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2 Breeding Habits and Sex in Families Closely Related to the Tephritidae: Opportunities for Comparative Studies of the Evolution of Fruit Fly Behavior

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2.1 INTRODUCTION

There are reasons to address the tephrit*oid* flies other than fruit flies, i.e., the Lonchaeidae, Ulidiidae (= Otitidae), Platystomatidae, Pyrgotidae, Tachiniscidae, Richardiidae, Pallopteridae, and Piophilidae, in a book devoted to the Tephritidae. Foremost is that comparative studies of tephritid behavior might be improved by the larger, more various data set created by inclusion of nontephritid flies. The potential advantages become clearer following a consideration of the nature of the comparative method itself.

Correlations between the variations in a particular type of behavior and the different ecological circumstances in which the variations are performed are important means of suggesting how the behaviors evolved (e.g., Thornhill 1984). Such comparative studies have long played an important role in the study of fruit flies, a classic example being the relationship between the spatial distribution of larval foods and the types of places males forage for mates and the investments they are likely to make in courtship signals (Emlen and Oring 1977; Prokopy 1980; Burk 1981; see following section on Lonchaeidae).

While correlations of niches and behaviors can be very revealing, there are two types of errors that may occur in comparisons of organisms, and the likelihood of these errors is influenced by the scope of the comparison. The first is mistakenly ascribing similar traits to convergence and dismissing the importance of differences in particular selective contexts. This can result from comparing closely related insects which may share a trait simply because of recent common descent. There may have been insufficient opportunity, perhaps due to lack of time or shared genomic coadaptations, for natural selection to result in divergence. The second error is to compare distantly related organisms and underestimate the role of phylogeny in restricting convergence; for example, a hypothesis that large wings will evolve in a certain habitat should not be weakened because a wingless centipede was collected along with broad-winged flies from some particular site.

Thus, the justification for the consideration of other tephritoid families is that they may provide material for comparisons that do not suffer from being made among insects that are either "too closely" or "too distantly" related. I offer no formula that predicts when such comparisons would be particularly useful, only urge fruit fly researchers to keep the Ulidiidae, Lonchaeidae, and other related families in mind and be aware of the opportunities they may afford to identify convergent evolutionary patterns and their ecological correlates. To that end, I briefly review the phylogeny and breeding habits of the nontephritid tephritoids, and comment on what they might reveal about mating behaviors in fruit flies.

2.2 TEPHRITOID FAMILIES

2.2.1 LONCHAEIDAE

Within the superfamily Tephritoidea there are three monophyletic subgroups (McAlpine 1989; Figure 2.1; but also see Korneyev, Chapter 1). One, consisting of the Lonchaeidae alone, is the sister group to the other subgroups and is distinguished by, among other things, its unpatterned wings and aerial-swarm mating systems (pigmented wings do occur in *Dasiops gracilis* Norrbom and McAlpine (1997) and various other lonchaeid species, but the patterns are usually faint and diffuse).

The function of wing patterning in tephritoids is obscure, although when the folded wings of some fruit flies are seen from behind, the bands appear to mimic a salticid spider. This resemblance can deter spider attacks (e.g., Greene et al. 1987). While both sexes typically have similarly patterned wings (Foote et al. 1993), it is possible that bands and spots on slowly moving wings serve as sexual or agonistic signals of some sort (Sivinski and Webb 1986). If wing patterns are signals, then they would be of lesser value in insect swarms, such as formed by lonchaeids, since the rapidly moving wings would obscure the pattern (Sivinski and Petersson 1997). Bold patterns on the wings of the largely nocturnal tephritoid family Pyrgotidae (Steyskal 1978) may be evidence against a universal intraspecific signaling role for the markings. In some tephritids, for example, *Trupanea* spp., male wing markings are fainter than those of females and some features may be interrupted or missing (Foote et al. 1993). This might also be inconsistent with sexual signaling since males typically have more elaborate displays.

Swarms are rarely found among the cyclorrhaphous Diptera, especially in acalyptrate families, but the lonchaeids are exceptions. For example, 12 species were discovered swarming at the same time of year on a hilltop in Quebec (McAlpine and Munroe 1968). Several to ten aggregated males engaged in rapid, spiral-like, zigzag flights over forest paths, typically in a beam of sunlight. Similar swarms of males, some much larger (>100 individuals) and others with females found crawling on adjacent branch tips, have been observed in different Canadian locations and in Australia (citations in McAlpine and Munroe 1968).

While lonchaeid swarms are unique in the Tephritoidea, male aggregations in the form of leks are common in the Tephritidae (Aluja et al., Chapter 15; Eberhard, Chapter 18). Could a comparison of the two families reveal similarities and differences that led to the evolution of two different group-based mating systems? The distribution of larval feeding sites seems to be correlated to the

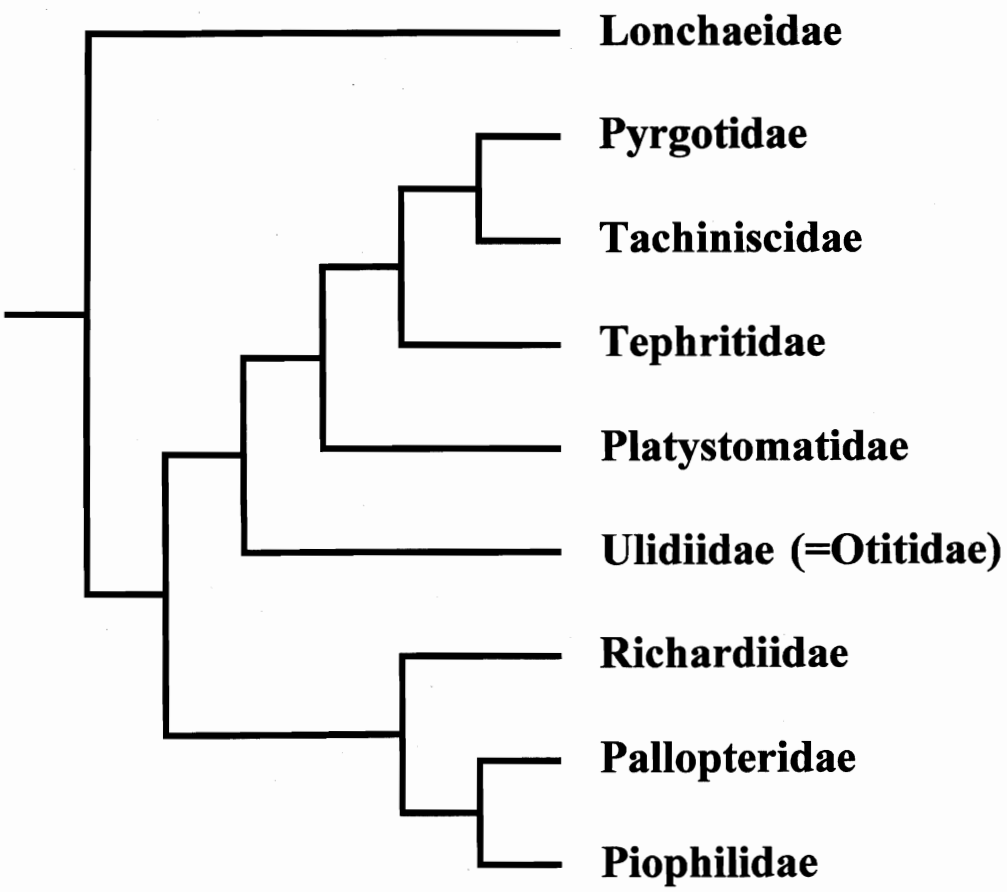

FIGURE 2.1 A cladogram representing the derivation of the tephritoid families. (Modified from McAlpine J.F., *Manual of Nearctic Diptera,* Vol. 3, Agriculture and Agrifood Canada, 1989. Reproduced with the permission of the Minister of Public Works and Government Services Canada.)

occurrence of certain kinds of insect mating systems. Prokopy (1980) and Burk (1981) brought to the attention of tephritidists that there are circumstances where female fruit flies cannot readily exercise precopulatory mate choice, for example, when oviposition sites are discrete, scattered, and relatively rare (see Emlen and Oring 1977). Males can wait by these resources and attempt to copulate with arriving females. Under these conditions it might benefit a female to mate immediately rather than expend time and energy choosing a particular male, all the while distracted from exploiting the resource. Where there is little opportunity for females to choose, there is little advantage for males to invest in courtship signals. However, where oviposition sites are relatively common and homogeneously distributed, females are not concentrated and their locations become unpredictable. Males have little chance to control access to resources and females are free to choose mates. Males may then compete through signals (Sivinski 1997), and perhaps aggregate (lek) away from oviposition sites (Alcock 1987).

Theories concerning the role of oviposition site distribution in the evolution of swarming, like those that address lekking, first suppose that males find it difficult to predict the presence of females near resources, and so participate in mating systems away from resources, where the sexes meet by "convention" (Sivinski and Petersson 1997). Swarm sites, hilltops, sunbeams, branch tips, etc. might originally have been useful as navigation markers (Sullivan 1981). Since moving insects pass over or near these markers, their vicinities would have contained unusually high densities of

otherwise rarely encountered females (Parker 1978; Alcock 1987); in the terminology of lek evolutionary theory such sites are "hot spots" (Bradbury 1979). One difference between leks, occurring as they do on a substrate, and aerial swarms is that males in leks have a platform from which to produce visual, acoustic, and/or chemical signals, all of which can presumably be tracked back to the emitter. This allows females to compare males and make informed mate choices. These signals are more difficult to track in aerial swarms, and appear to be rare in swarming species of flies (Sivinski and Petersson 1997). Thus, while leks and swarms may derive from similar conditions of female unpredictability, subsequent sexual selection may follow different paths.

What is the spatial-temporal distribution of resources used by lonchaeid females and are there any parallels with the resources used by lekking tephritids? In general, the Lonchaeidae are saprophages, with two main feeding types (Ferrar 1987). The first consume rotting fruit and vegetable material, and many follow attacks by tephritid fruit flies. A few are primary attackers of fruits and pine cones; for example, *D. alveofrons* McAlpine oviposits in apricots in a manner similar to that of tephritids (Moffitt and Yaruss 1961; see also figures of *Silba adipata* McAlpine in Katsoyannos 1983). The host ranges of Brazilian *Neosilba* spp. closely parallel those of local populations of *Anastrepha* spp. and *Ceratitis capitata* (Wiedemann) (as *Silba* spp.; Malavasi and Morgante 1980; Souza et al. 1983). The second feeding type is found under bark, in close association with wood-boring Coleoptera. Maggots consume weakened and dead beetle larvae and pupae (Ferrar 1987), although some can complete development on beetle frass alone. The large genus *Lonchaea* contains most of the larvae of this type.

Swarming species have been collected from genera that both secondarily attack fruit (e.g., *Silba horriomedia* McAlpine) and feed upon beetles under bark (numerous *Lonchaea* spp.). The first set of resources has obvious parallels with those exploited by fruit flies, and presumably generates similar selection pressures. It would be particularly interesting to compare the ecology and mating behavior of lonchaeids that oviposit into fruits previously attacked by lekking tephritids, such as the Brazilian *Neosilba* spp. mentioned above. Do these lonchaeids swarm? How similar are the larval resource distributions; for example, are the lonchaeid host ranges narrower? What factors might be responsible for the evolution of lekking in the one and swarming in the other? To what extent has the divergence between swarming and lekking influenced precopulatory courtship signals?

2.2.2 Ulidiidae

The Tephritoid subgroup containing the Tephritidae also encompasses the Ulidiidae, Platystomatidae, Pyrgotidae, and Tachiniscidae (Figure 2.1; see, however, Korneyev, Chapters 1 and 4, who subsumes the Tachiniscidae into the Tephritidae). All are characterized by patterned wings and sexual behaviors entirely completed while standing on a substrate (McAlpine 1989; see, however, rare aerial courtship components in species such as *A. robusta* Greene [Aluja 1993]). The Ulidiidae are separated from the remaining families in the subgroup largely on the basis of genital morphology (McAlpine 1989).

The ulidiids develop in a variety of breeding sites, the most common being rotting fruits and vegetables, and other decaying media such as pond muck, refuse, and dung (Ferrar 1987). However, there is a strong tendency to attack living plant tissue (e.g., *Euxesta stigmatias* Loew on sweet corn, *Zea mays* L.; Seal and Jansson 1989; Seal et al. 1995). These species tend to have narrow host ranges. Unlike the Lonchaeidae, those species that oviposit under bark appear to develop on beetle frass, rather than upon the beetles themselves.

Ulidiid behavior is diverse and sometimes spectacular. As in the Tephritidae, wing movements by individuals of both sexes are common. *Callopistromyia annulipes* (Macquart) "struts" with the wings upraised like a peacock's tail. The attitude so struck the well-known dipterist J. M. Aldrich that he mounted his specimens in the display position (Steyskal 1979). Wing waving by *Tritoxa incurva* Loew was thought by Allen and Foote (1975) to play some role in courtship, as does perhaps the frequent expulsion, and subsequent holding of, droplets in the mouth, a behavior which includes expansion of an orange-colored oral membrane.

While there are some behavioral similarities with fruit flies, other courtship behaviors in the Ulidiidae differ from those typical of tephritids. For example, in *E. stigmatias* females in the presence of males extend their aculeus (ovipositors), which stretch nearly as long as the body. Males then rub their labella down its length (Seal and Jansson 1989; see also similar activities reported by Perez (1911) as cited in Richards (1924); note that females of the tephritid *A. striata* Schiner may touch their ovipositors to the males' heads (Aluja et al. 1993)). Such a behavior might reflect different sensory systems in the two families (e.g., different chemosensillia on the ulidiid ovipositor) and/or a more saliva-borne pheromone in the male. The remarkable courtship of *Physiphora demandata* (Fabricius) consists of highly variable sequences of displays presented in territories held on twigs and grass stems. It includes (1) male drumming of the female's head and thorax with his forelegs; (2) vibration of the male's body; (3) wing waving; (4) wing flicking (supination?); (5) foreleg lift and wave; (6) midleg raise (abduction); and (7) the male quickly backing up several centimeters and then hurrying forward (Alcock and Pyle 1979). Female behavior is also complex and includes a bizarre episode where she places her extended proboscis on the male's back and appears to pull him backward in a spiraling course for several centimeters (Figure 2.2). Following a successful courtship, pairs remain coupled for over 2 h, which prevents females from mating again during the afternoon breeding period. The relationship between the opportunity to remate and copulation duration might likewise be profitably examined in the Tephritidae where pairings among species can be highly variable (see Sivinski et al., Chapter 28).

Larvae of *P. demandata* develop in dung and rotting vegetation, and Alcock and Pyle (1979) note that male dung-breeding flies are typically able to control access to oviposition resources and so do not advertise their suitability to females with elaborate/expensive signals. They suggest that the apparent paradox of an off-resource mating system containing elaborate male signals having evolved in a species exploiting a discrete and relatively rare oviposition site (dung) may be resolved by the flies' additional use of rotting vegetation. Such resources may be "... too widely distributed to be easily monitored or defended."

In addition to complex courtships, some ulidiid males have their eyes on stalks, which may be used by males to defend oviposition sites from sexual rivals (Wilkinson and Dodson 1997). Thus, sexual selection has generated a variety of adaptations used presumably to convince choosy females of male sexual suitability and/or deter rival males from occupying resources. The wide range of ulidiid behaviors, many of which resemble those of tephritids, and breeding sites, most of which are dissimilar to those of tephritids, seem to make them a particularly interesting group for comparison and contrast with fruit flies.

2.2.3 Platystomatidae

The Platystomatidae is the sister group of the remainder of the tephritid-containing subgroup (Tephritidae, Pyrgotidae, and Tachiniscidae), and differs from them by the largely saprophtyic feeding habits of its larvae (Figure 2.1; McAlpine 1989). Platystomatids breed in rotting tree trunks, bulbs, roots and fruit, dried flowers and dead grass stems, dung and fungus (Ferrar 1987). Mass graves dug in World War II sometimes produced prodigious numbers of *Platystoma lugubre* Robineau-Desvoidy (Hennig 1945, as cited in Ferrar 1987). Unlike ulidiids, a few species are predaceous; *Elassogaster linearis* (Walker) larvae are important predators of locust eggs in the Philippines (Greathead 1963) and *Euprosopia megastigma* McAlpine was found eating a scarab grub (McAlpine 1973a). Species of the cosmopolitan genus *Rivellia* typically attack the nitrogen-producing root nodules of legumes, occasionally reaching pest status (e.g., the soybean nodule fly *R. quadrifasciata* (Macquart); Koethe and Van Duyn 1988).

A striking component of platystomatid sexual behavior is the frequently encountered passing of fluids from the male's mouth to the female's (trophallaxis, Figure 2.3). The contents of these droplets are unknown. Alcock and Pyle (1979) suggest that the salivary substances passed in certain tephritids constitute a "food present," and that large investments of this sort would be presented in

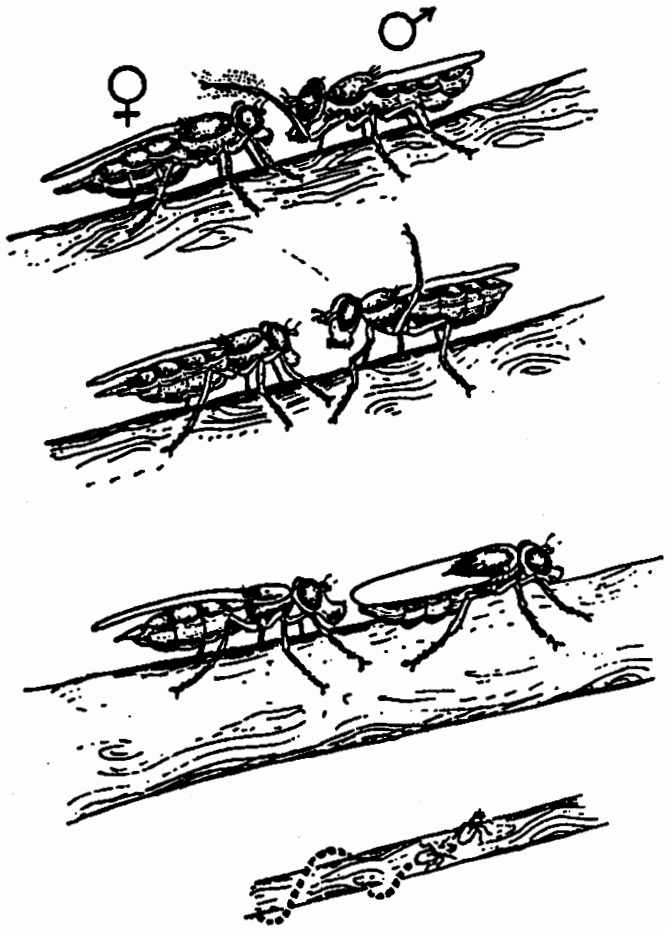

FIGURE 2.2 The courtship of the ulidiid *Physiphora demandata* is particularly complex, and contains such unusual features as the signals involving midlegs, and the female touching the male's abdomen with her extended proboscis and then "pulling" him in a spiral course backward along a twig. (From Alcock, J. and D.W. Pyle, *Z. Tierpsychol.* 49: 352–362, 1979. With permission.)

a "... courtship free from elaborate displays"; that is, a relatively large male investment would be valuable to the female and she would be selected to obtain the resource rather than waste opportunities by making fine precopulatory distinctions about the genetic qualities of potential mates. For example, male *Stenopa vulnerata* (Loew) stand next to froth mass deposits on leaves making the stylized wing movements similar to many (most?) Tephritidae (Novak and Foote 1975). Females are mounted as they arrive to feed on the male's cache. Similar behaviors are exhibited by *Icterica seriata* (Loew) (Foote 1967) and *Dirioxa pornia* (Walker) (Pritchard 1967, as *Rioxa pornia*).

However, platystomatid courtships containing trophallaxis often appear to be relatively complex, as is also the case in some more recently studied Tephritidae (see Headrick and Goeden 1994; Sivinski et al., Chapter 28). In *Rivella melliginis* (Fabricius) males fan their wings, sway their bodies, and rotate. After the arrival of the female they form the droplet and continue to wing fan. This is followed by foretarsal tapping, circling, and eventual mounting (McMichael et al. 1990). Females of *R. boscii* Robineau-Desvoidy run about in circles on leaves with the males in close pursuit (Piersol 1907). After mounting, male *R. boscii* produce multiple clear droplets which the female consumes, and in some cases he dismounts and run in circles around his mate while she consumes the regurgitant. He then remounts and produces another droplet (see also Michelmore's

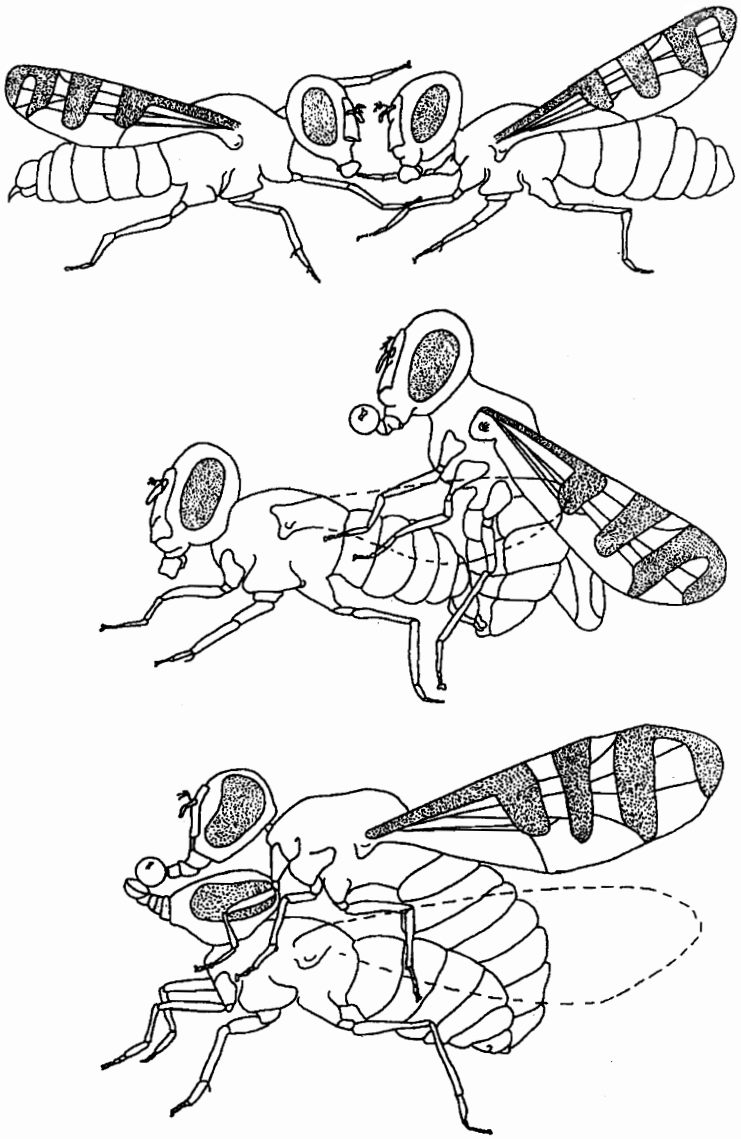

FIGURE 2.3 Trophallaxis occurs during mounting in *Rivellia melliginis*; transfers of fluids at this point in mating appear to be relatively common in the Platystomatidae. (From McMichael, B. et al., *Ann. Entomol. Soc. Am.* 83: 967–974, 1990. With permission.)

1928 description of trophallaxis in *Platystoma seminationis* (Fabricius)). McAlpine (1973b) observed three species of Australian *Euprosopia,* one of which presented the female with a regurgitant. One stage of courtship — the mounted stage prior to copulation where males of the other species stroke, tap, and comb the female — was indeed absent in this species, although the premounting stage seems to be well developed, with male displays of blackened foretarsi and tapping by the male's proboscis on the female's wings and abdomen.

A comparison of the regurgitant contents and courtship complexities in the "simple" tephritids and the Platystomatidae and "complex" Tephritidae might reveal different functions for trophallaxis. Those provided by some male tephritids seem to have a higher concentration of solids than those produced by Platystomatidae. In some *Eutreta* spp. the regurgitant is a frothy mass deposited on leaves, which collapses into a viscid mucus when probed with a needle (Stoltzfus and Foote 1965).

FIGURE 2.4 The eyes of a male *Achias* sp. from Papua, New Guinea occur on the ends of stalks, each of which is longer than the insect's body. (From Sivinski, J., *Fla. Entomol.* 80: 144–164, 1997. With permission.)

Froths are also produced by males of *S. vulnerata* and *I. seriata* (Novak and Foote 1975; Foote 1967). Foam ball "mating lures" are made by male *Afrocneros mundus* (Loew) (Oldroyd 1964), and male *Spathulina tristis* (Loew) transfer a viscous milky-white fluid to females *following* copulation (Freidberg 1982). While some tephritids produce a platystomatid-like clear droplet that is passed from labella to labella, this type of trophallaxis is relatively uncommon in fruit flies (Aluja et al. 1993; Headrick and Goeden 1994; see Sivinski et al., Chapter 28). If such viscous offerings are nutritionally more substantial than those of platystomatids, they could represent a greater reward to females which, given the validity of Alcock and Pyle's (1979) hypothesis, might ultimately lead to the relative simplification of courtships. There was no evidence in this case that the material influenced female longevity or fecundity, although the possible effects on the success of the offspring were not examined. However, trophallaxis increased female longevity and was associated with greater fecundity in the tephritid *A. striata* (Sánchez-Martínez 1998; Aluja et al., Chapter 15).

Other "wet" courtship activities in the Platystomatidae include males regurgitating on the thorax of mounted females and then imbibing their own fluids (*Euprosopia tenuicornis* Macquart), and the peculiar female production of an anal fluid which is ingested by the male prior to mounting (*E. anostigma* McAlpine) (McAlpine 1973b). In *E. anostigma* the males have a remarkable projection on the hind trochanter that is used to comb the "soft, downy pubescence" on tergite 3 of the female abdomen. The appearance of females that have been so combed "suggests that some liquid secretion contacts it during the combing process." Fluids that are not provided by males or not imbibed by females might be some sort of chemical or tactile signal, and may serve a different function than those that are consumed.

A number of platystomatid males have modification of their heads that are used in agonistic interactions with sexual rivals. These vary from broadening of the face into a surface used to push against the face of another male (McAlpine 1975), to extremely well-developed stalk eyes (e.g., *Achias* spp.; McAlpine 1979; Figure 2.4). The latter serve a similar role to the antlers projecting from the cheeks of tephritids in the genus *Phytalmia* (Wilkinson and Dodson 1997; Dodson, Chapter 8), a genus whose unusual breeding habits, oviposition into fallen timber rather than living plant tissue, is more typical of platystomatids. The parallel development of antlers and stalk eyes could be ascribed to similar opportunities to defend rare, discrete resources.

2.2.4 Pyrgotidae and Tachiniscidae

The pyrgotids are endoparasitoids of adult scarab beetles (or rarely Hymenoptera). They are further separated from the Tephritidae on the basis of their generally crepuscular or nocturnal habits and specialized ovipositors, both apparent adaptations for finding and then successfully penetrating the defenses of their largely nocturnal and armored hosts (exceptions include the diurnal *Peltodasia flaviseta* (Aldrich); Clausen et al. 1933, as *Adapsilia flaviseta*). Typically, female flies wait in the vicinity of feeding beetles for the host to take flight. The fly then pounces on the scarab, pierces the soft dorsal surface of the abdomen, and falls with the host to the ground where it lays one to several eggs (Forbes 1907). *Maenomenus ensifer* Bezzi oviposits in the anus of feeding hosts (Paramonov 1958). There are conflicting claims as to the effects of pyrgotid parasitism on populations of turf-feeding Scarabaeidae (e.g., Crocker et al. 1996), but the flies are, at least on some occasions,

locally abundant (e.g., Clausen et al. 1933). Male beetles are twice as likely as females to be parasitized by *P. flaviseta* (Clausen et al. 1933), a feature that might minimize their impact on pest populations.

There are few accounts of pyrgotid behavior, other than those involved with egg-laying. In general flies are captured at lights (Lago 1981), and actively hunting females are typically near or on the host plants of their prey (Clausen et al. 1933). As noted earlier, the presence of boldly patterned wings in a largely nocturnal family (Steyskal 1978) might not support the notion that the markings serve as intraspecific signals.

The Tachiniscidae are even more poorly known than the Pyrgotidae. Korneyev (Chapters 1 and 4) includes them in the Tephritidae, as the subfamily Tachiniscinae (this came to my attention only as this book was going to press). This is a tiny group. Only three genera with only four described species had been included (Ferrar 1987), although Korneyev (Chapter 4) includes five more genera. McAlpine (1989) also raised some doubt as to its familial status, but suggested that in the future it may be reclassified as a supergeneric taxon of the Pyrgotidae. Tachiniscids occur in South America, eastern Asia, and Africa. *Tachinisca* and *Bibundia* are burly, hairy flies that resemble tachinids, while *Tachiniscidia* mimic vespid wasps. The only host record is for a *Bibundia* sp. which emerged from the pupae of two species of African Saturniidae (Roberts 1969, as cited in Ferrar 1987). Apparently, nothing is known of the sexual behaviors of any tachiniscid genera.

2.2.5 Richardiidae, Pallopteridae, and Piophilidae

The third monophyletic group within the Tephritoidea consists of the Richardiidae, Pallopteridae, and Piophilidae (Figure 2.1; but also see Korneyev, Chapter 1, regarding the Richardiidae). The Richardiidae is considered the most generalized family within the subgroup, and is distinguished by heavily spinose hind femora, strong bristles on the second abdominal tergite, reductions in features of the male genitalia (the phallapodeme, gonopods, and parameres), and the presence of only two spermathecae (McAlpine 1989). The few breeding records suggest a larval diet of rotting vegetable matter, rotting fruit, decaying trunks, and flowers (Ferrar 1987). The ~30 genera are essentially restricted to the neotropics, with only eight species extending as far north as the United States.

Recently, interest has focused on the possibility of male genitalia having a communicative role; that is, the various projections, flanges, and enlargements of the aedeagus or phallus in certain insects may have evolved as tactile displays, perhaps through "Fisherian" runaway sexual selection (e.g., Eberhard 1996). A condition in females that would promote this kind of male display is the postcopulatory ability to choose which ejaculates will be used to fertilize eggs. Thus, a genitalic display provided during copulation would still be useful to a choosy female sampling various potential sires for her offspring. One means of doing this is to store sperm from different males in different spermathecae and preferentially use those from certain locations. For example, in the yellow dung fly, *Scathophaga stercoraria* (L.), sperm from larger males are stored separately and used more often to fertilize eggs (Ward 1993). Reductions in the Richardiidae of both phallic structures and the number of spermathecae (from three to two) may reflect less postcopulatory female choice and diminished male genitalic displays. Comparisons of sperm usage, genital complexity, and courtship in richardiids with some of the better-endowed tephritids may be particularly revealing. Fruit flies have a wide range of reproductive morphologies; for example, females of various *Rhagoletis* species have two or three spermathecae and *Oedicarena* species have four (Foote et al. 1993).

The Richardiidae are yet another tephritoid family containing stalk-eyed species (Wilkinson and Dodson 1997), and again offer opportunities to correlate breeding habits with the presence of these extraordinary male adaptations. A considerable sexual dimorphism in size in *Omomyia hirsuta* Coquillett is described by Barber (1908): "To these moist spots [on wood] came flies in large numbers, apparently two species, one of which was large, 6 mm in length, yellowish, covered with long yellowish hairs. The other was much smaller, black, shiny, with a distinct dark spot near the tip of the wing. The large wooly one appeared very aggressive, alighting often upon the black, shiny one and with his wooly legs outspread so as to hide his captive completely he would run

about on the moist wood as if he were a single specimen. But at last I saw a very small wooly specimen alight upon a large shiny black one and in this case saw copulation take place. Then the true state of affairs dawned upon me." Other richardiids (e.g., *Beebeomyia* sp.) also mate on or near host plants (Seifert and Seifert 1976).

The Pallopteridae are a small family of 52 species (+ 3 fossil species from Baltic amber). They occur mainly in the Palaearctic and Nearctic Regions with a scattering of species as far disjunct as the Falkland Islands, New Zealand, and Israel (Ferrar 1987). Unlike the Richardiidae, the parameres of male pallopterids are large and strongly sclerotized. In general, they infest shoots and stems of herbaceous plants, or live under bark, often in association with wood-boring Coleoptera. As with the Lonchaeidae, there is some question about the actual diet of the larvae living under bark. Some are clearly predaceous (Morge 1958, as cited in Ferrar 1987), but others have been collected in tree trunks with no evidence of beetles being present (Morge 1956, as cited in Ferrar 1987). Larvae of *Palloptera umbellatarum* (Fabricius) occupy the galls produced by tephritids in composite flowerheads, where they may be secondary consumers of the gall tissue (Niblett 1946). If this results in similar distributions of oviposition opportunities for both the tephritid and the pallopterid females, there may be a chance to examine further the relationship between resource distributions and mating system evolution (see previous section on Lonchaeidae). McAlpine (1989) notes that in the Pallopteridae the "habit of vibrating wings during sexual excitement [is] strongly developed," a characteristic they share with many tephritids (Sivinski et al. 1984; Aluja et al., Chapter 15; Sivinski et al., Chapter 28).

The Piophilidae, consisting of 71 species in 23 genera, is another relatively small family, and is the sister group of the Pallopteridae (Figure 2.1). The subfamily Neottiophilinae is composed of three species, one of which, *Neottiophilum praeustum* (Meigen), lives in birds' nests where larvae feed ectoparasitically on the blood of nestlings (Hutson 1978). Piophilinae develop in a variety of decaying materials, ranging from rotting leaves to the bones of whales to human corpses (including pupae found in a 2000-year-old Egyptian mummy; Cockburn et al. 1975). Because of their feeding habits and the ability of the larvae to flip themselves considerable distances, the maggots are sometimes called "bone-skippers." *Piophila casei* (L.), the cosmopolitan "cheese-skipper," has long been a major problem in human foods. Larvae feed deep inside such things as hams and cheeses with little outward sign of infestation. Not surprisingly, *P. casei* is a leading cause of human myiasis, and is the most common insect found in the human intestine (James 1947).

Species of *Protopiophila* occasionally occur together on a single piece of cervid carrion, where males of *P. litigata* Bonduriansky and *P. latipes* (Meigen) will unsuccessfully attempt heterospecific copulations (Bonduriansky 1995). However, male distributions and sexual behaviors in the two species are generally quite different. *Protopiophila litigata* larvae develop in the porous matrix of discarded cervid antlers. Some males defend aggregated territories on the upward surface of moose antlers, and remain coupled to females who later move toward oviposition sites following insemination. Other males position themselves near oviposition sites where they attempt to dislodge coupled males. Males of *P. latipes* fight with one another in and on corpses where females come to mate and lay eggs. They do not engage in mate guarding. Comparison of resource distributions in the two species may reveal the different selective pressures that have resulted in their behavioral divergence. (Is it important that discarded antlers are apt to be more abundant, persistent, smaller, and seasonally occurring than corpses? See similar patterns in Tephritidae of distinct mating behaviors on different parts of host plants in Headrick and Goeden, Chapter 25.)

Males of *Centrophlebomyia furcata* (Fabricius) are considerably larger than females, an atypical condition in the Tephritoidea and one shared with the previously mentioned richardiid *Omomyia hirsuta* (see Dodson, Chapter 8). Neither species engages in elaborate courtships, but both are described as "covering" their mates, presumably to prevent access to other males (Freidberg 1981). These mating systems may have evolved in response to the predictable nature of females at rare discrete resources (pockets of decay in wood and carcasses). The sexual dimorphism of *Amphipogon* spp. suggests interesting signaling/agonistic/courtship behaviors. Males have a long "beard" of

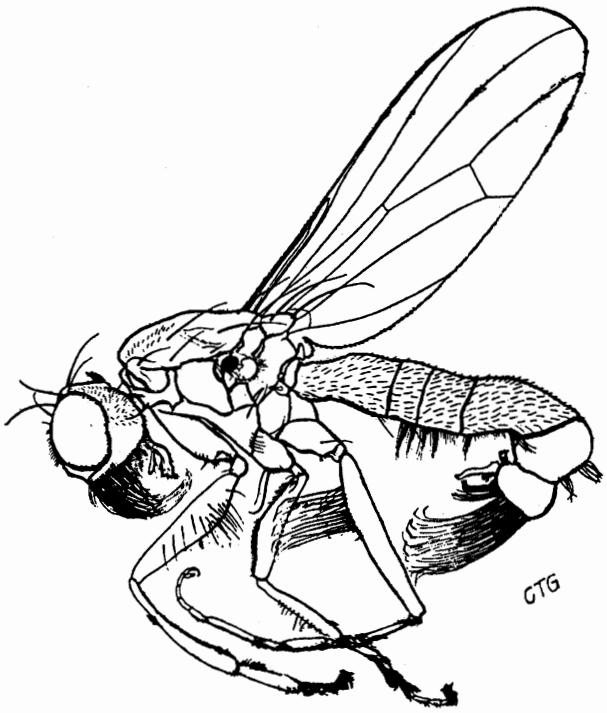

FIGURE 2.5 The males of the "bearded flies," *Amphipogon* spp. (Pilophidae), are considerably more hirsute than the females. (From Cole, F., *The Flies of Western North America,* University of California Press, Berkeley, 1969. With permission.)

curved and crinkly bristles, and swollen femora "adorned with clumps of setula, bristles and hairs" (McAlpine 1977; Figure 2.5). The hind leg is particularly elaborate, with additional spines, distortions, and setae. Larvae develop in fungi, but the role of the peculiar male pelage is unknown.

2.3 CONCLUSIONS AND FUTURE RESEARCH NEEDS

2.3.1 Sexual Selection in the Tephritoidea

There are 64 families of acalyptrate Diptera; in eight of these, some species (particularly the males of some species), bear eye-stalks and in five families males have "antlers" (Wilkinson and Dodson 1997). Four of the eight families with eye-stalks and three of the five with antlers are tephritoids, which suggests a particularly rich history of intrasexual selection within the superfamily. Ornaments used in courtships are likewise abundant in the Tephritoidea (Sivinski 1997). What might account for this concentration of elaborate (and presumably expensive) communication devices? Some characteristics that might bear examination are:

1. The relatively large size of many tephritoids relative to many other acalyptrates. Larger size might mean an increased ability for males to control access by females and sexual rivals to a resource. All other things being equal, large size reduces the numbers of offspring that can develop in a particular resource and so limits the number of opportunities for females to oviposit into it. This, in turn, would tend to make the resource more valuable to foraging females, and this could have consequences for the practicality of female mate choice.

2. The appearance of behavioral richness is due to chance. Perhaps any particular adaptation is more likely to occur in larger families, such as the Tephritidae with 4000+ species (although the Richardiidae with only ~30 genera have males with both stalk eyes or antlers).

3. Fisherian runaway sexual selection may be more likely to occur where females have the time to sample male displays and the capacity to remember the range of variation in displays. Long life and good memory allows females to choose the most extreme examples within the pool of potential mates. Alexander et al. (1997) have argued that these characteristics are rare in insects and that complex courtships and ornaments would more likely be due to "arms races" between choosy females and males advertising actual qualities than to Fisherian selection. The evidence supporting this argument is debatable (Eberhard 1997); however, it may be that long-lived insects with good memories are particularly "preadapted" to bouts of runaway sexual selection, and that extravagant signals resulting from Fisherian selection could accumulate in such taxa. Certain tephritids can be extremely long lived for flies; for example, *Anastrepha suspensa* (Loew) lives up to 1 year in the laboratory (Sivinski 1994), but at present little is known about the relative quality of their memories.

2.3.2 Opportunities for Comparative Studies

The similarities and differences among Tephritoidea provide an extensive pool of subjects for use in comparative studies that center on tephritid behaviors. Some of the problems in the evolution of fruit fly behavior that might be addressed by a consideration of related families are reviewed below.

1. Wing patterns and wing movements are common in the tephritids, but except for some cases of spider or wasp mimicry, their purpose, particularly their sexual function (if any), is obscure. The absence of wing markings in the Lonchaeidae, the only family that regularly forms aerial mating swarms, the presence of wing markings in the largely nocturnal Pyrgotidae, and the prevalence of wing vibrations in sexually excited Pallopteridae may offer opportunities to form hypotheses about the evolution of this striking phenomenon.

2. There has been considerable interest in the evolution of mating aggregations in the Tephritidae, and how males and females perform within leks. Swarming by the Lonchaeidae offers an alternative aggregated mating system to compare and contrast with fruit fly leks. Investigations into lonchaeid larval resource distributions, which in some instances seem to parallel that of lekking tephritids, might offer insights into why males aggregate, and once aggregated, why some swarm and others lek.

3. The Ulidiidae have many complex intersexual and intrasexual signals reminiscent of the Tephritidae. However, their breeding habits are very different, as they largely oviposit in decaying plant material rather than live plants. Resource distribution over space and time has been implicated in the evolution of complexity in courtships and agonistic encounters. These different resource sets would permit comparative tests that are more independent of the nature of the resource, and allow more confidence to be placed on the distributional characteristics of the resource.

4. While the Ulidiidae, and other tephritoid families, share some courtship behaviors with Tephritidae, there are also differences, such as the male mouthing of the extended aculeus. Do these differences reflect different sensory systems, different types of information passed by advertising males to choosy females, or are they evidence of Fisherian sexual selection leading to an arbitrary distribution of displays within and between taxa?

5. Platystomatid courtships often include trophallaxis, but the materials passed from males to females seems to be of a different nature than those transferred by many tephritids; they are described as clearer and less viscous than the froths commonly produced by tephritids. In addition, the courtships of platystomatids that include trophallaxis may be more complex than those performed by males of some (but not all) tephritids with oral secretions. This correlation may represent a greater investment by these male tephritids in their fluids and foams.

6. Male genitalia may have a role in communication as well as being organs of insemination; that is, they may be tactile displays that are judged by females who may make decisions about the paternity of their offspring after sampling multiple sexual partners. One means by which females

could exercise control of different ejaculates would be to sort them into different spermathecae. In the Richardiidae there is both a simplification of male genitalia and a reduction in the number of spermathecae. Does this loss of complexity reflect a lesser role for male genitalic displays and female sperm control? If so, can simplification in the Richardiidae help illuminate the evolution of the broad range of phallic complexities and spermathecal numbers in the Tephritidae?

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Fruit Flies (Tephritidae): Phylogeny and Evolution of Behavior

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