LEPIDOPTERA AND WITHERED PLANTS

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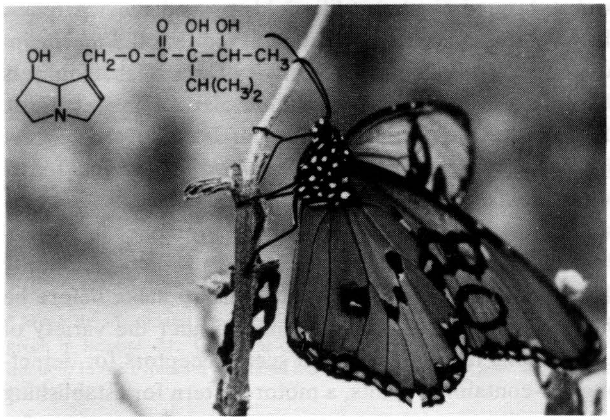
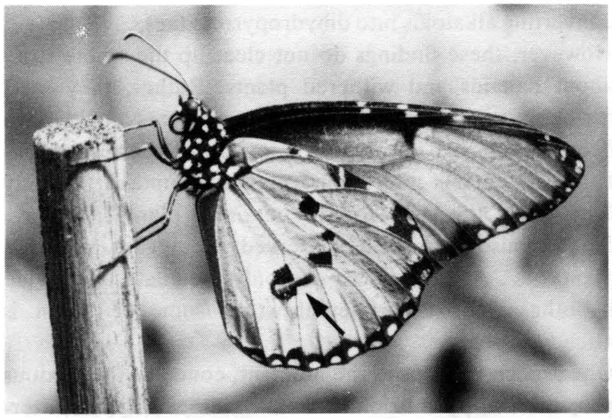
In 1927 G.H.E. Hopkins and P.A. Buxton observed male *Euploea* butterflies sucking at dead twigs of *Tournefortia.* Since then several field-workers have published notes on the attraction of adult Danaidae to various withered plants, but its biological significance long remained unknown. It was considered to be a phenomenon like the attraction to and feeding from decaying meat, mammalian urine, faeces, and other strange diets, which some butterfly species—often only the males!—show. A few years ago, in the course of studies on the sexual communication of danaids, it was discovered that the males have to take up certain secondary plant substances to become acceptable to their females. Meanwhile, the whole affair has proved to be rather complicated, and it is the purpose of this article to arouse the interest of field-workers the world over, in the hope of enlisting their help in studying Lepidoptera and withered plants.

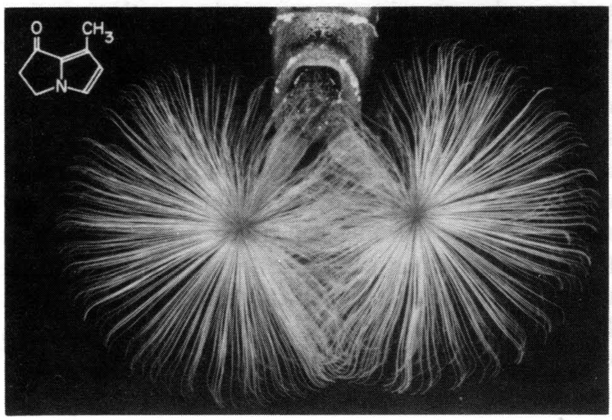
During courtship flight, male danaids protrude and expand abdominal hairpencils (cf. Fig.) and disseminate tiny cuticular particles. These carry pheromones which stimulate the females. Males which have had their hairpencils artificially removed show drastically reduced courtship success. But intact males also have a poor chance to mate if they have been raised and kept in captivity. This lack of courtship success is now known to be due to the lack of dihydropyrrolizines, major components in many species of the hairpencil odour 'bouquet'.

The chemical structure of the dihydropyrrolizines is strikingly similar to the heterocyclic moiety of pyrrolizidine alkaloids (PAs; cf. Fig.). PAs are secondary metabolites of plants like, for example, *Tournefortia, Heliotropium, Senecio*, and *Crotalaria*—and these are the very plants on which adult danaids have been observed feeding! Extensive studies have now demonstrated that male danaids have to ingest pyrrolizidine alkaloids before they can synthesize the dihydropyrrolizine pheromones which are necessary for courtship success. The males gather PAs either from withered plants by releasing droplets of fluid from the proboscis onto dry stems, leaves, or seed-pods, and then reimbibing the fluid with dissolved alkaloids, or sucking directly at broken twigs or stems. Danaids also feed on flowers of PA-containing plants, and studies now in progress are intended to discover if the nectar of such plants can be used as an alkaloid source.

Knowledge of the precursor dependency for pheromone biosynthesis led to the understanding of another phenomenon in danaid biology: besides the abdominal hairpencils, most male danaids possess glandular organs on the







Top: Male *Danaus chrysippus* (no. 80) sucks PAs from a broken stem of *Heliotropium steudneri.* Inset: The pyrrolizidine alkaloid 'lycopsamine'. Centre: Male *D. chrysippus,* which has had its hind wing pockets excised, engaged in 'contact' activity: the left abdominal hairpencil can be seen passed through the hole in the wing.

Bottom: Everted abdominal hairpencils (*D. petiverana*): length of hairs: ~ 4.5mm. Inset: 'danaidone', a dihydropyrrolizine pheromone component.

wings, formed as pocket-like folds or as distinct patches. In several species it has been observed that the males, independent of courtship activity, establish contacts between the hairpencils and these alar organs (cf. Fig.). What is the function of the alar glands and of the contact behaviour? We examined *Danaus chrysippus* and found these contacts to be another prerequisite for the production of the dihydropyrrolizine pheromones in physiologically normal amounts.

Imagine the efforts a male danaid has to make before he has even a chance to mate! And consider the variety of adaptations involved, such as scent receptors for detecting PA-containing plants, a motor-pattern for establishing hairpencils-alar organ contacts, the enzyme system for converting alkaloids into dihydropyrrolizines, . . . !

However, these findings do not clear up the whole story about danaids and withered plants. Rather, they raise further questions. What selective pressures could have been responsible for the development of such a complicated system? Is pheromone precursor uptake the only function of the visits to PA-containing plants? Why are females also sometimes observed sucking at withered plants? ... At present we can only speculate to provide hypotheses for experimental work—some of which is already in progress.

One aspect, in focus at the moment, concerns the noxious properties of pyrrolizidine alkaloids. Since PAs are bitter-tasting and very poisonous to vertebrates, the question naturally arises, do danaids also use the PAs for defence against vertebrate predators? So far, this hypothesis has not been investigated experimentally; there is, however, some circumstantial evidence available. The bodies of male and female danaids of several species, which were caught in the field and then kept without access to PAs for several days, contained unconverted pyrrolizidine alkaloids; this means that the butterflies are able to retain, or even store these compounds. Although it seems quite likely that the PAs do serve defensive purposes, studies with alkaloid-fed danaids and potential predators must be carried out.

The hypothesis on the use of PAs by danaids in defence puts a new complexion on danaids with respect to their mimicry associations. Classical studies with *Danaus plexippus* have shown that cardiac glycosides obtained from asclepiad plants by larval feeding and passed on to the adults are responsible for the emetic properties of the insects, and thus for their protection. One was inclined to think that the same would be true for the other danaids. However, some danaid foodplants provide only minor amounts of cardiac glycosides, others none at all, and some danaid species seem not to store these substances in the adult stage. Even in *D. plexippus* not all individuals of a population contain cardenolides.

Could it possibly be that pyrrolizidine alkaloids are the original defence mechanism and that cardiac glycosides are an additional defence employed by some species only? This idea would also explain why females go for PA-containing plants, and provide a hypothesis on the origin of the elaborate male pheromone system: At an early stage, following the adaptation to the use of PAs for defence, the PA-containing plants (as sources of the defensive substances) might have been employed also as mating sites by the butterflies. This would have had the advantage of separation from any Batesian mimics (likely already to have evolved) during sexual communication. Males able to release PA-derivatives may then have developed higher reproductive fitness through being able to persuade females to mate away from the PA-plants. During speciation of danaids, specific mate recognition signals were probably elaborated mainly by changes in the pheromone system and (due to selection by predators) not or to a lesser extent by changes to the outward appearance, which not only led to Müllerian mimicry associations but also to the very complex male scent organs and the use of multi-component chemical signals.

This is hugely speculative, of course, and other hypotheses exist, e.g. that the system developed from an ancestral situation where larval danaids might have fed on plants containing both cardiac glycosides and pyrrolizidine alkaloids.

Danaid butterflies are not the only Lepidoptera attracted by withered PA-containing plants. Adult arctiids, ctenuchiids, and ithomiids also visit such plants and take up PAs—in many species this behaviour is male-biassed. Do they need PAs for the biosynthesis of sex pheromones, too? Do they use PAs for defence? The adaptive significance of visits to PA-containing plants by these Lepidoptera awaits further investigation. Ithomiids do apparently elaborate male pheromones from the plant metabolites: the androconial secretion of some species of these butterflies closely resembles the acid moiety of PAs! We also know that male *Utetheisa* moths, which feed as larvae on PA-containing plants, disseminate dihydropyrrolizines from their coremata.

It goes without saying that the brief outline given here involves much simplification and generalization*. However, a number of species have been investigated and the facts reported above seem to be true for the majority of danaids at least (*D. plexippus* is an exception; in this species pheromones do not seem to play any role in courtship). But there are more unanswered questions than answered ones. Some aspects require experimental studies, but others require field-observations of the sort which can only be made by lucky accident. In order to get a better survey on danaid (and other insect) associations with PA-containing plants (e.g. *Parsonsia, Heliotropium, Senecio, Crotalaria, Eupatoria, Tournefortia*) major questions for field-observations are: Which insect species suck from withered plants? Which plant species are involved? Is there a preference of certain insects for certain plant species? What is the sex-ratio of visiting insects? Which Lepidoptera feed as larvae on the respective plants?

May we ask any reader who has made relevant observations to let us know her or his findings? Even anecdotal observations may be very helpful. We would also greatly appreciate getting in contact with colleagues who could provide us with living material of the insects (danaids, ithomiids, arctiids, ctenuchiids).

* More details on the aspects discussed above as well as references are given in Boppré, M.: Chemical communication, plant relationships, and mimicry in the evolution of danaid butterflies. *Ent. exp. & appl.* **24,** xxx–xxx (1978). 264–277