

The Evolution and Parasitic Habit of the Tachinidae (Diptera)

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The family Tachinidae is generally regarded as a relatively recent, actively radiating group of parasitic flies (Crosskey 1976). It may be the most speciose family of the order Diptera in the world (Crosskey 1980). Currently the family is outnumbered in described species (8200 worldwide; Cantrell and Crosskey 1989) only by the Tipulidae. Tachinid flies are morphologically diverse, ranging in size from a few millimeters (e.g. *Siphona* sp.) to several centimeters (e.g. *Paradejeania rutilioides*) and they display a wide variety of color and setal patterns. Tachinids are found on every continent (except Antarctica), most large islands, and many smaller islands throughout the world. They are abundant in almost all environments, and at times may constitute the majority of flies observed in particular habitats (pers obs.). All tachinids with known life histories are parasitoids of other arthropods, ranging from caterpillars, the most common hosts, to spiders and scorpions (Vincent 1985; Williams et al. 1990). The majority of tachinid hosts are phytophagous insects. Due to this preference, they may significantly influence community structure by regulating herbivore populations in natural and artificial ecosystems. Many species have been introduced to various parts of the world in order to control pests of crops and forests. In several cases the introduced tachinids have become established and are able to regulate the pests to low densities (e.g. see refs in Hawkins 1994). Despite the abundance, diversity, and importance of tachinids, relatively little is known about their evolution and ecological interactions. Even basic biological information concerning hosts, mating systems, and habitat requirements is known for less than half of the species in the most well-studied regions (i.e. Europe; Mellini 1990). In this paper I will outline what is known about the evolution and parasitoid habit of this large and diverse family of flies. I will suggest areas of their biology that deserve scientific attention and discuss the problems associated with these studies. I will also examine how the study of tachinid biology may be valuable in understanding broader issues of insect evolution and ecology.

It is quite likely that the Tachinidae represents a monophyletic group (Wood 1987, Pape 1992). The family can be readily distinguished from related groups by the presence of a

subscutellum and meral bristles in the adult, and by first instar larva in which the anterior cephalopharyngeal skeleton (probably the labrum) extends forward as a hook or axe-like beak; the mandibles being vestigial or absent (Wood 1987). The fact that all species with known larval habits are parasitoids of arthropods also provides evidence for a monophyletic origin of the family.

Tachinids belong the superfamily Oestroidea within the Calyptratae, along with the Sarcophagidae, Calliphoridae, Oestridae and a few other small families. Their placement within the Calyptratae is unquestionable due to the large number of synapomorphies they share with other members of the group (e.g. large lower calypter, dorsal seam on pedicel; also see Griffiths 1972, McAlpine, 1989) and their inclusion within the Oestroidea is well founded (Hennig 1958 cited in McAlpine 1989). However, within this assemblage relationships are uncertain.

McAlpine (1989) places the Tachinidae as sister group to the Rhinophoridae (a small family of isopod parasitoids once included within the Tachinidae) on the basis that both share the parasitoid habit. He considers this assembly to then be a sister group of the Oestridae on the basis of the shared parasitic habit and concomitant changes in the larval feeding apparatus. The union of these two families, with all their morphological differences and completely disparate host associations, is probably incorrect. Larval characters associated with feeding in these parasites are probably convergent due to the similar environments and resources they experience. It seems more likely that the oestrids are more closely associated with the Calliphoridae which contains many vertebrate parasites with similar habits to the Oestridae, and the Tachinidae share a recent common ancestor with the Sarcophagidae which they superficially resemble. This was the general (though rather weak) conclusion of Pape (1992) who performed a cladistic analysis based on morphological characters to elucidate relationships within the superfamily. Many sarcophagids are parasites of arthropods (Shewell 1987) and according to Clausen (1940) they are the only other family of Diptera besides the Tachinidae that contain parasitic species which form a respiratory funnel (although Pape 1992, disputes this). If sarcophagids are indeed the sister group to the Tachinidae, it is possible that the parasitoid habit arose in the ancestor of both of these groups. It is also feasible that tachinids are derived from a group of parasitic sarcophagids, making the latter family paraphyletic. The reverse hypothesis (i.e. sarcophagids being derived from tachinids) is unlikely due to the well-supported monophyly of tachinids, though Shewell (1987) suggests that

the sarcophagids are a “younger” group than the Tachinidae (and Calliphoridae). The only phylogenetic reconstruction of the Oestroidea using molecular characters (28s rRNA; Vossbrinck and Friedman 1989) that I know of, failed to resolve the position of the Tachinidae. In fact, this analysis (in a consensus tree) split up the three tachinid taxa used, so that each had a different family as its sister group. Each of these hypotheses for the origin of tachinids and their parasitoid habit has profound effects upon our understanding of the evolution of oviposition methods and the relationships among taxa within the family.

The relationships within the Tachinidae are confused and ambiguous. All of the authorities on the systematics of the family appear to agree that the “taxonomy of the family is difficult and confused” (Sabrosky and Arnaud 1965), they are “one of the most difficult families of Diptera in which to make practical identifications” (Crosskey 1976), and there is “no consistent classificatory scheme within the family” (Wood 1987). The current state of tachinid systematics and taxonomy can best be summarized with this quote from Wood’s (1987) comprehensive treatment of the Nearctic Tachinidae:

“...Descriptions of new taxa, even today, sometimes neglect to mention unique features, but instead, present further combinations or recombinations of the same limited suites of characters. Furthermore, these character suites are usually not correlated with internal structure, life cycle, larval characters, or other character states...Such convergence, multiplied many times over because of the vast number of superficially similar species, has resulted in a long history of incorrect identifications and misunderstanding of relationships, a trend that still continues...even the most recent classifications still rely mainly on arrangements of bristles and probably contain few monophyletic taxa.”

However, some researchers have recently begun to examine characteristics of eggs, larva, life history, genitalia, and other previously neglected characters in their analyses (e.g. Cantrell 1988), and a somewhat clearer picture of the relationships between tachinids is slowly emerging.

Despite the uncertainty of tachinid systematics, it is generally agreed that the family consists of four (Wood 1987) or five (Crosskey 1973, 1976) major groups (subfamilies) which tend to share characteristics of life history and morphology. These groups are briefly described below with reference to their evolutionary relationships, oviposition methods and host range.

The Phasiinae is the smallest subfamily of tachinids in species number, but probably the most diverse in morphological appearance (many mimic bees or wasps). They are generally considered to be the most “primitive” subfamily due to their oviposition method which consists of laying unincubated macrotype eggs on or in the host. This feature is one of the few characters that unite the group, and it is likely that the Phasiines are not monophyletic. Their basal position, at least with respect to the Goniinae and Tachininae, is supported in Pape’s (1992) analysis. Another character uniting the group is their tendency to utilize Hemiptera (mostly large forms such as Pentatomidae, Coreidae, and Lygaeidae) as hosts, though they are not completely confined to this group, also attacking some Lepidoptera, Coleoptera, Orthoptera and mantids. Phasiines are atypical in their attack of adult insects and, in some groups (e.g. *Cylindromia*) the possession of an elongate piercing ovipositor derived from sternite 10 (Wood 1987). The fecundity of these species is generally low, ranging from 100-400 eggs per female (O’Hara, 1985).



The Dexiinae is the only recognized subfamily that is united by a clear synapomorphy: a distinct aedeagus morphology in which a hinge is present between the basiphallus and distiphallus, the former of which is extended as a tapering process beyond the hinge (Wood 1987). This complex character is not likely to be convergent and supports the monophyly of the group. Although Crosskey separates out the Dufourinae, which shares the hinged aedeagus, as a distinct subfamily (Crosskey 1973, 1976). Generally, dexiines tend to be large, rather long legged flies that most commonly parasitize larval Coleoptera (mostly Scarabaeidae) and Lepidoptera. They have also been reared from Diptera (e.g. Tabanidae), Hymenoptera, and Orthoptera. All dexiines have a uterus or “ovisac” in which they incubate eggs. Consequently, larvae are fully formed when eggs are deposited and they often hatch within minutes or even seconds of deposition (Clausen 1940). A large proportion of the Dexiinae, notably the tribe Dexiini, do not contact their hosts directly, but rather they broadcast their eggs in the vicinity or appropriate microhabitat of the host. The planidial larvae then burrow into the substrate in search of suitable hosts. This allows the parasitization of hosts that are concealed underground, in wood, or in plant tissues. Species with this form of oviposition produce relatively

large numbers of eggs (500-3000; O'Hara 1985).

The majority of tachinids belong to the subfamilies Tachininae and Goniinae, which cannot at present be separated on the basis of well defined synapomorphies. Generally the Tachininae are defined by the presence of a bare prosternum, though there are several exceptions, and it is quite possible that the subfamily is not monophyletic. Tachinines are a diverse group morphologically, representing the extremes of both small and large sizes. The species used in the introduction to demonstrate the range of size are both tachinines. They also exhibit a diversity of oviposition methods and host preferences. Lepidoptera constitute the majority of their hosts, but they also attack a wide variety of other insects including Coleoptera, Diptera, Orthoptera, Hymenoptera, Dermaptera, Embioptera, and even centipedes and spiders (Wood 1987). Aside from a few species that lay embryonated eggs on hosts (e.g. *Siphona* sp), adult tachinines do not contact the host directly but rather they distribute their eggs in areas which are likely to contain hosts. This is most often accomplished by laying eggs on the foliage of plants on which their hosts feed; usually on those plants that exhibit evidence of herbivore damage. Soon after deposition the eggs hatch, and instead of heading off in search of hosts, the larvae remain at the site of oviposition. These larvae "stand" upright or recline on the remnant egg shell, waiting to ambush passing hosts (Clausen 1940; O'Hara 1985; Wood 1987). When a host approaches, the larvae flail their bodies about in order to contact the host or they may leave their positions in order to intercept the host. Tachinine larvae are often covered by sclerites that fit tightly together to prevent desiccation and they may persist for up to ten days after hatching if a host is not encountered (Clausen 1940). Like the Dexiini, the tachinines that broadcast their eggs are able to attack hosts that would otherwise be inaccessible due to their concealment in silk bags or tents, under bark, underground, or in leaf rolls. As these types of hosts emerge in the evening to feed in relative asyllum from most predators and parasitoids, they come in contact with the larvae of tachinines. This strategy of parasitization requires large numbers of eggs (500-3000; O'Hara 1985), as many larvae are doomed to never encounter an appropriate host.

The Goniinae is the largest subfamily of tachinids, comprising about half of all described species and the vast majority of species that are regularly recorded as parasites of insect pests (Crosskey 1980). The subfamily is not easily definable and it is currently in a state of flux, with some groups being transferred to and from the Tachininae depending on which of several

authorities is followed. It also contains some of the most confusing and undefinable taxonomic groups. In this paper I follow the classification of Wood (unpub. class.).

This subfamily exhibits an extremely wide range of oviposition habits, encompassing every strategy of egg deposition and egg/larval morphology found in the other three subfamilies, plus several unique types. Some genera such as *Exorista* and *Phorocera* lay unincubated eggs directly on or in the host, the supposed ground plan state for the family. Others (e.g. *Drino*, *Lespesia*) lay incubated eggs on or in the host, or, as in the case of *Carcelia reclinata*, “shoot” their eggs onto the host from a distance (pers. obs.). Like the Tachininae and Dexiinae, some goniines (e.g. *Lydella*, *Lixophaga*) have larvae that contact hosts either by waiting in ambush or via mobile planidiaform larvae. However, the most impressive innovation of the Goniinae is the evolution of the microtype egg. These tiny eggs (.02-.2mm) are laid on vegetation near potential hosts or on plant parts that the hosts are likely to feed upon. The eggs are incidentally ingested by the host while it feeds. Stimulated by digestive enzymes, the eggs hatch and the larvae burrow through the foregut wall and into the haemocoel where the tachinid larvae feed. A large group of goniines (formerly all in the tribe Goniini) share this habit of laying microtype eggs and it is presumed that this synapomorphy establishes their monophyly. As might be expected with this strategy, goniine tachinids with microtype eggs have extremely large fecundities (1000-6000+; O’Hara 1985).

Coinciding with the wide variety of ways in which goniines parasitize their hosts is a wide variety of types of hosts. Though the Goniinae are primarily parasites of Lepidoptera, which they exploit to an impressive degree both in levels of parasitism and diversity of species attacked, they also attack Coleoptera (primarily chrysomelids), Hymenoptera, Orthoptera, Blattaria, Phasmida, Dermaptera, and Diptera (O’Hara 1985; Wood 1987).

The extreme range in hosts that tachinids parasitize (in all 14 orders of insects and other arthropods; Eggleton and Belshaw 1993) and the wide variety of methods by which they attack these hosts (discussed briefly above), make this family unique among the Diptera and among parasitoids in general. The complex and intriguing chronicle of evolution that has resulted in this incredible diversity of forms and habits is largely unknown. But, some processes and pressures shaping the evolution of tachinids have been suggested.

Oviposition methods

As mentioned above, it is thought that laying unincubated eggs on hosts is the ancestral

habit of tachinids (Wood 1987). This scenario seems to make sense, i.e. it is unlikely that a common ancestor possessed microtype or other highly specialized oviposition methods, but it relies heavily on which of the oestroid families is the sister group. If all or part of the Sarcophagidae is the sister group to the Tachinidae, then it is probably more parsimonious to assume that the most basal condition is one of ovolarviparity (given that all sarcophagids are ovolarviparous or larviparous). The Phasiinae, a highly derived group morphologically and in host utilization, are considered to be basal among the Tachinidae due almost solely to the fact that they lay unincubated eggs on their hosts. There may be factors associated with their host usage, mostly adult Hemiptera, that have actively selected for the evolution of unincubated macrotype eggs (from ovolarviparity) that must be deposited directly on the host. For example, the high mobility and lack of obvious feeding damage characteristic of most Hemiptera may require contact with the host directly, larvae that are not exposed when entering hosts, and the ability to lay many eggs quickly. All these features are consistent with unincubated macrotype eggs and their oviposition. This egg type and oviposition method are also found in each of the other subfamilies (O'Hara 1985) and in some cases in divergent groups within subfamilies (e.g. Exoristini and Blondeliini in the Goniinae).

Regardless of whether the ancestral state of tachinid oviposition strategy consists of embryonated or unembryonated eggs, there appears to be a trend in many lineages towards methods of parasitization that do not require direct host contact by the adult female. Without a specialized ovipositor akin to that found in the hymenopteran Parasitica which allows parasitization of concealed hosts, and with the constraining diurnal habits of the vast majority of muscoid flies, many potential hosts must have been inaccessible to early tachinids. The evolution of host searching first instar larvae that can burrow through soil or into galleries of insects concealed in living plants or dead wood, of larvae that can wait to ambush nocturnally feeding caterpillars on their host plants, and of microtype eggs that can be ingested by nocturnal or heavily defended hosts, all served to expand the range of hosts that are vulnerable to attack. These innovations opened an enormous adaptive zone for tachinids to colonize. An additional benefit of attacking hosts with these sorts of life histories is that they may be less susceptible to attack by predators or other parasites. Tachinids that can effect entry into these concealed hosts may be less likely to be destroyed by enemies of the hosts themselves. This may help to explain why

herbivores with an intermediate level of concealment, tend to have the highest parasitoid loads (though tachinids do not appear to follow this pattern; Hawkins 1994).

These varied mechanisms that allow parasitism without direct contact by the female fly may have also given tachinids the ability to utilize hosts that have formidable morphological defenses. Tachinids, and dipteran parasitoids in general, often oviposit very rapidly and can avoid host defensive behaviors easily with their remarkable flying abilities. In many cases oviposition is accomplished so quickly that a slowed motion picture is necessary to witness the process (e.g. *Apocephalus* sp. (Phoridae), *Calodexia* sp. (Tachinidae); pers. obs.). Therefore, dipteran parasitoids generally have access to some hosts or host stages that other parasitoids (e.g. the Parasitica) may find difficult to attack. With the evolution of microtype eggs, tachinids are able to attack an even further range of seemingly invulnerable hosts, such as Lepidoptera larvae that are protected by urticating bristles or long hairs (e.g. many arctiids, saturniids), or beetles that are protected by heavy sclerotization of body parts (e.g. adult Tenebrionidae, parasitized by *Eleodophaga pollinosa*; Arnaud 1978).

Despite the arguments made above, many of the hosts attacked by tachinids via life stages other than the adult, have no special characteristics such as concealed feeding habit or formidable morphological defenses that appear to justify these indirect methods of attack (see Arnaud 1978 for tachinid/host associations and Hawkins 1994, for the relative concealment of tachinid hosts). Perhaps, time is the currency that makes these strategies efficient. Theoretically, it may be possible for a tachinine or goniine female to lay a thousand or more eggs in a single day, if it needs only to find the damaged leaves of a tree, rather than individual (cryptic) hosts with their time consuming behavioral defenses. Host contacting first instar larvae and eggs may have evolved in order to minimize the search and handling time taken to parasitize hosts, and later these methods were subverted for use in attacking concealed hosts that the adult could not contact directly.

These specialized mechanisms by which tachinids contact their hosts have almost certainly evolved a number of times within the family. Though it is thought that the distinctive microtype egg evolved only once (as mentioned above), other methods by which the female flies can exploit hosts without directly contacting them must have evolved several times due to the dispersed distribution of these characters in extant taxa. Exactly how many times, or even the range of times

is difficult to estimate due to the lack of phylogenetic resolution within the family. Around half of the females of all tachinid species do not contact their hosts directly (Eggleton and Belshaw 1992). This suggests that the clades which have evolved these innovations in oviposition may have undergone considerable diversification, as seems to be the case in the microtype goniines. Comparative phylogenetic studies will reveal whether these innovations have indeed resulted in increased diversity in the clades which possess them relative to their sister groups.

The ability to incubate eggs internally until they are completely developed has probably also been an important factor contributing to the success of tachinid flies. The egg stage of many insects including tachinids is vulnerable and susceptible to predation and parasitism. Tachinid eggs that must develop outside the female may be actively destroyed by the host or shed during ecdysis before they are completely developed (Gross 1993, Terkanian 1993). With uterine incubation, the amount of time that vulnerable life stages are exposed to the environment is minimized.

Host Utilization

The Tachinidae, as a family, have by far the greatest range of hosts of any group of dipteran parasitoids, and they rival the range of the entire Parasitica clade of the Hymenoptera (Eggleton and Belshaw 1993). This diversity in the use of hosts may be due in part to the aerial agility and dexterity of tachinids, their diversity of oviposition methods, the plasticity of the female post-abdomen, and/or the active nature of dipteran larvae (Eggleton and Belshaw 1993). However, physiological characteristics may also be important. Tachinids are well known for their formation of a respiratory funnel in the host (though not all species form these structures; Clausen 1940). Unlike the Parasitica, most tachinids maintain direct contact with atmospheric air via posterior spiracles that either traverse the host's external integument or the walls of major tracheal branches. Around these connections, a sheath of cells derived from wound tissue and defensive hemocytes of the host forms and partially envelops the parasitoid. In many hymenopterans these encapsulatory sheaths can suffocate parasitoid larvae. Members of this group have been forced to evolve biochemical means by which to thwart the host immune defense response (Strand 1986; Godfray 1994), which may lead to coevolutionary arms races between parasitoid and host. Tachinids, on the other hand, are generally not vulnerable to these encapsulating host defenses because of their contact with outside air. This may allow them to ecologically or evolutionarily

“explore” new hosts more easily, and expand the range of hosts utilized. This idea is supported by the finding that tachinids that remain free in the haemocoel without forming a respiratory funnel exhibit a significantly lower degree of polyphagy than the average for the family (Belshaw 1994).

Many tachinids also do not appear to be seriously affected by toxins actively or inadvertently ingested by their hosts. This notion has been used to explain geographical patterns in the diversity of dipteran parasitoids (Gauld et al. 1992). Some species that are well known parasitoids of relatively innocuous hosts (*e.g. Exorista mella*, often reared from lasiocampids; Arnaud 1978) are occasionally reared from taxonomically distant hosts that are thought to be extremely distasteful to predators such as *Danaus plexippus*. Mallampalli et al.’s (1996) experiment with parasitized gypsy moth caterpillars raised on diets laced with secondary plant compounds showed no ill effects of the toxins on their tachinid parasitoids (though see Bouchier 1991 for a contrary result). Due to a lack of information, it is unknown if this apparent reduction in susceptibility to toxins is a general phenomenon within the family; there are certainly some exceptions (*e.g.* English-Loeb et al. 1993). If it is a general characteristic, perhaps it might be explained as an exaptation derived from the ancestral saprophagous habits of the group (Eggleton and Belshaw 1992) which must have evolved ways to cope with the various toxins produced by the bacteria and fungi found in the larval environment. It could also be related to the position of the larvae within the host; most tachinids do not remain free in the haemocoel but embed themselves in specific tissues at least in early life (Belshaw 1994).

A reconstruction of the ancestral host of the Tachinidae would probably result in an equivocal state of either an adult hemipteran or a larval lepidopteran. The former would be supported by the basal position of the Phasiinae, the latter by the cumulative signal of all other tachinids. The Phasiinae are an extremely derived group, morphologically and ecologically unlike the rest (and vast majority) of tachinids, or their close relatives (Crosskey 1973; Wood 1987). Larval Lepidoptera constitute a large majority of tachinid hosts (Arnaud 1978). It is probable that either a lepidopteran was the ancestral host of the Tachinidae, or that they were colonized early on in tachinid evolution at which point a massive radiation took place.

Lepidoptera are heavily utilized by tachinids for a number of reasons. First, many Lepidoptera are relatively large insects. By definition, an individual parasitoid must complete development on only a single host individual. Therefore, the host must be at least as massive as

the parasitoid, and given the inefficiency of energy transfer and assimilation between trophic levels, it probably must be considerably larger. Tachinids and their relatives are generally medium to large flies, and thus require large hosts. Other hosts, suitable for hymenopteran parasitoids such as aphids and dipteran larvae, may simply be too small for tachinids to parasitize. Of course, in this situation it is difficult to separate cause from effect.

Second, lepidopteran larvae are abundant. The Lepidoptera is one of the four largest (in terms of species number) orders of insects (Strong et al. 1984). They are extremely widespread, and form a major if not dominant component of the herbivorous community in nearly all terrestrial ecosystems. Janzen (1988) goes so far as to say that "...in most forests of the world [caterpillars] consume more living leaves than all other animals combined." Thus, even if tachinids selected hosts randomly, butterflies and moths would comprise a significant proportion of their hosts.

Finally, and probably most important, larval Lepidoptera are vulnerable. The majority feed exophytically where they are exposed to parasitoids. They have thin cuticles. They cannot locomote rapidly. They do not have large limbs or mandibles with which to fend off enemies. Their customary defenses such as sequestered toxins, long hairs, or crypsis are probably not effective against tachinids (see above). In general they are a life stage that is designed for bulk feeding, like the larvae of many other holometabolous insects, and in this respect they have become like bags of protein whose primary defense is remaining undiscovered by their enemies.

Larval sawflies and beetles are also fairly common hosts of tachinids (Arnaud 1978). These insects often share the characteristics of the Lepidoptera that make them vulnerable to parasitoid attack such as limited mobility and relatively soft unsclerotized bodies. Tachinids probably began parasitizing those species with feeding niches similar to the Lepidoptera, and subsequently evolved the means to attack more concealed hosts such as subterranean scarabs. With the ability to attack hosts rapidly, the evolution in some groups of cuticle piercing ovipositors, and active larvae able to burrow into heavily sclerotized hosts, there were few barriers to keep tachinids from augmenting their range of hosts with relatively agile and heavily defended adult insects. This has been accomplished to an unparalleled degree by these flies which are known to parasitize adult scarabaeids, chrysomelids, curculionids, carabids, acridoids, gryllids, mantids, phasmids, coreids, pentatomids, tabanids, spiders and a wide variety of other insects and arthropods (Clausen 1940; Arnaud 1978; Smith and Kok 1983; Vincent 1985; Wood 1987; refs in

Belshaw 1994). Selective pressure due to competition with hymenopteran parasitoids or other tachinids may have been a factor in the colonization of adult host stages, which, aside from the relatively defenseless Homoptera, are only sparsely utilized by the Parasitica.

If any generalizations can be made about large scale taxonomic host affinities in the Tachinidae aside from the overall bias towards the Lepidoptera, they would have to include the tendency of the Phasiinae to attack Hemiptera, and the preponderance of coleopteran hosts in the Dexiinae. The radiation of the phasiines onto hemipteran hosts may have been spurred in part by their method of host location. It has been shown that several species within the Phasiinae locate hosts via sex pheromones produced by the adult bugs (e.g. *Trichopoda* sp., Harris and Todd 1980). This may be a widespread phenomenon within the subfamily, and provide a general explanation for their tendency to attack adult hosts, predominantly of one sex (Clausen 1940). The use of this type host location cue may serve to restrict phasiine host ranges to insects that produce these types of cues, and could have led to the divergence of lineages among hosts with differing pheromonal compositions or phenologies of pheromone distribution. The utilization of coleopteran hosts by dexiine tachinids may be fairly old trait within the group, though a considerable portion of the subfamily attack Lepidoptera and sawflies. The majority of these coleopteran hosts are scarabaeid grubs that live in decomposing vegetable matter and underground (Arnaud 1978). Cerambycids and members several other coleopteran families are also attacked, though less frequently. There does appear to be an association between those dexiines that attack beetles and those with host searching first instar (Arnaud 1978).

The remarkable diversity of hosts exploited by the family Tachinidae is mirrored by the breadth of hosts used by some of the individual species. Tachinids generally have much larger hosts ranges than would be expected given their koinobiont status (Eggleton and Gaston 1992; Hawkins et al 1992; Belshaw 1994; see Godfray 1994 for definitions). As a whole, they are even more polyphagous than idiobiont hymenoptera (Belshaw, 1994). The extreme of this is manifested in species such as *Compsilura concinnata* which has been reared from over 100 different host species in three different orders (Arnaud 1978). This high level of polyphagy is probably the most important functional ecological distinction between tachinids and hymenopteran parasitoids. That is to say, this feature is likely responsible for much of the difference in the effects of the Tachinidae versus Hymenoptera on the population dynamics, ecology, and evolution of their

hosts. Due to their polyphagy, tachinids may in effect, act more like a predator in an ecological community than a koinobiotic braconid, which is functionally more equivalent to a parasite. The extent and breadth of tachinid polyphagy is not fully known, for there are several inherent problems in estimating the host ranges of parasitoids such as biases in the types of hosts investigated, host and parasitoid misidentification, and a lack of quantitative data (Shaw 1994). Given that hosts are not known for most species of tachinids (Mellini 1990) and they are notoriously hard to identify (Crosskey, 1980), generalizations about tachinid-host associations must be made carefully.

The relatively high level of polyphagy found within the Tachinidae has commonly been explained by the habit of forming respiratory funnels within the host (Askew and Shaw 1986; Eggleton and Belshaw 1992; Hawkins et al. 1992). This hypothesis generally assumes that these respiratory funnels provide the larvae with some immunity from the host's encapsulatory response (as described above) and that this immunity allows a wider range of hosts to be attacked. In one of the few quantitative analyses of parasitoid host ranges, Belshaw (1994) attempted to determine which life history characteristics of tachinids might be responsible for their large host ranges. Using a large database of rearing records (Palearctic), he found that the location of the larvae in the host and developmental synchronization with the host were associated with significant deviations from a standard regression of host species versus rearing records. That is, he found that larvae that were located free in the haemocoel and those that were highly synchronized developmentally with their hosts, had significantly lower levels of polyphagy than that for the family as a whole. The first relationship appears to provide support for the respiratory funnel hypothesis. The second suggests that the rapid development of many tachinids may be important in allowing a diversity of hosts to be parasitized. Surprisingly, there was no relationship between polyphagy and reproductive strategy (e.g. host searching first instar vs. direct contact). Note however, that these explanations do not deal with how the behavior of attacking a wide range of hosts evolved. It only explains how this may have been accomplished developmentally or physiologically. The methods of host location and choice of adult females have probably also played a role, and the differences between tachinids and Hymenoptera in these respects may be telling.

Host location and Selection

The processes and methods by which tachinids locate and select hosts are not well known for most species. Notably lacking is information from species in which the adults do not contact the host directly. The few cases in which information is known indicate that tachinids are capable of using a wide diversity of olfactory, visual, auditory, and possibly tactile cues to locate their hosts. One of the most famous and well studied tachinid host location systems is that found in the cricket parasitoid *Ormia ochracea*. This nocturnal fly uses “ears” located on its thorax to detect the songs of male crickets which it then locates and parasitizes (Cade 1975; Walker 1993). Corresponding systems have been discovered in related species that attack similar song-producing hosts (Allen 1995). As mentioned above, some phasiines such as *Trichopoda pennipes* have been shown to use sex pheromones of their hemipteran hosts as cues by which to locate them (Harris and Todd 1980). This may occur in some other phasiine species, and quite possibly in other tachinid groups that attack adult insects (Clausen 1940). Cues derived from plants have also been shown to be used by tachinids in locating hosts (Montieth 1955, 1964; Roland et al. 1989, 1995; Roth et al. 1982). Most of the studies demonstrating the use of plant derived olfactory cues by female tachinids, showed both whole plants and extracts to be attractive to the flies. The response of males to these cues is generally much reduced or absent (e.g. Martin et al. 1990). Cues associated with host secretions (vomit, frass) have also been shown to attract female tachinids (Clement et al. 1986).

The use of visual cues, though seemingly underplayed by researchers on hymenopteran parasitoids (Godfray 1994, and references therein), is probably very important for many tachinids (Monteith 1956; personal obs.). All tachinids have large eyes, some enormously so. In accordance with their remarkable aerial agility and the need to precisely control flight, muscoid Diptera have acute vision, especially in relation to motion detection (see Chapman 1982, for the related *Calliphora*). This, combined with their tendency to attack exposed hosts (Hawkins 1994), makes vision a useful, easily co-opted tool with which to find hosts (at least at close ranges). Of course, most species of tachinids probable utilize many types of cues with varying degrees of specificity and reliability. As a consequence of their broad host ranges, It might be expected that very general cues associated with microhabitats or non-specific plant damage are of primary importance to tachinids, and that more specific types of information are less commonly used. Little can be said about the evolution of host location mechanisms in the Tachinidae due to the relatively few taxa

for which anything is known and their sporadic distribution within the family. Though there is probably some phylogenetic coherency to these mechanisms, I would suggest that the ecology of the host(s) is of upmost importance in determining which sorts of cues are used.

The process of host selection in tachinids has received even less attention than host location. Some observations suggest preferences for particular sizes or instars of hosts (Terkanian 1993; pers. obs.), but few quantitative studies have been conducted. This is partially due to the lack of behavioral studies on tachinids in general, but it may also be related to the prevalent notion that tachinids are rather indiscriminant in their choice of hosts. For example, females of the species *Carcelia reclinata* readily deposit eggs on the old exuviae of their hosts (unpub. data), a situation in which they have no hope of survival. Many researchers (e.g. Askew 1971) have also pointed to the high levels of superparasitism that have been recorded for tachinids (e.g. 72 eggs of the solitary parasitoid *Ptychomyia remota* larvae on one zygaenid moth larva, reference in Godfray 1994) as evidence of their lack of discrimination. However, a recent study has demonstrated the ability of two species of tachinids to discriminate parasitized from unparasitized hosts (Lopez et al. 1995), and it is likely that future research will reveal that many tachinid species evaluate and actively discriminate between hosts.

Tachinids as models

There are many ways in which research on tachinid flies can be applied to the more theoretical disciplines of biology such as ecology, evolutionary biology, and behavioral ecology. Especially useful, may be the ways that tachinids deviate from theoretical expectations that are based on examinations of other parasitoid groups. One area that has received great attention in recent years is the general phenomenon of coevolution between parasites (or predators) and their hosts (or prey). Most tachinids probably lack the “tight” coevolution that results in co-cladogenesis due to their elevated host ranges, but on the other hand, most are extremely selective given the range of possible hosts available. It is also possible that the generality of tachinid host usage may only be realized at large geographical scales. Many species that appear to have broad host affinities as a whole may, on the local population level, be quite specialized (Thompson 1994). Regardless of the level of host specificity of tachinids, they must often represent a potent selective force to many of their hosts, and the hosts have likely responded to them evolutionarily via changes in behavior, morphology, and physiology. Analyses of tachinid parasite loads and

traits that influence vulnerability to parasitoids, either by manipulative selection experiments or in comparative phylogenetic studies, may aid in understanding the role that parasitoids have had, and are having, in shaping traits of the host (e.g. see Zuk et al. 1993). Complementary analyses using similar comparative studies of host-parasitoid relationships and manipulative experiments may elucidate the role of various host characteristics in shaping the parasitoid.

The enormous and rapid radiation of tachinids may also be useful in understanding the processes of speciation and diversification. Because tachinids are thought to be a relatively young and actively radiating clade, they may be an ideal group in which to understand how (and if) behavioral or morphological innovations lead to radiation, which sorts of processes actually lead to initial divergences between populations, and how this divergence is related to the types of hosts used and behaviors associated with locating and attacking these hosts. For example, it is tempting to suggest that the relatively high diversity of tachinid species is due to reduced extinction rates. This could be due to the lack of specialization and dependence upon a particular host.

Tachinids are exceptionally good fliers, and it might be suggested that most geographical barriers would not seriously restrict gene flow between populations. Many tachinid species are known to have large geographic distributions (e.g. species of *Exorista* and *Lespesia*, though oftentimes these wide ranging species may represent species complexes; Arnaud 1978, Crosskey 1980). Thus, it seems unlikely that the simple, vicariance form of allopatric speciation has been responsible for generating the diversity of species we see today. Speciation in tachinids may be closely tied to changing characteristics of hosts, or to shifts in host utilization. If tachinids tend to remain in areas where hosts are likely to be found, fragmentation of these habitats could lead to divergence, even if the host adults move freely between these patches. Tachinids may also track temporal changes in host phenology which could vary geographically among populations and lead to reproductive isolation. It is also possible that tachinids may undergo host-based sympatric speciation associated with host shifts or host divergence. This however could only occur if the flies mate somehow in association with the host or host's microhabitat, a phenomenon not known to exist in tachinids.

Another large and controversial topic that research on the Tachinidae may assist us in understanding is the evolutionary and ecological consequences of specialism versus generalism. The intimate relationship that tachinids have with their hosts would lead many to believe that they

must necessarily be highly specialized. Yet, there exists a wide range of specificity within the family, from monophagy to extreme polyphagy. How can this be? Several hypotheses have been suggested (see above), but we really do not know. What are the evolutionary consequences of being a specialist or generalist? Perhaps, if the systematics of this group were better understood, generalist and specialist lineages could be identified, and their relative diversities compared. I have already suggested that perhaps the generalized host ranges of tachinids may have resulted in a decreased extinction rate, contributing to their apparent diversity. The manner in which hosts are located, selected, and attacked by a tachinid must be heavily influenced by its level of specificity (and vice versa). Comparing these behaviors in tachinid species of varying host specificities may be extremely informative, and aid in our understanding of the ecological and behavioral characteristics that determine host range, and its subsequent consequences. Broad comparisons could also be made between the host related behaviors and specificities of tachinid and hymenopteran parasitoids. This would help revise generalizations made about parasitoids and their host ranges that are based solely on a relatively few members of the Parasitica.

Research on the role tachinids in ecological communities may also prove to be useful and interesting. Due to their abundance, diversity, and use of primarily phytophagous hosts, tachinids are certainly important members of terrestrial food webs. They likely serve to regulate the interactions between phytophagous insects and their host plants and thus, promote community stability. Their competitive interactions with other parasitoids, and sensitivity to predators of their hosts, may add to the complexity (and probably stability) of ecological systems. Studies of how tachinids affect the population dynamics of their hosts, how they interact (indirectly or directly) with the plants upon which their hosts feed, and how they are assembled into a parasitoid community can reveal much about the processes that shape and maintain the structure of ecological communities.

One of the areas that research on tachinid behavior could be most easily and readily applied is that of behavioral ecology, especially with regard to optimality theory. Much of the theoretical work on optimal foraging, patch use, clutch size, and sex ratios was based on or at least heavily influenced by models of hymenopteran parasitoids (e.g. Charnov and Skinner 1985). This has resulted in an enormous literature on optimality theory applied to parasitoids (see Godfray 1994). Tachinids appear to be almost perfect organisms with which to test many of these

models (notably excepting sex ratio theory). Tachinid resources are often distributed in a patchy manner, the flies travel between these patches at some cost, they have easily measurable handling times, they probably can assess resource quality, and their clutch sizes and egg loads are easily measured. All these variables are relatively easily definable for tachinids and can be transformed into models of their expected behavior, which may subsequently be tested in the lab or field. Tachinids however, differ from hymenoptera in many ways, and this could generate different predictions for how they and other animals should behave. For example, dynamic models of tachinids must include variables that reflect the number of incubated eggs (not just total egg load) available for deposition and the costs of not depositing completely developed eggs on a host (the eggs may have to be laid, on a host or not).

The Future of Studies on the Tachinidae

Though I have identified several areas in which the study of tachinid parasitoids may be useful, I believe that there are three main research directions that are exceptionally promising: One is the construction of a robust phylogenetic hypothesis based on numerical methods, on which the evolution of morphological, reproductive, ecological and behavioral characters could be examined; Two, is the study of interactions between tachinids and their hosts in natural ecological communities including examination of the population dynamics of parasite and host, the realized host ranges of tachinids, mechanisms of host defense and the tri-trophic interactions between host-plant, host, and parasitoid; and Three, explicit studies of host location, selection, and parasitization methods of tachinids with respect to their level of polyphagy and in comparison with their hymenopteran counterparts.

The importance of a testable phylogenetic hypothesis which resolves relationships among tachinid subfamilies and tribes has been alluded to throughout this paper. In order to understand nearly anything about how reproductive strategies, host usage, and host ranges have evolved within the Tachinidae a large scale phylogeny containing taxa from all the representative groups, especially within the Tachininae-Goniinae complex, is needed. A robust phylogenetic analysis would also enable comparative analyses of behavior and ecology to be conducted without the ever present confounding factor of shared ancestry rearing its ugly head (of course, characteristics of the behavior and ecology must also be known to perform these sorts of analyses, a problem which the other two research directions help to address). Analysis of the basic phylogenetic relationships

among tachinid groups could be performed with either morphological or molecular data, or both. However, if morphological characters are used, they must be chosen in such a way as to avoid the homoplasious traps that have burdened many taxonomists (as mentioned previously). Most of the larger taxonomic groups are distributed throughout the world (with the exception of the Australian Rutiliini and a few other groups), therefore sampling enough divergent taxa should not present a problem. Sampling should be more dense in the Goniinae and Tachininae given that they are the least resolved groups and that they exhibit the most variation in all life history characteristics.

Detailed studies of parasitoid-host interactions in the field are rare (Godfray 1994), and thus our knowledge of the role of parasitoids in natural communities is mostly speculative and inferential. Rearing studies of wild collected hosts and their parasitoids have been conducted (e.g. Schaffner and Griswold 1934, Schaffner 1959), but this provides only a snapshot of a complex dynamic relationship, and reveals little about the interactions that occur in nature. Also, the data in these studies is only beginning to be analyzed from ecological and/or evolutionary perspectives. Studies of parasitoid and host communities in nature are even more rare, and we know very little about broad ecological patterns in parasitoids (but see Hawkins 1994, Price 1994). Tachinids comprise an important part of these communities and they may be better suited than other parasitoids for observational studies in the field. They are generally large, easily caught, diurnal, and often abundant. They also tend to attack exposed hosts, which are usually the easiest types of insects for researchers to locate, collect, and rear if needed.

Long term studies of tachinid-host interactions in the field would be enormously valuable, and allow theoretical predictions of population dynamics and ecology to be tested. For example, one could examine whether populations of polyphagous tachinids are buffered from dramatic fluctuations in size by the ability to utilize alternate hosts when the primary host becomes rare. Long term ecological studies could also be useful in understanding whether tachinids actually use a selective subset of hosts that they can survive on, and why this may be so. As stated above, the seemingly polyphagous nature of tachinids may be a result of regional specialization and divergence in host preferences between populations (in the sense of Thompson's 1994 geographical mosaic model of coevolution). This would have profound effects on how tachinids behave within a population and how they impact their hosts.

Tritrophic interactions between plants, herbivores, and parasitoids have recently begun receiving considerable attention from ecologists. Studies have shown that the plants on which herbivorous insects feed can affect the success of their parasitoids (e.g. Tschamntke 1992, English-Loeb et al. 1993). Other studies have demonstrated that parasitoids can influence plant fitness by destroying phytophagous insects (e.g. Price et al 1980; Gomez and Zamora 1994). However, inquiry into the complex interactions among these three trophic levels is still in its infancy. Rigorous field and laboratory studies which correlate plant traits with the probability of parasitism, and demonstrate host-plant effects on parasitoid fitness are needed in order to understand the extent and importance of interactions between parasitoids and plants. Tachinids appear to be ideal organisms for these sorts of studies due to their apparent dependence on floral resources (Wood 1987; pers. obs.), their common use of plant related cues in host location (see above), and their tendency to attack phytophagous insects. If tachinid host ranges are determined more by microhabitat than taxonomy, they may have more impact on plant fitness than a specialized parasitoid that attacks only one pest species. On the other hand, their widespread polyphagy may dilute their effect on hosts and prohibit coevolved interactions with host plants.

The koinobiont-idiobiont dichotomy, used to characterize all parasitoids, does not apply well to tachinids (Hawkins 1994). While by definition tachinids are koinobionts (see Godfray 1994), they do not follow any of the patterns expected from the lifestyle. Hymenopteran koinobionts, which allow continued development of the host after attack, tend to be more specialized than their idiobiotic counterparts (Hawkins 1994). Tachinids, despite their koinobiotic status, surpass the host ranges of even the idiobiont Hymenoptera. The failure of this paradigm to apply to tachinid parasitoids suggests the need for a more comprehensive view of parasitoid life history. Our current perspectives on the ecology and evolution of parasitoids have been shaped almost solely by hymenopteran examples. Given the many differences between dipteran and hymenopteran parasitoids such as physiology, aerial agility, and larval activity, we might expect to see major differences in behavioral traits related to their parasitoid lifestyle such as host location and selection (as we have with host ranges). The term “parasitoid” refers to a group of organisms that have similar life histories and face the same general suite of ecological problems. Characterization of the differences in hymenopteran and dipteran host-related behaviors will allow a better understanding of what the parasitoid lifestyle actually entails, and how different solutions

to common ecological problems may be reached. Tachinids, which comprise the vast majority of all dipteran parasitoids, are an obvious choice with which to begin these investigations.

Detailed empirical studies of tachinid host-related behaviors in the field and laboratory are needed to understand the consequences of their many inherent differences from the Parasitica. More importantly, these sorts of specific behavioral studies will help researchers revise the current dogma of parasitoid biology by broadening the base of information both phylogenetically and ecologically.

Perhaps one of the most important ways in which tachinids will influence current conceptions of parasitoid biology is through their relative polyphagy. Most models of parasitoid behavior have focused on interactions with one or at most a few hosts (e.g. see examples in Godfray 1994). The predictions of these models may be quite different when there are ten or twenty potential hosts. The broad host range of many tachinids surely affects their host-related behavior in a variety of ways. Comparisons of host location, selection, and attack could be performed between tachinids exhibiting various degrees of host specialization in order to understand what traits enable polyphagy to evolve and what the behavioral consequences of host range are. These kinds of comparisons can only be performed if these behaviors are critically examined for many different species, preferably under natural conditions.

Conclusions

In conclusion, I would like to reiterate the understated and often overlooked importance of the Tachinidae. This family of parasitic Diptera is extremely diverse. Diverse not only in terms of the numbers of species, but in form, in reproductive habit, and in ecology. They are also abundant in many habitats and ecosystems. They are among the most commonly seen large flies in a variety of natural and artificial environments, from oak forests to back yards. Also, as I have suggested at several points in the discussion above, they must certainly play an important role in regulating plant-insect interactions and influencing community dynamics in many terrestrial ecosystems. It is lamentable that such a group as this has not attracted more attention from ecologists and evolutionary biologists. Despite the impact that tachinid parasitoids can have on “pest” insects in forest and agricultural systems (See Clausen 1940, and references in Hawkins 1994), the family does not even have a common name in English besides the rarely used “Tachina Fly.”

Only recently has interest in the evolution and ecology of tachinids spread beyond the realm of taxonomy and systematics (e.g. Eggleton and Belshaw 1992,1993; Belshaw 1994). As more information on tachinid life histories and behavior is acquired and placed in evolutionary and ecological contexts, we will approach a true understanding of the unique parasitoid lifestyle. We will also gain new perspectives on the processes of coevolution, specialization, and community structure. However, applying knowledge of tachinid life history and ecology to these issues will be limited by the problematic taxonomy and lack of well supported hypotheses of phylogenetic relationships within the family. Thus, the resolution of this problem is one of the most important and most promising directions for future work on the Tachinidae

As concern about the “environment” grows and people realize the need for sustainable agriculture more and more emphasis will be placed on the use of natural control methods to deal with pest species. Though many advancements have been made towards increasing plant resistance (e.g. genetic transformation), biological control using parasitoids and predators is still an important tool for agronomists. They will probably remain important in the future as well, for herbivores will find it hard to evolve resistance to their natural enemies for any appreciable amount of time. Tachinid flies have been important in controlling pests in the past (see review in Hawkins 1994), and it is likely that when we gain a better understanding of their ecology and behavior, they will become even more important. This paper is primarily concerned with less pragmatic aspects of tachinid biology, but the potential to use information derived from these more esoteric types of inquiry in an applied manner is enormous.

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