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REVIEW ARTICLE

Gall induction by hemipteroid insects¹

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The Thysanoptera and sternorrhynchous Hemiptera induce galls through feeding action, a behavior similar to that in the Cecidomyiidae. Salivary glands of gall-founding female thrips include greater quantities of hydrolyzing enzymes and soluble proteins than those in either males or pupae, which possibly alter the host-tissue metabolism, enabling galls to develop. Piercing-and-sucking mouthparts of the Hemiptera are adapted for an exclusively liquid diet – either the plant sap from vascular elements or the fluids from living nonvascular cells. Hemipteran-salivary chemistry alters the hormonal balance in the host, triggering gall development. Soluble proteins in the saliva of nymphs are critical. Gall-inducing Hemiptera vigorously take oxygen from the ‘gall’ tissue, which triggers auxin activity. Gall-inducing behaviors in the Thysanoptera and Sternorrhyncha are similar in that gall induction occurs by the feeding action of a single female, and gall-founding females disperse over short distances seeking young host-plant organs. Besides providing a comparative overview of gall induction by hemipteroids, this paper highlights the subtle but noteworthy differences in behaviors among these insects, thus offering pointers to their evolution within the specialist guild of herbivory.

Keywords: Hemiptera; physiology of galls; saliva; Sternorrhyncha; Thysanoptera; mouth parts

Introduction

Among phytophagous insects, certain species interact intimately with plants and induce specialized enclosing structures – the galls. Galls represent highly regulated growth manifestations on plants within which the inducing insects and their progeny live. Galls are the best examples for modified, usually symmetrical, natural-plant structures that arise solely because of messages from the inducing insects. These structures develop as an extension of the host-plant phenotype (Raman 2011). That the morphology and physiology of the plant influence the biology, ecology, and evolution of a plant-feeding insect is established: interactions between diverse species of flowering plants (e.g. *Quercus*, *Rosa*) and different species of gall-inducing Cynipidae (Hymenoptera) demonstrate that plant architecture influences the oviposition behavior of the Cynipidae (Abrahamson et al. 1998; Shorthouse et al. 2005). By inducing a gall, the insect ensures nutrition and shelter for either shorter or longer periods of its life. Because of their usually concealed habit (‘pit’ galls induced by some Sternorrhyncha excepted), compared with nongall inducing insects, gall-inducing insects generally show novel traits in their nutritional physiology and population dynamics (Raman et al. 2005a). Gall-inducing habit has evolved independently and multiple times among insects (e.g. Cook and Gullan 2004). Gall-inducing capability could be a characteristic of a

subgroup, e.g. Ophelimini (Hymenoptera: Eulophidae) (LaSalle 2005).

The capability to induce galls does not occur in all orders of Insecta. Within plant-feeding groups, gall-inducing capability principally occurs among insects belonging to Thysanoptera, Hemiptera, Diptera, and Hymenoptera, and in a lesser frequency among those of Lepidoptera and Coleoptera. Even in these orders, gall-inducing habit does not display any logical pattern. For example, gall-inducing capability in the Psylloidea is high in the Triozidae, but low among the Psyllidae, Phacopterionidae, and Calophyidae (Daniel Burckhardt, Basel, Switzerland, personal communication, email, 5 November 2010). A similar pattern occurs in the Thysanoptera as well, with a majority of gall-inducing taxa restricted to the Tubulifera (namely, Phlaeothripidae), whereas less than five taxa are known, as of today, as gall inducers in the Terebrantia (Ananthakrishnan and Raman 1989; Mound and Morris 2005). Considering gall-inducing capability at the order level, a majority of gall-inducing Hemiptera occur in the Sternorrhyncha. However, the reports of *Aphelaenus nigripectus* (Hemiptera: Aphrophoridae) as roll-gall inducers on the leaves of *Prunus speciosa*, *P. yedoensis*, and *P. pendula* cv. *pendula* (Rosaceae) (Sugiura and Yamazaki 2003), *Cicadulina bipunctata* (Hemiptera: Cicadellidae) on different species of Poaceae (e.g. *Zea mays*, *Oryza sativa*, and species of *Triticum*)

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¹To Warren Gene Abrahamson III (Bucknell University, Lewisburg, PA, USA), who blazed new trails in interpreting the evolutionary ecology of galls and inducing insects. Memories of my stay in his laboratory in 1990–1991 are pleasant.

(Matsukura et al. 2010), and a few scattered historical references to galls induced by species of Cercopoidea and Membracoidea (see Meyer 1987; Raman et al. 2005a) need to be recognized. In Western Kazakhstan (northeastern Kyzylkum desert near Baltakul, 43°12'N, 67°77'E), *Scenergates viridis* (= *Papyrina viridis*) (Hemiptera: Cicadellidae) induces closed leaf galls on a species of *Alhagi* (Fabaceae). Each gall on *Alhagi* would include one cicadellid, either an adult or an immature stage. Gall development commences with the feeding action of a young nymph on the midrib of a young leaf, which develops as a leaf fold, concealing the insect (Mitjaev 1968). *Copium* and *Paracopium* (Hemiptera: Tingidae) are the two taxa (plus three others: see Werner 2001) claimed as gall inducers on different species of *Teucrium* (Lamiaceae) and *Clerodendrum* (Verbenaceae) (Schaefer 2005). Four species of *Copium* remain tied to European *Teucrium*, whereas *C. japonicum* in the Eastern Palaearctic infests *Kesukea japonica*, also a taxon of Lamiaceae; about 40 species of *Paracopium* are hosted by species of *Clerodendrum* and *Scaevola* (Goodeniaceae) distributed in the Pantropics and Pan-Pacifica (Werner 2001). The most preferred host plant of *Copium clavicornis* is *Teucrium chamaedrys*. Yet, a few taxa from the Section *Teucrium chamaedrys* (*T. canum*, *T. marum*, and *T. flavum*) also host *C. clavicornis*. Host plants of *C. teucrii* occur on taxa of Section *Teucrium polium* (*T. montanum*, *T. polium*, *T. capitatum*, *T. aureum*) and also on *T. radicans* (Zalat et al. 2000; Lambinon and Schneider 2004). These Auchenorrhyncha taxa induce 'low' level alterations (namely, curls and crinkles) on leaves and flowers, and a few of them are specific to their hosts (Murphy 1989). However, these Auchenorrhyncha are generally polyphagous, whereas the gall-inducing taxa in the Cynipidae, Cecidomyiidae, Psylloidea, and Phlaeothripidae are highly monophagous. The debatable point is whether the Auchenorrhyncha induce 'true' galls as the Sternorrhyncha do. Alternatively, do the 'galls' induced by nonsternorrhynchan Hemiptera offer opportunities to explain the evolution of gall-inducing behavior among the hemipteroids? Is the high percentage of gall-inducing taxa in the Sternorrhyncha compared with Auchenorrhyncha a direct consequence of their feeding habits? (Daniel Burckhardt, personal communication, email, 5 November 2010). However, we know today that a majority of Auchenorrhyncha feed on phloem, similar to many of the Sternorrhyncha, but species of Cercopoidea and Cicadoidea feed on xylem; a majority of Cicadellidae feed on phloem, but the Cicadellinae and related subfamilies feed on xylem. Species of a single but diverse Typhlocybinae (Cicadellidae) feed from individual cells, and they are unique in displaying such behavior within Auchenorrhyncha (Roman Rakitov, personal communication, email, 10 November 2010).

Regional lists of arthropod-induced galls (e.g. Trotter and Cecconi 1902; Docters van Leeuwen–Reijnvaan and Docters van Leeuwen 1926; Felt 1965; Mani 2000) indicate that nearly 90% of the known galls occur on dicotyledons, few on monocotyledons, and still fewer on grasses (Mani 1964). Established examples of galls on grasses are those induced by *Orseolia oryzae* (Diptera: Cecidomyiidae) in Asia (Gagné 2004; Krishnaiah 2004) and *O. oryzivora* in Africa (Harris and Gagné 1982) on different varieties of *Oryza sativa* and *O. perennis* (Poaceae), respectively; at least four species of gall midges induce galls on *Phragmites australis* (= *P. communis*) (Poaceae) in Central Europe (Skuhrov and Skuhrov 1992); and a few Northern-European species of Chloropidae (Diptera) induce galls on different species of Poaceae (De Bruyn 2005). In such a context, the puzzling questions are 'why galls on monocotyledons are so few?' and 'are those claimed as galls on monocotyledons true galls?' The latter question gains significance because the structure of 'galls' induced by *Giraudiella inclusa* (Diptera: Cecidomyiidae) on *P. australis* (Rohfritsch 1975) defies established cecidogenetic patterns (Rohfritsch 1992). Gall induction reported on monocotyledons, on grasses in particular, needs to be examined closely to arrive at generic conclusions.

Specific differentiation processes control growth and development of galls. Among the different insect-induced galls, distinct variations in differentiation and in final gall shapes occur. Insects attack plant tissues resulting in the alteration of the subcellular environment and placing those tissues in a state of chemical shock. This shock evokes osmotic changes in the cells attacked, establishing the earliest recognizable stage in gall induction. To neutralize the stress arising consequent to osmotic changes, aggravated by wounding, the plant responds by developing usually one, sometimes 2–3, metaplasied cell(s). Localized metabolic changes diffuse from the metaplasied cell(s), but not throughout either the involved plant organ (e.g. leaves) or the plant (Rohfritsch 1978, 1980, 1992). When the shock is of low intensity, the plant responds with 'certain' chemical–molecular factors that disperse from the metaplasied cell(s) triggering gall development. When the shock factor is of high intensity, the cells under the influence of the insect (e.g. *Dasineura marginemtorquens*, Diptera: Cecidomyiidae; *Daktulosphaira vitifoliae*, Hemiptera: Phylloxeridae) die rejecting the inducing insect and thus defending the plant tissue (Ollerstam et al. 2002; Raman et al. 2009a).

Insects feed on gall tissue continuously for a specific period, throughout their developmental phase, and this behavior usually synchronizes with their life history. Osmotic-change related stress prevails during that period of time, which in turn stimulates a sequence of plant-mediated changes including alterations in gas exchange and synthesis

of growth promoters. Osmotic stress affects electrical properties of the plasma membrane and impacts on IAA activity, which in turn, also alters H^+ -transport systems. During the physical action of insect feeding, the host-cell wall breaks down, and the degenerated wall materials act as elicitors. Gall-hosting plants employ varied strategies to mitigate and neutralize stress arising sequel to gall induction. Although neutralizing strategies appear to exist in the genetic constitution of the host plants, they are mediated by complex molecular interactions. Plants generally use a flexible short-term strategy to respond to stress; organisms that can modify gene expression reversibly have an advantage in evolutionary terms, since they can avoid rearrangements and species diversification (Boyko and Kovalchuk 2008). Mechanisms of DNA methylation and histone modifications possibly regulate inheritance of stress 'memories'. Inherited genetic traits also play a role in gall morphogenesis, followed by roles played by correlating morphogenetic factors.

The sequence of steps in the process of gall development are: osmotic-shock related stress → establishment of either one or a group of metaplasied cells → growth promotor-mediated cell expansion → commitment of the metaplasied cell(s) starting the 'novel' cell-cycle patterns, cell multiplication, and programmed differentiation. Most critically, galls are controlled manifestations that are, usually, symmetrical – either radial or bilateral – when mature. Each gall is unique because the inducing insect species controls its shape (Raman 2011).

Gall initiation and development

Key phases in gall development are induction and growth; the latter includes increment in mass and qualitative differentiation. The earliest recognizable event is the isolation and insulation of either one or a few cells on the attacked plant organ (e.g. leaf) from their normal course of differentiation organizing a few metaplasied cells that are irreversibly changed by the stimulus from the inducing insect (Rohfritsch 1978, 1980, 1992; Meyer and Maresquelle 1983; Raman 1991, 1996; Raman et al. 2005b). A chemical factor obviously stimulates division activity in the metaplasied cell(s) triggering the gall (Bronner, 1973; Rey 1992; Rohfritsch 1992). The chemical factors variously implicated are high-molecular weight proteins (Carango et al. 1988), bruchins (Doss et al. 2000), and mitogenic lipids (Farmer 2000). This stimulus activates and regulates growth by triggering novel patterns of differentiation, which ensue at the metaplasied site (Harper et al. 2004).

During early stages, gall-inducing insects evoke stress responses at their attack sites, such as accumulation of active peroxisomes (Corpas et al. 2004) and glyoxysomes (Kim et al. 2004). The key role played by oxysomal microbodies in stress neutralization mediated by the production of reactive-oxygen

species is established (Pastori and Río 1994). Stress responses evoke gene expression from cells in the vicinity, which in turn, activate new growth and differentiation, resulting in a gall that offers nutrition and shelter to the inducing insect (Raman 2010, 2011). Continuing stimulus from the insect is essential to control gall shape and structure (Rohfritsch 1971). Gall development, in principle, involves two counter-acting events: the insect stresses the host organ; the host counters it with new physiological activities supplemented by newly differentiated tissues. In the galls induced by *Phacopteron lentiginosum* (Hemiptera: Phacopteronidae) on the leaves of *Garuga pinnata* (Burseraceae) (Raman 1987a; Burckhardt 2005), a sac-like gall develops from within the leaf, the most complex gall type among those induced by different species of Phacopteronidae (Malenovský et al. 2007). A vegetative mersitem differentiates within the primordial mesophyll, which grows into the saccular gall housing developing stages of *P. lentiginosum*. *Phacopteron lentiginosum*'s action has limited impact on the adaxial and abaxial epidermal cells of the host leaf. The gall, which shoots through the leaf, expresses itself differently on either side of the lamina by differentiating its own epidermises with varying structures: cells at the gall summit are similar to those of the host leaf, whereas those along the mid and lower regions, differentiated through intercalary meristematic activity, vary in their morphologies and even generate multicellular trichomes that are absent on normal leaves (Raman 1993).

Among the known gall-inducing insect taxa, nearly 90% of them have been shown to be specific to their hosts (Raman et al. 2005b). Levels of their host fidelity are remarkable compared with those of related, but nongall-inducing, plant-feeding taxa (Raman 1996). Fidelity of gall-inducing species of North-American Cynipidae (Hymenoptera) to *Quercus* (Fagaceae) demonstrates a high degree of monophagism (Abrahamson et al. 1998); many similar examples from other groups of gall-inducing insects are available (Raman 1996; Gagné 2004; see various chapters in Raman et al. 2005a). This trait is conservatively preserved among gall-inducing insects. For example, out of the nearly 250 insect species known to utilize *Mangifera indica* (Anacardiaceae), the 25 established taxa are gall-inducing Cecidomyiidae (Diptera), most of which are species of *Procontarinia* (Cecidomyiidae: Cecidomyiini) (Gagné 2004). Adaptive radiation of *Procontarinia* on *M. indica* has progressed conservatively among the diverse *M. indica*-infesting gall-inducing Cecidomyiidae, with a majority of them continuing to utilize the leaf. Species of *Procontarinia* on *M. indica* exhibit minimal variation in their overall gall shapes, in patterns of tissue differentiation, in the nature of dehiscence at maturity, on their location on leaves,

and in the numbers of larval chambers per gall (Raman et al. 2009b).

Although concrete evidences explaining how gall-inducing insects recognize their specific host plants and organs are not available, subtle evidences point to that host-plant surface waxes and lectin-recognizable carbohydrates (Smith 2005) facilitate recognition. Chitosan (a polymer of β -1, 4-linked glucosamine) with a strong affinity for DNA was localized in the nuclei of leaf cells of *Solanum dulcamara* (Solanaceae) punctured by *Aceria cladophthirus* (Acarina: Eriophyidae) and also at the feeding sites on leaf-cell walls (Bronner et al. 1989). Chitosan transmitted by *A. cladophthirus* induced changes in the DNA in cells under the direct feeding impact; accumulation of chitosan within nuclei and at feeding points on the walls could be the trigger factor (or, one of many factors?) for division activity in cells in the neighborhood of the laminae of *S. dulcamara* eventuating in the gall. Polygalacturonase activity in the saliva of *Aceria caulobia* on *Suaeda fruticosa* (Chenopodiaceae) (de Lillo and Monfreda 2004; Monfreda and Spagnuolo 2004) has also been shown to be a stimulus-recognition factor eliciting response signals. Incompatible subcellular responses have been demonstrated in the *A. cladophthirus*–*S. dulcamara* system (Westphal 1980; Westphal et al. 1981). Vacuolar alkalization in the epidermal cells punctured by feeding *A. cladophthirus* within 24 min of attack has been shown as a key resistance response (Westphal 1982). During incompatible reactions, callose accumulates in unattacked cells and auto-fluorescent, phytolaxin-like materials accumulate in cells around the lesion; pathogenesis-related proteins also build up in resistant tissues (Westphal 1992). Building up of pathogenesis-related proteins (e.g. osmotines) in alkaline vacuoles indicates accelerated senescence similar to host-plant resistance to microbial-plant pathogens (Memelink et al. 1990), but no more is known in the context of gall-inducing arthropods at early stages of their interactions with plants.

Whereas we know much of cell structure and physiology of plant galls, the nature and functions of signal receptors and steps involved in the signal-transduction pathway have not been convincingly explained. Genes analogous to the 'Nod' factors (Dénarié et al. 1996; Crespi and Gálvez 2000) involved in the signal transduction in the development of root nodules induced by *Rhizobium* (Lerouge et al. 1990) have been implicated in galls induced by *Diplolepis spinosa* (Hymenoptera: Cynipidae) on *Rosa spinosa* (Rosaceae) (Schonrögge et al. 1998), suggesting that these genes act as signal molecules in triggering gall induction. The Nod factors interrupt cytokinin-signal transduction pathway, by introducing concurrent changes in auxin-related responses during root-nodule initiation, in high likelihood, through increased levels and action of flavonoids

(Mathesius et al. 1998). Flavonoids occur at 'low-negligible' levels in insect-induced gall systems (Nyman and Julkunen-Tiitto 2000; Motta et al. 2005), although soluble phenolic materials and tannins are usually high. Isolation of castasterone-4 (a brassinosteroid) from insect-induced galls of *Castanea crenata* (Fabaceae) (Yokota et al. 1982) prompts the exploration of brassinosteroids in triggering signal-transduction pathways in galls.

Because considerable literature on the gall-inducing behavior of the specialist gall-inducing insects belonging to Cecidomyiidae (Diptera) (Skuhravá et al. 1984; Yukawa and Rohfrisch 2005) and Cynipidae (Hymenoptera) (Askew 1984; Csóka et al. 2005) exists, in this paper, I restrict myself to a précis of gall-inducing behavior among Thysanoptera and sternorrhynchous Hemiptera. Hemipteroid insects induce galls through feeding action by either juvenile stages or adults, sometimes by both, which in principle, is similar to the gall-inducing behavior in the Cecidomyiidae (Diptera). The Hymenoptera (Tenthredinidae, Braconidae, Chalcidoidea, and Cynipidae), on the contrary, induce galls by inserting their eggs into plant tissue. For an understanding of the role of oviposition and eggs in triggering gall development among the Hymenoptera, the reader is referred to Bronner (1973), Rey (1976), and Csóka et al. (2005), and several citations in them.

Thysanoptera

Thysanoptera (thrips)-induced galls, at maturity, house several individuals in different developmental stages. Thrips-induced galls occur on leaves in far greater frequency than those induced on vegetative buds and flowers (Ananthakrishnan and Raman 1989). An extensive variation in final gall shapes usually manifests: from simple leaf distortions and puckering to leaf folds and rolls, and of complex shapes. Extreme gall shapes include rosettes (e.g. *Thilakothrips babuli* [Phlaeothripidae] – *Acacia leucophloea* [Fabaceae: Mimosoideae]), pouches (e.g. *Austrothrips cochinchinensis* [Phlaeothripidae] – *Calycoperis floribunda* [Combretaceae]), and horn-like growths (e.g. *Liothrips ramakrishnae* [Phlaeothripidae] – *Schefflera racemosa* [Araliaceae]). Numbers in thrips populations are vital for the final gall form (Krishnamurthy et al. 1975; Raman et al. 1978; Raman 2003); a staggering number of a little more than 100,000 individuals of *A. cochinchinensis* are known in a single pouch gall on *C. floribunda* (Ananthakrishnan and Raman 1989). Several studies made in the last decade confirm eusocial behavior among gall-inducing thrips (see Mound and Morris 2005). Greater levels of humidity benefit thrips (Crespi et al. 1997). Thrips usually attack a tender plant organ (e.g. a developing leaf) that has the morphogenetic potential to redirect its course of development and grow into a gall. An exception is the multilocular woody stem gall-inducing

Iotatubothrips crozieri (Phlaeothripidae) on *Casuarina cristata* (Casuarinaceae) in Australia (Mound and Crespi 1992).

Several species of tropical and subtropical Tubulifera induce galls; on the contrary, only five species of Terebrantia, throughout the world, are the known gall-inducing taxa (Raman 2003). Gall-inducing thrips, as known from subtropical southern India, have an almost uniform life cycle. Terebrantia insert their colorless and smooth-shelled eggs singly into plant tissue with their saw-like ovipositor (Childers and Achor 1995). Tubuliferans, on the contrary, lay their eggs exposed on plant surface in clusters. Life-cycle periods vary with species, temperature, photoperiod, and food availability; the shortest known is 10–15 d; in subtropical peninsular India. Thrips show a life-cycle time of 30–40 d and occur throughout the year with 8–10 generations (Ananthakrishnan and Raman 1989).

Mouth parts of thrips form a cone that occurs on the underside of the head. Much of the cone occurs beneath of the first thoracic segment in a resting thrips. When extended, it is directed downward and backward. Mouth parts are characteristically asymmetrical because of the vestigial right mandible. In species of Phlaeothripidae (Tubulifera), maxillary stylets are usually longer and more deeply retracted into the head than they are in either Thripidae or Aeolothripidae (Terebrantia) (Mound 1971). Tubuliferan cones are usually longer than those of the Terebrantia, and this endowment, in high likelihood, enables the Tubulifera to explore host tissues with greater efficacy (Mound et al. 1980; Childers and Achor 1995). Musculature of the head and pharynx enables ingestion of cell sap with their contractile and pumping action (Moritz 1995). Leaf-feeding thrips rasp epidermal cells with their left-mandibular stylet and then insert the paired maxillary stylets. They empty the host-cell contents through maxillary stylets and use them to probe and feed on deeper-lying leaf tissues. When a thrips commences feeding, it presses the tip of its mouth cone against the host-plant surface and the labral pad, thus maintaining the closest contact with the host surface. Thrips feed through rapid protraction and retraction of the mandibular stylet by contracting the mouth cone. The mandibles, however, can move only within certain limits because of the nature of their orientation, musculature, and articulation within the head capsule (Heming 1978; Moritz 1982). For a detailed description of thrips' mouth parts, refer to Kirk (1997).

In *Frankliniella occidentalis* (Terebrantia: Thripidae), a nongall inducing taxon on *Phaseolus vulgaris* cv. Prelude (Fabaceae), the stylets utmost extend to about 30 μm reaching the first and second cell layers of mesophyll immediately beneath the epidermis (Kindt et al. 2003). However, in the infested leaves of *P. vulgaris* cv. Prelude, the further-lying

tissues suffer subcellular changes ('damage'), although not by wounding. The damage could be due to either the chemicals in the saliva of *F. occidentalis* (Kindt et al. 2003) or desiccation (Wardle and Simpson 1927) or both acting concurrently. Similar observations are available for *F. bispinosa*-fed *Citrus* flower tissues (Childers and Achor 1991). However, what needs to be recognized here is that a subtle difference exists between the nongall-inducing, plant-feeding Thysanoptera (e.g. species of *Frankliniella*, Thripidae) and gall-inducing Phlaeothripidae (e.g. species of *Gynaikothrips*). Gall-inducing thrips elicit a defined response which includes the organization of a specialized tissue of nutrition with pumped-up levels nutrients (Raman and Ananthakrishnan 1983a; Ananthakrishnan 1992), whereas the nongall-inducing taxa never elicit a similar response in their host tissues. For example, the feeding action of *Crotonothrips* (Tubulifera: Phlaeothripidae) that induces galls on the leaves of *Memecylon* (Melastomaceae) in southern India evokes a specific response in the host, by establishing specialized transfer cell-like cells which increase surface areas of nutritive cells, thus enabling short-distance nutrient transport (Raman 1987b).

A gravid female (the gall founder) selects and occupies the potential gall site. Her progeny feeds at that site contributing to gall development. Salivary glands of the gravid females of *Arrhenothrips ramakrishnae* (Phlaeothripidae) that induce fold galls on the leaves of *Mimusops elengi* (Sapotaceae) include greater quantities of hydrolyzing enzymes (e.g., proteases, amylases, and lipases) than those in either males or pupae (Raman et al. 1991). Maximum levels of amylases occur in the first and second larvae. The pupae have shrunken (nonfunctional?) salivary glands; neither proteases nor amylases occur, except for insignificant lipase values. Compared with any other development stages, the males and pupal stages, the saliva of the gravid female includes a wide range of soluble proteins. In high likelihood, salivary proteases and soluble proteins in the gravid female alter the host-tissue metabolism in enabling them to develop into galls. Higher concentrations of hydrolyzing enzymes in the saliva of *A. ramakrishnae* show them to be a better adapted taxon for mesophyll feeding.

Final gall shape, be it either a simple fold or roll or a complex pouch, materializes by the collective feeding action of several individuals – the progeny from the gall-founding female. During early stages of gall development, 4–5 individuals occur at a gall site. From the time of unfurling and expansion of the lamina, host leaves remain susceptible for a specific period of time as evident in the studied examples in subtropical southern India: *Pavetta hispidula* (Rubiaceae), the host of *Teuchothrips longus* (Phlaeothripidae) – 5 d; *Ventilago maderaspatana* (Rhamnaceae), the host of *Schedothrips orientalis* (Phlaeothripidae) – 7 d. If thrips invade after the susceptible period,

chances of galls developing are unlikely. Usually in 48–72 h, the invaded tissue responds with dramatic changes leading to gall development. The period of existence of thrips in old galls and the time necessary for the completion of gall growth generally coincide with the preoviposition period of the inducing thrips (Varadarasan 1979).

The developmental stage of the host organ and the size of thrips population together regulate variations in gall shapes. For example, when ± 20 adults and 10 larvae of *Gynaikothrips flaviantennatus* inhabit, partially rolled galls develop on the leaves of *Casearia tomentosa* (Salicaceae: Samydeae); when ± 80 adults and 90 larvae inhabit, completely rolled galls develop (Raman et al. 1978; Raman 2003). Similar effects have been confirmed in the horn galls on the foliage of *Schefflera racemosa* (Araliaceae) induced by *Liothrips ramakrishnae* (Phlaeothripidae), where smaller populations inhabit galls made of 7–12 layers of parenchyma, whereas larger populations inhabit galls made of 25–35 layers (Krishnamurthy et al. 1975). For remarks on the unique ‘company’ galls induced by thrips, refer to Ananthakrishnan (1992).

Thilakothrips babuli inducing rosette galls on *Acacia leucophloea* shows a unique behavior. *Thilakothrips babuli* not only induces galls on the axillary vegetative meristems but also on the florets. In an annual cycle, peak populations of *T. babuli* exist for c. 90 d: c. 60 d in galls induced on vegetative meristems, c. 30 d in galls on florets. When galls on meristems dry, thrips populations decline, but a few apterous adults survive diapausing. With the onset of flowering, these apterous adults move to the flower head, and initiate galls on the florets. The floret-gall-inhabiting *T. babuli* populations exhibit wing polymorphism, whereas the meristem-gall-inhabiting populations of *T. babuli* do not (Ananthakrishnan and Raman 1989). Such a capability of *T. babuli* inducing galls both on vegetative meristems and florets is striking because even among the sophisticated gall-inducing insects (e.g. Cecidomyiidae, Cynipidae), such a behavior seldom occurs (Raman 2007): two of the rare examples are *Asphondylia* (Diptera: Cecidomyiidae) on *Larrea tridentata* (Zygophyllaceae) and *Andricus* (Hymenoptera: Cynipidae) on species of *Quercus* and *Cerris* (Fagaceae) which show radiation of the inducing-insect taxon occurring between organs in the same host (Cook et al. 2002; Joy and Crespi 2007). However, in the evolution of insect phytophagy, fidelity to feeding site is more critical for speciation than fidelity to host plants (Favret and Voegtlin 2004).

Sternorrhyncha

The Aphidoidea, Psylloidea, Coccoidea, and to a limited extent the Aleyrodoidea include gall-inducing taxa. For an understanding of the range of galls they induce, refer to chapters by Wool (2005), Burckhardt

(2005), Gullan et al. (2005), and Byrne (2005). The number of insects in mature galls would vary with groups: several occur in galls induced by the Aphidoidea and Coccoidea, whereas usually one and rarely two occur in galls induced by the Psylloidea; exceptions certainly exist. Hemipteran mouth parts are of piercing-and-sucking nature, adapted for an exclusively liquid diet. The liquid diet could be either the plant sap from vascular elements or the fluids from living nonvascular cells. Social behavior and incidence of a special class of gall-inducing Aphididae (the *samurai* aphids) have been reported by Aoki and Aoki et al. in Japan between 1977 and 2000 (see Wool 2005 for references).

Several papers have appeared in recent times explaining the morphology of mouth parts of plant-feeding Hemiptera. For contextual clarity, a brief note is provided here. Mouth parts of plant-feeding Hemiptera (for a comprehensive review of the nutritional physiology of plant-feeding Heteroptera, see Hori 2000) include the labrum, labium, and a sclerotized stylet bundle that includes two mandibular and two maxillary stylets. The mouth part complex is essentially tubular and devoid of either labial or maxillary palpi. The labral cone, usually endowed with sensilla, is attached proximally to the clypeus and occurs overlying the labial groove. The included stylets are sharp tipped and are elaborately sculptured both at the tips and along the edges. The first maxillae are closely pressed to each other so that the oppositely lying grooves along their interfaces are arranged in such a manner that they bear two superposed capillary tubes. Through one of the tubes, the hemipteran flushes its saliva and through the other sucks plant sap. Endowed with a variety of sensilla, the distal tip of the labium guides the stylet into the host organ. The second maxilla fused into a labium constitutes the rostrum, with a groove in which the distal parts of the stylets slide. Each stylet is manipulated by two sets of retractor and protractor muscles. Large muscles attached to the ceiling of the cibarium enable a suction force which helps in either drawing or injection through the food and salivary canals that lie between the maxillary stylets. The two maxillary stylets interlock with each other along their full length, thus constituting a smooth hollow tube that bears an armature of denticles at the tips (Hori 2000). The articulation on the opposite side of the stylet bears the salivary canal which opens terminally between the denticles and the extreme end of the stylets. Although each maxillum is similar in shape and dimension, length of stylets changes as the insect develops: first nymphal instars: 300–600 μm ; adults: 1000–1400 μm . Because stylet bundles become longer with each successive moult of the nymphal instar, developing nymphs shift their feeding sites from superficial cells to deeper-lying tissues as they mature. Gall-founding aphid females change their feeding sites several times during gall development; they

usually generate and introduce new stylets at different sites (Rohfritsch and Anthony 1992).

During feeding, the labium does not pierce the plant tissue, but is positioned perpendicular on the surface to insert the stylets into the host. Although a majority of the Sternorrhyncha feed passively on the contents of phloem, several studies on gall-inducing Sternorrhyncha, especially on the nymphal instars, indicate them to be nonvascular tissue feeders (e.g. parenchyma) (Raman 1991; Rohfritsch and Anthony 1992; Raman et al. 1996). Because we know more about the saliva of nongall-inducing aphids, we will use them as a model here. Aphids produce two types of saliva. The first is dense and proteinaceous, which jels around the stylets forming stylet sheaths, isolating plant tissues from the mouth parts, and preventing any possible adverse plant reactions (Felton and Eichenseer 1999). On reaching the phloem, aphids secrete the second type of saliva which is less dense and is injected directly into the vascular system of the plant. The watery saliva contains diverse digestive and lytic enzymes. The aphid's feeding action inflicts a 'fine' wound, but the salivary proteins interact with Ca^{++} of host-plant tissues (Will et al. 2007) preventing possible wound-healing effort by the plant. In general, wounding does not induce cell necrosis. Nongall inducing aphids impress as more sophisticated taxa than their allies because they avoid plant-based allelochemicals and indigestible compounds by their elegant feeding mechanism (Schoonhoven et al. 2007). In *Bemisia argentifolii* (Aleyrodidae), the adult stylet bundle enters the labial groove of the labium between the first and second segments and is included within the labium except during feeding; stylet length is equal to the combined length of 2, 3, and 4 labial segments; the physical force necessary for adult stylet penetration is derived from changes in the position of the *B. argentifolii* head during feeding; the head is bent over the labium which is attached to the leaf surface, forcing the stylet bundle down the labial groove, and into the host tissue (Freeman et al. 2001).

Miles (1999) provides the state-of-the-art knowledge on aphid saliva; a few key points are summarized here: (1) Several amino acids occur in the watery saliva, but their concentrations vary with species. In high probability, the amino acids that occur are the same that occur in the sieve-tube sap, and they represent 'unused dietary products absorbed into the haemolymph and excreted via the salivary glands' (Srivastava 1987). (2) Watery saliva has reducing and surfactant properties to lubricate stylet activity. (3) Watery saliva is of pH 8–9, similar to that of many Pentatomomorpha (Taylor and Miles 1994). (4) Pectin-hydrolyzing enzymes such as pectinesterases and polygalacturonases occur. (5) Cellulase, arabinogalactan breaking down 1, 3-glucosidases, and exopolygalacturonase also occur. (6) In the nonaphidid aphids, α -amylases exist; in the aphid taxa, α -amylases are not from the saliva, but are from the

gut tissues that house a bacterium. (7) Glucose-breaking α -glucosidases occur in both saliva and gut tissues. (8) The sheath material and watery saliva of *Rhopalosiphum padi* release *p*-nitrophenol from both *p*-nitrophenyl- α -D-glucopyranoside and *p*-nitrophenyl- β -D-glucopyranoside, indicating a salivary α -glucosidase and β -glucosidase, respectively (Urbanska and Leszczynski 1997). (9) The watery saliva and the stylet sheath contain polyphenol oxidase originating from the accessory glands occurring near the salivary glands; the difficult-to-demonstrate peroxidases have been shown in *Aphis pomi* (Aphididae) (Leszczynski et al. 1996). (10) Salivary soluble proteins vary considerably between species (Miles and Harrewijn 1991). The saliva of *Therioaphis trifolii* (Aphididae) includes soluble proteins of molecular weights 6–200 kDa, and the three that showing oxidase activity had molecular weights of 20, 90, and 200 kDa (Madhusudhan and Miles 1998); the saliva of a nongall-inducing species *Acyrtosiphon pisum* (Aphididae) includes two minor and two major soluble protein fractions (120–300 kDa), and the three that showed oxidase activity with molecular weights 120, 180, and 300 kDa.

Stylet tracks (the proteinaceous sheath) left in the host tissues by gall-inducing and nongall-inducing Sternorrhyncha after the withdrawal of the stylets accept coloring by cationic dyes (e.g. methylene blue, bismark brown) and can be easily detected in a light microscope. In some species, the track is straight (e.g. *Eriosoma lanigerum* [Pemphigidae] on *Malus domestica* [Rosaceae]), whereas in other species it is meandering and branched (e.g. *Adelges abietis* [Adelgidae] on *Picea excelsa* [Pinaceae]). Sternorrhyncha extensively probe the plant surface before they commence feeding (e.g. *Hormaphis hamamelidis* [Aphididae] on *Hamamelis virginiana* [Hamamelidaceae]; Lewis and Walton 1958), whereas others do not (e.g. *Daktulospheria vitifoliae* [Phylloxeridae] on *Vitis vinifera* [Vitaceae]; Raman et al. 2009a). In a majority of instances, the stylet path travels intercellularly dissolving the middle lamella – principally made of pectic compounds – which cements adjacent cells (Rohfritsch 1976, 1988). Pectinase activity in aphid saliva is known from the 1960s (Auclair 1963; Ma et al. 1998; Miles 1999).

One key characteristic of gall-inducing Sternorrhyncha is that their first-instar nymphs (the crawlers) are mobile. Settling at the most-suitable feeding site by these nymphs is vital because movement over greater distances after they moult into subsequent stages is generally not possible. Byrne and Bellows (1991) in the whiteflies and Gullan and Kosztarab (1997) in the scale insects have shown that the crawlers disperse over short distances before settling under favorable conditions. Crawlers of the Coccoidea show different kinds of movements. For example in a species of *Matsucoccus* (Margarodidae), the crawler movement combines thigmotactic behavior

and negative phototaxis over a short distance away from the mother (Gullan et al. 2005). Crawlers of *Anonidiella aurantii* (Diaspididae) move upward in light, downward in dark, and settle beneath either in leaf sheaths or at stem angles. Crawlers of *Aulacaspis tegalensis* (Diaspididae) respond phototactically and geotactically, generally clustering at leaf tips, enabling their wind dispersal (Greathead, 1990). Once at the periphery of the plant, the first-instar nymphs can orientate themselves toward wind currents and get easily dispersed over long distances (Washburn and Washburn 1984). The first-instar nymphs of Aleyrodidae also move either short distances on the same plant or long distances between plants. For example, those of *Aleurotrachelus jelinekii* (Aleyrodidae) crawl for 1–2 days on the abaxial leaf surface before they settle (Southwood and Reader 1976). Young nymphs of *Bemisia argentifolii* move for about 50 mm on the same plant and travel as far as 200 mm during interplant movement; 80–100% of *B. argentifolii* crawlers settle on the abaxial surface, but the behavioral cues for site selection are undetermined as of today (Summers et al. 1996).

The first-instar nymphs of *Trioza jambolanae* (Trioziidae) (Raman 1991) and *Diaphorina truncata* (Psyllidae) (Balakrishna and Raman 1992) settle on the abaxial side of their host leaves to initiate a gall. Neonate nymphs of *T. jambolanae* crawl to venal angles along the abaxial leaf surface. The choice of settling site is dictated by the availability of stomata. After settling, these nymphs feed on the primordial-mesophyll parenchyma cells lying immediately below the abaxial epidermis by inserting their stylets through a stoma. The potential cues, which the nymphs of *T. eugeniae* use when discriminating between the two morphological sides of a leaf, include the differences in external cuticular chemistry, differences in internal leaf chemistry, presence of stomata or other structural features, gravity, and light (Luft and Paine 1997). Walker (1987) determined that adults of *Parabemisia myricae* (Aleyrodidae) discriminate between young and mature lemon leaves from leaf-surface cues picked up by the sensilla on the rostral tip. Probing by first-instar nymphs could be limited by physical and/or chemical factors in leaf cuticle (Walker 1985). For instance, sucrose, in high likelihood, is a phagostimulant for inducing the settling response (Walker and Bednar 1986). Actively growing tissues rich in nutrients could be another factor for sternorrhynchan nymphal preference for young leaves (Walker and Aitken 1985). Consequently, settling is a response to the presence and absence of both inhibitory and stimulatory behavioral cues. Direct-contact chemoreception could be playing a reduced role in discrimination. Adaxial and abaxial faces of leaves could be producing a different quantity and quality of volatiles that nymphs use in discrimination. Discrimination of

host quality is critical for the fitness of insects with less mobile further stages during nymphal growth.

Sea urchin-shaped galls induced by *Mangalorea hopeae* (Coccoidea: Beesoniidae) arise on the shoots of *Hopea ponga* (Dipterocarpaceae) along the western coastal plains of peninsular India. The gall consists of a 1–1.5 cm wide head-like structure (the columella) on which several, compactly arranged sharp lance-like structures arise. The neonate wingless female nymphs of *M. hopeae* invade axillary angles of vegetative meristems of *H. ponga*, exploiting the space made available by their extra-axillary positions on the stem, shortly after monsoon rains (Raman and Takagi 1992). How they invade new sites remains a supposition. The conjecture is that the older winged brothers transport female nymphs enabling them to occupy new sites, similar to what occurs in the gall-inducing Australian Eriococcidae (Gullan and Cockburn 1986). Immediately after settling, the female nymph of *M. hopeae* starts feeding on the cortical tissues of the vegetative bud. A gall develops arching over the nymph, enclosing it nearly completely. The trapped female nymph grows into an adult fitting snugly in that space. In between the lance-like appendages that develop through the modification of the multicellular trichomes along the outer edges, male nymphs – arising from the trapped adult female – live feed on the columellar tissue. When the gall dries, the lance-like appendages separate enabling the males which would have grown into adults by that time to escape. Galls induced by *M. hopeae* stand distinctly from the remainder of the known galls induced by Coccoidea (Gullan et al. 2005) because of the following characteristics: (1) two life stages of *M. hopeae* contribute to gall development, (2) a first-nymphal instar initiates the gall on the vegetative shoot bud, exploiting the axillary gap, and (3) several male nymphs that emerge from the entrapped female after its maturation and mating occupy the spaces between the lance-like appendages. Although occupation of a maternal gall by several males is usual among galls induced by Coccoidea (Gullan et al. 2005), the feeding behaviors of the inducing female and the male progeny are strikingly different: the inducing female *M. hopeae* feeds on cortical parenchyma, whereas the *M. hopeae* males feed on phloem elements. An adult male from outside mates with the female trapped within the gall, through an aperture that occurs close to the stalk of the gall. This aperture not only enables mating but also the discharge of nymphs that develop viviparously within the females' saccular body.

Verification of oviposition-preference patterns of *Trioza apicalis* (Trioziidae) that lives on *Daucus carota* as the preferred host plant, on different plants of Apiaceae, and its alternate host *Picea abies* (Pinaceae) provide the following results (Valterová et al. 1997): the number of eggs laid by *T. apicalis* per day varies from 18 on *Daucus carota* subsp. *sativus* to zero on

Aegopodium podagraria; individual *T. apicalis* occupy quickly and oviposit earlier on *D. carota* subsp. *sativus* compared with *Anethum graveolens*; *T. apicalis* survive on *P. abies* for more than 30 weeks, but die on *Phleum pratense* and *Brachypodium sylvaticum* in 15 d. Day length was a factor that regulated hibernation; at 20°C, light regimes shorter than 17 h induced hibernation, while longer light periods led to reproduction. The Apiaceae taxa and *P. abies* released monoterpene hydrocarbons, but with distinct differences among tested species. *Daucus carota*, the most preferred host plants, released (+)- and (-)- α -pinene and (+)-sabinene, whereas the other lesser preferred Apiaceae released either (+)- or (-)-limonene. *Picea abies* included (-)- α -pinene, (-)-J3-pinene, and (-)-limonene as the principal volatiles.

Among the different Indian Anacardiaceae-infesting psyllids, *Apsylla cistellata* (Calophyidae) infesting *Mangifera indica* induces fir-cone shaped galls. *Apsylla cistellata* is restricted to the Indo-Gangetic Plains and the lower valleys of the Himalaya (20–34°N; 77–85°E; Singh 2003). Gravid females lay 75–150 eggs on leaves, burying them partly into leaf tissue. Eggs hatch approximately in 200 d and adult development occurs in 140 d. The first-instar nymphs feed on the leaves on which the eggs were laid and their feeding action ‘triggers’ gall development in the vegetative axillary buds that occur approximately 10 cm away. The feeding effect of many neonate nymphs induces the modification of nearby vegetative buds into galls in about 30 d. Stimulation of gall development at a site farther away, viz., the vegetative axillary bud, is implicated by the translocation of a ‘stimulus’ over a distance of 10–15 cm. Such a behavior is unusual among the gall-inducing psyllids (Burckhardt 2005), but is analogous to the behavior of *Adelges cooleyi* (Adelgidae) that induces galls on the vegetative buds of the hybrid interior spruce (*Picea glauca* \times *P. engelmannii*) in North America, where a dose-dependent chemical stimulus is transported over long distances from the point where the gall-founding female settled (Sopow et al. 2003). In spite of an apparent similarity, in the bud galls of *M. indica*, the first-instar nymphs of *A. cistellata* are the purported gall inducers, whereas in the bud galls of *Picea glauca* \times *P. engelmannii*, adult females of *A. cooleyi* induce galls. Burying eggs – either partly or fully – into host tissue by the gravid female is unusual among the Psylloidea. Among the Triozidae such behavior is unknown (Boujou and Nguyen 1974; Ratsimialarivo-Ravoahangiarisoa 1983; Raman 1991; Raman et al. 1996). However, the gall-inducing females of *Phacopteron lentiginosum* (Phacopteronidae) bury their eggs in the leaves of *Garuga pinnata* (Burseraceae) in southern India. Leaf tissues of *G. pinnata* respond to the buried eggs with metabolic changes (e.g. accumulation of phenolics) with features of reaction tissue, similar to that shown in the leaves

of *Lactuca sativa* (Asteraceae) consequent to mechanical wounding (Choi et al. 2005). The emerging nymphal instars of *P. lentiginosum*, living within leaf tissues, initiate galls by their feeding action. The gall assumes its complex shape with the further development of *P. lentiginosum* (Raman 1987a).

Injection of aphid saliva alters the hormonal balance in the host, thus leading to gall development. However, apart from three triacylglycerides containing (E,E,E)-octa-2,4,6-trienoic acid isolated from the gall induced by *Colopha morioakaensis* (Pemphigidae) on the leaves of *Zelkova serrata* (Ulmaceae) responsible for cell hypertrophy, no potential gall-inducing compound has been determined so far (Otha et al. 2000). Soluble proteins in the saliva of the nymphs of *Trioza jambolanae* have been shown to be a critical factor for gall development in the leaves of *Syzygium cumini* (Rajadurai et al. 1990). In the saliva of *Trioza apicalis*, an undetermined amine exists in addition to plant-derived sugars (Markkula et al. 1976). Gall-inducing Hemiptera vigorously take up oxygen from gall tissue (several examples in Miles 1999), along with a stimulation of auxin activity. Use of oxygen in the tissues under arthropod attack might be so great that the IAA-oxidase activity that regulates the concentration of IAA might be deprived of oxygen and therefore inhibited. Such a deprivation of oxygen (Florentine et al. 2002) results in the concentration of IAA increasing disproportionately at feeding sites with a consequential hypertrophy of meristematic plant tissues. Although the specific agent in the hemipteran saliva that induces galls has not been determined, salivary oxidases should be playing a role in the disruption of IAA-oxidase pathway.

Concluding remarks

Rohfristch (1992) indicated that the pattern evident in the feeding and gall-induction behaviors of Thysanoptera and Sternorrhyncha is, in principle, similar to that evident in the feeding and gall-induction behaviors of the Cecidomyiidae (Diptera). Her argument is based on her study of the gall-inducing behavior of *Hartigiola annulipes* (Cecidomyiidae) on leaves of *Fagus sylvatica* (Fagaceae) and that of different species of Sternorrhyncha (Rohfristch 1971, 1976, 1988). Neonate larvae of *H. annulipes* (and many other Cecidomyiidae, for that matter) initiate galls by sucking cell sap using their sharp, but short mandibles (Rohfristch 1978, 1980) eliciting a covering growth. She has also argued that in a majority of the Cecidomyiidae-induced galls, covering growth is the common pattern which is also the basic pattern in the galls induced by Thysanoptera and Sternorrhyncha (Rohfristch 1992).

A comparison of gall-inducing behaviors in the Thysanoptera and Sternorrhyncha presents at least two similarities: (1) gall induction occurs by the feeding action of a single female; (2) gall-founding females disperse over short distances seeking young

host-plant organs (e.g. differentiating leaves). More importantly, thrips' saliva is considered 'similar' to that of the Sternorrhyncha in several ways (Kirk 1997). Differences, however, exist in gall-inducing behaviors. Among the Thysanoptera, a gravid female founds the gall. Collective feeding effort of her progeny is critical in achieving the final-gall shape. In a majority of galls induced by thrips, a marked level of wounding occurs because of their feeding action with asymmetrical mouth parts and their probing behavior (which includes rasping) followed by piercing and sucking. Cell necrosis occurs to a limited extent at the wounded sites of host plants. Among gall-inducing Aphidoidea (e.g. Adelgidae) and Coccoidea (e.g. Eriococcidae, Beesoniidae), a first-instar female nymph initiates the gall. Among Psylloidea (e.g. Triozidae), a first-instar nymph initiates the gall by settling on the stomatal aperture on the abaxial side of the leaf; however, in the Triozidae, whether it is a female nymph, similar to what is known among gall-inducing Aphidoidea and Coccoidea, or whether it is a male nymph is uncertain presently, although chances of a male inducing a gall are highly unlikely. Studied examples from the Triozidae indicate that their galls house a single individual (Raman 1991; Raman et al. 1996). The trait of occupation of a gall as a colony is shared between the Thysanoptera on the one hand and the Aphidoidea and Coccoidea on the other. In the Psyllidae, e.g. *Diaphorina truncata* that induce galls on the leaves of *Strychnos nux-vomica* (Loganiaceae), gravid females colonize young leaves and by feeding on their abaxial surfaces they initiate galls which require the feeding-action support from her progeny (Balakrishna and Raman 1992). Such behavior is similar to those in a majority of leaf-roll, leaf-fold gall-inducing Phlaeothripidae (e.g. *Arrhenothrips ramakrishnae*, *Gynaikothrips flaviantennatus*), which require at least 8–15 individuals to reinforce their mother's feeding initiative.

Among the Psylloidea, gall-inducing behaviors of *Apsylla cistellata* (Calophyidae) and *Phacopteron lentiginosum* (Phacopteronidae) are different compared with those of the Triozidae and Psyllidae. In gall-inducing Triozidae, gravid females deposit their eggs on the potential site where galls would develop, and only the egg stalks remain buried in the leaf tissue. However, *P. lentiginosum* buries its eggs entirely in the host-leaf tissue, although gall initiation is triggered only by the feeding action of the neonate nymph. Young leaves of *Garuga pinnata* respond to oviposition by generating a reaction tissue. On the contrary, in *Apsylla cistellata*, Singh (2003) reported that the egg is 'partly buried' on the leaves of *Mangifera indica* and the emergent nymphs feeding on the leaf initiate galls on the axillary vegetative buds, at least 10 cm away. Samui and Jha (2009) described *A. cistellata*'s oviposition behavior as follows: eggs are laid singly in slits dug by ovipositor,

eggs remain embedded in midrib tissues along the under sides of new leaves, eggs are inserted alternatively by puncturing the tissue along both sides of the dorsal face of the midrib, the intensity of egg laying depends on the availability of new flush of tender leaves and number of adults emerging at a particular time in an orchard, and if many females had only a few leaves for egg laying, then they lay eggs along both sides of lateral veins along the under sides of *M. indica* leaves. Burying eggs in host tissue, therefore, emerges as a nonTrioziidae character in the Psylloidea, shared only in species of Phacopteronidae and Calophyidae.

Claims of gall induction by the Tingidae and Cicadellidae need to be discussed. In terms of their general biology, the Tingidae prefer to feed on the abaxial-leaf sides seeking humid microenvironments – a trait shared by a majority of gall-inducing Sternorrhyncha. Nonetheless, among the purported gall-inducing Tingidae, their gregarious occurrence on host organs (e.g. leaves, flowers) stands out (Schaefer 2005). Their preference for flowers and capability to induce floral galls impress as specialized traits among the gall-inducing hemipteroids because floral galls induced by Sternorrhyncha and Thysanoptera are rare. The singular near match is the southern-Indian phlaeothripid *Thilakothrips babuli* that induces galls on the florets of *Acacia leucophloea* (Raman and Ananthakrishnan 1983b). Gall-bearing *Teucrium polium* (Sinai desert, Egypt; 29°30'N, 33°50'E) include leaves and floral axes reduced in size compared with the uninfested, although the petals in galled flowers are 'enlarged' ('hypertrophied?') (Zalat et al. 2000). The other key behavior that distinguishes gall-inducing Tingidae (e.g. *Copium*) from that of the gall-inducing Sternorrhyncha is that they insert their eggs in host plants to trigger gall development (Behr 1952; Monod and Carayon 1958). Evidences of a differently structured internal reproductive system in *Copium* show it to be better adapted for such a specific behavior (Schaefer 2005). Nonetheless, without arguing how relevant the following could be, the oviposition behavior of gall-inducing Tingidae indicates a situation parallel to what occurs in the few gall-inducing Terebrantia (Thysanoptera) which insert their eggs into plant tissues triggering gall development. Among the reported instances of gall-induction in the Cicadellidae (Mitjaev 1968; Matsukura et al. 2010), a common behavior is that both nymphs and adults are gall inducers, which is strikingly different to the behavior in the gall-inducing Sternorrhyncha; however, the purported 'gall'-inducing behavior of the Cicadellidae reminds us of the behavior known in gall-inducing Tubulifera in that both immature stages and adults participate in gall induction. Nymphs and adults of *Cicadulina bipunctata* induce galls not only at the locations they feed but also on distant leaves through dose-dependent stimulation (Matsukura et al. 2009); this

behavior is similar to the gall-inducing behaviors of *Apsylla cistellata* and *Adelges cooleyi*. Nevertheless, the polyphagous behavior of *Copium clavicornae* and *C. teucris* (Drake and Ruhoff 1965) infesting different species of southern Palearctic and Middle-eastern *Teucrium* and *Cicadulina bipunctata* on different Poaceae in south-east Asia raises the question ‘could these be considered true gall-inducing taxa because of the low level of tissue complexity in their so-called galls and their polyphagous nature?’

A trait shared in all of the gall-inducing Tubulifera (Phlaeothripidae) (*Iotatubothrips crozieri* excepted), the few gall-inducing Terebrantia, and a majority of the gall-inducing Sternorrhyncha is that they induce galls on soft plant organs (e.g. leaves, vegetative shoot buds, and flowers) of tree species, and that capability is considered an evolved trait. Molecular investigations (Morris and Mound 2003) and evolutionary reconstructions based on fossil evidences (Grimaldi et al. 2004) suggest Phlaeothripidae as the most derived family in Tubulifera and this family includes the highly diverse set of taxa including a majority of gall-inducing species. Gall-inducing Phlaeothripidae radiated in the Cenozoic (or at the latest, in the Cretaceous) in conjunction with the evolution of flowering plants (Grimaldi and Engel 2005). Preference to tree species by these specialist phytophages could be interpreted as reliance on a ‘predictable resource’ (*sensu* Raffa 1989). However, their strong level of fidelity to respective plant species, and even plant organs, does not impress as an evolutionary advantage. Considering species of *Procontarinia* and *Mangifera indica* interactions, Raman et al. (2009b) proposed that the gall midges have progressed conservatively specializing along the host-plant lines to match with the plant phenology and to minimize competitive interactions with the parasitic, predatory, and inquiline arthropods. Established schemes outlining the phylogeny of plant-feeding Sternorrhyncha indicate that changes in feeding preferences enabled their radiation historically: for instance, the Cretaceous coccoids fed on conifers (Grimaldi et al. 2000); host switching from conifers to angiosperms that occurred in the Cretaceous triggered radiation of aphids in the Tertiary (c. 40 MYA) (von Dohlan and Moran 1995). At the other end of the spectrum, the gall-inducing arthropods have limited neurological capacity to process different hosts, and therefore different diets, which has restricted them to specific plants and organs. We need to factor here Labandeira and Phillips’s (1996) explanation that in the later Middle Pennsylvanian coal-swamp forests of Euramerica, the dominant arborescent plants possessed vascular tissues unavailable to insects because they were either deeply embedded in a thick layer of cortical tissues or protected by outer indurated, peridermal tissues. Subsequent tree-fern forests of the Late Pennsylvanian provided accessible vascular and other tissues to

surface-dwelling insects with stylet mouthparts – a condition which continued into the Permian and propelled the radiation in the Hemiptera. By Middle Pennsylvanian–Late Pennsylvanian period, a rapid expansion of phytophagy occurred, from simple foliage feeding to complex gall-inducing capability (Labandeira 2006).

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