarpaceae in the tropics and their association with temperate Fagaceae is a secondary trait, consequent to their diversification from tropical Asia into temperate eastern Asia. Beesoniidae diversification seems to be strongly influenced by the richness of species in Dipterocarpaceae (circa 650 species under 17 genera) in tropical Asia and Fagaceae (circa 900 species in eight genera throughout the world, and nearly 700 species in temperate Asia) in temperate Asia, similar to the pattern of diversification of Eriococcidae (Hemiptera: Coccoidea) on the Eucalyptus bon (measured as $\delta^{13}C$, nitrogen measured as $\delta^{15}N$), and the TNC signatures presented significantly different values, when assayed through the development of galls induced by Epiblema strenuana (Walker) (Lepidoptera: Tortricidae) on the shoots of Parthenium hysterophorus Linn. (Asteraeaceae) (Raman et al. 2006). The $\delta^{13}C$ values in galls were consistently more negative than those from the plant parts above the gall. The $\delta^{15}N$ values in galls, on the contrary, were either similar or less negative than those from the plant parts above the gall. TNC levels varied within the compared plant populations. Overall, the stem distal to the gall functioned more efficiently as a nodal channel than the stem proximal to the gall, especially in the translocation of nitrogenous nutrient materials. In Mayetiola destructor (Say) (Diptera: Coccidomyiidae) interactions with Triticum (Poaceae), the genes coding for virulence in M. destructor operate on a gene-for-gene basis with those for resistance in Triticum, presenting a strong evidence for a coevolutionary “arms race” between M. destructor and Triticum (Rausher 2001, Zantoko and Shukle 1997, Nicholls et al. 2018).
Benefits to Plant From Gall Induction

In some instances, nevertheless, gall-inducing insects benefit the plant in terms of pollination. The North-American *Tegeticula* (Lepidoptera: Prodoxidae) adult females collect pollen of *Yucca* (Agavaceae) into a ball and carry them to another blossom before depositing them there, thus effecting intercrossing. The *Tegeticula* female also oviposits in the recipient flower, initiating a gall in the process. The emerging larvae feed on the newly developing gall tissue within the flower (Pellmyr 2003, Powell and Opler 2009). Among the Agaonidae (Hymenoptera), the alate females complete their development within the complex syconium of *Ficus* (Moraceae), mate with the wingless males, and emerge through the exit hole, picking up pollen in the process. These females then disperse aerially to another syconium and enter it, effecting cross-pollination. There they oviposit into newly developing tissue, initiating galls, which may be augmented by the hatching larvae (Kjellberg et al. 2005, Borges 2013). These examples illustrate secondary mutualisms, as phylogenetic evidence suggests they have evolved from an ancestral state of parasitism (Godfray 1994, Cook and Rasplus 2003). We may go further and refer to such mutualisms as reciprocal exploitation, since both the plant and the gall-inducing insect appear to have reached an evolutionary steady state, although subject to breakdown at any time, as evidenced in the “hugus” Prodoxidae (Riley 1880, Pellmyr 2003) and nonpollinating Agaonidae (Cardona et al. 2013, Jandér and Steidinger 2017).

Commensalism implies interspecific interactions in which one party benefits without either harming or aiding the other (van Beneden 1876). Commensalism can arise as a result of “attenuated antagonism” (Thompson 2005), in which selective pressures on plant parasites gradually favor reduced fitness costs to the host plant, such that gall-inducing insects only rarely inflict significant harm to plants. Nevertheless, we need to recognize that a modest level of metabolic changes will occur consequent to invasion by foreign organism, viz., the insect (Raman 2011b). Therefore, these could be regarded as commensals, rather than damaging parasites, although this is of limited use in enabling our understanding of the relations of gall-inducing insects and their host plants. Other than this, galls attract a few other unrelated organisms, which neither contribute to the gall induction and development nor inflict any damage to the gall (e.g., Synerginae associated with several galls induced by the Cynipidae in North America; Buss 2008) referred to as inquilines, which are clear-cut commensals in insect-gall systems, since they stand to gain in terms of shelter and much literature exists on this subject (Sanver and Hawkins 2000).

Synthesis

Distribution of Gall-Inducing Insects

It would be pertinent to summarize the present knowledge on the distribution of gall-inducing insects. The first *proviso*, however, would be that galls arise on unrelated plants of unrelated families induced by unrelated insect groups distributed in disjointed regions (Raman 2007b). Gall-inducing Tubulifera are confined to the tropics (Ananthakrishnan and Raman 1989), whereas the Cynipoidea are to the Holarctic (Askew 1984). The gall-inducing Coccoidea occur chiefly in the subtropical and tropical regions of the world (Beardsley 1984, Gullan 1984). The gall-inducing Cecidomyiidae occur all over the world, except the Alpine and polar regions (Gagné 1989, Skuhrává and Skuhrává 1998). No striking pattern in the broad distribution of these specialist insects is apparent, although some patterns have been shown at local scales in recent years (see Giertych et al. 2013). Subtle differences in insect behavior and levels of plant susceptibility are the implied factors in regulating the distribution of these specialist insects (Felt 1940). Gall richness, nonetheless, manifests in specific bioregions. For example, Australia includes a rich dose of gall-inducing Chalcidoidea (Hymenoptera) and Coccoidea, and to a lesser degree, the gall-inducing Psyllioidea and Thysanoptera, whereas the Aphidoidea (Hemiptera) and Tenthrindinidae (Hymenoptera) are almost unrepresented (Blanche 2012). About 40 species of *Apionomorpha* (Hemiptera: Coccoidea) known today occur confined to Australia and Papua New Guinea. Of these, 28 live only on species of *Eucalyptus* subgenus *Symphyomyrtus*, 12 on species of *Eucalyptus* subgenus *Eucalyptus*, and two on species of *Eucalyptus* subgenus *Eudesmia* (Mills et al. 2016). The gall-inducing Aphidoidea, Tenthrindinidae, and Cynipoidea are distinctly absent in warm and humid peninsular India (Raman 2007a), whereas the Aphidoidea and Cynipoidea occur in reasonable numbers in the temperate Himalaya (Mani 2000). To take another example, similar temperature regimes and rainfall patterns in south-eastern Australia and the distribution of the species of *Eucalyptus* subgenus *Eucalyptus* are the potential regulatory factors in confining the gall-inducing taxa of *Glycaspis* (*Syngycaspis*) to south-eastern Australia. The restriction of the gall-inducing species of *Glycaspis* (*Syngycaspis*) to the south-eastern segments of the Australia indicates that their evolution is tied with 1) the spread and diversification of *Eucalyptus* and 2) the physiognomy of temperate-closed forests that naturally constitute the forest biome of this region influenced by the specific geomorphology and climate, reinforcing the proposal advanced by Price et al. (1998) that temperate warm forests support maximal diversification of gall-inducing arthropods.

Evolutionary Aspects of Host-plant Selection by Gall-Inducing Insects

Evolutionary pressure between random search and choice of plants depends on the delicate balance between cost in time and energy spent in locating the potential host and the level of difficulty in detecting and processing information from plants (May and Ahmad 1983). Yet, it is still a matter of speculation how gall-inducing insects remain committed to particular plant species and how they are able to locate the preferred plant in a complex, natural environment. Moreover, these insects also display a high level of intimacy with the chosen plant, driven by their concealed (embedded) habit and compounded by the nutrition and shelter they derive.

The concealed stages of insects have few to no choices before them and these organisms have evolved to achieve the best outcomes in spite of such ecological and physiological restrictions. What is generalizable here is that the plant that offers the least resistance to the insect is armed with a battery of proteins, which obviously attract the insect. The — susceptible — plant responds suitably to the ovipositing female and the feeding juvenile stages of the inducing insect, because of its inherited protein machinery. For instance, Detoni et al. (2011) indicate elevated metabolic activity and especially a 1.5- to 4.5-fold greater protein concentration in the galls induced on *Bahinia brevipes* Vogel (Fabaceae) by *Schizomyia macrocapillata* Maia (Diptera: Cecidomyiidae) than in comparable tissues of *B. brevipes*. Detoni et al. (2011) further clarify that different tissues from susceptible and resistant plants showed distinct protein concentrations and protein fractionation showed specific polypeptides. They conclude that specific proteins are involved in the physiological processes that determine whether the plant shows either total or partial resistance to *S. macrocapillata* populations. The best adaptation in insect-induced galls, in summary, is the differentiation...
of the specialized tissue of nutrition (the nutritive tissue) (Bronner 1992, Diamond et al. 2008). Certain other plants, under exceptional conditions, become hosts because of the continuum of preferences that exists among the insects, with the rejected plants existing beyond a threshold of acceptability (Futuyma 1999).

The selection of a site to initiate a gall is necessarily constrained by the evolutionary history of association that links the insect with its particular plant taxon (Futuyma and Moreno 1988, Moran 1988). As a rule of thumb, gall-inducing insects are extreme specialists (Abrahamson et al. 1998, Shorthouse et al. 2005); a majority of these insects is restricted to a single species. Only occasional reports indicate them as occurring on two or more, but closely related species. This could be a consequence of the highly intricate trophic relationship between the insect and the plant (Lawton and Strong 1981, Thompson 1994). Even when the most appropriate, preferred plant is available, still a variety of factors bears on the precise selection of a site for gall induction, which results in differential herbivory (Mopper and Simberloff 1995). In particular, the host–plant health as well as spatial attributes within a population of neighboring host plants are key factors mediating site selection for gall induction.

Lipids in Host–plant Selection

The other prevailing question presently is whether the plant lipids (e.g., phospholipids, chloroplast-specific membrane glucolipids, and sterols) play a role in plant selection by the specialist gall-inducing insects. Differences in evolutionary pressures on insects in utilizing plant metabolites, especially lipids and sterols, influence them to behave as either a generalist or a specialist (Behmer and Nes 2003). The best examples among specialist plant-feeding insects are the gall-inducing insects. In insects, cholesterol is an essential requirement to reinforce cell-membrane integrity, to synthesize molting hormones (e.g., 20–OH ecdysone), and to regulate the genes controlling growth. The inadequacy of not being able to synthesize cholesterol without a steroid precursor (Douglas 2009), in high probability, directs their reliance on specific plants. More vitally, the plant-feeding insects lack the ability to introduce Δ5 bond into plant-derived sterols (Behmer and Grebenok 1998, Morgan and Moynihan 2000). Therefore, the gall-inducing insects rely on sterols with preexisting Δ5 or Δ7 bonds (e.g., spinasterol and ergosterol) for synthesizing the hormones necessary for their growth and development. The necessity of gall-inducing insects for sterols with Δ5 or Δ7 bonds, possibly, narrows their host–plant range, thus making them operate as high-fidelity organisms. This has been clarified in the E. macrorhyncha—Glycaspis (Synglycaspis) gall system from the central-western New South Wales (Australia) (Sharma et al. 2016). The levels of ergosterol (396.3 molecular weight, a Δ5 bond-including sterol) increase in gall tissues that include the early instars (second, third, and fourth) and decrease in gall tissues that include fifth stage instars of Glycaspis (Synglycaspis). Ergosterol is produced in E. macrorhyncha from the time of oviposition by the gravid females of Glycaspis (Synglycaspis) and commencement of feeding by the first-stage instars. Ergosterol contents build up through gall development and get utilized by the gall inhabitants. Impressively high levels of sterol 440.3 (which could not be determined due to paucity of information in the databases, and hence referred by its molecular weight) in young leaves of E. macrorhyncha, the leaf stage on which gall induction commences, and its significantly low levels in mature leaves point to the fact that 440.3 sterol is critical in the host choice by species of Glycaspis (Synglycaspis) (Fig. 4).

Hypotheses on Adaptive Value of Galls

The evolutionary mechanism of natural selection has, presumably, favored and maintained the capacity of cecidogenous insects to induce galls. This adaptive process involves several alternative hypotheses, none of them exclusive of the others. Three hypotheses consider the host–plant quality as a critical variable in influencing

Fig. 4. Sterols in young and mature uninfested and infested leaves of Eucalyptus macrorhyncha. The labeling Gall 1–Gall 5 represent the stage of the gall inhabited by developing instars of stages 1–5. The sterol 440.3 (an unnamed lanosterol analogue), predominant in young leaves of E. macrorhyncha, is the likely phytosterol that regulates the specificity of the gall-inducing Glycaspis (Synglycaspis). x-axis—molecular weights of sterols; y-axis—mole % of sterols. Vertical bar represents the SE value.

Plant-vigor Hypothesis
The plant-vigor hypothesis supports the notion that gall-site selection and reproductive success are a function of the susceptible plant’s health. The most vigorous, fast-growing plants, therefore, attract and bear, the greatest density of galls. Conversely, slow-growing and/or senescent plants support the lowest density of galls (Price 1991). The plant-stress hypothesis explains that those plants experiencing physiological stress, for instance, because of either poor-soil health or drought, or perhaps those plants already weakened by a microbe-induced disease or attack by other herbivores, are the most likely targets of gall-inducing insects (Mattson and Haack 1987, De Bruyn 1995). This hypothesis generates predictions precisely at odds with those generated by the plant-vigor hypothesis. Support for the plant-stress hypothesis has been equivocal, however, with evidence suggesting that plants experiencing intermediate levels of stress may support the highest populations of gall-inducing insects (McKinnon et al. 1999, Wool 2005). As indicated earlier in this review, the plant-apparency hypothesis proposes that the rate of infestation by herbivorous insects, including gall-inducing species, is a consequence of the facility with which the host plant is located by them (Rausher 1983, Strauss and Cacho 2013). Hence, individual plants more apparent in the landscape, either because of isolation or because of greater size, are more likely targeted by gall-inducing insects. Such an apparent may be especially important for the diverse array of minute gall-inducing species, such as the Aphidoidea and Cecidomyiidae, which are generally weak fliers, and therefore are heavily dependent on favorable air currents for dispersal to new plant sites (Gagné 1989, Dixon 1998).

The Nutrition Hypothesis
Under the nutrition hypothesis, selection of a plant for gall induction results in the most favorable conditions for the inducing insect: the most essential function of the gall, therefore, is provisioning of nutrients for the inducing insect (Kuster 1930). This takes the form of a source–sink relationship, in which plant assimilates are redirected toward the gall and its occupant. Feeding behaviors of the occupants of the gall (the inducing insect only as in the instances of the Cecidomyiidae and Cynipoidea; the inducing insect and her progeny as in the instances of Acarina, Phlaeothripidae, and many Sternorrhyncha) accelerate the accumulation of nutrients in gall tissues (Kirst and Rapp 1974). In the instance of galls induced by E. strenuana on the stems of P. hysterophorus, Raman et al. (2006) have clarified that the pumping of nutrients to gall site is essentially driven by the effort made by P. hysterophorus to heal the wound inflicted by E. strenuana; the ongoing feeding action of E. strenuana does not facilitate healing to occur; instead the inhabiting larval stages of E. strenuana utilize the nutrients for their benefit.

Evidence in support of the nutrition hypothesis for gall development has been shown in experiments in which host plants were manipulated with the addition of synthetic fertilizers. For example, Purdy and Miller (2013) treated Arctostaphylos (Ericaceae) that hosts populations of Tamalia coweni (Cockerell) (Aphidoidea: Aphididae) with nitrogen enrichments. The Tamalia clones within the galls responded to a gradient of nitrogen enrichment by skewing brood sex ratios increasingly toward females, a pattern consistent with the Trivers–Willard hypothesis for conditional sex allocation. Thus, clones of T. coweni responded adaptively by producing female offspring rather than males, reflecting investment in high-quality offspring under improved nutritional conditions. Manipulation of host–plant quality by insects occurs in populations of Sorbhis chaetosipho Shaposnikov (Aphidoidea: Aphididae), whose galls on Sorbus (Rosaceae) accumulate high concentrations of amino acids (Koyama et al. 2004). Alternatively, gall-inducing insects may manipulate host plants by decreasing levels of defense compounds, such as tannins in Quercus (Fagaceae). For example, gall induction by a species of Trigonaspis (Cynipoidea: Cynipidae) on Quercus crispula Blume and Quercus serrata Murray (Fagaceae) lowers tannin levels in inner gall tissues from which the Trigonaspis larvae feed, whereas their levels remain high in outer gall tissues and ungalled leaves (Ikai and Hijii 2007). Nonetheless, increased nutrient levels in plant tissues especially that of nitrogen is not necessarily beneficial to the inducing insect (Hartley and Lawton 1992), whose performance is potentially an adaptation to the gall environment. Using an innovative approach to avoid any confounding effects of superior nutrition and adaptation of herbivores to the gall, Diamond et al. (2008) transferred the larvae of nongall-inducing Hellinsia glenni (Cashatt) (Lepidoptera: Pterophoridae) into galls induced by the Eurosta solidaginis (Diptera: Tephritidae), which also utilizes the same host plant, S. gigantea (Asteraceae). In its novel environment, H. glenni gained greater mass than it did in its normal feeding environment in the stem, offering further support for the nutrition hypothesis.

The Preference–Performance Hypothesis
An insect-induced gall may be regarded as an extension of the insect phenotype, arising as an outcome of intricate interaction between insect and plant genotypes (Dawkins 1982, Nyman et al. 2000). As a phenotype, the gall may be acted upon by natural selection, potentially yielding local-fitness optima under either stabilizing or divergent selective regimes (Arnold et al. 2001). In an inclusive sense, insect-induced galls may also be considered a form of parental care, as they are critically important for the development of the juveniles within (Clutton-Brock 1991, Danks 2002). This applies especially when the gravid female, as in many of the Hymenoptera, chooses the most appropriate site for gall induction and initiates the gall. Accordingly, selection is predicted to favor those females selecting optimal sites for gall induction, consistent with the preference–performance hypothesis, sometimes referred to as the “mother-knows-the-best” hypothesis (Craig et al. 1989, Gripenberg et al. 2010). Attractive though this hypothesis may be, it has not gained widespread support (Burstein and Wool 1993, Kagata and Ohgushi 2001).

The Natural-Enemy Hypothesis
Under the natural-enemy hypothesis, the gall protects the inducing, inhabiting insect from natural enemies (Price et al. 1987). Parasitoids are rare in the open and thin-walled galls induced by the Thysanoptera and Aphididae, whereas predators are rare in the closed and thick-walled galls induced by the Cynipidae and Cecidomyiidae (Price et al. 1987). Possibly, the parasitoids fail to locate gall-inducing Aphididae and Thysanoptera efficiently within galls, although some parasitoids, such as the species of Chalcidoidea exploit the other gall-inducing insects, such as the Cynipidae effectively (Godfray 1994). Hence, a diverse range of parasitoids succeeds in exploiting the closed, complex galls induced by the Cynipoidae and Cecidomyiidae. Selective pressures from parasitoids and vertebrate predators may be responsible for the evolution of large, thick-walled galls (e.g., galls induced by Izeniola obesula Dorchin and Stefanola defoliata Dorchin [Cecidomyiidae] on Suaeda monoica
Forssk. ex G.F. Gmel [Chenopodiaceae] including extensive insulating layer of sclerenchyma, Dorchin et al. 2002, also see Meyer 1969 for several examples) in which the inducing insects gain some measure of protection from natural enemies; however, even thick-walled galls suffer attacks from parasitoids and vertebrate predators (Godfray 1994). Indeed, small mammals such as squirrels (Sciuridae) and birds (e.g., woodpeckers, Picidae) may preferentially attack large galls, such that stabilizing selection may favor galls of intermediate size (Abrahamson and Wei 1997, László et al. 2014).

Stone and Schönenroge (2003) argue that the apparent diversity in gall morphologies, especially as evident in nonnutritive tissue components of galls, is most likely a consequence of selection pressures exerted by natural enemies, although this hypothesis requires further testing. In some gall-inducing taxa, notably in the Thysanoptera and Aphidoidea, sterile “soldiers” (or defender morphs) have evolved to defend the brood from predators (Aoki 1977, Stern and Foster 1996, Crespi et al. 2004). These morphs bear a weaponry such as frontal horns, or display certain specialized behavioral responses such as stabbing or the injection of a “venom”, which deter predatory Diptera (Aoki 1977, Moran 1993). Here again, the inter-gall dispersal threats to undermine the benefits of such defender morphs, as conspecific “cheaters” enter galls and feed without aiding in defense of the gall (Abbot et al. 2001). Some of the gall-inducing Cynipoidea exploit extrafloral nectaries activated as a consequence of their feeding activity as a tool to recruit ants, which, in turn, aid in protection of these galls from parasitoids and inquilines. For example, Disobolaspis eldoradoensis (Beutenmuller) (Cynipoidea: Cynipidae) induces galls on Quercus lobata (Fagaceae), which produce copious nectar highly attractive to ants. Exclusion experiments have confirmed significant gains in the safety of gall occupants as a result (Washburn 1984, Fernandes et al. 1999, Nicholls et al. 2018). Gall-inducing insects avoid enemies through escape in time as well as in space (Yukawa et al. 2016). In some species, distinct generations of galls are induced, thus lowering the risk of attack by predators and parasitoids. Such galls often differ morphologically and represent alteration of generations in the life history of the gall-inducing taxon. A well-studied example is Andricus quercuscalicus (Burgsdorf) (Cynipoidea: Cynipidae) in Europe, whose two generations of galls support distinct communities of natural enemies. In A. quercuscalicus, the larval stage is more intensely parasitized in the sexual generation than in the asexual generation (Schönenroge et al. 1995). In the univoltine Andricus quercuscalifornicus (Bassett) (Cynipoidea: Cynipidae) in North America, parthenogenetic females emerge from galls in autumn (September–November) and oviposit on twigs of Quercus. In spring (March–May), concomitant with bud burst, the enclosed larvae induce galls rupturing plant stems. The galls expand to as large as 12 × 8 cm before the larvae pupate within, emerging in autumn (September–November) (Russo 2006). However, a portion of the overwintering eggs delays eclosion until the following summer (June–August), when plants produce leaves for the second time in a year. The late-emerging larvae subsequently induce galls and pupate; adult wasps emerge as a single generation in autumn. By spreading out the timing of gall induction over the growing season, the wasps may reduce the risk of predation and parasitism (Joseph et al. 2011).

The Microenvironment Hypothesis

The microenvironment hypothesis for the adaptive value of gall induction explains that the gall’s internal environment provides ideal physical conditions for insect development, especially by enabling them to overcome adverse environmental conditions (Price et al. 1987). Because most galls are small, they confer little protection from the dynamic external temperatures (Layne 1991, Williams 2002), but they may provide refuge from hygrothermal stress (the combined effects of low moisture and high temperature). At minute insects, gall-inducing species generally have a high ratio of body–surface area to volume, thus increasing the risk of desiccation especially in xeric habitats (Chapman 1982, Danks 2002). By developing and sometimes reproducing within galls, the insects avoid adverse environmental conditions, and remain active even when hygrothermal stress peaks (Price et al. 1987). Gall induction also aids in the attachment of the insect to host plant, which can, otherwise, pose a critical risk to juvenile insects (Strong et al. 1984). Such “beneficial” effects of galls have been more often predicted than verified (Felt 1940, Danks 2002), although a few empirical evidences exist. Experimental support for the microenvironment hypothesis has been shown in the populations of A. quercuscalifornicus on Q. lobata Née (Miller et al. 2009): internal levels of relative humidity approach saturation within gall tissues, and the high relative humidity within galls extend the survival times of A. quercuscalifornicus larvae significantly under experimental conditions. Thus, galls of A. quercuscalifornicus on Q. lobata serve to buffer the inhabiting larvae from adverse environmental conditions. More generally, the gall-inducing insect species are disproportionately diverse in xeric environments such as warm deserts in which the hygrothermal stress is severe. Such habitats have presumably fostered accelerated rates of speciation and radiation, in part because of reduced selective pressures from natural enemies (Fernandes and Price 1992).

Conclusion

The gall-inducing insects, as a more specialized group, present an astonishing taxonomic and ecological diversity, yet share the distinct capacity to redirect developmental programs of plants by generating galls—the structures within which the inducing insects live, feed, and propagate their progeny. Specific groups of insects, such as those of the Thysanoptera, Hemiptera, Diptera, and Hymenoptera seem to have acquired this capability at different scales of times living mostly on dicotyledonous plants. Curiously, this habit also prevails in the Eriophyoidea (Acari) and in the Coleoptera and Lepidoptera to some extent. Although we are unable to explain why and how this habit emerges sporadically among arthropods (Insecta and Acari), the propagation of the progeny appears as the key driving factor for gall induction among the hemipteroids and in the Acari, whereas this reasoning does not appear that critical in the more-evolved gall-inducing groups, such as the Cecidomyiidae and Cynipidae. Considerable scope presently exists to achieve a better understanding of the mechanisms involved in gall induction as well as further exploration of host–plant relationships of these specialist insects, especially in the context of how these insects utilize various microbes as associates and their potential effects on gall hygiene. Such explorations can have profound implications in understanding the mechanisms of plant pathology and the manner in which they hold promise for better-management tactics in agriculture and forestry, particularly in the context of clarifying mechanisms of resistance and susceptibility of plants to insects. It is clear that gall-inducing insects are easy to monitor because of galls, which are an advantage in this direction. The gall-inducing insects could be regarded as “ecosystem engineers” (Jones et al. 1994) in the sense they manipulate plant development and architecture to create novel habitats for themselves. In the Anthropocene, gall-inducing insects may prosper especially in expanding dry habitats due to climate change, and the widening urban environments will doubtlessly support a multitude
of gall-inducing species (Hamilton 2016). The impacts on host plants will continue to bear scrutiny, especially in regions where gall-inducing insects have been introduced and, released from their natural enemies, potentially threatening various other plants. Examples of this include N. saltatorius on its novel host-plant Quercus garr ryana Douglas ex Hook. (Fagaceae) in western Canada (Prior and Hulcr 2016), A. quercuscalicis on various species of Quercus in Western Europe (Schönrogge et al. 1995), and Dryocosmus kuriphilus Yasumatsu (Hymenoptera: Cynipidae) on Castanea sativa Mill. (Fagaceae), also in Europe (Nicholls et al. 2018).

The most critical stage in gall development is induction, which occurs within the first 24–48 h of attack on the plant by the inducing arthropod. In the instance of the gall induced on E. sylvatica leaves by H. annullipes, Rohrfritsch (1980–1981) provided details of changes that occur in E. sylvatica leaf tissue between 0 and 24 h at the site where the galls subsequently develop (Rohrfritsch 1978, 1980–1981). The <24 h changes in the physiology of host-plant cells are generally referred as cell metaplasia (Maresquelle and Meyer 1965). The chemical and molecular influences that occur during this earliest phase of insect attack, i.e., <24 h, need resolution.

A comparison with how pathogenic fungi access plant cells would be relevant and appropriate here. Spores of pathogenic fungi first invade and attack 1–2 cells of the host plant by applying a battery of cell-wall degrading enzymes (e.g., cellulases, hemicellulases, pectinases, cutinases, and proteases). High levels of production of reactive-oxygen-species, induction of necrosis- and ethylene-inducing proteins, and a range of other secondary metabolites such as salicylic acid usually eventuate at this stage of infection (Arenas Mendel et al. 2004), and Dryocosmus kuriphilus Yasumatsu (Hymenoptera: Cynipidae) on Castanea sativa Mill. (Fagaceae), also in Europe (Nicholls et al. 2018). The ability of pathogenic fungi to overcome the host's immunity and establish is the most significant step here.

We have referred to the high level of fidelity of gall-inducing insects to their respective host plants at great length. However, the papers on Leptocybe invasa Fischer & La Salle (Mendel et al. 2004) and Quadristichus erythrinae Kim (Kim et al. 2004) (both Hymenoptera: Eulophidae) are proving to be striking exceptions to the preceding statement. L. invasa and Q. erythrinae have been reported as gall-inducing agents on various species of Eucalyptus (Myrtaceae) and Erythrina (Fabaceae) in their new environments introduced for either commercial or ornamental reasons. However, what remains to be seen is whether L. invasa or Q. erythrinae induces the abnormalities (termed as galls) on the shoots of Eucalyptus and Erythrina or whether a microbe (possibly a fungus) induces the tumor, and the insects have possibly evolved the ability to live in those tumors successfully.

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