

Feeding biology and nutritional physiology of Psylloidea (Insecta: Hemiptera): implications in host–plant relations*

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About 3500 species represent the Psylloidea across the world. Many Psylloidea live on a wide range of agriculturally and horticulturally important plants and some of them also act as vectors of plant pathogens. Generally they show a narrow host–plant range and feed on plant sap. Endosymbiotic bacteria are shown to be associated with some of them, enabling them to live on a nutritionally imbalanced plant diet. During feeding, the Psylloidea induce changes in plant tissues. Salivary enzymes such as pectinases enable them to mobilize primary metabolites rapidly to feeding sites from uninfested parts. Specific proteins (64 and 58 kDa) occur in the saliva of free-living Psylloidea (e.g. Aphalaridae) as well as in host–plant phloem. These insects live either freely or by constructing lerps or by inducing galls. Variations in guilds and feeding behaviour determine the nutritional ecology and physiology of the Psylloidea. Varying nutrient levels in leaves regulate populations of the gregariously feeding Psylloidea. The lerp-constructing Psylloidea utilize more of sugar-based nutrients, while the group-feeding Psylloidea induce more intense changes in amino-acid, fatty-acid, and mineral levels in host plants. High C and low N ratios in leaves influence psyllid growth rates negatively. For instance, the gall-inducing Psylloidea achieve only two generations a year. High levels of the sterol (440.3 molecular weight) and ergosterol and low levels of complex lipids in young leaves of *E. macrorhyncha* appear to regulate the specificity of the gall-inducing species of *Glycaspis* (*Synglycaspis*) (Aphalaridae). About 100 plants are indicated as hosts of Indian Psylloidea. Curiously no lerp-forming psyllid is known in India.

Keywords: Auchenorrhyncha, feeding behaviour, Heteroptera, nutritional requirements, primary metabolites, Sternorrhyncha.

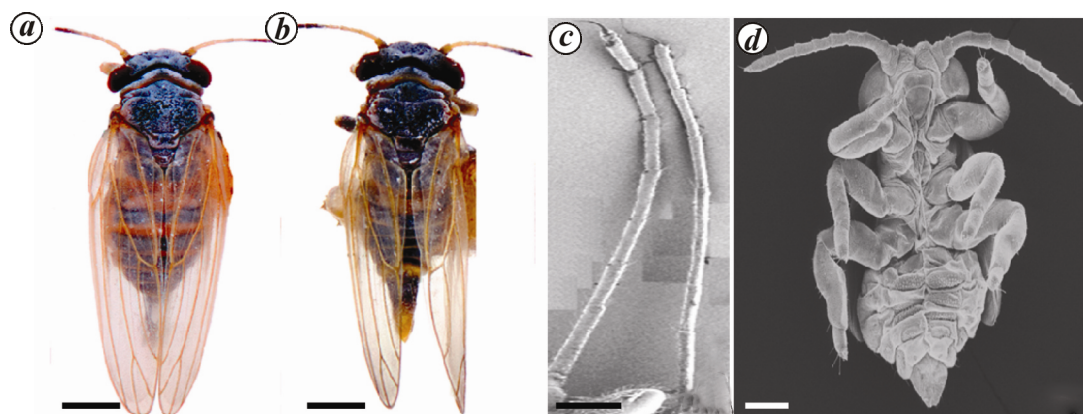
GLOBALLY the Psylloidea are represented by c. 4000 species, which are treated under Phacopteronidae, Aphalaridae, Carsidaridae, Homotimididae, Liviidae, Calophyidae, Psyllidae, and Triozidae¹. Many pestiferous Psylloidea

live on a wide range of annuals and timber trees of agricultural and horticultural importance. These insects are mostly known from the tropical and subtropical regions of the world, while the temperate fauna is relatively less species rich, very few are known from the Arctic region². Life cycles of tropical Psylloidea are generally contiguous, presenting multiple generations a year (e.g. *Diaphorina citri*², *D. truncata* (Liviidae)³, *Trioza jambolanae* (Triozidae)⁴). Development rates and voltinism of the warm-temperate taxa are generally slower and lower than those of the tropical and subtropical regions. The multi-voltine life cycles of the Psylloidea, over time, have undergone considerable modifications in different bioregions of the world, enabling them to radiate onto more than one plant species².

Adult Psylloidea are usually 1–10 mm in length. Two pairs of membranous wings are held over the body horizontally, particularly when resting. The hind legs with well-developed coxae are suitable for jumping. The antennae are 10-segmented⁵ (Figure 1). Many of the known Psylloidea are monophagous (e.g. *T. jambolanae*, Triozidae); some are oligophagous (e.g. *Acizzia obscura*, Psyllidae), and a small number are polyphagous (e.g. *Bactericera cockerelli*, Aphalaridae; *Russelliana solani-cola*, Psyllidae). Lerp-forming Psylloidea (Figure 2) occur in Australia in greatest diversity⁵. The Indian Psylloidea live either freely or inducing galls. No lerp-forming Psylloidea are known in India thus far. Yet, some free-living Psylloidea such as *D. citri* that secrete copious sugary exudates along with waxy filaments are known⁶. Sugary-exudate secreting behaviour also occurs in their Sternorrhyncha allies (the Aphidoidea, Phylloxeroidea, Coccoidea, and Aleyrodoidea), because they too feed on sugar-rich phloem sap diet. About 120 plants are reported as hosts of Indian Psylloidea^{6–10}. These reports, however, need re-verification in the light of recent explanation of host plants of Psylloidea by Burckhardt *et al.*¹¹. General biological and lifecycle details are available in Hodkinson^{2,12,13} and Burckhardt^{14–17}. The bionomics of *Apsylla cistellata* (Aphalaridae) on *Mangifera indica* (Anacardiaceae)¹⁸, *Trioza obsoleta* (Triozidae)¹⁹, *Pauropsylla depressa*²⁰, *P. longispiculata*²⁰, *T. hirsuta*²¹, *T. jambolanae*⁴, *Trioza minor* (= *T. fletcheri minor*) (Triozidae)²², *Diaphorina truncata* (Liviidae)³, *Phacopteron*

*This article celebrates Ram Nath Mathur's (1903–1977) contributions to Indian Psylloidea.

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Figures 1. *a*, Dorsal view of adult *Ctenarytaina eucalypti* (Aphalaridae) female (bar = 500 µm); *b*, adult *Ctenarytaina eucalypti* male (bar = 500 µm); *c*, 10-segmented antennae (*Glycaspis* sp. Aphalaridae) (bar = 250 µm); *d*, fifth instar of *C. eucalypti* showing well developed hind legs (bar = 500 µm).

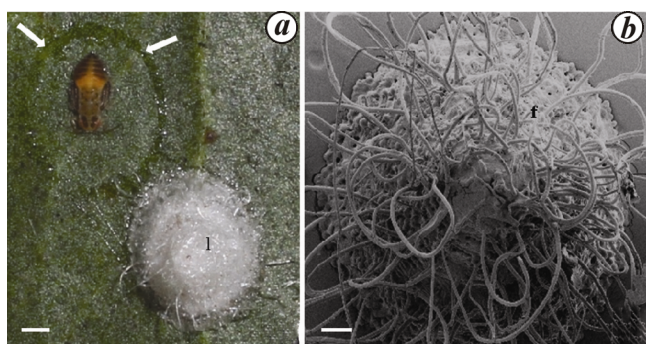


Figure 2. Lerp of *Glycaspis* sp. on *Eucalyptus sideroxyylon*. *a*, Lerp site of the 4th instar (arrows) and the dislodged lerp (l) (bar = 1 mm); *b*, lerp constructed by the second instar (f – sugary filaments) (bar = 100 µm) (source: Sharma *et al.*³³).

*lentiginosum*²³, and *Pseudophacopteron tuberculatum* (Phacopteronidae)²⁴ are known from the subcontinent.

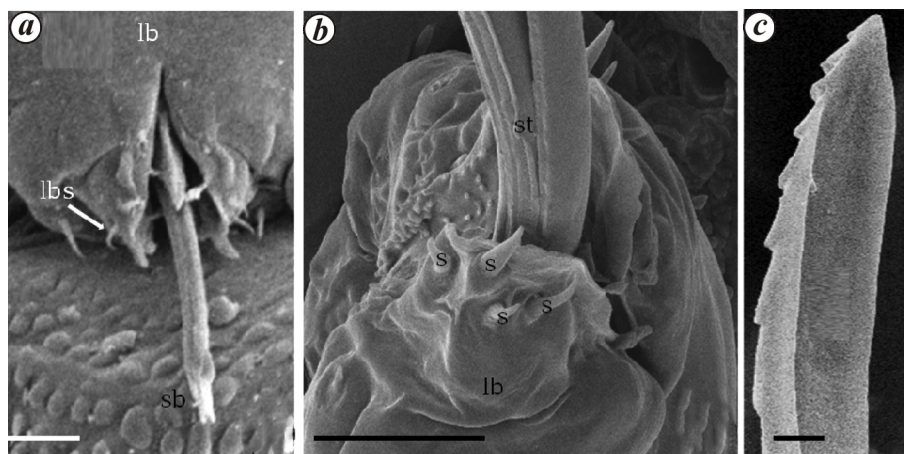
Apsylla cistellata^{25,26} occurs only along the Indo-Gangetic Plains (27°15'–27°25'N, 80°30'–80°50'E) and lower Himalaya (27°59'–27°98'N, 86°55'–86°92'E), whereas *D. citri*, the vector of Citrus Greening Disease (CGD) occurs, wherever *Citrus* is cultivated²⁷. *Diaphorina citri* transmits 'Candidatus Liberibacter', which induces²⁸ CGD, inflicting severe loss to Indian *Citrus* industry⁵. Both *T. minor* and *T. hirsuta* induce galls on the leaves of *Terminalia catappa*, *T. arjuna*, and *T. tomentosa* (Combretaceae) – important timber taxa of India, further to being the preferred hosts of *Antheraea mylitta* (Saturniidae). Differing from a majority of gall-inducing psylloids, which are generally host and site specific¹⁷, *T. minor* induces galls not only on the leaves of *T. tomentosa* and *T. arjuna*, but also on those of *T. catappa*, *T. paniculata* and *T. tomentosa* × *T. arjuna*²⁹ and in flowers of *T. arjuna*^{30,31}. Chromosome numbers from determined adult male populations of *T. minor* from *T. tomentosa* and *T. arjuna* revealed no significant differences. Therefore Raman *et al.*²² concluded that the same species, viz.

T. minor induces galls on both *T. tomentosa* and *T. arjuna*²².

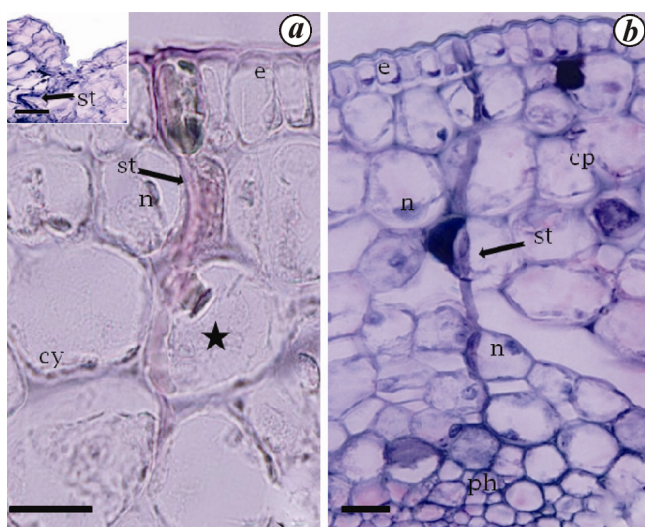
Plants respond to infestations by Psylloidea variously. The details of their actions on plants and the responses they elicit from plants, however, are not yet well clarified. In such a context, we clarify, in the following sections, the feeding biology, nutritional physiology, and host–plant relations of selected Aphalaridae, as representative examples of the Psylloidea. This article also aims at relating those known details towards a better understanding of the nutritional ecology and physiology of Indian Psylloidea.

Feeding biology

Psylloidea feed on plant sap² with their piercing-and-sucking mouthparts, made of two pairs of clasping stylets – the modified mandibles and maxillae. The distal end of the labium bears four equidistally and bilaterally placed sensilla, which enable them to recognize plants (Figure 3). The Psylloidea, similar to their Sternorrhyncha allies, form a proteinaceous stylet sheath during feeding. Adults feed on phloem (e.g. *D. citri*, *D. truncata*). In adult Psylloidea, the stylets vary in length (from 600 to 950 µm). The stylet length appears to depend on the guild to which the psylloid belongs, although the relationship between the body size and stylet length³² cannot be overlooked. For example, free-living *Ctenarytaina eucalypti* (Aphalaridae) bear c. 600 µm long stylets, the lerp-forming, unnamed species of *Glycaspis* c. 850 µm, and the gall-inducing, unnamed species of *Glycaspis* (*Synglycaspis*) c. 950 µm (refs 33–35). Singh¹⁸ indicates that the neonate nymphs of *A. cistellata* feed on the tender leaves of *Mangifera indica* (Anacardiaceae) and stimulate gall growth on nearby vegetative axillary buds by translocating a chemical of unknown details. Singh¹⁸ also indicates that the neonate nymphs of *A. cistellata* bear 'very long' stylets. Such a behaviour of the insect living at one



Figures 3. Mouthparts (*Ctenarytaina eucalypti*). **a**, lb – labium; lbs, labial sensilla; sb, stylet bundle (bar = 10 μ m); **b**, sensilla (s) on labium; lb, labium; st, stylet (bar = 10 μ m); **c**, serrated mandibular stylet tip (bar = 1 μ m) (Source: Sharma *et al.*^{34,35}).



Figures 4. Feeding sites (*Ctenarytaina eucalypti*) on *Eucalyptus globulus* leaves (cross sectional views). **a**, stylet tip terminating in mesophyll parenchyma (st, stylet pathway); n, nucleus; cy, hyaline cytoplasm along the walls; e, epidermis; *, fed cell that includes the stylet tip (bar = 100 μ m); Inset: caving in of dorsal leaf segment aligning with the shape of the rostrum of the 1st instar (st, stylet track) (bar = 100 μ m). **b**, feeding site of adults along the midrib: stylet pathway from the abaxial surface reaching phloem; ph, phloem; cp, cortical parenchyma; e, epidermis; n, nucleus (bar = 100 μ m) (Source: Sharma *et al.*³⁴).

location and inducing gall at a different and distant location is unusual among the known gall-inducing Psylloidea¹⁷. This behaviour, however, appears similar to that of the European and North American Adelgidae (Aphidoidea) infesting different species of *Picea* (Pinaceae)^{36–38}.

Leaf tissues attacked by free-living Aphalaridae (e.g. *C. eucalypti*) display more intense stress symptoms than those attacked by gall-inducing Aphalaridae (e.g. species of *Glycaspis* (*Synglycaspis*) on *E. macrorhyncha*). The feeding action of early instars of the free-living *C. eucalypti* induces greater level of cellular alterations at and

around the stylet path than those of lerp-forming and gall-inducing Aphalaridae. The feeding action of the early instars of Aphalaridae, irrespective of the guild, plasmolyzes the epidermal and palisade cell cytoplasm of the host-leaf cells, particularly along the stylet path. The cells around the stylet include thin and hyaline cytoplasm and show unusually thick walls. Plasma membranes of cells surrounding the stylet retract from walls consequently (Figure 4), enabling greater apoplastic mobility of nutrients³⁴. Such retracted cell membranes and the newly formed apoplastic spaces also indicate localized subcellular alkalization and production of reactive-oxygen species, sequel to development of oxidative stress due to feeding pressure inflicted by the Aphalaridae³⁴. The lerp-forming Aphalaridae (e.g. *Glycaspis* on *E. sideroxylon*) show that they require greater quantities of sugars than what are generally required by the free-living Aphalaridae, because the former build characteristic sugary lerps. The lerp-forming and gall-inducing Aphalaridae draw sugar-based reserves more rigorously from their hosts and that too at a far greater proportion than what their free-living counterparts do.

During feeding, a modest level of mechanical damage eventuates during stylet insertion and movement in plant tissues. In contrast, the chemical injury by salivary enzymes induces intense transcriptomic changes³⁹. Feeding action of Psylloidea alters the photosynthetic activity in host tissues significantly, which, in turn, affects primary-plant metabolism⁴⁰. Feeding action involves flooding of saliva and ingestion of sap from either parenchyma (1st–3rd instars) or phloem (older instars and adults) (Figure 4). Their mouth parts are so well developed that they can both salivate and ingest plant sap, not only concurrently, but also efficiently, similar to other Hemiptera^{41,42}. Psylloid saliva includes cellulases, amylases, and pectinases enabling the movement of stylets within plants inflicting minimal mechanical damage. The

structure of the salivary-gland-complex of the Hemiptera is generally understood to be made of a principal gland and an accessory gland⁴³. In *C. eucalypti*, the principal gland is highly lobed and the accessory gland is tubular (Figure 5), which is similar to that known in some Aphidoidea (e.g. *Myzus persicae*, Aphididae)⁴².

Nutritional physiology

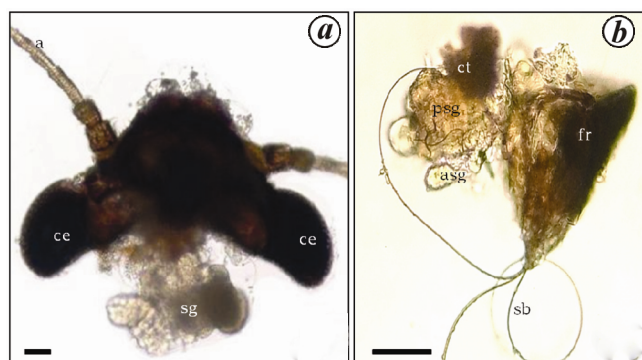
The Psylloidea extract primary metabolites, minerals, and water from plant sap, which is rich in sugars but poor in nitrogenous materials⁴⁴. Sugars usually occur at greater levels than optimally necessary for the Psylloidea. The incidence of sucrase-transglucosidase in the digestive system of Psylloidea, which is indicated to be highly likely, enables these insects to convert excess sugar into honeydew⁴⁴. Association of endosymbiotic microorganisms in the digestive tracts of the Psylloidea is another critical factor. Psylloidea harbour one primary endosymbiont (Ca. *Carsonella*) and at least one other secondary endosymbiont, the latter meant to compensate for *Carsonella* genome reduction⁴⁵. Such an association is unique, because the Psylloidea feed on a nutritionally imbalanced diet, which is deficient in essential amino acids, vitamins, and lipids^{46,47}. The obligate endosymbiotic bacteria (e.g. Ca. *Carsonella*) live in specialized cells – the bacteriocytes – constituting a ‘new’ functional system, ‘the bacteriome’, confined to the haemocoel⁴⁷. The bacteriocytes provide space and nourishment to the endosymbiotic bacteria. The endosymbiotic bacteria and Psylloidea share nutrients (e.g. vitamins, amino acids, carotenoids) necessary for mutualistic living. The endosymbiotic bacteria synthesize one or more essential amino acids, which the psyllid cannot synthesize; in turn, the psyllid produces and supplies certain other essential amino acids, which the bacterium cannot produce. Such obligatory endosymbionts have been shown to be maternally inherited in the Aphidoidea and their phylogeny

is congruent with that of the Aphidoidea^{45,46}. Probably the bacterial association in the Psylloidea is of a similar functional relationship.

Many Psylloidea bear an intimate association with plant-pathogenic viruses, phytoplasmas, and bacteria. However, our present knowledge of the psyllid–microbe relationship is limited. This association could benefit the Psylloidea, because the pathogen-induced changes may render plants amenable to the Psylloidea nutritionally and also by reducing levels of defence materials⁴⁸. For example, species of *Cladosporium* (Fungi: Dothideomycetes: Davidiellaceae) and *Alternaria* (Fungi: Dothideomycetes: Pleosporaceae) growing on either the nymphal excreta or the honeydew secreted by Psylloidea on plants (e.g. *Cacopsylla pyricola* (Psyllidae) on *Pyrus* (Rosaceae))² generally support psyllid infestations, because such fungal association prepares plants by weakening their natural immunity levels⁴⁹. Microbial-disease agents are ingested by the Psylloidea during feeding and later introduced into plants through their saliva. Phytoplasmas and Liberibacter-s occur in the sieve-tube elements and circulate in plant sap, thus making them suitable for transmission. Once within the psyllid, the microbes cross through the gut wall, multiply in the haemolymph, and migrate to salivary glands for transmission *via* the saliva. Both nymphs and adults can transmit microbial agents.

Psylloidea infestations trigger physiological changes in plants enabling them to obtain nutrition. For instance, populations of *Cardiaspina densitexta* (Aphalaridae) enhance the physiological quality of *Eucalyptus fasciculosa* (Myrtaceae) leaves by rapidly mobilizing soluble nitrogen to feeding sites⁵⁰. The Aphalaridae feed on parenchyma during 1st–2nd instar stages and on phloem during 3rd–5th instar stages^{33–35}. The biosynthesis of primary metabolites in infested host leaves varies, rather dramatically, depending on whether the psyllids live either freely or forming lerps or inducing galls. The solitary- or gregarious-feeding behaviour defines the nutritional ecology of Psylloidea. For instance, the effect of solitary-feeding Psylloidea (e.g. gall-inducing Triozidae) is strikingly different from the gregariously-feeding Psylloidea (e.g. free-living Aphalaridae). Feeding pressure placed by gregariously feeding taxa results in the rapid mobilization of nutrients from uninfested to infested parts of the host plant⁵⁰. In contrast, the feeding action of solitary feeding Psylloidea (e.g. gall-inducing *T. jambolanae*, Triozidae on *Syzygium cumini*, Myrtaceae) stresses plant parts, such as leaves by inducing galls, where the galls function as ‘nutrient sinks’ enabling the inducing psyllid to extract their nourishment^{4,51}.

Varying nutrient levels in different parts of the same leaf regulate populations of free-living, gregariously feeding Psylloidea. For example, a c. 3.5 cm long juvenile leaf of *Eucalyptus globulus* (Myrtaceae) would harbour a population of 60–100 actively feeding *C. eucalypti* of varying



Figures 5. Salivary gland (*Ctenarytaina eucalypti*). **a**, Position of the salivary glands (dorsal view) in relation to dissected head: ce, compound eye; sg, salivary gland; a, antenna (bar = 500 μ m); **b**, principal and accessory salivary glands: asg, accessory salivary gland; ct, connective tissue; fr, frons; psg, principal salivary gland; sb, stylet bundle (bar = 500 μ m) (Source: Sharma *et al.*⁴³).

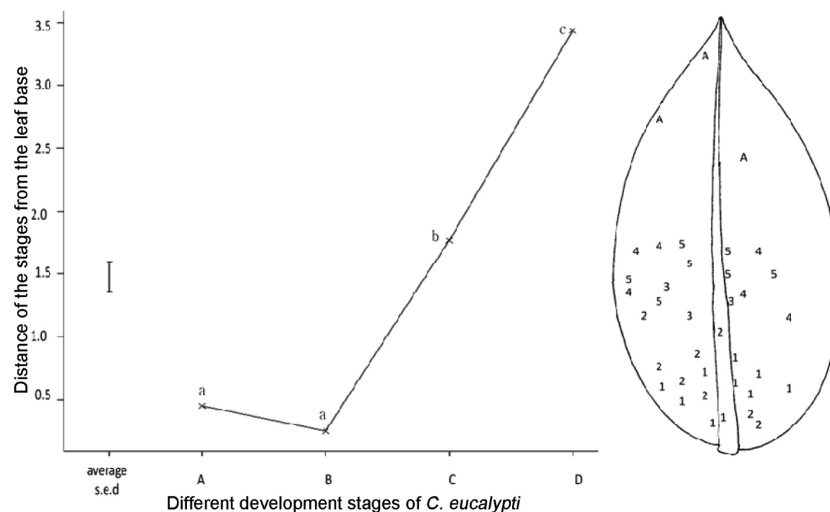


Figure 6. Feeding preference and partitioning (*Ctenarytaina eucalypti* on *Eucalyptus globulus*). Points with the same letter of alphabet indicate that they do not differ significantly ($P = 0.05$). Left: A, egg population; B, 1st and 2nd instar population; C, 3rd, 4th and 5th instar population; D, adult population ($df = 3$; $F = 0.5013, 1.1085, 1.7742$), ($n = 10$ leaves, 3.5–4 cm long). Right, reconstruction of one 'representative' leaf (3.5 cm) showing the preference pattern of different instars (1st–5th) and adult (A) populations (eggs not shown) (Source: Sharma *et al.*³⁴).

instars and adults at one point of time. In that actively feeding population, the 1st and 2nd instars usually remain confined to leaf bases, whereas the 3rd, 4th and 5th instars occur restricted to mid-leaf parts, and the adults to leaf tips indicating a defined, development-specific preference (Figure 6). Such a 'partitioning' behaviour among different developmental stages and adults of *C. eucalypti* reinforces that different nymph and adult populations acquire nutrients of varying qualities from different segments of the same leaf to achieve the best growth and reproductive efficiency. Distribution of metabolites within segments of individual leaves is demonstrated to vary. Lipids, sugars, amino acids, organic acids, nutritive cations and anions, and secondary compounds in *Arabidopsis thaliana* (Brassicaceae) leaves measured along the basipetal trajectory show variations in their quantity and quality in different parts of the same leaf: for instance, glucosinolates, raffinose, and galactinol occur at high levels along leaf bases than other parts of the same leaf⁵². Similar variations, particularly in lipids, occur in *Triticum aestivum* cv. Hereward (Poaceae) leaves⁵³. Significant differences in nitrogen and phenolic levels at apical and basal regions of the same leaf explain the unique distribution of *C. eucalypti* on *E. globulus*³⁴. Nutrient-material acceptability is exquisitely demonstrated in the Psylloidea in their feeding preference. In contrast, nutrient material availability to the Psylloidea depends on their population sizes being restricted to specific leaf segments. A variable nutritional gradient from the proximal to distal parts of a leaf influences the distribution and thus partitioning of resources in the free-living Aphalaridae³⁴.

Carbon and nitrogen levels vary in leaves that host Aphalaridae. Maximal variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios (ratios between isotopic carbon and nitrogen) occur in *E.*

macrorhyncha leaves that host gall-inducing Aphalaridae, followed by *E. sideroxylon* leaves hosting the lerp-forming Aphalaridae, and the least in *E. globulus* leaves hosting the free-living Aphalaridae. Generally insects living on plants with high $\delta^{13}\text{C}$ and low $\delta^{15}\text{N}$ ratios grow slowly in a temporal sense, because of high levels of defence compounds (e.g. phenolics) and low-nitrogen availability⁵⁴. This applies truly in the feeding biology of the Psylloidea: the gall-inducing Aphalaridae complete two generations in a year, feeding on high $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ ratio bearing host-leaf tissues⁵⁵, followed by the lerp-forming Aphalaridae, which complete 3–4 generations in a year feeding on relatively low $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ ratio bearing leaf tissues³³, and the free-living Aphalaridae, which complete 5–6 overlapping generations in a year, living on host leaves with the least $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ ratios³⁴. The maximum decrease in total non-structural carbohydrates and $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ ratio in *E. globulus* leaves infested by free-living Aphalaridae indicates a drop in carbon levels sequel to infestation. The drop in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ ratio in *E. globulus* leaves could be due to greater level of mechanical damage these free-living, gregariously feeding Aphalaridae inflict than the lerp-forming and gall-inducing Aphalaridae do⁵⁵. Amino acids occur maximally in leaves infested by the free-living Aphalaridae compared with those infested by the lerp-forming and gall-inducing Aphalaridae, indicating that the free-living, gregariously feeding Aphalaridae stimulate mobilization of amino acids to infestation sites, possibly to repair the damage.

The Aphalaridae canalize primary metabolites to feeding sites mostly *via* the symplast and occasionally *via* the apoplast⁵⁶, similar to the feeding action of the other Sternorrhyncha⁵⁷. Free-living Aphalaridae (e.g. *Cardiaspina retator*), while feeding on leaves of *E. camaldulensis*

stimulate rapid mobilization of lipids, amino acids, and soluble proteins to feeding sites⁵⁸. Usually mature leaves of *Eucalyptus* include low levels of soluble nutrients, particularly the usable nitrogenous material such as amino acids⁵⁹. Other primary nutrients, e.g. amino acids, enable regulation of osmotic pressure in body fluids and energy conservation in the Sternorrhyncha⁶⁰. Protein-strong diets are necessary for egg production, development, and viability⁶¹. Infestations by different Aphididae and Aleyrodidae on the foliage of *Pisum sativum* (Fabaceae) and *Gossypium hirsutum* (Malvaceae) respectively, redirect amino acids to infestation sites, further to accelerating localized biosynthesis of amino acids^{62,63}, which is critical for the growth and development of feeding insects⁶². In contrast, Dubey *et al.*⁶³ indicate that feeding by different Hemiptera intensify amino-acid biosynthesis as a plant response to ward off invading insects *via* decarboxylation of amino acids. In Aphalaridae–*Eucalyptus* interactions, recanalization of amino acids occurs aggravated in the interaction that involves the gregariously feeding, free-living Aphalaridae⁶⁷ indicating that this aggravation is because of the plant response to the intensity of stress arising due to group feeding (Figure 7a). When the Hemiptera (Psylloidea included) attack plants, they inflict a modest level of injury. The Hemiptera maintain the injury they cause to plants by retaining their inserted stylets and salivary chemicals flooding the injured site. Eventually the nutrients mobilized to the damaged site subserve the nutritional needs of invading insects.

Lipids, besides being the key sources of energy, are vital for membrane construction and hormone synthesis. Insects require dietary sterols such as cholesterol and ergosterol for their growth and development⁶⁴. Fatty acids control egg development, whereas phospholipids are critical-membrane constituents facilitating osmoregulation⁶⁵. In *E. globulus* infested by the free-living Aphalaridae, levels of unsaturated fatty acids increase modestly, whereas the values of saturated fatty acids remain nearly the same in both uninfested and infested leaves (Figure 7b). In contrast, when *Aphis glycines* (Aphididae) feed on *Glycine max* (Fabaceae) leaves, saturated fatty acids (e.g. palmitic acid) increase and unsaturated fatty acids (e.g. linoleic and linolenic acids) decrease⁶⁶. These indicate that striking variations in the feeding behaviours within free-living Sternorrhyncha exist, reinforcing that nutritional requirements vary among the Aphidoidea and Psylloidea, particularly in terms of utilization of lipids.

Minerals in plants influence the growth and development of plant-feeding arthropods. In Insecta, minerals enable enzyme activation; trigger regulatory mechanisms, besides participating in organ formation during embryogenesis⁶⁷. P, K, and Mg are the major elements, which occur abundantly in insect tissues, usually obtained from host plants, although at varying levels^{67,68}. In contrast to what has been shown in the Aphidoidea⁶⁷, high levels of Mg occurs in *E. globulus* leaves, fed by the gregariously

feeding populations of free-living Aphalaridae – compared with the populations of lerp-forming and gall-inducing Aphalaridae on *E. sideroxylon* and *E. macrorhyncha* leaves – emphasizing the more rapid growth rate of free-living taxa than those of the other two guilds. Moreover, greater levels of minerals in leaves of *E. globulus* infested by the free-living Aphalaridae reiterate the influence of group feeding on mineral abundance in host tissues (Figure 8).

Host–plant relations

Those Psylloidea, known to occur on more than one plant species, generally remain restricted to species of the same plant genus: e.g. *T. minor* on different species of *Terminalia*. Prevalence of highly specific plant association among Psylloidea is considered a ‘critical’ step in the co-evolution of Psylloidea and their hosts¹¹, although, we require molecular phylogenetic data to validate this statement. Available global information on the verified host relations and diversification behaviour of the

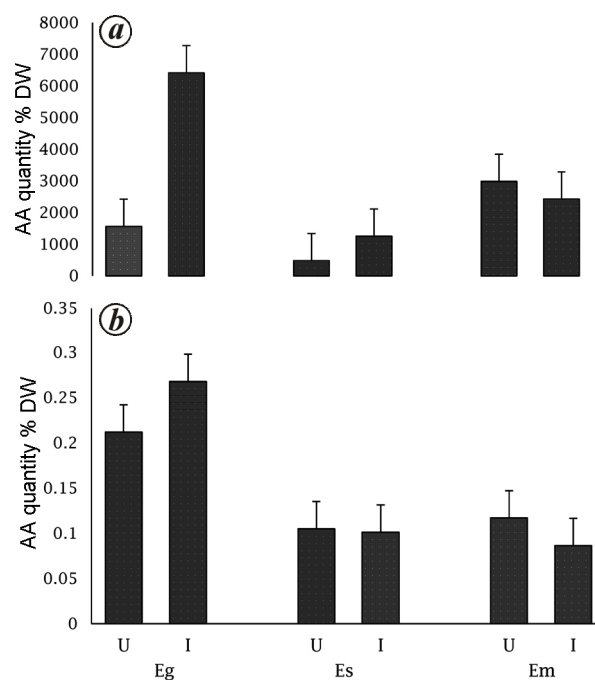


Figure 7. a, Total amino acid (AA) (% DW = per cent dry weight) in leaves of *E. globulus* (Eg) infested by *Ctenarytaina eucalypti*, *E. sideroxylon* (Es) infested by *Glycaspis* sp. and *E. macrorhyncha* (Em) infested by *Glycaspis* (*Synglycaspis*) sp.(x axis); (uninfested leaves – U, infested leaves – I). b, Total fatty acids (FA) (% DW, per cent dry weight) in leaves of *E. globulus*, *E. sideroxylon* and *E. macrorhyncha* (x axis); (uninfested, U, infested, I). (For overall comparisons between the three systems (*C. eucalypti*–*E. globulus*, *Glycaspis* sp.–*E. sideroxylon*, and *Synglycaspis* sp.–*E. macrorhyncha*), the host–plant data were pooled for the five instars of *Glycaspis* on *E. sideroxylon* and *Glycaspis* (*Synglycaspis*) on *E. macrorhyncha*, whereas the data for *C. eucalypti* were already combined because all developmental stages co-occur on the same leaf and graphs were generated using Microsoft Office Excel 2007. The vertical bars represent standard errors).

Psylloidea among related plants is inconsistent. Abrupt evolutionary changes possibly enable host switch among the Psylloidea⁶⁹. A majority of the Indian Psylloidea, too, are similar to their global relatives in this behaviour, influenced by their patchy distribution⁷.

The Sternorrhyncha, and a majority of plant-feeding insects belonging to other Orders as well, rely on plant sterols to metabolize cholesterol, vitally necessary for their metamorphosis⁷⁰. The exclusive reliance of the gall-inducing species of *Glycaspis* (*Synglycaspis*) on *E. macrorhyncha* leaves has been clinched recently. Surveys made in field revealed that the populations of this unnamed species live only on *E. macrorhyncha* and never on either related or unrelated species of *Eucalyptus* that occur in the neighbourhood in equal frequency. We chose *E. dives* and *E. rossii*, since *E. macrorhyncha*, *E. dives*, and *E. rossii* belong to *Eucalyptus* subgenus *Eucalyptus* + *Primitiva*, Sections *Capillula* (*E. macrorhyncha*), *Aromatica* (*E. dives*), and *Cineraceae* (*E. rossii*), as the 'closest' relatives of *E. macrorhyncha*, the host of gall-inducing *Glycaspis* (*Synglycaspis*)^{71,72}. High levels of the sterol of molecular weight 440.3 in young leaves of *E. macrorhyncha* (the primary sites of colonization by the gall-inducing neonate nymphs) hold the key to host-plant selection by this species⁷³. Levels of ergosterol – a $\Delta^{5,7}$ nucleus sterol (Δ^7 -bond is critical for the synthesis of steroid-based moulting hormones) – rise steeply in galls of *E. macrorhyncha* occupied by the 1st and 2nd instars of *Glycaspis* (*Synglycaspis*) indicating its greater requirement for them to grow. Further, low levels of complex lipids (mono- and di-galactosyl-di-acylglycerides) levels in young leaves of *E. macrorhyncha* render those young leaves susceptible to neonate nymphs of *Glycaspis*

(*Synglycaspis*). A critical difference in the levels of the sterol of molecular weight 440.3 occurs in uninfested, young leaves of *E. macrorhyncha*, *E. rossii* and *E. dives*. The 440.3 molecular weight sterol in young leaves of *E. rossii* and *E. dives* occurs in far smaller quantities than what occurs in similar-aged leaves of *E. macrorhyncha*. High levels of the 440.3 molecular weight sterol in young leaves of *E. macrorhyncha* indicate that this sterol dictates the preferential colonization by the 1st instars of *Glycaspis* (*Synglycaspis*), and influences its building populations to remain committed on *E. macrorhyncha*⁷³.

Variation in patterns of feeding by the free-living, lerp-forming, and gall-inducing Psylloidea influences the levels of complex lipids, sterols, and minerals in host leaves. In *Eucalyptus* leaves hosting the group feeding, free-living Aphalaridae (e.g. *C. eucalypti*), high levels of stigmaterol (which, the insects in general have a limited capability to use)⁶⁴ occur, whereas low levels of stigmaterol occur in the *Eucalyptus* leaves hosting the solitary feeding, lerp-forming, and gall-inducing Aphalaridae (e.g. species of *Glycaspis* and *Glycaspis* (*Synglycaspis*)). These indicate that high levels of stigmaterol accumulate due to group-feeding effect of *C. eucalypti*. Physiological adaptability in *C. eucalypti* to utilize stigmaterol⁷⁴, possibly enables *C. eucalypti* populations to accumulate stigmaterol, as also shown in generalist Lepidoptera raised on exclusive stigmaterol diets⁷⁵. Similarly low levels of complex lipids and high levels of minerals in the leaves fed by free-living species compared with the high levels of complex lipids and low levels of minerals in host of lerp-forming and gall-inducing species reiterate the distinct variation in the nutritional requirements of Psylloidea with different feeding behaviours⁷³.

Salivary enzymes of a majority of Sternorrhyncha are known to cause stress in plant cells, whereas those of a minority modify host-plant defences⁷⁶. Detoxification of plant-defence compounds is one critical function of Sternorrhyncha saliva. Cell-degrading enzymes, such as amylases, proteases, and lipases, occur in the saliva of the gall-inducing *T. jambolanae*⁷⁷. In free-living *C. eucalypti*, 64 and 58 kDa proteins characterized in both the saliva and phloem sap indicate that these proteins are vital in *C. eucalypti*–*E. globulus* interactions. The other identified salivary proteins of *C. eucalypti* include oxidoreductases and hydrolases, which enable mitigation of defence and detoxification of plant allelochemicals via cell degradation. The enzyme battery enables *C. eucalypti* to pierce leaf tissues of *E. globulus* and feed (Figure 9)⁴³.

The Sternorrhyncha form stylet sheaths during feeding; whereas the Auchenorrhyncha and Heteroptera rupture plant cells during feeding^{39,41}. Although the stylet pathway of Psylloidea is intercellular, they probe and puncture mesophyll cells randomly along the path. The Psylloidea make fewer probes than the Aphidoidea³⁹. The adult Psylloidea (e.g. *B. cockerelli*) occasionally feed from xylem similar to the Cicadellidae (e.g. *Homalodisca*

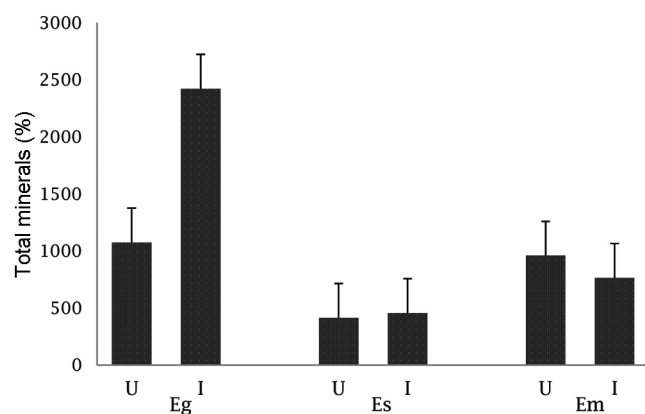


Figure 8. Total minerals (%) in leaves of *E. globulus* (Eg) infested by *Ctenarytaina eucalypti*, *E. sideroxylon* (Es) infested by *Glycaspis* sp. and *E. macrorhyncha* (Em) infested by *Glycaspis* (*Synglycaspis*) sp. (x axis); (uninfested – 0, infested – 1). (For overall comparisons between the three systems (*C. eucalypti*–*E. globulus*, *Glycaspis* sp.–*E. sideroxylon*, and *Synglycaspis* sp.–*E. macrorhyncha*), the host-plant data were pooled for the five instars of *Glycaspis* on *E. sideroxylon* and *Glycaspis* (*Synglycaspis*) on *E. macrorhyncha*, whereas the data for *C. eucalypti* were already combined because all developmental stages co-occur on the same leaf and graphs were generated using Microsoft Office Excel 2007. The vertical bar represents standard error.)

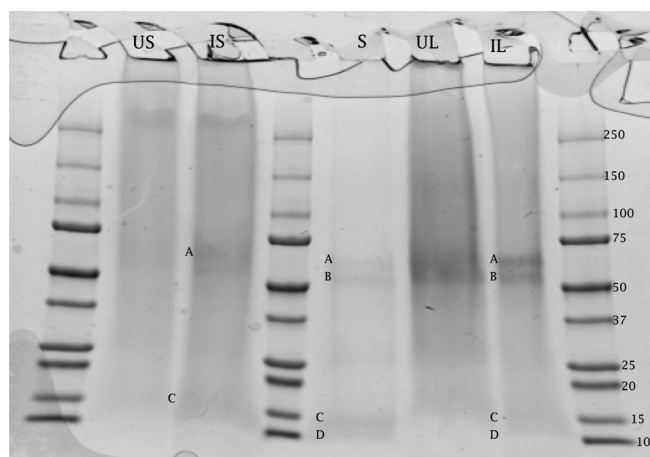


Figure 9. SDS-PAGE analysis of salivary proteins of adult *Ctenarytaina eucalypti* (0.05 g total protein/lane) from an uninfested shoot (US) and infested shoot (IS) (fed by populations of *Ctenarytaina eucalypti*; S – salivary protein; UL – uninfested leaves; IL – infested leaves (fed by populations of *Ctenarytaina eucalypti*) of *Eucalyptus globulus*. Unlabelled lanes (3X) contain a 10 kDa molecular mass ladder (Bio-Rad) (Source: Sharma *et al.*⁴³).

vitripennis)⁷⁸ and other plant-sap sucking Auchenorrhyncha and Heteroptera⁴¹. Nutritional behaviour of the sap-sucking Hemiptera is complex. Most of the nutrients are available in the diets the Hemiptera choose. Some of the extracted nutrients, such as carbohydrates, proteins, and fatty acids are stored in their tissues and carried through their metamorphoses, whereas amino acids (e.g. arginine) are supplied by the symbiotic microorganisms⁷⁹. The amino acids, carbohydrates, and lipids are generally necessary in greater quantities than vitamins for the Hemiptera⁶⁵.

Conclusion

Nutrients and the way the Psylloidea acquire them dictate the life-history performances of these insects. In general, the ability to enhance the quality of specific sites of the host plant and the occurrence of microbial endosymbionts in their gut facilitate them to perform better on nutritionally poor diets. However, within that realm, the nutritional requirements of Psylloidea vary. Variations in guilds (e.g. free living, lerp forming, gall inducing) and feeding behaviour (solitary, group feeding) appear to play a role in determining the nutritional ecology and physiology of the Psylloidea. Intense utilization of sugar by the lerp-forming and gall-inducing Aphalaridae because of their need to construct special structures (lerps, galls) and the maximum utilization of amino acids by the free-living species due to their gregarious feeding behaviour underscore basic variations in the nutritional eco-physiology of this group of insects. The role played by lipids in regulating the choice of specific plant taxa and in regulating Aphalaridae's fidelity to a single plant taxon is striking.

Compared to the available knowledge on the nutritional physiology of other plant-sap sucking Hemiptera (e.g. Aphidoidea, Aleyrodidae), little is known of the Psylloidea. Among the Indian Psylloidea, substantial variations are recorded in their life-cycle patterns and they vary substantially in different segments of the sub-continent. *Trioza minor* shows diversification behaviour onto different taxa of *Terminalia*, which exemplifies that in an otherwise conservative group – the Psylloidea – a capability to widen its host range occurs. Two other examples of highly flexible Psylloidea are *C. eucalypti* and *Glycaspis brimblecombei* (Aphalaridae). *Ctenarytaina eucalypti* populations occur intensely on *E. globulus* and less on *E. bicostata* and *E. leucoxylon* in its native Australian landscape. However, with the introduction of *E. globulus* and other taxa such as *E. maidenii*, *E. bico-stata*, *E. dunnii*, *E. nitens*, *E. benthamii*, *E. camaldulensis*, and *E. pulverulenta*, for commercial reasons, into the Mediterranean (Italy), subtropical and tropical South America (Chile, Brazil), and parts of South Asia (Sri Lanka), and with the ability of *C. eucalypti* to establish successfully in new environments, *C. eucalypti* has spread today as an invasive species in the above regions³⁴. Similarly *G. brimblecombei*, another Australian native, occurs on *E. blakelyi*, *E. camaldulensis*, *E. dealbata*, *E. tereticornis* and *E. nitens* in Australia. The recognized principal host of the *G. brimblecombei* outside Australia is *E. camaldulensis*, but it also occurs on 15 other species of *Eucalyptus* in the introduced landscapes of Mexico and the United States of America⁸⁰. A contrasting behaviour is apparent in *A. cistellata*, which remains restricted to *M. indica* populations in the Indo-Gangetic plains and Himalayan foothills. Although *M. indica* populations occur in equally high intensities in Peninsular India, *A. cistellata* populations are never known from here.

Although a majority of the Psylloidea feed on either one or on a narrow range of plants, their ability to be vectors of pathogens makes them a threat to agricultural and forestry plants. Given that almost nothing is known about the nutritional behaviour and physiology of economically important Psylloidea (e.g. *D. citri* and *A. cistellata*) of India, a critical gap exists to study the feeding biology and nutritional physiology and related bioecology of Indian Psylloidea.

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ACKNOWLEDGEMENTS. We thank Donald Miller (California State University, Chico, California, USA) and Igor Malenovsky (Masaryk University, Brno, Czech Republic) for helpful reviews and insightful remarks.

Received 6 February 2017; revised accepted 6 May 2017

doi: 10.18520/cs/v113/i08/1543-1552