THE AMERICAN MONARCH: COURTSHIP AND CHEMICAL COMMUNICATION OF A PECULIAR DANAINE BUTTERFLY

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ABSTRACT. The androconial organs, courtship behavior, and the roles of chemical signals and allelochemicals in *Danaus (Danaus) plexippus plexippus*, the American monarch, are discussed in comparison with other danaine butterflies. In the monarch, and in other members of *Danaus* sensu stricto, a change in mating strategy has evolved so that chemical communication plays a minor role in comparison with butterflies in other danaine genera. To date, there is no plausible explanation for this curious evolutionary change because many basic questions on the behavioral and chemical ecology of the monarch remain unanswered.

The monarch butterfly could well be designated nature's prime example of the male chauvinistic pig.
Miriam Rothschild (1978)

INTRODUCTION

Considering how much is known about the biology of the monarch butterfly, *Danaus (Danaus) plexippus plexippus* (L.), it is curious how poorly understood courtship and chemical communication is in this widely distributed species. The literature on these aspects of monarch biology is strikingly scant, and one can summarize the available information almost in one sentence: Compared to most of its danaine relatives, *D. plexippus* has abolished elaborate androconial organs and complex courtship rituals, as well as complex bouquets of male pheromones; instead, it employs comparatively simple mating behavior where male pheromones play a minor role and in which rape is common.

This paper reviews evidence for the simplicity of monarch reproductive behavior and compares the morphology, histology, and chemistry of the androconial organs of *D. plexippus* with some other danaines. Because little information on the behavioral and chemical ecology of reproduction in the American monarch is available, neither its sexual peculiarities can be interpreted from an ecological perspective, nor is an evolutionary explanation yet possible. The discussion and the new data establish the questions that require investigation, and my aim is to stimulate further work on the monarch's sex life.

The chemical ecology of the subfamily Danainae, the milkweed butterflies, as well as their reproductive biology, has recently been reviewed extensively by Ackery and Vane-Wright (1984) and Boppré (1978, 1984a, 1986).

MALE SECONDARY SEXUAL CHARACTERS— RUDIMENTARY FEATURES?

MORPHOLOGY AND HISTOLOGY OF MONARCH ANDROCONIAL ORGANS

Binate androconial organs, used to secrete and disseminate pheromones during courtship, are one of the basic characters of the Danainae. The males possess extrudable abdominal "hairpencils," and in most species they are also equipped with alar glands. Male *D. plexippus* possess hairpencils as well as wing pockets, and their basic morphology has long been known (Müller, 1877 [see Fig. 1]); Illig, 1902). More recent investigations (Hausman, 1951; Urquhart, 1958, 1960, 1976) have added little information to the widely "forgotten" early papers. Instead, our understanding of the "scent organs" in the American monarch is confused and even misleading in part. Therefore, I summarize and illustrate the basic morphology and histology of monarch androconial organs (cf. Boppré and Vane-Wright, 1989, for basic features of danaine androconial organs and terminology).

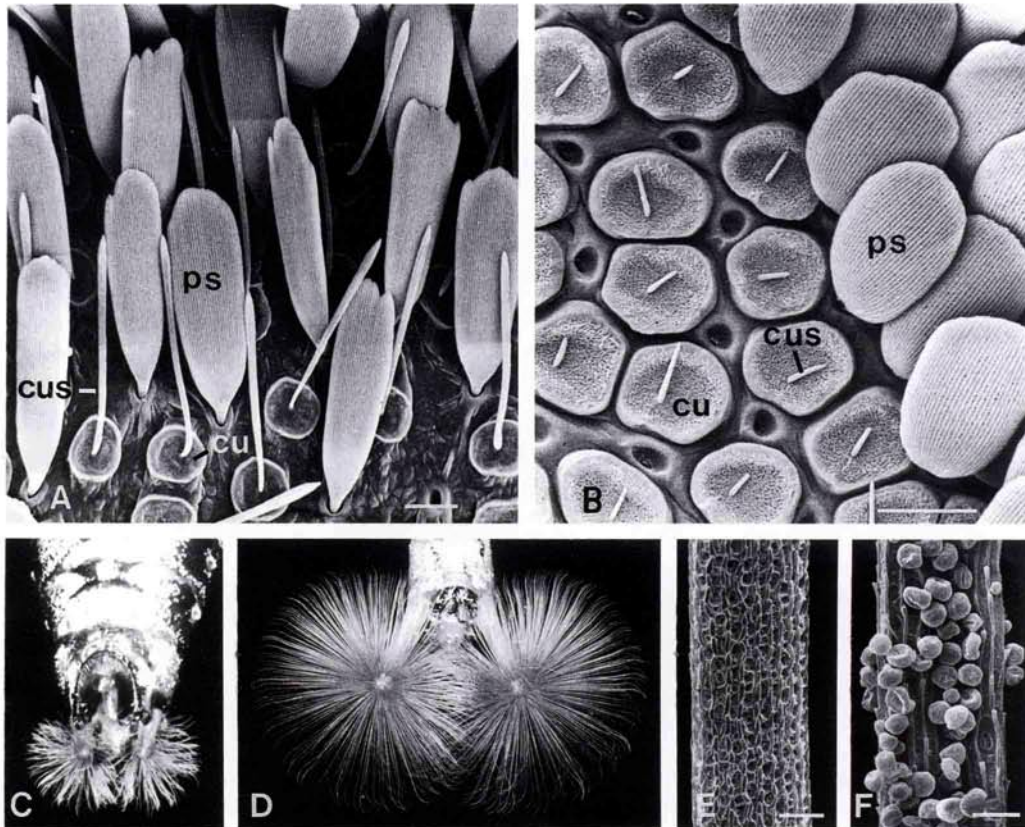The alar androconial organs of *D. plexippus* are
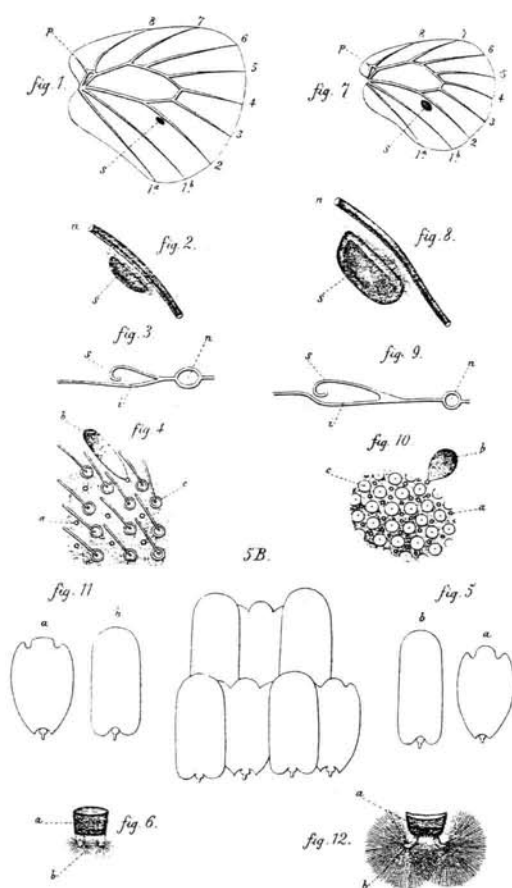
Figure 1. Figure reproduction from Müller (1877) comparing the androconia of *D. erippus* (1–6) with that of *D. gilippus* (7–12). (*Danaus* (*Danaus*) *erippus* and *D. plexippus* are similar; *D.* (*Anosia*) *gilippus* resembles *D.* (*A.*) *chrysippus*.) 1 and 7, position of pockets on hindwings; 2 and 8, magnified pocket (3.2×); 3 and 9, transverse section through pocket (9.7×); 4 and 10, pocket scale, cushions, and cushion scales inside pockets (120×) (cf. Fig. 2A and 2B); 5 and 11, ordinary scales from the upper surface of the hindwings (120×); 6 and 12, expanded hairpencils (1.3×) (cf. Fig. 2C and 2D).

located on the hindwings adjacent to vein Cu_{1b} and show up as pocketlike cavities (folds of the upper wing membranes) with orifices toward the inner margin of the hindwings (cf. Fig. 1.1–1.3). The inside of these alar pockets (Figs. 1.4 and 2A) is lined by "pocket scales," which (1) are larger and less densely arranged than the ordinary covering scales (Fig. 1.5) and (2) have a double lattice structure (cf. Boppré and Vane-Wright, 1989). Intermittently, roundish projections ("cushions") occur, each with a long hair ("cushion scale") arising from the center (Figs. 1.4 and 2A). While the alar organs of *D. plexippus* and *Danaus chrysippus* are located on corresponding hindwing areas and are made of the same structural elements (cf. Fig. 2A and 2B), the

pockets of the two species differ significantly in their histology: In *D. chrysippus* the cells under the pocket scales are the most prominent structures (Fig. 3B), but in *D. plexippus* large cells occur under both pocket scales and cushions (Fig. 3A; see also Figs. 4 and 5, and respective legends). In addition, vein Cu_{1b} of the monarch contains specialized cells (like other danaines) and is, thus, strikingly different from all other veins, as well as from all female wing veins. Hence, vein Cu_{1b} must be considered as part of the androconial organs.

The hairpencils are usually hidden inside the abdomen, but they can be everted by hemolymph pressure from the end of the abdomen to appear as two spheres of hair at the tips of stalks (Figs. 1.6 and 1.12 and 2C and 2D). In *D. plexippus*, each hairpencil consists of about 400 hairs, which are 2.1 mm long and 10 μm in diameter (Table 1), and their surface is sculptured (Fig. 2E). Viewed macroscopically, hairpencils of the monarch appear miniaturized compared to those of other danaines such as *D. chrysippus* (Fig. 2D), which has about 1,300 hairs, each 4.5 mm long (Table 1). Unlike *D. chrysippus*, *D. plexippus* also possesses only one type of hair and lacks pheromone-transfer particles (PTPs) (cf. below and Fig. 2E and 2F) entirely. Histologically, the hairs are very similar to *D. chrysippus*, and in freshly hatched males (<24 hr) prominent cells (80 × 25 μm) are found beneath the sockets of the hairs, which contain large nuclei and microvilli. These cells appear very similar but are slightly larger in *D. chrysippus*, at approximately 115 × 30 μm (Table 1), and in both species they are probably glandular and release a secretion into the hair shafts. In contrast to the glandular cells of the alar pockets, the hairpencil cells atrophy very early in adult life. *Danaus plexippus* also differs in that the glandular cells contain round to oval inclusions of 1–2 μm, and their number increases with age. At present, these inclusions cannot be properly interpreted, and their possession of a capsule and a membrane contradicts the assumption that they would represent secretions. Nevertheless, they appear to be typical for the monarch and were found in preparations of both indoor-raised and field-caught males (O.W. Fischer, pers. comm.).

In all other Danaini, except *Danaus* sensu stricto, both the hairpencils and the alar organs are much larger compared to those of *D. plexippus*, and often they are very elaborate (Boppré and Fecher, 1977; Boppré and Vane-Wright, 1989). For example, the hairpencils of *Amauris* comprise up to five structurally different hair types, which unfold sequentially. The Amaurina and the genera *Danaus* (*Salatura*), *Danaus* (*Anosia*), and *Tirumala* produce (in different ways) cuticular, pheromone-bearing particles, or PTPs (Boppré, 1976), which are disseminated during courtship behavior. In comparison with such specialized and complex structures, the androconial organs of *D. plexippus* appear considerably less complex and unspecialized. Nevertheless, the abdominal and alar secondary char-

Figure 2. Scanning electron micrographs (**A, B, E, F**) and macrophotographs (**C, D**) of androconial organs in *D. plexippus* (**A, C, E**) and *D.* (*A.*) *chrysippus* (**B, D, F**) to contrast respective structures. **A** and **B**, inside alar pockets (cu = cushion; cus = cushion scales; ps = pocket scales); **C** and **D**, artificially expanded hairpencil; **E** and **F**, hairpencil hair (Fischer and Boppré, unpubl. originals). Scale bars: **A** and **B** = 20 μm; **C** and **D** = ca. 3×; **E** and **F** = 5 μm.

acters in male monarchs consist of all the microscopical and histological elements, with the exception of PTPs, which are typical of androconial organs in all Danainae, and there are no signs of an atrophied secretory function in these structures. The organs are simply smaller in the monarch, and also in the doubtfully distinct species *Danaus erippus* and the *plexippus/erippus* sister-species *Danaus* (*D.*) *cleophile*. As can be seen in Boppré and Vane-Wright (1989), the androconial organs of *Danaus* sensu stricto are secondarily modified and do not represent an early stage of phylogenetic development.

CHEMISTRY OF MONARCH ANDROCONIAL ORGANS

With respect to the chemistry of the androconial secretions, prior to the recent study by Schulz (1987) there was little information available. Some authors reported that the hairpencils emit a "flower-like aroma" (Urquhart, 1958), or a "faint, fragrant odor" (Hausman, 1951). By chemical analyses, Meinwald et al. (1968, 1969) identified two bishomoterpenes ((*E,E*)-10-hydroxy-3,7-dimethyl-2,6-decadienoic acid and (*E,E*)-3,7-dimethyl-2,6-decadiendioic acid) in extracts of hairpencils. Bellas et al. (1974) found benzyl caproate, and a ketone with unknown configuration, in extracts of abdominal tips. Schulz (1987) reinvestigated the hairpencils and found, in addition to the above-mentioned chemicals, numerous acetogenins, aromatic esters, and terpenoids in extracts of hairpencils. In extracts of alar pockets, he detected only traces of the major hairpencil compounds but larger amounts of ubiquitous fatty acids and hydrocarbons, which are typical cuticular components. Table 2 lists the compounds and Figure 6 shows representative gas chromatograms (cf. Schulz, 1987).

Compared with other danaine butterflies (Schulz, 1987; Schulz et al., 1988; see also Ackery and Vane-Wright, 1984), the American monarch thus seems similarly equipped with chemicals that could serve as male pheromones. However, male *D. plexippus* lack plant-derived dihydropyrrolizines, which are the characteristic, major hairpencil components in
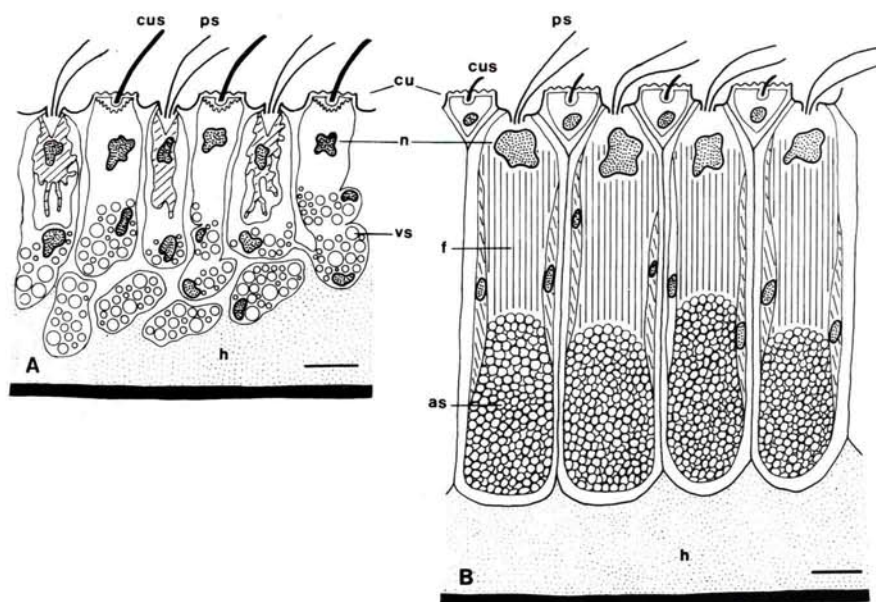
Figure 3. Schematic sketches of the cellular situation in the alar pocket of *D. plexippus* (**A**) and *D. chrysippus* (**B**), reconstructed from light and electron micrographs (O.W. Fischer, unpubl.). Within the area of a pocket, the space between the wing lamellae is widened and filled with hemolymph (h) as well as with prominent cells, aligned toward the lumen of the pocket and containing large nuclei (n). Two major differences between the species are evident: (1) the cells underneath the cushions (cu) are very small in *D. chrysippus* but prominent in *D. plexippus*; and (2) the intermittently located cells underneath the pocket scales (ps) in *D. chrysippus* contain an amorphous substance (as) at their bases, and fibrous structures (f) medially, while in *D. plexippus*, all cells are filled with vesicles (vs). In addition, the arrangement of the glandular cells in *D. chrysippus* is quite regular, while in *D. plexippus* the basal parts of the cells form interleaved processes. Because the cellular structure of the alar organs undergo marked differentiation during the first days of adult life, 14-day-old males were used for comparison. The thick black line marks the cuticle of the outer wing membrane. Scale bar = 20 μm.

other Danainae (see below). Apart from dihydropyrrolizines, the bouquets of volatiles released by male danaine hairpencils are not understood functionally. They may serve a role in species recognition, but proof is most difficult to establish, and comparison with other danaine butterflies does not help interpret monarch behavior.

Thus, in contrast to previous understanding, the histology and chemistry of androconial organs in the monarch do not indicate that chemical communication should be less elaborate than in other species of the subfamily. However, more detailed comparisons among danaine androconia are required for a fuller interpretation.

## BEHAVIORAL USE OF ANDROCONIAL ORGANS— NO FUNCTION?

In most species of the tribe Danaini, male hairpencils in general are used in two different contexts. First, independent of courtship, hairpencils are protruded and introduced into the alar pockets, or fanned out on the alar patches. For *D. chrysippus*, it has been demonstrated that this contact behavior

is required for biosynthesis of the important pheromone component "danaidone" (see below) in physiologically normal amounts. For *Tirumala* species, similar mechanical contacts between the two organs load the hairpencils with PTPs produced in the alar pouches. Second, during the last phases of courtship flight, a male briefly expands its hairpencils close to a female's antennae and disseminates the volatile secretions and PTPs.

Other danaine groups (e.g., *Lycorea, Euploea*) either have no alar organs or contact behavior has never been observed. However, after visual courtship initiation, the use of hairpencils in close-range stimulation of the female with pheromones seems generally to be required by the female to accept a mate. The most detailed proof for the importance of hairpencil secretion comes from studies on *Danaus gilippus berenice* by Brower et al. (1965) and Pliske and Eisner (1969). These authors clearly demonstrated that hairpencilling by the male is a necessity for successful courtship and, moreover, that danaidone is a key stimulus. Although the behavioral role of hairpencils may be partially modified in other danaine species, the findings obtained with *D. gilippus* basically seem to hold true for
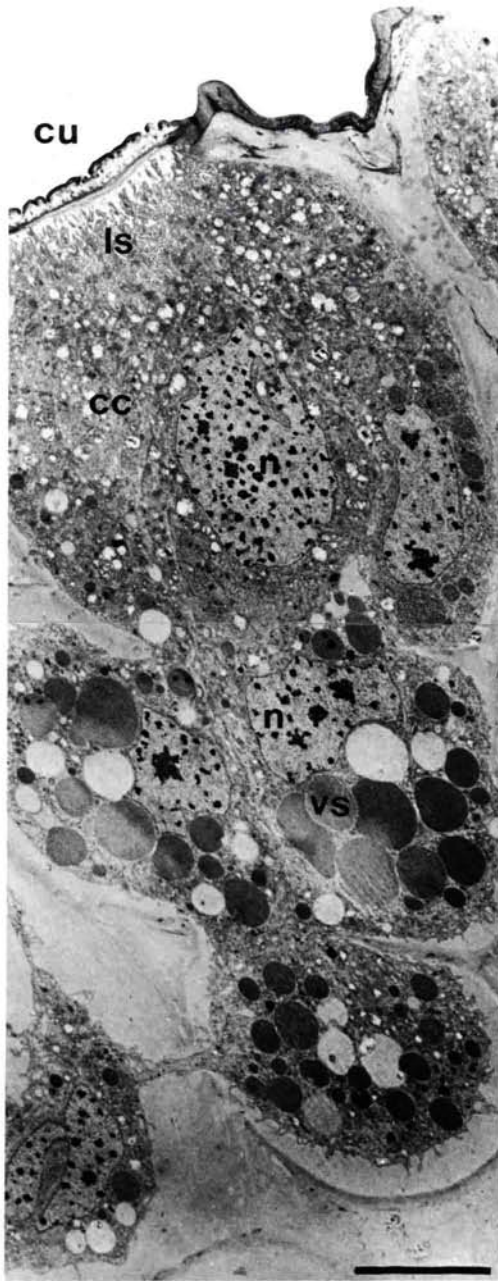
Figure 4. Transmission electron micrograph of an alar pocket of a 14-day-old *D. plexippus* male showing the functional unit of glandular cells underneath the cushions (cu) (cf. Fig. 3A). A central cell (cc) is bordered with a heavily lamellated structure (ls) at the thin, perforated cuticle of the cushion and shows many empty vacuoles. Basal to the central cell, further interlaced cells occur, characterized by numerous vesicles (vs), which appear gradually during adult life (O.W. Fischer, unpubl. original). n = nucleus. Scale bar = 10 μm.
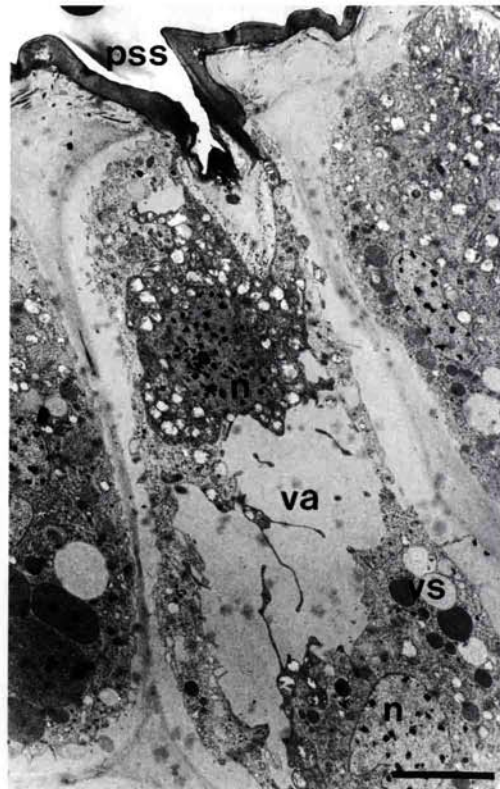
Figure 5. Transmission electron micrograph of an alar pocket of a 14-day-old *D. plexippus* male showing glandular cells underneath a pocket scale (cf. Fig. 3A). The cell close to the socket of the pocket scale (pss) is characterized by dense cytoplasm and a prominent nucleus (n) and is surrounded by the glandular cell type shown in Figure 4, with which it is also connected (O.W. Fischer, unpubl. original). va = vacuole; vs = vesicles. Scale bar = 10 μm.

most danaines (Seibt et al., 1972; Boppré, 1977; Boppré and Schneider, unpubl.). However, thorough analyses have not been performed.

In contrast to other Danaini, androconial contact behavior has never been observed in the American monarch, and Urquhart (1960) believes that it does not occur. Despite speculation by Urquhart on the role of the androconial organs, no evidence indicates a function. Male "hairpencilling" during courtship is not required, because when hairpencils are removed artificially there is no reduction in sexual vigor or "courtship" success (Pliske, 1975b); nevertheless, the abdominal organs are occasionally expanded prior to copulation (see the next section).

RAPE—AN ALTERNATIVE TO SEDUCTION?

The mating behavior of *D. plexippus* was analyzed in detail by Pliske (1975b; Fig. 7). According to this study, monarch courtship has an aerial phase and

Table 1. Comparison of morphometric data of alar and abdominal androconial organs in *D. plexippus* and *D. chrysippus* (Fischer and Boppré, unpubl.).

	D. plexippus	*D. chrysippus*
Alar organs		
Size of pocket scales (μm)	70 × 15	50 × 30
Cushion diameter (μm)	20	23
Cushion density (mm^{-2})	≈500	≈1,000
Size of cushion scales (μm)	55 × 2	7 × 1
Abdominal organs		
Hair diameter (μm)	10	10
Hair length (mm)	2.1	4.5
Number of hair types	1	2
Pheromone-transfer particles	no	yes
Number of hairs	≈400	≈1,300
Size of glandular cells (μm)	≈80 × 25	≈115 × 30

a ground phase. The aerial phase includes nudging, pursuit, hairpencilling, and takedown behaviors by the male, and the ground phase concludes courtship with landing and antennal palpation by the male, followed by copulation and postnuptial flight. Unlike other, closely related danaines, hairpencilling is not necessary for male reproductive success and occurs only in some courtships. Instead, aerial takedowns predominate.

The literature also contains several observations on parts of *D. plexippus* mating behavior. Urquhart (1960) describes male aerial pursuit of females to which females either respond with an ascending, pre-nuptial spiral flight or a fast, zig-zag escape flight. Like Urquhart (1960), Miller and Clench (1968), Pliske (1975b), Hill et al. (1976), Rothschild (1978), and Shull (1979) recorded male monarchs as the active partner in courtship. Hill et al. (1976) also described male aerial pursuit of other monarchs, followed by capture, rapid descent to the ground, and contact discrimination between male and female. Attempts at copulation on the ground were vigorous, and males occasionally extruded hairpencils during struggles with females.

In her account of male monarch mating behavior, Rothschild (1978) emphasizes the apparently indiscriminate and violent chauvinism often observed in both intra- and interspecific interactions with reproductively active males. Like Rothschild's (1978) observations, there are several reports of faulty discrimination by males (see also Van Hook, this volume). Tilden (1979) noted numerous attempts at mating between male monarchs at an overwintering site in California during dispersal from the site when sex ratios are strongly male-biased (see also Van Hook, this volume). Winter (1985) illustrated a male

monarch pinning a *Vanessa virginiensis* to the ground after the monarch had attacked the nectaring butterfly.

Although Tuskes and Brower (1978) and Brower (1985) assumed that monarchs mate randomly at overwintering colonies in Mexico and California as the butterflies disperse in spring, Van Hook (this volume) shows that they do not mate randomly. Instead she found that the aggressive mating behavior of small, worn males resulted in their nonrandom copulation with large females in good condition. Such active aerial pursuit and takedown of females by males precluded female mate choice. Furthermore, Zalucki (this volume) shows that male presence at patches of host plants also influences mating patterns.

All these reports are basically consistent with Pliske's study, and there is little doubt that the American monarch has drastically changed its mating strategy from the typical danaine pattern. Although its courtship contains elements that are found in other Danainae, the monarch is unusual in the absence of both female choice and use of pheromones during courtship.

PLANT CHEMICALS— REQUIRED TO INCREASE FITNESS!?

It is another basic feature of danaine butterflies that males, and in a few species occasionally females, are strongly attracted to withering and decaying parts of plants containing pyrrolizidine alkaloids (PAs) and that they ingest these secondary plant chemicals (for review, see Boppré, 1986). PAs are required by the males for biosynthesis of dihydropyrrolizine pheromone components such as "danaidone," "danaidal," and/or "hydroxydanaidal," which make up the quantitatively major components of the hairpencil secretion (up to 500 μg) in the majority of Danainae, and appear as key chemicals in female mating decisions. Not only is male courtship success thus dependent on the plant chemicals, but the insects also store unconverted PAs in their body as a distasteful protective device against predation (see below).

Danaus plexippus can also be seen visiting dead and decaying PA plants, particularly *Senecio*, *Heliotropium*, *Crotalaria*, and *Parsonsia* (Edgar et al., 1973, 1974; Pliske, 1975a), and they gather PAs with nectar from plants such as *Eupatorium* (Edgar et al., 1976). Rothschild and Edgar (1978) have also shown that the larvae of both sexes of *D. plexippus* can sequester and store PAs sprayed onto a milkweed host plant, but that males store more PA than females. However, despite such abilities to handle PAs in *D. plexippus*, numerous investigations have clearly demonstrated that hairpencils of monarchs do not secrete PA derivatives (Meinwald et al., 1968; Edgar et al., 1971; Schulz, 1987).

Edgar et al. (1976) found unmodified PAs in extracts of the bodies of field-caught *D. plexippus* and first suggested that PAs might contribute to the

Figure 6. Gas chromatograms of methylated extracts of pockets (upper trace) and hairpencils (lower trace) of *D. plexippus* (50m CP-sil-8-CB, programmed from 60–300°C with 3°C/min) (original, courtesy of S. Schulz).

Table 2. Compounds identified from extracts of andro-
conia (hairpencils and alar pockets) of *D. plexippus* (cour-
tesy of S. Schulz, Hamburg; cf. Schulz, 1987) (cf. Fig. 6).
* = tentative identification; +++ = major component;
++ = minor component; + = trace component.

	Hair-pencils	Alar pockets
1 Heptanoic acid	+	
2 Contamination	+	
3 Benzoic acid	+	
4 Linalool	+	+
5 Nonanal	+	
6 Oxoisophorone	+	
7 Nonanoic acid	+	
8 Ethyl benzoate	+	
9 Methyl salicylate	+	
10 Decanoic acid	+	+
11 Nerolic acid	+	
12 Geranic acid	++	
13 Undecanoic acid	+	
14 Benzyl butanoate	+	
15 Benzyl pentanoate	+	
16 (1R*, 3R*, 6S*)-1,3,7,7-Tetra-methyl-2-oxabicyclo[4.4.0]-9-decen-7-one	+++	+
17 2-Phenylethyl pentanoate	+	
18 Pentadecane	+	
19 Benzyl caproate	+++	+
20 Lactone	+	
21 (E)-Nerolidol	+	
22 Unknown terpene	+	
23 2-Phenylethyl caproate	+	
24 Unknown compound	+	
25 3,7-Dimethyl-10-hydroxy-2,6-decadienoic acid	+	
26 (E,Z)- and/or (Z,E)-α-Farnesol	+	
27 3,7-Dimethyl-10-hydroxy-2,6-decadienoic acid	++	
28 (E,E)-α-Farnesol	++	+
29 Myristic acid	++	+
30 Benzyloctanoate	+	
31 Contamination	+	
32 (E,E)-3,7-Dimethyl-10-hy-droxy-2,6-decadienoic acid	+++	+
33 (E,E)-Methyl farnesenoate	+	
34 Unknown compound	+	
35 (E,E)-3,7-Dimethyl-2,6-deca-dien-1,10-dioic acid	+++	
36 14-Hydroxy-3,7,11-trimethyl-2,6,10-tetradecatrienoic acid*	+	
37 Pentadecanoic acid	+	+
38 Contamination	+	+
39 Hexadecenoic acid	+	++
40 Palmitic acid	+++	+++
41 Heptadecanoic acid	+	+
42 Octadecadienoic acid	++	+++
43 Octadecatrienoic acid	+++	+++
44 Octadecenoic acid	+++	+++
45 Stearic acid	++	+++
46 Tricosane	+	
47 Eicosanoic acid	+	++
48 Pentacosane	+	++
49 Docosanoic acid	+	++
50 Heptacosane	+	++
51 Tetracosanoic acid	+	+

unpalatability of the species. Kelley et al. (1987) found that female monarchs overwintering in Mexico contained more PA than males (means of 119 and 59 µg, respectively), and that monoesters comprised 90% of the PAs identified. Of the monoesters, echinatine was the most abundant in males and lycopsamine was the most abundant in females. Two macrocyclic diesters were also found in most monarch samples. Recently, Stelljes and Seiber (1990) also reported details of PA sequestration by monarchs overwintering in California and suggested that monarchs alter sequestered flower PAs to other PAs, like retronecine, that are more toxic to potential predators.

Since Edgar et al. (1976) suggested an additional defensive role for PAs, storage of PAs gathered by larvae and adult Lepidoptera of several families has been well documented (Edgar et al., 1979; Eisner, 1982; Brown, 1984a,b; Dussourd et al., 1984, 1988; for overviews, see Boppré, 1986, 1990). According to studies with various vertebrates, as well as invertebrates, PAs are taste-rejected, and it appears possible that PAs are the primary chemical defense of the entire danaine subfamily (see Ackery and Vane-Wright, 1984; Boppré, 1986, 1990; Glendinning, this volume; Schneider, this volume). Thus, in the Danainae in general, PAs establish a link between chemical communication and chemical defense. Individual differences in the amounts of hairpencil pheromones among males may reflect amounts of defensive chemicals gathered by males during adult life. An attempt to interpret this link was advanced by Eisner (1980) and Conner et al. (1981), who suggested that the amount of dihydropyrrolizine pheromone could be an indication of the defensive vigor of the male and, thus, decisive for the female in sexual selection.

Large amounts of PAs can be transferred from the male to the female via the spermatophores, as has been demonstrated for ithomiine butterflies, *Danaus gilippus*, and the moth, *Utetheisa ornatrix* (Brown, 1984a,b: Dussourd et al., 1984, 1988; Eisner and Meinwald, 1987). Thus, the male pheromone content might not only indicate to the female the defensive vigor of a pursuer, but also how much PA she can expect to receive from him during mating. However, it is yet to be proven that females actually discriminate among males on the amount of dihydropyrrolizine pheromones.

A lot more could be said about PAs in the context of sexual selection, but for *D. plexippus* these

plant-derived chemicals have become less important than for other danaines; in common with reduced androconia and reluctant use of hairpencils in courtship. Despite the retention of PA-gathering behavior in adult monarchs, PAs are not needed for male courtship success, and so male monarchs have become emancipated from the danaine dependency upon plant chemicals for reproductive success. Nevertheless, *D. plexippus* may utilize PAs as defensive chemicals (see also Glendinning, this volume, and Schneider, this volume); perhaps, male monarchs donate PAs to females with their spermatophores during mating to enhance protection of females and eggs (see also Wells et al., this volume).

A discussion of chemical defense of the American monarch is not possible without considering cardenolides (cardiac glycosides) (reviewed by Brower, 1984). The predation experiments of J.V.Z. Brower (1958), the pharmacological research of Parsons (1965), and the chemical characterization of Reichstein (1967) established the American monarch as the first proven case of secondary plant chemical use by insects as a defense against predators and heralded the discipline of "ecological chemistry" (Brower and Brower, 1964; Brower, 1969)—now more often referred to as "chemical ecology" or "chemoecology." In summary, milkweed host plants (Asclepiadaceae) of *D. plexippus* contain varying quantities and kinds of cardenolides. These are ingested by monarch larvae and retained and stored by the adults. The cardenolide content of a butterfly is thus a characteristic fingerprint of its larval host plant, although it is modified with respect to the kind and amount of cardenolide stored (see Lynch and Martin, this volume; Malcolm et al., this volume; Nelson, this volume). Cardenolides have been clearly recognized to protect *D. plexippus* from several potential predatory bird species. However, because the cardenolide content of monarchs depends on available host-plant cardenolides, there is a "palatability spectrum," with individuals ranging from completely palatable to highly unpalatable. Furthermore, because no protection is perfect, some predators can circumvent or tolerate the cardenolide-based defenses of monarchs (Arellano G. et al., this volume; Glendinning, this volume).

As important as cardenolide sequestration must be for *D. plexippus*, I am certain that PAs significantly enhance monarch defense against predation—especially for individuals with little, or no, cardenolide content and against cardenolide-tolerant predators. Apart from the chemical analyses by Edgar et al. (1976), Kelley et al. (1987), and Stelljes and Seiber (1990), no experiments have been performed on the defensive potency of PAs in *D. plexippus*. However, studies with other "PA insects" clearly demonstrate the defensive use of PAs (Eisner, 1982; Brown, 1984a,b; Vasconcellos-Neto and Lewinsohn, 1984; Dussourd et al., 1988). Therefore, these allelochemics must not be ne-
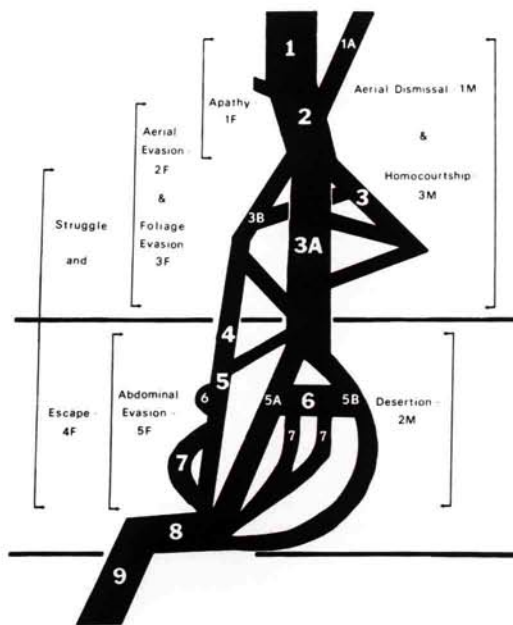
Figure 7. Sequence of mating behavior in *D. plexippus* (from Pliske, 1975b). The flow diagram illustrates monarch mating behavior: (1) male nudging, (1A) female nudging, (2) aerial pursuit, (3) aerial pounce, (3A) aerial takedown, (3B) aerial hairpencilling, (4) pair alighting, (5) lateral copulation attempt, (5A) dorsal copulation attempt, (5B) ventral copulation attempt, (6) antennal palpation (occurs with all copulation attempts), (7) female proboscis extension, (8) copulation, (9) postnuptial flight. 1–3 = aerial phase I, 4–8 = ground phase, 9 = aerial phase II. Brackets indicate female (left) and male (right) terminations.

glected when considering the ecology of chemical defense and communication in the American monarch.

Bird predation studies at the Mexican overwintering sites of the American monarch revealed that orioles and grosbeaks prey heavily on the butterflies (Calvert et al., 1979) and kill them randomly with respect to cardenolide content (Fink and Brower, 1981). Nevertheless, although most overwintering monarchs contain <1 emetic unit of cardenolide, observations of 98 oriole and 92 grosbeak attacks showed that 75 and 65, respectively, were released without apparent harm (Fink and Brower, 1981). Do such contradictory findings not indicate that a noncardenolide element is involved in the chemical defense of American monarchs? Most of the accepted butterflies may have been females since they seem to be reluctant PA-feeders and are likely to contain little or no PAs to enhance their chemical defense, particularly while they are unmated. Thus it is a pity that the sex of the eaten and rejected butterflies was not determined. However, it is interesting that Arellano G. et al. (this volume) found that grosbeaks killed more male than female mon-

archs at a Mexican overwintering colony, particularly in view of the fact that Kelley et al. (1987) found more PA in female than in male monarchs. This suggests that PAs do have a role in enhancing the chemical defense of overwintering monarchs, especially at a time when their cardenolide defenses are diminished (Malcolm and Brower, 1989).

It is also unfortunate that the series of force-feeding experiments (in which birds are fed powdered monarchs in capsules) were not designed to determine aversion to PAs, because, like cardenolides, their defensive potency is mediated by taste-rejection. However, Glendinning et al. (1988) and Glendinning (this volume) showed that one mouse species, *Peromyscus melanotis,* fed preferentially on male monarchs overwintering in Mexico (much like the grosbeaks described by Arellano G. et al., this volume). Presumably PAs in males had little influence on the foraging mice. Glendinning (this volume) also suggests that monarch consumption by *P. melanotis* was probably not influenced strongly by PAs, but that cardenolides were important in excluding three additional mouse species as predators of overwintering monarchs.

Despite different published conclusions as to the roles of PAs and cardenolides, research that takes both of these groups of chemicals into consideration, and includes possible synergism, is likely to make the story of sequestered plant chemicals that protect adult insects even more fascinating and instructive. In this context, it needs to be stressed that there are basic differences in the source and utilization between cardenolides and PAs and in their modes of action. Whereas cardenolides are ingested erratically with food by the larvae, PAs are actively searched for by adults and taken up independently of feeding behavior, i.e. pharmacophagously (cf. Boppré, 1984b). It also needs to be emphasized that the pharmacologically well-known noxious effects of PAs on vertebrate metabolism (e.g., hepatotoxicity) cannot be directly responsible for their protective potency in insects. Instead, it is their "bad" taste that deters predation. Although both PAs and cardenolides are thought to be bitter tasting to predators, there are basic differences between their activities in vertebrates. Cardenolides often produce an immediate emetic response, whereas PAs are nonemetic and do not harm an organism instantly. However, because mixed-function oxidases in the liver of vertebrates produce toxic metabolites of PAs, and some are carcinogenic, PAs can be severe vertebrate poisons (Robins, 1982).

The chemical defense of the American monarch seems to be still more complicated yet since Rothschild et al. (1978) suggested that *D. plexippus* may also contain self-produced cardio-active chemicals. Furthermore, Rothschild et al. (1984) suggested that 2-methoxy-3-alkylpyrazines in monarchs function as warning odors to deter predators (Guilford et al., 1987). In any case, while all Danainae utilize PAs, cardenolide-containing Asclepiadaceae are exclusively exploited by *Danaus* species (cf. Ackery

and Vane-Wright, 1985), including those with typical danaine courtship behavior. Thus, a consideration of chemical defenses does not help explain the monarch's unusual mating habits.

PECULIAR SEX LIFE— ECOLOGICALLY MEDIATED?

Although the American monarch's chemical communication should be reconsidered, it is beyond doubt that *D. plexippus* is a peculiar danaine butterfly with respect to its mating habits (although not necessarily a peculiar lepidopteran). Its evolutionary shift in mating behavior from the general danaine pattern must have an ecological basis.

The American monarch is the only danaine that inhabits cool-temperate northern climates (apart from the Asian *Parantica sita*), and its extraordinary annual migration is thought to relate to the exploitation of the asclepiad (milkweed) flora of North America (Brower, 1985; Vane-Wright, 1986; Malcolm and Brower, 1989; Malcolm et al., 1989; Cockrell et al., this volume; Malcolm et al., this volume; Vane-Wright, this volume). By extending its range a long way north, did the monarch leave behind the rich tropical resources of PAs? This, and perhaps less selective pressure from tropical Batesian mimics (see Ritland and Brower, this volume), might well have caused adoption of a novel mating strategy (cf. Boppré, 1978). However, such thinking appears to be too simple. On one hand, *D. plexippus* is partly sympatric with other danaine species in which male courtship success depends on gathering PAs. On the other hand, other species of the genus *Danaus* sensu stricto, such as *D. erippus* and *D. cleophile,* together with the tropical American races of *D. plexippus,* all have androconial organs that are morphologically similar to those of the American monarch in that they are also secondarily reduced in size. Unfortunately, we know virtually nothing about the courtship behaviors and the androconial secretions of the closest relatives of *D. plexippus plexippus.* Thus, we have as yet no meaningful hypothesis as to what might have caused the American monarch to adopt such a modified mating strategy.

CONCLUSIONS— LEADING TO CONSEQUENCES?

In conclusion, courtship and chemical communication in the American monarch is a fascinating subject, although as yet it is rather incompletely investigated. Questions of importance for further research on the monarch include the following. (1) Are contacts between hairpencils and alar pockets definitely not established? Doubleday (1846) noted in some males of *D. erippus* (which is doubtfully recognized as a distinct species by Ackery and Vane-Wright, 1984) that a small portion of the wing, close to the orifice of the pocket, was denuded of scales, as if they had been rubbed away by introducing something into the slit. This observation would indicate that contact behavior may occur, but the

observation has never been investigated further. (2) What are the androconial secretions and courtship behaviors of other members of the genus *Danaus* sensu stricto? Only comparative studies can shed light on why the American monarch became such a peculiar danaine. (3) Is the search for PAs, and their uptake and sequestration, a significant behavior in *D. plexippus*? At present, seemingly contradictory statements are found in the literature. While Pliske (1975a) provided some evidence for the monarch's reduced visitation to PA sources (compared to *D. gilippus*), Edgar et al. (1973) and Rothschild and Marsh (1978) state that male *D. plexippus* are avid feeders on PAs. (4) Are there subspecific or regional differences in PA use and PA occurrence? (5) Last, but by no means least, further work should be carried out on the likely supplementary roles that cardenolides and PAs play in the chemical defense of the American monarch. As outlined above, both cardenolides and PAs need to be considered to understand fully antipredator mechanisms in the American monarch. Combined efforts at both behavioral and chemical levels would be more than useful. Unlike most other insects sequestering secondary plant chemicals, danaines can be reared on various host plants and the amount of cardenolides a specimen contains can be determined, and adult danaines can be fed PAs in varying amounts. Thus, feeding experiments with an array of predators can be easily manipulated without unnatural treatment of the insects.

It is likely that more detailed knowledge of the chemical ecology of *D. plexippus* will not only aid in understanding monarch courtship, but will also lead to understanding the dual relationship that danaines have with both cardenolide- and PA-containing plants. The debate on automimicry (Brower et al., 1967; Gibson, 1984) could also receive a helpful interjection.

I hope to have shown here that we need to know much more about the reproductive and defensive biology of *D. plexippus*, and that there are challenging and rewarding avenues to be followed in the future. By virtue of our poor understanding, it seems to me that it is too early to designate the American monarch as nature's prime example of the male chauvinistic pig.

ACKNOWLEDGMENTS

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