

'DRUG-ADDICTED' INSECTS IN AFRICA

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Abstract: Pharmacophagy and its diverse functional aspects is introduced using examples from studies on relationships between insects and pyrrolizidine alkaloids (PAs) in Africa. Remaining open questions are outlined, emphasizing the over-riding need for natural history information from the field on 'PA-insects' and 'PA-plants'.

Key words: Lepidoptera, Danainae, Arctiidae, Coleoptera, Alticinae, insect-plant relationships, pharmacophagy, pyrrolizidine alkaloids, chemical ecology, pheromone biology, chemical defences, mimicry, hostplants.

Introduction

"Observe the butterflies, sombre black fellows ..., flying in a crowd round a shrub with thick silvery-looking leaves. ... A branch is broken, and the leaves are hanging dry and wilted. The butterflies settle on the dead leaves in swarms, almost pushing and jostling one another to get a good place. Notice that it is the withered leaves and flowers that they prefer, and seem to become half-stupid in their eagerness to extract the peculiar sweetness, or whatever it is, that the leaves contain." (Woodford 1890)

The 'peculiar sweetness' of a dried *Tournefortia* (Boraginaceae) branch, so attractive to *Euploea* (milkweed butterflies, Danainae) was subsequently found to be a toxin gathered to improve their fitness.

This paper provides a brief introduction to the general subject of such non-nutritional uses of plants by insects ("pharmacophagy") illustrated by the results of my personal field studies on relationships of insects to plants containing pyrrolizidine alkaloids (PAs) primarily conducted in Kenya during numerous visits between 1979 and 1990 but with some observations made in Bénin, Togo and Uganda. In combination with laboratory analyses such field observations have provided insights into various aspects of lepidopteran biology and chemical ecology. However, lack of knowledge on the natural history of PA-plants and PA-insects continues to curtail our understanding. This article, then, is a plea for information from readers with an interest in lepidopteran natural history, and an invitation for further collaboration in this area.

Non-nutritional insect-plant relationships

So-called secondary plant substances* extend the relationships between insects

* Chemicals that are not required for the general metabolism and do not occur in each cell of a plant; most serve defensive purposes, but there are many which mediate mutualistic relationships with animals (e.g., the scents of flowers). Caffeine, nicotine, herbal medicines as well as the smells and tastes of fruit are secondary plant metabolites, however, most are undetectable for the human senses.

and plants beyond nutrition: plants' secondary metabolites render them unacceptable for unadapted herbivores / phytophages and can also play a major role in mediating host localization and host recognition. Many insects sequester noxious plant chemicals for their own protection against predators and other antagonists. Such specialists are physiologically adapted to avoid noxious effects, but generally the utilized secondary chemicals are ingested incidentally in the course of feeding – often they are not perceived by the insects and even if they are, they alone do not modify insect behaviour, for instance, by eliciting feeding behaviour.

However, the special non-nutritional relationship between insects and plants called "pharmacophagy" (Boppré 1984) is exclusively mediated by and directed towards plant secondary compounds. This insect-plant interface is quite separate from the primary insect/hostplant relationship.

The utilization of pyrrolizidine alkaloids (PAs) provides a widespread example. Numerous insects gather PAs as adults, usually from withered and dry plants of certain taxa which are unrelated to their larval hostplants. Generally, they store PAs (which are taste-deterrent for non-adapted phyto- as well as zoophages) for their defence, but among the Lepidoptera several taxa use PAs in addition as precursors for the biosynthesis of male courtship pheromones. Details of insect-PA relationships are reviewed by Boppré (1986, 1990, 1994, 1997), Schneider (1987), Eisner & Meinwald (1995), Hartmann & Witte (1995).

Insects pharmacophagously associated with PA-plants in East Africa

The literature contains very few reports on adult Lepidoptera 'feeding' at dry PA-plants in Africa (Schneider *et al.* 1975; Smith 1975; Boppré 1981), and I myself have only rarely encountered such interaction during many months spent in the field. Spectacular congregations of insects gathering PAs only occur when PA-sources are very scant and PA-insects very abundant at the same time; usually, a single individual insect obtains PAs from a small wound or a small withered part of a PA-plant which escapes the eyes of an observer – or the observer does not recognize the interaction as anything 'special'. However, by using dry *Heliotropium indicum* or *H. pectinatum* (Boraginaceae) plants or PAs extracted and purified from *Crotalaria scassellatii* (Fabaceae) as baits (cf. Figs 1, 5), I have been able to lure insects of four orders (see Schneider *et al.* 1975; Boppré 1981; Boppré & Scherer 1982; Boppré *et al.* 1984; Boppré & Pitkin 1988; Fischer & Boppré 1997; Häuser & Boppré 1997; Scherer & Boppré 1997; M. Boppré unpubl.):

Lepidoptera. Nymphalidae: Danainae: All species known from Kenya (*Amauris albimaculata*, *A. echeria*, *A. ochlea* (Fig. 6), *A. niavius*, *Danaus chrysippus*, *Tirumala formosa*, *T. petiverana*), with the exception of *A. niavius* (and *A. tartarea?*), only males.

Arctiidae: Arctiinae: 10 species of *Amerila* (Figs 3, 11-14), 3 of which undescribed, no sex-bias.

Arctiidae: Nyctemerinae: *Nyctemera coleta* (Fig. 7) and 4 yet undetermined species (Fig. 5).

Arctiidae: Euchrominae: *Euchromia amoena* (Fig. 4), *E. lethe* (Fig. 8), *E. interrupta*.

Arctiidae: Hypsinae: *Digama* spp. (Fig. 9), *Aganais speciosa* (Figs 2, 10).



Plate 1. Lepidoptera gathering pyrrolizidine alkaloids: *D. chrysippus*, *A. ochlea* and *T. petiverana* at a gauze-bag with withered material of *Heliotropium pectinatum* (1); *Aganais speciosa* at dry *Heliotropium* (2), *Amerila* sp. applying 'solvent' to a dry root of *Heliotropium* (3), *Euchromia amoena* at *Gynura scandens* (4), *Euchromia* and *Nyctemera* at a dish with pure PAs (5).

Coleoptera. Chrysomelidae: Alticinae: Males only of 18 spp. of *Gabonia* (Figs 16, 17), 13 of which undescribed, both sexes of a new species (*Nzerekorena filicornis*, Fig. 15), several species of other alticine genera.

Diptera. Chloropidae: Species of at least 2 subfamilies (Chloropinae, Oscinellinae) and 4 genera (*Melanochaeta*, *Chlorops*, *Eutropha*, *Oscinella*), no sex-bias. (These catches have not been fully evaluated.)

Orthoptera. Pyrgomorphidae: In South and West Africa, all stages and both sexes of *Zonocerus elegans* and *Z. variegatus* (Fig. 18).

This list is hardly comprehensive for insects gathering PAs from dry plant matter; it simply reflects my own experience in limited areas and limited time. In other habitats and/or at different times of the year, the composition of species is different as is the number of individuals at baits. Also, similar to the scarcity of encounters of congregations of insects at natural PA-sources (cf. above), visitation of baits depends on competition with natural sources of PAs, the abundance of respective insects in the area etc.; I have experienced attraction of 'any number' of insects, from none to many dozens.

PA-containing plants in East Africa

Because of the pharmaceutical importance of PAs, almost 400 species of plants have been analysed chemically for their presence; the 400 or so structures elucidated are found in some 90 genera of 11 families. However, only those PAs with the necine bases heliotridine or retronecine (Figs 19, 20) are known to be associated with insects, and these molecules occur in a smaller number of plant taxa – but those are the more abundant ones and include the following genera represented in Africa:

Asteraceae: *Ageratum*, *Emilia*, *Gynura*, some *Eupatorium*; Boraginaceae: *Heliotropium* (Fig. 23), *Tournefortia*; Fabaceae: *Crotalaria* (Fig. 24).

Adult insects obtain PAs usually from withering or even completely dry fruits, seeds, foliage or roots; which plant part is most attractive depends on the species and also on the stage of decomposition. With their proboscides butterflies and moths apply a fluid onto the dry plant matter and imbibe it with dissolved PAs.

Over a distance, insects cannot detect and recognize PAs in living tissue where they are concealed in the cell vacuoles; in addition, it is not the intact PA molecules but a volatile breakdown product which mediates attraction. This 'volatile principle' (Boppré *et al.* in prep.) appears in tiny amounts after cells have been mechanically damaged by wounding or drying. (Because the occurrence of this scent requires hydrolysis, the attractiveness of dry PA-plants used as bait can be increased by moistening.) In many species PAs are synthesized in the roots which then contain highest concentrations and make particularly good baits although they are not accessible naturally to butterflies and moths.

Interestingly, *T. petiverana* have been observed gathering PAs from living tissue of *H. pectinatum*: they scratched green leaves with their tarsi to get access to the chemicals. However, the leaves had been fed upon previously by leaf beetles (*Longitarsus* sp.), the dry edges of their feeding holes releasing the volatile principle (Boppré 1983).

There are, however, also plants which have PAs in their nectar. For example,

flowers of *Gynura scandens* are exclusively visited by PA-gathering species and avoided by other nectar foragers, an observation that led to the discovery of new PAs in this species (Wiedenfeld 1982); puzzlingly, dry leaves and roots of *Gynura* are not attractive and fail as baits. Guided by insect behaviour, we have also demonstrated for the first time PAs in *Heliotropium pectinatum* (Schneider *et al.* 1975), *Crotalaria scassellatii* (Wiedenfeld *et al.* 1985) and others.

On the biology of PA-pharmacophagous species

Identifying certain insect taxa to be PA-pharmacophagous and certain plants to contain PAs, finding new PAs or describing new species provides the basis of our search for functional commonalities and differences, and of general conclusions regarding PA-pharmacophagous species.

A significant character of PA-pharmacophagy is that in many cases only males gather PAs, but there are others with no sex-bias or with female sex-bias. This already indicates basic differences in function.

So far, all species investigated chemically store unconverted plant PAs. Several research groups found that by storing PAs insects can gain protection from a large suite of vertebrate as well as invertebrate predators. Most such PA-insects exhibit aposematism in their appearance both morphologically (colour) and behaviourally (slow flight, day-active moths). Some species store part of the ingested plant metabolites in a slightly modified structure ("insect PAs", e.g., Hartmann *et al.* 1990).

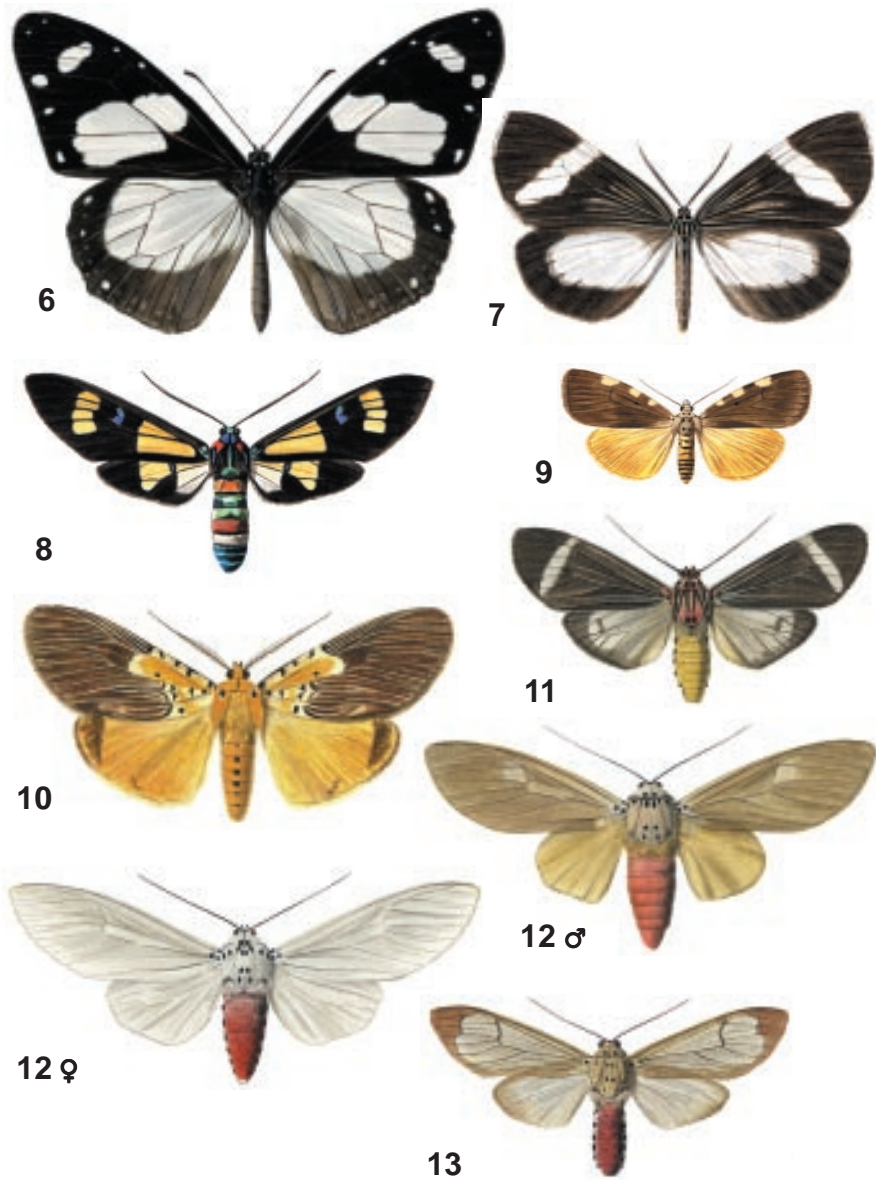
Males of many PA-utilizing Lepidoptera not only use PAs as defensive chemicals for themselves but also transfer large amounts to the females with their spermatophores; these, in turn, are incorporated into their eggs for protection (see Dussourd *et al.* 1989).

In addition, plant-derived PAs are used by males of many species to manufacture dihydropyrrolizine pheromone components (cf. Figs 21, 22) (Schneider *et al.* 1975; cf. Boppré 1990; Hartmann & Witte 1995), however, the use of PAs as precursors for pheromone biosynthesis is not a general feature of PA-insects. Not in all PA-insects do the males possess androconial organs, and even those which do need not necessarily produce PA-derived pheromones.

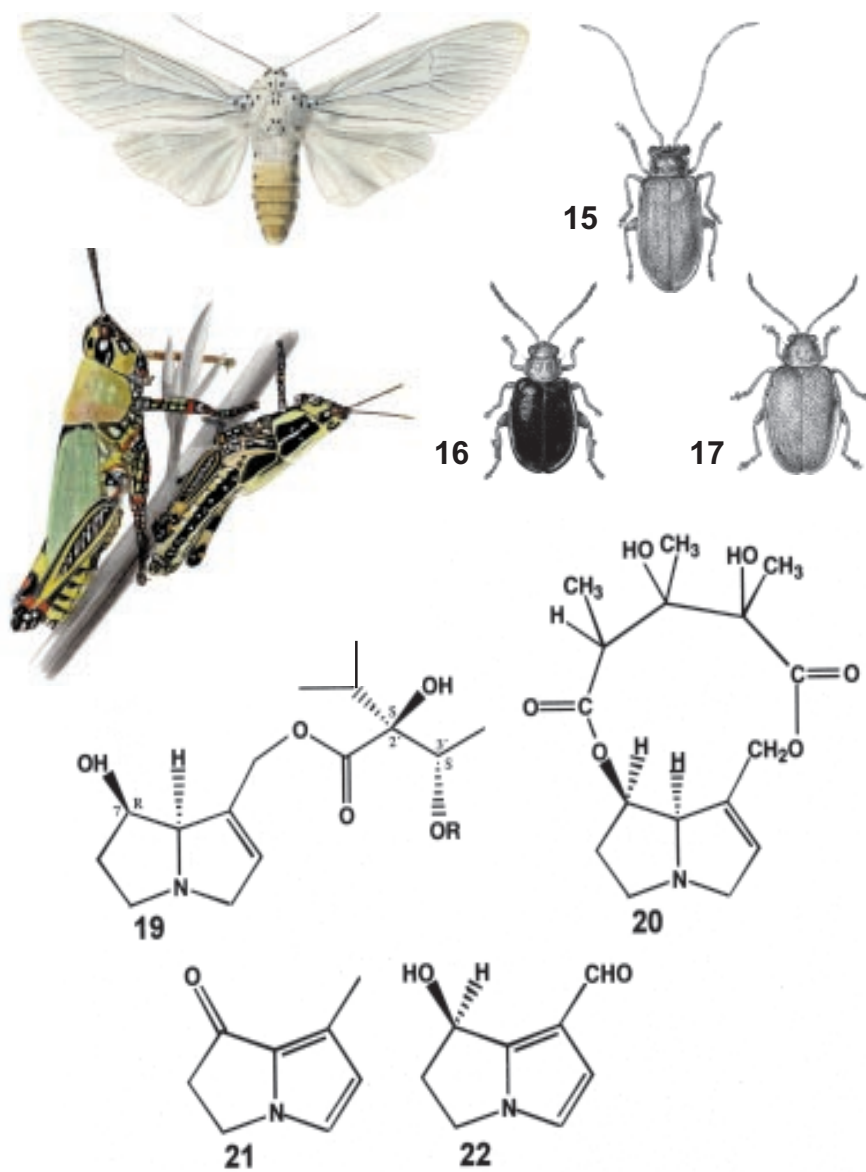
The extrudable abdominal hairpencils of male danaine butterflies (cf. Boppré & Vane-Wright 1989; Vane-Wright *et al.* 1992) emit species-specific bouquets of up to 80 volatiles, including components derived from PAs (e.g., danaidone, Fig. 21) (e.g., Schulz *et al.* 1993). The amount of these dihydropyrrolizines vary individually and seem to provide an indication to females of the amount of PAs that might be received through a spermatophore to protect the eggs (cf. Eisner & Meinwald 1995).

Within *Amerila*, androconial organs show great diversity; for example, expandable tubes at the claspers, hairbrushes at the abdomen, and glands on the wings (Fischer & Boppré unpubl.). They also emit bouquets of volatiles but – in contrast to danaines – only in some species are these PA-derived.

Our knowledge on the other PA-pharmacophagous Lepidoptera is very limited, but interesting data can be expected. For example, *Nyctemera* visit sources of PAs although the larval hostplants known for this are PA-plants. This is contrary to the expectation that they would have no need to undertake the costly search for and uptake of these chemicals as adults.



Plates 2 & 3. Examples of taxa attracted to dry PA-plants and pure pyrrolizidine alkaloids in East Africa: *Amauris ochlea* (6), *Nyctemera* sp. (7), *Euchromia lethe* (8), *Digama* sp. (9), *Aganais* sp. (10) *Amerila syntomina* (11), *A. phaedra* (12, ♂, ♀),



♀, *A. vitrea* (13), *A. bubo* (14), *Nzerekorena filicornis* (15), *Gabonia bicolor* (16), *G. bicaveata* (17), *Zonocerus variegatus* (18). Examples of molecular structures of pyrrolizidine alkaloids [heliotrine (19), monocrotaline (20)] and of PA-derived male dihydropyrrolizine pheromones [danaidone (21), hydroxydanaidal (22)].

The biology of *Gabonia* beetles is completely unknown; there are no records of primary hostplants, and for many species the females are quite unknown. Since the males of many species possess elaborate glandular structures on their antennae, elytra or legs (cf. Scherer & Boppré 1997), PA-visitation might relate to biosynthesis of pheromones as in many of the Lepidoptera.

General conclusions

Insect-plant relationships are generally highly specific, involving many adaptations, for instance, specialized receptors to detect appropriate plants for egg-laying. Pharmacophagous species exhibit 'double' insect-plant relationships, necessitating two sets of adaptations as the primary and secondary / supplementary hostplants are not taxonomically related.

The dual function of PAs as defensive chemicals and as precursors for pheromone synthesis intimately links chemical defence and sexual communication. Thus, finding individual variation and even temporal variation within an individual in pheromone content as well as in defensive outfit poses various new questions relevant to mate-choice and discussion of mimicry. The fact that pharmacophagous uptake of PAs is independent of uptake of nutrients and/or energy permits challenging experimental approaches on defence, mate-choice, mimicry, and the cost of sex.

It is interesting to note that the knowledge on lepidopteran associations with PAs led to the discovery of new techniques for management of *Zonocerus* grasshoppers, a pest in many countries of West Africa (Fischer & Boppré 1997).

Insects using PA-plants as primary hostplants

PA-plants are not only utilized pharmacophagously by certain adult insects but also used by many taxa as primary hostplants to obtain nutrients. Some species do not take advantage of PAs (rather they break-down and/or excrete these noxious compounds) while others take advantage of both the nutrients and the secondary metabolites of PA-plants. Again, storage for defence with associated aposematic characters is common as is the use of PAs to manufacture dihydropyrrrolizines as male courtship pheromones. To date, only a few African arctiid species have been looked at (e.g., Rothschild *et al.* 1979), including *Amphicallia* (Fig. 27) (larvae on *Crotalaria*), *Utetheisa* (Fig. 28) (larvae on *Heliotropium*, *Crotalaria* and *Argina* (Fig. 29) (larvae on *Crotalaria*) and *Nyctemera* (Figs 7, 26) (larvae on *Senecio*, *Gynura*). *Utetheisa*, for instance, use dihydropyrrrolizines in mate-choice as originally demonstrated with an American species by Thomas Eisner's group (see Eisner & Meinwald 1995).

Larvae using PA-plants are usually linked with certain taxa, that is they do not respond to a wide range of PAs as described above for adult PA-pharmacophagy. In fact, host choice appears not to be determined by the presence of PAs. However, larvae of the polyphagous Asian *Cretonotos* species (Arctiidae) are pharmacophagous: they consume even glass-fibre disks if they are impregnated with small amounts of pure PAs. *Cretonotos* not only utilize PAs for defence and male pheromone biosynthesis, PAs also act as morphogens regulating the size of the androconial organs quantitatively (e.g., Boppré & Schneider 1990). The African *C. leucanoides* (Fig. 30) shows the same features (Boppré *et al.* unpubl.).

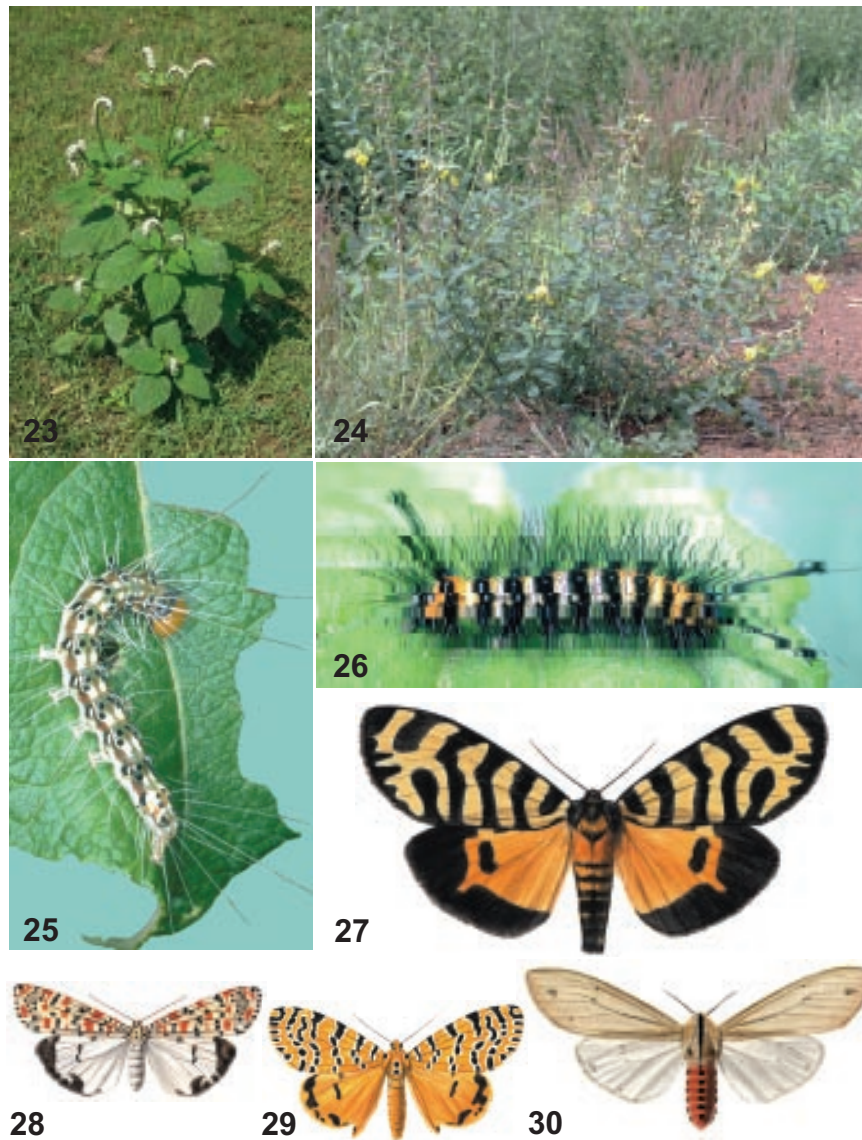


Plate 4. Examples of plants providing pyrrolizidine alkaloids for insects [*Heliotropium indicum* (23); *Crotalaria* sp. (24)], larvae of PA-pharmacophagous species [*Amerila bubo* (25), *Nyctemera* sp. (26)], and examples of arctiids using PA-plants as larval hosts [*Amphicallia bellatrix* (27), *Utetheisa* sp. (28), *Argina* sp. (29), *Cretonotos leucanoides* (30)].

Open questions / Call for cooperation

Looking at insect-plant(-predator) relationships not from a (plant or insect) taxonomic point of view but focussing on a group of plant chemicals and studying the diverse taxa of plants and insects linked with it appears as a rewarding approach. Done in a multidisciplinary way, news is gathered on many – at first sight seemingly unrelated – aspects. However, this point of view also reveals non-predictability: if we find an insect at a PA-plant we cannot predict if and, in case, how it utilizes the PAs. Even with more knowledge this situation will remain – but this does not make further studies less interesting or less relevant.

Despite significant findings, we are only at the beginning of understanding PA-pharmacophagy. For example, further laboratory analyses on selectivity, specificity and variation of storage of PAs and, in case, pheromone production will provide further insight into the chemical ecology of insects. Also, experimental field-studies on, e.g., mimicry and mate-choice, are made possible by the fact that secondary chemicals (and in consequence pheromones, too) can be modified qualitatively and quantitatively without artificial manipulations.

Yet, there are basic gaps in our knowledge of the natural history of PA-associated species, gaps that could be filled by basic observations and simple tests in the field (cf. Appendix). For example:

- There are surely many more plants which provide insects with PAs than the ones named above. These are, by the way, all ruderal plants; so, what are the PA-sources of species living in forests? (In a Kenyan forest, we have accidentally found a rhizome without overground parts which is very attractive to PA-insects. Chemical analyses have revealed several PAs – but we can't even have a good guess as to which plant species the rhizome belongs) Knowing further PA-sources would, for example, permit general chemotaxonomic conclusions and a better understanding of the specificity of insect-PA associations. Finding 'new' PA-plants is a matter of chance but awareness of pharmacophagy provides an insight into the possibilities inherent in noticing an insect at a dead plant part. Simple tests can make the discovery of a 'new' PA-source very likely.
- Certainly, there must be many more species of insects that gather PAs pharmacophagously. These can be collected by baiting in as many habitats as possible and in as many seasons as possible.
- For many PA-insects their larval hostplants and their general natural history is – if at all – poorly known. Knowledge on their primary hostplants and their behaviour provides important pieces for the general "puzzle" and is likely to reveal interesting evolutionary interpretations.
- Several *Amerila* are sex-dimorphic (Fig. 12) while for some species only one sex is known. Of most *Amerila* not only larval hostplants but even larval characters (cf. Fig. 25) are unknown.
- Feeding guilds at PA-plants have not been investigated in the tropics at all but an inventory of insect species associated with PA-plants is most relevant to understand if PAs are peculiar secondary plant metabolites and to find further uses of PAs, in case.

Pharmacophagy, of course, is not an uniquely African syndrome. PA-plants as well as PA-insects known from other continents belong to the same families; in South America Ithomiinae utilize PAs for defence and for male pheromones

(e.g. Brown 1984), also very many species of the Ctenuchinae are involved in PA associations. As in Africa, in South America and in Asia / Australia there is great demand for natural history information on PA-pharmacophagy.

Also, pharmacophagy is not restricted to pyrrolizidine alkaloids and there are non-nutritional relationships of insects with other natural products – but they are not the subject of this paper.

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Appendix

Specific tasks on the natural history of PA-plants and PA-insects

Baiting tests with PAs

In order to improve our knowledge on which adult insects (species, sex) are attracted to sources of PAs, baiting tests are required in as many habitats at as many times of the year and at all times of a day.

Since adults searching for PAs seem not to be hooked on a given PA-containing plant species, putting out dried plants (including roots) of *Heliotropium* sp. (Figs 1, 23) is the most simple technique, and a very efficient one as well. A dried plant remains attractive at least for a week or so, and its attractiveness can be reinforced by moistening it (after drying).

Alternatively – or in addition – pure PAs, extracted from *Heliotropium*, *Crotalaria* or other PA-plants, can be used. Such bait dishes (Fig. 5) last for many months (unless spoiled by rain or 'eaten up' by insects). They should be exposed where there is some wind to carry the 'PA-odour' (e.g. hung up).

Reference specimens should be collected for proper determination. Since species of *Amerila* and *Gabonia* resemble each other greatly and cannot be separated easily, a good number of reference specimens should be taken in case a sample comprises several species.

Searching for natural sources of pyrrolizidine alkaloids

Finding individual Lepidoptera or small groups of butterflies or moths at a dry or wounded part of a plant is suggestive for PA-pharmacophagy. To test it, fresh parts (including roots) can be dried artificially and offered in a different area and or at a different time to see if more specimens / other species are attracted.

Biology of insects visiting PA-sources as adults

Plants providing adult insects with PAs are quite different from their primary hostplants. For *Amerila* and *Gabonia* there is hardly any hostplant record. Of most *Gabonia* the females are unknown, it is also an open question if the plants providing *Gabonia* adults with nutrients are the same as those on which the larvae develop.

Guilds of insects using PA-plants as primary hosts

Of no tropical plant containing PAs the feeding guild is known because research so far concentrated on some conspicuous species. Which taxa (Lepidoptera, Coleoptera, Orthoptera, others; leaf-feeders, stem and root borers, pollinators) utilize PA-plants as primary larval / adult hosts?

Readers in Africa or elsewhere who are interested in the subject and in collaboration are most welcome to contact us (boppre@fzi.uni-freiburg.de). We can provide PA-baits for screening tests, an artificial diet for rearing many species of moths (Bergomaz & Boppré 1986), pictures of larvae to help searching for natural hostplants, etc.. Also, our website (<http://www.fzi.uni-freiburg.de>) provides additional information (e.g., information on artificial diet, keys to *Amerila* and *Gabonia*).