

Mirid (Hemiptera: Heteroptera) Specialists of Sticky Plants: Adaptations, Interactions, and Ecological Implications

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Annu. Rev. Entomol. 2015. 60:393–414

The *Annual Review of Entomology* is online at ento.annualreviews.org

This article's doi:
10.1146/annurev-ento-010814-020932

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Keywords

omnivory, intraguild predation, tritrophic interactions, mutualisms, enemy-free space, carnivorous plants

Abstract

Sticky plants—those having glandular trichomes (hairs) that produce adhesive, viscous exudates—can impede the movement of, and entrap, generalist insects. Disparate arthropod groups have adapted to these widespread and taxonomically diverse plants, yet their interactions with glandular hosts rarely are incorporated into broad ecological theory. Ecologists and entomologists might be unaware of even well-documented examples of insects that are sticky-plant specialists. The hemipteran family Miridae (more specifically, the omnivorous Dicyphini: Dicyphina) is the best-known group of arthropods that specializes on sticky plants. In the first synthesis of relationships with glandular plants for any insect family, we review mirid interactions with sticky hosts, including their adaptations (behavioral, morphological, and physiological) and mutualisms with carnivorous plants, and the ecological and agricultural implications of mirid–sticky plant systems. We propose that mirid research applies generally to tritrophic interactions on trichome-defended plants, enhances an understanding of insect–plant interactions, and provides information useful in managing crop pests.

Metabolites: intermediates and products of plant metabolism; exudates from glandular trichomes often contain secondary metabolites that perform ecological functions

INTRODUCTION

The plant surface serves as a dynamic, multifunctional boundary between plants and their external environment (53). Interactions of insect herbivores with plant surfaces remained underappreciated into the 1980s (48), but herbivore adaptations to surface features such as trichomes (epidermal hairs) might be as important as nutrition, odor, and taste in determining their host specificity (51). Trichomes not only provide information on a plant's suitability for colonization (70), but also play key roles in shaping herbivore communities, densities, and tritrophic interactions (8, 20, 77, 81, 114).

Trichomes are morphologically diverse and can be glandular or eglandular (nonglandular). Eglandular trichomes vary from soft fuzz-like hairs to rigid Velcro-like hooks to sharp stalks that can impale soft-bodied insects. Glandular trichomes secrete fluids (exudates) (39, 58, 117). The exudates are primarily metabolites that serve various functions, including UV absorption, toxin excretion, and herbivore defense (26, 39, 121). Metabolites typically are synthesized in the glandular trichome itself, although carbon can be supplied by the epidermis as a precursor for massive exudate synthesis (121). Glandular plants often contain glandular and eglandular trichomes of multiple morphotypes, creating a complex three-dimensional surface that can restrict arthropod movement and prevent mouthparts from reaching the plant cuticle (e.g., 39).

Approximately 30% of all vascular plants produce glandular trichomes (39), including major crops such as pima cotton (*Gossypium barbadense*), tobacco (*Nicotiana tabacum*), and tomato (*Solanum lycopersicum*). Sticky plants have unique ecological interactions and support a diverse group of arthropod specialists. We focus on mirids because they are the best-studied arthropod specialists of glandular plants. The interactions we describe, however, should apply generally to glandular-plant ecological networks, which often involve specialists such as berytids (44), harpactorine reduviids (125), and oxyopid spiders (88).

We discuss adaptations that enable mirids to circumvent sticky-trichome defenses, highlight their mutualisms with carnivorous plants, and examine ecological and agricultural implications of mirid-sticky plant systems. Our main intent is twofold: (a) to document the widespread, important, and widely ignored interactions between sticky plants and their specialist mirids, and (b) to show that our topic, far from esoteric, applies broadly to ecological theory and crop management and can enhance our understanding of insect-plant interactions in natural and managed systems.

STICKY PLANTS: DEFINITION AND USE OF TERM

Sticky plants, though found in numerous families, are particularly common in the Asteraceae, Lamiaceae, and Solanaceae (39). We define sticky plants as those bearing glandular trichomes that secrete adhesive, viscous fluids, which excludes plants with physical (Velcro-like) clinginess, although our findings might also apply to such plants. Sticky plants, often termed clammy, glandular, glutinous, gummy, resinous, or viscid, tend to inhibit the movement of, or entrap, generalist arthropods. Common and scientific names sometimes reflect glandularity (e.g., sticky purple geranium, *Geranium viscosissimum*).

Stickiness represents a loosely defined continuum and is dynamic owing to plant growth state, herbivory, and environmental factors (dust, rain, wind) (74). Garden tomato, at the low end of the continuum, has exudates that impede the movement of (but do not exclude) most generalist insects (52) and entrap some small arthropods. Petunia (*Petunia* spp.) and tobacco, near the middle of the continuum, are moderately sticky, entrap numerous arthropods, and exclude even large generalist species (e.g., 23). Species of the carnivorous plant genus *Roridula* have extreme stickiness that entraps large arthropods and excludes virtually all arthropods except specialist mirids. Many of

the plants we will mention trap large numbers of arthropods, and the carrion becomes a key food resource in arthropod–sticky plant communities.

Sticky hosts of mirids include certain species of *Rhododendron* (108) that exhibit early-season stickiness. One of the few generalist mirids that use sticky plants is *Lygus hesperus*, which includes a sticky composite, *Deinandra kelloggii* (41), as a host. Glandular-plant specialists often use woolly eglandular hosts; glandular and densely pubescent, eglandular plants can have similar herbivore-deterrent effects and other plant-insect interactions (8).

A formal quantification of stickiness is a critical next step in developing broad theory on plant stickiness and its consequences. Few examples of precise measurements (29, 117, 118), however, are available.

Measurements of glandular-trichome densities and surface areas of exudate droplets are more straightforward to conduct and are common in the literature (e.g., 90). These measurements describe the extent of glandularity but do not necessarily measure stickiness, which combines the extent of glandularity with the adhesive force of the glandular exudate on a substrate and trichome strength. Studies that actually measured adhesion forces of plant surfaces (29, 117, 118) used similar methods. A freshly cut plant sample with sticky trichomes is attached to a platform. The material of interest (e.g., insect cuticle) is then attached to a force sensor and pushed onto the plant material at a standardized force for a standardized time. The force sensor is retracted unidirectionally at a constant rate until contact between the plant and material of interest is broken, at which point the force is recorded (e.g., 29, 117). Ideally, measurements of adhesive force and the extent of glandularity would be combined to produce measurements of the adhesive potentials of certain parts of the plant. This apparently has never been done, and in reality it would be complicated because of the dynamic stickiness and interactions between exudate adhesion and insect cuticle.

GLANDULAR TRICHOMES: A SYNOPSIS

Glandular trichomes probably evolved in response to different selection pressures (39), representing convergent structures that evolved via divergent developmental pathways (102). Before an essential role of glandular trichomes in herbivore defense was demonstrated (10, 43, 58; see also 13), their contents often were considered metabolic waste products (92). Furthermore, the contents of glandular trichomes can be cytotoxic, and selection for avoiding autotoxicity by sequestering metabolites and pinpointing their delivery might have influenced their evolution (26).

Eglandular trichomes pose physical barriers to herbivores, but the combined physical and chemical effects of glandular trichomes are more difficult for herbivores to overcome (34, 114). Biologically active exudates from glandular trichomes are diverse and include fatty acid derivatives, phenylpropanoids, polyketides, and terpenoids (92).

The odor, taste, stickiness, and toxicity of glandular-trichome contents (50) can attract, repel, trap, and kill insects and impede insect movement (8, 52, 71). Most studies have examined foliar trichomes, rather than those found on inflorescences (46) or stems (but see 52). Voigt et al. (117) provided detailed descriptions of foliar trichomes, including their position (abaxial, adaxial, or on both surfaces) and arrangement (e.g., sparse, dense).

Glandular exudates can be sticky and toxic to arthropods (39) and are secreted by two broad types of glandular trichomes: capitate and peltate. Capitate trichomes typically consist of a basal cell and one to several stalk cells with one or several secretory cells at the distal end that secrete compounds directly onto the trichome surface, then potentially onto the leaf epidermis. Peltate trichomes comprise a stalk cell with a head having several secretory cells and a large, common, subcuticular storage cavity (39); the cuticle of this cavity is easily ruptured by mechanical disturbance,

Jasmonic acid: a fatty acid derivative in the jasmonate class of plant hormones; involved in regulating production of defensive traits

Defensive transcript: genes related to defense against herbivores

similar to a bubble bursting. Peltate trichomes tend to contain more volatile and sticky exudates than do capitate trichomes. The rapid oxidation that occurs when peltate trichome storage cavities rupture, for example, causes acyl sugars and polyphenol contents to become sticky, entrapping, suffocating, or poisoning arthropods that make contact (39). Wild tomato species (*Solanum* section *Lycopersicon*) have greater trichome densities and diversity of specialized metabolites and are more resistant to insect herbivory than the cultivated tomato (52, 63, 67, 103). Among tomato's glandular-trichome types (63), type IV contains acyl sugars and type VI is the main site of terpenoid production (52, 67). Together they confer maximal herbivore resistance in tomato (52, 103). The diverse antiherbivore alkaloids secreted by glandular trichomes can poison herbivores via direct feeding, contact, or volatilized compounds that function as fumigants (24, 28, 60).

Glandular-Trichome Inducibility

Trichome densities vary according to availability of resources (e.g., light, water; 131), but herbivory can induce increases in densities and amounts of volatiles released, and changes in proportion of glandular to eglandular trichomes (49, 83). Jasmonic acid, which triggers the expression of defense genes, is linked with glandular-trichome production; its effects vary by plant species. In some species, trichome abundance can be altered by plant-defense induction, whereas in other species it appears to be fixed. In the tarweed *Madia sativa* (Asteraceae), wounding induces increased production of glandular trichomes when ample water is provided (40). Low-water conditions also induce increased glandular-trichome production, but only in undamaged tarweed plants; an upper limit to production might prevent damage and drought from contributing additively to glandular-trichome production (40). Tomato plants (*S. lycopersicum*) with jasmonic acid biosynthesis and reception mutations produce lower trichome densities than comparable wild types (59); application of methyl jasmonate to tomato plants induces increased trichome densities (12). Application of methyl jasmonate to *Datura wrightii* does not alter trichome density or the concentration of alkaloids in exudates, but it increases acyl sugars in exudates by 44% (42).

Peiffer et al. (78) demonstrated that glandular trichomes in *S. lycopersicum* function in the detection of herbivores and induction of the jasmonic acid pathway. Trichomes ruptured by walking caterpillars or moths induce the expression of defensive transcripts; feeding is not required for induction, so tomato plants could prepare for herbivory before it occurs. A tiptoeing (avoidance) strategy (**Figure 1a**) of mirids (Dicyphina) on sticky plants might interact with an early-sensor defense strategy by rupturing fewer trichomes than other arthropods. Caterpillars on sticky plants sometimes consume glandular exudates (e.g., 124), which could function to mute early sensors, although that possibility has not been studied.

Genetic Determinants of Glandular Trichomes

Glandular-trichome production is heritable and plastic. Many systems provide evidence for genetic determinants of glandularity (39), including studies on gene suppression (122) and trait-heritability values (47). Glandular and eglandular populations often are found within a species (e.g., sticky or fuzzy *D. wrightii*). A single gene in *D. wrightii* determines trichome phenotype; the sticky allele is dominant (32). Populations of glandular and eglandular conspecific tarweeds can be found at different times of the season in the same locations. Although the genes have not been identified, the differences persist when plants are grown under common garden conditions, suggesting the trait is genetically determined (17).

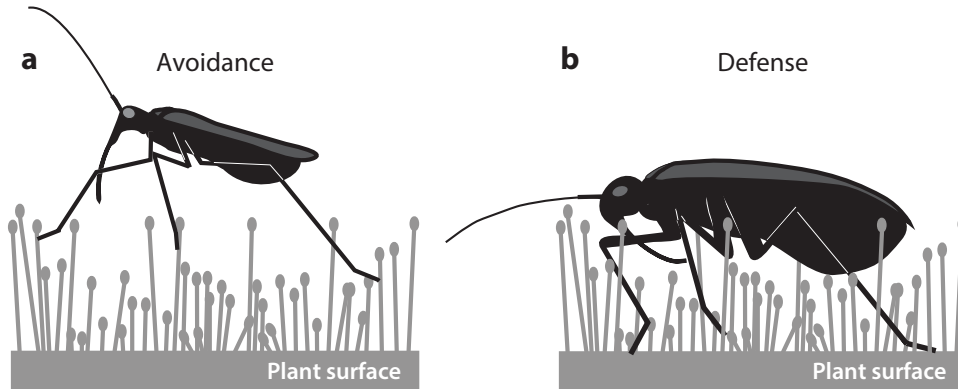


Figure 1

Hypothesized strategies of dicyphine mirids (Bryocorinae: Dicyphini: Dicyphina) in walking on plant surfaces with glandular trichomes. (a) Avoidance strategy: Slender, lighter-bodied bugs use long legs to hold their bodies above glandular exudates. (b) Defense strategy: Heavier, tougher-bodied bugs (*Pameridea*) often contact sticky exudates; the bugs are able to slough off exudates using an antiadhesive, epicuticular grease layer on the cuticle. Modified from Reference 120 with permission from Springer Science + Business Media, Dagmar Voigt, and Stanislav Gorb.

OVERVIEW OF MIRIDAE

The Miridae, comprising more than 11,000 species (14, 44), represent the most species-rich heteropteran family and include both crop pests and their predators; several species have been used successfully in classic biological control. Ancestrally predacious (18, 97, 127; but see 110), the family includes both generalist predators and specialists of particular prey [e.g., mites (Acari), lace bugs (Tingidae), thrips (Thysanoptera); 127]. Omnivorous mirids can be key crop pests or key predators, depending on host-plant quality, prey densities, and availability of alternative food (38, 127). As a result, a species can be beneficial or detrimental to crops, depending on environmental conditions (127).

MIRID SUBFAMILIES ASSOCIATED WITH STICKY PLANTS

The use of sticky plants by mirids correlates with omnivory, although this has not been studied formally. Sticky-plant specialization has arisen in at least four subfamilies (**Figure 2a**). Such specialists, however, are well documented only in the Bryocorinae (97, 105, 114), where they are restricted to the tribe Dicyphini: subtribe Dicyphina (14). Other bryocorine groups apparently are associated with nonsticky hosts (and are strict phytophages) (**Figure 2b**). Glandularity (and hairiness) in this subtribe might be as important as plant architecture, phylogenetic relatedness (129), and secondary plant chemistry in determining host-plant ranges. Within Dicyphina, research has focused on species that belong to key ecological systems or are potentially useful in managing crop pests. Associations with sticky hosts, therefore, remain unknown for the majority of world dicyphines.

Compared with knowledge of dicyphines, less is known about the use of sticky plants by mirids within other groups. Publications often list host plants without mentioning glandularity or possible restriction to sticky species, making difficult the linking of species with these host-plant traits. We suggest that the subfamily Phylinae will prove rich in sticky-plant specialists, although

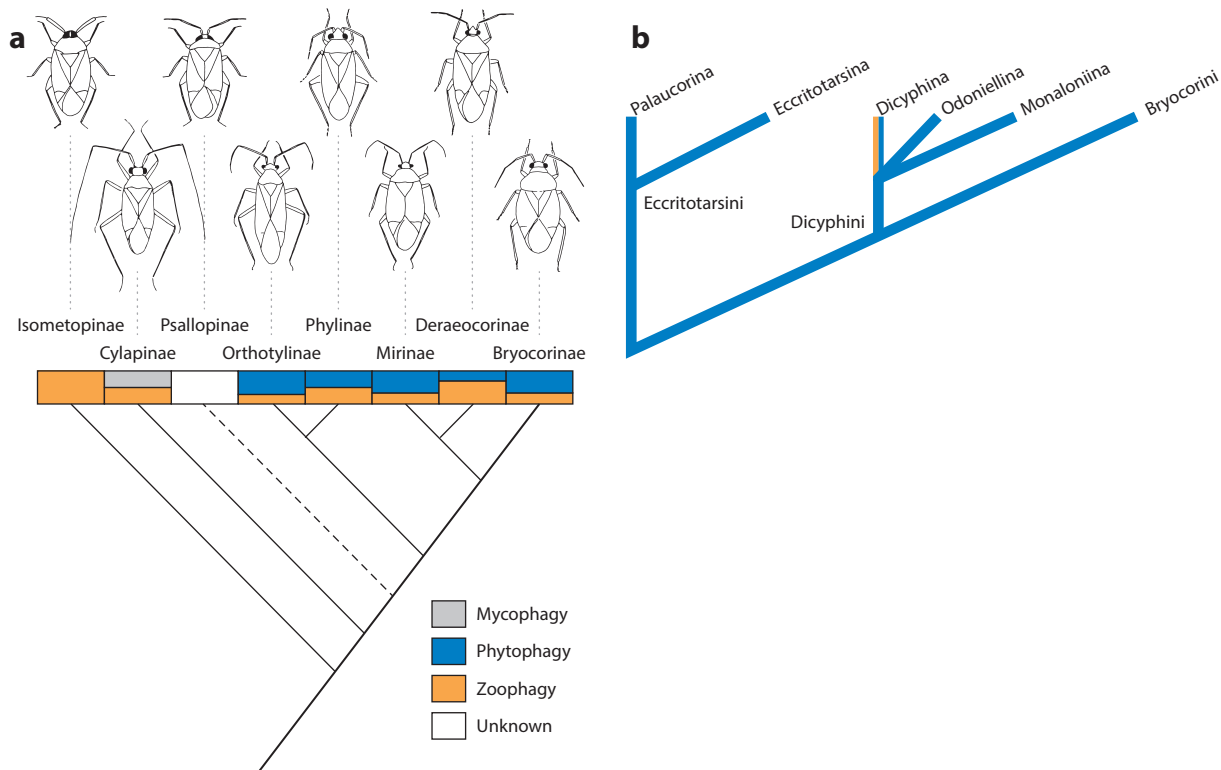


Figure 2

Mirid phylogenetic relationships and feeding (trophic) habits. (a) Subfamilies with the relative proportions of their feeding habits estimated. Modified from Reference 127 with permission of Cornell University Press. (b) Subfamily Bryocorinae with tribes (-ini) and subtribes (-ina). Color codes for feeding habits: mycophagy (fungivory) (*gray*), phytophagy (*blue*), zoophagy (carnivory) (*orange*), and unknown (*white*). Omnivory is indicated by *blue* and *orange*. Modified (with a phylogenetically unresolved subtribe, Odoniellina, added) from Reference 94 with permission of the American Museum of Natural History and Randall T. Schuh.

relatively few species (e.g., *Macrotylus ponticus*, *M. quadrilineatus*; 101) have been noted to use sticky hosts. That several North American species of the phylinae genus *Plagiognathus* specialize on sticky hosts can be inferred from known plant associations (95). In the Orthotyliinae, insect carrion is essential for *Orthotylus gotoi* on a sticky species of *Rhododendron* (108). The use of glandular hosts in Orthotyliinae also can be inferred from the literature (e.g., certain *Pseudopsallus* species; 107). Specialization on sticky plants probably is more common among orthotyliines than is documented but is unlikely to occur in all tribes, especially those in which omnivory is unknown (127).

In the largest mirid subfamily, Mirinae, associations with sticky hosts seldom have been mentioned (e.g., *Lygus convexicollis*; 98). Even though specialization can be inferred from lists of plant associations, the extent of mirine specialization on glandular hosts remains unknown.

MIRID ADAPTATIONS FOR LIVING ON STICKY PLANTS

Insect competence on plant surfaces should be under strong selection pressure (11). An insect's success in coping with plant defenses, including glandularity, is thought to be inversely proportional

to its amount of contact with the defense (8); most mirid (and other) specialists of sticky plants avoid contact with glandular exudates while moving along the plant surface.

Omnivory is common in the Miridae, especially so in specialists of sticky plants, and is considered a key innovation promoting insect diversification (33). An ability to specialize on sticky plants—and consume their diverse resources—might have allowed the Dicyphina to diversify relative to other subtribes within Dicyphini that do not use sticky plants. The omnivorous Dicyphina are more speciose (210 species) than the phytophagous subtribes Monaloniina (171 species) and Odoniellina (54 species) (96) (**Figure 2b**). Omnivorous mirids possess behavioral, morphological, and physiological adaptations that allow them to consume phylloplane resources (e.g., carrion) and prey (19, 21, 33, 127). This trophic flexibility probably is a key adaptation allowing them to thrive on sticky plants. Mirid adaptations for omnivory, however, are not without costs; plant feeding by *Dicyphus hesperus*, for example, results in wear of the mandibular stylets (87).

Pretarsal claws (curved, elongated) and behavior allow Dicyphina to attach to and live on sticky hosts (e.g., 101, 105, 117; but see 94). These elongate bugs have long, slender legs and walk on tiptoe to minimize contact with exudates (105, 117, 118) (**Figure 1a**); early instars, however, can be susceptible to entrapment (64). Pretarsal claws also are used to remove exudates from the antennae, proboscis, and body (89, 105, 114). Exudate-affected dicyphines groom more effectively than do generalist heteropteran predators (27, 57).

Fine-tuned adaptations in the dicyphine *Pameridea roridulae* allow it to walk unimpeded on sticky surfaces. Though similar in size to other dicyphines, the heavier *Pameridea* bugs apparently have more muscle mass and produce stronger forces during walking. Holding the body close to the surface, often contacting sticky trichomes (defense strategy) (**Figure 1b**), they employ a thick (516–713 nm) cuticular grease layer that adheres to sticky secretions and is sloughed off (cohesion failure; 118, 120).

Adverse effects of trichomes are inversely related to body size (74), but larger and heavier true bugs usually are overlooked as sticky-plant specialists. An exception is *Corizus byoscyami* (Rhopalidae), which is able to plow between glandular trichomes (99). Whether large mirids can slog through stickiness in a similar manner is not known.

MIRID RELATIONSHIPS WITH CARNIVOROUS AND PARACARNIVOROUS PLANTS

Carnivorous (insectivorous) plants, which typically grow in nutrient-poor soils, have evolved strategies for obtaining macronutrients (e.g., nitrogen and phosphorus) that are in short supply. Not all carnivorous plants are sticky, but species of several genera use digestive-mucus-secreting, adhesive traps to capture arthropod prey from which they can extract nutrients. Carnivory has evolved independently in five or six plant lineages (1, 55). Trichomes, ranging from tentacle-like to stalked glands that resemble the glandular trichomes of noncarnivorous plants (22), have exudates with enzymes that allow direct nutrient absorption. Traps and digestive enzymes incur metabolic costs, resulting in ecological trade-offs between photosynthesis and nutrient uptake. Cost-benefit models assume that nutrient uptake offsets the costs of prey capture and digestive structures (1, 16, 55).

Researchers disagree on the attributes needed to classify a plant as carnivorous; some require that plants produce their own mucus with digestive enzymes, although other pathways for nutrient absorption are possible. We follow Rice (85): Carnivorous plants should have adaptations for capturing prey; a mechanism for degrading prey, using their own enzymes or indirect means (e.g., bacteria, insects); and a pathway providing nutrient absorption.

Phylloplane: the leaf surface considered as a habitat

Pretarsal claw: last segment of insect leg; in mirids, it bears structures useful in higher classification

Fynbos: ecoregion of heathland and shrubland in South Africa's Cape Floral Region, which is noted for exceptional biodiversity and endemism

Vicariant: referring to fragmentation of a group of organisms by a geographic barrier leading to differentiation of the ancestral group into new taxa

Cospeciation: concordant speciation in which one species causes speciation in the other; resulting phylogenies can be mirror images of one another

An Obligate Mutualism: *Roridula*-*Pameridea* System

The plant family Roridulaceae comprises a single genus of two species, *Roridula dentata* and *R. gorgonias*; their allopatric populations are patchily distributed in the fynbos of South Africa's cape (3). Roridulas differ from other carnivorous plants in that they trap prey with a lipid-terpene resin (versus aqueous mucilage) that enables larger prey to be trapped and resists desiccation during the dry fynbos summers (119). *Roridula*-dicyphine interactions thus qualify as carnivory, even though roridulas do not produce proteases. Phosphatase activity recently was discovered in the epidermis of *Roridula* leaves (80), although it is not clear what the effects of this activity are. Phosphatases might digest phosphate-containing nutrients from entrapped insects or mirid feces; or the enzymes might indicate only high metabolic activity in general (80).

The mirid genus *Pameridea* similarly contains only two species, which also are fynbos endemics, each specializing on a species of *Roridula*: *Pameridea marlothi* on *R. dentata* (but see 69) and *Pameridea roridulae* on *R. gorgonias* (3, 25). The bugs are major pollinators of their *Roridula* hosts (7). Anderson (3) hypothesized that a *Roridula*-*Pameridea* association predated a single vicariant event that split the ancestor of extant roridulas, allowing allopatric speciation (cospeciation) of plant and bug genera.

Because roridulas were thought incapable of producing digestive enzymes, they were not always considered carnivorous. Dicyphines, however, feed on entrapped insects and defecate on leaves of *Roridula*, and the plants rapidly (<72 h) absorb nitrogen (as much as 70% of their needs) through cuticular gaps on leaves. This indirect means of nutrient absorption reduces the costs of producing digestive enzymes and structures and is regarded as a digestive mutualism (2, 3). This apparently coevolved system warrants inclusion among classic examples of plant-insect mutualisms. Similar mutualisms with mirids have been considered for few other plant systems, but fecal fertilization might prove important in noncarnivorous sticky plants, particularly in systems where sticky trichomes do not have clear antitherbivore functions.

Outcomes of the *Roridula*-*Pameridea* digestive mutualism are potentially variable and density dependent. Roridulas grown in the greenhouse without mirids show negative growth rates, and those with intermediate densities exhibit positive growth, but high mirid densities can result in negative growth rates. At high densities, the positive effects evidently are offset by costs of their plant feeding (6). The experimental conditions (greenhouse), however, were not representative of natural conditions. Soil without phosphorous or nitrogen was used (plants in the field may get as much as 30% of their nitrogen from soil; 6), and mirid density was higher than observed in the field, with intermediate levels slightly higher than the average field maximum; high levels were an order of magnitude higher. The experiment still demonstrates the potential for dynamic and variable outcomes of the mutualism. A disruptive nonmutualist, the crab spider *Synaema marlothi*, preys on the mirid, reducing the mutualism's strength on *R. dentata*. Mirid and spider densities are inversely related, but plants still receive about 40% of their nitrogen from bugs at peak spider densities. Even with high spider densities, the benefits of mutualism might outweigh the costs (5).

Relationships with Other Carnivorous Plants

Dicyphine mirids (**Figure 3**) are found on certain enzyme-producing carnivorous plants (*Byblis* spp., *Drosera* spp., and *Pinguicula* spp.) with adhesive traps (69, 127, 132). The bugs' relationships with their hosts are unknown but could include robbing nutrients, removing excess prey (62), and engaging in mutualisms (69). Collembolan carrion trapped on an Australian sundew (*Drosera erythrorhiza*) provides plants with as much as 100% of their nitrogen and phosphorous needs (123). The possibility that sundew dicyphines (*Setocoris* spp.; formerly *Cyrtopeltis*) also provide nutrients was not tested; these bugs could be parasitic or mutualistic.



Figure 3

Setocoris sp., a dicyphine mirid on glandular trichomes of the sundew *Drosera binata*. Reproduced from Reference 69 with permission of Stewart McPherson.

Relationships with Paracarnivorous Plants

Sticky plants often are called paracarnivorous (hemi- or protocarnivorous) when they possess attributes similar to carnivorous plants, such as trapping large amounts of insects and producing leaf proteases, but are not known to digest captured carrion. Some of these plants could be carnivorous via digestive mutualisms (84, 106). Anderson et al. (4) presented methods for determining the nature of symbiotic relationships between mirids and other potentially carnivorous plants. According to this framework, scavenging mirids are mutualists if plants absorb their fecal nutrients, and parasites or commensals if plants do not. Another possible interaction not included in the methods of Anderson et al. (4) is that scavenging mirids could provide indirect plant defense by feeding on herbivores (e.g., 54, 88). In general, researchers should determine if sticky plants harbor dicyphine Miridae; if the bugs are present, the possibility that mirids provide plants with indirect nutrition or defense should be considered in the experiment design.

MIRID AND STICKY-PLANT FOOD WEBS

Importance of Carrion

In addition to carnivorous plants, noncarnivorous sticky plants trap large amounts of carrion (22)—would-be herbivores, predators, and passersby (tourists) (105)—which provide a critical resource for mirids. Mirids on sticky plants with entrapped insect carcasses apparently scavenge carrion. *Pameridea* bugs rapidly consume the carcasses of entrapped insects on their *Roridula* hosts. Even though scavenging by mirids on sticky plants has been observed in many other systems, we found only one study that measured the consequences of scavenging for mirid growth. *Orthotylus gotoi* scavenges carrion to survive on a sticky rhododendron (*Rhododendron macrosepalum*), which increases growth rates and adult survival and decreases instar duration; the bug also benefits from phytophagy (108). How plant fitness might be affected by *O. gotoi* is unknown. Fecal fertilization by the mirid is possible but unlikely (4), and it is not known if *O. gotoi* contributes to indirect herbivore defense.

The effects of scavenging by mirids on sticky plants are little known, as are other aspects of their feeding behavior on such hosts. To what extent do they also consume live prey, and what

Paracarnivorous plants: species with some attributes of carnivorous plants but lacking some necessary to meet strict criteria for carnivory

Zoophytophagy: feeding by predators (carnivores) on plants

Intraguild predation: the killing and eating of species that use similar resources and represent potential competitors

do they require from host plants other than carrion? Scavenging by mirid specialists on sticky plants, however, is ubiquitous and probably a central component of their food webs (**Figure 4**). Even mainly phytophagous mirids living on nonsticky hosts consume carrion, underscoring their ability to exploit available resources. *Lygus lineolaris* and *Adelphocoris lineolatus*, key pests of alfalfa, scavenge mummified aphids and fungus-killed flies on host surfaces (126). Species of the phylinae genus *Ranzovius* are specialists in spiderwebs, where they scavenge small arthropods ignored by spiders or too small to trigger their feeding responses (128). The mirid-spider interactions are similar to those in systems involving sticky plants and mirids.

Glandular Exudates as Food

Dicyphine mirids feed on exudates of certain sticky hosts (56, 114), but the nutritional benefits they derive are unknown. A dicyphine (*Tupiocoris notatus*) might sequester defensive compounds from exudates of *D. wrightii* (114), but this hypothesis is untested. Exudate chemical composition varies greatly among plant taxa. Exudates of *D. wrightii* are toxic to herbivores, but exudates from other glandular plants might simply be sticky or involved in detection of herbivores. In wild tobacco (*Nicotiana attenuata*), exudate feeding by caterpillars tags them for predators; ants can use volatile exudate constituents in caterpillar feces to locate prey (124). Functional differences between exudates from different plants, though rarely categorized, probably are critical in structuring arthropod-plant interactions; the assumed differences make it difficult to postulate effects of exudate feeding on mirid ecology. In some systems, mirids might sequester chemicals, whereas in others, they might obtain sugars and minerals (or microbes) from exudates.

Other Plant-Trapped Resources

Organic materials—pollen, fungal spores, bacteria, and materials from nearby plants—that become stuck on trichomes might provide food for mirids. Nectar from flowers of *Lyonia ovalifolia* that falls on *R. macrosepalum* is fed on by resident mirids (108). Whether sticky-plant mirids forage for fungal spores (fungal spores have been found in guts of clypeate mirids; 130) is not known, but many plant bugs consume pollen as an important food source (127). Because pollen accumulates on sticky surfaces, it might also represent an important phylloplane food source for mirids; predatory mites consume phylloplane pollen, and their association with trichome-bearing host plants might be due in part to increased phylloplane pollen on such plants (93). Also untested is whether mirids might obtain minerals from dust-coated sticky plants or nutrition from bacteria living in exudate.

Ubiquity of Omnivory on Sticky Plants

A key aspect of sticky-plant food webs involving mirids is their trophic flexibility (e.g., zoophytophagy; 127) (**Figure 4**). Omnivory, especially common in the Dicyphina, includes cannibalism and intraguild predation (127). Omnivory appears to be more prevalent in mirids specializing on sticky plants than in those specializing on nonsticky hosts; entrapped carrion might be important in selecting for their predation. The heteropteran labium (e.g., stylet flexibility), use of nitrogen-rich food (e.g., pollen), and polyphagy are considered preadaptations for omnivory (21, 33). These attributes appear to have been important in not only the evolution of omnivory (33) but also the success of mirids on sticky plants, enabling them to use diverse resources.

Little is known regarding what mirids obtain from phytophagy on sticky hosts (37) and whether the benefits of plant feeding differ for nymphs and adults. How the bugs feed likely depends on other available resources (45). An enhanced understanding of their trophic behavior, including how

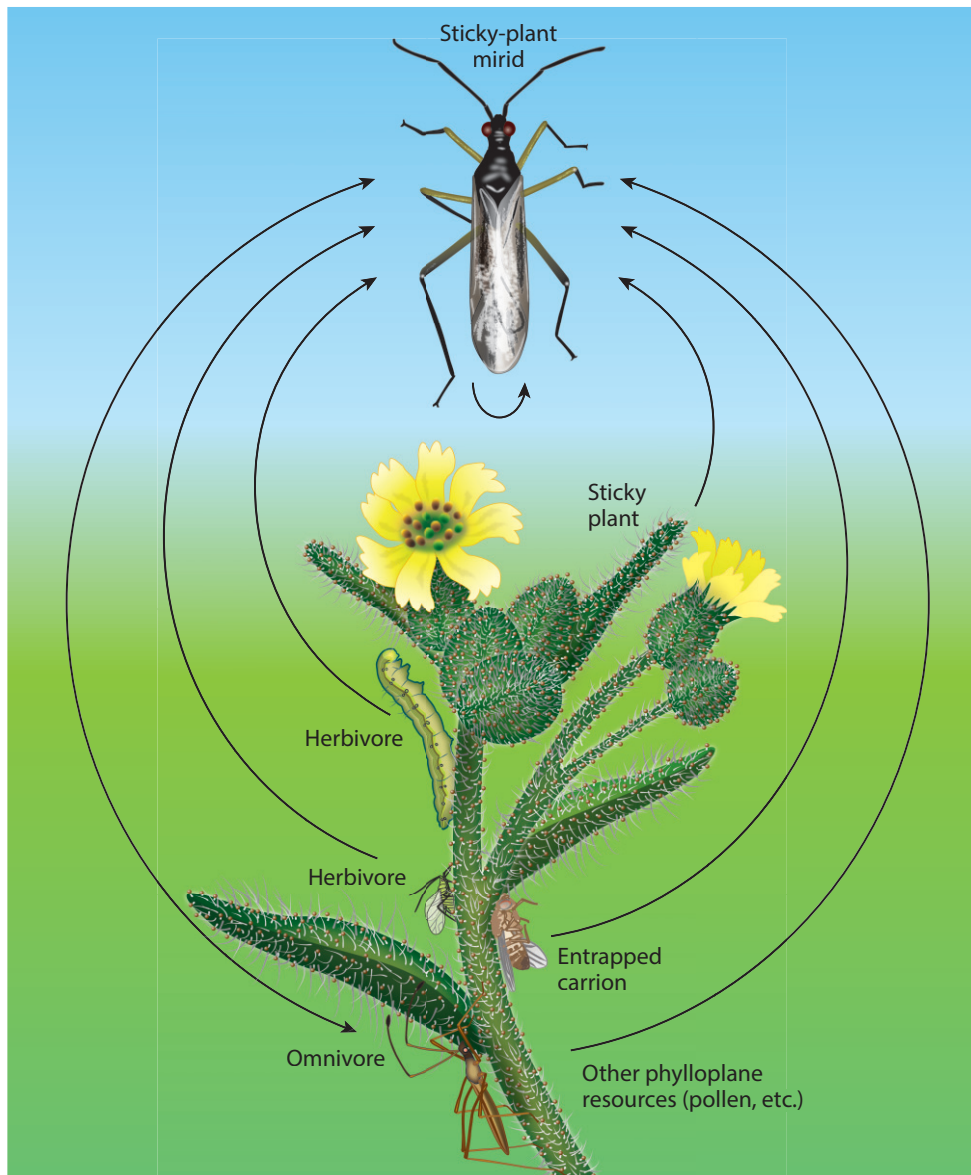


Figure 4

A theoretical food web for a sticky plant, showing only feeding interactions for the mirid. Mirids feed as broad omnivores on sticky plants, consuming phylloplane resources (e.g., entrapped carrion), herbivores, other omnivores, conspecifics, and their host plants. The arthropod community is a simplified representation of that found on slender tarweed (*Madia gracilis*; Asteraceae) and is meant to depict a typical sticky-plant food web rather than formally quantified interactions.

dicyphines feed on plants, might help predict their exposure to soil-applied systemic insecticides (112) and their efficacy as biological control agents. The ability of *D. hesperus* to consume whiteflies is limited by water, which is obtained from feeding on various host plants (37). Because mirids digest prey extraorally (127), which requires water (19), water probably is a critical plant-provided resource, particularly when the bugs scavenge dry carcasses. In the absence of prey, *D. hesperus* persists on only a few plant species, suggesting it requires alternative food from other hosts (38). This result also implies that sticky-plant mirids with carrion available might be less constrained by host chemistry and access to live prey than are mirids on plants lacking carrion. Specialization for sticky-plant surfaces—and an ability to consume the diverse phylloplane resources on them—could lead to generalization with regard to host-plant phylogeny and chemistry, as well as trophic behavior (phytophagy, zoophagy, necrophagy).

TRITROPHIC INTERACTIONS ON STICKY PLANTS

Enemy-Free Space

Ecologists often assume that sticky-plant herbivores live in enemy-free space because their predators are excluded (e.g., 30, 81). This assumption typically is based on greenhouse or laboratory studies, but effects of trichomes on tritrophic interactions can differ dramatically under field conditions (e.g., 74). The use of generalists (e.g., coccinellids, geocorids, nabids), rather than sticky-plant specialists, as surrogate predators also has led to this conventional view (e.g., 30, 35). The omnivorous mirid *T. notatus*, a dicyphine sticky-plant specialist, damages glandular more than eglandular *D. wrightii* because of decreased top-down control by generalist predators, including heteropterans (*Geocoris pallens*, *Nabis* sp.; 35). Decreased top-down control on *Datura* sp. also was observed for a chrysomelid specialist (*Lema daturaphila*) using the same predators. Numerous dead coccinellids stuck to the Velcro-like hairs of *Mentzelia pumila* led Eisner et al. (30) to conclude that the plant paid an indirect cost for the hairs via decreased indirect defense. When coccinellids are used to determine the effects of glandular trichomes on predator foraging (e.g., 75), results are similar: inhibition of top-down control.

A recent review (86) of trichome effects on predator effectiveness highlights a generalist-predator bias; sticky-plant specialists were used in only 3 of the 47 systems. Most studies were conducted in the laboratory or greenhouse, coccinellids were the most common surrogate predators, and the 7 studies that measured trichome effects on predator abundance (rather than just behavior) showed no significant pattern.

Three criteria often are used to determine enemy-free space (9): (a) predators are important (they lower prey fitness outside enemy-free space), (b) prey benefit from predator exclusion (prey fitness is greater within enemy-free space than it is outside enemy-free space when predators are present), and (c) enemy-free space involves a cost (lower prey fitness in the absence of predators). Laboratory studies using surrogate generalist predators can satisfy the three criteria even if predators whose relative importance increases within enemy-free space (e.g., sticky-plant mirids) are ignored. We propose that ecologists studying tritrophic interactions on sticky plants consider how plant trichomes affect the relative importance of each predator species, and the overall predator community. A coccinellid might be the most important predator of aphids on glabrous plants, but a dicyphine mirid might be more important on sticky plants, where it is most abundant. Instead of comparing the efficacy of coccinellids on glabrous versus sticky plants, it would be better to compare their top-down strength on glabrous plants with the top-down strength of dicyphines on sticky plants. Predator diversity and abundance on sticky versus nonsticky hosts, when combined with the predation strength of each predator on its host, will yield more accurate predictions for

the magnitude of predation risk than simply comparing the locomotion of a single predator species on preferred and nonpreferred hosts.

Even though host stickiness can reduce locomotion by sticky-plant specialist predators and increase their grooming time, it might not reduce top-down control by predators. Stickiness can increase carrion abundance, thus supporting higher densities of specialist predators that suppress herbivory on sticky plants (54, 88), even if predators walk slower and must groom more often. Stickiness also could inhibit herbivores more so than predators on sticky plants, enhancing top-down control by predators. Measuring only the effects of stickiness on predator behavior is insufficient for inferring its effects on tritrophic interactions. The relative effects of stickiness on predators versus herbivores must be tested to infer the effects of stickiness on top-down control and indirect defense.

Arthropod Specialization and Composition of Exudate Chemicals

To better understand proximate and ultimate mechanisms affecting interactions on sticky plants, researchers should demonstrate that arthropods are sticky-plant specialists and determine the functional chemistry of exudates. Conclusions from studies involving sticky plants and generalist insects probably do not apply to specialist mirids. Moreover, plants with toxic, sticky, or volatile exudates likely differ in their suitability for insects.

Use of Volatiles from Glandular Exudates

Volatiles from glandular exudates play diverse roles in plant-arthropod interactions. The moth *Diaphania nitidalis* uses volatiles from squash (*Cucurbita pepo*) as oviposition cues (79). Trichome volatiles also can be toxic. In tomato, 2-tridecanone from glandular trichome type VI (52, 63) increases larval mortality in lepidopterans (60), but volatiles of sticky *D. wrightii* do not affect survival of *Manduca sexta* (113).

We are not aware of studies that have measured effects of glandular-trichome-produced volatiles on sticky-plant mirids, although responses to volatiles from their nonsticky hosts are known (68, 72). Volatiles released by insects rupturing glandular trichomes could provide honest signals to predators seeking mobile prey or entrapped, struggling insects, but this hypothesis remains untested.

STICKY PLANTS AND AGROECOSYSTEMS

Difficulty of Biological Control on Sticky Plants

Important sticky crops include alfalfa (*Medicago sativa*), hops (*Humulus lupulus*), pima cotton, potato (*Solanum tuberosum*), tobacco, and tomato, and ornamentals such as geranium (*Pelargonium × hortorum*), petunia, and some mints (*Salvia* spp.). Biological control on such plants is difficult because many generalist predators, as well as hymenopteran parasitoids, are rendered ineffective (52, 81). Chrysopid larvae placed on petunia to control tobacco budworms (*Heliothis virescens*) became entrapped in glandular trichomes and were eaten by the budworms they were supposed to control (23). Tomato trichomes inhibit foraging efficacy of a syrphid (*Episyrphus balteatus*), resulting in ineffective aphid control (115).

Sticky-Plant Mirids as Biological Control Agents

Sticky-plant specialist predators make ideal candidates for biocontrol on sticky crops. Where generalist predators are unable to forage effectively, specialist dicyphine mirids that can walk relatively

Omnivore: organism that feeds at more than one trophic level

Syntopic: referring to species (often taxonomically related) that live in the same microhabitat or in proximity

unimpeded are widely used (15). Although typically small bodied and capable of consuming only eggs and small herbivores, sticky-plant mirids can have dramatic top-down effects on crop pests and their damage (127). Certain dicyphines, as omnivores, are important in greenhouse- and field-grown tomatoes as biocontrol agents of herbivores and their eggs (15). Omnivores are resilient predators because they can persist during prey shortages by consuming other resources (e.g., plant fluids, pollen; 37, 57, 127). This resilience, however, comes at a cost: Omnivores can damage the crop plants on which they live. Plant feeding by *D. besperus* can damage tomato fruits, but the bug prefers leaves (38). *Dicyphus tamaninii* can damage tomato, but estimates of mirid densities and those of their whitefly prey allow insecticides to be applied only when needed to limit potential damage by either insect (66).

Dicyphines will cannibalize (127), and syntopic species on tomato can prey on each other and engage in other antagonistic interactions (73). Dicyphines also compete with released parasitoids (but do not necessarily decrease pest mortality; 116). In the case of biocontrol of sticky weeds, resident dicyphines can prey on released herbivores, potentially interfering with weed suppression (127).

Plant Breeding and Trichome Engineering

When his classic work on insect resistance in crop plants appeared (1950s), Painter (76, p. 421) could report few instances when “knowledge of the cause of resistance has aided in plant breeding.” Even though some progress has occurred since that time, relatively few examples are available in which breeding for known resistance traits has achieved useful resistance to insect pests. Rapid breakthroughs in plant breeding and metabolic engineering will depend on knowing the source of resistance and its genetic basis. Thus, identifying enzymes and pathways involved in the synthesis of trichome-produced, specialized metabolites would be valuable. Trichomes possess attributes (e.g., heritability) that enhance their usefulness in metabolic engineering; other features (e.g., unusual biochemistry, correlations with other traits) inhibit such use (92, 111).

Taking Advantage of Crop Stickiness in Agriculture

Glandular trichomes, critical in structuring plant-arthropod food webs, can disrupt predator foraging; directly impede, entrap, or exclude herbivores; attract and provide food for predators; contribute to herbivore perception of plants and plant perception of herbivores; and potentially affect signaling and herbivore apparency to predators. Thus, on the one hand, manipulating glandular trichomes offers potential benefits to agriculture. On the other hand, these diverse effects complicate their potential application. Because trichomes mediate complex interactions at multiple trophic levels and studies often consider only one or a few interactions, little is known about how glandular-trichome manipulation might affect herbivory and plant yield at large scales.

Sticky plants can facilitate early colonization by dicyphine mirids in greenhouses or maintain their populations (91). *Macrolophus melanotoma*, however, is common on a sticky composite (*Dittrichia viscosa*), which can restrict the bug’s colonization of less glandular plants (e.g., tomato) (66). Even so, sticky-plant mirids used in biocontrol might benefit from having alternative sticky hosts nearby (e.g., 82) with large amounts of entrapped carrion. Sticky plants could be used in hedgerows adjacent to sticky crops to support dicyphine populations. Bees (e.g., *Apis mellifera*, *Tetragonisca angustula*) incorporate resins from sticky plants into their nests for various purposes (e.g., defense against predators, parasites) (36, 104), and many sticky plants thrive in arid conditions. Thus, the use of sticky plants in hedgerows could be advantageous.

Maluf et al. (65) and Wang et al. (122) showed that plants with higher glandular-trichome densities can resist arthropod pests, but neither study considered the effects of trichome densities on plant-resource allocation and tritrophic interactions. In the case of *D. wrightii*, these factors appear more important in determining plant fitness than direct herbivore resistance, with glandular plants showing lower fitness, even though they produce more herbivore-defense compounds and suffer less herbivory (31).

Sticky plants have potential in crop protection. Understory malvaceous weeds (*Pavonia odorata*, *Pavonia zeylanica*) are used as trap plants in teak plantations in India to control populations of a defoliating moth (*Hyblaea puera*). Caterpillars (mainly early instars) dislodged from teak or ballooning on silken threads can become trapped in the glandular trichomes of *Pavonia* spp. and die (61). Legumes in the genus *Stylosanthes* entrap and kill large numbers of ticks (*Rhipicephalus microplus*) in their glandular trichomes and potentially could be grown in pastures to reduce tick infestations of cattle (109).

SUMMARY POINTS

1. Diversity of sticky-plant specialists in the heteropteran family Miridae (plant bugs)—and generally in other Heteroptera (e.g., berytids, harpactorine reduviids) and other arthropods (e.g., oxyopid spiders)—remains underappreciated. Mirids of glandular plants are best known in the subfamily Bryocorinae (tribe Dicyphini: subtribe Dicyphina). We anticipate the documentation of similar specialists in other mirid subfamilies, especially Phylinae.
2. Mirid adaptations to sticky plants can be behavioral, biomechanical, or morphological. Fine-tuned adaptations allow species of the dicyphine genus *Pameridea* to walk unimpeded on the exceptionally sticky surfaces of their carnivorous host plants (*Roridula* spp.).
3. The *Pameridea-Roridula* system comprises two species of each genus that are endemic to South Africa's cape; each mirid species specializes on a species of *Roridula*. Mirid feces deposited on leaves provide nitrogenous compounds that are rapidly absorbed by their hosts, which lack their own digestive enzymes (proteases). This species-specific digestive mutualism appears to represent tight cospeciation.
4. Additional studies of relationships between mirids and carnivorous plants (and those considered paracarnivorous) might illuminate the evolutionary stages leading to digestive mutualisms.
5. Omnivory and scavenging are ubiquitous and important in sticky plant–mirid systems. Sticky-plant specialists are restricted to certain groups (e.g., Dicyphina) and probably are highly correlated with omnivory.
6. Glandular trichomes have myriad functions; a given glandular plant's exudates could be toxic, volatile, sticky, and nutritious and serve as early sensors of herbivores.
7. More work is needed to develop coherent theory regarding tritrophic interactions on sticky plants to predict when plant–insect interactions are mutualistic or antagonistic, to determine the contexts in which herbivores are free of natural enemies, and to understand the consequences of manipulating stickiness in crops.

8. Sticky plants have agricultural potential for use in hedgerows, near open greenhouses, or among crops to promote mirid populations or trap pests.

FUTURE ISSUES

1. Biodiversity of mirids that specialize on sticky plants is inadequately known, particularly in the subfamilies Mirinae, Orthotylinae, and Phylinae. Ecologists and field biologists who study insect-plant interactions are encouraged to note glandularity (and its type) in their publications, as are taxonomists when they record host-plant relationships in describing new species.
2. Certain plants—paracarnivores—that do not meet strict criteria for carnivory might harbor overlooked dicyphine mirids (Dicyphina). Experiments to test whether paracarnivorous plants meet criteria for carnivory should include the possibility that mirids provide indirect nutrition.
3. Is a cuticular grease layer that allows species of *Pameridea* to walk unhampered over their sticky roridula hosts unique to that dicyphine genus, or has it evolved independently in other groups of sticky-plant mirids?
4. Do mirids use glandular-trichome-emitted volatiles as cues? Are these cues muted by walking behavior (tiptoeing) or consumption of glandular exudates? Do sticky-plant mirids indirectly defend their host plants?
5. Was the use of sticky plants an innovation that allowed specialist mirid (and other arthropod) groups to diversify?
6. A framework for characterizing glandular plants based on the chemical and physical properties of their exudates, and effective methods for measuring stickiness, would advance our understanding of interactions between arthropods and glandular plants.
7. What leaf-surface (phylloplane) resources (e.g., pollen, dust, microbes) are used by mirid specialists of sticky plants?
8. Studies in which trichomes are found to inhibit indirect defense (enemy-free space) often use generalist predators as surrogates rather than sticky-plant specialists that occur in natural settings. In systems where sticky-plant specialists exist, researchers should consider their roles before concluding that herbivores are in enemy-free space based solely on the behavior of generalists.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We are grateful to Stewart McPherson; Randall Schuh; Dagmar Voigt and Slanislav Gorb; and Cornell University Press, Springer Science + Business Media, and the American Museum of

Natural History for permission to reproduce material; and Peter Adler, Sanford Eigenbrode, Thomas Henry, Rick Karban, Ian Pearse, and Jay Rosenheim (and lab) for thoughtful feedback that improved an early draft of the manuscript. B.A.K. was supported by an NSF Graduate Research Fellowship.

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