TACHINIDAE: Evolution, Behavior, and Ecology

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■ **Abstract**   Tachinidae are one of the most diverse and ecologically important families in the order Diptera. As parasitoids, they are important natural enemies in most terrestrial ecological communities, particularly as natural enemies of larval Lepidoptera. Despite their diversity and ecological impact, relatively little is known about the evolution and ecology of tachinids, and what is known tends to be widely dispersed in specialized reports, journals, or texts. In this review we synthesize information on the evolutionary history, behavior, and ecology of tachinids and discuss promising directions for future research involving tachinids. We provide an overview of the phylogenetic history and geographic diversity of tachinids, examine the evolution of oviposition strategies and host associations, review known mechanisms of host location, and discuss recent studies dealing with the ecological interactions between tachinids and their hosts. In doing so, we highlight ways in which investigation of these parasitoids provides insight into such topics as biogeographic patterns of diversity, the evolution of ecological specialization, the tritrophic context of enemy-herbivore interactions, and the role of host location behavior in shaping host range.

INTRODUCTION

The Tachinidae are one of the most speciose families of Diptera, with approximately 10,000 described species worldwide (71). One of the few traits that unites this diverse assemblage of flies is that all tachinids (with known life histories) are parasitoids of insects and other arthropods. In this respect, they are second only to the parasitic Hymenoptera (e.g., Ichneumonoidea, Chalcidoidea) in diversity and ecological importance as insect parasitoids. Because of their predominance as parasitoids of the larval stage of Lepidoptera and other major groups of insect herbivores (e.g., Heteroptera, Scarabaeidae, Symphyta, Chrysomelidae), tachinids often play significant roles in regulating herbivore populations and structuring ecological communities, both natural and managed. On the order of 100 species have been employed in biological control programs of crop and forest pests, and many of these programs have been met with partial or complete success (49, 50). However,

introduced tachinids have also been implicated in devastating effects on nontarget organisms (17).

Tachinids are found in nearly all terrestrial environments throughout the world including deserts, forests, grasslands, mountains, and tundra, and at times may constitute a large proportion of flies observed in particular habitats. In addition, they are widely regarded as a relatively recent, actively radiating group of insects that we may be seeing in the full climax of evolutionary diversification (28). Despite this abundance, diversity, and ecological importance, relatively little is known about the evolutionary history, ecology, and behavior of tachinids. Even basic biological information on hosts, mating systems, and habitat requirements is known for fewer than half of the species in the most well-studied regions (i.e., Europe) (90). Most of our knowledge of tachinids comes from an extensive history of studies concerned with their potential application in controlling pests in managed agricultural and forest systems (50). However, owing to their ecological importance in natural systems as parasitoids of herbivorous insects, tachinids are attracting increasing attention from basic ecologists (47, 143). Novel host location mechanisms of certain species and associated implications for host-parasitoid coevolution have also attracted recent attention (e.g., phonotaxis to sexual calls of Orthoptera by the tribe Ormiini) (48). In addition, recent systematic analyses of morphology and at least one molecular phylogenetic study have begun to provide an initial foundation for understanding their evolutionary relationships, historical biogeography, and the evolutionary development of their host associations. In this review, we provide an overview of tachinid evolution and ecology, focusing on recent literature. We further examine four main areas in which we believe research on tachinids may be particularly rewarding: (*a*) evolution and biogeography of Tachinidae, (*b*) evolution of oviposition strategies and host associations, (*c*) behavioral mechanisms of host location, and (*d*) ecological interactions between tachinids and their hosts. These represent but a few of the many potential topics that could be discussed with regard to the Tachinidae. However, we hope that a review of these aspects of tachinid biology illustrates the remarkable diversity within the family and offers insight into more general issues in evolutionary biology, ecology, and behavior.

OVERVIEW OF TACHINID BIOLOGY

Tachinids are muscoid calyptrate Diptera belonging to the superfamily Oestroidea along with groups such as the flesh flies (Sarcophagidae), bottle flies (Calliphoridae), and bot flies (Oestridae). Tachinids exhibit an impressive diversity of morphologies (Figures 1 and 2), ranging in size over an order of magnitude from the diminutive (∼2 mm; e.g., *Siphona* spp.) to the impressively large (more than 20 mm; e.g., *Trixodes obesa*). A number of species are brightly colored with yellow, black, orange, and/or red markings, possibly mimicking aculeate Hymenoptera. Others are decorated with vivid metallic green, blue, or other tints (e.g., the

visually impressive Australian Rutiliini). However, many species, especially those belonging to the diverse subfamily Exoristinae, tend to be rather small, gray or blackish, and superficially nondescript. Closer inspection of these forms reveals a diverse array of morphologies and patterning, representing some of the most impressive radiations of tachinids, such as in the tribes Blondeliini, Eryciini, and Voriini.

All tachinid species are parasitoids, more specifically internal (endo-) parasitoids of other arthropods. As is typical for parasitoids, tachinids usually kill their hosts (but there are exceptions) (40). Although many tachinids emerge from the pupal stage of their hosts, none is known to attack pupae nor do any species attack the egg stage of their hosts. Most species of tachinids attack larval hosts, but a significant fraction, perhaps 5% to 10% of species, attack adults. Larval development is usually completed in one to three weeks, except for species that diapause in the host, where it can be prolonged over many months. Depending on the tachinid species, larvae develop either singly or gregariously and either pupate in the dead host or leave the host remains to pupate in soil litter.

Unlike parasitic Hymenoptera, tachinids lack a primitive piercing ovipositor. Thus, with the exception of a few groups in which piercing structures have evolved from modified sternites (e.g., most Phasiinae, many Blondeliini), tachinids must deposit eggs externally on or near the host, and the newly hatched larva must gain entry into the host. This lack of an ovipositor also prevents the injection of paralytic poisons, mutualistic polyDNA viruses, and other accessory substances that immobilize the host and/or its immune system. As a result, tachinids are classified as koinobiont parasitoids (9), that is, they allow their host to continue to feed and grow while they develop inside it rather than arresting its development in some way (as do idiobionts). Tachinids attack a wide range of hosts, comparable to that of the more diverse parasitic wasps (36) (Figure 3). The most commonly used hosts are phytophagous insects, primarily Lepidoptera, Coleoptera (Scarabaeidae and Chrysomelidae), Hymenoptera (Symphyta), Heteroptera, and Orthoptera. However, hosts in at least six additional insect orders, including Blattodea, Dermaptera, Diptera, Embioptera, Mantodea, and Phasmida, are attacked. Several genera of tachinids attack noninsect arthropods, specifically centipedes (e.g., tachinid genera *Loewia* and *Eloceria*) and scorpions (161). There is a single record of the parasitism of a spider (157). This great breadth of host use by the family is accompanied by broad host ranges in some tachinid species. Unlike parasitic Hymenoptera with similar life histories (koinobiont endoparasitoids) that tend to be highly host specific, many tachinid species are polyphagous, and a number have been reared from dozens of hosts in multiple families (37). At the extreme end, the tachinid *Compsilura concinnata* attacks almost 200 species of hosts in dozens of families and even multiple orders (Lepidoptera, Hymenoptera, and Coleoptera) (8). The striking variation in host range among species of Tachinidae makes the group particularly well suited for investigating the evolution, ecological consequences, and behavioral basis of host specificity.

Although this review focuses on the evolutionary history of tachinids and their ecological interactions with hosts, we draw attention to some aspects of the adult biology of tachinids that have received little attention. Adult tachinids can be found in most habitats, on leaves, tree trunks, flowers, rocks, or the ground. They are typically, but not always, diurnal or crepuscular and extremely active. Little is known about the mating behavior of tachinids aside from the general sexual aggregation sites of many species (e.g., hilltops, tree trunks) (1, 164). Adults of certain groups such as Phasiinae and Tachinini are often observed at flowers and may function as pollinators for a wide diversity of plant taxa, but their importance in this respect has been largely unexplored. At least one highly specific tachinid pollinates orchids in the genus *Trichoceros* via pseudocopulation, in which the female tachinid mimicking flowers lure tachinid males to attempt copulation and incidentally acquire pollinia (33). The importance of adult resources such as nectar, salts, leaf exudates, or potential sources of protein (e.g., pollen) is poorly known, as are patterns of adult dispersal.

EVOLUTION AND DIVERSIFICATION OF TACHINIDAE

Phylogenetic Relationships

The early history of the Tachinidae is poorly understood. There are surprisingly few fossils, the sister group has not been determined, the region of early evolution is uncertain, and basal relationships within the family are still under debate. Despite such fertile ground for discoveries of significance, this huge taxon has been understudied in favor of smaller families that are more amenable to phylogenetic investigation on a global scale.

The Tachinidae are the largest family of the Oestroidea, which includes, in addition to the Tachinidae, the Calliphoridae, Mystacinobiidae, Oestridae, Rhinophoridae, and Sarcophagidae. The relationships between these families have been explored by several authors, but a strongly supported phylogenetic tree remains elusive (89, 108, 118). The sister group to the Tachinidae has been postulated as the Rhinophoridae (89, 163) or Sarcophagidae (108, 118). Earlier regional catalogs of Tachinidae included the rhinophorids as a tachinid subfamily (54, 125), but this small group of flies has been universally regarded as a distinct family since Crosskey's (29) review of the group.

The fossil history of the entire oestroid lineage is markedly sparse and generally uninformative about the origin of the Oestroidea or Tachinidae. The oldest potential fossil in this lineage is a collection of puparia from Alberta, Canada, dating from the Upper Cretaceous. This specimen was originally assigned to the Calliphoridae (88) but is now unplaced beyond the Schizophora (52). All other known fossils of Oestroidea are Eocene or younger, and the oldest tachinid is described from an Eocene compression fossil from the United States (41).

The monophyly of the Tachinidae is well established on the basis of at least two synapomorphies, a well-developed subscutellum in the adult and the labrum extended forward and broadly fused to the rest of the cephalopharyngeal skeleton in the first instar (108, 117, 154, 164). Obligate endoparasitism of arthropods is a universal characteristic of the Tachinidae, but it has been suggested that this may not be a suitable character for inferring monophyly (108).

Early attempts to classify the Tachinidae into genera, tribes, and subfamilies were based mostly on the external features of adults. This was the principal modus operandi of the prolific C.H.T. Townsend, who proposed 1555 new species names and 1491 new generic names of Tachinidae throughout a career spanning the 1880s to 1940s (7). Unfortunately, there is much homoplasy in the external characters of tachinids, and most early authors, including Townsend, placed too much emphasis on such characters in the formation of their suprageneric classifications (111). Homoplasy within the family prompted Crosskey (28, p. 8) to write, "The Tachinidae...are certainly a group in which acquisition or loss of particular characters in different evolutionary lines has given rise to much confusing resemblance.... Few groups of Diptera give more difficulty in classification at the suprageneric level...."

Townsend's (151) classification of the Tachinidae also suffered from his propensity for describing monotypic genera (one species per genus). Indeed, the Neotropical Tachinidae are still largely arranged according to Townsend's classification (54). The Neotropical region has such an overwhelming number of small and almost meaningless genera that its fauna is currently almost impossible to compare with the more integrated classifications of other regions (22, 28, 30, 69, 105).

Most authors now recognize four tachinid subfamilies, the Exoristinae, Dexiinae, Phasiinae, and Tachininae (68, 69, 105, 154, 164). This is partly because of advancements in our understanding of tachinid relationships and partly because of a common desire to use a classification of convenience until a better classification is proposed. The characters that led Townsend and others astray still pose huge problems for modern systematists. However, the four subfamilies of Tachinidae are not entirely arbitrary in their composition. The Dexiinae are widely accepted as monophyletic because of derived features in the male genitalia (112, 153, 164). The Phasiinae comprise a morphologically diverse assemblage of species that was historically united chiefly because of their parasitism of Heteroptera (26). However, more recently the monophyly of the Phasiinae has been based primarily on a feature of the male genitalia (112, 153). There are some features that unite most Exoristinae and other features that unite most Tachininae such that these groups have some practical value, but neither is demonstrably monophyletic on morphological grounds. Nevertheless, Tschorsnig (153) concluded that the Exoristinae are probably monophyletic and Stireman (140) provided some molecular evidence that this subfamily may be largely monophyletic.

A complicating factor in resolving the relationships between tachinid subfamilies, in addition to the possible para- or polyphyly of the Exoristinae and Tachininae, is competing interpretations of oviparity/ovolarviparity and egg morphology

in the different subfamilies. The oviparous condition (the laying of unincubated eggs that have no appreciable embryonic development) is presumed to be primitive in the Tachinidae and is found in all Exoristini and Winthemiini, a few Blondeliini and Eryciini (all in Exoristinae), all Phasiinae (excluding Eutherini and Strongygastrini) (105, 164), and perhaps a few other as yet unexamined groups. The ovolarviparous condition (the laying of incubated eggs containing well-developed larvae) is present in the rest of the Exoristinae and all members of Dexiinae and Tachininae. Depending upon whether ovolarviparity is thought to have arisen once or multiple times changes the possible relationships among the subfamilies. Wood (162) argued that ovolarviparity is associated with complex modifications of the female reproductive system and probably evolved once. Other authors have taken the view that ovolarviparity developed at least twice, based in large measure on egg morphology, leading to other phylogenetic interpretations: Herting (66, 67) postulated the intersubfamilial relationships as Phasiinae + Exoristinae and Tachininae + Dexiinae, Richter (112) modified this interpretation into Phasiinae + (Exoristinae + (Tachininae + Dexiinae)), and Shima (129) proposed Phasiinae + Dexiinae and Exoristinae + Tachininae. Under the scheme of Herting (66, 67), the Tachinidae diverged early into two lineages, one in which the upper surface of the egg is thickened and convex and the lower surface is membranous (termed a planoconvex egg in tachinid literature) (Phasiinae + Exoristinae) and the other in which the whole egg is essentially membranous (Tachininae + Dexiinae).

Tachinid tribes are still undergoing refinement and reorganization as their phylogenetic affinities become better understood. Systematic studies have been focused generally on genera and species, so there have been few revisions of regional or world faunas at the tribal level in recent decades. Significant tribal revisions during the past 30 years have dealt with the Rutiliini (27), Uramyini (56), Blondeliini (162), Siphonini (5, 6, 101), Dexiini (11), Winthemiini (130), and Polideini (102). Interestingly, the two large tribes Goniini (Exoristinae) and Siphonini (Tachininae) are each recognized as monophyletic only on the basis of internal structures: the Goniini producing microtype eggs and the Siphonini having two rather than the usual three spermathecae in females. The monophyly of many tribes has yet to be investigated and the classification of Neotropical Tachinidae at all taxonomic levels is in great need of modernization. Further advances in the global suprageneric classification of the Tachinidae will benefit from integrating information from the study of eggs (45), first instars (100, 113–115, 149, 151), puparia (166), female terminalia (63), male terminalia (153, 156), molecular sequences (140), and host associations (8, 55, 131), coupled with a cautious interpretation of the external morphology of adults.

Diversity and Zoogeography

The Tachinidae are found worldwide and are one of the largest, if not the largest, families of Diptera. The distribution of Tachinidae by region is shown in Table 1, based on a recent enumeration of the genera (103) and variously dated sources of

TABLE 1 Distribution of tachinid genera and species by biogeographic region

Number	World	Neotropical[a]	Nearctic[a]	Palearctic	Afrotropical	Oriental	Australasian[b]
Species	9899[c]	2864[d]	1345[e]	>1600[f]	1006[g]	725[h]	808[i]
Genera[j]	1530	822	303	404	213	266	228
Endemic genera	1130[k]	644	61	153	93	54	125
% Endemic genera	—	78%	20%	38%	44%	20%	55%
Genera shared between regions[l]							
Neotropical	25[m]	—	173 (102)	70 (1)	40 (0)	48 (0)	40 (0)
Nearctic	—	—	—	133 (38)	50 (1)	72 (1)	43 (0)
Palearctic	—	—	—	—	98 (14)	171 (55)	71 (1)
Afrotropical	—	—	—	—	—	96 (12)	61 (1)
Oriental	—	—	—	—	—	—	92 (20)

[a]For the purposes of this paper, the boundary between the Nearctic and Neotropical regions is taken as the United States/Mexico border to correspond with the geographic coverage of the catalogues by Guimarães (54) and O'Hara & Wood (105). The true boundary between these regions is in southern Mexico (51).

[b]Australasian and Oceanian regions.

[c]Data from Reference 71.

[d]Data from Reference 54.

[e]Data from Reference 105.

[f]Data from Reference 154.

[g]Data from Reference 71.

[h]Data from Reference 28.

[i]Data from Reference 22.

[j]Data from Reference 103.

[k]Total number of genera found in only one region.

[l]Left number is total number of genera shared with another region; right number in parentheses is number of genera unique to two regions (data from Reference 103).

[m]Number of genera found in all regions.

species diversity (22, 28, 30 54, 105, 154). The species numbers are especially deceptive because only the faunas of the Palearctic and Nearctic regions are reasonably well known, with perhaps 90% of their actual faunas documented. The huge number of species recorded from the Neotropical region, which accounts for nearly one third of the described species of Tachinidae (Table 1), is but a portion of the total, as evidenced from the many specimens of new species that abound in collections. Similarly, the seemingly small faunas of the Afrotropical, Oriental, and Australasian regions are understudied and likely highly diverse. The continent of Australia (the largest land mass in the Australasian region), with a relatively small described fauna of nearly 500 species (22), was recently estimated to have a tachinid fauna "roughly in the order of 3500–4000 species" (104, p. 10). Considering the understudied nature of the world's tachinid fauna, it is possible that only half of the species have been described.

The geographic distribution of the Tachinidae is in agreement with the meager fossil history of the family in failing to show evidence of a pre-Tertiary existence. The most obvious indication of an earlier origin would be sister group relationships among Southern Hemisphere tachinids, thereby suggesting a vicariance of ancient faunas in the late Cretaceous or early Cenozoic. Most likely such relationships would be seen at the generic level, but there are no genera unique to South America, Africa, and Australia or to South America and Australia (Table 1). Only one genus, *Anacamptomyia* Bischof, is known exclusively from the Afrotropical and Australasian regions (Table 1), but this apparent disjunction has not been studied and the tachinid fauna of the intervening Oriental region is inadequately known. Cortés (25) postulated a relationship between the South American tribe Trichoprosopini and the New Zealand tribe Occisorini, but that association has not been explored in a phylogenetically rigorous manner.

There is no evidence from which to infer the region of origin of the Tachinidae. From a zoogeographic perspective, the Tachinidae have radiated with surprising thoroughness throughout the world. The faunas of adjacent regions show significant overlap in generic composition (Table 1) and all regions are diverse in the major lineages. However, each region also supports a significant endemic fauna. Most notable in this respect are the diverse tribes Rutillini and Occisorini, the first an essentially Australasian group (22) and the second endemic to New Zealand (34), both of which presumably diversified in situ after early colonization events. New Zealand has remained far removed from Australia throughout the Cenozoic, and as a result its tachinid fauna is highly endemic and apparently descended from few ancestors (34). The fauna of Madagascar, on the other hand, although rich in Tachinidae, has proportionally a far less endemic fauna than New Zealand (71). The Neotropical region boasts an endemic fauna of 644 genera, fully 78% of its genera (Table 1), but this is in part an artifact of the oversplit generic classification. Nevertheless, the Neotropical fauna is huge and diverse and tachinids must have had a long history there. The water gap between North and South America that closed in the Pliocene and resulted in the "great American biotic interchange," so evident in the New World megafauna (136), seems to have functioned more as a

"filter bridge" than as a barrier for tachinids during the Tertiary (101). A similar pattern of progressive enrichment probably took place in Australia as that continent and associated islands slowly edged toward the island archipelagos of Southeast Asia in the late Cenozoic. In the Northern Hemisphere, intermittent land connections between North America and Eurasia across the North Atlantic and through Beringia at various times during the Cenzoic (87) must surely have provided key pathways between the Old and New Worlds for Tachinidae, if indeed the family is too recent to have used Gondwanan corridors between southern continents.

Latitudinal Considerations

Certain parasitoid taxa such as the Ichneumonidae apparently lack a gradient of increasing diversity toward the tropics found in most insect groups (73). Hypotheses to explain these unusual patterns of diversity have suggested that specialized parasitoid populations experience difficulty persisting in the tropics because of resource fragmentation (73), a preponderance of chemically defended "nasty" hosts (46), and other factors. Although the tropical faunas of Tachinidae are not well known in the Old World, the Neotropical Region clearly harbors a fauna much larger than those in the temperate latitudes of the Nearctic and Palearctic regions. As an example of this diversity, Janzen & Hallwachs' (74) Lepidoptera-rearing program in Costa Rica indicates that approximately 330 species of tachinids (>80% undescribed) have been reared from caterpillars at a single tropical forest site. The reasons behind these disparate diversity patterns for Ichneumonidae and Tachinidae are not well explored, but the generally greater polyphagy and perhaps reduced susceptibility of tachinids to host chemical defenses may be involved (46, 60).

EVOLUTION OF OVIPOSITION STRATEGIES AND HOST ASSOCIATIONS

Oviposition Strategies and Egg Types

One of the most striking features of tachinids as a group is their wide diversity of oviposition strategies and associated egg morphologies. These strategies have been outlined several times in the literature, and the egg morphologies have been subjected to a variety of classification schemes (14, 24, 150, 154, 164). Perhaps the most significant division is between species that lay eggs on the host (direct oviposition) (Figure 1) versus those that lay eggs away from the host (indirect oviposition) (Table 2). The former type may be divided further depending on whether eggs are laid externally or injected into the host and whether the eggs are incubated (ovolarvipary) in a uterus and contain fully developed larvae when deposited or not (ovipary). Taxa with indirect oviposition can also be subdivided into two major groups: ovolarviparous species, in which larvae hatch soon after eggs are laid and either wait for passing hosts (e.g., many Tachininae) or actively search

TABLE 2 Types of oviposition strategies in Tachinidae

Oviposition strategy	Egg type	Taxa	Fecundity[a]
Indirect	Ingested by host (microtype)	Goniini, Blondeliini (e.g., *Anisia*, *Phasmophaga*)	1000–6000 (2420)
Indirect	Incubated	Tachinini, Dexiini, Polideini Few Exoristinae (e.g., *Lixophaga*)	500–8000 (1168)
Direct-external	Incubated	"Eryciini" (Exoristinae), Blondeliini (most), Voriini, Strongygastrini	30–600 (140)
Direct-external	Unincubated (planoconvex)	Phasiinae, Exoristiini, Winthemiini, some Blondeliini, *Aplomya* (Eryciini)	100–200
Direct-internal	Incubated	Blondeliini (e.g., *Blondelia*, *Eucelatoria*), Dexiinae (Palpostomatini)	65–250
Direct-internal	Unincubated	Phasiinae, Exoristiinae (e.g., *Phorocera*)	100–200

[a]Fecundities are rough ranges taken from the literature (primarily derived from References 14, 24, and 154) with averages in parentheses for some groups from Belshaw's (14) compilation.

for hosts (e.g., Dexiini), and species possessing "microtype" eggs, in which ova are ingested by hosts as they feed and hatch in the gut, and the emerging first-instar larvae burrow into the hemocoel (Figure 2). These diverse oviposition strategies have evolved in concert with host-searching and attack strategies, changes in fecundity, and the types of hosts attacked. As expected, given the probability of successful parasitization, indirect egg-layers exhibit high fecundities of sometimes thousands of eggs, whereas direct egg-layers tend to have more moderate fecundities (Table 2).

Interestingly, the taxonomic diversity of tachinids is approximately evenly distributed across oviposition strategies. For example, at least 40% of Palearctic species have indirect modes of oviposition (14), and the Tachinini (indirect "waiters"), Dexiini (indirect "searchers"), and Goniini (microtype) are among the most species-rich tribes of Tachinidae. Furthermore, these oviposition strategies may have been gained or lost multiple times over tachinid evolution. Piercers for example, which are present in about 7% of Palearctic tachinid species (14), have evolved in three of the four subfamilies and at least four times in the Exoristinae alone (137). This repeated evolution of piercing structures and consequent internal oviposition may be associated with selection to minimize the likelihood that eggs will be destroyed by the host or shed during host molting (53). Transitions from unincubated (presumably ancestral) to incubated egg types may also have occurred more than once, given the presence of both forms in Eryciini and Blondeliini of

the Exoristinae, but the absence of a credible phylogeny of Tachinidae prevents strong inferences concerning the evolution of egg type. Note that these categories are not entirely distinct, with the incubation of a single egg at a time occurring in some if not most species possessing unincubated macrotype eggs (65, 148). Even the highly derived strategy of laying minute eggs that are inadvertently consumed by the host appears to have evolved at least twice in different tribes [Goniini and Blondeliini (*Phasmophaga*, *Anisia*)] (162) and possibly has been gained or lost multiply in the Goniini (140).

Given that nearly one half of all tachinid species oviposit indirectly (37), these strategies appear to have been important innovations in tachinid evolution. Because tachinids generally attack active life stages of their hosts and do not possess paralytic poisons with which to subdue them, behavioral and morphological defenses of hosts may present formidable barriers to oviposition. Host defenses such as biting, thrashing, stinging hairs or spines, and gregariousness may have initially encouraged the evolution of indirect oviposition strategies and promoted the diversification of tachinid taxa possessing them. Furthermore, given the diurnal habits of most species and the lack of specialized ovipositors (as in the Hymenoptera), many concealed and/or nocturnal hosts must have been inaccessible to early tachinids. The evolution of host-searching first instars that burrow through soil or into galleries of concealed insects, of larvae that ambush nocturnally feeding caterpillars on their host plants, and of microtype eggs that can be ingested by nocturnal or well-defended hosts all served to expand the range of hosts that are vulnerable to attack. These innovations may have opened extensive adaptive zones for tachinids to colonize. Most microtype Goniini and many Tachininae, however, attack hosts that are apparently accessible to direct oviposition (i.e., diurnal exophytic Lepidoptera). Thus, although indirect oviposition may have been frequently exploited to allow the attack of inaccessible hosts, it may often be more profitably viewed as a strategy to reduce search time, handling time, and potential injury associated with oviposition (144).

HOST ASSOCIATIONS

Tachinids exploit a wide diversity of hosts belonging to many orders and families of insects (and a few other arthropods). Aside from a few taxonomically coarse associations of tachinid taxa with particular host orders and families, host associations are evolutionarily labile within Tachinidae, often varying considerably among congeneric species. Detailed host associations of tachinid taxa have been summarized for most regions (8, 13, 26, 28, 55, 64, 131); therefore only some of the general associations are summarized here (Figure 3). The strictest associations between tachinid and host groups are the restriction of Phasiinae to heteropterous hosts and Rutiliini to scarab hosts. Other broad associations include Scarabaeidae as hosts of Dexiini, Lepidoptera as hosts for most Tachininae and Exoristinae (as well as Voriini of Dexiinae), and Orthoptera as hosts for Ormiini (Figure 3). Even

where these broad associations occur, however, there is often little phylogenetic
signal in host use at finer levels (140, 144). This phylogenetic lability of host as-
sociations, along with our poor phylogenetic understanding of Tachinidae, makes
it difficult to draw many conclusions concerning the evolution of host associations
in the family. The widespread use of Lepidoptera in Exoristinae, Tachininae, and
Dexiinae suggests that members of this order may have served as ancestral hosts
of tachinids. This inference cannot be corroborated through outgroup analysis be-
cause the sister group to the Tachinidae is unclear and parasitism of insects may be
a derived character of the family absent in early ancestors. An early shift in host use
from Lepidoptera to Heteroptera apparently occurred in Phasiinae, a seemingly
primitive lineage that has retained the ancestral habit of producing unincubated
eggs.

Most tachinids attack exophytic caterpillars or other larvae of holometabolous
insects that are ecologically and morphologically similar to caterpillars, such as
larval sawflies and chrysomelid beetles (35). The predominance of these insects
as hosts of tachinids may be explained by their external feeding habit, generally
weak physical defenses, taxonomic diversity, adequate size, and perhaps most im-
portantly, their specialized associations with plants. In general, the most diverse
clades of parasitoids including Tachinidae, Chalcidoidea, and Ichneumonoidea at-
tack primarily phytophagous insects, and the tritrophic interactions between plants,
phytophagous insects, and parasitoids may play a central role in both herbivore
and parasitoid diversification. The indirect effects of plants on parasitoids, via
their role in host location by parasitoids and their use as defenses against para-
sitoids by herbivores (e.g., sequestered secondary compounds), should select for
increased specialization and encourage diversification in parasitoids. Explicit con-
sideration of the tritrophic framework of host plants, herbivores, and tachinids is
central to understanding patterns of tachinid host use at both microevolutionary
and macroevolutionary scales.

HOST RANGE

The apparent lability of host use among most Tachinidae may be due to a gen-
eral lack of host-specific adaptations relating to host physiological defenses. Lar-
val tachinids are well known for their formation of respiratory funnels derived
from host defensive cells. Rather than evading or destroying host hematocytes
as do many hymenopteran parasitoids (145), tachinids often coopt them to form
"breathing tubes." These structures allow many tachinids to maintain direct contact
with atmospheric air via their posterior spiracles through either the host's external
integument or major tracheal branches (24). The ability to capitalize on the im-
mune response by forming respiratory funnels may allow tachinids flexibility to
ecologically "explore" new hosts more easily, resulting in dynamic evolution and
diversification of host associations. This hypothesis is supported by the observa-
tion that tachinids that remain free in the hemocoel without forming a respiratory

funnel exhibit significantly narrower host ranges than average for the family (14). In addition, tachinids may be relatively tolerant of toxins actively or inadvertently ingested by their hosts (46, 83), allowing greater evolutionary plasticity in host range. This tolerance may be due to preadaptations associated with the ancestral saprophagous habits of the Oestroidea (37), in which larvae faced with highly toxic environments produced by bacteria and fungi accumulated adaptations to tolerate these toxins. The apparent tolerance of tachinids to host physiological defenses may be related also to the position of young larvae within the host. Many early larval stages of tachinids embed themselves in specific tissues rather than float free in the hemocoel (14), and at least one highly polyphagous species, *Compsilura concinnata*, undergoes most of its larval development in the gut (i.e., between the peritrophic membrane and gut wall) (70).

These arguments, that tachinids may overcome physiological defenses of the host via the formation of respiratory funnels, through adaptations to toxic environments, or by "hiding" in specific tissues, have also been used to explain the wide host ranges of many tachinid species (14). Some tachinids (e.g., *C. concinnata*, *Exorista mella*, *Lespesia aletiae*) are unusually polyphagous, attacking dozens of host species belonging to multiple families. Further, in analyzing host records of Palearctic species, Eggleton & Gaston (37) and Belshaw (14) found a strong correlation between the number of tachinid rearings and the number of hosts, suggesting widespread polyphagy in Tachinidae. This has led to the general perception that most or even all tachinids are polyphagous. However, this conclusion may be misguided. First, parasitoid rearing data is riddled with misidentifications of hosts and parasitoids (127). Second, generalists are reared far more often than specialists, acquiring undue influence on regressions (e.g., it is likely that few of the tachinid species for which no hosts are known are highly polyphagous). Third, widespread polyphagous tachinid species may often consist of relatively specialized, perhaps genetically differentiated, local populations. Finally, owing to the developmental permissiveness of tachinids, "mistakes" on alternative hosts end up as observed rearings that obscure otherwise narrow host associations. Recent analyses of tachinid-host associations from a long-term intensive caterpillar-rearing program in Costa Rica (more than 12,000 tachinid rearing records; 74) indicate that most tachinid species are relatively specialized at a local scale, attacking only one or a few host species, or a well-defined ecological category of caterpillars (D.H. Janzen, personal communication). However, these data also support the existence of a visible minority of highly polyphagous species.

Tachinids possess several additional traits that may permit broad host ranges, including external oviposition that does not expose the defenseless egg stage to host immune defenses, rapid larval development, and oviposition on host-frequented substrates. The notion that rapid larval development of tachinids may encourage polyphagy is supported by the finding that species exhibiting developmental synchrony with hosts exhibit significantly narrower host ranges than those lacking this synchrony (14). Another prediction that species with indirect oviposition

should exhibit broader host ranges (because larvae with a low probability of contacting a host should not be particularly selective) has not been borne out in analyses of the literature (14) or in studies of particular tachinid-host communities (144). This is likely related to the observations that indirectly ovipositing taxa deposit offspring on specific substrates (e.g., particular host plants) (120), use fresh feeding damage by hosts as a cue for oviposition (91, 92), and may visually or otherwise locate hosts and lay eggs in their vicinity (D.H. Janzen, personal communication). Interestingly, polyphagous tachinids are widely dispersed among tachinid lineages, often occurring in genera that contain many specialized species (141). This indicates that host range is not strongly conserved and not closely related to oviposition strategies or other major traits that define clades within Tachinidae. It also suggests that tachinids are well suited for testing the controversial hypothesis that host specialization promotes diversification (37a).

Host Finding and Host Range

The previous discussion of evolutionary patterns of host associations and host ranges proposes that, unlike many hymenopteran parasitoids (158), host associations of tachinids are not strongly limited by physiological suitability or host defenses. Assuming that hosts are generally physiologically permissive for tachinids and that even "generalist" tachinids use only a small fraction of potentially available hosts, the obvious question arises: What then determines host ranges of tachinids? One recurring observation concerning tachinid-host associations is that the set of hosts tachinids attack may be more closely related to their ecology (e.g., habitat use) than to their phylogenetic affinities (14, 30, 37, 42). This observation stems from the apparent ecological and evolutionary flexibility of tachinid-host associations and is supported by strong effects of host plant species on parasitism rates by tachinids in a variety of systems (43, 72, 82). It can be explained by the use of relatively specific cues by tachinids to locate host habitats (e.g., host plant volatiles) (119) and, once in the appropriate habitat, the use of relatively indiscriminate cues to locate and/or select hosts (see Host Location and Selection, below). Thus, the processes of host location and selection that determine proximate host use may ultimately shape broad-scale ecological and evolutionary patterns of host use. This suggests that it is the cues that determine which hosts are attacked rather than the more conventional perspective that it is the host that determines the cues used to locate it. In nature there likely exists a dynamic interplay between behavioral mechanisms of host location that determine which hosts are attacked and subsequent selection due to location efficiency and host-related performance that shapes the evolution of these mechanisms. Although the role of host location and selection behavior in shaping broader scale patterns of host use has been relatively ignored historically, it has recently received increased attention as a means of shaping host associations in phytophagous insects (15).

HOST LOCATION AND SELECTION

The mechanisms by which most tachinids locate and select hosts are not well understood. Notably sparse is information about species in which the adults do not contact the host directly. The information available on the small proportion of species studied indicates that tachinids are capable of using a wide diversity of olfactory, visual, auditory, and tactile-chemosensory cues to locate their hosts (Table 3). It is clear from an examination of host location mechanisms that many tachinids rely heavily on chemical cues derived from the host plants of their phytophagous insect hosts or from interactions between hosts and host plants (91, 93, 120). These cues may serve to attract tachinids to the habitats or microhabitats occupied by their hosts, at which point more reliable close-range cues can be utilized to detect the host or signs of the host's presence. Close-range cues include odors associated directly with the host, host secretions, or excretions (particularly frass), and visual detection of hosts (Table 3). Several studies have shown that tachinid oviposition behavior can be elicited in response to tactile-chemosensory cues associated with the host's cuticle (19, 38), recently damaged leaves (92), and/or host frass (123). In these cases females use chemosensors on their front tarsi (92, 123), which may function similarly to the chemosensors on the long antennae of many hymenopteran parasitoids. Such an explanation may account for the "drumming" of tarsi on the host observed in *Exorista* species (138, 146).

Visual Cues

The use of visual cues is apparently integral to host location and selection for many tachinids (94, 138, 139, 160, 165). Higher Diptera generally have well-developed visual systems, particularly with regard to motion detection (20), and this may have preadapted Tachinidae to rely on visual cues in locating and selecting hosts. In some species motion of hosts or host-like objects appears to act as a superstimulus, leading to indiscriminant oviposition, or at least ovipositor probing of feathers, forceps, and even fingers (94, 137). This strong excitatory effect of visual detection of host movement may play a role in generating patterns of host use in tachinids that are related more to ecology and habitat use than to phylogenetic affinities of hosts. Easily detectable cues such as volatile chemicals associated with plants or plant damage may serve to attract female tachinids to particular habitats. Once there, many tachinids may rely strongly on relatively indiscriminant visual detection of host movement for host location and selection, leading to apparent polyphagy within a habitat and perhaps rapid evolutionary changes in host use.

Learning

One phenomenon relating to host location and selection that has received little attention in tachinids is learning. Given that many tachinid species attack multiple host species, and that several forms of learning have been demonstrated in other insects including higher flies (107), it may be expected that sensitization or

TABLE 3   A survey of mechanisms of host location and/or selection in Tachinidae

Tachinid species	Subfamily (Tribe)	Host	Mode	Source	Cue	Reference(s)
Compsilura concinnata	Exoristinae (Blondeliini)	*Lymantria dispar* (Lymantriidae)	Visual	Host	Motion	160
Eucelatoria bryani	Exoristinae (Blondeliini)	*Heliothis* sp. (Noctuidae)	Olfactory	Host plant	Damaged plant volatile	86
Eucelatoria sp.	Exoristinae (Blondeliini)	*Heliothis* sp. (Noctuidae)	Tactile (chemosensory)	Host	Cuticular extract	19
Eucelatoria sp.	Exoristinae (Blondeliini)	*Heliothis* sp. (Noctuidae)	Olfactory	Host × host plant	Plant volatiles from herbivore?	97
Lixophaga diatraeae	Exoristinae (Blondeliini)	*Diatrea saccharalis* (Crambidae)	Chemosensory	Host	Frass	123
Lixophaga diatraeae	Exoristinae (Blondeliini)	*Diatrea saccharalis* (Crambidae)	Olfactory	Host × host plant	Plant volatiles × host interaction	122
Drino bohemica	Exoristinae (Eryciini)	*Neodiprion* spp. (Diprionidae)	Olfactory	Host plant	Plant volatiles	93
Drino bohemica	Exoristinae (Eryciini)	*Neodiprion* spp. (Diprionidae)	Olfactory	Host	Plant/frass volatiles?	93
Drino bohemica	Exoristinae (Eryciini)	*Neodiprion lecontei* (Diprionidae)	Visual	Host	Motion	94
Drino inconspicua	Exoristinae (Eryciini)	*Gilpinia hercyniae* (Diprionidae)	Visual tactile	Host	Motion + "firmness"	31
Eucarcelia rutilla	Exoristinae (Eryciini)	*Bupalus piniarius* (Geometridae) and others	Olfactory	Host plant	Plant volatiles	62
Exorista japonica	Exoristinae (Blondeliini)	*Mythimna separata* (Noctuidae)	Olfactory	Frass	Frass volatile	147

Exorista japonica	Exoristinae (Blondeliini)	*Mythimna separata* (Noctuidae)	Olfactory	Host plant	Damaged plant volatile	76
Exorista japonica	Exoristinae (Blondeliini)	*Mythimna separata* (Noctuidae)	Visual	Host	Motion	165
Exorista japonica	Exoristinae (Blondeliini)	*Mythimna separata* (Noctuidae)	Visual	Host	Color, size	146
Exorista mella	Exoristinae (Blondeliini)	*Grammia geneura* (Arctiidae)	Olfactory	Host plant	Damaged plant volatile	138
Exorista mella	Exoristinae (Blondeliini)	*Grammia geneura* (Arctiidae)	Visual	Host	Motion	138
Blepharipa pratensis	Exoristinae (Goniini)	*Lymantria dispar* (Lymantriidae)	Tactile (chemosensory)	Host plant	Damaged plant exudate	99
Cyzenis albicans	Exoristinae (Goniini)	*Operophtera brumata* (Geometridae)	Olfactory	Host plant	Plant volatile (Borneol)	58, 119, 120
Leschenaultia exul	Exoristinae (Goniini)	*Malacosoma disstria* (Lasiocampidae)	Olfactory	Host plant	Damaged plant volatile	91
Leschenaultia exul	Exoristinae (Goniini)	*Malacosoma disstria* (Lasiocampidae)	Olfactory	Host	Host frass	91
Leschenaultia exul	Exoristinae (Goniini)	*Malacosoma disstria* (Lasiocampidae)	Tactile (chemosensory)	Host plant	Damaged plant exudate	92
Patelloa pachypyga	Exoristinae (Goniini)	*Malacosoma disstria* (Lasiocampidae)	Olfactory	Host plant	Damaged plant volatile	91

(Continued)

TABLE 3   (*Continued*)

Tachinid species	Subfamily (Tribe)	Host	Mode	Source	Cue	Reference(s)
Hemyda aurata	Phasiinae (Cylindromyini)	*Podisus* spp. *Euschistus* spp. (Pentatomidae)	Olfactory	Host	Male pheromone	2
Gymnoclytia occidentalis	Phasiinae (Gymnosomatini)	*Euschistus conspersus* (Pentatomidae)	Olfactory	Host	Male pheromone	79
Euclytia flava	Phasiinae (Phasiini)	*Podisus* spp. *Euschistus* spp. (Pentatomidae)	Olfactory	Host	Male pheromone	2
Trichopoda pennipes	Phasiinae (Trichopodini)	*Nezara viridula* (Pentatomidae)	Olfactory	Host	Male pheromone	57
Linnaemyia (Bonnetia) comta	Tachininae (Ernestiini)	*Agrotis ipsilon* (Noctuidae)	Olfactory/ (chemosensory)	Host	Frass, vomit	124
Triarthria setipennis	Tachininae (Loewiini)	*Forficula auricularia*	Olfactory	Host	Host kairomones?	80
Homotrixia alleni	Tachininae (Ormiini)	*Sciarasga quadrata* (Tettigoniidae)	Auditory	Host	Sexual calls	3, 4
Ormia ochracea	Tachininae (Ormiini)	*Teleogryllus oceanicus* (Gryllidae)	Auditory	Host	Sexual calls	21, 159
Therobia leonidei	Tachininae (Ormiini)	*Poecilimon* sp. (Tettigoniidae)	Auditory	Host	Sexual calls	81
Archytas marmoratus	Tachininae (Tachinini)	*Heliothis virescens* (Noctuidae)	Tactile/chemosensory	Host	Protein	98

associative learning of host-associated cues is widespread in tachinids. Learning of habitat cues associated with hosts could be partially responsible for plant-specific patterns of parasitism by tachinids, and learning or reinforcement of host-associated cues may result in locally restricted host associations. However, the capacity to learn has been demonstrated for only two species, *Drino bohemica* (95) and *Exorista mella* (139). Interestingly, in both cases the tachinids learned to associate visual cues with hosts, reaffirming the importance of this modality in host location/selection.

Host Sexual Signals as Host Location Cues

One striking mode of host location by tachinids that has attracted a great amount of attention in recent years is phonotactic attraction to sexual calls of crickets and other Orthoptera by tachinids in the tribe Ormiini (Tachininae) (21, 96, 159). The relatively well-studied species *Ormia ochracea* searches for hosts at night using an "ear" located between the forecoxae to detect and locate calling male crickets, upon which eggs are laid (21, 116). Similar strategies are utilized by other species to attack other nocturnal song-producing hosts such as katydids (Tettigoniidae) (3) and mole crickets (Gryllotalpidae) (44). This mode of host location is particularly interesting because it results in trade-offs for calling males, which attract both potential mates and deadly parasitoids. Such conflicting forces of sexual and natural selection may result in strong coevolutionary dynamics between ormiine tachinids and their hosts (167).

A similar exploitation of sexual signals by tachinids is found in a number of Phasiinae that attack Heteroptera (2, 57). These tachinids, such as *Trichopoda pennipes*, utilize the volatile sexual pheromones of their heteropteran hosts for host location via chemotaxis (57). In at least one case, *Euclytia flava*, the tachinid species appears to consist of cryptic "pheromone races" that are differentially sensitive to particular pheromone components associated with different host species (even more sensitive than the hosts themselves) (2). As in the hosts of Ormiini, conflicting selection pressures associated with mate and parasitoid attraction may lead to coevolutionary "arms races" in which hosts are constantly selected to produce sexual signals unattractive to tachinids but attractive to mates ("new codes") and tachinids are constantly selected for greater sensitivity to these signals ("code-breakers"). Repeated cycles of these dynamics may facilitate speciation and evolutionary diversification of both players. Dependence on host pheromones in host location is probably widespread in the Phasiinae and may have been pivotal in their evolutionary radiation on heteropteran hosts.

ECOLOGY OF TACHINID-HOST INTERACTIONS

The long history of tachinids in biological control programs attests to their importance as enemies of phytophagous pest insects (12, 50). Yet, tachinids' roles as enemies of native herbivores and their larger roles in the structure and dynamics

of natural ecosystems have been largely uninvestigated. Recent data from several
large-scale caterpillar-rearing programs focusing on exophytic macrolepidoptera
have shown that mortality from tachinids is often equivalent and sometimes greater
than that due to hymenopteran parasitoids. For example, tachinids were responsible
for more than half of caterpillar mortality due to insect parasitoids in rearing studies
focused on a diversity of ecosystems including Southwestern United States desert-
savanna (143), Northeastern United States forests (128), Costa Rican tropical dry
forest (73), Costa Rican tropical wet forest (47), and Ecuadorian montane wet forest
(L.A. Dyer & H.F. Greeney, personal communication).

Tachinid Community Ecology

As the field of parasitoid community ecology has developed over the past two
decades (61), the number of studies dealing with the structure and dynamics of
tachinid-host associations has dramatically increased (47, 82, 128, 143). This is
due primarily to a broader emphasis on ecological communities (rather than single
species) and to a growing realization of the importance of higher trophic levels
in shaping the ecology and evolution of insect communities. The goals of these
studies have been largely to understand how and why parasitism frequencies and
richness of parasitoid species vary among host species. Several relationships be-
tween host traits and tachinid parasitism or diversity have been documented, some
of which appear to be consistent across ecosystems. For example, analyses of large-
scale caterpillar-rearing programs by both Sheehan (128) and Stireman & Singer
(143) found that abundant, gregarious, and host plant generalist caterpillars were
attacked by significantly more tachinid species than their rare, specialist, and/or
solitary counterparts. Both studies suggested that this pattern is associated with the
process of host finding. Stireman & Singer (143) also found that hairy caterpillars
exhibited significantly larger tachinid assemblages than did smooth caterpillars.
This result, along with positive associations between tachinid parasitism and both
gregariousness and shelter-building among caterpillars, has been used as evidence
that enemy-free space (75) may be important in determining patterns of tachinid
host use (47, 143). That is, hosts that are well defended against predators may be
particularly suitable for tachinid parasitoids because in these hosts an immature
parasitoid is less likely to be devoured by a predator.

Tachinid Population Ecology

Although the prominent insect population ecologist M.P. Hassell (59) developed
several of his influential ideas with a tachinid-host system (58), only recently
have other population ecology researchers become aware of the utility of tachinid-
host systems in understanding general ecological processes (23, 106, 109). This
usefulness is evident in a recent research program studying the spatial structure
of western tussock moth outbreaks (*Orgyia vetusta*) (85). Detailed work on this
system involving the tachinid *Tachinomyia similis* has carefully elucidated how
strong dispersal and density-dependent host searching by this tachinid result in a

patchy spatial structure of localized host outbreaks, dampening and weakening the spread of host population irruptions (18, 84, 155). Given well-developed flying abilities, most tachinids are likely excellent dispersers, suggesting that population interactions exemplified by *T. similis* and its host may be widespread.

As discussed previously, many studies have demonstrated that parasitism by tachinids is often highly dependent on habitat, particularly on the food plant of the host (10, 82, 142, 160). Recent detailed ecological research on spatial patterns of parasitism has also revealed that tachinids respond strongly to the spatial structure of habitats or host plants (23, 32). A particularly nice example is the work of Roland & Taylor (121). These authors showed that parasitism by three tachinid species and a sarcophagid pupal parasitoid on the forest tent caterpillar (*Malacosoma disstria*) responds strongly (and disparately) to forest structure, with larger bodied parasitoids being more sensitive to forest structure and less likely to parasitize hosts in small fragments. On the basis of these results, the authors inferred that forest fragmentation could interfere with host population regulation by this tachinid community. A recent study of the insect community associated with a bracket fungus in old-growth forests also indicates a strong dependence of parasitism on habitat structure (78). The primary parasitoid in this food chain, *Phytomyptera cingulata* (as *Elfia cingulata*; Tachininae), declined in frequency with the age of forest fragments and was completely absent from the oldest fragments (12 to 32 years). Because tachinids occupy higher trophic levels and may be relatively sensitive to habitat structure and composition, they (and other parasitoids) may be particularly well suited as indicators of ecosystem health.

Tritrophic Interactions

The frequent finding that tachinid parasitism varies strongly with habitat has important implications for the evolution and diversification of both tachinids and their mostly plant-feeding hosts. There is a growing consensus among researchers that to understand patterns of ecological specialization and evolutionary diversification in phytophagous insects, one must consider not only their interactions with their host plants but also tritrophic interactions involving natural enemies (16, 110, 152). Although much of the interaction between tachinids and plants may be via the cues plants provide in host location (Table 3), recent studies have indicated that tritrophic interactions may also take place between larval tachinids, hosts, and host food plants. One interesting example is the interaction between the arctiid caterpillar *Platyprepia virginalis* and the tachinid *Thelaira americana*, in which the host often survives parasitism despite emergence of mature *T. americana* larvae (39). Survival of the host, however, is strongly dependent on the food plant, with parasitized larvae preferring the plant *Conium maculatum*, which increases their chances of surviving parasitism (77). The work of Singer and colleagues (132–134) on interactions between tachinid parasitoids and polyphagous arctiids shows evidence of similar tritrophic interactions. In these studies, caterpillars exhibited increased survival via lower parasitism rates when fed diets of noxious plants,

which were poor for growth and survival in the absence of parasitoids. These results suggest that polyphagy in some insects may be maintained because some food plants are more suitable for efficient growth ("good" plants) while others provide benefits through protection against parasitoids such as tachinids ("nasty" plants) (133). These results also suggest that at least some tachinid species are susceptible to host plant toxins ingested by the host.

There has been a long and valuable history of applied and basic research on tachinid-host associations since the early 1900s (7, 24, 54, 64), but only recently has ecological research on tachinids been widely integrated into modern ecological and evolutionary theory (13, 60, 143). Despite a recent flourish of basic studies and the more extensive applied ecological research, our knowledge of the ecology of most tachinid species is at best rudimentary. Currently, certain lines of inquiry are hampered by practical issues such as the inability to breed most species in the laboratory. On the other hand, this paucity of knowledge, the potential of tachinid-host interactions as model systems in the field, and the important role of tachinids as enemies of many crop and forest pests suggest that ecological research involving tachinids offers both expansive opportunity and great reward.

CONCLUSIONS AND FUTURE DIRECTIONS

Given the many constraints of a review article, this review provides only a cursory overview of tachinid biology. Many interesting and active areas of research have been mentioned only in passing or have been omitted altogether. Perhaps most noticeable is the sparse coverage of biological control involving tachinids and tachinid-host interactions in managed agricultural systems. Our avoidance of these issues is not due to a lack of perceived importance but rather to the realization that we cannot possibly do justice to them in this limited space, and they have been summarized in various articles (50). However, we hope to have conveyed some appreciation of tachinid biology and the many ways in which the study of this diverse group can provide insight into larger issues of evolution, ecology, and behavioral ecology. Furthermore, we hope to have impressed upon students and researchers the fragmentary extent of our knowledge of tachinids and the many interesting questions and areas of research that have yet to be fully explored. The following are a few of the promising future directions of research on the Tachinidae:

■ Molecular ecology of tachinids. Little research has been conducted examining the genetic structure of tachinid populations and how this may vary according to geography and host use. We know of only a single study (126) that has examined population genetic structure in tachinids, and it focused on an introduced species in its introduced range. Evidence of cryptic pheromone races in Phasiinae (2) suggests that phylogeography and population genetic techniques could provide great insight into the evolutionary diversification and host relationships of Tachinidae.

■ Phylogenetic/comparative studies. The evolutionary relationships of Tachinidae remain largely unresolved, as is our understanding of the evolution of morphological, behavioral, and ecological traits in the family. Modern phylogenetic analyses, as well as basic taxonomic studies, are sorely needed and are likely to provide fundamental insights into the evolution of life-history strategies and host associations and their relationship to macroevolutionary patterns of diversity.

■ Tritrophic interactions. Initial research on tritrophic interactions involving tachinids, herbivorous hosts, and plants has produced some exciting results (82, 132, 133). These interactions are paramount in determining the ecological structure and dynamics of tachinid-host interactions, and given the significant roles of phytophagous insects in terrestrial ecosystems, they may frequently have broader community- and ecosystem-level impacts.

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Figure 1   A *Winthemia* species (Exorisinae: Winthemiini) depositing macrotype (unincubated) eggs on its sphingid host (photo courtesy of Robert W. Mitchell and Paul H. Arnaud, Jr.).

Figure 2 *Belvosia bifasciata* (Goniini), which deposits micro-type eggs that are ingested by the hosts on their food plants (photo courtesy of J.O. Stireman, III).
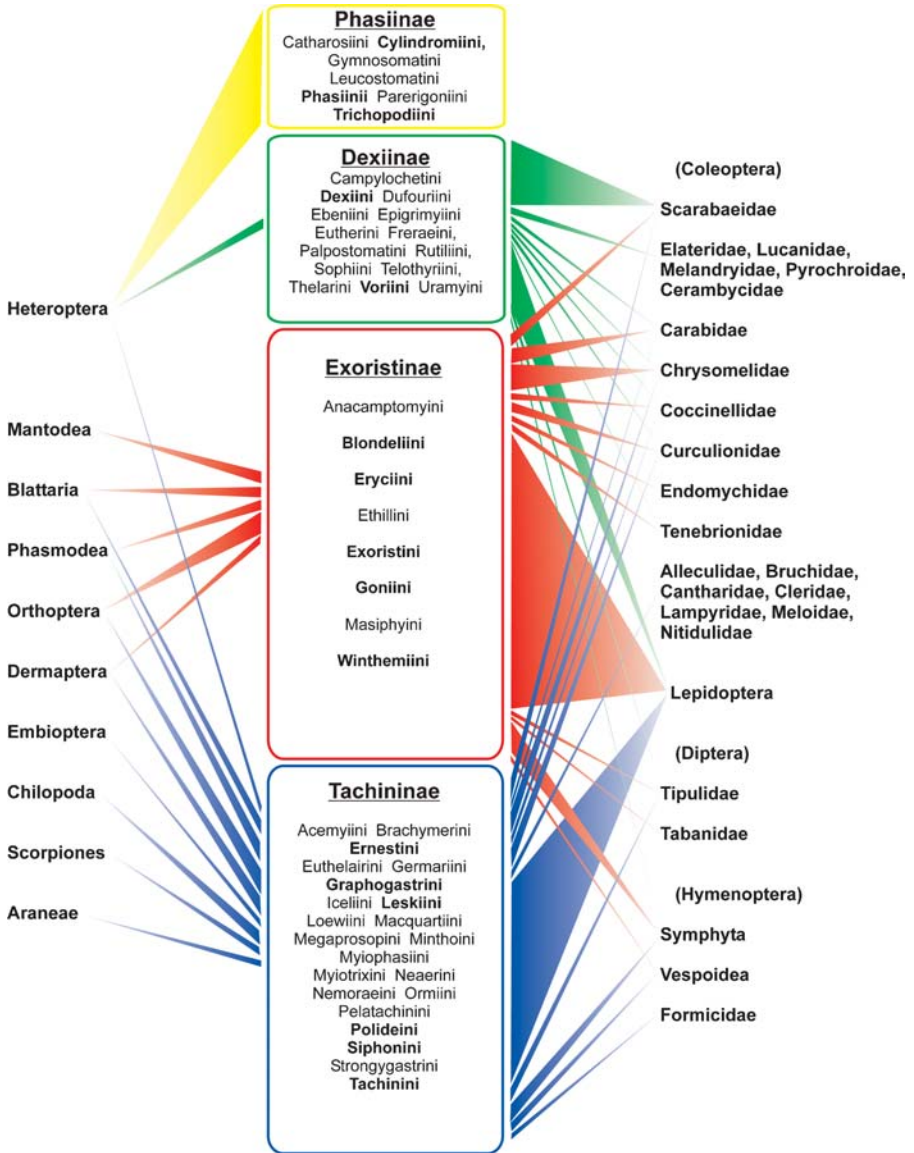
Figure 3   Host associations of the major subfamilies of Tachinidae and their included tribes. On the right are Holometabolous host groups; on the left are all other hosts. Box heights indicate relative species diversity of the four subfamilies (154). Tribal names in bold indicate major tribes in each subfamily (approximately >30 species). The width of the colored wedges indicates the rough proportion of use of different host groups by each tachinid subfamily as based on published records (8, 13, 26, 28, 55, 64).

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