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Host-plant relationships of gall-inducing Thysanoptera – the lack of patterns

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ABSTRACT. Adult Thysanoptera occur within plant galls for various reasons and use of the term "gall-thrips" without defining the particular relationship is uninformative and misleading. Apart from inducing a gall, a thrips may be found in a gall as a predator feeding on the galler, as a kleptoparasite feeding on plant cells and usurping the protective space induced by the galler, as a phytophagous inquiline breeding in low numbers in a gall without disturbing the galler, or as a casual visitor seeking protection from desiccation. These various relationships are discussed in the light of how little is known about the phylogenetic relationships amongst the Phlaeothripidae, the thrips family that includes most of the galling thrips species. Host associations amongst thrips, including the galling habit, are largely opportunistic, with few examples of a close relationship between thrips and plants above the level of genus in either group.

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Introduction

The insect Order Thysanoptera comprises more than 6000 species (ThripsWiki, 2020) and, although some are known to be phytophagous, with many mycophagous and a few predatory, remarkably little is known about the precise biology of most species (Mound, 2004). Amongst phytophagous thrips many species are associated with plant galls, the distortions to plant growth that are induced by the feeding of an adult thrips.

The galls which some thrips species induce on particular plants are wound reactions in response to feeding by one or more adults. A plant-feeding thrips, after first puncturing the epidermal cells of a leaf or young bud with its single mandible, inserts its maxillary stylets into the tissues and withdraws the contents from cells one at a time. In some plant species, the response to such feeding involves the cells around the dead cells becoming meristematic, with dense cytoplasm and changes in the cell walls, and the resultant growth can produce a structure that is highly species specific in form. Details of these structural changes for several thrips galls in India are summarized in Ananthakrishnan & Raman (1989) followed by many references in Ananthakrishnan (1992). However, there have been

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no similar detailed studies on the structure of the numerous galls induced by thrips in Africa, Australia, or South America. The objective here is not to review the mechanisms and physiology of gall-induction by thrips, but to consider the differing relationships that individual thrips species have to galls, and to seek any apparent phylogenetic patterns amongst both the galled plants and the thrips. All thrips taxa referred to below are members of the sub-family Phlaeothripinae, except where indicated, and full nomenclatural details are available in ThripsWiki (2020).

Problems

The search for patterns is an essential aspect of science, but there are several constraints to the process of looking for patterns in the relationships between insects and plants. Ehrlich & Raven (1964), in an extensive account of the evolutionary relationships between groups of butterflies and groups of plants, emphasized that an essential consideration is the reliability of the available data. They recognized that any review based on published literature must bear in mind the possibility of misidentifications, both of plants and of insects, as well as differing views on phylogenetic relationships. Such problems are clearly apparent when considering the relationships between thrips and plant galls, but of particular importance is the frequently ignored behaviour of a thrips in relation to a gall. The term "gall thrips" was used by Ananthakrishnan (1978) in what he claimed to be "a comprehensive sense so as to include all the primary and secondary thrips occurring in a gall". Also, in various publications he used the term "inquiline" for any thrips species found living in a gall yet not being the gall-inducer. These terms lack any precision for interpreting and understanding thrips behaviour and evolution in relation to gall-induction, because there are various reasons why a thrips may be found inside a gall. As a result, despite the many publications on thrips and galls in India there is almost no information concerning what each thrips species is actually doing in any particular gall.

Thrips behaviour

Apart from inducing the cells of a plant to become meristematic, with the consequent production of a gall, thrips may be present within a gall for several quite different reasons. Predatory, non-phytophagous, thrips invade a gall to feed on the adults, larvae or eggs of the gall-inducing thrips. Unfortunately, clear evidence for such predation is rarely available (Melo et al., 2013), but thrips species in several genera are known to feed on other small insects including other thrips species. Species in the genera *Karnyothrips* and *Mesandrothrips* are free-ranging predators that are found occasionally in galls, whereas species of *Androthrips* appear to be specific predators of various gall-inducing thrips in the Old World tropics including northern Australia (Mound & Minaei, 2007). Similarly, *Senegathrips coutini* appears to be a specific predator within galls induced by *Vuilletia houardi* on *Guiera senegalensis* [Combretaceae] in western Africa (Mound et al., 2014). A behaviour that is very distinct from predation is kleptoparasitism, in which a thrips species invades a thrips gall and kills or evicts the gall-inducing thrips but does not feed on it. Such kleptoparasites are phytophagous, feeding on the plant tissues within the gall and using the invaded gall as a breeding site. In Australia, kleptoparasitic thrips species in the genera *Koptothrips* and *Turmathrips* are known to invade the galls induced by *Kladothrips* species on various species of *Acacia* (Crespi et al., 2004). Similarly, *Pharothrips* is a kleptoparasitic invader of *Drypetothrips korykis* galls on the leaves of *Drypetes deplanchei* [Putranjivaceae] (Mound &

Wells, 2020; Fig. 2C). Although these kleptoparasites are phytophagous rather than predators, there is no evidence that they stimulate further cell division of the plant tissues on which they are feeding.

In addition to predators and kleptoparasites, each of which has a precise biological relationship to a gall, there are species in which one or more individuals may simply be casual invaders, presumably sheltering from exposure to the weather. This type of invasion may sometimes be no more than thigmotaxis, a behaviour exhibited by many thrips that involves an adult crawling into a confined space. The record of the grass thrips *Haplothrips aculeatus* in a leaf gall of a *Ficus* [Moraceae] tree (Ananthakrishnan, 1978) probably has no more biological significance than the presence of a grass thrips in a commercial smoke detector (Kirk, 2004). However, some invasive thrips in galls may actually feed and breed alongside the gall-inducer without apparently disturbing it, and such an invader could be considered a true inquiline. For example, the open leaf galls on *Tetrastigma nitens* [Vitaceae] induced by *Leeuwenia tetrastigmae* in eastern Australia sometimes have been observed to shelter a colony of a *Teuchothrips* species (Fig. 1A). A further variant on this behaviour has been observed with *Gigantothrips elegans* feeding and raising a colony on the external surface of a leaf gall of a *Gynaikothrips* species on *Ficus* without invading the actual gall chamber (Fig. 1B).

Ananthakrishnan (1978) coined the term "company galls" for situations where several thrips species have been recorded within a gall. However, he provided no precise data that the species he listed had ever been found together within a single gall, and his list contains serious errors. One such error was the assumption that the nine Phlaeothripinae species recorded by Mound (1971) from leaf galls on *Geijera parviflora* [Rutaceae] in Australia all came from the same gall. These nine species were recorded as taken from several different plant individuals, although they were sometimes found on various plants growing at the same locality. Similarly, Ananthakrishnan (1978) lists eight species from *Ficus* as an example of a "company gall" but, and allowing for previously published synonymies, three of the species are known only from Tonga, two from Samoa, and one from Fiji; these thrips species were never found together, not even on the same island. Even a list of eight Phlaeothripinae species from galls on *Ficus retusa* in India (Ananthakrishnan, 1992) was not supported by precise data, and appears to be no more than a list of the species that have been found at various times in galls on that tree species. The diversity of relationships between thrips and galls is of considerable biological, ecological and evolutionary interest. Referring to any thrips found in a plant gall as a "gall-thrips" is not merely uninformative, it seriously inhibits biological and behavioural investigation into the significance of the relationships involved.

Taxonomy and systematics

In a search for patterns, Mound (1994) approached the subject of thrips and galls rather uncritically by accepting the published literature on the subject as taxonomically and systematically valid. However, in the years since the publication of that review our understanding of the systematic relationships amongst thrips taxa has changed radically, although the systematics of the plants on which galls attributable to thrips have been found has remained reasonably stable. The systematic distribution of the plants involved is highly asymmetric. One fern species has been reported with a thrips-induced gall, also one species of *Gnetum*, and there are records of gall-inducing thrips on a few monocot plants.

Figure 1. A. Opened leaf gall induced by *Leeuwenia tetrastigmae* on *Tetrastigma nitens* with *Teuchothrips* species invader. **B.** *Gigantothrips elegans* larvae on external surface of *Gynaikothrips* leaf gall on *Ficus* sp. **C.** Rolled leaves of *Commelina cyanea* induced by *Chaetanaphothrips orchidii*. **D.** Curled leaves of *Olearia lirata* induced by *Klambothrips oleariae*.

In contrast, at least 90% of gall thrips records are from dicots, and even within this group only a few records are from magnoliids, apart from Piperaceae. It is from species of eudicots that most gall thrips are recorded, although the 40 or more plant genera involved come from several different eudicot groups. Thus, apart from a clear association with higher plants, there seems to be no evolutionary pattern amongst the plants on which thrips galls have been found. This is not entirely unexpected, because opportunism seems to be an essential aspect of thrips biology and evolution (Mound & Teulon, 1995), and remarkably few thrips genera are strictly associated with a particular group of plants. A greater problem is the classification of the thrips involved in gall-induction, because of significant changes in perceived phylogenetic relationships in recent decades. The Thysanoptera classification adopted by Ananthakrishnan throughout his career, including in his final taxonomic publication (Ananthakrishnan & Sen, 1980), was developed by H. Karny and H. Priesner during the 1920s and 1930s. It was published formally by Priesner (1960) primarily in response to Stannard (1957) who provided the first attempt to consider phylogenetic relationships amongst the Phlaeothripidae. The Priesner classification used by Ananthakrishnan was essentially typological, with little phylogenetic relevance, and although it has been used by some other authors it remains misleading or even fundamentally incorrect in the relationships indicated. Following Stannard, the classification of Thysanoptera continues to be revised progressively through the use of both morphological data (Mound & Marullo, 1996; Zhang et al., 2019; Wang et al., 2020) and molecular data (Buckman et al., 2013). Without a suitable phylogenetic classification of Phlaeothripinae genera, this being the group to which most gall thrips belong, there is limited scope for examining the patterns of evolution of this habit of gall induction among thrips.

Gall Diversity

A gall is presumably a response by a plant to limit the damage caused by an insect feeding. Leaf-feeding on *Acer saccharum* [Sapindaceae] by the Thripidae species *Taeniothrips inconsequens* results in leaves becoming seriously distorted, dying and falling from the tree. This is a great disadvantage to the tree. In contrast, a leaf on which a gall has developed, regardless of the complexity of the gall structure, maintains its photosynthetic function, and the plant continues to grow and reproduce even when bearing many galls. This mutually beneficial association is often species specific, but there is a continuous gradient between damage to leaves caused by a thrips feeding and wound responses to thrips feeding that result in the diverse multicellular growths that we refer to as galls. For example, the Thripidae species *Chaetanaphothrips orchidii* is polyphagous, and can cause serious damage to various unrelated plants including orchids, bananas and citrus. This species has been observed damaging leaves on an extensive stand of the weedy herb *Commelina cyanea* [Commelinaceae]. Some of the leaves had been induced to curl and thus provided protection to the developing thrips (Fig. 1C), and this leaf distortion is not entirely dissimilar to the irregularly curled leaves (Fig. 1D) induced on *Olearia lirata* [Asteraceae] in Australia by the feeding of a Phlaeothripidae species, *Klambothrips oleariae*. There is thus a progression from haphazardly distorted leaves to more precise reactions. These range from the simplest of curled, but not rolled, leaf margins on *Ficus macrophylla* due to feeding by *Gynaikothrips australis*, to more complex folding or curling on *Ficus microcarpa* in response to *Gynaikothrips ficorum*, and the emergent tubular "nail-galls" induced by some *Liothrips* species (Fig. 2A). But there is no evidence that this sequence is associated with phylogenetic relationships among the thrips, and the form and structure of each gall is largely an independent, albeit characteristic, reaction by a particular plant species to attack by a particular thrips species. Particularly unusual thrips-induced galls occur on the woody stems of certain *Casuarina* [Casuarinaceae] trees in Australia (Mound et al., 1998). Two species of *Iotatubothrips* are known to induce the galls on these trees, one in Western Australia, the other in eastern Australia. The galls are multilocular and involve very hard wood, and those of both species are invaded by the same two species of kleptoparasites, *Thaumatothrips froggatti* and *Phallothrips houstoni*. But such a precise association between a particular thrips species and a particular plant species is known to have broken down in *Klambothrips myopori*. This is a specific gall-inducer on *Myoporum insulare* in Tasmania and southeastern Australia (Cameron & Mound, 2014), but the thrips has been inadvertently introduced into both California and Hawaii. In both countries it attacks and eventually kills two species of *Myoporum* with which it is not co-adapted; in California the widely planted but introduced New Zealand plant *M. laetum*, and in Hawaii the native plant, *M. sandwichense*.

Gall inducer diversity

Gall induction by thrips clearly has multiple, independent origins, and the thrips involved are members of two distantly related families, Thripidae and Phlaeothripidae. Among Thripidae, gall induction is known only among members of the Thripinae, one of the four recognized subfamilies. The growth abnormalities induced by the feeding of Thripinae species are almost all irregular leaf deformities, rather than precisely formed galls. These deformities are usually rather insignificant, although a population of adults and larvae of *Anaphothrips carlylei* can induce a large convoluted mass of flower-bud tissues on species of *Dianella* [Asphodelaceae] in southern Australia (Fig. 2B). A remarkable exception to such imprecise deformities is the reaction by leaves of *Austrosteenisia blackii* [Fabaceae] to the feeding of the Thripinae species *Cyrilthrips cecidis* in Queensland, Australia. This plant is induced to produce neat leaf folds, but many of these leaf-folds include a small second fold along the leaf edge similar to the flap on an envelope (Tree & Mound, 2009). This second fold closes the gall and is of biological significance, because those galls in which it is present have been found rarely to have one or other of the invasive predatory thrips *Androthrips monsterae* or *Mesandrothrips austrosteensia*.

It is amongst the Phlaeothripinae that most gall-inducing thrips are found. Many of these galls are relatively simple leaf deformations, although some are remarkably precise in their form (Fig. 2C). In contrast, galls induced on buds can be large and contain considerable populations of thrips. *Ocnothrips austrochinensis* induces large axillary pouch galls on *Getonia floribunda* [Combretaceae] (Mound, 2020), whereas *Acaciothrips ebneri* and *Thilakothrips babuli* on *Vachellia nilotica* and *Vachellia leucophloea* [Fabaceae] respectively, induce vegetative apical buds to form an irregular mass of distorted, entwined leaflets (Fig. 2D). Phylogenetic relationships among genera of Phlaeothripinae remain unclear, but three main supra-generic lineages are distinguishable within this subfamily (Mound & Marullo, 1996). Of these three, the *Liothrips*-lineage includes most of the gall-inducing species. Mound (1994) tabulated a series of about 40 genera from the Old World tropics that are possibly members of this lineage. The genera *Liothrips*, *Gynaikothrips* and *Acaciothrips* are certainly closely related, but the relationships of genera such as *Ocnothrips* and *Thilakothrips* are far from clear. Moreover, many of the listed genera are monotypic and inadequately diagnosed, and these remain of doubtful phylogenetic significance.

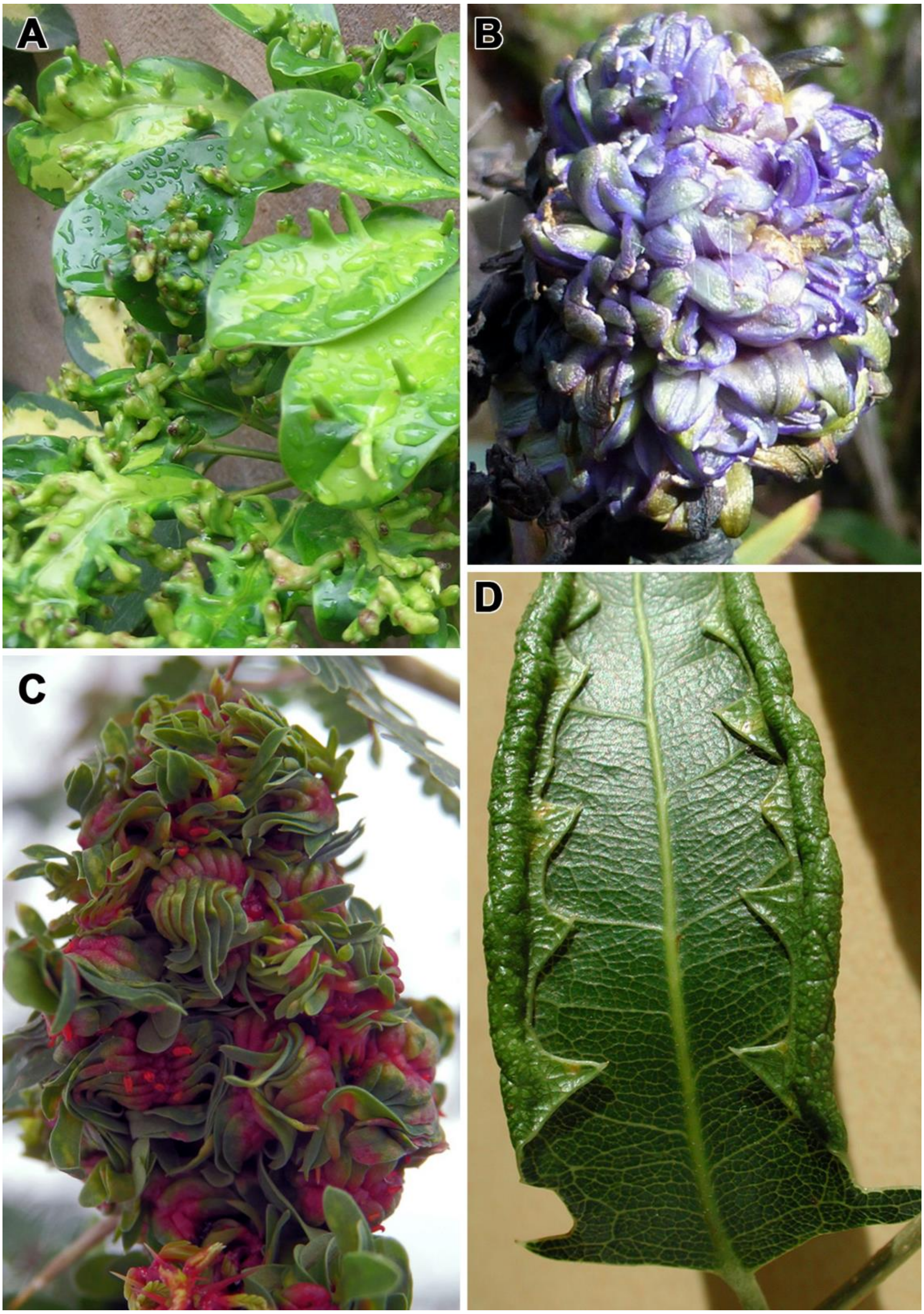

Figure 2. A. *Schlefflera* sp. leaves with nail galls induced by *Liothrips* sp. **B.** Galled flower on *Dianella* sp. induced by *Anaphothrips carlyleyi*. **C.** Leaf margin gall on *Drypetes deplanchei* induced by *Drypetothrips korykis*. **D.** Leaf bud gall on *Acacia nilotica* induced by *Acaciothrips ebneri*.

The *Haplothrips*-lineage within the Phlaeothripinae is now considered the Tribe Haplothripini (Mound & Minaei, 2007) and comprises mainly flower-inhabiting species. However, members of the genera *Euoplothrips* and *Mesothrips* are commonly referred to as "gall-thrips" because they are always found within leaf galls. But there is no evidence that any species in either of these two genera actually induces a gall. In Australia, *Euoplothrips bagnalli* is a gall-invader that has been found breeding in leaf galls induced by various species of Phlaeothripinae on plants in the following genera: *Acronychia*, *Alyxia*, *Callistemon*, *Ficus*, *Smilax*, *Piper* and *Tetrastigma*. Similarly, *Mesothrips jordani* appears to be an invader of *Gynaikothrips* leaf galls on *Ficus*, but in the absence of careful behavioural observations it is unclear if these thrips are kleptoparasites.

The third major group of Phlaeothripinae, the *Phlaeothrips*-lineage, comprises large numbers of genera of fungus-feeding species. One such genus, *Hoplandrothrips*, includes about 120 fungus-feeding species worldwide, but in East Africa two species have become phytophagous and induce rolled-leaf galls, with one a minor pest of coffee (Mound, 1994). Species in the genera *Choleothrips*, *Moultonides* and *Sacothrips* that are associated with galls on *Geijera parviflora* in eastern Australia, *Vuilletia houardi* that induces galls on *Guiera senegalensis* in western Africa, and the American *Amynothrips andersoni* that induces galls on *Alternanthera philoxeroides* [Amaranthaceae] have all been considered members of the *Phlaeothrips*-lineage. The phylogenetic relationships among these genera that are apparently involved in major host-shifts require investigation using molecular data. Particularly enigmatic are the relationships of the genus *Holopothrips*, the major Neotropical group of gall-inducing thrips. The character states of the many species in this genus (Lindner et al., 2018) are such that no clear relationships to any other Phlaeothripinae have been suggested. These species induce galls on many different plant genera, although a few of them are invaders of old, abandoned galls induced by cecidomyiid flies, thus emphasising yet again the behavioural opportunism so common amongst Thysanoptera.

Discussion

The weakest aspect of much of the published literature on thrips associated with galls is the absence of behavioural observations beyond the mere presence of these insects. The continued use of undefined terms such as "gall-thrips" and "inquiline" inhibit studies into functional relationships among these insects. Precise observations are needed on why any particular thrips is present in a gall: is it a gall-inducer, a predator, a kleptoparasite, an invader, or merely a visitor? The lack of such precise observations, together with the lack of a sound supra-generic classification within this Order, limit any conclusions that can be drawn concerning evolutionary patterns of host exploitation by thrips. Description by taxonomists of thrips structural diversity is only one step in our search for a broader understanding of the biological diversity and evolutionary radiation among Thysanoptera.

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Conflict of Interests

The author declares that there is no conflict of interest regarding the publication of this paper.

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روابط گیاه-میزبان و تریپس‌های گال‌زا، نبود الگو

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چکیـــده: حشرات بالغ تریپس‌ها به دلایل مختلف درون گال‌های گیاهی فعالیت دارند و استفاده از اصطلاح تریپس‌های گال بدون مشخص‌کردن یک ارتباط خاص، فاقد ارزش علمی و گمراه‌کننده است. یک تریپس، علاوه بر ایجاد گال ممکن است به عنوان شکارگر موجود ایجاد کننده گال، به عنوان کلپتوپارازیت تغذیه کننده از سلول‌های گیاهی و اشغال کننده زیستگاه ایجاد شده توسط موجود گال‌زا، به عنوان مستاجر گیاه‌خواری که با تعداد اندک بدون آنکه مزاحم موجود گال زا باشد یا به عنوان بازدیدکننده اتفاقی به منظور حفاظت خود از خشکی، حضور دارد. این روابط مختلف با تاکید بر این‌که اطلاعات اندکی در مورد روابط فیلوژنتیک خانواده‌ی Phlaeothripidae با بیشترین تعداد گونه‌های گال‌زا وجود دارد، مورد بحث قرار گرفت. روابط میزبانی تریپس‌ها در گال‌ها تا حد زیادی از نوع فرصت‌طلبی است. در عین حال مثال‌های محدودی نیز از روابط نزدیک بین تریپس‌ها و گیاهان در سطح جنس در هر دو گروه وجود دارند.

واژگـان کلیدی: Phlaeothripidae، تریپس‌های گال، کلپتوپارازیت‌ها، مستاجرین، شکارگرها