

## ORNAMENTS IN THE DIPTERA

JOHN SIVINSKI

USDA, ARS, Center for Medical, Agricultural and Veterinary Entomology  
Gainesville, FL 32604

## ABSTRACT

Occasionally, flies bear sexually dimorphic structures (ornaments) that are used, or are presumed to be used, in courtships or in aggressive interactions with sexual rivals. These are reviewed, beginning with projections from the head, continuing through elaborations of the legs and finishing with gigantism of the genitalia. Several functions for ornaments are considered, including advertisement of genetic properties, subversion of female mate choice and "runaway" sexual selection. Neither the type of ornament nor the degree of elaboration necessarily indicates which of the above processes is responsible for a particular ornament. Resource distribution and the resulting possibilities for resource defense and mate choice explain the occurrence of ornaments in some species. The phyletic distribution of ornaments may reflect foraging behaviors and the type of substrates upon which courtships occur.

Key Words: sexual selection, territoriality, female mate choice, arms races

## RESUMEN

Ocasionalmente, las moscas presentan estructuras sexuales dimórficas (ornamentos) que son utilizados o se cree sean utilizadas en el cortejo sexual o en interacciones agresivas con sus rivales sexuales. Dichas estructuras han sido evaluadas, comenzando con proyecciones de la cabeza, continuando con las estructuras elaboradas de las extremidades y terminando con el gigantismo de los genitales. Se han considerado distintas funciones para dichos ornamentos, incluyendo la promoción de sus propiedades genéticas, subversión de la elección de la hembra por aparearse, y el rehusarse a la selección sexual. Tanto el tipo de ornamento como el grado de elaboración no necesariamente indicaron cual de los procesos mencionados es el responsable de un ornamento en particular. La distribución de los recursos y la posibilidad resultante de un recurso de defensa y de elección de apareamiento pudieran explicar la aparición de ornamentos en algunas especies. La distribución filial evolutiva de los ornamentos pueden reflejar comportamientos relacionados con la búsqueda del alimento y con el tipo de sustratos sobre los cuales el cortejo sexual se lleva cabo.

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In general, the body shapes of flies fall into a few familiar categories, ranging from the willowy (e.g., Tipulidae) to the robust (e.g., Muscidae). Sporadically added onto these ordinary forms are extraordinary elaborations apparently fashioned by sexual selection. These have been called "ornaments," but it is useful to think of them as "organs of propaganda," designed to communicate with, and manipulate, potential mates and/or sexual rivals (c.f., Krebs & Dawkins 1978). In considering the ornaments of Diptera, first I survey their types and locations, starting with the head and working back to the genitalia. Then I will address whether the nature of ornaments provides clues to their "messages" and for whom the messages are intended. Finally, I attempt to correlate certain forms of decoration with different types of mating systems in various taxa of flies.

## I. THE HEAD

## A. Eyes

Sexual dimorphism of the eyes is commonplace in the Diptera, but ornamented eyes are rare. In order to make this distinction clear, the term "ornament" needs to be clarified. Males flies, particularly those that swarm, often have larger eyes with portions modified to locate the motions of incoming females (e.g., Sivinski & Petersson 1996). However, this sexual difference does not constitute ornamentation. For one thing, these dimorphic eyes are not suspected of being signaling devices. Colors and patterns, common in eyes in families such as Tabanidae, Dolichopodidae and Tephritidae, and which could act as signals, will not be considered ornaments either. Rather, ornaments will be defined, perhaps somewhat arbitrarily, as elaborated or novel structures, sculptures rather than paintings. An example of ornate eyes are those of the male Brazilian drosophilid *Zygotricha dispar* Wiedemann (Fig. 1b). They are much enlarged, and prolonged into sharpened horns that resemble those of a water buffalo (Bristowe 1925). In certain congeners, the tip of the eye curls like a ram's horn (Grimaldi 1987; Grimaldi & Fenster 1989).

## B. Extensions of the Head Capsule (Stalk-eyes and Antlers)

In eight acalypterate families, male's heads, and occasionally female's heads, are sometimes stretched laterally until the eyes are supported at the ends of remarkable "stalks" (Fig. 1a; Wilkinson & Dodson 1996). There is a considerable literature regarding the behavior of stalk-eyed Diopsidae that will be addressed when the significance of ornaments is discussed (e.g., Burkhardt & de la Motte 1983; de la Motte & Burkhardt 1983; Shillito 1960, 1976; Wilkinson 1993; Wilkinson & Dodson 1996).

Antlers, projections from the head capsule, occur, to one extent or another, in five families of flies (Wilkinson & Dodson 1996). Those of the tephritid genus *Phytalmia* originate under the eyes and are by far the most elaborate (Fig. 1c; see McAlpine & Schneider 1978; Schneider 1993). In his classic "The Malay Archipelago", Wallace (1869) describes his collection of four species from New Guinea: "... these horns (of *P. cervicornis* Gerstaecker) are nearly as long as the body, having two branches, with small snags near their bifurcation, so as to resemble the horns of a stag. They are black, with the tips pale ... the eyes (when alive) are violet and green. ... The horns (of *P. megalotis* Gerstaecker (= wallacei)) are about one third the length of the insect, broad, flat, and of an elongated triangular form. They are of a beautiful pink color, edged with black, and with a pale central stripe. The front of the head is also pink, and the eyes violet pink, with a green stripe across them, giving the insect a very elegant and singular appearance. ... The horns (of *P. alcicornis* (Saunders)) are very remarkable, being suddenly dilated into a flat plate, strongly toothed round the outer margin, and resembling the horns of an elk (*moose*) ... the head (of *P. brevicornis* (Saunders)) is compressed and dilated laterally, with very small, flat horns ..."

## C. Mouthparts and Face

Mouthparts are occasionally ornamented in the Dolichopodidae. Males of the tiny *Chrysotus pallipes* Loew have much enlarged labial palps (see Van Duzee 1924), which emit silver flashes as males signal from the surface of leaves (Sivinski 1988a). The expanded gold-silver palpi of the Hawaiian *C. pallidipalpus* Van Duzee reflect light as males pursue females (Parmenter 1952). The palpi of males in the closely re-

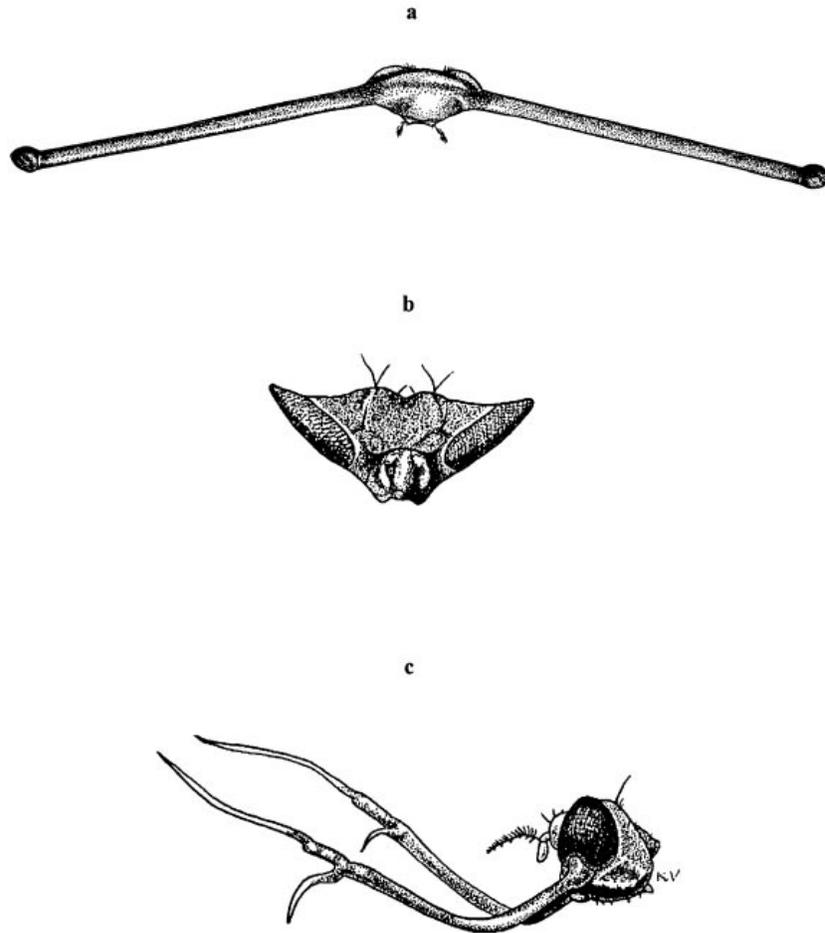


Fig. 1. Projections from the heads of acalypterate flies:

a) Stalk-eyes on a male *Achias* sp. (dorsal view), a large platystomatid fly from New Guinea. Similar projections in diopsid flies are perceived as signals by both males and females in the contexts of aggression and mate choice respectively.

b) The head (frontal view) of a male drosophilid, *Zygotricha dispar*, a tiny, but pugnacious, fly from Brazil that uses its horn-like eyes in intrasexual combats and perhaps as an advertisement of size directed to potential mates and rivals.

c) The antlered head (lateral view) of a male *Phytalmia cervicornis*, a large and aggressive tephritid fly from the rain forests of New Guinea where males defend oviposition sites from other males and mate with females that come to lay eggs.

lated genus *Asyndetus* are also sometimes ornate. Those of *A. flavipes* Van Duzee are bright yellow and covered with long yellow hairs (Van Duzee 1932). A male of *Aphrosylus raptor* Walker, searching for mates on seaweed covered rocks, flashes his large silver palpi "as he swings his shoulders and head in his stride" (Parmenter 1952). Silver reflections are found on the elongated faces of certain male dolichopodids. In *Poly-*

*medon* spp. the face extends to form a "plate or ribbon" that hangs down over the proboscis (Van Duzee 1927).

#### D. Setae

Male tephritids often have highly modified setae. Some species of *Ceratitis*, tephritids that include the infamous Mediterranean fruit fly, *C. capitata* (Wiedemann), bear orbital setae on the face above the antennae. These hairs can be strikingly long; those of *C. caetrata* Munro reach more than twice the width of the head in length (Munro 1949). The setae, tipped with either black or white expansions (Bezzi 1924), are "waved" about during courtships (e.g., Arita & Kaneshiro 1989).

#### E. Antennae

Many flies, such as mosquitoes and chironomid midges, bear sexually dimorphic antennae (see Sivinski & Petersson 1996). In most cases, these differences result from one sex, usually the male, being adapted to perceive pheromones or acoustic cues. However, some antennae appear to be modified to emit a signal of their own. Chloropids are rarely dimorphic, but males of the sole species of *Gampsocera* in Hawaii have various unique markings and thickened and black aristae (Kanmiya 1989). Males of *Camposella insignata* Cole, an acrocerid from Ecuador, have "an astonishing development" of the third antennal segment that renders it enlarged, flattened and patterned (Cole 1969). Dolichopodid males sometime have elongated antennae which are plumed at the tip (e.g., *Tachytrechus* spp. (Greene 1922)), or in the case of *T. binodatus* Loew, plumed at the tip and in the middle. Tachinids commonly have sexually dimorphic antennae. Some, such as those of male *Lispidae triangularis* Aldrich which contain a much broadened third segment, seem decoratively large (Aldrich 1929). Exaggerated and plumed antennae occur in some tephritids (White 1988).

## II. THE THORAX

#### A. Forelegs

Various dolichopodids wave and/or touch potential mates with ornamented forelegs (Gruhl 1924; Fig. 2a). Males of *Neurigonia quadrifasciata* Fab. and *Poecilobothrus nobilitatus* (L.) approach a female from the rear and reaching over her, curve their plumed tarsi over her head (Smith 1959). They then wave their tarsi alternately, one over each eye. Male *Dolichopus omnivorax* Van Duzee wait for foraging females on floating vegetation (Steyskal 1938). When a potential mate is found, he approaches with his forelegs extended laterally. The tibiae hang down and forward, displaying a large black pad on the terminal tarsi. If the female remains still, the male's advance will bring the pads almost into contact with her eyes. Sometimes the front femora of dolichopodids are decorated. Those of *Tachytrechus olympiae* Aldrich are swollen and marked with a dark spot (Greene 1922). The pinnacle of foreleg ornamentation in the Dolichopodidae is occupied by *Campsicnemus magius* (Loew), whose limbs are so swollen, pendant, hairy and bizarre that the dipterist Gerstaecker accused his colleague Loew of describing a species from a specimen deformed by fungus (Verrall 1905; Lundbeck 1912; Fig. 2b). Some male asilids in the genera *Heteropogon* and *Cryptopogon* bear decorated front tarsi (Bromley 1933; Wilcox & Martin 1936). Curiously, only American species of the latter genus, and not those from Europe, have tarsal elaborations (Hull 1962). In addition to waving their ornaments, robber fly males

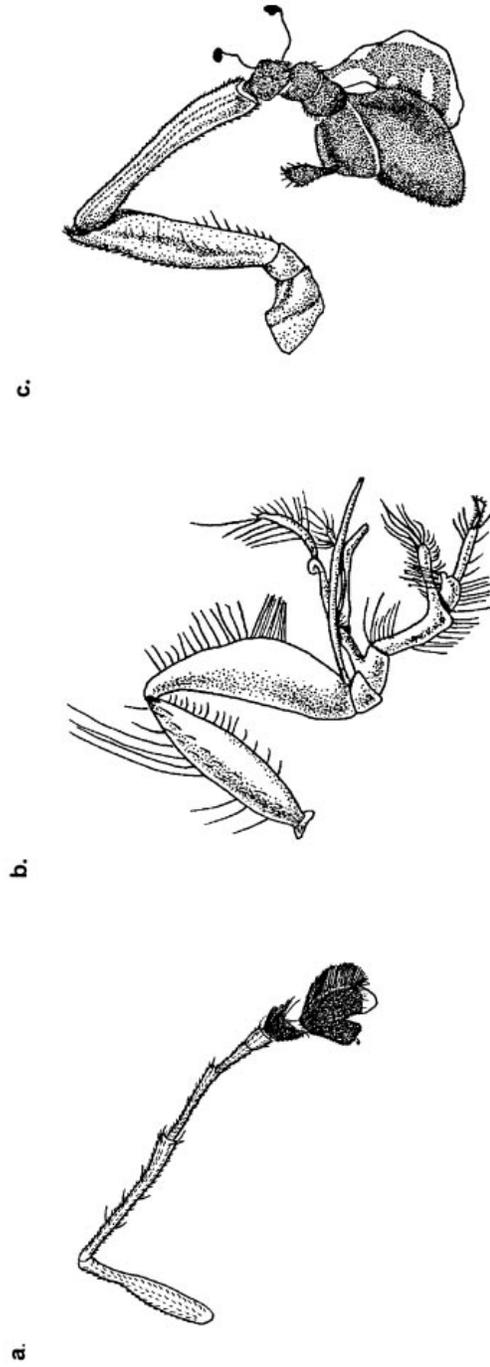


Fig. 2. Ornaments on the legs of flies:

- a) The front legs of the dolichopodid *Dolichopus pulchrimanus* bear a dark plume of setae and what appears to be a reflector.
- b) The front legs of the paleoarctic dolichopodid *Campsicnemus magius* are contorted into one of the more elaborate male ornaments to be found in the Diptera.
- c) The hind legs of *Calotarsa insignis*, a platypezid from North America, are drooped below swarming males in flight. They have reflective patches and glitter in the sunlight.

may stroke the female's head and thorax. It is not uncommon for male syrphids to have dilated front legs, spotted with clumps of setae (e.g., Verrall 1901). This tendency achieves the fantastic in the complex decorations of the west African species *Tityusia regulas* Hull (Hull 1937). The fore tibiae are "enormously thickened, grooved, twisted and distorted" with an "extremely long, extremely matted" dark pile of fringe. The fore tarsi are "extravagantly flattened . . . the lateral edges of the second, third and fourth segments prolonged into narrow, down curving lobes." Among acalypterates, the yellow front legs of the tephritid *Ectopomyia baculigera* bear a large down-pointing projection on the femur, while the front basitarsis of the male *Euphranta maculifemur* is broadened and concave (Hardy 1973).

#### B. Midlegs

A mosquito, *Sabethes cyaneus* (F.), bears elongated, iridescent blue and gold scales that transform the midlegs into "paddles" (Hancock et al. 1990; smaller setae occur on the other legs as well; *S. tarsus* Dyar & Knab and some other congeners also bears leg paddles; Fig. 3; smaller setal expansions occur on the legs of certain *Wyeomyia* spp.). Males fly toward resting females with their ornate legs held perpendicular to their bodies. After landing on twigs, they suspend themselves by their forelegs, then swing and wave their paddles. Undulating waving motions persist after the initial coupling, until the genitalia are fully clasped. "Wagging," during which the midlegs rise and fall, continues throughout the copulation (see Eberhard 1994 for a discussion of courtship during mating). Remarkable middle tarsi occur in males of the empidid *Rhamphomyia scaurissima* Wheeler (Wheeler 1896). The first joint consists of a globular base beset with prominent hairs and a scale-like appendage, the second is large and symmetrical and has a club-shaped extension clothed in a pencil of long hairs, and the third is enormously enlarged into a boat-shaped structure. A few tephritids of the genus *Ceratitis* have either mid and/or hindlegs expanded and feathered along the margins (Silvestri 1914). Male dolichopodids sometimes employ ornate midtarsi in courtship displays (e.g., Qvick 1984). Those of *Sympycnus cuprinus* are dilated and fringed with black bristles (Cole 1969; see also Harmston & Knowlton 1943). The midlegs of certain species of *Campsicnemus* are much more elaborate (e.g., Curran 1933; Harmston & Knowlton 1942). Robber flies of the genus *Cryptopogon* often bear tufts of black or silver hairs on the tarsi of both the front and middle legs (Wilcox & Martin 1936). In general, ornaments upon the midlegs of flies appear to be rare relative to forelegs (Wheeler 1896).

#### C. Hindlegs

Some of the most amazing ornaments in the Diptera adorn males of the platypezid genus *Calotarsa* (Fig. 2c). Three species are found in widely separated North American locations. Their enlarged hindlegs bear a variety of curious projections and glittering aluminum-colored flags (Kessel 1963). Snow (1884) noted how swarming males ". . . allow their hindfeet to hang heavily downward and look as if they were carrying some heavy burden." There is a degree of convergence between the design of the posterior tarsi in *Calotarsa* and the fore tarsi of the syrphid *T. regulus* (Hull 1937; see section on front legs), but the hover fly has a peculiarity upon its hind tarsi as well, "an enormous brush of dark, matted hair." Conspicuous hairs decorate the hind tarsi of certain asilids (Wilcox & Martin 1936). The entire hindleg of males in the genus *La-godias* is fringed in long flattened setae (Hull 1962). Male anthomyids sometimes have patterned legs with elongated setae. The hind tibia of *Rhynchtrichops aculeipes*



Fig. 3. The middle leg of the male mosquito *Sabethes cyaneus* ends in an iridescent blue, purple and gold plume made up of flattened setae. These feather like objects are employed in the various displays that make up the only complex courtship described in the Culicidae.

Zett. has an odd projection that renders it reminiscent of a wishbone (Seguy 1923). Males of the dolichopodid genus *Scellus* are remarkable not only for their caudal ribbon-like projections (see below), but for the enlarged corkscrew-like spines and long hairs that project from the hindlegs (e.g., Greene 1924). If these are ornaments, and not a grooming apparatus for the abdominal projections (or something else), their being on the hindlegs is noteworthy. It is my impression that dolichopodid hindlegs bear fewer peculiar modifications than the midlegs, which in turn are less often ornamented than the front (e.g., Van Duzee & Curran 1934). Perhaps the presence of a caudal appendage creates a posterior focus of attention in females, into which the hindlegs can be profitably included. Female empidids of the genus *Rhamphomyia* have large scale-like setae on their legs. These are held away from the body while in flight and glitter in the light (Evans 1988).

#### D. Wings

Like the antennae, wings are commonly sexually dimorphic in size, although this is often because of adaptations to different flight requirements (e.g., Sivinski & Dodson 1992). Wings are sometimes dimorphically marked, or have sexually distinct venation (e.g., Alexander 1936; Kanmiya 1989), and serve important roles in courtships and aggressive interactions (e.g., Land 1993; Lunau 1992), but, for present purposes, these are not considered to be ornamented. Possible exceptions occur among the oddly shaped, rounded and patterned wings of certain female empidids who participate in sex-role reversed swarms (see Cumming 1994) and the combined peculiar wings and modified tarsi of the dolichopodid *Collinellula magistri* Aldrich (Aldrich 1932).

### III. THE ABDOMEN

#### A. Enlargement of the Abdomen

Females of the empidid *Rhamphomyia longicaudata* Loew inflate their abdomens with air until the pleural membranes are greatly stretched and collapse when punctured (Steyskal 1941; Newkirk 1970). Similarly, the membrane of the third abdominal segment in females of the New Zealand species *Hilara flavinceris* Miller forms an extensible bladder that stands out to the sides (Miller 1923). Cumming's (1994) examination of the extensive holdings of Empididae in the Canadian National Collection of Insects and Arachnids (Ottawa) revealed that 29% of the described species of *Rhamphomyia* and 26% of *Empis* (583 species total) had females with pinnate scales on the legs or abdomen and pleural sacs. Male abdomens may sometimes be modified as well; that of the swarming Ugandan stratiomyid *Platyna hastata* F. is expanded and flattened, and "... brilliantly reflects a white light. . . . The glistening appearance of the upper surface . . . is very striking" (Carpenter 1923). Unfortunately, no females were observed, or at the time had ever been collected, and a sexual dimorphism is only presumed.

#### B. Modified Glandular Projections

Females of the chironomid *Palpomyia brachalis* evert long glandular strings from their abdomens as they participate in sex-role reversed female swarms (Edwards 1920). These have been interpreted as pheromone organs, but their bright orange color contrasting with the black body suggests a visual role as well. Since similar tubes in other species of *Palpomyia* and the related genus *Bezia* are colorless, their great size may not be ornamental but a means of increasing surface area for pheromone dispersal.

### C. Caudal Ribbons

Males of the dolichopodid genus *Scellus* have odd, twisted, ribbon-like structures projecting from the dorsum of the abdomen (Green 1924). Some are as long as the abdomen itself, fringed and tufted with hairs, or tipped with a spoon-like enlargement. Often white in color, with black bases and yellow ends, their function is mysterious. These strange appendages may have evolved solely for communication, or perhaps they are ornate elaborations of structures that serve an additional purpose (pheromone dispersion?). In addition to long, twisted, reddish or orange-yellow ribbons, male *S. virago* Aldrich have enlarged fore tibia furnished with a large blunt protuberance and tufts of curly hairs on the middle tibia. Despite these multiple male ornaments, the female appears to be more sexually aggressive (Doane 1907); “. . . she seemed suddenly to become very much excited, now squatting low, now rising high and waving the wings frantically. The cause of this extra excitement was a male fly. . . He seemed to paying but little attention to her. . . (After) facing each other, going through the curious performance. . . The male then turned away and seemed about to leave, but the female quickly flew in front of him again and began her antics.”

### D. Modified setae

Males of the large ropalomerid *Scatophga gigantea* Aldrich have “very striking long, dense . . .” hair on their abdomens (Aldrich 1932). Tephritid fruit flies sometimes bear modified setae on the abdomen; e.g., males of *Trupanea brunnipennis* have a mass of strong yellowish bristles along the posterior margin of the 5<sup>th</sup> tergite (Hardy 1973). *Copiolepis quadrisquamosa* Enderlien is perhaps the most dramatically plumed tephritid (Enderlein 1920). It somewhat resembles the Birds of Paradise with which it shares habitats in New Britain and New Guinea.

### E. Genitalia

It has been argued that the notorious complexity of some male insect genitalia, including those of certain Diptera, is in fact ornamentation, but ornamentation on a tactile level (Eberhard 1985). Giant male genital regions in dolichopodids are employed in courtships prior to physical contact. A number of species carry enlarged terminalia (hypopygium) slung under the abdomen. In *Dolichopus omnivagus* this is raised and lowered during the male's courtship advance (Steyskal 1938). I observed a more dramatic effort by an unidentified male on the upper surface of a leaf. It raised itself up on its long legs, beat its wings and then lowered the hypopygium until it hung perpendicular to the body. At this point the genitalia began to slowly twirl. As in some other structures discussed previously, it is not clear whether the terminal segments are enlarged to send a message or if the great size serves a mechanical function and is secondarily used in courtships.

## WHAT DO ORNAMENTS “MEAN”?

### A. Size and Aggression in Horn-eyed, Stalk-eyed and Antlered Flies

The evolution of horn-eyes, stalk-eyes and antlers illustrates how organs of communication and manipulation might arise through aggression among members of the same sex. McAlpine (1979) offers a diabolical hypothesis of how a blunt instrument (the head) could evolve through deceit into a sophisticated piece of propaganda. Male flies often fight head to head. The broad head and abundant cheek bristles of the Aus-

tralian platystomadid *Pogonortalis doclea* (Walker) are used in such combats (McAlpine 1975). The enlarged and hairy surface area better applies force and prevents slippage. Bristles may even become interlocked to grip an opponent, a technique that may have been further perfected by the clusiid *Clusoides gladiator* McAlpine, whose males' facial vibrissae are spiraled (McAlpine 1976), perhaps to twist into those of a rival's. These elaborations serve as practical weapons, but are they organs of communication; i.e., are they ornaments? Perhaps not, but proceed one step further. Suppose, as is often the case, a smaller fly retreats from a confrontation after determining that his opponent is too large to successfully engage. If the size of the rival is assessed by the breadth of his head, as gauged by the degree of overlap between the two sets of eyes, then males can appear large and conquer psychologically by simply widening the head. As deceitfully widened heads become common, even further exaggeration is required to sustain a bluff and the resulting "arms race" pulls eyes farther and farther out until they are held at the ends of extraordinary stalks, each of which may be longer than the body (e.g., an 8 mm long male of an undescribed diopsid from Borneo supported eyestalks with a combined span of 20 mm; Burkhardt et al. 1994).

In the end though, there are practical conclusions to arms races. Accumulating expenses and increasing vulnerability may dictate the final state of an ornament. Perhaps truly extraordinary ornaments, such as stalked-eyes in certain *Achias* spp. (McAlpine 1994), are cases where selection has exploited every opportunity and no further mechanical demands can be made on the overall "fly design." Wilkinson & Dodson (1996) found the relationship between antler size and body size within *Phytalmia* spp. reached a plateau. At this point signals are no longer deceptive, they are genuine burdens that reflect the qualities of their bearers. Wilkinson & Dodson (1996) suggest that since there is a strong positive allometric correlation between body size and projections from the head, "(ornament) size is an honest indicator of overall size, which itself is a predictor of fighting success . . . (ornament) size could be used by males to assess an opponents fighting ability, thereby avoiding unnecessary contests." One might ask why body size should be advertised by an ornament that does not increase in size at the same rate as the actual body; i.e., why do larger males have proportionately longer projections? Positive allometry might allow more accurate judgements of size; i.e., since a small increase in body size results in a larger and more obvious increase in the ornament, "the projection span scale will be finer than the body length scale." Allometry might also suggest that the cost of stretching the head, in terms of energy and maintenance, does not increase at the same rate as that of enlarging legs and guts and the other sophisticated and enervated body parts that make up "size." If so, larger flies might spend a similar proportion of their resources to advertise their bulk as smaller individuals but obtain a relatively greater return on their advertising budget. Still another hypothesis for the existence of allometry is that larger individuals may be more likely to use force in their interactions with other males. As a consequence they might invest more in weapons and propaganda (see Green 1992).

Females in some diopsid species are found in groups associated with individual males. However, these harems in *Cyrtodiopsis whitei* are not the result of males excluding rivals, but of a female preference for males with long stalks (Burkhardt & de la Motte 1988). Allozyme markers have revealed that males with longer stalks sire relatively more offspring (Burkhardt et al. 1994). In *C. dalmanni*, females likewise prefer longer stalked males (Wilkinson & Reillo 1994). What may have originally been propaganda to intimidate rival males has come under scrutiny from females and is now used as a factor in mate choice.

Like eye-stalks, antlers are both weapons and symbols of prowess. Males of *Phytalmia mouldsi* clash by rising up on their legs and pushing hard against each other's remarkable heads, although the antlers themselves do not play a major role in

the battle (Moulds 1978). However, those whose horns are experimentally lengthened or shortened are respectively more and less likely to win fights (Dodson 1989). In addition, males with their horns removed are treated by their rivals like females (Wilkinson & Dodson 1996). Hence antlers serve, at least in part, as signaling organs. The massive antlers of *P. alicornis* are more involved with actual pushing.

#### B. Material Resources and Deception in the Empididae

Horns and stalks have been depicted as evolving through interactions among males (intrasexual selection), although females might come to prefer a particular state of ornamentation and influence its form. The ornaments considered from this point forward are presumed to have originated in a different context, that of interactions between the sexes, i.e., intersexual selection. They are employed, or are believed to be employed, in courtships or in attracting the opposite sex.

A number of male empidids present mates with insects they have killed or stolen from spider webs (e.g., Chvala 1976). Often these are the only animal meals females will have as adults. Female mate choice is sometimes based on this nuptial gift and in certain cases the importance of the gift is so great that a sex-role reversal takes place. Females swarm and choosey males examine a series of potential mates before feeding and inseminating a particular individual (Svensson et al. 1989). The addition of a resource to courtship has consequences for ornamentation. Both sexes have "goods," the nuptial gift of the male and the eggs of the female, that can be advertised to a potential "customer."

Male *Rhamphomyia scaurissima* have peculiar growths protruding from the mid-legs (Fig. 4a). I have found no behavioral records for *R. scaurissima*, but other species in the genus form swarms. Congeners provide females with a nuptial gift of a small dead insect which they hold in their legs (Downes 1970; Fig. 4b). Only males with a gift succeed in mating. Could this mass of swellings and projections deceitfully suggest a resource the insect doesn't have or exaggerate the size of one that it does?

On the other side of sexual bartering are females whose apparent fecundity might influence whether or not they obtain a valuable meal. Females of many *Rhamphomyia*, *Empis* and *Hilaria* species inflate their abdomens while participating in sex-role reversed swarms (Cumming 1994). It is tempting to think that such swellings may be exaggerated promises of fecundity directed toward males who provide a nuptial gift. Larger females are preferred by resource-providing males in other empidids (e.g., Svensson et al. 1989). Like stalk-eyes, abdominal enlargements may evolve into "honest advertisements" if only the largest females can fly with the most swollen abdomens. In *Rhamphomyia* species females bear glittering setae on their legs. When extended in flight these ornaments may call attention to the females' abdomens, as might the coloration of another empidid, an unidentified Alaskan species "garishly marked with an extensive silvery abdominal 'saddle' which flashes conspicuously as she crosses beams of sunlight." (Frohne 1959).

#### C. Good Genes, Manipulation and Runaway Selection

Some ornaments suggest original functions; the air-filled abdomens of female empidids may have been false advertisements of fecundity, just as stalk eyes exaggerated size and dangles from midlegs gave the impression that a male empidid has a nuptial gift. But putting these instances with perhaps more obvious histories aside, a number of very puzzling objects remain. Just why does stroking a female's head with tarsal plumes improve the reproductive success of a male robber fly? If simple species isola-

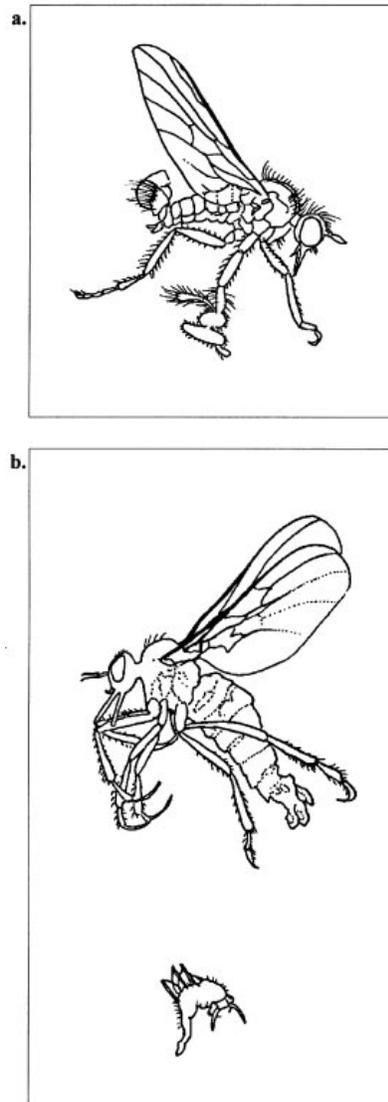


Fig. 4. A comparison of the appearance of two species of *Rhamphomyia*:  
 a) The middle legs of males of the empidid *R. scaurissima* end in a remarkable complex of swellings and projections (from Wheeler 1896).  
 b) These peculiarities are absent from the legs of *R. ursinella*. However, the ornaments of *R. scaurissima* might bear a resemblance to the more mundane species carrying a nuptial gift, such as the chironomid *Smittia* sp. (smaller insect figured below; from Downes 1970). Perhaps originally, ornamented males appeared to be holding a gift and so were allowed to copulate with females who would otherwise have mated only when provided with a prey item.

tion is involved in ornamentation, why are such decorations relatively uncommon? Are ornamented species in some particular danger of engaging in unprofitable hybridizations? The opposite is often the case (e.g., West-Eberhard 1984). The spectacular genus *Calotarsa*, for example, consists of three widely separated North American species, one so rare it appears to have never been recollected.

There are a number of other paths that might lead to ornamentation, any one of which could result in a world with only a single species being inhabited by ornamented animals.

1) The production and use of expensive and unwieldy growths may provide a potential mate (or sexual rival) with an estimate of genetic (or phenotypic) quality; i.e., the displayer has foraged well enough or avoided debilitating infections long enough or is big enough to put on his show (e.g., Sivinski 1988b). Body symmetry is a correlate of genetic quality and a trait preferred by choosing females in some animals (Moller 1992; Thornhill 1992; Watson & Thornhill 1994). The flags and feathers of some displays could test the genome's ability to produce symmetry.

2) The receiver may be manipulated by an ornament. Nervous systems are imperfect. A flaw in perception or information processing can be exploited by the behavior of others (cf. Dawkins 1982). For instance, a resting dragonfly can be "hypnotized" by tracing a narrowing spiral in the air. Such an event is presumably so rare that selection has not favored a brain resistant to the influence of a moving finger. Perhaps flaws in female nervous systems allow them to be approached and handled by rhythmically waving, plumed, or otherwise ornamented, males.

3) A female preference for extreme examples of a certain characteristic in a mate begins an episode of "runaway sexual selection." That is, when females prefer the most ornate male available, genes for both choosing the very elaborate (expressed in daughters, but present in both daughter and sons) and being very elaborate (expressed in sons, but present in both daughters and sons) can generate a sort of "chain reaction" self selection for the increasingly extreme. A lucid explanation of this complex procedure can be found in Dawkins (1986). This form of selection requires that females sample the range of male decoration and mate with the most ornate. It has been suggested that such mate comparisons are not typical of insects, who are presumed to have a limited time to acquire courtship experiences and little capacity to remember those that they had (Alexander et al. 1997). If so, perhaps only rare circumstances, where potential mates are compared simultaneously or where females have unusually good memories, give rise to the occasional "runaway monstrosity" (Sivinski & Petersson 1997).

Could these various kinds of "messages" be recognized by the nature of the ornament that carries them? This categorization may prove to be difficult. I can imagine many ornaments of the "puzzling" variety (those not originally exaggerating size or a resource) resulting from any of the above. The male robberfly rhythmically stroking the female's head with leg plumes could be displaying his coordination, seducing her "hypnotically," or satisfying her taste for an extreme in courtship.

Though similar *types of ornaments* could be derived from different types of selection, might the different types of selection generate different *degrees of ornamentation*? To the entomologist's eye not all ornaments are equally elaborate. Some dolichopodid legs seem to be practical semaphores, others appear contorted and absurd (Fig. 2a & b). Would advertisers of genetic quality tend to invest as much in their displays as participants in a "runaway" situation, or vice versa? Unfortunately, this to might be a difficult approach to finding meaning. Each type of selection could direct varying amounts of resources to ornaments, so that complexity and simplicity may not be indicative of particular sets of selection pressures. For example:

1) There are several explanations for variance in ornaments evolved to advertize "genetic quality." A simple ornament may sometimes be sufficient; i.e., there might be

types of messages that are just not improved by increased broadcasting. Genetic identity (species identification or lineage identification) is one possibility. Under some circumstances, mate choice based on symmetry might select for simplicity. If complexity can overwhelm perception and hide asymmetry, females may come to prefer simpler ornaments, clearly displayed.

However, there may be few such inherent limitations on how elaborate ornaments that reflect genetic quality can become. If an ornament is "improved" from the signaler's perspective by exaggeration, then potential mates or sexual rivals with new and higher criteria for what they find attractive or intimidating will be better adapted than "gullible" individuals with out-of-date tastes, and so on and so on (see discussion of stalk-eyes). An alternative to linked escalation of ornamentation and discrimination is selection for a new ornament that will, at least temporarily, be a more honest indicator of genetic quality (see also Iwasa & Pomiankowski 1994). Multiple male ornaments are commonly found in the Dolichopodidae (e.g., the genus *Scellus*; see above).

It is unlikely that all ornaments are equally burdensome or that all bearers of ornaments would have similar resources to spend on advertisement. Different limits would lead to variety in ornamentation. On the other hand, some signal systems may be relatively simple because they have not been in existence long enough for arms races to bring them to the brink of being maladaptive handicaps to their carriers.

2) Males may exploit weaknesses in female nervous systems, but females might evolve "immunity", and this could ultimately lead to interspecific differences in the elaborateness of male ornaments. If the subversion of females' ability to choose a mate has a sufficiently negative effect on their reproductive success, then flaws in their brains might be eventually corrected and the degeneration of their sexual control stopped. Males might then respond with more potent stimuli, escalating yet another arms race. Assuming different female susceptibilities and different costs to being manipulated, a range of ornamentation could develop in various males.

3) Where runaway sexual selection occurs (if it occurs) the ability of the receiver to discriminate differences in signals would influence the capacity to choose among mates, and eventually how far "taste" can dictate male ornamentation. The abilities of different males to bear the burdens of their "beauty" could also determine how elaborate any particular display may become. What is extreme in an aerial predator might appear simple in a fruit fly. Parenthetically, the male empidids who carry objects as diverse as flower petals (Hamm 1913) and silk balloons, (Kessel 1955; which sometimes, but not always, contain a prey item), into mating swarms may be using a disposable "ornament" that would not interfere with the other parts of their lives.

Another characteristic of an ornament that might help translate its meaning is the *variance* in the display among the individuals of a population. It has been suggested that when females choose a male trait in lekking species, "modifier genes" to generate variance in that trait might be selected as well (Pomiankowski & Moller 1995). The explanation is that the combination of the highest mean value of a character along with its greatest variance will produce the most extreme manifestations of that trait in the next generation. In both "runaway selections" and "arms races" extreme individuals can be the most successful (up to a point), perhaps enough so to make up for extremely unattractive sons that a large variance also produces. But again, an unusual degree of variance in an ornament could be due to either runaways and many of the hypothetical arms race causes we have considered. This unenlightening conclusion suggests that perhaps the best strategy is to consider the function of each ornament individually and not expect that the form of an ornament will immediately reveal its significance.

## Ornamentation and Mating Systems

Let us assume that ornate signals are advertisements of male (or less frequently, female) qualities directed to potential mates and / or sexual rivals. Do these organs of propaganda occur in any sort of pattern? Are they associated with certain behaviors and are these behaviors typical of particular mating systems?

There are circumstances where an individual can profitably advertise and situations where it cannot (Burk 1981; Prokopy 1980). One place where there is little profit in investing in an ornament is where females are predictably located at resources, (e.g., oviposition sites), and these resources are discrete, scattered and rare. Males can then wait by the resource and attempt to copulate with an arriving female. Under these conditions it might be more beneficial for her to immediately mate rather than spending time and energy choosing a particular male, all the while being distracted from exploiting the resource. Where there is little opportunity for females to choose, there is no reason for males to advertise (e.g., Sivinski 1984). If the resource is small enough for a male to exclude its rivals, then signals directed to competitors can evolve. Where males cannot predictably locate females by waiting by a resource (e.g., the resource is common relative to females), then the costs of mate choice are lower, females may be able to afford to discriminate among males, and males may compete for attention by producing signals.

Can this scheme explain the occurrence of ornaments in flies? Some instances seem to be textbook examples of the "resource distribution model of sexual selection". For example, antlered males of *Phytalmia* spp guard rare, scattered oviposition sites, "pin holes" in the freshly fallen trunks of particular trees. They dispute with rivals for control of the resource, through displays of their horns and combat, and females that attempt to use it must mate with the resident male (Dodson 1987, 1989). The elaborate leg decorations of *Calotarsa* and the facial setae of *Ceratitis*, which are presumably used to communicate with females, adorn males that participate in swarms and leks, respectively. These male aggregations are formed solely for the purpose of mating and in the absence of any of the resources females require (e.g., Sivinski & Petersson 1996). The sex life of many ornamented flies is unknown, and how well resource distribution explains ornamentation in general remains to be seen.

## THE PHYLETIC DISTRIBUTION OF ORNAMENTS

While resource distribution seems to be successful in explaining why ornaments have evolved in certain instances, there are puzzling phyletic patterns (Table 1). Eye-stalks and antlers are concentrated among the acalypterate families. Resource guarding is commonly described in acalypterates, but is also found in a number of other Diptera, including the calypterates which are conspicuous by the scarcity of their ornaments. Also puzzling is the apparent scarcity of elaborate ornaments displayed in acalypterate courtships (outside of the Tephritidae and related families). Mating behaviors are often complex and include movements of head and legs, organs ornamented in other taxa (e.g., section "Conclusion: the locations of ornaments"). Rather there seems to be a concentration of intersexually selected ornaments in the more primitive Brachycera.

There is considerable variance in the range of ornamentation within a family. Why are the Dolichopodidae so rich in decorations? Or perhaps even more curious, why does ornamentation sporadically evolve in otherwise ordinary appearing taxa? The complicated waving of huge blue leg paddles in *Sabethes* spp. make up the *only* courtships described in the Culicidae! Can resource distributions alone account for either

the commonness or the rarity of ornaments within various taxa? Are there other factors involved?

Why do dolichopodids seem to bear so many and such various ornaments, on antennae, faces, mouthparts, legs and abdomens? As predators, females may not be concentrated onto a small resource that males can control and this might encourage male advertisement. But other orthorrhaphous Brachycera, such as the similarly predaceous asilids and the closely related empidids, are only occasionally ornamented. One possible explanation is that dolichopodids, unlike many asilids and empidids, generally feed on small prey that they glean from a surface; i.e., they spend a good deal of time standing and walking (e.g., Chvala 1976). It may be easier to present a complicated display involving the movement of patterned body parts while both parties have their feet upon the "ground" (or the water's surface in the case of some *Campsicnemus*). At least some of the ornamented robber flies both forage for food and display to mates on substrates, e.g., tree trunks (Wilcox & Martin 1936). Those insects that reveal their ornaments in flight (e.g., *Calotarsa*), fly in a slow dignified manner that allows their decorations to be seen (Sivinski & Petersson 1996).

Why *Sabethes* should differ so much from other mosquitoes is a mystery, although there are two factors that might contribute to their unique ornamentation. First, the tribe Sabethini is diurnal. Shannon (1931) in Brazil and Haddow & Corbet (1961) in Africa noted that diurnal mosquitoes were more brightly colored than the drab species active at twilight or during the night. They presumed that coloration was useless in the dark. Second, the mating system of *Sabethes* does not include male swarms or males waiting by emergence sites, both common behaviors in the Culicidae (see Hancock et al. 1990). Rather, males patrol areas searching for resting females on twigs, or occasionally pursue flying females until they land. As in the dolichopodids, there is more of a stage available for their showmanship than is typical for a mosquito.

#### CONCLUSION: THE LOCATIONS OF ORNAMENTS

Wonders occur everywhere along the bodies of flies. Ornaments that appear to be used in aggressive interactions with members of the same sex seem to be concentrated on the head. Since the head is often used in the pushing style of confrontation and combat typical of Diptera, such elaborations are probably embellishments of weapons or advertisements of size and the ability to use weapons. They may then take on a presumably secondary function by advertising sexual competitiveness to potential mates (e.g., stalk-eyes). The rare instances of female ornamentation, swellings and glandular (?) projections are concentrated on the abdomen. The reproductive organs are likely to be a focus of male interest and where females would center their propaganda. Male ornaments that appear to be solely directed to females are more widespread, but still are concentrated in the anterior regions of the body, the head, and fore and mid legs.

The prominence of legs as platforms for signals may be because of their mobility. Movement might enhance perception of the ornament because objects in motion are more apparent to insect compound eyes. Alternatively, it could be the movement itself that is embellished by the ornament; i.e., displays of coordination, timing and flexibility made more impressive by the equivalent of a cheerleader's pom poms (or as W. B. Yeats might say . . . "how can we tell the dancer from the dance").

Evidence for it being the motions that are enhanced by the ornaments comes from the common employment of unornamented legs in communications between flies. Male forelegs, without decoration, are often used by flies to brush the female's face and eyes during courtship and copulation. For example, when mating, male *Platystoma*





*seminaionis* F. signal the start of a bout of nuptial feeding with a regurgitant by moving their front legs from the base of the female's wings to the inner margins of her eye (Michelmore 1928). In a similar vein, copulating males of the micropezid *Cardiacephala myrmex* alternatively scratch and regurgitate onto their mate's eyes (Wheeler 1924). In Mexico, mounted males of the asilid *Efferia cressoni* (Hine) rest their foretarsi on the females eyes (Dennis et al. 1986). However, in Wyoming they do not. Perhaps the mechanics of copulation remain the same, while selection on signaling does not. In addition to the actual placing of tarsi on the females' eyes, male flies may wave relatively unmodified front legs from a distance (e.g., Alcock & Pyle 1979; Spieth 1982). Both forms of signaling, the placing of the foretarsi on (or very near) the female eye and motions from a distance, might provide more information (or misinformation) when a more conspicuous front leg is employed. Plain midlegs are also sometimes used to signal. For example, the particularly complex courtship of the ottiid *Physiphora demandata* (F.) includes sessions where the male raises the middle leg with its light colored tarsi on the side away from the female (Alcock & Pyle 1979). Mounted males of the dolichopodid *Scapius platypterus* rest their front legs over the female's head while the midlegs are held to the side near her eyes and waved back and forth (Grootaert & Mueffels 1988). The unornamented mosquito, *Sabethes chloropterus* (Humboldt), quivers its plain midtarsi against its mate's antennae during copulation (Hancock et al. 1990). Its relative, *S. cyaneus*, has apparently escalated the display by using spectacularly plumed midlegs in a complex visual and tactile sexual performance.

Though wings are mobile, ornamented examples are rare in true flies. Perhaps the single pair is too critical to survival to bear the additional costs of carrying elaborate signals. The same combination of mobility and relative expendability characteristic of fly legs may have concentrated many of the more spectacular displays of birds' onto their tails.

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