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Danainae (Lep.) and 1,2-dehydropyrrolizidine alkaloid-containing plants – with reference to observations made in the New Hebrides

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Male butterflies of the closely related nymphalid subfamilies Danainae and Ithomiinae visit and feed at dead and withering plants containing 1,2-dehydropyrrolizidine alkaloids. These visits are associated with the acquisition of alkaloid precursors of chemicals used by the males during courtship and for territory marking. A number of aspects of this unusual association, including its origins, are discussed with special reference to observations made in the New Hebrides.

1. INTRODUCTION

The clustering of large numbers of predominantly male butterflies of the genus *Euploea* (subfamily Danainae) on dead twigs and broken branches of the tree *Messerschmidia argentea* (L.) Johnst. (family Boraginaceae) was first reported by Hopkins & Buxton (1927) after they had observed the phenomenon in Samoa and Tonga and on the island of Tanna in the New Hebrides. Lever (1936) observed the same behaviour in the Solomon Islands and reported that the butterflies appeared to feed on moist, damaged parts of the tree.

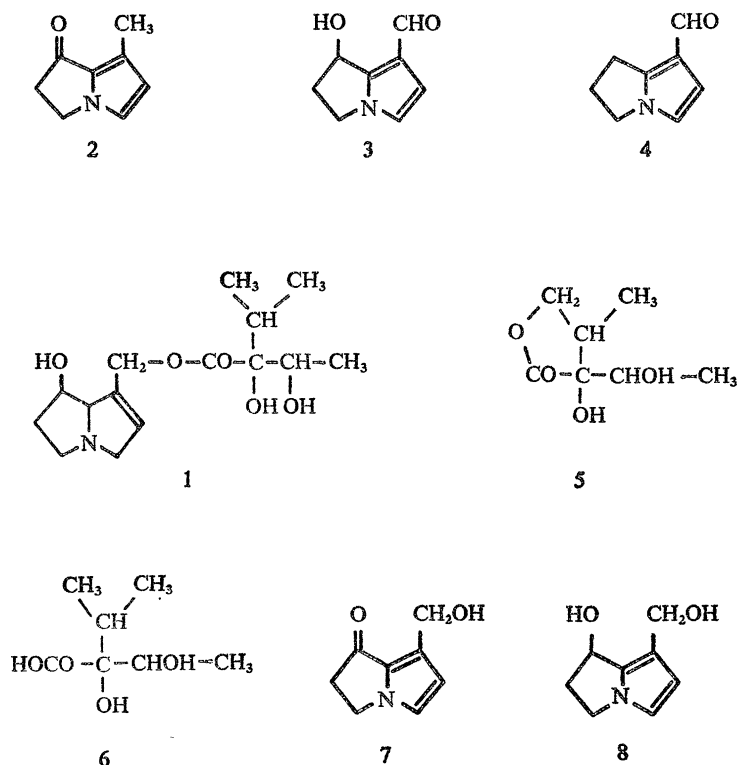
Withering *Heliotropium indicum* L., another Boraginaceae, also attracts Danainae (Morrell 1960). The remarkable powers of *H. indicum*, as a 'bait' for certain Lepidoptera, were discovered by Hagmann in 1921 in South America (Moss 1947). There it attracts primarily male Ithomiinae (close relatives of the Danainae which are scarce in that region) and moths of the families Ctenuchidae and Arctiidae (Moss 1947; Beebe 1955; Pliske 1975*a*). More recently Owen (1971), in Africa, has observed large numbers of *Danaus chrysippus* L. feeding on the exudates from *H. indicum* leaves which had been damaged by feeding grasshoppers. Other Boraginaceae, such as *Heliotropium amplexicaule* Vahl and *Cynoglossum amabile* Stapf and Drummond, also attract and cause male Danainae to feed (Edgar, Culvenor & Robinson 1973). The plants which act as attractants and induce feeding behaviour are not, however, restricted to the Boraginaceae. Thus McCann (1952–53) and Atkins (1974) have observed *Danaus* and *Euploea* on *Crotalaria* (Leguminosae) and Pliske (1975*a*) has observed male Danainae feeding on the genera *Senecio* and *Eupatorium* of the Compositae.

The plants which attract male Danainae are not normally larval food plants for the Danainae nor are their flowers especially used as sources of nectar by these butterflies (see, however, Pliske 1975*c*). The reason for this unusual sex-biased behaviour was therefore an intriguing mystery at the time of the Royal Society and Percy Sladen Expedition to the New Hebrides in 1971.

2. RESULTS AND DISCUSSION

It had been recognized, before the expedition, by Dr C. C. J. Culvenor and the author and independently by several other groups, that the plants which attract male Danainae have at

least one feature in common – they all contain 1,2-dehydropyrrolizidine alkaloids, e.g. **1**, suitable for metabolic conversion into the dihydropyrrolizine derivatives, **2–4**, found on male danaine ‘hairpencils’ (Meinwald *et al.* 1966*b*; Meinwald, Meinwald & Mazzocchi 1969; Edgar, Culvenor & Smith 1971; Meinwald, Thompson, Eisner & Owen 1971; Edgar *et al.* 1973; Meinwald *et al.* 1974). The ‘hairpencils’ are glandular organs, normally retracted within the males posterior abdomen, which, when displayed, appear as stalks tipped with hairs. These brush-like structures disseminate chemicals (including the dihydropyrrolizines, **2–4**) and are



used during courtship to seduce females (Brower, Brower & Cranston 1965; Myers & Brower 1969; Pliske & Eisner 1969). In some species they appear to perform other functions as well but these have not yet been clarified (see below).

(a) *Origin of the hairpencil dihydropyrrolizines*

Meinwald *et al.* (1966*a, b*), who first isolated the ketone (**2**) from *Lycorea ceres ceres* Cramer, pointed out the similarity in chemical structure of **2** and certain pyrrolizidine alkaloids and suggested that the ketone may be derived from a food source. Pliske & Eisner (1969) later found that when *Danaus gilippus berenice* Cramer was raised in captivity, on a normal larval food plant, the males lacked **2** which is normally present on their hairpencils. A similar deficiency was found in male *D. chrysippus* raised in captivity (Meinwald *et al.* 1971; Edgar *et al.* 1973) and an occasional newly emerged danaine captured in the field was also found to lack the appropriate dihydropyrrolizine(s) (Edgar *et al.* 1973). These results suggested that the butterflies do not obtain their hairpencil dihydropyrrolizines from larval food plants but that they require an exogenous source not available to the laboratory reared butterflies and not yet visited by the dihydropyrrolizine-deficient butterflies captured in the field. Attention then

focused on the plants visited by adult male Danainae, particularly when it was realized that these plants contained 1,2-dehydropyrrolizidine alkaloids.

Feeding experiments (Edgar *et al.* 1973) with male *Danaus chrysippus petilea* Stoll, raised in captivity either with or without access to a pyrrolizidine alkaloid-containing plant (*H. amplexicaule*), established that they required access to the *H. amplexicaule* in order to produce **2** (figure 1). In addition one dihydropyrrolizine-deficient *D. chrysippus petilea* was given a pure pyrrolizidine alkaloid (rinderine, a diastereoisomer of **1**) as well as its normal laboratory diet of sugar and water. It consumed the aqueous alkaloid solution avidly but died within 24 h of feeding;

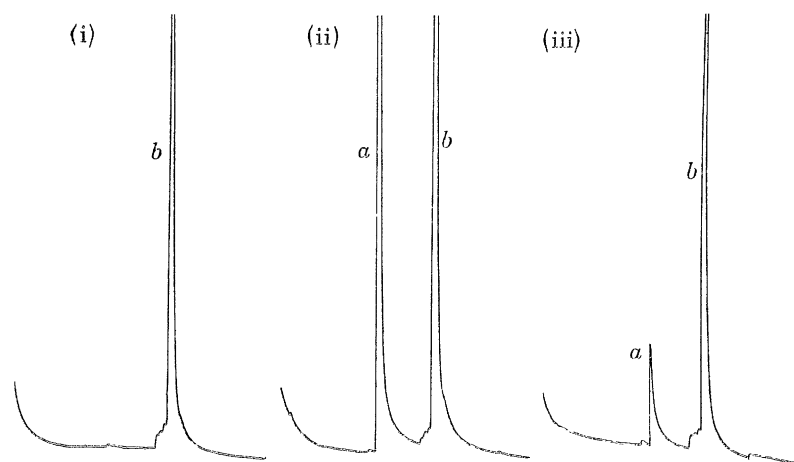


FIGURE 1. Typical gas chromatograms† of the hairpencil extracts of male *D. chrysippus* reared in the laboratory and given (i) sugar and water only, (ii) access to *H. amplexicaule* and sugar and water and (iii) approx. 100 µg of rinderine, a diastereoisomer of **1**, as well as sugar and water. The two components have been identified by their mass spectra as (a) the ketone (**2**) and (b) 3,7-dimethyloct-2-en-1,8-diol. The latter component (b) was first identified in *D. chrysippus* from Sierra Leone by Meinwald *et al.* (1971).

† Obtained on a Varian MAT III gas chromatograph-mass spectrometer with a 1.5 m × 3 mm glass column packed with 2% SE 30 on Chromosorb G, mesh size 80-100 with temperature programming from 80 to 200 °C at 4 °C/min.

nevertheless extracts of its hairpencils showed a significant level of **2** (figure 1 (iii)). A similar experiment has been carried out by Schneider (1974) who fed an alkaloid of the same type, derived from *Heliotropium*, to male *D. chrysippus* raised in the laboratory and later found the normal amount of **2** on their hairpencils. We (Edgar & Culvenor 1974) have recently identified a likely precursor of the hairpencil dihydropyrrolizines, the alkaloid lycopsamine (**1**), in hairpencil extracts of two danaines, *Euploea tulliolus tulliolus* Fabricius and *Danaus hamatus hamatus* Macleay, captured in the field. These results would appear to establish that male Danainae visit 1,2-dehydropyrrolizidine alkaloid containing plants in order to acquire the alkaloid precursors of their hairpencil dihydropyrrolizines.

(b) Dihydropyrrolizines and their functions

(i) *Danaus*

The hairpencil secretions of at least twenty-three species of Danainae have now been analysed, including nine from the New Hebrides (Edgar *et al.* 1973), and patterns of hairpencil dihydropyrrolizines, characteristic of particular genera, are beginning to emerge. In the genus *Danaus*, for example, dihydropyrrolizines are dominant volatile hairpencil components. Each species,

particularly within the same geographical area seems to possess its own dihydropyrrolizine or mixture of dihydropyrrolizines (table 1). It is in this genus also, with *D. gilippus berenice*, that the dihydropyrrolizine ketone **2** has been firmly established as an 'aphrodisiac' which induces females to mate (Pliske & Eisner 1969; Schneider & Seibt 1969). During *D. gilippus berenice*

TABLE 1. DIHYDROPYRROLIZINES IN *DANAUS* HAIRPENCIL SECRETIONS

species	locality†	components		
		(2)	(3)	(4)
<i>D. hamatus hamatus</i> ‡	Au }	+	+	-
<i>D. hamatus moderatus</i> ‡	NH }			
<i>D. affinis affinis</i> ‡	Au }	+	-	+
<i>D. affinis albistriga</i> ‡	NH }			
<i>D. pumilus hebridesius</i> ‡	NH	-	+	-
<i>D. chrysippus petilea</i> ‡	Au }	+	-	-
<i>D. chrysippus dorippus</i> §	Af }			
<i>D. ferrugineus</i>	NG	+	+	+
<i>D. plexippus</i> ‡	NH }	-	-	-
<i>D. plexippus</i> ‡	Au }			
<i>D. plexippus</i> §	US }			
<i>D. gilippus berenice</i> §	US }	+	-	-
<i>D. gilippus strigosus</i> §	US }			
<i>D. formosa mercedonia</i> §	Af	-	-	-
<i>D. limniace petiverana</i> §	Af	+	-	-

† Au = Australia, NH = New Hebrides, Af = Africa, NG = New Guinea, US = United States.

‡ Edgar *et al.* (1971, 1973).

§ Meinwald *et al.* (1969, 1971, 1974).

|| Identification based on thin layer chromatography (Culvenor, Edgar, Smith & Tweeddale 1970) of hair-pencil extracts before and after sodium borohydride reduction and comparison with authentic samples and their reduction products.

courtship the male brushes the hairpencils against the female antennae and head in flight. She responds by alighting and after further 'hairpencilling' copulation takes place. Male *D. gilippus berenice*, raised in captivity and therefore lacking **2**, show a marked reduction in their ability to seduce females but their competence can be restored by addition of synthetic **2** to the hairpencils (Pliske & Eisner 1969). It seems likely that the females of any one *Danaus* species may respond only to the dihydropyrrolizine, or mixture of dihydropyrrolizines, disseminated by the males of that species (table 1) so that these chemicals may have played an important part, among other cues, in establishing and maintaining the reproductive isolation of *Danaus* species.

(ii) *Euploea*

In direct contrast, of the seven species of *Euploea* so far examined, five contain the hydroxy-aldehyde (**3**) as the primary, if not the only (see below) dihydropyrrolizine derivative (table 2) so that no species-specific role can be ascribed to this chemical in *Euploea*. In addition gas chromatography/mass spectrometry of *E. tulliolus tulliolus* hair-pencil extracts (figure 2) has revealed that, unlike the prominence of dihydropyrrolizines in *Danaus* hair-pencil secretions, **3** is only one component among a series of volatile, non-pyrrolizidine-derived chemicals (figure 2).

Some *E. tulliolus tulliolus* hair-pencil extracts have been found to contain an additional dihydropyrrolizine; the diol (**8**) (see figure 2). This chemical is unstable and not very volatile

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TABLE 2. HYDROXYALDEHYDE (3) IN *EUPLOEA* HAIRPENCIL SECRETIONS†

species	locality‡	hydroxy- aldehyde (3)
<i>E. tulliolus tulliolus</i>	A, NH	+
<i>E. sylvester sylvester</i>	A	+
<i>E. core corinna</i>	A	-
<i>E. nemertes</i>	NH	+
<i>E. treitschkei jessica</i>	NH	+
<i>E. boisduvalii</i>	NH	-
<i>E. lewinii lilybaea</i>	NH	+

† Edgar *et al.* (1971, 1973).

‡ A, Australia; NH, New Hebrides.

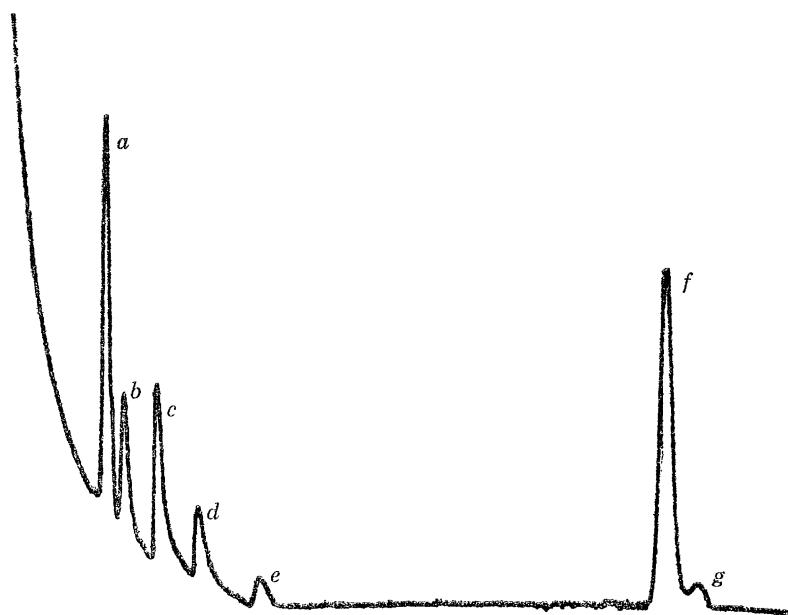


FIGURE 2. A gas chromatogram† obtained from the hairpencil extract of a male *E. tulliolus tulliolus* captured in the field.‡ Components identified by their retention times and mass spectra are: (a) β -ocimene, (b) 'Indole'§, (c) unknown ($M^+ 100$), (d) unknown ($M^+ 132$), (e) methylsalicylate, (f) unknown ($M^+ 195$), (g) hydroxyaldehyde (3).

† Column and conditions as described in figure 1.

‡ This chromatogram may not be typical of *E. tulliolus tulliolus* in that the extract of this individual and eleven others captured at the same time, contained the diol (8) and lycopsamine (1). Their presence might indicate a recent visit to a pyrrolizidine alkaloid plant and incomplete conversion to the full complement of hydroxyaldehyde (3) normally present.

§ This peak has the retention time and characteristic mass spectrum of indole. The diol (8), which has been identified in this hairpencil extract, rearranges and dehydrates in the injection block of the gas chromatograph to give 'indole' so that this peak is probably an artefact.

(Culvenor, Edgar, Smith & Tweeddale 1970). It is therefore probably not present as a pheromone but is more likely to be an intermediate in the metabolic conversion of alkaloids such as 1 to the hydroxyaldehyde 3.

In the New Hebrides male *Euploea* were often seen patrolling open, sunlit clearings with their brightly coloured hairpencils displayed in the manner previously described by Latter & Eltringham (1935) and others (Brower *et al.* 1965). This behaviour, which is not seen with *Danaus*, was thought by Latter & Eltringham (1935) to attract females from a distance. If so

the hydroxyaldehyde (**3**) is probably not involved since it was tested, without success, as a female attractant in the New Hebrides. An alternative explanation for this behaviour is that patrolling males are defining a territory by releasing a male repellent and there is circumstantial evidence to support the view that **3** may be fulfilling this role. Similar behaviour is performed by male Ithomiinae which secrete a pyrrolizidine alkaloid-derived lactone (**5**) from erectile pheromone-disseminating glands (costal fringes) on the costal margin of the hind wing (Edgar, Culvenor & Pliske 1975). The lactone **5**, like the hydroxyaldehyde in *Euploea*, is common to a number of ithomiine species and is thought to function, at one level at least, as a non-species specific male recognition/repellent chemical (Pliske 1975*b*; Edgar *et al.* 1975). By analogy, **3** may serve a similar role for *Euploea* species. It may also be significant, in this regard, that while the *H. amplexicaule*, used as a danaine attractant in the New Hebrides, attracted male *Euploea* from a distance it seemed to repel them at close range and, unlike male *Danaus*, they were never observed to settle and feed at the 'bait' (Edgar *et al.* 1973). The hydroxyaldehyde **3** has since been isolated from the surface of *H. amplexicaule* prepared in the manner used to render it attractive to Danainae in the New Hebrides (Edgar *et al.* 1973).

The possible role of the hydroxyaldehyde as a male repellent does not exclude the possibility that it also functions as an 'aphrodisiac' like the ketone **2** in *D. gilippus berenice* courtship since female *Euploea* are 'hairpencilled' by the male, in the manner observed with *Danaus*, prior to copulation (Brower *et al.* 1965).

(c) Chemicals involved in attraction

The volatile chemicals which attract male Danainae to withering pyrrolizidine alkaloid-containing plants and the chemicals which induce feeding are still unknown. The acids (**6**) (viridifloric and trachelanthic), which constitute a part of certain pyrrolizidine alkaloids, are known to attract male Ithomiinae to pyrrolizidine alkaloid-containing plants where the unmodified alkaloids cause them to feed (Pliske, Edgar & Culvenor 1975). The same chemicals may be involved in danaine attraction and feeding and this possibility is currently being tested.

There are some indications which suggest that genus-specific chemicals may be involved in the attraction of danaines. Few *Danaus*, for example, have been reported feeding on *Messerschmidia* (Hopkins & Buxton 1927; Lever 1936). This may be a coincidence or may suggest that *Euploea* and *Danaus* are attracted by different substances and that the *Danaus* attractant is not produced by *Messerschmidia*.

We reported earlier (Edgar *et al.* 1973) that male New Hebridean *Danaus* were attracted to and fed on hairpencil extracts and, on one occasion, the bodies of dead male danaines which had been partly consumed by ants. We now consider this attraction and feeding to be associated with unmetabolized alkaloids and their volatile derivatives, such as the acids (**6**), present in the bodies of butterflies which had recently fed on a pyrrolizidine alkaloid source.

(d) New Hebridean sources of pyrrolizidine alkaloids

Messerschmidia argentea is the only New Hebridean plant so far observed to attract male Danainae (the *H. amplexicaule* employed as an attractant during the expedition was brought from Fiji by Dr G. S. Robinson) but the pyrrolizidine alkaloid-containing genera *Eupatorium*, *Senecio* and *Crotalaria* also occur in the New Hebrides and these may be alternative sources of dihydropyrrolizines for New Hebridean Danainae.

(e) Origin of the requirement for pyrrolizidine alkaloids

The study of the unusual association of male danaine and ithomiine butterflies with pyrrolizidine alkaloid-containing plants tempts one to speculate on its origins (Edgar *et al.* 1974). Two broad, not entirely exclusive, possibilities exist. They are: (1) that 1,2-dehydropyrrolizidine alkaloid-derived chemicals possess intrinsic properties which predispose them for use as pheromones and that danaines and ithomiines have sought them out for this reason or (2) that butterflies ancestral to modern danaines and ithomiines had, at one time, a long association with 1,2-dehydropyrrolizidine alkaloid-containing plants during which the present dependence developed. Subsequent evolutionary changes in both plants and insects have since modified the original situation so that now only the remnants of it remain.

I favour the second of these two proposals. In particular I believe that 1,2-dehydropyrrolizidine alkaloids may have been important constituents of food plants of butterflies ancestral to modern danaines and ithomiines. Such an association would seem to provide a reasonable basis on which the present behaviour might have developed.

Three zones of chemical influence can be envisaged in the space surrounding the ancestral, 1,2-dehydropyrrolizidine alkaloid-containing plants. Furthest out the more volatile pyrrolizidine alkaloid-derived chemicals (e.g. the acids (6)) may have attracted both male and female butterflies towards the ancestral larval food plant in the same way that these chemicals now attract male (and some female) danaines and ithomiines. Less volatile chemicals (the dihydropyrrolizines 2–4) may have formed an intermediated zone in the vicinity of the plants. Here females became receptive to males and mating occurred. Finally chemical cues of low volatility, of which I will say more later, on or near the surface of the plants provoked ovipositing behaviour in females.

It is envisaged that a small group of males later developed the capacity, now displayed by *Danaus*, to produce and disseminate the chemicals (dihydropyrrolizines) which induced receptivity in females. They used these to seduce females in the absence of the food plant. Females which had mated remote from the food plant were then required to seek out suitable plants in order to lay their eggs. They may have used the normal volatile chemicals associated with pyrrolizidine alkaloids to find suitable larval food plants or become attuned to other volatile chemicals more directly associated with the ovipositing cues.

At this point let us consider the nature of the cues which induced ovipositing behaviour in females. Present day danaines oviposit primarily on plants in the Asclepiadaceae and Apocynaceae (Ehrlich & Raven 1965). They are particularly fond of cardenolide-containing species in these two families and have, in some cases at least, developed the capacity to store these vertebrate heart poisons in their body tissues (Reichstein, von Euw, Parsons & Rothschild 1968). This makes them unpalatable and protects them from potential vertebrate predators (Reichstein *et al.* 1968; Brower 1969). Their association with cardenolide-containing plants is therefore likely to have been preserved through ovipositing cues directly or indirectly associated with cardenolides. It is therefore also possible that cardenolides provided the ovipositing cues in the postulated ancestral larval food plants so that these plants originally contained both pyrrolizidine alkaloids and cardenolides. If this were the case feeding pressures imposed by the ancestral butterflies would have favoured survival of plants deficient in one or other (or both) of these chemicals since deficient plants would fail to either attract the butterflies or provoke ovipositing. Inevitably therefore the ancestral larval food plants would split into three possible

branches – one containing cardenolides, another 1,2-dehydropyrrolizidine alkaloids and the third having neither of these chemicals (figure 3). It is conceivable that some species could have survived this development by continuing to use pyrrolizidine alkaloid plants as loci for mating with females then seeking out cardenolide-containing plants for egg laying. The long term advantage, however, would lie with males capable of producing the chemicals which induced receptivity in females (albeit by gathering precursors from pyrrolizidine plants), and with females who responded to these chemicals yet were capable of finding (via different olfactory cues) plants in the cardenolide branch for ovipositing.

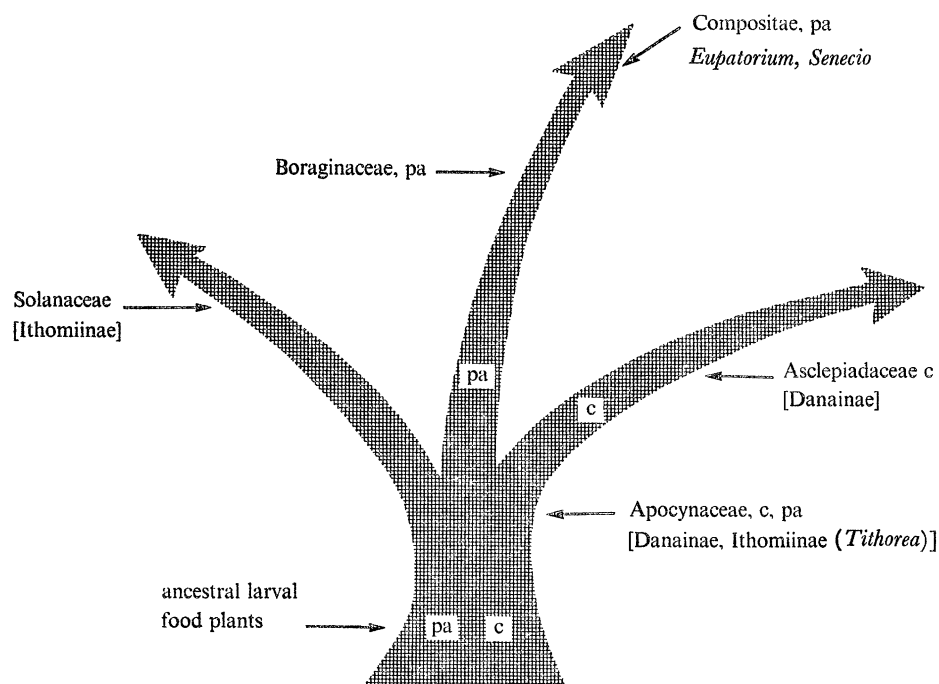


FIGURE 3. Proposed evolution of plants used by Danainae and Ithomiinae as larval food plants [] or visited by males of both subfamilies for the acquisition of pyrrolizidine alkaloids; showing the distribution of cardenolides (c) and 1,2-dehydropyrrolizidine alkaloids (pa).

The above proposal suggests a phylogenetic relationship between the pyrrolizidine alkaloid-containing plants visited by male danaines (and ithomiines) and the cardenolide containing plants they use as larval food plants (figure 3). This suggestion is encompassed within the broader phylogenetic proposals of Cronquist (1968) and Takhtajan (1969) who have proposed that the Orders containing the relevant families have had a common origin.

In an endeavour to find additional support for our hypothesis we collected data on the danaines larval food plants. Among the information sent to us was a report, from A. Muyschondt, that the larvae of the ithomiine *Tithorea harmonia salvadores* Staudinger feed on *Fernaldia pandurata* (A.D.C.) Woodson (family Apocynaceae) (previously called *Urechites karwinsky*) a plant which is closely related to the cardenolide containing genera *Urechites* and *Echites* of the Apocynaceae. The roots of *F. pandurata* are used to kill small animals (Borges del Castillo, España de Aguirre, Bretón, Gonzáles & Trujillo 1970) so that it too may contain toxic cardenolides. In addition extracts of *F. pandurata* have yielded a dihydropyrrolizidine (7) (which we believe is of 1,2-dehydropyrrolizidine alkaloid origin) closely related to the danaine hairpencil

dihydropyrrolizines (Borges del Castillo *et al.* 1970). *F. pandurata* may therefore contain both 1,2-dehydropyrrolizidine alkaloids and cardenolides and represent a conservative development of the ancestral larval food plants we have postulated.

The genus *Tithorea* is also noteworthy because it belongs to the 'primitive' tribe Tithoreini (Fox 1956) and has larvae and pupae which resemble those of certain Danainae (Gilbert & Ehrlich 1970). Unlike other ithomiines, whose larvae feed exclusively on Solanaceae, *Tithorea* larvae feed, like some danaines on Apocynaceae (e.g. *Echites*) (Gilbert & Ehrlich 1970). The genus *Tithorea* may therefore be a conservative development of the ancestral butterflies we have postulated. Further support for this view has come from T. Pliske (1975*a*) who has found that, in marked contrast to the normal attraction of predominantly male ithomiines and danaines to pyrrolizidine-containing plants, a very high proportion (up to 80%) of female *Tithorea* are attracted.

The presence of both cardenolides and 1,2-dehydropyrrolizidine alkaloids in *F. pandurata* has not yet been confirmed but recently we have identified the alkaloid lycopsamine (**1**) and its diastereoisomers intermedine and/or indicine in the genus *Parsonsia* which is in the same tribe (Parsonsiace) as *Fernaldia* (Edgar & Culvenor 1975). This finding represents the first definite evidence of 1,2-dehydropyrrolizidine alkaloids in the Apocynaceae. It is also significant that the pyrrolizidine alkaloids found in *Parsonsia* have only been found previously in the Boraginaceae and that diastereoisomers, rinderine and echinatine, occur only in the genus *Eupatorium* of the Compositae as well as in the Boraginaceae (Bull, Culvenor & Dick 1968). Thus sections of the Compositae, Boraginaceae and Apocynaceae can now be linked phytochemically in agreement with our hypothesis.

Parsonsia attracts male danaines (Atkins 1974) and is reported to be used occasionally as a larval food plant by *Euploea core corinna* Macleay (G. Sankowski, personal communication) and perhaps *D. hamatus hamatus* (Common & Waterhouse 1972). It is also used as a larval food plant by the ithomiine *Tellervo zoilus zoilus* Fabricius (Common & Waterhouse 1972) which differs from other ithomiines in not having costal fringes. *Tellervo* is believed by Fox (1956) to be the most primitive ithomiine genus, even more primitive than *Tithorea*. Of the two danaines mentioned above only *D. hamatus hamatus* is known to secrete dihydropyrrolizines (Edgar *et al.* 1971) and it will be interesting to discover whether, after being reared on *Parsonsia*, male *D. hamatus hamatus* emerge with dihydropyrrolizines on their hairpencils.

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