

## SCENTS AND EVERSI­BLE SCENT STRUCTURES OF MALE MOTHS

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### INTRODUCTION

Males of many species of Lepidoptera have scent-organs located on the abdomen, thorax, legs, and wings. Such organs vary from simple scales and hair-tufts to complex eversible structures with storage areas and intricate mechanisms for expansion or exposure. These male scent-organs have many descriptive terms such as androconial scales, scent fans, costal hairs, brushes, hair-pencils, and coremata. Some authors use a different name for each type of scent-organ, while others use only one. This article concerns the eversible structures found on male moths but excludes similar ones found in butterflies, flies, and other orders. Butterfly male courtship pheromones and scent structures have been reviewed recently (34, 64, 168), and new ones are often being discovered (e. g. 112).

The male scent structures consist of hypertrophied trichogen cells and their associated scent scales or hairs. In earlier reports, these scales and hairs formed the basis of a system for the classification of male semiochemical glands, designed to indicate the increasing complexity of the glands (12-19, 97). Cells of the glands usually occur in groups, and their scent scales or hairs may form a brush or a "pencil" which can be concealed within a pocket and can be everted by means of sclerotized levers (24, 29). Such glands include coremata (inflatable tube-like organs), androconia, and hairs (28, 117, 169, 175). Swinton proposed a radial "family tree" of butterflies and moths based

on their scent-organs (162), but his system has little bearing on currently accepted systematic divisions and is, in any case, based on a character found in one sex only.

In some species, volatile chemicals are emitted from these organs when the male is close to the female, but in only a few species have they been proved to have a pheromonal function. According to many reports, the volatile chemicals produced by male organs are involved in copulation or courtship, and any identified chemicals are therefore thought to be male pheromones even though behavioral proof is lacking. The original definition of pheromone included the need for a specific reaction from members of the same species (100); there needs to be some kind of response evoked by the volatile before the term pheromone can be strictly applied. We follow the development of these male organs and volatiles through taxonomic families and then try to explain their possible evolution.

## TORTRICIDAE

Males of many tortricid species have modified scales, pockets, and eversible structures, but little is known of their function (78). In one species, however, *Grapholita molesta* (Oriental fruit moth), the morphology, behavior, and chemical ecology have been studied, not only because it is a pest, but also because courtship occurs in daylight, during which time the male abdominal hair-pencils are displayed close to the female (6, 7, 70).

Courtship involves a stereotyped sequence of behaviors culminating in an elaborate hair-pencil display performed one or two centimeters from the female. Displays consist of multiple rhythmic extrusions and retractions of the white hair-pencil organs and claspers at the end of the abdomen (6, 70). The paired terminal hair-pencils are a tuft of 93 hollow scales with honeycombed, porous walls, typical of structures that continually secrete, store, and disperse volatile material (71). The lumen of each scale is continuous with an underlying reservoir within a fibrous space, which in turn is bounded by microvilli of an enveloping trichogen cell. A blend of four volatile chemicals (Table 3e) is propelled by the male's vibrating wings toward a female (10). The female is attracted to the hair-pencils, and when she contacts the male's abdomen she stops walking. The male immediately turns and attempts copulation (6).

Only the ethyl *trans*-cinnamate and the methyl-2-epijasmonate are known to be pheromone components, attracting females from 2 cm away (10, 129). Interestingly, the cinnamate can be sequestered from the larval diet, but adults also can imbibe and sequester it, possibly from natural sources (129). Jasmonic acid is a common constituent of apples and other fruits (123). Adult males deficient in ethyl *trans*-cinnamate yet allowed to imbibe this compound from

sugar water were shown to be more successful in courtship than males that drank sugar water alone. Their dependence on these compounds has perhaps waned after years of laboratory breeding in small mating boxes (115).

Baker & Cardé (6) suggested that this courtship behavior may have evolved primarily by means of female-choice sexual selection (55, 66), and they were the first to implicate this mechanism in the evolution of lepidopteran male scent structures and displays (see Discussion). They viewed the display as a form of clasper extension behavior that became "ritualized" through the process of sexual selection (6). The fitness-related trigger that would cause the original female preference of clasper-odor would be a factor such as mating mistakes due to sex pheromonal cross-attraction of congeneric species or perhaps defensive ability (6). This attraction does occur between *G. molesta* and at least one sympatric and synchronic species, *Grapholita prunivora* (8), in New York State. *G. prunivora* males also display abdominal hair-pencils to their females, but the rhythm is much faster. Males must back into the females while displaying, forcing them to stop walking forward so that a copulatory attempt can be made (T. C. Baker, R. T. Cardé, unpublished data). Cross-specific male courtship display is readily evoked between males and females of these two species owing to the similarity in female sex pheromone blends. However, such courtships are not successful: *G. molesta* males wait for the touch that never comes from the unattracted females of *G. prunivora*; *G. prunivora* males disturb *G. molesta* females by continually bumping and backing into them rather than waiting for them to be attracted (T. C. Baker R. T. Cardé, unpublished observations).

Very few other courtship behaviors of tortricid moths have been described. In male *Choristoneura fumiferana* (Spruce budworm moth), androconia are located on the wings and abdominal tip, but it is not clear how they function. The male behavior is never clearly directed toward the head of the female (138). In descriptions of courtship in *Laspeyresia pomonella* L. (Codling moth) (43) and *Argyrotaenia velutinana* (Redbanded leafroller) (9), male androconia were not discussed. However, males of *Cryptophlebia leucotrata* (False codling moth) have three androconial areas. One is a notch on the hindwings; a second consists of small coremata between the seventh and eighth abdominal segments; and a third is a modification of a tibial spur on the hindlegs that is hidden by large scales covering the whole leg (181). All three types of androconia are successively involved during an original courtship sequence, but their function is not clear since they are not essential to mating success. Zagatti & Castel (181) stated that courtship behavior in *C. leucotrata* is one of the most complex described for Lepidoptera. The function of the androconia may also involve aggregation of males and perhaps defensive behavior.

## ARCTIIDAE

There are 10,000 arctiid species, many of which possess coremata, eversible sacs or tubes covered with scales or hairs (Table 1). These emerge from pockets between the seventh and eighth abdominal sternites or in the genital valves. Air enters a large tracheal sac connected to the lateral tracheal trunks and at the base of the tubes. The sac inflates and everts the coremata; a small amount of haemolymph also enters the inflated coremata (16, 127). The coremata in some species are quite small, but those of *Cretonotus gangis* show how large the coremata can be (twice the size of the moth) and still remain capable of eversion (137, 179).

**Table 1** Chemicals identified from and behavior elicited by coremata of male arctiid moths

Species	Volatile chemicals (*Pheromone)	Effect of coremata extrusion	References
<i>Cretonotus transiens</i> (Walker) [Asian arctiid moth]	R(-)Hydroxydanaidal*	Female and male attraction	(21, 156, 179)
<i>Cretonotus gangis</i> (L.) [Asian arctiid moth]	R(-)Hydroxydanaidal*	Female and male attraction	(21, 156, 179)
<i>Utetheisa ornatix</i> (L.) [Ornamental Utetheisa]	Hydroxydanaidal*	Female acceptance	(50, 51)
<i>Utetheisa pulchelloides</i> (Hampson)	Hydroxydanaidal	None known	(53)
<i>Utetheisa lotrix</i> (Crampton)	Hydroxydanaidal Danaidal	None known	(53)
<i>Pyrrharctia isabella</i> (J. E. Smith) [Isabel Tiger moth]	Hydroxydanaidal* Danaidal*	Female ultrasonic clicks	(103, 106)
<i>Phragmatobia fuliginosa</i> (L.) [Ruby Tiger]	Danaidal* Hydroxydanaidal*	Female ultrasonic clicks	(103, 105, 106)
<i>Estigmene acrea</i> (Drury) [Salt Marsh moth]	Hydroxydanaidal	Female and male attraction	(106, 178)
<i>Ciseps fulvicollis</i> (Hübner)	Hydroxydanaidal*	Female and male attraction	(104)
<i>Cycnia tenera</i> (Hbn.) [Dogbane Tiger Moth]		Female acceptance, if male ultrasonic emission is lacking	(48)

\*Danaidal, 6,7-Dihydro-5H-pyrrolizine-1-carboxyaldehyde

\*Hydroxydanaidal, 7-Hydroxy-6,7-dihydro-5H-pyrrolizine-1-carboxyaldehyde

At dusk, males of the North American Salt Marsh moth, *Estigmene acrea*, display inflated abdominal coremata and form male aggregations. Both sexes fly into aggregations, where mating occurs (178). The inflated coremata are about the same length as the body. Female *E. acrea* also release a sex pheromone which attracts males (91), but they do so three or four hours after dusk. Thus, there are two different mate-finding behaviors in this species (178). However, only circumstantial evidence suggests the involvement of a male pheromone.

Similarly, males of *Cretonotus gangis* and *C. transiens*, two sympatric Asian arctiid spp., also aggregate. When a male has inflated his coremata, he attracts other males so a male group develops with all their coremata inflated and emitting scent (179). Females are attracted to the male group; when a female contacts a male, the coremata are deflated and mating follows. After a couple of hours the male group disbands. Any remaining virgin females emit a sex pheromone that attracts males and so more matings occur (179).

The coremata of *C. gangis* contain R(-)-hydroxydanialal in varying amounts up to 500  $\mu\text{g}$  (Table 1) (21, 38, 179). Both the size of the coremata and the pheromone content depend on the larval ingestion of pyrrolizidine alkaloids (PAs), which are the plant-derived precursors of hydroxydanialal (38, 156, 179). The huge and pneumatically eversible coremata lie in a cavity between abdominal sternites 7 and 8. They are comprised of two pairs of tubes, up to 37 mm long: One large coremata is one-and-a-half times a male's body length and is covered by 3000 scales. A direct correlation exists between amounts of PAs ingested and the size of the coremata, but the PAs are not essential dietary factors for the general development of the moths. The morphogenic effect is restricted to the coremata (38). There is, as yet, no known disadvantage with regard to mating success, for males possessing stunted coremata.

The male aggregations in *Cretonotus* spp. and *E. acrea* have been called leks (178, 179). In a lek, a male group attracts the females without offering any resource except the opportunity to mate (20, 39). In *Cretonotus* the females do not seem to select a specific male or the biggest coremata (155, 179). However, Schneider suggests that these experiments may be misleading since they were done indoors (155). Certainly much more valuable information is to be gained by studying the selection of males by females entering male assemblages of *E. acrea* and *Cretonotus* spp. in the wild.

The pyrrolizidine alkaloids are complex products thought to be manufactured secondarily by plants for defense. Specialized herbivores can overcome this chemical defense and sequester the PAs to become chemically protected (153, 155). Thirty-two genera of Lepidoptera are known to visit PA-containing plants (145). Some Lepidoptera, including *Rhodogastria* spp., visit wilting plants, scratch the surface, and deposit fluid from their proboscis

which they reimbibe with the PAs (35, 36). *Rhodogastria* moths emit a defensive froth when disturbed. The froth comes from the prothoracic glands and contains N-oxides of PAs (35, 36). In arctiid moths, there is often no sex bias in the number of visits of adults, in contrast to danaid butterflies among which only males visit the PA-containing plants. In *Cretonotus* spp., the larvae are said to be pharmacophagous (35, 36). They not only gain possible protection from predators, they also use the PAs as precursors for the biosynthesis of male pheromones and the quantitative growth of the pheromone-producing coremata in the pupa (35-38, 155).

Three *Utethesia* spp. have inflatable coremata: *Utethesia pulchelloides*, *U. lotrix* in Australia (53) and *U. ornatix* in North America (49, 50), but their morphology is different. Each corema is situated in the side of a genital valve, a thin-walled, invaginated cuticular sac covered with specialized scales and everted by inflation of the abdomen (50). The principal chemical in the coremata is hydroxydanaidal (Table 1), which again is derived from defensive PAs obtained from their larval foodplants (*Crotalaria* spp.). Unlike the "lekking" males of *Cretonotus* and *Estigmene*, a *U. ornatix* male approaches a calling female, hovers beside her, then makes antennal and tarsal contact. Next, he everts the coremata while thrusting his abdomen toward the female's head and thorax (49). The female raises her wings, exposes her abdomen and the pair make genital contact and copulate. The hydroxydanaidal [(+)- and (-)-] induces the wing raising of the female (50). Conner et al (50) suggested that the hydroxydanaidal in male coremata signals to the female the degree of his chemical PA-based protection. The amount of hydroxydanaidal in the coremata averages 1.4  $\mu\text{g}$  per male, and the amount of PAs ingested is dependent upon the part of the plant the larvae had fed upon. The seeds are the richest source of PAs (51). If males are severely deficient in producing hydroxydanaidal, as may occur with a diet lacking PAs, they are less likely to succeed in courtship (50). It is not known whether females discriminate against males with the slightly lower titres that would occur from feeding as a larva on the wrong part of a plant (51).

The North American temperate arctiids, *Phragmatobia fuliginosa* (Ruby tiger) and *Pyrrharctia isabella* (Isabel tiger moth) have coremata between the seventh and eighth sternites of the abdomen. These species are in the *Spilosoma* group of the tribe Arctiini, subfamily Arctiinae, which includes *Cretonotus* spp. and *E. acrea* (64). *P. isabella* coremata are relatively large, about three quarters of the body length, in a form like those of *E. acrea* and *Cretonotus* spp., whereas *P. fuliginosa* coremata are much smaller, about one fifth of the body length. Both *P. fuliginosa* and *P. isabella* males evert their coremata only briefly during the courtship flight while they approach a calling female (102, 103, 106, 128). In the coremata of both species are hydroxydanaidal and danaidal (106). Males collected from the field exhibit a

bimodal distribution of their hydroxydanaidal or danaidal titres. The hydroxydanaidal in *P. isabella* coremata is either in the 0–10 ng or 1–10  $\mu\text{g}$  range, with little if any danaidal. On the other hand the coremata of *P. fuliginosa* contain danaidal in either the 0–30 ng or in the 0.3–3  $\mu\text{g}$  range, with little, if any, hydroxydanaidal. Females of both species are more sensitive to compounds from males of their own species, although both hydroxydanaidal and danaidal can elicit courtship responses in sexually receptive females of both species. Females respond with a distinctive wing-fluttering and ultrasonic clicking behavior (102, 103, 106). It is intriguing that although females respond (audibly) to the odor of the males, thus classifying the odor as a pheromone, the pheromone apparently does not function to increase courtship success (102, 103, 105). This appears to be the only known case in which an insect behaviorally signals its reception of a pheromone signal but does nothing about it.

Sonic emission also plays a role in the courtship of the arctiid *Cycnia tenera* (Dogbane tiger moth). Males must emit either pheromone from their coremata or ultrasound from microtymbals for optimal mating success (48).

Males of *Spilosoma lubricipeda* (White ermine) and *S. urticae* (Water ermine) also have coremata between abdominal seventh and eighth sternites that arise from a sclerotized bar extending in a circle around the abdomen and that are fused to the tergite of the eighth segment. In contrast, the related *S. lutea* (Buff ermine) has no coremata, but it has the same general appearance as *S. lubricipeda*, the same size and similar color. The larvae and adults of both species also have the same PAs in their bodies (150, 153). Rothschild (151) suggested that *S. lutea* might be a mimic of *S. lubricipeda*; but how the coremata of *S. lubricipeda* are used in courtship or in defense is unknown.

In Great Britain and Ireland, there are 32 arctiid spp. in two subfamilies that possess coremata. As judged by the structural differences alone, coremata and brushes appear to have evolved independently many times in the Arctiidae, possibly as many as seven times in the few British species checked (23, 29).

## NOCTUIDAE

“Scent fans are the perquisite of the males of many of the Noctuina whose eyes shine at night like those of the barn owl as they winnow the dewy flowers” (Swinton, 162). Male eversible structures in the Noctuidae are of diverse morphological types and can occur on the legs, thorax, or more often, on the abdomen: the abdominal structures are the most complex scent-distributing systems found in the Lepidoptera (Table 2).

Males of several species have eversible structures on the eighth abdominal sternite, although these brushes are sporadic among species in any of the

**Table 2** Chemicals identified from and behavior elicited by hair-pencils of male noctuid moths

Species	Volatile Chemicals (*Pheromone)	Effect of Hair- pencil Extrusion	References
<b>[a] Hadeninae—Anterior abdomen hair-pencils</b>			
<i>Mythimna impura</i> (Hub.) ( <i>Leucania</i> ) [Smokey Wainscot]	Benzaldehyde iso-Butyric acid	None known	(1, 2)
<i>Mythimna conigera</i> (Schiff.) ( <i>Leucania</i> ) [Brown-line Bright-eye]	Benzaldehyde iso-Butyric acid	None known	(1, 2)
<i>Mythimna pallens</i> (L.) ( <i>Leucania</i> ) [Common Wainscot]	Benzaldehyde iso-Butyric acid	None known	(2)
<i>Mamestra brassicae</i> (L.) [Cabbage moth]	2-Phenyl ethanol Benzyl alcohol	Female acceptance	(23, 31, 92, 95)
<i>Mamestra persicariae</i> (L.) [Dot]	2-Phenyl ethanol Benzyl alcohol Phenyl-acetaldehyde	None known	(2, 22)
<i>Mamestra configurata</i> (Walker) [Bertha Armyworm]	2-Phenyl ethanol	None known	(47)
<i>Polia nebulosa</i> (Hufnagel) [Grey Arches]	2-Phenyl ethanol Benzyl alcohol Benzaldehyde	None known	(27)
<i>Polia tincta</i> (Brahm) [Silver Arches]	2-Phenyl ethanol Phenyl-acetaldehyde	None known	(22)
<b>[b] Noctuinae—Anterior abdomen hair-pencils</b>			
<i>Peridroma saucia</i> (Hub.) [Pearly Underwing, or Variegated Cutworm]	2-Phenyl ethanol	None known	(30)
<b>[c] Amphipyriinae—Anterior abdomen hair-pencils</b>			
<i>Pseudaletia unipuncta</i> (Haworth) [Armyworm moth]	Benzyl alcohol Benzaldehyde Acetic Acid	Female acceptance	(67-69, 80, 93, 96)
<i>Pseudaletia separata</i> (Walker) [Southern Armyworm]	Benzaldehyde Benzyl alcohol Benzoic acid n-Butanoic acid	Possibly inhibits females' movement (inconclusive)	(45, 47, 92, 93)
<i>Phlogophora meticulosa</i> (L.) [Angle Shades]	6-Methyl-5-heptene-2-one 6-Methyl-5-heptene-2-ol 2-Methyl butanoic acid	Female acceptance	(2, 25)



Table 2 (Continued)

Species	Volatile Chemicals (*Pheromone)	Effect of Hair- pencil Extrusion	References
<i>Apamea monoglypha</i> (Hub.) [Dark Arches]	Pinocarvone	None known	(2)
<b>[d] Cuculliinae—Anterior abdomen hair-pencils</b>			
<i>Cucullia umbratica</i> (L.) [Shark]	2-Methyl butanoic acid	None known	(27)
<i>Agrochola helvola</i> (L.) [Flounced Chestnut]	2-Phenyl ethanol	None known	(22)
<b>[e] Pantheinae—Post abdomen brushes</b>			
<i>Trichoplusia ni</i> (Hub.) [Ni moth]		Female long- distance attraction, acceptance	(111)
<b>[f] Heliethinae—Male genitalia hair-brushes</b>			
<i>Raghuva albipuncta</i> De Joannis	Diethyl malonate	None known	(114)
<b>[g] Catocalinae—Post abdominal hair-pencils</b>			
<i>Anticarsia gemmatalis</i> (Hub.) [Velvetbean Caterpillar]	(Z,Z,Z)-3,6,9— Heneicosatriene*	Attracts males during court- ship	(87)

subfamilies. Male *Trichoplusia ni* (Pantheinae) have brushes (73, 74); these are spread out like a fan during the last stage of their courtship (72). Electro-antennograms (EAGs) showed that both male and female antennae detected brush extracts (73), although it was not until 1976 that Jacobson et al (98) identified a chemical from the brushes as 2-phenyl ethanol. No evidence of 2-phenyl ethanol was found in a later study (86). Recently, Landolt & Heath (111) discovered that male *T. ni* take up a calling posture and release a chemical from their terminal abdominal hair-pencils that attracts females from several metres away. Females fly upwind in a zigzagging flight path to extracts from these hair-pencils, but not to extracts from abdominal brushes located on the third to fifth segments. There appears to be a dual system once again in this species, with male attraction to females occurring in the middle of the scotophase and female attraction to males occurring throughout the scotophase, but with a peak towards dawn (111). The chemical causing this female attraction has not yet been identified, but it is not 2-phenyl ethanol.

Many other Plusiinae spp. have brushes very similar to those found in *T. ni*. These brushes can easily be everted by squeezing the male abdomen, causing the hair tufts to suddenly spread out into a fan. Males of *Heliothis virescens*

(Noctuidae) (Tobacco budworm) have a dense pair of brushes on the ventro-lateral side of the base of the ninth abdominal sternite; these brushes extend and spread to a fan shape when a male approaches a calling female to mate (164). Male brush extract or brush eversion has been reported to cause females to cease calling (88).

Male *Anticarsia gemmatilis* (Catocalinae) (Velvetbean caterpillar moth) possess two pairs of brushes, one pair on the center of the eighth abdominal segment and a terminal pair on the ninth segment. The chemical in the eighth brush is (Z,Z,Z)-3,6,9-heneicosatriene, which is one of the major components of the female sex pheromone (87). Males are attracted to extracts of the male brushes, but it is hypothesized that if a male everted its brushes during courtship after arriving at a calling female, other males flying up the plume of female pheromone might cease upwind progress as the ratio of pheromone components changed (87). This remains to be demonstrated, as does the effect of the brush-derived compound in evoking female acceptance of males. Brushes are found on the middle tibiae of *Catocala nupta* (Catocalinae) (Red underwing moth). The brushes lie in a groove in the tibiae and are concealed by enlarged scales (29). Other Catocalinae spp. have similar male leg brushes, but how the brushes are everted, or even if they have volatile chemicals, is unknown. In Hypheninae, like *Paracolax derivalis* (Clay fan-foot moth), males have tufts of hairs on the coxae, tibiae, and femora of the forelegs, but nothing is known about these.

The noctuid male scent organs commonly referred to as hair-pencils are unusually complex organs found at the front of the abdomen of many males in the subfamilies Noctuinae, Hadeninae, Cuculliinae, and Amphipyriinae, within the trifine group of the Noctuidae. The structures are remarkably constant in all the species in which they were found (24): the system consists of paired brushes, scent-glands (Stobbe's gland) (160), and storage pockets. Each brush is attached to a sclerotized lever arising from the posterior angle of the second (apparent first) abdominal sternite. The brush is extended by muscles acting at the base of the lever, and the hairs are fanned out by a muscle at their base. Scent secretion originates from Stobbe's glands in the second abdominal segment, which are active only in the pharate adult. The scent is stored on the brushes within the pocket and the lattice-like structure of the brush-hairs provides a huge surface area both for storage of scent and for evaporation when the brushes are everted. This "typical" system is found in *Phlogophora meticulosa* (Amphipyriinae) (Angle shades moth) (24), *Mamestra configurata* (Hadeninae) (Bertha armyworm), *Pseudaletia separata* (Amphipyriinae) (45-47), and *Mamestra brassicae* (Hadeninae) (Cabbage moth) (101).

Volatile chemicals from some of the above species have been identified (Table 2) and are easily perceived by the human nose. In some species the biochemical pathways to these compounds have been proposed. In *M. con-*

*figurata*, plant-derived phenyl ethyl- $\beta$ -glycoside is thought to be the precursor of 2-phenyl ethanol (47). However, a crucial question remains as to the actual role of most of these compounds. Here, we consider three well-studied noctuid spp. to see the functions, if any, of the hair-brushes and volatile chemicals disseminated from them.

*Phlogophora meticulosa* has a complete brush-organ that contains at least three compounds (1) (Table 2). Males fly upwind to calling females and evert their brushes when they attempt to copulate (25). Fifty-five normal males were used in small cages: of these, 38% of males everted their brushes, and 33% succeeded in copulation. Thirty males with their hair-pencils cut off flew to calling females, but none were able to mate. Male compounds possibly acted as an aphrodisiac pheromone, but there is no direct evidence, only the inference from the ablation studies (25).

Male *M. brassicae* have anterior abdominal hair-pencils from which chemicals have been isolated (Table 2). Szentesi et al (163) conducted preliminary investigations which showed that an aphrodisiac from brush extracts caused a female to adopt a "calling" position and quiver her wings. Toth found that male *M. brassicae* everted scent brushes during courtship in almost every case, but ablated males also courted and mated successfully (166). Thus, hair-pencil eversion is unnecessary for some successful courtships. Similarly, males without hair-pencils mated just as successfully as unoperated males, and there was no evidence that male compounds attracted females or affected the behavior of other males (31). It must be noted, however, that eversion of hair-pencils by males had not been observed on video (31) until recently, when using a new stock (G. Poppy, unpublished observations).

In *Pseudaletia unipuncta* (Armyworm moth) Hirai et al claimed that the male scents acted at close range as a sexual stimulant to females (96), but a more obvious effect of the same scent was upon other males, inhibiting their approach to the same female. This was the first claim for a male-to-male inhibitory moth pheromone which prevented other males from competing for a single female. Fitzpatrick et al (67, 68) disagreed, believing the results of Hirai et al were due to disruption of the female pheromone plume by stimulus introduction and not the result of pheromone-induced repulsion (93, 94, 96). The hair-pencils were not observed to be everted during courtship (67, 68). However, males whose hair-pencils had been excised were unable to mate as successfully as did sham-operated males. Benzyl alcohol and acetic acid were compounds identified from the hair-pencils, but they have not been demonstrated to evoke acceptance by females. This is true despite their being the most abundant compounds in the brushes and despite the extirpation results that go together with data showing how these compounds vary with diet and photoperiod (67-69).

At present it seems that the majority of noctuid spp. lack hair-pencils. In

300 British species studied, 40% have fully developed brush-organs as described, or at least some of the structures involved: The remaining 60% have no trace of them (27). Some species have complete brush-organs, others have only a portion of the sclerotized structures, and the remainder show no evidence of them at all. A full structure is present in 20 of 59 species of Hadeninae, 37 of 56 species of Cuculliinae, 41 of 89 species of Amphipyriinae, and only 1 of 52 species of Noctuinae (27, 29). There is also variability within a genus. In the genus *Apamea* half of the species have them: *A. furva* has a complete brush-organ, whereas *A. remissa* has the sclerotized lever only (26). Most species in the genus *Mythimna* have complete brush-organs. Two species have no brush-organs (*M. pudorina* and *M. loreyi*), and three species have large inflatable coremata where the brushes would be located in other noctuids (*M. comma*, *M. obsoleta*, and *M. putrescens*) (27, 29). So far there has been no research to see how the brush-organs are used, if at all, in the courtship behavior of these species or whether there is cross-attraction among congeners to their female-emitted sex pheromones. The hair-pencils in three *Mythimna* spp. (*M. impura*, *M. conigera*, *M. pallens*) contain the same compounds (2) (Table 2), not yet known to be pheromones, in the same ratios.

In the Noctuinae, only *Peridroma saucia* has any trace of the noctuid-type of hair-pencil. It contains 2-phenyl ethanol (30) (Table 1), which has not been shown to be used in courtship. In all other respects, however, this genus appears to be closely related to other genera in the Noctuinae (27). One British Noctuinae sp., *Ochropleura plecta*, has a single median abdominal corema with a red brush (27, 29).

The noctuid structures are an example of both the consistency and the lability of the male brush-organ/hair-pencil structures. The consistency is demonstrated by the unique position, at the anterior end of the abdomen, of the complex structure found in many species throughout four subfamilies. Lability is emphasized by the total absence of the structure in some species, partial loss in others, and the evolution of completely different eversible organs in yet others.

## HAIR-PENCILS IN OTHER MOTH FAMILIES

### *Pyralidae* (Table 3c)

Several species of male phycitine moths possess a characteristic gland located on the basal costal margin of each forewing, where a membranous flap overlies specialized scales which can be everted during wing-fanning (13, 52, 107, 149). Quite a lot of work has been done on a few phycitine species that infest stored products.

In males of *Ephestia kuehniella* (Mediterranean flour moth) there are tufts

of modified scales between the seventh and eighth abdominal segments (52). The trichogen cell secretes the modified scale and withdraws, forming a microvillous lumen into which the volatile chemicals are secreted; the tormogen cell forms the hair-pencil scale socket. The morphology has been described for *Plodia interpunctella* (Indian meal moth) (78), *Vitula edmandsae* (Bee moth) (77, 174), and *Cadra cautella* (Almond moth) (78). Male courtship pheromones from the basal glands of the forewings function in the mating success of males in *P. interpunctella* (79, 118), *C. cautella* (11, 79), and *V. edmandsae* (78). The female behaviors evoked by the as-yet-undefined compounds ranged from acceptance to turning to face the male.

Synthesized or natural pheromone of *Ephestia elutella* (Tobacco moth) (143) (Table 3) elicits a stereotyped courtship response from conspecific females (107, 143). All five species in the stored-product moths share the same primary component in the female sex pheromone, (Z, E)-9,12-tetradecadien-1-ol acetate (107). These species can be sympatric and sexually active at the same time of day (107). There is considerable cross-attraction of males to nonconspecific females (141).

However, courtship interactions result in very few interspecific matings, mainly due to differences in male courtship behavior and male chemicals from the costal fold hair-pencils (76, 79, 139). Courtships between *E. elutella* and *Cadra figulilella* (Raisin moth), for instance, are unsuccessful because most females lower their abdomens following the copulatory strike by the male, during which he brings his abdomen over the top of his head to contact the female's head. The lowered female abdomen makes copulation difficult and functions as a rejection by the females. In intraspecific courtships, the female's abdomen becomes elevated in the acceptance posture in the vast majority of the cases following the copulatory strike. Phelan viewed the behavioral differences in courtship among these species as less important in preventing interspecific mating mistakes than were chemical blends themselves (139). The behavior was considered merely the stage upon which the chemical message is played out.

Male behavior can be very complex in some species such as *E. elutella*, *C. figulilella*, *Vitula edmandsae*, *C. cautella*, *Ephestiodes gilvescentella*, and *Sosipatra rileyella*, involving the dissemination of wing gland pheromones followed by a "headthump" that apparently delivers yet another chemical blend to the female's head from the abdominal hair-pencils (79, 107, 139). In other species the behavior is simpler; some such as *Plodia interpunctella* and *Ephestia kuehniella*, hold the abdomen stationary over the female's head. In the latter species, the abdominal hair-pencils are not displayed when the abdomen is raised (139). Other species lack courtship movements entirely, in addition to lacking the wing-glands and abdominal brushes [*Paramyelois transitella* (Naval orange moth) and *Laetilia coccidifivora* (Coccid moth) (139)].

**Table 3** Chemicals identified from and behavior elicited by eversible structures of other male moths

Species	Volatile Chemicals (*Pheromone)	Effect of Scent Structure Eversion	References
<b>[a] Hepialidae—Big hindleg scale-brushes</b>			
<i>Hepialus hecta</i> L. [Swift Moth]	6-ethyl-2-methyl-3,4-dihydro-2H-pyran, 1,8-dimethyl-3-ethyl-2,9-dioxabicyclo-[3.3.1]non-7-ene 1,8-dimethyl-3-ethyl-2,9-dioxabicyclo-[3.3.1]non-7-en-6-one	Attracts female	(157)
<b>[b] Agaristidae—Anterior abdomen hair-pencils</b>			
<i>Phalaenoides glycinae</i> Lewin [Vine Moth]	2-Phenyl ethanol 2-Phenyl ethanacetate	None known	(58)
<b>[c] Pyralidae—Forewing gland and brushes (see each species)</b>			
<b><u>Phycitinae</u></b>			
<i>Ephestia elutella</i> (Hüb.) [Tobacco moth] [Wing gland and brush]	(E)-Phytol* gamma-Decalactone* gamma-Undecalactone*	Causes female acceptance posture	(107, 140, 143)
<b><u>Galleriinae</u></b>			
<i>Eldana saccharina</i> Walker [African Sugar Cane Borer] [Abdominal HPs/Vanillin: Wing gland/(E)-3 . . .]	Vanillin p-Hydroxy-benzaldehyde (E)-3-Methyl-4-dimethylallyl-gamma-lactone	Wing gland: Stimulates searching by walking females  Abdominal HP's: Evoke ♀ wing vibration and acceptance	(109, 170, 180)
<i>Paralipsa (Aphomia) gularis</i> Zeller [Stored Nut Moth] [Forewing gland]	2-Phenyl ethanol n-2,6-Nonadien-4-olide	Short range female attraction	(110)
<i>Galleria mellonella</i> L. [Greater Wax Moth] [Gland & brush, base of forewing]	n-Undecanal* n-Nonanal*	Attracts females	(65, 113, 149, 158)
<i>Achroia grisella</i> (Fab.) [Lesser Wax Moth] [Gland & brush, base of forewing]	n-Undecanal* (Z)-11-Octadenal*	Activates females for orientation to ultrasound	(54, 84, 159)
<i>Corcyra cephalonica</i> Stainton [Rice Moth] [Gland & brush, base of forewing]	(E,E)-Farnesal (Z,E)-Farnesal	Attracts female	(182)

Table 3 (Continued)

Species	Volatile Chemicals (*Pheromone)	Effect of Scent Structure Eversion	References
<b>[d] Geometridae—Brushes (bases of genitalia)</b>			
<i>Bapta temerata</i> (Schiff) [Clouded Silver Moth]	n-Butyric acid	None known	(2)
<b>[e] Tortricidae—Posterior abdominal hair-pencils</b>			
<i>Grapholita molesta</i> (Busck) [Oriental Fruit Moth]	Mellein Methyl jasmonate Methyl 2-epijasmionate* Trans-ethyl cinnamate*	Attracts female	(6, 10, 129)

Phelan observed a general trend in the Phycitinae towards an increasing reliance upon abdominal hair-pencils rather than the costal fold hair-pencils.

In male *Galleria mellonella* (Greater wax moth), there is a scent perceptible, by humans, as "bitter-aromatic" or "musklike" (13, 171) which was traced to a gland on the forewing (13). This scent attracts females (65); the active compounds are a blend of n-undecanal (149) and n-nonanal (113). A blend of the compounds is needed for optimal attraction (65), although ultrasound emitted from the males' vibrating wings also plays a role in stimulating females (158). In *Achroia grisella* (Lesser wax moth), males vibrate their wings and emit two pheromone components, undecanal plus (Z)-11-octadecenal, from similar glands located ventro-basally on the forewings (84). Together the two components evoke female activation, but ultrasound emitted as a result of wing vibration causes the orientation of females towards the male (159).

Male *Eldana saccharina* (African sugarcane borer) emit a long-range attractant for the female. A male adopts a typical calling posture by fanning his wings and displaying his large abdominal hair-pencils to emit the pheromone (Table 3) (108, 109, 170, 180). The female walks over the grass blades from several meters to locate the male. The wing glands stimulate walking by females, and the abdominal hair-pencils evoke female wing vibration and acceptance (180). As in other Galleriinae, males of *Corcyra cephalonica* (Rice moth) emit a pheromone which attracts females who locate the males by walking upwind (182). Scales are inside a pouch which runs along the costal vein very close to the wing articulation, in a way similar to the gland of *G. mellonella* and *E. saccharina*. It was noted that in the Galleriinae, the typical response of attracted females is to walk to males (182). Also the idea that localized resources such as bee hives are at the root of such

long-distance attraction of females to males (84) does not appear to be supported by *E. saccharina* or *C. cephalonica* (182).

### *Yponomeutidae*

Although there is no significant gene flow among the many species in the genus *Yponomeuta* in Europe (121, 121a, 122), and the female sex pheromone blends are specific enough to result in very little cross-attraction (114), under some conditions interspecific attraction of males to females occurs at high levels (89). In these cases, females refuse males of the wrong species (89, 90), apparently owing to differences in the chemicals emitted from the prominent male abdominal brushes (89). In three species, *Y. evonymellus*, *Y. cagnagellus*, and *Y. padellus*, the male wing fanning seems to inhibit the response of other males to female sex pheromone (90). No chemicals have been identified from the hair-pencil organs of *Yponomeuta* spp.

### *Thyrididae*

A possible function of a male hair-pencil scent dispersal mechanism is given for the *tibiaria*-group of species of *Striglina*. There are 40–50 scales forming the pencil that arise from a patch near the inner margin of the hind wing, probably as a modification of the fringe scales (177).

### *Gelechiidae*

Male *Phthorimaea operculella* (Potato tuber moth) have hair brushes on the hind wings which are displayed in their copulatory behavior (133–136). There is no known behavioral response in females to the display of male brush organs during normal courtship. Whether the excision of their hair-pencils has any influence on the courtship and mating of males remains to be established.

### *Geometridae* (Table 3d)

In many Geometrid spp., males have brushes or coremata, but there appear to be no published studies on behavior. Coremata in geometrid males were mentioned in two species, *Xanthorhoe ferrugata* and *X. fluctuata*. These may function to prevent mating mistakes (25, 28), but no data confirm this. Coremata, the morphology of which have been studied (99), are present in *X. montanata*, but no volatile chemicals have been found in the coremata of any *Xanthorhoe* spp. Male *Bapta temerata* (Clouded silver moth) have brushes on the genitalia, and they expand when the genitalia are open. There are no observations on courtship, but the hairs of the brushes form groups like "palms", which may release n-butyric acid when they are open (2).

### *Hepialidae* (Table 3a)

Many male Hepialids have hind-tibial brushes in which the hind leg has lost its normal function. Males of *Hepialus hecta* (Swift moth) hover, sit, or loop



back and hover on the spot in leks; and females aggregate, fly into male aggregations, and mate there (116, 167). Three chemicals have been identified from hind-tibial brushes of *H. hecta* (157), but it is not known whether they function as female attractants. Some hepialid spp. lacking male brush-organs use the more standard lepidopteran mate-location method in which females emit pheromone and attract males (116, 173). This is an interesting contrast to the more conspicuous and oft-cited lek-formation by hepialid males, but it is believed that these quite common female pheromone-based mating systems are actually ancestral in hepialids (173). In the North American species *H. sequoiolus*, males sit on foliage and display their hind tibial brushes. Males form small aggregations to which females are attracted, and mating occurs. Aggregations of males attract more females than do solitarily displaying males (172).

#### *Palaephatidae*

This family is a primitive monotrysian heteroneuran in southern South America and in Australia. Males of several South American palaephatid spp. and genera have hair-pencils and pockets with specialized scales on the wings and abdomen (56). In Australia, the males of *Azaleodes* spp. possess an impressive array of hair-pencils and pockets with specialized scales on wings and abdomen (126). However, nothing is known about the behavior of *Azaleodes* nor about the many secondary organs in the males, including their color-pattern and sizes. It can only be speculated (126) that these may play an important role in courtship in this genus.

#### *Sphingidae*

Rothschild & Jordan stated that male brushes are present in all sphingids (154), but it is now known that about half of the species do not have brushes. Before 1903, male brushes were known in *Acherontia atropos* (130). A strong scent is emitted by these males, and Swinton describes how "a male held in the hand squeaked and spread out large, whirling, orange coloured fans (like stars) which distributed a scent smelling first of jasmine, later becoming aluminous and disagreeable." It was believed that the scent, dust, and stridulation by male *A. atropos* in flight caused "blindness in humans" (162). However, Swinton (161) stated that his moth "had not that power." A very good history of the discovery and description of male brushes in this species and of the whole organ is given by Stobbe (160). The male brushes produce a musky odor in several species of sphingid moths (124, 125, 152).

*Manduca sexta* (Tobacco hornworm) has two ventral brushes arising from the second abdominal segment that are contained in a pair of slitlike shallow pockets that extend across the second and third segments. The scent brush scales arise from large cells, but the male scent is probably produced by large glandular cells at the base of the pocket scales. The scent substance passes

through a reservoir system and through a cuticular tube to the pocket scales (81). The scent disseminates when the brushes are everted. Volatile secretions are released (75), but no chemicals have been isolated nor has their use during courtship been ascertained. There is a similar male brush organ in *Deilephila elpenor* (Large elephant moth) in which the white hairs are visible against the pink abdominal scales. Normally the hairs are concealed in pleural pockets into which complex glands open through ducts and tiny pores (29). In *M. sexta*, *D. elpenor*, and other species with brush organs, the structure of the brushes suggests the dissemination of chemicals produced by these glands. However, no chemicals have been isolated, and there have been no behavioral experiments to see how these brushes are used.

The behavioral function of sphingid male brushes can only be conjectured. Both the volatile chemicals from the brushes and genital stridulation (147, 148) are thought to be used primarily in courtship behavior and secondarily in defense. When males are picked up, grabbed by their wings, or disturbed in any other way, the brushes are everted (29, 81). It is curious that the Sphingidae have few large predators, except for the people working on them who want large moths of their collections. This is the only family of large moths in which the males have large brushes, and it is curious that there are no data concerning how or even if the male brushes are used during courtship.

#### EVOLUTION OF MALE SCENTS AND EVER-SIBLE SCENT-DISSEMINATING STRUCTURES

Baker & Cardé first used behavioral data to link Darwin's ideas (55) about female-choice sexual selection with the possible evolution of hair-pencils. They demonstrated that males whose scent disseminating ability had been made deficient had reduced mating success (6), and they favored Fisher's original model (66) for how sexual selection upon dissemination abilities would proceed. First, a fitness-related trait involving odor in males would become preferred by females. Included in Baker & Cardé's list of possible preference traits were odors that indicated the courting male was of the correct species, that males had acquired the ability to defend themselves, and odors that indicated male vigor (6). These, of course, are not mutually exclusive. They pointed out that if there were also conditions present that promoted differential mating success between males, then both the preference and the preferred trait could be driven to extremes by the directional, runaway aspect of the selection until other selective forces put a limit on them (6, 66, 131, 132). Such conditions might include a skewed operational sex ratio caused by, for example, protandry or females being limited to fewer potential matings than males.

In our opinion, Fisher's is still the most robust, all-encompassing model for

the evolution of male moth scents and eversible organs. In the current literature several interesting issues pertain to this evolutionary process. First are the factors underlying the initiation of female preference. Does this preference arise as an adaptive response to interspecific mating mistakes, or as an incidental result of ecological factors favoring habitat-specific, mate-recognition traits in temporarily separated allopatric populations? Second is the nature of the selection that causes the exaggeration of the trait. Is it due to sexual or natural selection? If the former, is it due to direct female choice on the trait, or to indirect selection, after males have already in effect done the selecting themselves due to male-male interactions? Third is the nature of the male trait itself, continually linked to inclusive fitness as an indicator of another, physical, investment such as a nutritional gift from males transferred directly to females to increase fecundity or survival of offspring? Or is the trait itself the gift that is only triggered by, but not continually linked to, the fitness-related advantage (6)? The male scent and apparatus inherited from the father would thus be handed down through the choosy mother to her sons in the next generation, and the sons will be favored for mating by the discriminating females in that generation (66). Perhaps we can learn much about the evolution of these scents and structures by studying details of these male traits and the behaviors they elicit in females.

### *The Origin of Male Scents*

**THE LINK TO MINIMALLY ALTERED PLANT COMPOUNDS** The above review of scents, courtship pheromones, and eversible scent-disseminating structures in male Lepidoptera establishes the link between volatile production and feeding on plants. This is true for courtship compounds that are also related to defensive compounds, as well as for compounds that have no known relationship to defense. True pheromones are nearly always closely related structurally to compounds found in plants (4). Unlike female-emitted sex pheromones (32), most of the courtship pheromones emitted by males derive directly from ingested compounds peculiar to certain plants, and not to general nutritional building blocks such as carbohydrates, lipids, and proteins (4). Thus, any discussion of the evolution of male scents must account for this one overriding feature.

**WHY PLANTS?** One logical reason for the tendency for male scents to consist of minimally altered plant products is that foodplant odors are the chemicals for which females are likely to have already existing receptors and behavioral responses (59). That is, if olfaction functioned in hostplant selection by females, they would already have an appropriate sensory system to sense hostplant metabolites emanating from males. The only thing lacking

would be female preference for this odor during *mating*, in addition to during host-finding.

Evidence for the host-odor link is known for some species. In *G. molesta*, gravid females in the field are known to be attracted from a distance to one of the hair-pencil constituents, ethyl *trans*-cinnamate (129), and cinnamic acid is a common alleopathic constituent of plants. In one species of moth, *Cisseps fulvicollis*, females as well as males are attracted to hydroxydanaidal baits as well as to plant parts containing pyrrolizidine alkaloids (PAs). Hydroxydanaidal is found in the male coremata and may be a courtship pheromone; these results suggest that the compound used in the location of such plants and in courtship are one and the same (104).

**ASSESSMENT OF DEFENSIVE FITNESS OF MALES** The hypothesis that females of some species assess, through his hair-pencil display, a male's ability to locate, imbibe, sequester, and possibly even deliver defensive chemicals in his ejaculate (49, 62, 63) deserves further scrutiny. As pointed out by Baker (5) this hypothesis is inherently untestable because it posits a motive on the part of the female. He also noted that evidence that runs counter to this hypothesis exists in the extensive data on danaid butterfly courtship compounds, including the strongly male-biased adult feeding on plants containing PAs and the apparent lack of cardenolide use by males in their displays (5). Thus, a discussion of such butterflies is relevant here.

Why is there a male bias in adult feeding; why do females not visit PA-containing plants and augment their own chemical defense and that of their offspring? The Queen butterfly, *Danaus gilippus*, nicely illustrates this problem. Pliske (145) reported that only males feed on the available *Crotalaria*, *Eupatorium*, *Heliotropum* and *Senecio* plants rich in PAs. He recorded over 400 males feeding on such plants (no females). Adult males need to obtain PAs for danaidone synthesis. Males without this courtship pheromone are only 20% as successful as males containing danaidone (146).

It should pay *D. gilippus* females to feed on these compounds directly from the plants rather than take the unnecessary risk of waiting for an insufficiently endowed male to give them to her. The risk of predation while searching for such plants should be minimal: both sexes are already protected with cardenolides ingested as larvae (40, 42). They also benefit by being conspicuous, because bird predators learn quickly to avoid all members of the population (42). In addition, if PAs augment the cardenolide defense (62, 63), it would seem that egg-bearing females need more protection than males, and females should take every opportunity to imbibe PAs for themselves.

Interestingly, the male bias in adult feeding on PA-containing plants extends also to the monarch butterflies, *D. plexippus*, although the overall frequency of visits by males is very low compared to *D. gilippus* (145). The

male hair-pencils of the monarch do not contain danaidone, the PA-derived courtship pheromone used by *D. gilippus* and *Lycoreia ceres* (33, 60, 61, 119, 120). Monarch males do not need this compound for successful mating, although it is often overlooked that 33% of males gave a hair-pencil display and evoked settling by females without their being forced to alight (144). The chemicals inducing female quiescence, if any, are not known. As in *D. gilippus*, it would seem unnecessary for males to display evidence of defensive ability or pass on PAs to females, when they would do better to get them themselves.

Another question involves cardenolides; if male hair-pencil displays evolved to indicate defensive prowess, why aren't cardenolides or their metabolites used? Cardenolides are the most powerful and best-studied defensive compounds in insects, yet curiously, danaiids that feed on them do not display to females how much they have ingested. The ability of *D. gilippus* butterflies to sequester cardenolides from their *Asclepias* host plants as larvae is nearly as good (77%) as that of monarchs (41), yet instead males visit other plants to acquire PAs for manufacturing danaidone. Edgar et al (59) hypothesize that the reason for the male bias in danaid butterflies visiting plants rich in PAs may be the plants' status as former host plants. Males need to obtain the associated odor itself, consisting of danaidone, hydroxydanaidal, or danaidal in order to provoke females to alight, a process based on this hostplant preference-linked courtship system that has persisted due to the courtship value alone (5, 59).

For male butterflies an extra benefit may accrue to PA-ingesting males in the form of defense because some species do evert their hair-pencils during handling (124, 125). In butterflies, this behavior only occurs in a few genera (*Lycoreia*, *Ituna* and in the *Euploea*) (42, 44), but, curiously, not in *Danaus* (42). Again, the male bias is surprising because females should have a greater need than males for a large concentration of these compounds and the associated warning display. Thus, these displays may be only of secondary value in defense; the male bias may indicate that the primary value is as a courtship display.

An extra fitness-related factor that could promote preference by females for PA-emitting males is the potential transfer of PA-based protection of eggs from males to females (51, 62, 63). However, data from a recent study (57) show that the PAs transferred by males to females in their ejaculate did not enhance the defense of *U. ornatrix* eggs unless the female was completely devoid of PAs herself, a situation that apparently cannot occur in nature because they are obligate feeders on *Crotalaria* spp., all of which have at least some level of PAs in their tissues (5).

It is interesting that in another species, *Pyrrharctia isabella*, a value for passage of PAs via the ejaculate to the female has now been demonstrated,

and it lies not in defense but in the pheromonal competence of the sons (106). This species is only a facultative feeder on PA-containing plants, and thus under field conditions there may be adult females lacking PAs in their body tissues. When PA-deprived females were mated with PA-fed males, the coremata of their male offspring were able to evoke the ultrasonic click from females that indicated they had detected the pheromone, hydroxydanaidal; male offspring from parents that had both been deprived of feeding on PAs were unable to evoke this response (106). Thus, as Baker (5) argued, the evidence in moths suggests that nuptial transfer of PAs has evolutionary significance due to this transfer's transovarial pheromonal value, and not to its defensive value. There is a direct inheritance of male signalling competence, in this case the very chemicals themselves from the father through the mother's egg.

These findings (106) support still further the hypothesis that whatever the fitness-related factor triggering the initiation of a female preference, the evolution of male lepidopteran pheromones proceeded primarily by the inheritance of the mating advantage by sons, gained from the chemical's pheromonal effect (5, 6). Such transovarial transfer of pheromonal competence should be looked for in species, such as in the Danainae, which practice male-biased adult feeding on PA-containing plants; the adult females are devoid of PAs initially (5). This perhaps reveals that the true value of PA acquisition by males and discrimination of it by females is in the direct transfer of the chemicals from females to their sons (in addition to the genetic transfer of the behavior) to ensure mating competence in the next generation (5).

**OTHER POTENTIAL LINKS WITH PARENTAL INVESTMENT** Apart from endowing eggs with defensive compounds, another possible fitness-related factor linked to the courtship pheromone might be the amount of nutrients to be passed to the female in the male ejaculate. These would include proteinaceous materials in the accessory secretions which could aid oogenesis and hence fecundity. Greenfield (82) demonstrated via radiolabelling studies that males of *Plodia interpunctella* do pass proteinaceous materials in their ejaculate to females, who incorporate these compounds into their eggs (82). Larger males produce more ejaculate, and females mate more frequently with them. However, females that received a larger ejaculate were no more fecund in terms of number of hatched eggs laid than those females that had mated with smaller males (82). Thus, no fitness advantage was to be gained by mating with males that gave females a greater amount of nutrients, but a potential advantage remains to females that choose larger males if such males transfer more courtship chemicals (see next section).

### *The Nature of the Selective Force*

Although Baker & Cardé (6) viewed the mating advantage of hair-pencil-competent males as evidence of female choice, their evidence of the sexual selective nature of the process remained speculative, resting on the fact that so many of the structures appeared to be grossly exaggerated scales and highly modified appendages that could have resulted from runaway sexual selection. They viewed the sporadic occurrence of the structures across groups, even within genera, as further proof of the effects of rapid, runaway sexual selection.

However, there is now direct evidence for sexual selection in at least one species. Females of the tobacco moth, *Ephestia elutella*, preferentially mate with larger males, which also contain approximately twice as much wing-gland courtship pheromone as do small males. Females actively reject smaller males (140). In courtships with large or small males that were allowed an equal chance to proceed indefinitely without copulation due to the removal of one clasper from each male, females terminated courtship with smaller males after only three bouts, whereas they allowed large males to proceed through over fourteen bouts. Females that mate with larger males were shown to benefit in several ways. They produced larger offspring than females that mated with smaller males, and thus the larger sons in the next generation would also be expected to be at a mating advantage. Also, such females produce more offspring, and their daughters are larger, which further improves inclusive fitness (140).

If female-choice sexual selection results in higher pheromone emission displays by larger males, why aren't all displays and males equally grand in size? The existence of alternative routes to mating success may be the answer: Smaller males or males with deficient displays find a way to mate successfully (3). If this ability is heritable, then this will maintain diversity in the mating system, in which smaller as well as larger males can mate successfully. An example is found in *G. molesta*, in which the elaborate, usually obligatory, hair-pencil display is sometimes not used by males that arrive at a female during a display by a first-arriving male (3). Such late arrivals will "sneak" a copulation by intercepting a female walking towards the first male's hair-pencil display. If successful, the sneak mating occurs without regard to the sneaky male's hair-pencil pheromone, and thus these males could possibly pass on this sneaky ability, and potential lack of pheromone to their sons. The variation does not appear to occur necessarily only across the population; it also occurs within individuals, because the same males that practice an alternative mating behavior such as sneaking, often later display their hair-pencils and successfully mate in the conventional way (3).

The question of sexual selection also arises in the disappearance of displays. From a review across families (24, 78), it can be seen that many of these scents and structures are apparently in a state of atrophy. Some are completely vestigial, where only the pocket exists, with no scent scales, or at least no glands to produce the scent (24, 78). In other species the scent, even the pheromonal integrity of the scent in evoking a female behavior, is operational, yet the female mating discrimination is apparently lacking (105).

A case in point is the above-described *Phragmatobia* and *Pyrrharctia* systems (103, 105). These species are facultative feeders on PA-containing plants, and their host ranges include many other types of plants, including grasses. Krasnoff (102) hypothesizes that the primitive condition was one of obligate PA feeding when these moths' ancestors were found only in the tropics and that there has been a "trend away from host-plant specialization towards the more generalized feeding habit that characterizes the arctiinae lineage, to which they belong." Krasnoff & Roelofs (105) hypothesize further that the use of danaidal and hydroxydanaidal during courtship has atrophied due to the link between the host odor and courtship pheromone and the shift in preference by females of these species away from PA-containing plants.

The monarch butterfly hair-pencil system is also viewed as vestigial (63, 144). Then there is also the above mentioned possible loss of hair-pencil pheromone function in oriental fruit moths after more than 13 years of laboratory breeding in densely populated mating boxes (115). Lastly, *M. brassicae* moths, from a semiwild stock reared for only three generations on artificial diet, used their hair-pencils in courtship, and males with their hair-pencils removed were less successful in mating (G. Poppy, unpublished observations). Prior to this, when using an inbred stock Birch et al had not found any difference in success, nor were the hair-pencils everted (31).

Vestigiality makes sense with regard to the capricious nature of sexual selection, the rapidity with which it proceeds (131, 132), and the possible waxing and waning of different female preferences arising at different times. The apparent vestigiality needs further scrutiny. In contrast to most female sex pheromone systems, in which emission is required for mating, male courtship pheromone is rarely obligatory, even in such classically overt male pheromone systems as the Queen butterfly or *Utethesia ornatrix* (49, 143). Usually 20% or more of those males completely lacking detectable amounts of the pheromone still manage to mate. In most experiments the differences in mating success between males whose scent structures have been ablated and those that were sham-operated are rarely more than 50% in favor of the latter. Thus, the ready acceptance of pheromone-deficient males by females always occurs, even in nonvestigial systems. It would only take an event favoring females that execute such a choice to promote selection toward pheromone loss. If we understood why so many courtship pheromones were



lost, we might better understand how such systems were initiated. The subject of female preferences for males is greatly neglected.

Another system that accords with sexual selection theory is lekking, or male aggregations. It is clear that even in the majority of species that do not use leks, male-emitted scents attract, not repel, conspecific males. In the Oriental fruit moth, late-arriving males are attracted at close range by each other's pheromone (3). Sometimes they display simultaneously at a single female. It is possible that in species in which solitary pheromone-emitting males attract females from a distance, other males might be attracted to the area and begin emitting pheromone, thereby increasing the chance that available females would arrive at that location (111). Also, as runaway selection proceeds, males may reach a physiological and anatomical limit in their ability to emit more pheromone (4). The fact that males of species that form leks possess the largest eversible structures known thus far is consistent with the hypothesized solution that the need for higher emission rates leads to forming groups (4). In the hepialid moth, *Hepialus sequoiolus*, an increase in the number of pheromone-emitting males does help to attract more females (172). The pheromone emission rates are not known for these species but could be correlated with size of the individual and hence surface area. At this point in the progression, if the female preference for yet higher amounts of emitted pheromone is elevated another notch by the success of males that join leks and add to the emissions, then the benefits of joining outweigh those of emitting pheromone solitarily. To emit solitarily might be in effect not to emit at all, given the elevated thresholds of the females. Another factor favoring male aggregations is that the attraction of extra males to emitting males also would be favored if some late-arrivals had little or no scent to emit, because they would gain by intercepting females attracted to the first male's display, and thus would act as satellite males. Thus, there are many reasons why male leks should occur, given the initial evolution of attraction of females to single males.

#### *The Nature of the Initiation of Female Preference: Adaptive or Incidental?*

The discussion over whether the initial female preference for a male trait arises only as a result of forces from within a population, or as an adaptation against interpopulational mating mistakes, has direct bearing on the speciation process itself (142). Proponents of the former (incidental) model accept sexual selection as the mechanism driving both the trait and the female preference to extreme levels (165); so also do some of the proponents of the adaptive model (66, 142). The extreme levels presumably would become so high that mating with individuals from previously acceptable populations

would now be impossible. Thus, restricted gene flow among groups, and speciation, could occur.

In male moth courtship systems, evidence for the adaptive rather than the incidental origin of the female preference should include the finding that eversible structures are positively correlated with the potential for interspecific mating mistakes. This would come from, among other possibilities, cross-attraction of congenics that are sympatric and mate at the same time of the day or night. There are many examples in the above review of males with functional courtship pheromones involved in such cross-attraction with other species. For example, calling females often induce significant levels of cross-attraction in the stored-products moths in the Phycitinae (141), the genus *Grapholita* containing the Oriental fruit moth (6) and the genus *Yponomeuta* (89). Conversely, in some groups that lack known eversible male organs (some Sesiidae, for instance) there is no reported cross-attraction due to several factors, including differences in seasonal and daily times of activity, habitat differences, and specificity of the female sex pheromone itself (83, 85).

Data concerning the probability of cross-specific courtship is of course difficult to obtain and mostly lacking for moths. Phelan & Baker (142), however, reasoned that records of two congeneric species sharing source host plants should be the best available indication that cross-courtships could occur, because of the ties to geographic region, habitat, and seasonality. They also scored males for the presence or absence of scent organs. They found a significant positive correlation between overlap of host plant and possession of such male organs in all but one of the groups they examined. They considered this to indicate an adaptive origin of female preference. Of course the specificity of the sex pheromone blends of two species sharing the same host plant, as well as their times of sexual activity, are not available from the host records, and so error will result. However, such error should obscure, rather than enhance, the positive correlation that they found, as would lack of knowledge of whether eversible structures were functional.

Baker (5) pointed out that even the danaine butterflies support the adaptive origin of female preference, due to possible long-distance visual cross-attraction among individuals in mimicry complexes associated with these distasteful, mostly aposematically colored, insects. This idea was first discussed by Boppré (33), although he did not include sexual selection as part of the evolutionary pathway. The adaptive response to interspecific mating mistakes (6, 142), by members of a mimicry complex that all rely primarily on vision to make their long-distance approach to females, could trigger a female preference based on odor. This would allow the individuals to maintain their visually similar appearance (33) for purposes of defense based on cardenolides (59), while sexual selection could drive PA-based courtship systems to extremes (6).

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