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# LETTER TO THE EDITOR

# REDEFINING "PHARMACOPHAGY"

MICHAEL BOPPRÉ

*Universität Regensburg, Zoologie—SFB 4/B6,*
*D-8400 Regensburg, Federal Republic of Germany*

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In his classification of *Papilio* butterflies, Haase (1892) named a subgenus *Pharmacophagus*. The larvae of some of the species were known to feed on *Aristolochia* plants, and Haase assumed that they utilized noxious chemicals obtained from their hosts for their own defense. Subsequently, a few authors informally referred to other insects as "pharmacophagous" because they shared this habit of feeding on "toxic" plants. Considering today's much more detailed knowledge of insect-plant relationships, I plead here for a redefinition of this term so that it can be used with a precise meaning to characterize a particular type of insect-plant association.

Chemical techniques applied during the last 20 years or so have demonstrated that noxious secondary plant substances are indeed sequestered by a huge array of insects (for review and references, see Blum, 1981; Brower, 1984). It appears that the only feature which insects feeding on so-called toxic plants all have in common is that they take advantage of food sources avoided by most herbivores. However, this does not imply that the insects recognize the respective secondary plant chemicals or that they utilize them. On the one hand, insects can sequester toxic plant products without being able to detect them, i.e., they merely take them up automatically with their food.[1] On the other hand, ingested toxic plant substances are not necessarily retained or stored by insects, there being many examples where they are degraded

[1] In the case of *Danaus plexippus* (Lepidoptera: Danainae), for example, a classic aposematic insect frequently protected by cardiac glycosides obtained from milkweed plants on which the larvae feed (for review and references, see Brower, 1984), neither the egg-laying females nor the caterpillars show an apparent interest in cardenolides (Dixon et al., 1978; Cohen and Brower, 1982). As a consequence, cardenolide-free asclepiadaceous plants are also chosen as food, and so storage of cardenolides is not a constant feature of the species. Only the potential to do so is.

and/or eliminated (see, e.g., Rothschild, 1972). Thus, pharmacophagy in the broad sense, as previously used (see above), embraces fundamentally different relationships between insects and plants.

Generally, plants are sources of nutrients for insects, with their particular secondary plant substances often mediating herbivory by serving either as attractive or as repellent stimuli. Sequestration of secondary plant products in most cases is only a side effect of the consumption of food (see above). In recent years, however, we have learned of insect–plant associations which are independent of the need to obtain energy and which concern the plants' allelochemicals only. It has been recognized that several insects require—and even can depend on—certain secondary plant substances and that they can gather these by specific behavior which can be different from and additional to ordinary feeding. Examples include the following: adult danaine butterflies are attracted to withered plants containing pyrrolizidine alkaloids (PAs); with their proboscises, they apply a fluid capable of dissolving PAs and then reimbibe it. Under certain conditions, they can obtain PAs by scratching fresh leaves and ingesting the sap oozing out. Gathering PAs is thus a special activity and is separate from feeding behavior (although from some plants, insects can get PAs with nectar, i.e., with food). This is indicative of a peculiar importance of PAs, which has been shown: both sexes store PAs for defense, and males depend on PAs as precursors for the biosynthesis of a pheromone component essential for courtship success. (For details and references, see Boppré, 1978, 1984.)

This example demonstrates that plants are not only "grocery stores" but can also be "pharmacies" which—sometimes in addition to food but even exclusively—supply insects with chemicals not needed for their primary metabolism but significantly affecting their fitness. In the insects, basically different adaptations are involved if interactions with plants concern food, on the one hand, or "drugs," on the other, and so separate terminology should be applied. This leads me to suggest restricting the term "pharmacophagous" to the following usage: *insects are pharmacophagous if they search for certain secondary plant substances directly, take them up, and utilize them for specific purpose other than primary metabolism or (merely) foodplant recognition.*[2] Thus, calling an insect pharmacophagous requires demonstration that it takes up plant allelochemicals in pure form—even if these are normally ingested together with food—and evidence that this is of advantage for its fitness. Of course, the plant chemical(s) must be known; it may be, but need not be, noxious to other organisms.

Redefining pharmacophagy is not just a semantic issue. To apply the

[2]It is stressed that for convenience, i.e., to avoid the need for further terms, pharmacophagy is not to be understood literally; in this context, "pharmaco-" means secondary plant substances in general and not only those having curative effects, and "-phagy" means gathering, which can, but need not, be ingestion.

term, experiments are needed and these should give some insight into the function(s) of the plant metabolite(s) for the insect. That tests for pharmacophagy can be worth pursuing is shown by example of *Creatonotos* (Lepidoptera: Arctiidae): the males emit an odor from their androconial organs which was assumed to be derived from PAs. By breeding insects with or without access to PAs and checking whether PAs are detected and ingested by the larvae in pure form, we established not only that PAs serve as precursors for the odor, but also that PAs specifically regulate the growth of the androconial organs (Schneider and Boppré, 1981; Schneider et al., 1982; Boppré and Schneider, in preparation).

Apart from Danainae and *Creatonotos*, which were used as examples only, other Lepidoptera have been proved to be pharmacophagous or seem likely to be. Many Ithomiinae, Arctiidae, and Ctenuchiidae obtain PAs from dry plants (in experimental situations they are attracted to and ingest pure PAs; cf. Figure 1) and store them, and some use them additionally as pheromone precursors (references given by Pliske, 1975; Boppré, 1978, 1984). PAs also bait various species of flea beetles (Chrysomelidae) and grasshoppers (*Zonocerus*), which also ingest crystals of PAs (Boppré and Scherer, 1981; Boppré et al., 1984; Boppré, unpublished). A rather different example which also meets the definition of pharmacophagy appears to occur in golden bees (Hymenoptera: Euglossinae): the males visit flowers of orchids and some other plants which do not contain nutrients but certain fragrances. They collect the fragrances in their hind legs and utilize them to attract other male bees of their species and form leks where mating takes place (such a pheromonal role of these plant substances in the behavior of the bees needs further substantiation). Fragrance components displayed in the field are attractive and are collected. [See, e.g., Vogel (1966), Dodson (1975), and Dressler (1982) for details and references.]

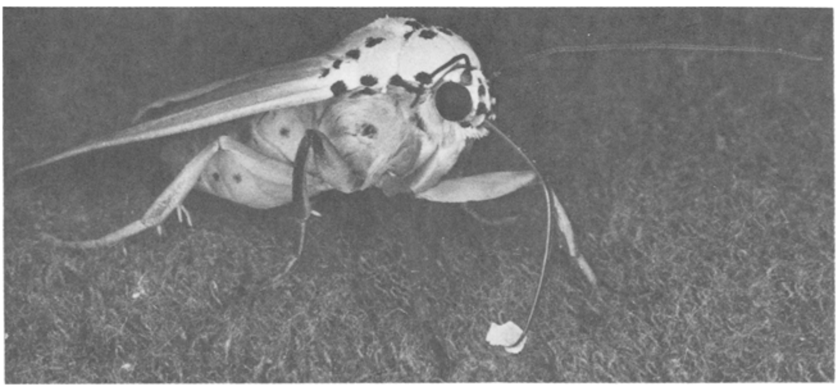

FIG. 1. *Rhodogastria phaedra* (Arctiidae) ingesting monocrotaline by dissolving a crystal of this PA with a fluid applied via its proboscis and reimbibing it.

It seems very probable that many other insects are pharmacophagous, but few have been investigated in this light.

In analogy to the definition of pharmacophagy given above, one might create a term for those insects which utilize certain secondary plant substances for a specific purpose other than primary metabolism but do obtain them together with food exclusively. However, to be complete, other types of insect–plant relationships would also need to be named, and it is thought that this should await a thorough classification of insect–plant interactions.

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