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CHEMICAL COMMUNICATION, PLANT RELATIONSHIPS, AND MIMICRY IN THE EVOLUTION OF DANAID BUTTERFLIES

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The knowledge on pheromone biology in danaid butterflies, on relations between adult danaids and pyrrolizidine alkaloid-containing plants, and on relations between danaid larvae and cardiac glycoside-containing foodplants is briefly reviewed and hypotheses on the phylogenetic origin and development of these phenomena are discussed.

Close range chemical communication mediated by male pheromones is essential in the courtship of danaid butterflies, and their pheromone biology shows particularly elaborate peculiarities (see Boppré, 1977). One of the most striking is that phytochemicals obtained by adult feeding serve as precursors for pheromone components found in many species of Danaidae.

Danaids, however, are not only associated with these plants which can provide pheromone precursors for the adults, but also with their larval foodplants, the bitter tasting toxins of which are often utilized by the insects for defensive purposes. This latter association has become very well known because it is the basis for the butterflies' conspicuous role as mimicry models.

It is the aim of this paper to review briefly the knowledge on pheromone biology of danaids as well as on their associations with plants, and to point out open questions. The information given will be compared with similar phenomena in other Lepidoptera and taken as a basis for discussing hypotheses on the possible phylogenetic development of both chemical communication in danaids and danaid/plant relationships, considering the role and influence of mimicry at the same time.

MALE PHEROMONE SYSTEM OF DANAIDS

During courtship behaviour, male danaids protrude and expand glandular abdominal hairbrushes ("hairpencils") which disseminate aphrodisiac pheromones necessary for the acceptance of a male by a female (Brower *et al.*, 1965; Myers & Brower, 1969; Pliske & Eisner, 1969; Seibt *et al.*, 1972). Chemical analyses of hairpencil extracts revealed that the distinctive hairpencil odour is composed of several components, the bouquet apparently providing a basis for species recognition (Petty *et al.*, 1977; Schäfer, unpubl.).

Morphologically, the hairpencils show remarkable differentiations within the subfamily Danainae. In most species of the genus *Danaus* the hairpencils are built up from one hairtype only, whereas in most species of the genus *Amauris* the organ is composed of up to five morphologically distinct hairtypes (see Eltringham, 1915; Boppré & Fecher, 1977). Tiny cuticular particles are found in masses in the hairpencils of most *Danaus, Amauris,* and *Parantica* species. These particles, which are produced in different ways (Boppré & Fecher, 1977, Boppré, unpubl.), are coated with pheromones and disseminated onto the female during courtship flight (Pliske & Eisner, 1969). Male danaids thus deposit "pheromone-transfer-particles" (Boppré, 1976) capable of providing a long lasting stimulus for the females.

In addition to the hairpencils, glandular organs formed as patches or as pocket-like folds are found on the wings. In *Amauris, Danaus,* and *Parantica,* and perhaps in *Euploea*, mechanical contacts between the abdominal and the alar glands are established by a special motor pattern, independent of courtship: The hairpencils are applied to the patches or introduced into the pockets (for refs. see Brower & Jones, 1965; Boppré *et al.*, 1978).

The function of the alar glands, or rather of the contacts between hairpencils and wing glands, is not yet fully understood. In one species, it was shown that contacts are a prerequisite for the biosynthesis of a pheromone component (see below); in some species (*e.g. D. formosa*) pheromone-transfer-particles are produced inside the alar pockets, and here contacts at least serve for the transfer of particles from the pockets onto the hairpencils (Boppré & Fecher, 1977).

Contrary to many other lepidopteran groups, where it is thought that male scent organs developed independently several times, in all danaid species scent organs occur (previous reports that *Ideopsis* species lack hairpencils are in error); and there is strong evidence, that all abdominal hairpencils are homologous and that this is also true of many alar organs. Morphological characteristics of the hairpencils (such as number of hairtypes, number of hairs, surface structure, mechanism of particle production) as well as of the alar organs (shape and density of scales and hairs, shape and size of the patches *etc.*) not only provide key information for determining the species but also make it possible to trace their apparent differentiation during the course of evolution (Boppré, unpubl.).

RELATION OF DANAIDS TO PYRROLIZIDINE ALKALOID-CONTAINING PLANTS

Pyrrolizidine alkaloids as pheromone precursors

In the pheromone biology of danaids, a group of dihydropyrrolizine derivatives play an extraordinary role. In many species of the genera *Danaus* and *Amauris*, as well as in *Lycorea*, a heterocyclic ketone (6,7-dihydro-1-methyl-5H-pyrrolizine-7-one = "*danaidone*", Fig. 1a) was found to be a common major component of the hairpencils' odour bouquet (Meinwald *et al.*, 1966, 1969, 1971, 1974; Edgar *et al.*, 1971, 1973; Schneider, 1975). In the genus *Euploea* the corresponding aldehyde and/or hydroxy-aldehyde ("*danaidal*", "*hydroxy-danaidal*") occurs, and two *Danaus* species possess danaidone and danaidal or hydroxy-danaidal respectively (Edgar *et al.*, 1971, 1973).

For *D. gilippus* and *D. chrysippus*, danaidone was proved to be an arrestant pheromone necessary for courtship success (Pliske & Eisner, 1969; Boppré & Schneider, unpubl.). The same function is assumed for other species, and the use of dihydropyrrolizine derivatives by many species of several genera suggests very strongly that this feature was to be found in the common ancester of all living Danaidae.

Surprisingly, when raised indoors, males of both *D. gilippus* and *D. chrysippus* had no danaidone on the hairpencils (Meinwald *et al.*, 1971, 1974) and had a reduced courtship success, whereas in field-caught males amounts of danaidone of up to 400 μg were detected. There are several reports that danaids (especially the males) are strongly attracted to certain plants, mainly belonging to Asteraceae (=Compositae; *Senecio, Eupatorium*), Boraginaceae (*Heliotropium, Tournefortia*), and Fabaceae (=Leguminosae; *Crotalaria*) where they suck at withered leaves, stems, and seed-pods (Beebe, 1955; Morrell, 1955; Edgar *et al.*, 1973; Atkins, 1974a,b; Schneider *et al.*, 1975; Pliske, 1975b; and others). These attractive plant species are well known as sources of pyrrolizidine alkaloids (**PA**; = *Senecio*-alkaloids) (Bull *et al.*, 1968), and the heterocyclic moiety of these secondary plant substances is strikingly similar to danaidone (Fig. 1). Extensive studies with *D. chrysippus* established a relationship between danaidone-deficiency and visits to PA-containing plants by the males: PAs ingested by the adult males from withered plants serve as precursors for the biosynthesis of danaidone (Edgar *et al.*, 1973; Schneider *et al* ., 1975). The butterflies locate the plants by means of olfactory stimuli; after palpating the surface of the plants with their antennae and proboscis they apply droplets of fluid which they then re-imbibe. Sucking at one spot for more than half an hour is quite common.

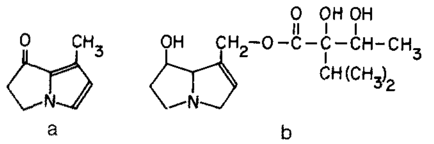

Fig. 1. Danaidone, major pheromone component of several species of Danaidae, (a) and the pyrrolizidine alkaloid lycopsamine (b).

The use of PA-derivatives as pheromone precursors obtained by adult feeding is apparently widespread among danaids:

- hairpencils of 23 species were tested for the presence of danaidone, danaidal, and hydroxy-danaidal; 17 gave positive results (see Edgar, 1975; Schneider, 1975),
- 5 species, known to contain danaidone when caught in the field, lacked these compounds when raised indoors with no access to PAs (Boppré & Schneider, unpubl.).

— several species, the hairpencils of which are not yet analysed chemically are attracted to PA-containing plants.

Further observations on which danaid species are attracted to PA-containing plants and further chemical analyses of male scent organs are needed in order to obtain a good survey of the use of PA-derivatives. Also, the function of PA-derived male pheromones should be worked out in various species.

The discovery of the dependence of danaidone biosynthesis on alkaloid precursors enabled us to understand the significance of the aforementioned contacts between abdominal and alar glands: Amounts of danaidone comparable to those found in field-caught males were only found in indoor-raised individuals, after the males had ingested PAs and had in addition established contacts between both glandular organs (Boppré *et al.*, 1978). Biochemical details are under investigation.

Thus, danaidone biosynthesis in physiologically normal amounts has two prerequisites: i) ingestion of PA and ii) contacts between abdominal and alar glands. So far, this statement is only corroborated for *D. chrysippus*, but it is probably valid for other species too. Further studies are needed to test this assumption and to investigate whether or not the alar glands and the contact-behaviour serve alternative or additional functions in this and other species.

Pyrrolizidine alkaloids as protective substances ?

Edgar *et al.*, (1976b and unpubl.) analysed bodies of field-caught danaids of various species: Even after 20 days without access to PAs, these phytochemicals occurred unconverted in the bodies of males and females. This strongly suggests that the alkaloids are retained or even actively stored by these insects.

The relevant PAs are known to be bitter tasting and extremely noxious compounds for vertebrates (Schoenthal, 1968; Bull *et al.*, 1968; McLean, 1970; Mattocks, 1973). Therefore, it might be assumed that PAs not only serve as pheromone precursors but also as protective substances (Edgar *et al.*, 1976b). Evidence on the defensive role of PAs comes from Eisner *et al.* (unpubl., cit. in Edgar *et al.*, 1976b) who demonstrated that PAs are distasteful to some insect predators. Nevertheless experiments are required to test the presumed protection of danaids by PAs. There are a number of Arctiidae, for example, which are avoided by many predators and these species store PAs obtained from larval foodplants; however, in these cases other potentially defensive compounds are also involved and it has not yet been shown that the PAs contribute to the unpalatability of the moths (Aplin *et al.*, 1968; Rothschild & Aplin, 1971; Aplin & Rothschild, 1972).

RELATIONS OF DANAIDS TO CARDIAC GLYCOSIDE-CONTAINING PLANTS AND IMPLICATIONS FOR MIMICRY

In addition to the association between adult danaids and PA-containing plants, danaids show a close association with Apocynaceae, Asclepiadaceae, and

Moraceae. These plants, which serve as major foodplants for the larvae, as a rule contain cardiac glycosides (CG; = cardenolides) known to be bitter tasting and noxious for vertebrates (Ehrlich & Raven, 1964; Roeske *et al.*, 1976).

Nearly a hundred years ago, danaids were thought to be protected from predators by storing toxic compounds from their larval host plants (for reference see Reichstein *et al.*, 1968). It was argued that this was the reason for danaids being aposematic and thus involved in both Batesian and Müllerian mimicry associations (for ref. on mimicry: Rettenmeyer, 1970).

Meanwhile, extensive studies with the American Monarch, *Danaus plexippus*, clearly demonstrated that it is unpalatable to bird predators (J. V. Z. Brower, 1958a) and also that the emetic property of the butterflies is due to storage of cardenolides obtained from the larval foodplants (Parsons, 1965; Reichstein, 1967; Brower *et al.*, 1967). Consistent with the theory of Batesian mimicry, it was further demonstrated that after a bad experience birds reject Monarchs as well as outwardly similar (and palatable) butterfly species by sight (J. V. Z. Brower, 1958b).

Detailed studies revealed not only that the cardenolide content of Asclepiadaceae varies markedly in quality and quantity, but that the amounts of cardenolides stored by Monarchs varies also (*e.g.* Brower, 1969, 1970; Brower *et al.*, 1968, 1972). Thus, Brower (considering only CGs!) postulated that "the palatability of these insects to vertebrate predators must consist of a spectrum from completely acceptable to completely unacceptable" (Brower, 1970). As a consequence, Brower formulated the concept of automimicry (Brower *et al.*, 1967). (for refs. Roeske *et al.*, 1976, and Rothschild & Reichstein, 1976).

The American Monarch[1] is one of the best documented examples of an unpalatable insect, utilizing toxic compounds from plants. However, very little information exists about the unpalatability of other danaid species. There is some evidence that the findings obtained for *Danaus plexippus plexippus* are not applicable to Danaidae in general. For example, *Danaus chrysippus* was found to be a poor storer of CGs (Brower *et al.*, 1965; Rothschild *et al.*, 1975), and in addition differences exist between East and West African populations which do not merely reflect the CG content of their larval foodplants (Rothschild *et al.*, 1975); the subspecies *Danaus plexippus erippus* stores only small quantities of CGs (Rothschild & Marsh, 1978); Swynnerton (1915) found *Amauris* to be unpalatable to birds, but the usual host plants of the larvae lack CGs, as did some chemically analysed specimens of *Amauris* (Rothschild *et al.*, 1970), however *Pergularia*, said to be an occasional larval host of *Amauris*, is rich in cardenolides (Rothschild *et al.*, 1970); *Euploea core* completely loses emetic potency during the earlier pupal stage (Marsh *et al.*, 1977). It has also to be noted that CG-storing insects are not protected

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[1] It needs to be pointed out that *D. plexippus* is an atypical danaid with respect to sexual communication; it has reduced male scent organs which do not emit stimuli necessary for courtship success (Pliske, 1975d) and the hairpencils do not contain danaidone (Meinwald *et al.*, 1968; Edgar *et al.*, 1971). However, males and females are attracted to PA-containing plants and both sexes store PAs (Edgar *et al.*, 1976b).

against all predators (for ref. see Reichstein *et al.*, 1968; Rothschild & Kellett, 1972).

These examples demonstrate the need for detailed studies with an array of danaid species on the unpalatability and its causes. Such investigations should not only consider CGs but also other compounds, since it is most probable that danaids are protected by a whole set of toxins: plant-derived substances like CGs and PAs, and others (see also Rothschild & Marsh, 1978; on aspects related with toxic Lepidoptera see Rothschild, 1972a, b; Rothschild & Reichstein, 1976; Rothschild *et al.*, 1970). The various components may have synergistic effects but it is also very likely that different poisons affect different predators. Further studies should also involve not only chemical analyses but also bio-assays with naturally occurring potential predators, to insure that biologically meaningful data are obtained. Such tests must consider the repellent properties (*e.g.* bitter taste) besides the "toxic" (noxious) ones. — In this context the importance of food plant records and chemical analyses of food plant toxins (as well as studies on oviposition stimuli) should be emphasized in order to obtain more data for testing phylogenetic speculations (*cf.* below); from the records available it seems probable that the larval foodplants of *Amauris, Parantica,* and *Ideopsis* generally lack CGs (Ackery & Vane-Wright, unpubl.) which would imply that the use of CGs as defensive compounds is a more recent specialisation evolved by certain danaid groups only.

RELATIONSHIPS OF OTHER LEPIDOPTERA TO PA-CONTAINING PLANTS

Withered PA-containing plants are not only attractive for Danaidae but also for Ithomiidae, Ctenuchiidae, and Arctiidae (Beebe, 1955; Beebe & Kennedy, 1957; Pliske, 1975b). While in ithomiids and danaids visitors are nearly all males, among the arctiids and ctenuchiids many species show either un-biased, male-biased, or female-biased attraction patterns (Pliske, 1975b).

The males of some species of Ithomiidae (a butterfly group closely related to Danaidae) secrete a lactone on the hairs of hindwing fringes (Edgar *et al.*, 1976a), which serves as an aphrodisiac for the female and/or as a male-male recognition signal (Pliske, 1975a). This lactone is most probably derived from the acid moiety of PAs which the males ingest from withered plants (Edgar *et al.*, 1976a). Ithomiidae, it should be noted, are also aposematic and are the models for many mimetic associations; the majority of species feed as larvae on Solanaceae (some "primitive" members of the group feed on Apocynaceae; see below) (Drummond, 1976).

The function of visits of Ctenuchiidae and Arctiidae at PA-containing plants is not yet understood. However, the males of most species in the ctenuchiid and arctiid genera having a large proportion of male-biased visitors, possess conspicuous abdominal hairpencils (Pliske, 1975b): but their chemistry awaits investigation.

Finally, it is worth mentioning that males of some *Utetheisa* moths secrete danaidal and hydroxy-danaidal on abdominal coremata (Culvenor & Edgar, 1972).

The production of these compounds which apparently serve as aphrodisiac pheromones is not dependent on the ingestion of PA by the adults, rather PA-containing plants are the larval foodplants. Therefore, one can assume that the males obtain precursors for the pheromone as larvae; possibly both sexes are protected by stored PAs derived from the larval foodplants.

SPECULATIVE CONSIDERATIONS ON PHYLOGENETIC ASPECTS

Most aspects of danaid biology discussed so far are certainly not unique within the insects. Many other Lepidoptera possess male pheromone systems, many other insects utilize noxious secondary substances for defence, and danaids are only one example of the aposematic life-style. However, the concurrence of these phenomena, their complexity, and the fact that males obtain pheromone precursor from plants by adult feeding, makes the study of the danaids (and of the ithomiids) a particularly challenging one.

This invites speculation on possible correlations between the various aspects of the insects' biology and also on their phylogeny. Two general questions will be focused upon:

1. How could one imagine the development of the relationship between danaids and PA and/or CG-containing plants?
2. Which selective pressures might be responsible for the evolution of the male pheromone system and its differentiation?

Origin of PA- and CG-containing plants?

Edgar *et al.*, (1974) (see also Edgar, 1975, and Pliske, 1975b) have put forward the hypothesis that the danaids' use of, and dependence on, PAs may have developed during a period when these alkaloids were constituents of their larval foodplants. These authors suggested that the ancestral foodplants contained both PAs and CGs and that under the pressure of ancestral danaids which depended on both substances, the plants split into three lines, one containing only PAs, one only CGs, and one containing none of these compounds.

As evidence for their hypothesis, these authors refer to Cronquist's (1968) and Takhtajan's (1969) phylogenetic classification of flowering plants, which include Apocynaceae, Asclepiadaceae, Boraginaceae, Compositae, and Solanaceae into a subclass Asteridae. Furthermore, Edgar *et al.* (1974) pointed out that the apocynad plant *Fernaldia pandura,* used as larval host of the primitive ithomiid butterfly *Tithorea harmonia salvadores,* contains a dihydropyrrolizine (another *Fernaldia* species contains CG); also the apocynad genus *Parsonsia* contains PA, attracts danaids and is occasionally used as a larval foodplant by *Euploea core* and *Danaus hamatus*. Finally, Muroya *et al.*, (1967) reported that *Parsonsia* is a foodplant of *Idea leuconoe*.

Unfortunately, whether or not the relevant butterfly species utilize these PAs as protective substances and/or as pheromone precursors has not yet been tested. It is interesting however, that approximately equal numbers of male and female *Tithorea* are drawn to *Heliotropium indicum* baits (Pliske, 1975b).

Assuming that the ancestral foodplants were CG + PA-containing, Edgar *et al.* (1974) envisaged that "mating of early danaids occurred in the vicinity of the larval foodplants and that males subsequently developed the means of storing and disseminating volatile pyrrolizidine alkaloid-derived plant substances, then used by the females to locate the larval foodplants. By disseminating these substances in the vicinity of a female in flight they would be able to make her settle and thus effect mating in a place remote from the larval foodplant. Such a development would have offered an expanded habitat for the insects and would have become essential for their survival during divergence of the original foodplants when the females were being selected for their ability to find and oviposit on cardenolide plants, which gave their offspring protection from predators, while the males were seeking out pyrrolizidine plants."

This hypothesis leaves several questions unanswered, *e.g.*:
— What made ancestral danaids dependent on both CGs and PAs?
— Was the male pheromone system already in existence?
— Can larval feeding put such a pressure on plants that they lose defensive properties?
— Can one assume that PAs (later CGs) were stimuli for finding the larval foodplants and for oviposition? (Fresh PA-containing plants are not attractive; CGs apparently do not provide oviposition stimuli for female danaids (they lay eggs on CG-deficient plants; Brower, 1969; Brower *et al.*, 1968)).
— What is the explanation of the fact that female danaids are sometimes attracted to and suck from withered PA-containing plants?

In addition, it has to be acknowledged that neither *Crotalaria* (Fabaceae) nor Moraceae, which are danaid PA-sources and foodplants respectively, fit into the phylogenetic proposals of Cronquist (1968) and Takhtajan (1969), which in any case are controversial (see *e.g.* Kubitzki, 1977). Finally, PAs (and CGs) are much more widespread in the plant kingdom (see *e.g.* Rothschild & Reichstein, 1976, and Bull, *et al.*, 1968) which suggests that PAs as well as CGs, like many other secondary plant substances, have been evolved several times independently.

The arguments given above do not rule out the hypothesis of Edgar and others that the association between danaids and several plant families originate from a proposed ancestral larval foodplant containing both CGs and PAs. However, their arguments do not convince me in all respects and it seems plausible to assume that the danaids' utilisation of CGs and PAs are two independent developments, which today complement each other.

In thinking about the origin and evolution of the male pheromone system and danaid/plant relationships, any hypothesis must take the following factors into account: PAs serve two functions; danaids are involved in mimicry; PA-derived pheromones are a primitive feature of danaids; and danaid scent organs are complex, differentiated mostly homologous. The hypothesis set out below is an attempt to account for all of these.

Hypothesis on the origin of danaids' male pheromone system and the association with PA- and CG-containing plants

Ancestral danaid butterflies obtained nutrition from nectar of various plant species. Those individuals which could tolerate the toxic properties of PA-containing nectar had a selective advantage because PAs protected them.[1]) Following this postulated "accidental" uptake of PAs, danaids not only developed a preference for PA-containing plants but also a storage system for PAs and they then became adapted for obtaining PA from withered plants, a more effective and long-term PA-source than nectar. Parallel with the development of unpalatability due to PAs, aposematic signals evolved, followed by the evolution of mimicry.

The use of PAs or PA-derivatives for sexual communication would then be a second step. PA-plants may have acted as mating sites which not only brought the sexes together but also separated danaids from mimicking butterfly species. To avoid courtship or even mating with mimetic species female danaids might have been selected to accept a male only when "PA-odour" was present. Subsequently, those males which disseminated "PA-odour", or PA-derivatives, had a selective advantage over non-disseminating males, because they could persuade a female to mate away from the normal mating sites without a loss of specificity.

This argument might also be extended to give a possible explanation for the development of pheromone-transfer-particles: Applying PA-odour to the females by means of particles provides a long lasting stimulus, similar to that of the postulated earlier mating site. (Species not producing particles (like *Euploea core*) — in contrast to particle-producing species — expand the hairpencils close to the female for a longer time.).

The danaids are now widely involved in Müllerian mimicry associations with other danaids and also with other chemically protected butterflies. The fact that many danaids are Müllerian co-mimics could explain the fact that the male pheromone system is elaborate and highly differentiated (see above) (also see Brower, 1963), if we assume that in the speciation of danaids specific mate-recognition systems were mainly elaborated by changes of the pheromone system and not, or to a lesser extent, by changes of outward appearance. For unpalatable butterflies it is of advantage to keep external characters constant, as predators mainly perceive their visual features.

With regard to the association of danaids with CG-containing plants, it is not in conflict with my general ideas to assume either that the association of danaids to CG-containing larval foodplants developed earlier than the one to PA-containing plants or *vice versa*. It is possible that the aposematic characters of danaids, their shared warning coloration, and Batesian mimicry of them by other butterflies already existed before the association with PA-plants evolved; in this case, those

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[1]) Pliske (1975b) indicated that feeding at PA-plants may originally have arisen in connection with nutritional requirements that were not sex-biased: — PAs were found in the nectar of *Senecio* by Deinzer *et al.* (1977). — Inflorescences (even dead ones) are highly attractive for danaids and some danaids were found to pollinate PA-plants (Pliske, 1975c).

using PAs would have the advantage of being better protected than with CGs alone. On the other hand, the advantage of using CG-plants as larval foodplants would not only make the adults better protected but would also protect the larvae. In addition, it is of advantage for insects to feed on plants which are toxic to vertebrates and thus not be consumed by larger herbivores accidentally (Rothschild, 1972a).

SYNOPSIS

These ideas on the origin of danaid/plant relationships and of the male pheromone system are highly speculative and I have mainly discussed the general aspects leaving out intermediate situations as well as more recent adaptations (*e.g.* behavioural ones). However, it has been shown that one can envisage the evolution of danaid/plant relationships without assuming an ancestral foodplant containing both PAs and CGs. Although not discussed above, such ideas can also be applied to the Ithomiidae.

It is necessary to emphasize that plant species containing both CGs and PAs and danaids feeding on them need not necessarily represent an ancestral condition; such situations might also be explained as relatively recent specialisations. It is especially striking that many insect groups seem to have a predilection for CGs and PAs or even both substances for their defence (and communication) system (Rothschild, 1972a, b; Rothschild *et al.*, 1970, 1973), and it would be a most interesting field for research to investigate "reasons" for this preference. In this context it is relevant that larvae of *D. plexippus* accept *Asclepias* which was sprayed with an extract of *Senecio* and that the resulting butterflies contain PAs (Rothschild & Edgar, 1978).

Finally, it should be stressed that the hypothesis presented here includes the idea that the existence of mimetic species puts a selective pressure on the communication system of a model species. In the context of mimicry the sexual communication within individuals of the model species, within individuals of the mimetic species, and between models and mimics have to be considered. Independent of what the selective pressures are, the development of mimicry in the Lepidoptera has had general consequences for the communication of the species involved. This aspect has had little attention to date but work is in progress on the development of these ideas.

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ZUSAMMENFASSUNG

CHEMISCHE KOMMUNIKATION, PFLANZEN-BEZIEHUNGEN UND MIMIKRY IN DER EVOLUTION DER DANAIDEN (LEPIDOPTERA)

Monarchfalter (Danaidae) haben ein ausgeprägtes männliches Pheromon-System und spezielle Beziehungen zu Pflanzen, die Pyrrolizidin-Alkaloide (PA) bzw. herzwirksame Glykoside (CG) enthalten.

— Die Imagines (besonders Männchen) nehmen von vertrockneten Pflanzen verschiedener Arten der Familien Boraginaceae, Asteraceae und Fabaceae PA auf; die Raupen fressen an Asclepiadaceae, Apocynaceae und/oder Moraceae, die meist CG enthalten. PA und CG sind Bitterstoffe und für Vertebraten toxisch; die Fähigkeit der Danaiden, diese Substanzen zu speichern, ist ein Schutz vor Freßfeinden.

— Außerdem stehen PA und CG in Beziehung zu dem chemischen Kommunikations-System der Danaiden: PA dienen als Vorstufen für die Biosynthese männlicher Pheromonkomponenten, die bei mehreren Danaiden-Arten auftreten; die Ungenießbarkeit der Danaiden (aufgrund der Speicherung von PA und CG) hat zur Ausbildung von Bates'scher und Müller'scher Mimikry geführt, die vermutlich einen Selektionsdruck auf das männliche Pheromonsystem ausübten.

Die vorliegenden Arbeit referiert die Pheromonbiologie bei Danaiden und die Danaiden-Pflanzen-Beziehungen und diskutiert Hypothesen zum Ursprung und zur Evolution des Kommunikations-Systems und der Beziehungen zu Pflanzen.

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