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COUMARINS AND CATERPILLARS: A CASE FOR COEVOLUTION

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Ehrlich and Raven (1964) were among the first to focus on coevolution as a distinct evolutionary process. In their formulation, insect-plant coevolution is a five-step sequence: 1. by mutation and recombination, angiosperms produce novel secondary substances; 2. by chance, these new secondary substances alter the suitability of the plant as food for insects; 3. the plants, released from the restraints imposed by herbivory, undergo evolutionary radiation in a new adaptive zone; 4. by mutation or recombination, insects evolve mechanisms of resistance to the secondary substances; 5. able to exploit a plant resource hitherto excluded from herbivores, the adapted insects enter a new adaptive zone and undergo their own evolutionary radiation.

This scenario was inspired by broad patterns of hostplant utilization among families of butterflies (Rhopalocera). Although the schema gained widespread acceptance, to date no specific example demonstrates most or all of the steps in the sequence. This lack of empirical evidence has been the subject of considerable criticism (e.g., Jermy, 1976; Janzen, 1980). Recent experimental work on associations between various insects and plants containing furanocoumarins and related compounds (Berenbaum, 1978, 1980, 1981a, 1981b, 1981c), however, provides a case study with either direct or circumstantial evidence for each part of the coevolutionary process.

(1) Production of Novel Secondary Substances by Mutation or Recombination

Natural products with a 2H-1-benzopyran-2-one nucleus (Fig. 1), broadly called coumarins, are widespread in the plant kingdom. Various modifications of the benzopyran-2-one nucleus exist in nature. By far, simple coumarins are the most common, characterized by the lack of additional fused ring systems. More than 30 simple coumarins have been reported from a total of 33 plant families (Hegnauer, 1964-1973; Gray and Waterman, 1978). Coumarins with an oxygen-containing substituent at the 7-position, such as umbelliferone (Fig. 1), appear to be biosynthetically distinct from those, such as coumarin, that lack such a function; umbelliferone and related hydroxycoumarins are derived from p-coumaric acid whereas coumarin is derived from the unsubstituted cis-cinnamic acid (Brown, 1960; Brown, 1970). Paracoumaric acid, an intermediate in lignin biosynthesis, is widespread among angiosperm plants, occurring in at least 100 plant families; hydroxycoumarins are more restricted in distribution, reported to occur in less than three dozen plant families (Table 1). Hydroxycoumarins are known to possess biocidal properties and act as phytoalexins and germination inhibitors in many species (Bose, 1958; Hughes and Swain, 1960; Berrie et al., 1968; Jurd et al., 1973; Williams and Hoagland, 1982).

In many natural coumarins, a third ring is fused to the benzopyran-2-one nucleus, thus incorporating the 7-oxygen atom into a new heterocyclic ring. Incorporation into a 5-membered ring gives rise to furano-

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COUMARIN



- а. Coumarin
- 2H-1-benzopyran-2-one ь.

LINEAR FURANOCOUMARIN



Psoralen а. b. 7-H-furo [3,2-g]-1-

benzopyran-2-one

HYDROXYCOUMARIN



- Umbelliferone (7-hydroxycoumarin) a. b.
- 7-hydroxy-2H-1-benzopyran-2-one



4'8 S Angelicin a. 2-H-furo[2,3-H]-1b. benzopyran-2-one

FIG. 1. Basic coumarin structural types with nomenclatural and numbering systems. (a) semi-rational nomenclature (first number at each position). (b) IUPAC nomenclature (second number at each position).

coumarins. All furanocoumarins share the precursor umbelliferone (7-hydroxycoumarin). In contrast with hydroxycoumarins, furanocoumarins are restricted to eight families (Table 2) and occur with regularity and diversity in only two of those families, the Umbelliferae and the Rutaceae. The two structural types of furanocoumarins-angular, with the furan ring attached at the 7, 8 positions, and linear furanocoumarins, with the furan ring attached at the 6, 7 positions (Fig. 1)-are biosynthetically distinct, although both types derive from enzymatic prenylation of umbelliferone. The enzymes that prenvlate umbelliferone appear to be site-specific. Dimethylallylpyrophosphate: umbelliferone dimethylallytransferase, which participates in the biosynthesis of linear furanocoumarins, attaches the prenyl unit to the 7-position only (Ellis and Brown, 1974). In that the enzyme is unable to prenylate umbelliferone at the 8-position, a separate enzyme is thought to mediate the biosynthesis of angular furanocoumarins (Ellis and Brown, 1974). Angular furanocoumarins are even more rare than linear furanocoumarins, occurring in only two genera of Leguminosae and in less than ten genera in the Umbelliferae (Baskin et al., 1967; Nielsen, 1970).

Furanocoumarins have been found in all parts of plants, although roots and seeds are the organs which have been investigated most thoroughly (Karrer, 1958). Where furanocoumarins are reported in roots and seeds, they are frequently found in foliage as well after further investigation, although foliar composition and concentrations may differ from that of roots (Fahmy et al., 1955; Steck, 1970). Depending on the taxon, fruits or roots appear to be the primary storage sites for furanocoumarins. Concentrations in roots can exceed 9%, calculated on a dry weight basis (e.g., Heracleum canescens—Kumar et al., 1976). Yields from fruits vary depending on the stage of maturity but most often reach maximum concentrations of 1% to 5% while fully formed yet still green (Beyrich, 1966; Simsova and Blazek, 1967; Balbaa et al., 1972; Stahl and Herting, 1976). Foliage typically contains far less material, on the order of 0.1% to 1.0% dry

| Apocynaceae | Moraceae |
|-------------------|----------------|
| Araliaceae | Nepenthaceae |
| Caprifoliaceae | Oleaceae |
| Caryophyllaceae | Passifloraceae |
| Compositae | Pittosporaceae |
| Convolvulaceae | Ranunculaceae |
| Ebenaceae | Rosaceae |
| Euphorbiaceae | Rubiaceae |
| Fouquieriaceae | Rutaceae |
| Hippocastaneaceae | Sapindaceae |
| Labiatae | Saxifragaceae |
| Leguminosae | Solanaceae |
| Loganiacae | Sterculiaceae |
| Magnoliacae | Theaceae |
| Meliaceae | Thymelaeaceae |
| | Umbelliferae |
| | |

TABLE 1. Plant families containing hydroxycou-marins (from Hegnauer, 1964–1973).

weight (Beyrich, 1965*a*, 1965*b*, 1966; Steck, 1970). Linear furanocoumarins invariably make up the greatest proportion of total furanocoumarin content, irrespective of botanical source. When angular furanocoumarins are present, they generally occur at levels ranging from .001% to .15% dry weight (Steck and Bailey, 1969; Kumar et al., 1976) and thus comprise, on average, less than 10% of the total furanocoumarin content of plant tissue (Spaeth and Simon, 1936; Hata and Kozawa, 1961; Nielsen and Lemmich, 1964; Ignat'eva and Nikonov, 1966).

According to Beyrich (1967), the site of storage or accumulation of furanocoumarins is also the site of synthesis; reciprocal root graft studies with *Levisticum officinale* and *Pastinaca sativa* demonstrated a fundamental inability to translocate furanocoumarins away from the site of synthesis. Brown and Steck (1973), however, established that skimmin, the glucoside precursor of furanocoumarin biosynthesis, can be translocated from petiole cut ends to leaf blades, where biosynthesis is thought to take place.

Irrespective of taxon, furanocoumarins occur in special organs. In seeds of *Psoralea subaucalis*, a legume, furanocoumarins are restricted to the seed coat and are completely absent from the endosperm (Baskin et al., 1967); in the rutaceous ge-

TABLE 2. Plant families and genera with furanocoumarins. Data from Hegnauer (1964–1973); Nielsen, 1970; Gonzalez et al., (1976); Gray and Waterman (1978).

| Family | Number of genera in family | Number of genera with furano- coumarins |
|----------------|----------------------------------|--|
| Umbelliferae | 200 | 23 |
| Rutaceae | 140 | 19 |
| Leguminosae | 550 | 2 |
| Moraceae | 73 | 1 |
| Solanaceae | 85 | 1 |
| Pittosporaceae | 9 | 1 |
| Thymelaeaceae | 40 | 1 |
| Compositae | 950 | 1 |

nus *Citrus*, furanocoumarins are localized in oil glands in the peel (Fisher and Trama, 1979); and in the seeds of Umbelliferae, Ladygina et al. (1970) found furanocoumarins primarily in the segmented secretory ducts overlying the seed coat, where they form small needle-like crystals. In shoots of Heracleum lanatum (Umbelliferae), furanocoumarins occur in oil channels associated with each vascular bundle in the petioles of unexpanded leaves (Camm et al., 1976), and in roots of Pastinaca sativa (Umbelliferae), Beyrich (1966) found that furanocoumarins occur only in the outer cylinder. Localization of secondary substances in special organs has been suggested as a mechanism for avoiding autotoxicity in plants (McKey, 1979), and thus is often associated with allelochemic, as opposed to internal physiological, activity (Whittaker and Feeny, 1971).

(2) New Secondary Substances Alter the Suitability of Plants as Food for Insects

Linear furanocoumarins are more toxic to polyphagous insects than their hydrocoumarin precursors by virtue of a double bond in the furan ring that allows ultraviolet light to inactivate DNA (see references in Berenbaum, 1978). *Spodoptera eridania*, the southern armyworm (Lepidoptera: Noctuidae), readily eats plants or artificial diets containing hydroxycoumarins; this caterpillar cannot consume fuTABLE 3. Coumarin chemistry and number of species of plant genera in the umbelliferae. From Willis, 1966; genera according to Drude, 1898; chemical data from Gonzalez et al., 1973.

| Genera | Number of species | Genera | Number of species |
|-----------------|-------------------------|-----------------------------|-------------------------|
| Without furance | oumarins coumarins | or with dihydro only (*) | furano- |
| Echinophora | 10 | Capnophyllum | 4 |
| Anisosciadium | 2 | Dorema | 16 |
| Dicyclophora | 1 | Leptotaenia* | 16 |
| Pycnocycla | 10 | Lomatium* | 80 |
| Scandix | 15 - 20 | Zozimia* | 10 |
| Myrrhis | 2 | Guillonea | 1 |
| Molospermum | 1 | Laserpitium | 35 |
| Astrodaucus | 4 | Thapsia | 6 |
| Torilis | 15 | Melanoselinum | 7 |
| Zizia* | 3 | Exoacan tha | 2 |
| Cryptotaenia | 4 | Artedia | 1 |
| Carum | 1 | Ammodaucus | 1 |
| Athamanta* | 15 | Daucus | 60 |
| Pteryxia | 2 | | |

Average number of species per genus = 12.1 ± 3.6 .

With linear furanocoumarins only

| Chaerophyllum | 40 | Agasyllis | 1 |
|----------------|----|--------------|-----|
| Coriandrum | 2 | Cymopterus | 18 |
| Cachrys | 22 | Levisticum | 35 |
| Conium | 4 | Phellopterus | 5 |
| Hippomarathrum | 12 | Ferula | 133 |
| Prangos | 30 | Ferulago | 50 |
| Apium | 1 | Xanthogalum | 3 |
| Cicuta | 10 | Malabaila | 10 |
| Petroselinum | 5 | Laser | 3 |
| Anethum | 1 | Siler | 1 |
| Cnidium | 20 | | |
| Foeniculum | 5 | | |
| Libanotis | | | |
| Sphenosciadium | 1 | | |

Average number of species per genus = 17.4 ± 5.8 .

With linear and angular furanocoumarins

| Ammi | 10 | Angelica | 80 |
|----------------|--------------|--------------------|---------|
| Bupleurum | 150 | Archangelica | 2 |
| Pimpinella | 150 | Pastinaca | 15 |
| Ligusticum | 60 | Peucedanum | 120 |
| Selinum | 3 | Heracleum | 70 |
| Seseli | 80 | | |
| Average number | r of species | per genus $= 67.3$ | ± 16.8. |

* Plants containing dihydrofuranocoumarins.

ranocoumarins or grow on plants containing them (Soo Hoo and Fraenkel, 1966; Berenbaum, 1978). Toxic effects are attributable to the furan ring. Artificial diet containing levels of furanocoumarins lethal in the presence of ultraviolet light does not cause great mortality in the absence of ultraviolet light (Berenbaum, 1978); toxicity dependent upon UV light is consistent with the mechanism of phototoxicity via furanocoumarin-induced inactivation of DNA.

Angular furanocoumarins are toxic to oligophagous insects that are able to ingest and tolerate linear furanocoumarins (Berenbaum and Feeny, 1981). Fecundity of the black swallowtail (Papilio polyxenes), an umbellifer-feeding specialist that is capable of ingesting and assimilating linear furanocoumarins, is drastically reduced by angelicin in an artificial diet. These observations suggest that the change of configuration of the furan ring from the linear to the angular position affects the properties of furanocoumarins. In the angular position, the furan ring double bond is incapable of photobinding with DNA (see references in Berenbaum and Feeny, 1981) so phototoxicity is theoretically an impossibility; some other mode of action must be responsible for the adverse response noted in swallowtails.

(3) Plants Undergo Evolutionary Radiation in a New Adaptive Zone

That plants underwent evolutionary radiation as a result of producing linear and angular furanocoumarins is suggested by patterns of species diversification and endemism within the Umbelliferae. With its 1,950 species, the Apioideae, the only group in the family containing any type of coumarin, far outnumbers the plants in the subfamilies Hydrocotyloideae (320 species) and Saniculoideae (250 species). Within the Apioideae, the vast majority of monotypic genera and genera with extremely restricted geographic distributions are those that produce no furanocoumarins (Table 3). At the opposite extreme, the majority of holarctic genera in the family (Bupleurum, Ligusticum, Angelica, Pastinaca, and Heracleum) are plants containing both linear and angular furanocoumarins; monotypic genera are the exception in this group of plants.

As for the new "adaptive zone" that plants producing furanocoumarins presumably entered, there is little direct evidence that such exists. However, it can be argued that furanocoumarins facilitated the colonization and expansion of the Umbelliferae into progressively drier habitats (Mathias, 1965). Root elongation in several species of Umbelliferae is reduced by ultraviolet light, and, in these species, synthesis of flavonoid pigments that absorb ultraviolet light and screen the plants from its harmful effects is stimulated by light (Wellman, 1976). Enzymes in phenylpropanoid metabolism (and thus furanocoumarin metabolism) are similarly induced by light (Heller et al., 1979). Since furanocoumarins are highly UV-absorbing, they may also act as screens for damaging sunlight and may thus have facilitated establishment and growth in open habitats. After establishment plants may have experienced reduced herbivory as well due to the phototoxic properties of furanocoumarins.

(4a) Insects Evolve Physical Resistance to Novel Secondary Substances

Polyphagous lepidopteran herbivores cannot digest or detoxify furanocoumarins (Yajima et al., 1977; Berenbaum, 1978; Gebreyesus, 1980), yet caterpillars of species adapted to feeding on umbelliferous plants are immune to the effects of some furanocoumarins. This immunity can be conferred by physiological mechanisms, as in Papilio polyxenes (discussed above); it can also be enhanced by behavioral adaptations. In the case of leaf-rolling oecophorids that feed exclusively on Umbelliferae, resistance to the chemicals may simply be the result of the leaf-rolling habit. Rolled leaves shield the caterpillar from ultraviolet light and thereby from UV-induced phototoxicity (Berenbaum, 1978).

Leaf-rolling is by no means restricted to caterpillars that feed on phototoxic plants. However, a remarkable number of hostplants for the oecophorid genera *Depressaria* and *Agonopterix* contain photoactive secondary substances (Table 4). Of the families reported as hosts for *Agonopterix* species, Guttiferae, Leguminosae, ComTABLE 4. Coumarin chemistry of hostplants of de-pressariinae (Lepidoptera: Oecophoridae) in NorthAmerica (Hodges, 1974).

| TRIBE A | MPHISBATINI |
|---------------|----------------------|
| Machimia, Ea | upragia, Psilocorsis |
| Ulmaceae* | Salicaceae* |
| Juglandaceae* | Rosaceae° |
| Fagaceae* | Cornaceae* |
| Betulaceae* | Aceraceae* |
| Tiliaceae° | Oleaceae° |
| | |

TRIBE DEPRESSARIINI

Himmacia, Nites, and Bibarrambla

Juglandaceae,* Fagaceae,* Betulaceae,* Aceraceae,* Salicaceae*

Apachea and Semioscopis

Betulaceae,* Rosaceae,° Rutaceae†

Martyrhilda

Betulaceae,* Malvaceae,* Salicaceae,* Compositae†#

Agonopterix

Juglandaceae,* Myricaceae,* Lythraceae,* Salicaceae,* Rosaceae,° Leguminosae,† Guttiferae,°# Rutaceae,† Umbelliferae,† Araliaceae,° Boraginaceae,* Compositae†#

Depressaria

Umbelliferae,† Compositae†#

* Families containing p-coumaric acid.

° Families containing hydroxycoumarins.

† Families containing furanocoumarins.

Families containing phototoxins other than furanocoumarins

positae and Umbelliferae contain photoactive secondary substances. Hypericum species in the Guttiferae, hosts for A. hyperella, A. lythrella and A. nubiferella, contain hypericin, a dimeric quinone that acts as a primary photosensitizer in mammals (Pathak, 1974; Galitzer and Oehme, 1978). In the Leguminosae, Psoralea spp., hosts for A. psoraliella and A. posticella, contain phototoxic furanocoumarins (Baskin et al., 1967). The composite host plants Antennaria, Artemisia, Eupatorium, Coreopsis, Bidens, Senecio and Erigeron contain several polyacetylenic substances, notably tridecapentayene, thiophene derivatives such as α -terthienvl, and matricaria ester, with antibiotic and phototoxic properties (Towers et al., 1977). In the case of α -terthienyl and derivatives, phototoxicity to nematodes, fungi and insects depends on the presence of longwave ultraviolet radiation (Gommers and Geerligs, 1973; Wat et al., 1981), as does the phototoxicity of phenylheptatryene (Wat et al., 1979). Wavelengths below 400 nm are necessary for the photoactivation of furanocoumarins in such Agonopterix hosts as Angelica, Cicuta, Heracleum, and Pastinaca in the Umbelliferae, Ptelea and Xanthoxylum in the Rutaceae, and Psoralea in the Leguminosae.

The proportion of phototoxic species among the foodplants of *Agonopterix* caterpillars is higher than among other groups within the family Oecophoridae. The Oecophorini, the largest tribe in the family, feed almost exclusively on detritus, particularly on fungus under bark (Hodges, 1974); *Hofmannophila* feeds on hides and *Martyringa* and *Endrosis* feed on stored grain, flesh and wool. Members of the tribe Amphisbatini feed primarily on tree species in the families Fagaceae, Rosaceae, Betulaceae and Juglandaceae; there are no species known to be photoactive in these families.

Specialization on plants containing phototoxic substances may have developed as a consequence of the leaf-rolling habit of oecophorids feeding on material with low water content. For tree feeders, low water content is often a factor limiting to larval growth (Scriber, 1977, 1979). For detritus feeders such as the Oecophorini, low water content is even more of a problem (Hodges, 1974). The water content of most species of hostplants for genera in the Depressariini other than Agonopterix and Depressaria is considerably lower than the water content of hosts of Agonopterix and Depressaria (Berenbaum, 1980); leaf-rolling acts to minimize water loss by maintaining high humidity and, in fact, enhances the rate of transpiration (O'Toole et al., 1979). Though undoubtedly biochemical and physiological adaptation has taken place within Agonopterix and Depressaria to furanocoumarin-containing plants, leafrolling, a vestige of the tree-feeding habits of their evolutionary predecessors, may well have facilitated the adoption of phototoxic plants as hosts.

(4b) Insects Evolve Biochemical Resistance to New Plant Secondary Substances

Comparisons between polyphagous and oligophagous species provide the best evidence of biochemical adaptation by insects to furanocoumarins. Black swallowtail caterpillars (*Papilio polyxenes*—Lepidoptera: Papilionidae), which feed exclusively on the family Umbelliferae (Tietz, 1972; Tyler, 1975) appear to be unaffected either behaviorally or physiologically by dietary levels of xanthotoxin (a linear furanocoumarin) ten times greater than those that kill 100% of the polyphagous Spodoptera eridania. In fact, growth is actually enhanced in the presence of the chemical (Berenbaum, 1981c). The physiological mechanism of resistance to furanocoumarins in these oligophagous insects is unknown. Papilio polyxenes caterpillars feed externally on plants, fully exposed to natural levels of ultraviolet light, yet manifest no short-term physiological symptoms of phototoxicity. High concentrations of furanocoumarins in artificial diet are excreted in the feces (pers. observ.), but metabolism or uptake of these chemicals has not been established.

Indirect evidence suggests adaptation to angular furanocoumarins by oligophagous insect herbivores of umbellifers. While the black swallowtail (P. polyxenes) suffers reduced fecundity from naturally occurring levels of angular furanocoumarins in its diet (Berenbaum and Feeny, 1981), the short-tailed swallowtail (P. brevicauda), feeds almost exclusively on plants containing angular furanocoumarins, which are generally avoided by P. polyxenes. Of 24 genera recorded as hosts of P. polyxenes, only two genera (Angelica, Pastinaca) contain angular furanocoumarins; of six genera reported as hosts of *P. brevicauda*, four (Heracleum, Angelica, Ligusticum and Pastinaca) contain angular furanocoumarins (Tietz, 1972; Tyler, 1975; Jackson, 1979). Moreover, Depressaria pastinacella, the parsnip webworm (Lepidoptera: Oecophoridae), feeds entirely on those few

North American umbelliferous genera that contain angular furanocoumarins (Angelica, Pastinaca, Heracleum), and occurs with statistically greater frequency within a Pastinaca sativa (wild parsnip) population plants containing angular furanocoumarins (Berenbaum, 1981a).

(5) Adapted Insects Can Enter a New Adaptive Zone and Undergo an **Evolutionary** Radiation

"Adaptive zone" has been an ill-defined concept as used by Ehrlich and Raven (1964). If number of species can be used as a measure of evolutionary diversification, then, at least in the two major herbivore groups associated with furanocoumarin-containing plants, the Oecophoridae and the Papilionidae (Table 5), there has been considerably more speciation in groups of feeding on plants containing furanocoumarins than there has been in those groups most closely related to them on hosts lacking furanocoumarins.

(6) Parallel Evolution of Insects Adapted to Particular Noxious **Phytochemicals**

According to Ehrlich and Raven (1964), similar coevolutionary pressures along different phylogenetic lines should generate parallel evolutionary series. Such series have been dismissed as rare (Jermy, 1976), but these series may escape detection for at least two reasons. First, phylogenetically distinct plant species can share similar chemistry. For example, Ficus in the Moraceae shares a biosynthetic pathway for furanocoumarin production that is identical in all respects to that of the Umbelliferae and Rutaceae (Caporale et al., 1970; Caporale et al., 1972), despite the lack of any close taxonomic affinity. Second, closely related insect species may feed on the same plant species but heterogeneity in production and distribution of secondary substances may create a situation in which insects, by feeding on different plant parts, actually encounter different secondary chemicals (e.g., Agonopterix clemensella and Depressaria

TABLE 5. Diversity of insect taxa and hostplant chemistrv.

| A. Depressariini (Oe | cophoridae) ¹ | | |
|----------------------|--|----------------------|--|
| Genus | Hostplant chemistry (# host families) | Number of species | |
| Depressaria | LFC, AFC, HC (2) | 100 | |
| Agonopterix | LFC, HC (12) | 125 | |
| Martyrhilda | HC (4) | 38 | |
| Semioscopis | HC (3) | 12 | |
| Apachea | LFC, HC(1) | 1 | |
| Bibarrambla | NC (5) | 1 | |
| Nites | NC (5?) | 5 | |
| Himmacia | NC (5?) | 3 | |
| B. Genus Papilio (P | apilionidae)² | | |
| Section | Hostplant chemistry (# host families) | Number of species | |
| Section II | LFC, AFC, HC (9) | 139 | |
| Section IV | LFC, HC (5) | 34 | |
| Section V | HC (2) | 18 | |
| Section I | HC(2) | 9 | |
| Section III | HC (13) | 8 | |

 1 North American species only (Hodges, 1974). 2 From Scriber (1973). NC = no coumarins. HC = with hydroxy-coumarins. LFC = with linear furancoumarins. AFC = with angular furanocoumarins.

pastinacella feed on leaves and seeds of Pastinaca sativa, respectively. Leaves contain only linear furanocoumarins whereas seeds of some individuals contain angular furanocoumarins as well as linear furanocoumarins [Berenbaum, 1981a]).

Among the taxa associated with Umbelliferae, there are several striking examples of convergence in hostplant usage patterns. These patterns are consistent with patterns of coumarin chemistry and could well be construed to be parallel series arising independently through the process of coevolution.

(6a) Lepidoptera

The greatest biomass, numerical abundance and species diversity of herbivores associated with Umbelliferae are lepidopterous larvae. In the Oecophoridae, the genera Agonopterix and Depressaria, in addition to feeding on furanocoumarincontaining Umbelliferae, Leguminosae (Psoralea), and Rutaceae (Ptelea and Xanthoxylum), are found on plants in the Guttiferae, Rosaceae, Leguminosae, Araliacae, and Compositae, all families con-

TABLE 6. Hostplants of the genus Papilio (Scriber,1973).

A. Sections of the genus in North America (Munroe, 1960)

Section II, machaon complex

Rutaceae,† Umbelliferae,† Compositae†

Section III

Lauraceae, Magnoliaceae, Platanaceae,* Ulmaceae,* Juglandaceae,* Betulaceae,* Tiliaceae,° Salicaceae,* Rosaceae,° Rhamnaceae,* Aceraceae,* Rutaceae,† Oleaceae°

Section IV

- Lauraceae,° Rutaceae,† Piperaceae, Nyssaceae, Salicaceae*
- B. Sections of the genus outside North America Section I

Magnoliaceae,° Lauraceae°

Section II, excluding machaon complex

Leguminosae,[†] Meliaceae,[†] Rutaceae,[†] Sapindaceae,[°] Araliaceae,[°] Umbelliferae,[†] Verbenaceae,^{*} Labiatae,[°] Rutaceae[†]

Section IV

Magnoliaceae,° Lauraceae°

* Families containing p-coumaric acid.

Families containing hydroxycoumarins
 Families containing furanocoumarins.

taining hydroxycoumarins. The remainder of host families for *Agonopterix*, while lacking coumarins per se, almost universally contain p-coumaric acid, the biosynthetic precursor of umbelliferone (Brown, 1960). While p-coumaric acid has an extremely broad distribution among plant families (Hegnauer, 1964–1973) and thus is hardly suggestive of a coevolutionary relationship, it nonetheless is a prerequisite for coumarin synthesis and its presence, in lieu of ferulic, sinapic, or cinnamic acid, indicates the phytochemical relationship of the plant taxon to coumarin-producing forms.

The host plants of the genus *Papilio* are much the same as *Agonopterix* and *Depressaria* (Table 6). The section of the genus most closely associated with the Umbelliferae is Section II of Munroe (1960). Outside the *machaon* complex, which feeds exclusively on the furanocoumarin-containing families Umbelliferae, Rutaceae and Compositae, other *Papilio* species in the section feed on Leguminosae, Meliaceae, Sapindaceae, Araliaceae, Labiatae and Rubiaceae—all families that contain hydroxycoumarins (the single exception being a single record on Verbenaceae). Sections I, IV and V of the genus, thought to be less advanced phylogenetically than Section II, feed on Magnoliaceae and Lauraceae, primitive plants that nonetheless possess hydroxycoumarins; Section III species fed on virtually the same plants as do genera in the tribe Amphisbatini in the Oecophoridae, plants in families containing either hydroxycoumarins or p-coumaric acid.

The family Noctuidae, known for its many highly polyphagous species (e.g., Spodoptera), nevertheless contains several species that are restricted as caterpillars to plants in the family Umbelliferae (Table 7). Papaipema marginidens and P. harrisi are both stem borers of furanocoumarincontaining umbelliferous genera. The majority of Papaipema species feed on plants containing hydroxycoumarins (Oleaceae, Ranunculaceae, Compositae) or furanocoumarins; of the two leguminous genera reported as hosts for Papaipema, one, *Psoralea*, is one of only two genera in the family producing furanocoumarins. The remainder of host families, with the exception of Polypodiaceae and Tiliaceae, contain p-coumaric acid. In the genus Platysenta, P. sutor is recorded as feeding on celery (Apium); its congeners all feed exclusively on Compositae, a family known to contain both hydroxy- and furanocoumarins.

(6b) Diptera

Two genera of Diptera in separate families mine leaves of Umbelliferae (Table 8). *Euleia fratria* is a blotch miner associated primarily with plants in the Umbelliferae and incidentally with plants in the Compositae. Both of these plant families are reported to contain furanocoumarins as well as hydroxycoumarins. The genus *Phytomyza*, an enormous and poorly understood genus in the Agromyzidae (Griffiths, 1973), contains a number of species that feed exclusively (e.g., *P. an*- TABLE 7. Genera of Noctuidae containing at leastone Umbellifer specialist (from Crumb, 1956; Tietz,1972).

A. Papaipema

- P. marginidens UMBELLIFERAE—Cicuta P. harrisi UMBELLIFERAE—Angelica
- P. cerina LILIACEAE—Lilium, BERBERIDACEAE—Podophyllum
- P. cataphracta GENERALIST
- P. duovata COMPOSITAE—Solidago
- P. pterisii POLYPODIACEAE—Pteris
- P. lysimache PRIMULACEAE—Lysimachia
- P. nebris GENERALIST P. polymniae
- COMPOSITAE—Polymnia
- P. circumlucens LEGUMINOSAE—Psoralea, COMPOSITAE—Senecio?, Vernonia, APOCYNACEAE
- P. insulidens COMPOSITAE—Senecio
- P. pertincta COMPOSITAE—Petasites, LEGUMINOSAE—Lupinus
- P. beeriana COMPOSITAE—Liatris
- P. eupatorii COMPOSITAE—Eupatorium
- P. impecuniosa COMPOSITAE—Aster, Helenium
- P. arctivorens COMPOSITAE—Cirsium, Arctium DIPSACACEAE—Dipsacus
- P. nelita COMPOSITAE—Rudbeckia
- P. frigida RANUNCULACEAE—Thalictrum P. sciatra
- SCROPHULARIACEAE—Veronica
- P. maritima COMPOSITAE—Helianthus
- P. cerussata COMPOSITAE—Vernonia
- P. merrickata BERBERIDACEAE—Podophyllum (Emboloecia) sauzalitae COMPOSITAE, SCROPHULARIACEAE—Castilleja,

TABLE 7. Continued.

POLYGONACEAE—Rumex. GRAMINEAE—Zea P. furcata OLEACEAE—Fraxinus, ACERACEAE—Acer B. Platysenta P. sutor UMBELLIFERAE—Apium P. apameioides COMPOSITAE—Bidens P. vecors COMPOSITAE-Lactuca P. discitriga COMPOSITAE-Chrysothamnus P. videns COMPOSITAE—Aster, Solidago

gelicae, pastinacae, chaerophylli, sii, cicutae, etc.) or incidentally (P. albiceps, fallociosa, obscurella) on the Umbelliferae. In addition to Umbelliferae, these insects feed on Compositae, Leguminosae, Caprifoliaceae, and Ranunculaceae, all families that contain hydroxycoumarins (the single exception to the pattern is P. obscurella, which feeds on Aquifoliaceae and Crassulaceae in addition to five families containing coumarins).

(6c) Coleoptera

The only beetle eating the foliage of Umbelliferae to any great extent in eastern North America is *Apion*, a curculionid. Host records for foliage-feeding *Apion* species (Table 9) are far from complete, but all recorded hosts (with the single exception of *Arctostaphylos* in the Ericaceae) for *Apion* species north of Mexico are species of plants in families with hydroxycoumarins. In fact, *Apion* feeds on members of three families that are reported to contain furanocoumarins—several genera in the Umbelliferae, *Psoralea* in the Leguminosae and *Xanthoxylum* in the Rutaceae.

(7) Overview and Case in Point

There is not a single example of an insect in eastern North America feeding exclusively on furanocoumarin-containing

TABLE 8. Hostplants of North American Diptera occurring on Umbelliferae.^a



TABLE 8. Continued.

^a Hostplant records from Frost (1924) and Griffiths (1973). —a plant species with more than a single record constitutes a major hostplant.

plants (Berenbaum, 1981b) that is not also closely related to species that feed on plants containing hydroxycoumarins. Given the limited distribution of coumarins in nature, it is difficult to believe that hydroxycoumarin-feeding insects are related to furanocoumarin-feeding insects by phylogenetic accident. The genus Psoralea, for example, is the only North American genus in the Leguminosae reported to contain furanocoumarins (Baskin et al., 1967) and is at the same time a hostplant of Apion, Agonopterix, Papaipema and is the sole leguminous host recorded for the genus Papilio (Scriber, 1973)-all genera with strong associations with furanocoumarin-containing umbellifers. At best, it is unconvincing to invoke coincidence as an explanation for the pattern; considering the vastly differing ecologies of the insect genera, no other consistent explanation comes to mind except that these insect genera have independently evolved resistance to furanocoumarins from progenitors adapted to plants containing hydroxycoumarins.

It is difficult, if not impossible, to prove coevolution—indeed, it has even proved difficult simply to define it (Janzen, 1980). Janzen (1980) defines coevolution as an evolutionary change in a trait of an array of populations or species, followed by reciprocal change in the array of species exerting the initial selective pressure. Such appears to be the case in at least three taxa of insects (Coleoptera, Diptera and Lepidoptera). Insects that feed on plants containing furanocoumarins almost invariably feed also on plants containing hydroxycoumarins or are closely related to species that feed on plants containing hydroxycoumarins. Synthesis of hydroxycoumarins is a necessary prerequisite for formation of furanocoumarins; thus, it seems eminently reasonable that insects that feed on plants containing hydroxycoumarins are most likely over evolutionary time to encounter plants containing furanocoumarins and are thus most likely to evolve resistance to them. Similarly, since angular furanocoumarins are not commonly produced in the absence of linear furanocoumarins, insects that feed on plants with linear furanocoumarins are most likely to encounter angular furanocoumarins and are most likely to evolve resistance to them. That these particular insects are capable of generating sufficient selective pressure to effect evolutionary changes in plant chemistry is suggested by the work of Hendrix (1979), who observed that *Depressaria pastinacella* is capable of reducing seed set of *Pastinaca sativa* by half, a substantial reduction in fitness.

TABLE 9. Hostplants of Apion (Curculionidae) Northof Mexico (Kissinger, 1968).

SUBGENUS FALLAPION

| A. | ance | eps – |
|----|------|-------|
| | 003 | ED OC |

- COMPOSITAE
- A. ellipticum UMBELLIFERAE—Chaerophyllum
- A. erraticum COMPOSITAE—Chrysothamnus
- A. impunctistriatum COMPOSITAE—Ambrosia, Heterotheca, Rudbeckia
- A. melanarium COMPOSITAE—Bidens
- A. minutum UMBELLIFERAE—Ptilimnium
- A. occidentale COMPOSITAE—Helianthus
- A. pennsylvanicum UMBELLIFERAE—Cicuta
- A. robustum COMPOSITAE—Xanthium?
- A. coracellum¹ UMBELLIFERAE—Cicuta, Sium, Angelica

SUBGENUS IXIAS

- A. xanthoxyli RUTACEAE—Xanthoxylum
- A. frosti CAPRIFOLIACEAE—Viburnum
- A. heraculanum CAPRIFOLIACEAE—Viburnum A. idiastes
- CAPRIFOLIACEAE—Viburnum
- A. umboniferum CAPRIFOLIACEAE—Viburnum

SUBGENUS TRICHAPION

- A. proclive LEGUMINOSAE—Lupinus
- A. simile BETULACEAE—Betula
- A. glyphium LEGUMINOSAE—Diphysa
- A. cordatum LEGUMINOSAE—Psoralea ERICACEAE—Arctostaphylos
- A. dolosum LEGUMINOSAE—Robinia
- A. rostrum LEGUMINOSAE—Baptisia
- A. griseum LEGUMINOSAE—Phaseolus A. oriotes
- LEGUMINOSAE—Phaseolus
- A. sayi LEGUMINOSAE—Strophostyles

A. metallicum COMPOSITAE—Ambrosia, Aster, Dahlia, Helenium, Xanthocephalum A. troglodytes COMPOSITAE—Artemisia A. commodum LEGUMINOSAE—Psoralea A. patrueleLEGUMINOSAE—Apios A. perforicolle LEGUMINOSAE—Amorpha, Tephrosia A. procatum LEGUMINOSAE-Robinia A. roseae LEGUMINOSAE—Desmodium? A. cribicolle LEGUMINOSAE—Lotus A. tenuirostrum LEGUMINOSAE—Krameria, Petalostemum

(8) A Scenario of Coumarin-Insect Coevolution

Host records and experiments with bioassays of relative toxicity and resistance suggest the following scenario in the evolution of coumarin chemistry: 1. Pcoumaric acid, an important intermediate in lignin biosynthesis in many angiosperm plant families, is the evolutionary precursor of hydroxycoumarins found in approximately three dozen plant families. 2. Umbelliferone and related hydroxycoumarins possess toxic properties lacking in their pcoumaric acid precursors (Jurd et al., 1973; Williams and Hoagland, 1982). 3. Plants producing hydroxycoumarins are freed from constraints imposed by certain enemies (e.g., fungi, bacteria and plant competitors). 4. By mutation or recombination, several groups of insects evolve mechanisms of resistance to hydroxycoumarins. This mechanism may be a generalized detoxication response present in polyphagous species such as Spodoptera eridania (Lepidoptera: Noctuidae) (Scriber, 1981). 5. As a result of adaptation to feeding on plants containing hydroxycoumarins, insects can specialize on these plants (tribe Amphisbatini in Oecophoridae; Section II Papilio excluding machaon complex). 6. In response to selective pres-

TABLE 9. Continued.

sure of herbivores adapted to hydroxycoumarins, plants in three dozen plant families proliferate possessing an enzyme prenylating umbelliferone at the 7-position and leading to formation of linear furanocoumarins. Due to the acquisition of a furan ring, linear furanocoumarins possess toxic properties lacking in their hydroxycoumarin precursors, i.e., phototoxicity (Berenbaum, 1978). 7. Plants producing linear furanocoumarins are freed from constraints imposed by certain enemies adapted to feeding on hydroxycoumarins. 8. Insects feeding on plants containing hydroxycoumarins encounter linear furanocoumarins; some develop mechanisms of tolerating furanocoumarins (machaon complex in the genus Papilio (Berenbaum, 1981c); genus Ago*nopterix* in the Oecophoridae). Those species that do not develop such a mechanism either drop furanocoumarin-containing plants from their diets or become extinct. 9. As a result of adaptation to feeding on plants containing linear furanocoumarins, insects can specialize on these plants. 10. In response to herbivory of specialist herbivores, plants in two families proliferate that possess an enzyme that prenylates umbelliferone at the 8-position, leading to the formation of angular furanocoumarins. 11. Angular furanocoumarins possess toxic properties to herbivores lacking in linear furanocoumarins produced in the same plants (e.g., *Papilio polyxenes*) (Berenbaum and Feeny, 1981). 12. Insects feeding on plants containing linear furanocoumarins encounter angular furanocoumarins; some develop mechanisms of tolerating the toxicity of angular furanocoumarins. Those species that do not develop such a mechanism either drop these plants from their diets or become extinct. 13. Insects adapted to feeding on plants containing angular furanocoumarins begin to specialize on these plants (genus Depressaria in Oecophoridae, P. brevicauda in Papilio machaon complex?) (Berenbaum, 1981a).

This scenario is speculative; many of the proposed steps (e.g., 12) have yet to be tested experimentally and even in those

cases where experimental evidence is available, the generality of the test results has not been demonstrated (e.g., steps 4, 6 and 11). Nonetheless, the scheme provides at least a partial explanation for observed patterns of insect herbivory and plant resistance. Moreover, it can be used to facilitate qualitative prediction within the system. The genus Artemisia in the Compositae, for example, is a hostplant for Phytomyza, Euleia, Apion, Agonopterix, Depressaria and is the only Compositae host known for the genus Papi*lio*—all genera with strong associations with furanocoumarin-containing plants. Artemisia, already known to contain hydroxycoumarins (Hegnauer, 1964), may well prove to be a rich source of furanocoumarins.

DISCUSSION

This study adds to the growing body of information the chemistry of insect-plant interaction, reinforcing and clarifying patterns observed in other systems (e.g., glucosinolates-Feeny, 1977; Rodman and Chew, 1980). Despite its limitations in scope, this system—coumarin-containing plants and associated herbivores-can serve as a paradigm for similar systems, i.e., plants containing "qualitative" toxins (sensu Feeny, 1976) and their associated specialized herbivores. Insofar as taxonomy reflects chemistry, insect-plant coevolution often appears to follow consistently. Yet there are many examples of hostplants perceived as anomalies in hostplant usage patterns because they do not follow along taxonomic lines. These anomalies may well be resolved with greater understanding of the biochemistry of the "aberrant" hostplants; taxonomic inconsistency may obscure independent evolution of biosynthetic pathways in disparate groups of plants. Preadaptation on the part of the insect with subsequent specialization could generate such anomalous usage patterns. Coumarins provide a case in point. Section II of the genus *Papilio* is associated primarily with the furanocoumarin-containing Rutaceae and, within the machaon, demolion and demoleus groups,

Umbelliferae. Within the demoleus group there is a species restricted to the genus Psoralea in the Leguminosae (J. M. Scriber, unpubl.). This pattern is anomalous taxonomically—yet is compatible with host chemistry, Psoralea being one of only two leguminous genera that synthesize furanocoumarins. Taxonomically anomalous hostplant "omissions" can be accounted for by chemical coevolution as well. The absence of hostplant records for the machaon group on Araliaceae, a family with some herbaceous representatives sympatric with and closely related to Umbelliferae (Heywood, 1971), is understandable in that the family is chemically distinct from the Umbelliferae, lacking flavones and furanocoumarins altogether (Hegnauer, 1964-1973; Heywood, 1971). Similar patterns of omissions or inclusions in other herbivoreplant systems may be resolved with a closer examination of the underlying biosynthetic relationships among the plants. By the same token, the documentation of parallel series of herbivorous groups across broad phyletic lines may provide insights into hitherto unsuspected chemical similarities among plants.

SUMMARY

Ehrlich and Raven (1964) proposed a stepwise coevolutionary mechanism for insects/plant relationships based on extensive examination of hostplant usage patterns in rhopaloceran Lepidoptera. This mechanism is examined with respect to the interactions between insect herbivores and plants sharing the biosynthetic pathway for production of hydroxycoumarins and derivatives. Biochemical evidence indicates that enzymatic changes in plants give rise to novel secondary substances-sequentially, hydroxycoumarins, linear furanocoumarins and angular furanocoumarins. These substances are sequentially less suitable to polyphagous insects, yet some oligophagous species have counteradapted to furanocoumarins by both behavioral and physiological means (e.g., certain Agonopterix spp., Papilio polyxenes). Finally, diversity in groups of coumarin-containing plants is greater than in related groups lacking coumarins (e.g., Umbelliferae), and insect groups associated with coumarincontaining plants are more diverse than related groups on plants without coumarins (e.g., Oecophoridae and Papilionidae). This is consistent with the idea that reciprocal evolutionary interactions, focusing on secondary plant chemistry, greatly augment the organic diversity of both herbivorous insects and plants.

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There will be a joint meeting of

Society for the Study of Evolution Genetics Society of America American Society of Naturalists Stadler Symposium

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Symposia will be held on Molecular Evolution, Plant Genetics, Immunogenetics, Mass Extinctions, Chromatin Structure, Genetic Epidemiology, and Human Evolution, and there will be contributed paper sessions and a poster session. Additional information can be obtained from:

> The Organizing Committee Evolution 83 Department of Botany Washington University St. Louis, Missouri 63130