ABSTRACT
The Psylloidea, >4000 named species known today, are plant-feeding, sap-sucking insects sleeved under the Sternorrhyncha. Most species of Psylloidea are confined to the tropics. They occur as galling, free-living, and lerp-forming taxa. Lifecycles and generations of galling Psylloidea vary in temperate and tropical worlds. The Triozidae, Aphalaridae, and Psyllidae include several taxa that induce galls of diverse morphologies, from simple pits and leaf-margin rolls to complex pouches and of two-tier structures. The feeding mechanism and nutritional physiology of the galling taxa of the Psylloidea differ from those of the free-living and lerp-forming species. A majority of the galling Psylloidea are associated with the dicotyledons and a small number with the monocotyledons. The galling Psylloidea are specific to certain plants. Their host specificity is regulated by specific lipids and sterols. The galling Psylloidea show conservative behavior in terms of geographical distribution. Although the life histories of several galling-inducing Psylloidea are known today, aspects explaining their association with host plants are little known. Details of nutritional physiology of galling-inducing Psylloidea are less known presently compared with that of the free-living species. A better understanding of the association and level of relationship between galling Psylloidea and their host plants is necessary.

Gall-inducing Psylloidea (Insecta: Hemiptera) – plant interactions*

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Introduction
The Psylloidea are sap-sucking, exclusively plant-feeding superfamily of the Hemiptera. About 4000 species are currently named and classified under the Aphalaridae, Carsidaridae, Mastigimataceae, Liviidae, Calophyidae, Psyllidae, and Triozidae (Burckhardt et al. 2021). The Psylloidea occur as free-living, lerp-forming, and galling taxa. Most adult Psylloidea measure between 2 and 4 mm in their overall body length. Their hind legs include well-developed coxae that enable them to jump, and therefore, are referred to as the ‘jumping-plant lice’ (louse – singular) in common parlance. Several species of the Psylloidea, e.g. Diaphorina citri (Psyllidae), Triozoa erytreae (Triozidae), Cacopsylla pyricola (Psyllidae), Heteropsylla cubana (Psyllidae), and Bactericera cockerelli (Triozidae) damage plants of agricultural and horticultural relevance (Hodkinson 2009). By their sucking – feeding habit, they transmit microbial-plant pathogens, similar to their plant-feeding allies of the Auchenorrhyncha. Diaphorina citri and T. erytreae transmit species of Candidatus Liberibacter (Proteobacteria: Rhizobiaceae) thus inducing the citrus-greening disease (the Huanglongbing disease) in different species and cultivars of Citrus (Rutaceae) in Asia, Africa, and the Americas (Hall et al. 2013; Barnett et al. 2019). In contrast, some Psylloidea are useful in the biological management of weedy plants: e.g. Calophya latiforces (Calophyidae) in managing populations of Schinus terebinthifolia (Anacardiaceae) in the USA (Diaz et al. 2015). Some Psylloidea species are invasive. One well-known example is the lerp-forming Glycaspis brimblecombei (Aphalaridae) that lives on various species of Eucalyptus (Myrtaceae) in Australia, and commonly on E. camaldulensis, E. rudis, and E. reticulata cultivated in many countries for commercial reasons (Brennan et al. 1999). Glycaspis brimblecombei spread from Australia to North America in 1998 and to Europe in 2009 (de Queiroz et al. 2013), when species of Eucalyptus were introduced in those parts of the world for plantation forestry.

The taxonomy of the Palaearctic Psylloidea is reasonably well clarified presently (Hodkinson and White 1981; Hodkinson 1986, 1989; Burckhardt and Mifsud 2003; Burckhardt 2005a, 2009; Burckhardt et al. 2004; Batta and Burckhardt 2018; den Bieman et al. 2019; Burckhardt et al. 2021). Ram Nath Mathur’s Psylloidea of the Indian Subcontinent (1975) is one comprehensive document on the taxonomy and biology of the Psylloidea of the Indian subcontinent. A 2018-checklist of the Indian Psylloidea by Burckhardt et al. is an up-to-date addendum to Mathur (1975). Knowledge of the Psylloidea of the Afrotropical and Neotropical realms is poor, whereas that of the other biogeographical realms is better known (Hodkinson and White 1981; Hodkinson 1986, 1989; Burckhardt et al. 2004; Burckhardt and Mifsud 2003; Burckhardt 2005a; den Bieman et al. 2019; Halbert and Burckhardt 2020).

Distribution of gall-inducing Psylloidea and the types of galls they induce
Whereas free-living Psylloidea occur almost throughout the world, the lerp-forming Psylloidea – mostly of the...
Aphalaridae – are especially diverse in the Australian landmass, represented by c. 50% of the known lerp-forming taxa of the world (Hollis 2004). The distribution of gall-inducing Psyllioidea vis-à-vis that of the lerp-forming taxa does not present any consistency in the pattern. However, what appears consistent among the gall-inducing Psyllioidea is that they are species-rich and more diverse in the tropics (Burckhardt et al. 2018). For instance, c. 5% of the gall-inducing Psyllioidea known globally occur in the Indonesian Islands and the Philippines (Docters van Leeuwen and Docters van Leeuwen-Reijnvann 1914; Uichanco 1919; Partomiharjo et al. 2011). Among the Psyllioidea, the Triozidae, Aphalaridae, and Calophyidae include high numbers of gall-inducing taxa, whereas the Carсидaridae, Liviidae, and Psyllidae include relatively fewer numbers (Burckhardt 2005a; Yang and Raman 2007; Burckhardt et al. 2021). Among these, the Triozidae and Aphalaridae include most of the gall-inducing taxa (Burckhardt 2005a; Raman 2012).

Galls induced by the Psyllioidea present highly varied morphologies: from simple leaf rolls to complex two-tier structures (Yang and Raman 2007). For example, Lauritrioza alacris (previously Trioza alacris) (Triozidae) induces leaf rolls on Laurus nobilis (Lauraceae) in Europe (Bouyjou and Nguyen 1974) (Figure 1(a)). Psyllipsis fraxini (Liviidae) induces leaf-margin rolls on Fraxinus excelsior (Oleaceae) in Europe (Schindler and Ehrhardt 1964). Trioza ocoteae (Triozidae) induces pit galls on Ocotea acutifolia (Lauraceae) in South America (Lizer Trelles and Molle 1945) (Figure 1(b)). Schedotrioza multitudinea (Triozidae) induces urn-shaped galls on Eucalyptus obliqua (Myrtaceae) in Mount Lofty Ranges, South Australia (Taylor 1990) (Figure 1(c)). Pseudophacopteron tuberculatum (Aphalaridae) induces spherical, pouch galls on Alstonia scholaris (Apocynaceae) in India (Mathur 1975; Mani 2000; Albert et al. 2011). Pseudophacopteron aspidosperrmi and P. longicudatum (Aphalaridae) induce globular and beutel galls on Aspidosperma macrocarpon and A. tomentosum (Apocynaceae), respectively, in Brazil (Malenovský et al. 2015). Trioza bullatae (Triozidae) induces globular galls on Ocotea bullata (Lauraceae) in South Africa (Burckhardt et al. 2012). Trioza jambolanace (Triozidae) induces near-spherical, closed galls on Syzygium cumini (Myrtaceae) in India (Mathur 1975; Raman 1991). Pachypsylla celtisdismedia (Carсидарidae) induces closed pouch galls on Celtis occidentalis (Cannabaceae) in North America (Riley 1881; Beisler and Baker 1992) (Figure 1(d)); Psyllipsis udei (Triozidae) induces spherical, closed galls on Ficus fulva and F. variegata (Moraceae) in the Indonesian islands, Philippines and in New Guinea (Rübsaamen 1899; Uichanco 1919; Percy et al. 2015) (Figure 1(e)). Schedotrioza eucalypti (Triozidae) induces spherical galls on Eucalyptus dives in (authors’ unpublished work) (Figure 1(f)). An unnamed species of Glycaspis (Synglycaspis) (hereafter ‘Glycaspis’ (Synglycaspis) sp. A’) belonging to the Aphalaridae induces globular, closed, pouch galls on Eucalyptus macrorhyncha (Myrtaceae) in Central-West New South Wales, Australia (Sharma et al. 2015a) (Figure 1(g)). Apsylla cistellata (Aphalaridae) induces fir-cone-like galls on the axillary vegetative buds of Mangifera indica (Anacardiaceae) along the Indo-Gangetic plains of India (Mathur 1975; Singh 2003) (Figure 2(a)). Pha-copteran lentiginosum (Aphalaridae) induces complex two-tier galls on Guraga pinnata (Bursaraceae) in subtropical peninsular India (Mathur 1975; Raman 1987; Mani 2000) (Figure 2(b)).

**Biological Galls of Indo-Pacific Psyllioidea**

Juvenile stages of the Psyllioidea (previously ‘nymphs,’ ‘nymphal instars,’ ‘larvae’) will be referred to as ‘immatures’ in this article, following Burckhardt et al. (2014). Immatures of different species of Psyllioidea show striking variations in their...
morphology in accordance with the plant parts they infest (White and Hodkinson 1985). For instance, the immatures of those Psylloidea living in pit galls have near-circular outlines with sclerotized dorsal surfaces almost covering the pit: e.g. Calophyta clavuligera (Calophyidae) on Litracae brasiliensis (Anacardiaceae) in Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Burckhardt and Bassett 2000). In contrast, those living in closed galls have short legs and weakly sclerotized bodies, compared with those in pit galls. Short legs and weakly sclerotized bodies are considered an adaptation for living in closed galls (e.g. Glycaspis (Synglycaspis) sp. A) (Burckhardt 2005a). The lerp-forming taxa, e.g. species of Glycaspis construct dome-shaped lerps using sugary secretions on the leaves of Eucalyptus sideroxylon (Myrtaceae), within which an individual of Glycaspis will reside until becoming adults (Figure 3). Immatures of both free-living and gall-inducing Psylloidea also secrete sugary filamentous material, but not as intensively as the lerp-forming taxa do (Sharma and Raman 2017). Almost all known gall-inducing Psylloidea secrete sugary filamentous and retain them within the galls they induce (e.g. Glycaspis (Synglycaspis) sp. A on E. macrorhyncha, Figure 1(g), Celtisaspis sinica (Carcidariidae) on Celtis sinensis (Cannabaceae) (Yang and Li 1982; Yang and Raman 2007; Sharma et al. 2015a). Pachysyrella cohabitan (Carcidariidae) occupies the galls induced by other species of Pachysyrella (e.g. P. celcidismamma) on different species of Celtis in North America (Yang et al. 2001; Burckhardt 2005a).

Life stages of the Psylloidea include an egg, five immature, and adult stages. Females are usually 0.15x larger than males and live 7–10 d longer than males (Sharma et al. 2013, 2014a, 2015a). Life cycles of gall-inducing Psylloidea are univoltine in temperate, subarctic, and subantarctic regions, supplemented by inactivity in winter (e.g. Lauritrioza alacris, Triozidae). In the tropics, in contrast, they are multivoltine, completing several generations in a year (e.g. Trioza jambolanae, Triozidae; Diaphorina truncata Psyllidae) (Balakrishna P. Raman 1992). Populations of gall-inducing T. jambolanae on the leaves of S. cumini present varied biologies in different parts of India under different climatic conditions: in humid and warm peninsular India, T. jambolanae completes 6–8 generations in a year (Raman 1991), whereas in the cooler Mussoorie Hill Ranges, proximal to the Himalaya, the same species presents only one generation in a year with a long diapause from late autumn (late October–early November) to early spring (late February–early March) (Mathur 1975). The gall-inducing Aphalaridae in Central-west New South Wales (e.g. Glycaspis (Synglycaspis) sp. A on leaves of E. macrorhyncha) complete two generations in a year. In contrast, the lerp-forming Aphalaridae (e.g. unnamed species of Glycaspis on Eucalyptus sideroxylon, Myrtaceae) complete 3–4 generations, and the free-living Aphalaridae (Ctenarytaina eucalypti on E. globulus) complete 5–6 overlapping generations in a year (Sharma et al. 2014a). Compared with other major gall-inducing taxa belonging to the Cynipidae and Cecidomyiidae, only a few parasitoids are presently known to be associated with gall-inducing Psylloidea. Psyllaephagus bliteus (Hymenoptera: Encyrtidae) is a non-specific parasitoid that is commonly associated with various species of gall-inducing Psylloidea, irrespective of geographical distances. In recent years, Psyllaephagus ramamurthyi, P. bachharidis, P. garuga, P. phacopteron, P. caillardiae, P. longiventris, P. ogazae, Aprostocetus essugenjaoi (Eulophidiae), one unnamed species of Eurytoma (Eurytomediae), one unnamed species of Tornyoides (Tornauidae), and one unnamed species of Synopeas (Platygastridae) have been described from galls induced by the Psylloidea (Hollis 2004; Cuevas-Reyes et al. 2007; Singh and Singh 2011; Hayat et al. 2013; Veenakumari et al. 2018; Zhao et al. 2021).

**Gall development (Cecidogenesis)**

Feeding action of the first-instar immatures of Psylloidea triggers gall initiation (Burckhardt 2005a; Raman 2011).
(Figure 4). Eggs deposited by *Trioza flavipennis* (Triozidae) on leaf surfaces of *Aegopodium podagraria* (Apiaceae) induce pit galls in Europe (den Bieman et al. 2019). Incitement of a gall by the egg and not by a first-instar immature is rare among the gall-inducing Psylloidea. We will use the gall systems induced by *T. jambolanae* and *A. cistellata* on *S. cumini* and *M. indica*, respectively, as examples in this article. Gall development on the leaves of *S. cumini* – from initiation to dehiscence – gets completed in c. 40 d in subtropical – tropical southern India. Growing immatures of *T. jambolanae* shift their feeding sites within galls, synchronizing with gall growth. Mature galls dehiscence because of specific physiological changes in cells in the gall wall, which differentially produces starch and polyphenolic materials. Cells that include secondary metabolic products (polyphenolic materials) turn into sclereids (dead cells with thick lignified cell walls) during later stages of gall growth, i.e. when occupied by the usually non-feeding, fifth-stage immatures. Sclereids occur in linear files, alternating with files of living, thin-walled parenchyma. The functionally antagonistic sclereids and parenchyma, supplemented by the tension caused by water deficit, facilitate the mature gall to dehisce from a weak point in the gall’s roof, splitting along the files of thin-walled parenchyma (Raman 1991). Feeding action of the first-instar immatures of *A. cistellata* (‘embryonic stages’ according to Gajendra Singh 2000, p. 2003) triggers the gall, which grows for the next c. 120 d. The immatures, partly remaining enclosed in their eggshells, feed on the same leaf where the adult female had oviposited (Singh et al. 1975). The feeding action of several first-instar immatures stimulates the gall through the modification of the nearest vegetative axillary bud, usually at a distance of 3–6 mm from the leaf on which the first-instar immatures feed. First-instar immatures crawl and occupy the spaces between the unfurled leaves and stem axis in the shoot bud as it transforms into the gall (Figure 2(a)) that resembles a fertile cone of *Abies* (Pinaceae).

In the *Psidium myrtoides* (Myrtaceae) – *Nothotrioza myrtoidis* (Triozidae) gall system, an increase in biomass is indicated due to pronounced hyperplasia of the median and outer cortical cell layers (Carneiro and Isaias 2015a, 2015b). The globoid shape of the gall is the outcome of centrifugal gradients between tissue hyperplasia and cell hypertrophy (Carneiro et al. 2014). Demethyl-esterified homogalacturonans denoted the activity of pectin methylesterases especially during the senescent phase, increasing the stiffness of cell walls, which, which according to Carneiro et al. (2014) triggers gall dehiscence.

**Gall initiation**

Salivary enzymes (the effector proteins) released by the feeding immatures trigger gall initiation. A 58 kD protein isolated from the saliva of *Eurosta solidaginis* (Diptera: Tephritidae) is indicated as the key trigger in the induction of ball galls arising on the stems of *Solidago altissima* (Asteraceae) (Carango 1988). The role of a specific protein, viz., cysteine-tyrosine-cysteine residue, has been recently demonstrated as the key trigger factor in gall initiation by *Hormaphis cornu* (Hemiptera: Aphididae) on *Hamamelis virginiana* (Hamamelidaceae) (Korgaonkar et al. 2021). Although we liberally speak of the role of plant-growth hormones (PGRs) in gall induction, the establishment of either one or a small group of activated cells – the metaplasied cell (s) (*sensu* Küster 1911; Maresquelle and Meyer 1965) – is the earliest ≥24 h recognizable response to feeding by any gall-inducing arthropod. The discharge of a protein (or a cluster of proteins), however, remains to be verified in the instance of gall-inducing Psylloidea. The second key trigger is chitin discharged from the mandibles of the feeding arthropod. Chitin – a glucosamine polymer – is a principal constituent of arthropod mouthparts (Brożek et al. 2015). Plants include chitinases (Collingel et al. 1993) and are capable of recognizing chito-oligosaccharides during attack by an invading organism, be it a plant-pathogenic fungus or a plant-feeding arthropod. The chitin, in principle, acts as an elicitor (Sharma et al. 2019) provoking the first attacked plant cell to recruit a novel pathway negotiating either a susceptible or a resistant response (Rohfritsch 1988; Westphal et al. 1990; Puszthelyi 2018). Chitin stimulates mitogen-activated protein kinase (MAPK) cascades and a network of transcription factors (Schweitzer et al. 2013; Bi et al. 2018). Activation of MAPKs provokes osmotic changes in the cytoplasm of the attacked cell, resulting in the establishment of one or more metaplasied cell(s). Wounding of plant cells by the feeding immature stage of the psylloid, accompanied by a chemical ‘shock’ resulting from the action of chitin and salivary proteins (Sharma et al. 2014b; Sharma and Raman 2017) induces rapid chemical alterations, such as vacuolar alkalization, in the subcellular environment of host-plant cells (Westphal...
Proteins specific to the inducing psylloid species interact with the host-plant’s genomic material and dramatically alter the developmental pathway resulting in a gall in a specific timeframe. The dissipation of various, newly synthesized metabolites remains restricted to the gall and its immediate neighborhood in the attacked plant organ, explaining why the altered physiology of the gall – when fully organized – is limited to that part of the plant only.

PGRs (especially the auxins) have been demonstrated in mature galls of *Metrosideros polymorpha* (Myrtaceae) induced by an unnamed Triozidae in Hawaii (Bailey et al. 2015). Bailey et al. suggest significant enrichment of auxin-response gene action during gall induction. During later stages of gall growth, i.e. when inhabited by the third-, fourth-, and fifth-stage immatures, PGRs kick in enabling the realization of the final shape of the gall (Miller and Raman 2019; Raman 2021). Other secondary metabolites, such as volatile phenols, especially the ortho-dihydric phenols, as shown in the galls of *Pauropsylla depressa* (Triozidae) on the leaves of *Ficus glomerata* (Moraceae) influence the lignification, anti-auxin activities, and IAA-oxidase inhibition (D'Souza and Ravishankar 2014). During gall induction by *Glycaspis* (Synglycaspis) sp. A on the leaves of *E. macrorhyncha*, membrane-bound galactolipids (mono- and di-galactosyl-diacyl-glycerols: MGDG, DGDG) occur in greater levels than storage triglycerides, which point to substantially changed physiology of cell membranes (Sharma et al. 2016). The DGDG level increases during the inhabitation of the first- and second-stage immatures of *Glycaspis* (Synglycaspis) sp. A reinforcing that physiological compatibility materializes between *Glycaspis* (Synglycaspis) sp. A and the host *E. macrorhyncha*.

Plants hosting gall-inducing insects employ diverse strategies to mitigate the stress (Hirano et al. 2020) that materializes during gall induction and ensuing growth- and differentiation phase. These stress-neutralizing strategies are necessarily dictated by the genetic constitution of host plants. Plant responses are inevitably mediated by molecular changes, but those responses vary dramatically with the kinds of protein triggers provided by the psylloids. During gall induction, susceptible plants use a flexible, short-term strategy responding to the stress inflicted by the psylloid. That short-term strategy involves mobilization of energy and other metabolites to the injured site as a reparative effort to heal the injury, which the inducing insect exploits the plant for its nourishment. This becomes clear when we recognize that the plant returns to its normal physiology the moment the insect ceases to feed (Rohfritsch 1971, p. 1992). Genetic factors play a role in controlling the shape of the gall, coordinated by the innate correlating morphogenetic factors that normally operate in the plant (Miller and Raman 2019; Raman 2021).

**Mouthparts, feeding biology, and nutritional physiology of the Psylloidea**

Psylloidea have long, at least 500 μm, piercing-and-sucking mouthparts, made of two pairs of interlocking styletes (also referred to as ‘stylet,’ ‘stylet bundle’), which are the modified mandibles and maxillae (Figure 5). Their mouthparts can function for both salivation and ingestion of plant sap. The salivary glands consist of one principal and one accessory gland (Sharma et al. 2014b, 2015b). Psylloid saliva includes...
cell-digesting enzymes: cellulases, amylases, and pectinases, which facilitate delicate styllet movement within plant tissue, inflicting minimal physical damage. Salivary dehydrogenases polymerize phenolics sequestered in the plant-cell apoplast and evoke induced-defence responses (Sharma et al. 2013, 2014b, 2015b). The known gall-inducing Psylloidea possess longer styllet bundles than those of the free-living and lep- forming species. For example, the styllet bundle of a gall-inducing species *G. (Synglycaspis)* sp. A is c. 950 μm long, whereas its adult body length is 4.6–4.8 mm. In a free-living species, *viz.*, *Ctenarytaina eucalypti*, the styllet bundle is 600 μm, whereas the body length is 2.5–2.8 mm. In a lep-forming, unnamed species of *Glycaspis*, it is 850 μm, whereas the body length is 3.2–3.6 mm. During the early stages of gall development, the inhabiting first- and second-stage immatures, and occasionally the third-stage immature feed on undifferentiated parenchyma made of thin cell walls and rich, dynamic cytoplasm. Feeding activity of the third- and fourth-stage immatures usually shifts to phloem ducts (Sharma et al. 2015a; Miller and Raman 2019).

Among the biologies of different gall-inducing Psylloidea known today, gall induction by *A. cistellata* is noticeably different from the better known Triozidae and other Aphididae, although finer details of the feeding biology of *A. cistellata* are yet to be clarified. Simultaneous feeding by several first-instar immatures of *A. cistellata* stimulates gall induction by translocating a ‘stimulus’ of unknown chemistry, invariably over a distance of 3–6 mm (Burckhardt 2005a). Gall induction by *A. cistellata* is vaguely similar to the gall-induction behavior of *Adelges cooleyi* (Aphidoidea: Adelgidae) on the vegetative shoot buds of *Picea glauca × P. engelmannii* hybrids (Pinaceae) in North America (Havill and Footitt 2007; Holman 2009). In the *A. cooleyi* – *Picea glauca × P. engelmannii* system, a dose-dependent chemical stimulus translocates over a ‘long’ distance from the point where the gall-founding female first settles and commences feeding (Sopow et al. 2003). The similarity between the shoot galls induced by *A. cistellata* on *M. indica* and *A. cooleyi* on *P. glauca × P. engelmannii* needs to be treated as ‘apparent,’ because, in the galls arising on the vegetative axillary shoot buds of *M. indica*, the first-instar immatures of *A. cistellata* induce the gall, whereas, in the vegetative axillary shoot-bud galls of *Picea glauca × P. engelmannii* hybrids, adult females of *A. cooleyi* induce galls. The distance between the site of gall-inducing agent(s) and the site where galls manifest is greater in *A. cooleyi* – *P. glauca × P. engelmannii* system than what is known in *A. cistellata* – *M. indica* system.

Feeding action of the first-instar immatures of gall-inducing Aphalaridae (e.g. *Glycaspis* (*Synglycaspis*) sp. A) plasmolyzes the cytoplasm of the attacked epidermal and palisade cells in plant tissues in less than the first six h of attack (Figure 6). The cells around the styllet rapidly respond (i.e. within the first six h of attack) to the psyllid by present- ing hyaline cytoplasm and unusually thick horizontal walls. Apoplastic nutrient movement occurs in these cells (Sharma et al. 2015a, 2015b), which include large intercellular spaces, reinforcing the production of reactive oxygen species (Sattelmacher 2001). The feeding action of gall-inducing Psylloidea induces subcellular alterations of relatively low intensity (Sharma et al. 2015a, 2015b) when compared with those cells attacked by free-living taxa. In addition to the mechanical damage caused by the insertion of the styllet, the discharged salivary chemicals (especially the proteins) inflict a chemical injury, activating a cascade of transcriptomic changes as shown in the feeding sites of *D. citri* (De Vos et al. 2005). In the Psylloidea, the salivary-enzyme profiles are complex. For instance, in the free-living species *C. eucalypti*, 60–65 kD proteins such as oxidoreductases, dehydrogenases, and esterases and 58 kD proteins such as trehalases, amylases, lipases, and cytochrome P–450 occur (Sharma et al. 2015b). Enabled with such a wide range of enzymatic proteins, the amylases help the feeding Psylloidea to pierce host-plant tissues; the oxidoreductases, dehydrogenases, and esterases detoxify host-plant allelochemicals (Sharma et al. 2015b). In the gall-inducing Psylloidea, the role of detoxifying enzymes is not yet adequately clarified: however, cell-degrading enzymes, amylases, proteases, and lipases have been demonstrated in the saliva of the gall-inducing *T. jambolanae* (Rajadurai et al. 1990). On the other hand, the galls induced by *P. depressa* on *F. glomerata* show the intense activity of amylases and invertases compared with normal leaves. Although the saliva of gall-inducing Psylloidea include both degrading and detoxifying enzymes, the association of the spherical pouch gall-inducing *P. tuberculatum* on a latex-producing *A. scholaris* is intriguing because *A. scholaris* includes secondary metabolites such as picrinine, schloracine, and many triterpenes that are generally toxic to any feeding arthropod (Waliwitiya et al. 2012), leaving the question how the immatures of these Psylloidea are able to detoxify such secondary metabolites and feed on these plant materials. Similar questions arise in the interactions between gall-inducing psyllids on various Anacardiaceae (e.g. *Calophyia on Schinus, Apsylla on Mangifera*) that usually include a wide suite of secondary metabolite compounds, such as alkyl- and alkenyl phenols.

Leaves of *E. macrocarpi* hosting *Glycaspis* (*Synglycaspis*) sp. A show a high δ13C–δ15N ratio. An increase in δ15N and a decline in δ13C occurs consequent to *Glycaspis* (*Synglycaspis*) sp. A’s feeding action indicating that the populations of this taxon utilize carbon-based materials and the mobile nitrogenous material that occur in relatively high concentrations at the feeding sites (Sharma et al. 2015c). During gall induction, rapid mobilization of nutrients occurs
from the normally biosynthesizing plant parts to the injured – feeding – sites. Consistent mechanical wounding by the feeding immature is restricted to gall sites only, but the stress caused by the mechanical injury spreads centrifugally into tissues in the vicinity (Sharma et al. 2015a). Infestation by Eucalyptus macro-rhyncha. (nutritive cells, nc; vascular trace, vt; stylet track, st; stomatal aperture, s; proliferating epidermal cells, pe; neotformed meristem, nm; dividing cells, circled area) [bar = 100 μm]. (b) submicroscopic changes in E. macrorhyncha leaf (cross-sectional view) due to feeding by Glycaspis (Synglycaspis) A; (endosome, es; chloroplast, ch; secondary metabolic inclusion, sm; autophagic vacuole, av; cell junctions, cj; mitochondrion, m; desmosomal condensation, dc; oil inclusion, oi; dissolved middle lamella, ⇔; stylet track, circled area) [bar = 1 μm] (Source: Sharma et al. 2015a).

A majority of the free-living Psylloidea extract carbohydrates and fatty acids from the phloem sap, although the phloem diet is known to be generally deficient in essential amino acids, vitamins, and lipids. Symbiotic microorganisms (e.g. Carsonella rudii, and other Enterobacteriaceae [Proteobacteria]) occurring in the bacteriome of the Psylloidea compensate for the deficiency of nitrogenous materials (Nakabachi et al. 2006). The nutritional ecology of gall-inducing Psylloidea is strikingly different from that of the free-living Psylloidea. For instance, the feeding pressure imposed by a free-living and gregariously feeding, unnamed species of Cardiaspina on a species of Eucalyptus results in the rapid mobilization of nutrients from uninfested to infested parts of the host plant (White 1970). In contrast, the feeding pressure imposed by solitarily occurring, gall-inducing T. jambolanae stresses leaf tissues of S. cumini creating ‘nutrient sinks’ in galls to extract concentrated levels of nutrients (Raman 1991; Mani and Raman 1994). Galls are ‘nutrient sinks’ for carbon-based and nitrogenous nutrients translocated from normal plant parts to galls (Kirst and Rapp 1974; Raman et al. 2006). Once the gall is initiated, the hosting plant pumps minerals and nutrients to repair and heal the injured site. The nutrients, however, are utilized by the inhabiting immature psylloid and the gall turns into a site supplying nutrients to the actively feeding immature (or, immatures, as the case may be) (Raman et al. 2006).

Galls as the site of concentrated nutrients also attract non-gall-inducing Psylloidea, which occupy the space in galls induced by other arthropods during certain portions of their life cycles to utilize the readily available nutrients for a longer period than what will be available in ungalled leaves. For example, a few unnamed species of the Psylloidea and Aphidoidea feed on leaves of Rhamnus cathartica (Rhamnaceae) that bear galls induced by Trichochermes walkeri (Triozidae) (McLean 1994; Burckhardt 2005a). Populations of Pachypsylla cohabitans inhabit galls induced by P. celtidismamma arising on the leaves of Celtis occidentalis, utilize the nutrients available in galls, and in the process negatively affect the performance of the immatures of the inducing P. celtidismamma (Yang et al. 2001). Occupation by inquilinous Hymenoptera and consequent modification of gall tissues by their feeding are amply demonstrated in...
the galls induced by Cynipidae in North America (Brooks and Shorthouse 1998).

**Association between gall-inducing Psylloidea and plants**

A majority of the Psylloidea are associated with dicotyledons. Very few gymnosperms are known hosting the Psylloidea (Burckhardt 2005b; Raman et al. 2005; Yang and Raman 2007): e.g. two species of *Ehrendorferiana* on *Austrocedrus* and *Fitzroya* (both Cupressaceae) in Chile and *Trioza colorata* and *T. dacrydii* on (Podocarpaceae) in New Zealand (Burckhardt 2005b). Fewer than 2% of gall-inducing Psylloidea live on monocotyledons: e.g. Juncaceae, Cyperaceae (Ouvrard et al. 2015). Particularly the species of *Livia* (Liviidae) are associated with species of Juncaceae (Hodkinson and Bird 2000; Burckhardt 2005a). For instance, *L. junci* induces organoid galls on the shoots of *Juncus articulatus* (Juncaceae) (Schmidt 1966; Schmidt and Meyer 1966; Hodkinson 1986; Meyer 1987) (Figure 8). A study in Portugal suggests that *L. junci* vectors a phytosystem that induces the witches-broom disease on *Juncus fontanesii* (Juncaceae), previously indicated as ‘*L. junci*-induced galls’ (Jarzembowski et al. 2013). A vast majority of gall-inducing Psylloidea are associated with species of Myrtaceae, and Asteraceae (Burckhardt 2005a; Ouvrard et al. 2015). Gall-inducing taxa belonging to the Triozidae, Aphalaridae, and Calophyidae are generally associated with species of Magnoliidae, Myrtales, Sapindales, and Malvales (Burckhardt 2005a). The Asteraceae (Campanulid/Asterid II: Asterales) host more of gall-inducing Aphalaridae and a few of the gall-inducing Triozidae (Burckhardt and Mifsud 2003; Burckhardt 2005a). The Asteraceae-associated Triozidae induce galls on the floral capitula, in addition to inducing leaf rolls and bean-shaped galls, whereas the members of monophyletic Calophyidae induce pit, cone-like, disk-shaped, spherical, and beutel galls on various species of Anacardiaceae (Malvids/Rosid II: Sapindales) (Burckhardt 2005a). A majority of the Oriental gall-inducing Psylloidea are tied to tree taxa of the families classified under the Eurosids (Yang and Raman 2007; Yang et al. 2009, 2013).

The gall-inducing Psylloidea and those of the lerp-forming and free-living guilds are narrowly specific to plants. A vast majority of the gall-inducing Psylloidea, similar to the gall-inducing Cecidomyiidae (Diptera) and Cynipidae (Hymenoptera), are highly selective of host plants and

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**Figure 7.** Isotopic carbon and nitrogen values in the normal and gall-bearing leaves of *Eucalyptus macrorhyncha* hosting *Glycaspis* (*Synglycaspis*) sp. A in Australia. (a) $\delta^{13}C$ values in uninfested (U) and infested (1C–5C: five developmental stages of *Glycaspis* (*Synglycaspis*). (b) $\delta^{15}N$ values in uninfested (U) and infested (1N–5N: five developmental stages of *Glycaspis* (*Synglycaspis*). Error bars are shown along the y axes of the graphs (source: Sharma et al. 2015c).

**Figure 8.** Galls modifying the vegetative shoot buds of *Juncus articulatus* (Juncaceae) induced by *Livia junci* distributed in Continental Europe (*sensu* Epstein 2014). Gall development inhibits leaf expansion and the elongation of internodal segments. (Source: Jiří Kameníček: Biolib.cz) (b) A line sketch of the gall (Source: Schmidt and Meyer 1966). (No scale bars are indicated by respective authors).
remain committed to them (Raman 2009). Different species of Schinus (Anacardiaceae) host more than one species of different genera of gall-inducing Psylloidea, such as Tainarys schini and T. maculipicta (Aphalaridae), Calopha clausa, C. hermitiae, and C. mammifex (Calophyidae) on different species of Schinus (Burckhardt and Bassett 2000). Trioza fletcheri minor (Triozidae) induce galls of nearly identical morphologies on different species of Terminalia (T. tomentosa, T. arjuna, T. catappa, T. paniculata, and T. tomentos x T. arjuna, Combretaceae) in the Indian subcontinent (Mathur 1975; Raman et al. 1996; Burckhardt et al. 2018). Several species of the same genus of gall-inducing Psylloidea also, although infrequently, occur on the same host. For example, three gall-inducing Calopha, viz., C. mammifex, C. rubra, and C. scrobicola occur on Schinus polygamus (Anacardiaceae) in Central Chile; similarly, C. catillicola, C. gallifex, and C. orbicola on S. fasciculatus in Argentina (Burckhardt and Bassett 2000; Burckhardt 2005a). Burckhardt (2005) attributes this pattern to efficient utilization of food resources and indicates that this is an adaptive strategy to evade predators and parasitoids by co-exisiting in and utilizing the same space. Such a behavior suggests a coevolutionary thread between the Psylloidea and their host plants (Hodkinson 2009; Burckhardt et al. 2014; Ouvrard et al. 2015). An apparent discontinuity of the association of the Psylloidea and their host plant is the probable central reason for the patchy distribution of the Psylloidea.

Psylloidea-induced galls occur mostly on leaves, although a small number develops on flowers and stems. A specificity to sites usually manifests among the gall-inducing Psylloidea. For example, more than 20 gall-inducing species of Gyscasps (Syngylycasps) in Australia induce galls only on leaves of different species of Eucalyptus (Sharma et al. 2015a), whereas the species of Pachypsylla induce galls on buds, twigs, and leaf blades of species of Celtis in North America (Hodkinson 1984; Yang 1995; Burckhardt 2005a). Pseudophacopoter tuberculatum (earlier Pauropsylla tuberculatum) traditionally known to induce galls on the leaves of A. scholaris are being presently found to infest and induce galls on the flowers of A. scholaris (Chauhan et al. 2020). Reports of Trioza fletcheri minori (Triozidae) inducing galls both on the leaves (Mathur 1975) and flowers (Sokhi and Kapil 1984, p. 1985) of T. arjuna exist. One widely indicated generalization with gall-inducing insects is that they are highly host and site-specific (Raman 1996). Therefore, it is highly likely that gall-inducing psylloids infesting two plant organs of the same plant belong to a cryptic species complex rather than being the same species. Based on ecological, behavioral, and molecular studies, cryptic species have been indicated (Dhileepan et al. 2017) and determined among the Cecidoomyiidae (Dorchin et al. 2015; Fitzpatrick et al. 2013). An approach integrating morphological and molecular tools with ecological and behavioral studies is currently necessary to determine the taxonomy of the Psylloidea that infest different plant organs simultaneously. Yang (1995) suggests that Pachypsylla species that attack the same plant organ form a monophyletic group, whereas the phylogenetic relationships of Psylloidea inducing galls on different plant organs follow an evolutionary sequence of gall position shifting from leaf to petiole to bud to the branch.

How and why the gall-inducing Psylloidea are tied to specific plants remains to be clarified. Gall-inducing Hemiptera bear specialized sensory appendages, that can be different from non-gall inducing Hemiptera, on their antennae, mouthparts, legs, and abdomen enabling them to select the right site on the right plant for oviposition and resulting in gall induction (Sharma et al. 2015a). For example, the immatures of Gyscasps (Syngylycasps) sp. A bear unequal apical antennal bristles that are olfactory in function. Besides them, specialized terminal antennal bristles enable the gall-inducing Psylloidea to select the oviposition site. The gall-inducing species of G. (Syngylycasps) include unique, cupola-shaped rhinaria on each of the flagellar segments 2, 4, 6, and 7 in subapical positions. These rhinaria act as chemoreceptors and facilitate the adults to determine and choose the most-suitable host in a heterogeneous natural environment (Sharma et al. 2015a) (Figure 9). Further, gall induction necessarily requires specific molecular signals that can be activated only by a specific species of Psylloidea endowed with specific salivary proteins. The natural habitat of E. macrorhyncha – the preferred host plant of Gyscasps (Syngylycasps) sp. A – includes closely co-occurring populations of E. rossii and E. dives. Ian Brooker (2000) treats these three taxa under ‘Eucalyptus subgen. Eucalyptus + Primitiva.’ The pouch gall-inducing Gyscasps (Syngylycasps) sp. A never occurs on either E. rossii or E. dives. Significant levels of sitosterol, ergosterol, and stigmastanol were detected in young leaves of E. macrorhyncha, susceptible to gall induction by Gyscasps (Syngylycasps) sp. A. Moreover, sitosterol and three other undetermined sterols of molecular weights 354, 382, and 440 g mol⁻¹ occurred maximally only in the young leaves of E. macrorhyncha (Table 1), that were distinctly absent in E. dives and E. rossii leaves of comparable age. A unique ‘440 g mol⁻¹ sterol’ was found as the key in the selection of E. macrorhyncha by Gyscasps (Syngylycasps) sp. A, because of the high levels in the young, gall-susceptible leaves of E. macrorhyncha (Table 1) (Sharma et al. 2016). The level of the sterol of 440.3 µg molecular weight was high in young leaves of E. macrorhyncha, the colonization site by the gall-inducing first-instar immatures of Gyscasps (Syngylycasps) sp. A (Figure 10). Moreover, the levels of ergosterol, a sterol with a Δ⁵,7 nucleus (Festucci-Buselli et al. 2008) occurred maximally in young galls of E. macrorhyncha occupied by the first- and second-stage immatures of Gyscasps (Syngylycasps) sp. A reinforcing that ergosterol plays a key role in the successful metamorphosis of subsequent immature stages of Gyscasps (Syngylycasps) sp. A (Sharma et al. 2016). This clarifies the choice of E. macrorhyncha by Gyscasps (Syngylycasps) sp. A. in a mixed community of E. macrorhyncha, E. dives, and E. rossii, underpinning that the gall-inducing Psylloidea choose specific plants to meet their sterol requirements (Sharma and Raman 2017). Variation in the nature and types of lipids and sterols is one strong indicator of the host fidelity in interactions between gall-inducing arthropods in general, applicable to the gall-inducing Psylloidea as well and their host plants (Behmer and Nes 2003; Miller and Raman 2019).

Concluding remarks

With more than 4000 described species, the Psylloidea include diverse gall-inducing species. Unlike the Hymenoptera, which induce galls by inserting eggs into plant tissues, the known Psylloidea predominately induce galls by the feeding action of the first-instar immatures, except T. flavipennis.
in Western Europe. Feeding biology of the Psylloidea is closely similar to that of the gall-inducing Cecidomyiidae (Rohfritsch 1992). The role of PGRs (plant growth regulators) and consequent gene manipulation due to their action have been widely indicated in galls of arthropod origin, including those by the Psylloidea (Bailey et al. 2015). Greater levels of secondary metabolites such as the phenols and terpenes have been determined in the interactions between gall-inducing Psylloidea and flowering plants as critical physiological alterations (Dsouza and Ravishankar 2014; Agudelo et al. 2018). The role and effect of effector proteins released from the salivary glands are currently widely considered in gall induction by the Cecidomyiidae suggesting the function of a novel class of effector proteins in disabling the innate defence mechanism of the host plants (Zhao et al. 2015; Shih et al. 2018). However, this aspect has not been clarified in the specific context of gall-inducing Psylloidea.

Another challenging issue in the context of gall induction by the Psylloidea (for that matter by every other known gall-inducing arthropod) is how galls are induced. The critical stage will be to determine the metabolic changes that occur during early two phases of gall induction, viz., initiation and triggering of new differentiation pathways. These phases necessarily involve the activation of molecular messengers responding to the signals by the host plant arising due to insect action. The widely promoted idea of the key role of PGRs in gall induction needs to be viewed with extreme caution, since the endogenous PGRs are synthesized during the occupation of a gall by either the late second or the third stage immature only. The elementary reason being the production of PGRs at a greater intensity in galls necessarily requires a trigger, which should be either one or a cluster of high-molecular-weight proteins. An interplay of abscisic acid and ethylene along with auxins and cytokinins manifests in about-to-senesce galls (Raman 2021).

Table 1. Sterols in normal and developing stages of galls induced by *Glycaspis* (*Synglycaspis*) sp. A on the leaves of *Eucalyptus macrorhyncha* (adapted from Sharma et al. 2015c).

| Sterols’ molecular weight (mole %) | 0 | 1’ | 2’ | 3’ | 4’ | 5’ |
|----------------------------------|----|----|----|----|----|----|
| 326.4                            | 0.0233 | 0.0265 | 0.0183 | 0.0219 | 0.0263 | 0.0253 | 0.0233 |
| 354.1                            | 0.0788 | 0.1129 | 0.0690 | 0.0738 | 0.0797 | 0.0689 | 0.0581 |
| 382.1                            | 0.1287 | 0.1987 | 0.1358 | 0.1648 | 0.1676 | 0.1764 | 0.1196 |
| 396.3                            | 0.0054 | 0.0177 | 0.0063 | 0.0094 | 0.0103 | 0.0136 | 0.0095 |
| 410.2                            | 0.0489 | 0.2454 | 0.0595 | 0.1181 | 0.1245 | 0.1787 | 0.1333 |
| 412.4                            | 0.0500 | 0.0458 | 0.0495 | 0.0497 | 0.0452 | 0.0488 | 0.0500 |
| 414.3                            | 0.1130 | 0.1244 | 0.1244 | 0.1649 | 0.1801 | 0.1569 | 0.1851 |
| 424.4                            | 0.0028 | 0.0147 | 0.0052 | 0.0055 | 0.0070 | 0.0120 | 0.0075 |
| 426.2                            | 0.0627 | 0.0496 | 0.0801 | 0.0738 | 0.0676 | 0.0696 | 0.1045 |
| 440.3                            | 0.3768 | 0.0591 | 0.3349 | 0.2324 | 0.1668 | 0.1442 | 0.1735 |
| 454.2                            | 0.0164 | 0.0285 | 0.0180 | 0.0253 | 0.0319 | 0.0255 | 0.0537 |
| 534.3                            | 0.0227 | 0.0002 | 0.0329 | 0.0072 | 0.0222 | 0.0033 | 0.0067 |

0: uninfested leaves, 1: infested leaves.
Y: young uninfested leaves, M: mature uninfested leaves.
1’, 2’, 3’, 4’, 5’: galls harboring populations of the first, second, third, fourth, and fifth instars (n = 50 each category).
Figure 10. Sterols in young (●) and mature (▲) uninfested leaves of Eucalyptus macrorhyncha hosting gall inducing Glycaspis (Synglycaspis) sp. The sterol 440.3 mol % (an unnamed lanosterol analog indicated by ◊) predominant in young leaves of E. macrorhyncha, is the potential sterol that regulates the specificity of the Glycaspis (Synglycaspis) sp. A. x-axis – molecular weights of sterols; y-axis – mole % of sterols. Vertical bar represents the SE value. (Source: Sharma et al. 2016).

From the available, but disjointed, literature on gall-inducing Psylloidea and extrapolating what we know in other gall-inducing insect groups, e.g. the Cecidomyiidae and the Cynipidae (Favery et al. 2020), we can propose that, in general, during gall initiation, the gall-inducing psylloids overcome the innate immunity of the plant and provoke a susceptible response. The tricky question is whether the gall is a defence response of the plant to limit the localized irritation and damage by the psylloid or whether a symbiotic relationship occurs between the Psylloidea and chosen plants. Presently, no firm answer to this question is available, since different studies have supplied answers in support of both contentions. Osmotic change-related metabolic pressure builds up when gall-inducing psylloids attack plant cells activating a train of events in the immediate environment of those plant cells. The following sequence of events includes alterations in gas exchange and synthesis of PGRs. Gall induction involves the vigorous uptake of oxygen from the reactive-oxygen species generated consequent to insect attack, which in turn stimulates auxin synthesis and activity. Osmotic stress alters the electrical properties of the plasma membrane and impacts on IAA synthesis and activity, which, alters the H⁺ transport. From what we know thus far, it is possible to infer that the plant actively mobilizes nutrients to mitigate the stress and repair the injury right from the time of attack by the psylloid. The gall-inducing psylloid, incidentally, utilizes the nutrients mobilized at this site to its advantage. A summary, nonetheless, would be that the metabolic changes consequent to changes in the vacuolar pH in the metaplasied cell produces certain ‘novel’ chemicals (of unknown details presently), which diffuse from the dedifferentiated metaplasied cell into its immediate neighborhood. But we need to recognize here that the dissipation of these novel chemicals is localized to a narrow window in the plant organ, viz., the gall, because of their obviously weak nature. This necessarily means that the effect of these novel chemicals does not spread throughout either the involved organ or the plant, explaining why galls and their effects are highly localized.

The inhabiting immatures of the Psylloidea are fascinatingly adapted to the design of galls they provoke. How the development of the gall synchronizes both morphologically and physiologically with that of the inducing agent is clearly illustrated in the study of P. lentiginosum that induces two-tier galls on the leaflets of G. pinnata (Raman 1987). The shape of galls is generally consistent in some of the families of the Psylloidea, for instance, Baccharis (Asteraceae) hosts c. 25 species of Triozidae that induce similar galls on the floral capitula in the Americas, whereas that behavior varies considerably in other taxa; for example, species of Calophya induce galls of varied morphologies on different species of Schinus, also in the Americas: e.g. Calophya schini (Calophyidae) induce open-pit gall, C. andina induce nipple or conical galls, C. orbicola induce disc-shaped galls. Similar to the gall-inducing Cecidomyiidae and Cynipidae, the gall-inducing Psylloidea are host and site-specific, although a few exceptions exist. The fidelity of gall induction in the Psylloidea is determined by sterols, as demonstrated in Glycaspis (Synglycaspis) sp. A–E. macrorhyncha interactions.

The free-living Psylloidea are better adapted to different climatic regions, whereas the gall-inducing Psylloidea show conservative behavior in terms of geographical distribution. For instance, in Australia, various species of Eucalyptus host several species of free-living, lerp-forming, and gall-inducing Psylloidea. However, within the same biogeographical realm, the free-living Psylloidea display a greater number of generations than the gall-inducing taxa. Life-history performances are known of gall-inducing Psylloidea inducing a variety of galls, however, aspects of their association with host plants are less known. Several factors of nutritional physiology of gall-inducing Psylloidea are also less known presently compared with that of the free-living, species. Since most of the gall-inducing Psylloidea are solitary inhabitants within a gall, their nutritional requirement varies starkly from the free-living Psylloidea. The gall-inducing Psylloidea manipulate the synthesis of a greater quantity of sugars in the galls and utilize them, as against the free-living Psylloidea. A better comprehension of the association and commitment between gall-inducing Psylloidea and their host plants is needed presently. Moreover, several aspects of the nutritional physiology of Psylloidea and
especially that of the gall-inducing Psylloidea remain to be clarified.

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