Annu. Rev. Entomol. 1990. 35:319–343 Copyright © 1990 by Annual Reviews Inc. All rights reserved

EVOLUTION OF SPECIALIZATION IN INSECT-UMBELLIFER ASSOCIATIONS

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Introduction

The plant family Umbelliferae (Apiaceae) consists of almost 3000 species worldwide (112). Members of the family occupy a wide variety of habitats, including deserts, basaltic bluffs, salt and freshwater marshes, chaparral, forests, waste places, and subalpine tundra. Despite the ecological diversity, however, family members display remarkable morphological conservatism. The integrity of the family as a taxonomic unit has been recognized for centuries, from Theophrastus' establishment of *Narthekodes* as one of the natural plant families to Tournefort's unification of its current elements in 1694 (38).

Also characteristic of the family is a relatively distinctive insect fauna. Acknowledged as a plant taxon disproportionately free from insect attack (105), the Umbelliferae nonetheless supports a fauna that is primarily oligophagous—restricted to Umbelliferae and, rarely, a few closely related families. Thus, it is not surprising that interactions between umbelliferous plants and their insect associates have received considerable attention from both ecological and evolutionary perspectives. In this review, the fauna of the Umbelliferae is evaluated in the context of recent discussion of the evolution (and implications) of specialization in insect-plant associations. Emphasis is placed on the mediation of insect-host interactions by umbellifer chemistry.

Working Hypotheses To Account for Specialization in General

The extraordinary ubiquity of oligophagy in herbivorous insects has given rise to extensive speculation on the forces involved in creating and maintaining specialized feeding habits. Two basic classes of explanations exist. Adaptive explanations of specialization advance the idea that oligophagy confers a selective advantage in terms of efficiency of host utilization. Possible advantages include precise ecological tolerances due to habitat predictability (utilizing a narrow range of hosts can reduce the environmental variability experienced over the range of a species) ("The milieu of the specialist is highly predictable so that, by selection, the animal may become well adapted to its environment;" see Ref. 106); enhanced host-finding capabilities, such as an increased ability to detect and orient to host chemical cues; enhanced metabolic capabilities, such as specific detoxification pathways for host allelochemicals (74); or reduced losses to predation through the evolution of morphologies or behavior particularly appropriate for a narrow range of hosts (18).

Implicit in adaptive explanations of oligophagy is the assumption of ecological optimization and, accordingly, trade-offs in performance, when such species are compared to nonspecialists. For example, trade-offs in enhanced host-finding capabilities may involve oviposition on plants that contain appropriate host recognition cues for the female but that also contain substances toxic to larvae (75). Trade-offs in metabolic capabilities would presumably be manifested in lower growth rates or efficiencies of utilization of nonhosts; dedicated detoxification mechanisms presumably leave oligophagous species susceptible to nonhost toxins. Trade-offs in defense against predators would be manifested by higher mortality on nonhosts, ostensibly due to the breakdown of crypsis, chemical sequestration, or to other specialized antipredator morphologies or behavior (18).

A number of alternative explanations for specialization in herbivorous insects assume that it is essentially nonadaptive in nature and do not involve the assumption that species numbers are valid criteria for estimating evolutionary success. These explanations maintain that specialists are numerous due not to ecological superiority in performance or competitive ability but rather to evolutionary predisposition to speciate—reproductive isolation is perhaps an inevitable consequence of close association with a narrow range of hosts. Specialist taxa thus tend to give rise to descendant specialist taxa. Moreover, according to Feeny (62), "at least in some circumstances specialist feeders may remain specialists not because this is their optimal strategy but because once they have become specialists they have little evolutionary opportunity to reverse the process." Specialization is thus perceived as a "dead end" (125), and phylogenetic constraints act as a brake on ecological diversification and acquisition of new hosts.

Taxonomy and Ecology of the Umbelliferae

The family Umbelliferae is currently distinguished by the umbellate inflorescence, pentamerous perianth and androecium, two-carpellate bilocular inferior ovary, and schizocarp fruit (112). Like many of the natural families, morphological uniformity within the family obscures relationships within the family. Generally, however, three subfamilies are recognized, based on anatomical features of the fruits. The Hydrocotyloideae consists of 320 species distinguished by woody endocarp and a southern hemisphere distribution. The Saniculoideae contains 250 species in both northern and southern hemispere floras. The largest subfamily, Apioideae, consists of approximately 1950 primarily temperate herbaceous plants (119, 120). Two centers of differentiation are recognized for apioid umbellifers: the Mediterranean, and the western United States and Mexico. There are over 200 endemic species in the western United States alone. Many of the holarctic species display a typical Arcto-Tertiary distribution. Considerable controversy surrounds the assignation of tribal affiliations (which number, depending on treatment, between 10 and 31); in this review, the tribes of Drude 1898 (49) will be followed.

Taxonomically, the family with which the Umbelliferae is most closely allied is almost universally recognized as the Araliaceae (the two families have even been unified by a number of workers, most recently Thorne—164). The similarity between the families is reflected in unique aspects of fruit and flower morphology, as well as chemistry (89, 139). The Umbelliferae-Araliaceae may then represent "a number of divergent lines arising from a theoretical pre-Araliaceae" (42).

Ecologically, the family is quite diverse. In general, umbellifers are associated with "difficult" environments, typically early successional stages and disturbed sites. The largest genus in North America, *Lomatium*, with over 80 species, is found in a variety of habitats ranging from chaparral to serpentine outcrops. In terms of life histories, the family is unusual in its large proportion of biennial or facultatively biennial species; these plants comprise 30% of the British umbelliferous flora (116). Breeding systems in the apioid Umbelliferae are primarily protandrous and andromonoecious, although many other types can also be found (3).

Chemistry of the Umbelliferae

The phytochemical diversity of the Umbelliferae (Table 1) is reflected at least in part by their global popularity as spice plants and potherbs (73). All members of the family are aromatic, due to the presence of essential oils and resins in schizogenous canals in both above- and below-ground parts (89). Essential oil constituents are primarily terpenoids and phenylpropanoids.

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Characteristic of the Umbelliferae are ligustilides as well as germacranolide and guainolide (sesquiterpene) lactones (77, 97, 98). Phenylpropanoid diversity includes both hydroxycinnamic acid derivatives and phenylpropenes. Of the hydroxycinammic acid derivatives, chlorogenic acid is universal in the family (87). Phenylpropenes occur primarily, if not exclusively, in the Apioideae (87). Considerable diversity among flavonoids exists in the family and may have some taxonomic significances. Whereas flavonols and their glycosides predominate in Hydrocotyloideae and Saniculoideae, flavones and their glycosides are more or less restricted in occurrence to more advanced or specialized taxa in the Apioideae (87); these include the tribes Scandiceae, Apieae, Dauceae, Laserpiteae, and Peucedaneae (114). Methylated flavonoids are found exclusively in the Apioideae, as are sulfonated flavonoids (86).

No other plant family can rival the Umbelliferae in the abundance and structural diversity of substituted coumarins. Although hydroxycoumarins are present in all of the subfamilies of the Umbelliferae, furanocoumarins are restricted in distribution to the Apioideae (128). Two distinct structural classes of furanocoumarins exist; linear furanocoumarins are restricted to six tribes, whereas angular furanocoumarins are known only from four tribes— Apieae, Peucedaneae, Scandiceae, and Dauceae. Pyranocoumarins are reported from Apieae, Peucedaneae, Laserpiteae, and Dauceae. Thus, there appears to be a progression in the family from simple to biosynthetically derived coumarins that parallels the progression from flavonols to flavones.

Polyacetylenes are also characteristic of the family and are documented from all three subfamilies (22). Chain lengths of C-17 and, to a lesser extent, C-13 and C-15 predominate. Falcarinone and its derivatives are the most widely distributed polyacetylenes in the family.

Triterpenoid sapogenins occur in all three subfamilies but are more frequently encountered in the Hydrocotyloideae and Saniculoideae (94, 95); whereas 28% and 35% of these subfamilies, respectively, contain triterpenoid saponins, only 7% of apioid umbellifers are known to produce them (87). Cyclitols are widespread throughout the family. Scyllitol has been isolated from five tribes, one in the Hydrocotyloideae and four from the Apioideae (137). Many of the perennial or biennial species store cyclitols along with carbohydrates in roots. Mannitol is the major six-carbon polyol in the family. The trisaccharide umbelliferose is ubiquitous in the Apioideae, whereas other forms of di- or tri-saccharides are more common in the Hydrocotyloideae and Saniculoideae (89).

Alkaloids have an erratic distribution in the family. For many years *Conium* maculatum was believed to be the only umbellifer that produces alkaloids [prompting Fairbairn in 1971 (61) to label the plant the "odd man out"]. However, subsequent work revealed that several other genera contain piperidine alkaloids, including *Heracleum*, *Daucus*, *Ferula*, *Hydrocotyle*, and Annu. Rev. Entomol. 1990.35:319-343. Downloaded from arjournals.annualreviews.org by University of Delaware on 02/03/09. For personal use only.

Table 1 Phytochemistry of the Umbelliferae^a

		A CONTRACTOR OF A CONTRACTOR O						
	Terpenes	Sesquiterpene lactones ^b	Phenyl- propenes	Alkaloids	Flavonoids ^c	Coumarins ^d	Polyacetylenes	Chromones
Subfamily Hydrocotyloideae								
Hydrocotyleae	×			×	FOL		x	
Mulineae	X				FOL	Н	x	
Subfamily Saniculoideae								
Saniculeae	x			×	FOL	Н	X	
Subfamily Apioideae								
Scandiceae	×		×		FO	H,L	X	
Coriandreae	×				FOL	H,L		
Smyrnicae	×	SL	×	×	FO	H,L,A	X	
Apieae	×	SQ	×		FO	H,L,A,P	X	×
Peucedaneae	×	SL	×	×	FO	H,L,A,P	X	×
Laserpiteae	×	SL	×		FO	Н, L, Р	x	
Dauceae	×	SQ	X	X	FO	H,L,A,P	Х	
^a From Refs. 31, 77, 87, 89, 97 ^b SL = sesquiterpene lactone; SV ^c FOL = flavonol; FO = flavon ^d H = hydroxycoumarin; L = lii	, 128, 137, 144 2 = sesquiterpe е. near furanocoum	ne. arin; A = angular fi	uranocoumarin;	P = pyranocou	marin.			

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Sanicula. In addition, *Daucus* species produce pyrrolidine derivatives (137). Other compounds with restricted distribution in the family include the chromones, which are known only from the Peucedaneae and Apieae, and naph-thalide-type lignans, reported from genera in Scandiceae and Apieae.

Phytochemical resemblances support the contentions of systematists that Araliaceae is strongly linked to the Umbelliferae. Triterpene sapogenins, C-17 polyacetylenes, essential oils, cyclitols, and lignans are characteristic of both families (85, 89). Strong phytochemical resemblance also suggests a relationship between Umbelliferae and Rutaceae, which share essential oils, substituted coumarins and pyranocoumarins, and chromones, and with Compositae, with which the umbelliferae shares essential oils, C-17, C-13, and C-15 polyacetylenes, triterpene sapogenins, chromones, guaianolides, germacranolides, and cyclitols (89, 90, 98, 137).

Taxonomic Distribution of Umbellifer Specialists

At least four orders of insects are represented among the species associated exclusively or almost exclusively with the Umbelliferae (Table 2). Absent from the umbellifer fauna are specialists from such phytophagous (or partially phytophagous) orders as Orthoptera, Thysanoptera, and Hymenoptera (Symphyta). The only conspicuous hemimetabolous specialists on umbelliferous plants are homopterans, where umbellifer feeding is ubiquitous in the Aphididae (heteropterans are represented by only a handful of species). All are phloem feeders; species range in specificity from only one or two host genera to over a dozen (*Cavariella*, e.g. Ref. 51).

Two possible (and admittedly entirely speculative) explanations exist for the relatively poor representation of hemimetabolous taxa in the umbellifer fauna. Hemimetabolous species may be at a general disadvantage in that they cannot achieve the high growth rates necessary to specialize on ephemeral plants (35). Even perennial umbelliferous species tend to have a very short growing season in the Pacific Northwest; *Cymopteris*, for example, is a perennial that flowers very early in the spring and is available for herbivores for a very short time (59, 116). Early successional species are associated with disturbance and hence are patchy in distribution and unpredictable in time (19, 20). Aphids, capable of cyclical parthenogenesis, have the capacity to develop rapidly and may thus be disproportionately represented on short-lived plants. Alternatively, if the Umbelliferae is a relatively recent group, then the major radiations of plant-feeding hemimetabolous groups may have occurred prior to the appearance of potential umbelliferous hosts.

In the Diptera, umbellifer specialists can be found in three families. Species in the Agromyzidae and Tephritidae are leaf miners, forming serpentine and blotch mines, respectively. At least 14 species of *Phytomyza* (Agromyzidae) feed exclusively on umbellifers, many on only a few closely related species

		Number		
		of specialists/	Feeding	
	Genus	Number in genus	habits ^a	Reference
Homoptera				
	Aphis	5/153	PS	140
	Cavariella	4/11	PS	149
	Hyadaphis	1/2	PS	168
Heteroptera				
Miridae	Orthops	1/11	PS	111
Diptera				
Psilidae	Psila	1/1	RM	23
Agromyzidae	Phytomyza	14/	LM	79
Tephritidae	Euleia	1/2	LM	71
Coleoptera				
Curculionidae	Apion (Fallapion)	4/10 (125 total)	SM	9
	Smicronyx	2/69	SM	57, 110
	Listronotus	1/28	RM	110, 178
Lepidoptera				
Incurvariidae	Greya	3/15	SM	O. Pellmyr,
		7/24	IF	pers. commun.
Oecophoridae	Agonopterix	//34		96
Enormaniidaa	Depressaria	18/21		90 20
Epermenndae Na stuida s	Epermenta Dan sin ana	2/2	SIVI, LIVI	22 70
Papilionidae	Papaipema Papilio	2/22	3B 1 E	14
Fapinondae	ғаршо	11/20	LF	107

Table 2	Specialist taxa in North	America exclusively or almo	ost exclusively associated with Umbel-
liferae			

 a PS = phloem sucker, RM = root miner, LM = leaf miner, SM = seed miner, LF = leaf and flower chewer, SB = stem borer.

(9, 79, 151). Two additional species feed on both Umbelliferae and Compositae. In contrast *Euleia* (Tephritidae) has a wide range of hosts within the family, encompassing 8 genera in two tribes (9, 71). Other dipteran associates of umbellifer develop in roots. *Psila rosae* (Psilidae) is a major economic pest of parsnip and carrot (23).

Umbellifer specialists in the Coleoptera are primarily species in the Curculionidae. Species in the genera *Apion* and *Smicronyx* are seed feeders while *Listronotus oregonensis*, the carrot weevil, is a root borer of some economic importance on carrots, celery, parsley, and related crop plants (7, 57, 178). In *Apion*, umbellifer feeding is restricted to the subgenus *Fallapion* (19). The three curculionid genera associated with umbellifers are in three different subfamilies; the relatively distant relationships among these insect taxa indi-

cate that the evolution of specialization on umbellifers may have arisen independently several times in the order. In Europe at least one chrysomelid genus is associated exclusively with umbelliferous plants (M. Rowell-Rahier, personal communication).

By far and away, lepidopterous larvae are the most conspicuous of umbellifer specialists, in terms of both absolute numbers and biomass. Umbellifer specialization occurs in at least five families, encompassing two suborders within the Lepidoptera. The monotrysian family Incurvariidae is represented by the genus *Greya*; caterpillars of *G. subalba* are seed miners of *Lomatium dissectum* in the Pacific Northwest (159, 160). One (169) and possibly two other species may also feed on umbellifers; based on relationships between these species and the rest of the genus, it is likely that umbellifer feeding arose only once in the family (O. Pellmyr, personal communication). Of ditrysian lepidopterans, umbellifer specialists include stem borers in the Noctuidae (*Papaipema*), seed and leaf miners (epermeniids), and leaf, flower, and seed feeders in the Papilionidae and the Oecophoridae. Specialization has undoubtedly arisen independently several times within the order. Epermeniids generally mine or bore plant reproductive parts or else they mine leaves (138); three species in North America are known to feed on umbellifers (39).

Even at the family level, parallel evolution of umbellifer specialization is apparent. In the Papilionidae, for example, according to Miller (122), associations with Umbelliferae, as well as associations with Rutaceae, arose at least three times in the genus Papilio. Worldwide, at least 20 species feed exclusively or almost exclusively on umbellifers (146). All but one of the species belongs to section II of the genus (127); the sole exception, Papilio paeon, belongs to section III. In North America, umbellifer feeding is restricted to the machaon complex, a group of 6 to 11 species (depending on taxonomic points of view). In this group, umbellifer feeding is probably ancestral (152). The species in the *machaon* complex have arguably the broadest host range within the Umbelliferae of any group of umbellifer specialists. P. polyxenes had been recorded on 25 genera in the family (165), encompassing two subfamilies [Hydrocotyloideae and Apioideae, although records on Hydrocotyloideae are suspect (69)] and on four tribes of the Apioideae. P. machaon is reported to feed on 18 genera in the same four tribes (167, 171, 172), and P. zelicaon on 27 species in 12 genera (60). All three species are reported occasionally on rutaceous plants.

In the Oecophoridae, umbellifer feeding is found exclusively in the subfamily Depressariinae. Within the subfamily, however, evidence suggests at least two independent origins of umbellifer feeding—at least one in *Depressaria* and one in *Agonopterix* (134). Whereas *Agonopterix* species vary in their degree of oligophagy, ranging from essentially monophagous on a single genus to, in the case of *A. clemensella*, oligophagous on over a dozen

umbelliferous genera (8), Depressaria species tend to associate with only one or two genera (33). Species of Agonopterix are primary leaf-rollers, although flower and seed feeding is not uncommon (14, 96). In contrast, Depressaria species tend to concentrate feeding on reproductive parts (33, 96, 117), although foliage and even stem feeding is known to occur as well (155-158). Species associated with umbellifers constitute approximately 20% of the North American Agonopterix (7/34 species); other major host families for the genus include the Leguminosae (Fabaceae) (8/34 species) and Compositae (Asteraceae) (12/34 species). Four species in the genus feed on rutaceous hosts. In comparison, umbelliferous plants are hosts for 18 of the 21 species of *Depressaria* for which records are available; *Artemisia* species in the Compositae (Asteraceae) are hosts for the remaining species (96). Of the umbellifer-feeders, D. cinerocostella probably has the widest host range within the family. Hosts include Oxypolis, Sium, Cicuta, Ligusticum, and Carum (96); because these plants grow primarily in marshes or swamps, D. cinerocostella may be a habitat specialist as well as a family specialist. Whereas all umbelliferous hosts for Depressaria are apioid umbellifers, primarily in only two tribes (Apiae and Peucedaneae), umbelliferous hosts for Agonopterix belong to five tribes in two subfamilies (8).

Although several generalist noctuids are incidental feeders on umbellifers (109), species in one genus are essentially specialists. Two species of stemboring *Papaipema* feed on *Angelica* and *Cicuta*, both typical of mesic habitats (39, 72).

Host Location by Umbellifer Specialists

The overwhelming importance of glucosinolates in host orientation and recognition by cruciferous herbivores (63, 64) has created unrealistic hopes and expectations in entomologists seeking a chemically based explanation for host-use patterns. In the Umbelliferae clearly no single "sign stimulus" suffices for host recognition by any species. Dethier has conducted a series of studies spanning four decades (44–48) attempting to determine the basis for host recognition in swallowtails in particular and phytophagous insects in general. In 1941, based on a series of observations of feeding responses of larvae to pure essential oil components, he suggested that such compounds were the primary determinants of host acceptability in Papilio polyxenes (then known as P. ajax). Dethier (44, 45) postulated a transition from Rutaceae, the host family for the majority of species in Papilio, to Umbelliferae, based on the presence of shared attractant chemicals. He suggested a progression of chemosensory responses in the genus from citral (typical of Rutaceae) to methylnonylketone (as found in herbaceous Rutaceae, such as Dictamnus, utilized by P. polyxenes) to anethole or methylchavicol (typical of Umbelliferae), but acknowledged that "an oligophagous species such as P. ajax may

be conditioned to more than one odor." Electrophysiological studies (47) confirmed the idea that swallowtail larvae perceive and respond to complex mixtures of chemicals rather than to a specific host-recognition signal.

The same dependence upon a response spectrum has been observed in host recognition by ovipositing swallowtail butterflies. Feeny et al (68) identified one of the oviposition stimulants for female *Papilio polyxenes* as luteolin 7-0-(6"-0-malonyl) beta-D-glucopyranoside. Luteolin glycosides are wide-spread in the subfamily Apioideae (87). Flavonoid glycosides are also oviposition stimulants for a number of swallowtails associated with Rutaceae (100, 130). In all of these studies, however, flavonoid glycosides alone did not elicit a complete response; other synergistic factors include chlorogenic acid (68, 100) and cyclitols (130), both ubiquitous in the family. Curiously, although flavonoid glycosides elicit oviposition behavior in papilionine swallowtails, they are not sequestered as extensively by these butterflies in wings as they are by leptocercine (graphine) swallowtails (177).

Host-recognition kairomones for *Psila rosae*, a root maggot restricted to several species in the Umbelliferae, have also been characterized recently. As is the case for black swallowtails, a mixture of compounds is more effective at eliciting oviposition than is any single compound or class of compound. Guerin and colleagues (82–84) confirmed by field bioassay and electroantennogram tests responses by adults to hexanal, a green leaf volatile, and trans-asarone. While these volatiles appear to play a major role in long-distance olfaction, contact chemoreception involves a different spectrum of compounds. Oviposition stimulants for adult females have been identified as trans-asarone, trans-methyl-isoeugenol (propenylbenzenes), bergapten, osthol (furanocoumarins), and falcarindiol (a polyacetylene) (153).

Larval host recognition in *Psila rosae* has also received a substantial amount of attention, particularly in view of the fact that the larvae are economically injurious to carrot and parsnip. Carrot cultivars display consistency in susceptibility to attack throughout Europe (55, 56); this consistency suggests a genetic component to resistance. Larvae display klinotaxis and klinokinesis in response to at least five compounds, including bornyl acetate, 2,4-dimethylstyrene, alpha and beta ionone, and biphenyl; trans-2-nonenal was repellent (143). Larvae also orient toward carbon dioxide and methyl eugenol (107, 108). In field populations, however, damage levels in carrot correspond to concentrations of chlorogenic acid (36, 37). Cultivars with high constitutive levels of chlorogenic acid not only sustain greater levels of infestation but also produce higher amounts in response to feeding damage by *P. rosae*, which leads to increased infestation.

Remarkably, even umbellifer-feeding aphids (a group not generally known for highly developed, chemically based host-finding abilities) display evidence of specific responses to umbellifer chemistry. Chapman et al (32) induced *Cavariella aegopodii* to land, from a distance of a meter or more, on visual targets baited with the monoterpene carvone. Upwind orientation was suggested by the pattern of collection data. The authors assert that theirs is the "first clear evidence of odor-induced orientation behavior in aphids." Carvone was an essential oil component singled out by Dethier (44) as responsible for one of the seven "common odors of the Umbelliferae" (45).

Metabolic Adaptations for Feeding on Umbellifers

While Dethier (44, 45) has ascribed the acquisition of new hosts to behavioral preadaptation to host recognition cues, host shifts may result from biochemical preadaptation to host allelochemicals (52). Futuyma (74) has argued, however, that biochemical resistance mechanisms may be a consequence rather than a cause of host shifts, that such adaptation may not be "immediately necessary for successful change of host but is a fine-tuning of adaptation that occurs only after the species has already become specialized on a particular host."

That umbellifer chemicals are toxic to nonspecialists has been documented abundantly. Characteristic umbellifer phenylpropanoids (myristicin—114, dillapiole and apiole—115, 118), terpenes (carvone—121), furanocoumarins (4, 30, 126), coumarins (24) and flavonoids (54) have been shown to be antifeedant or toxic to generalist herbivores. Indirect evidence also indicates that umbellifers may be difficult for nonadapted species to handle physiologically. Goeden & Rickers (76), for example, were surprised at the paucity of insect species associated with *Conium maculatum*, an umbelliferous weed introduced into the United States (in their words, "Poison hemlock hosted amazingly few insect species or individuals thereof"). The only common species on the plant was *Hyadaphis foeniculi*, a specialist on poison hemlock introduced from Europe. The authors speculated that the depauperate fauna was due to the presence of toxic piperidine alkaloids in the foliage and flowering parts. Coniine is phagodeterrent to *Locusta migratoria* (17) and as a vapor is toxic to fire ants (124, but see 131).

Those generalists that do feed regularly on umbellifers appear to rely heavily on avoidance mechanisms to deal with toxins. These avoidance mechanisms in all probability serve as preadaptations which may have initially conferred enhanced survival fortuitously on umbelliferous plants. Among the principal types of toxicants in the family are the furanocoumarins, p-coumaric acid derivatives activated by ultraviolet light to form highly reactive excited states which then proceed to bind to a variety of biomolecules, particularly DNA, and to disrupt many essential physiological processes (11). Light greatly enhances the toxic effects of furanocoumarins on generalist insects (4, 10, 11). *Spodoptera exigua*, a generalist noctuid which is a periodic pest on celery (*Apium graveolens*), displays developmental

differences in feeding site preferences. The first three instars feed preferentially on leaves, and the fourth and fifth instar on petioles and hearts; nutritional differences of plant parts did not account for the preference differences (80). Fifth instar larvae are strongly photonegative; the tendency to feed in the heart when exposed to light ostensibly protects the larvae from photoactivation of furanocoumarins. Early instar larvae may be able to feed on foliage because they are protected by a silken web (81). Jones & Granett (109) reported that Peridroma saucia, another generalist noctuid, also feeds preferentially in the heart, and Heliothis zea between overlapping leaves webbed together. The noctuid generalist Trichoplusi ni feeds on the undersides of foliage (109), where presumably exposure to ultraviolet light is decreased. Moreover, T. ni feeds in early instars by skeletonizing the leaves; by avoiding the major veins, the caterpillar may reduce its exposure to furanocoumaring, which are localized in vessels adjoining major veins (180). Two microlepidopteran generalists that are occasional pests on celery, *Platy*nota stultana (Tortricidae) and Udea profundalis (Pyralidae), feed in webbed rolled leaves (109). Feeding in leaf rolls effectively shields microlepidopterans from photoactivating wavelengths and may serve as a preadaptation to feeding on umbelliferous (or other phototoxic) plants (4, 145).

Sucking insects may also avoid toxins in umbelliferous hosts. The mirid *Lygus lineolaris* feeds selectively on embryos of umbelliferous seeds (70); since the furanocoumarins are localized in the seeds in the vittae or oil glands (14a), such selective feeding may reduce exposure to furancoumarins as well as to essential oil components.

Metabolic adaptation, in particular to furanocoumarins, is widespread among umbellifer specialists. In some cases, the basis for resistance is undetermined. *Aphis heraclella* and *Cavariella pastinacae* take up and "bind" furanocoumarins without suffering ill effects (28). Although furanocoumarins do not normally occur in phloem, the aphids tolerate their presence in cut stems of their cow parsnip host plants fed xanthotoxin in solution. In field situations, their stylets routinely penetrate vascular bundles containing furanocoumarin-rich oil ducts. Camm et al (28) recorded up to 4.5 micrograms of xanthotoxin per aphid.

In at least two orders, furanocoumarins are metabolized by cytochrome P450 monooxygenases. In the Lepidoptera, the furan ring double bond is oxidized, presumably through an epoxide intermediate, to form two dicarboxylic acid derivatives, neither of which is phototoxic or can bind to DNA (26, 101, 102). These metabolites have been characterized from the frass of *Papilio polyxenes* (101); thin layer chromatographic analysis of frass from *Depressaria pastinacella* revealed spots which resemble these metabolites as well (133). Metabolism of furanocoumarins in the dipteran *Phytomyza spondylii* is consistent with cytochrome P450 metabolism; these maggots also produce nonphotoactive metabolites in their frass (2).

The generalist noctuid Spodoptera frugiperda also metabolizes the furanocoumarin xanthotoxin via cytochrome P450 but can process xanthotoxin at rates only 1/50 those of which P. polyxenes is capable (25, 101). Moreover, in P. polyxenes, cytochrome P450 metabolism of xanthotoxin is induced by xanthotoxin-an increase of dietary levels, from endogenous levels in the host plant to 1.0% topically supplemented, results in an approximately sevenfold increase in activity (34). That overall amounts of P450 do not increase significantly with a sevenfold increase in activity suggests that only a small subset of the P450 complex is involved in furanocoumarin metabolism. Cytochrome P450 metabolism in P. polyxenes is relatively insensitive to inhibition by myristicin, a methylenedioxy-phenyl compound which normally acts as a synergist for P450 metabolism (13, 114). Enzyme activity in this species was ten times less sensitive to inhibition than enzyme activity in Heliothis zea, a noctuid generalist. Since myristicin is a common essential oil component of many swallowtail hosts, insensitivity to inhibition by P450 may represent adaptation by P. polyxenes to combinations of synergists and toxins in their host plants (129).

With a broad range of hosts within the Umbelliferae, *P. polyxenes* encounters variable levels of furanocoumarins in foliage. However, *Depressaria pastinacella*, which feeds exclusively on reproductive parts of species of *Pastinaca* and *Heracleum* (16), encounters furanocoumarin concentrations up to ten times greater than those experienced by *P. polyxenes* (6). Cytochrome P450 monooxygenases that metabolize xanthotoxin are also inducible by xanthotoxin in parsnip webworms and are up to ten times more active than those of *P. polyxenes* (133). It remains to be determined whether homologous isozymes are involved in xanthotoxin metabolism in the two oligophagous species.

The specificity of these monooxygenases toward umbellifer furanocoumarins remains to be determined. In the black swallowtail, metabolism of angelicin, an angular furanocoumarin, by cytochrome P450 is less efficient than metabolism of the linear isomer psoralen (101). Angelicin also causes a pronounced reduction in fecundity at ecologically appropriate levels in the diet; its presence in several genera of umbellifers may account for the fact that they are rarely utilized as hosts (12).

Although xanthotoxin has been shown to deter feeding in generalists and nonspecialists (4, 126, 179), it appears to stimulate growth in *Papilio polyxenes* (5) and *Depressaria pastinacella* (15), although it is not a feeding stimulant per se. Parsnip webworms are also differentially sensitive to furanocoumarins present in their hosts. Resistance of *Pastinaca sativa* to damage in the primary umbel by parsnip webworms in the field is associated with high levels of two furanocoumarins, bergapten and sphondin, in seeds (16). Although both compounds are isomeric with xanthotoxin, they may be less suitable substrates for P450 metabolism. Incorporated into artificial diets,

bergapten causes a significant reduction in relative growth rate and approximate digestibility of parsnip webworms (15).

Avoidance of Predation by Umbellifer Specialists

Blau (20, 21) and Thompson & Tiritelli (166) have conducted life table studies on mortality of swallowtail caterpillars on different umbelliferous hosts. In both species, the major source of mortality was invertebrate predation. Feeny et al (66) found an average 10% parasitism rate for *P. polyxenes* larvae on three hosts in central New York; in Costa Rica, Blau (19) reported very low parasitism of this species there (only 1/73 pupae were parasitized). Parasitism rates also appear to be low for *Depressaria pastinacella* on parsnip; Harrison (88) reported less than 1% mortality due to ichneumons, and Gorder & Mertins (78) found parasitism rates of 2.7% and 0.8% in two consecutive years. Similarly, for *Psila rosae* in Britain, Burn (27) discovered that "parasitism and egg mortality due to predation were relatively small," and there was no indication that parasitism is a key factor in population regulation of this species.

Many oligophagous species sequester host-derived toxins in order to reduce losses to predation; such phenomena have been described in detail for associates of Asclepiadaceae and cardenolides (50), and associates of Salicaceae and phenolic glycosides (135), among others. No such sequestration has ever been demonstrated to occur in umbellifer associates. Nevertheless, some evidence suggests that umbellifer associates may be toxic to a variety of predators. Ruzicka (141, 142) reported that, of 13 aphid species, *Cavariella theobaldi*, the only umbellifer specialist of the group, was consistently avoided by the predaceous syrphid larva *Metasyrphus corollae*; when ingested, the aphid causes a toxic response. *Aphis fabae*, a generalist, was not toxic to the syrphid when raised on the same umbelliferous host as *Cavariella theobaldi* (parsnip, *Pastinaca sativa*).

Swallowtail larvae are equipped with osmeterial glands that are presumably defensive in function. Secretions from the osmeterium of several species, for example, deterred ant predation (53, 99). However, the osmeterium is largely ineffective in defense of umbellifer-feeding swallowtails against vertebrate predators. Jarvi et al (104) demonstrated that decapitated larvae are equally distasteful to great tits; the "obnoxious properties" of the larvae are detectable in the cuticle. Further studies by Wiklund & Sillen-Tullberg (176) revealed that *P. machaon* larvae are more distasteful to Japanese quail (*Coturnix coturnix*) than are the larvae of the monarch *Danaus plexippus; P. machaon* larvae had a 92% probability of surviving encounters with four species of birds (175). Larvae of the North American *P. polyxenes* are also distasteful to *C. coturnix* (A. Leslie, M. Berenbaum, personal observation). The adult black swallowtail butterfly has long been assumed to be a palatable mimic of

the toxic troidine swallowtail *Battus philenor*; in view of the unpalatability of its larvae to avian predators, the possibility exists that *P. polyxenes* is actually a Muellerian mimic with distasteful properties of its own, perhaps due to sequestration of host chemicals.

Sequestration of host toxins, in a manner of speaking, does occur in at least one umbellifer specialist. *Depressaria pastinacella* incorporates unmetabolized xanthotoxin into its silken web (132). The silk glands, which constitute only a small fraction of total body weight, contain as much furanocoumarin and metabolites as the rest of the body (excepting the gut and its contents). The presence of furanocoumarins in the webbing may reduce microbial contamination and also deter predators and parasites that chew through silk to attack the webworm.

Evolution of Specialization on Umbelliferae

One of the alternative adaptationist explanations for specialization on a narrow range of host plants is the notion that specialization is likely to reduce the habitat variability experienced by the specialist. While this explanation may suffice for some groups, it seems unlikely for umbellifer specialization; the enormous ecological variability of the family would preclude a close correspondence between host taxonomy and host habitat. In central New York alone Agonopterix clemensella is found on 16 species of umbellifers in damp woods, wet meadows, waste places, and greenhouses (8). Hosts for Papilio polyxenes include species in woodland, meadows, oldfields, swamps, waste places, and agricultural fields (5), and P. machaon in Fennoscandia inhabits "fields, moors, and mountains from the very south of Sweden to the peninsula of Varanger, far north of the Arctic Circle" (172). In Britain, the number of agromyzid species attacking umbelliferous plants is positively correlated with the number of habitats in which a host grows (116).

If anything, specialization on umbellifers, far from being an evolutionary "dead end," would appear to be a windfall. Adaptation to umbellifers, due to the ecological diversity of the family, provides tremendous potential for colonization of new habitats and range expansion (see 52). *Papilio polyxenes*, for example, is reported on 25 genera (a respectable number even in comparison to polyphagous species) and ranges from Canada to Brazil (167), a range equalled by few of the generalists that feed occasionally on umbellifers. Perhaps this ecological opportunism is why so many species with "cosmopolitan" distributions are specialists (e.g. *Pieris rapae*, the cabbage butterfly).

An alternative explanation for specialization is that behavioral adaptations facilitate host-finding. According to Dethier (46) "the first barrier to be overcome in the insect-plant relationship is a behavioral one. The insect must sense and discriminate before nutritional and toxic factors become operative." Futuyma & Moreno (75) reasoned that, in the absence of compelling evidence

of trade-offs in performance among hosts, host shifts must involve changes in behavior in initial stages; biochemical adaptations then follow.

This idea of precedence of behavioral adaptation en route to specialization runs counter to the scenario of Ehrlich & Raven (52), who proposed that toxicological barriers must break down first in the process of acquisition of new hosts and that behavioral adaptations follow; "after the restriction of certain groups of insects to a narrow range of food plants, the formerly repellent substances of these plants might, for the insects in question, become chemical attractants." It is difficult to decide between these opposing points of view. Indeed, they may both come into play at different stages of the evolution of specialization (65). Oviposition "mistakes" by swallowtails are consistent with the idea that behavioral adaptation to recognition cues facilitates colonization of new hosts (67). Wiklund (174) described two types of oviposition behavior in Papilio machaon-"specialists" which oviposited preferentially (or exclusively) on host plants which supported larval growth, and "generalists" which occasionally oviposited on species unsuitable for larvae. Wiklund argued that this dichotomous behavior provides evolutionary flexibility and preserves a mechanism for adopting new host species. Larval performance and adult preference are ostensibly under separate genetic control, and selection is toward behavioral conservatism in adults and physiological generalization in larvae. Although swallowtail larvae generally refuse to feed on unsuitable hosts (147, 170, 171), they can be induced to feed on toxic plants; Finke & Scriber (69) reported that Zanthoxylum (a rutaceous plant) elicits feeding by *Papilio polyxenes* but does not support growth.

The genetics of both host preference and larval performance in umbellifer specialists has barely been examined, and the extent of genetic correlation between them is even more of a mystery (163, 173). Thompson (161, 162) has documented a genetic basis for oviposition preferences among hosts in two species of swallowtail, one of which (*P. oregonius*) is facultatively monophagous on a composite (*Artemisia*), and the other of which (*P. zelicaon*) is locally oligophagous on two umbellifers (*Lomatium* and *Cymopterus*). A gene for preference may to be located on the X chromosome; other genes on other chromosomes may also be involved.

On the other hand, evidence also suggests that umbellifer-feeding in certain groups of specialists may result from biochemical preadaptation. Stride & Straatman (154) noted that larvae of *Papilio aegus*, normally restricted to Rutaceae, readily developed on two umbellifers, parsley and celery. Moreover, populations of *Papilio polyxenes* feed on species in the rutaceous genera *Dictamnus* and *Ruta*, although there are no native North American rutaceous hosts for these populations. Similarly, *P. zelicaon*, whose native hosts are all umbelliferous, has recently incorporated *Citrus* as a host plant (60). If umbellifer feeding is derived from Rutaceae-feeding in the genus *Papilio*, then acquisition of new rutaceous hosts by umbellifer specialists may represent

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retention of ancestral traits conferring biochemical adaptation to rutaceous toxins. One such group of toxins are the furanoquinoline alkaloids, which are restricted in distribution to the Rutaceae (43). *P. polyxenes* is unaffected by ingestion of skimmianine, a furanoquinoline alkaloid (92), as is *Depressaria pastinacella*, a species in a genus that has never been reported to feed on rutaceous plants (113). That umbellifer specialists can tolerate toxins from plants rarely if ever naturally encountered suggests either that biochemical tolerance is retained from Rutaceae-feeding ancestors or that a common detoxication mechanism suffices for toxins in both groups of plants. The latter may be the case for these umbellifer feeders; furanoquinoline alkaloids are tricyclic phototoxins that are similar in structure to linear furanocoumarins and share a similar mode of action (136). They may also be metabolized by the same or related cytochrome P450 isozymes.

To gain insight into the evolutionary forces leading to specialization on umbellifers, it is instructive to examine patterns of host utilization of nonumbellifers by close relatives of umbellifer specialists (and indeed of umbellifer specialists as well). Two families consistently appear in the host lists of near-relatives of umbellifer specialists—Rutaceae and Compositae (Asteraceae). Rutaceae-feeding is reported in Agonopterix and in Apachea, another depressariine genus in the Oecophoridae (96), in Apion, and in Papilio (9). Composite-feeding is even more pervasive and occurs in Agonopterix, Depressaria, Papilio, Papaipema, Apion, and Euleia (see references in Table 2). Every aphid genus with umbellifer specialists (with the exception of Hyadaphis) also contains species that are composite specialists. Some species (e.g. Cavariella capreae, Aphis heracelella) feed on plants in both families (1, 149) as do mirids closely related to Orthops campestris (111). Almost every umbellifer specialist taxon is closely associated with taxa specialized on composites.

To find a biochemical explanation for the close association between feeding on umbellifers and on composites is not difficult. Striking chemical similarities exist between the two families in the occurrence of terpenes, sesquiterpene lactones, phenylpropenes, coumarins, lignans, C-17 polyacetylenes, flavone glycosides, cyclitols, guaianolides, and germacranolides (58, 89, 93, 98, 137, 150). In fact, apioid umbellifers are chemically more similar to some composites than they are to members of the Hydrocotyloideae or Saniculoideae. Host plant utilization patterns reflect the chemical similarities more than the taxonomic relationships; although Araliaceae is thought to be the family with the closest relationship to Umbelliferae, records of umbellifer feeders or their relatives on araliaceous hosts are quite rare (e.g. only one *Agonopterix* species in Europe and North America (96) and only two of over 200 species of *Papilio* worldwide—Scriber, 146).

The pattern of host association by Agonopterix within the Compositae is as strikingly nonrandom as are the associations within the Umbelliferae. The

composites are divided into two groups, Group I consisting of seven tribes and Group II of eight tribes (29, 117a). Every single oecophorid host plant in the Compositae belongs to tribes in Group II. This group is most similar chemically to the apioid umbellifers (Table I; 58, 89, 90, 93, 117a).

The remarkable similarity in chemistry does not provide a means for distinguishing between behavioral facilitation or biochemical preadaptation as the basis for the acquisition of new hosts and subsequent specialization. However, in this case, chemical similarities may provide some insights into the evolutionary processes underlying current host associations. Cronquist (40, 41) proposed an evolutionary sequence from Rutales to Umbellales to Asterales; this sequence is strongly supported by phytochemical patterns. The Rutaceae shares polyacetylenes, lignans, essential oils, chromones, and coumarins with both the Umbelliferae and Compositae (43, 91).

Conclusions

The process by which specialist taxa evolve is widely debated; alternative hypotheses include sequential evolution or host tracking (106) and reciprocal adaptive evolution or coevolution sensu lato (52, 103). In sequential evolution, preadaptation permits colonization of both related and unrelated plant taxa. In coevolution, reciprocal selection pressures generate series of related insect taxa associated with related plant taxa (123). The two processes are not easily distinguished in any practical way; it is in fact possible to create the same evolutionary pattern by invoking either process. Nonetheless, to examine the evolution of umbellifer association in the context of these arguments is instructive. In the case of umbellifer feeders, abundant evidence (perhaps greater than for any other group of insects) suggests that host finding depends on the detection of unique combinations of host chemicals. Moreover, there is evidence that biochemical adaptation to umbellifers also involves several unique groups of chemicals acting in concert (e.g. methylenedioxyphenylcontaining propenylbenzenes and furanocoumarins-13, 129). Oviposition mistakes and larval preadaptation are likely to occur on plants that are chemically similar to hosts, and chemical similarity is most likely to occur in related taxa. Colonization events are facilitated by chemical resemblance. Chemical similarity can arise either via common ancestry or by convergence, a fact that explains at least in part why related groups of insects are often associated with related groups of plants and at least in part why specialists often utilize chemically similar but phylogenetically unrelated plants. Sufficient chemical similarity may exist among distantly related plants to allow a colonization event to succeed. For example, the leguminous genus Psoralea is host to a number of umbellifer specialists or their close relatives (including Agonopterix, Papilio, and Apion); species in the genus are virtually alone in the Leguminosae (Fabaceae) in producing furanocoumarins (9).

Part of the debate on how new host plants are acquired stems from a lack of

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consensus on what exactly constitutes a host plant. A reasonable criterion would seem to be that a host plant is a species on which females will oviposit (for those species in which females oviposit on hosts) and on which larvae will feed. Such a statement borders on fatuous; however, much vituperative debate has centered around the significance of oviposition "mistakes" and larval growth on nonhosts. Each phenomenon is by itself incomplete. To draw a rather strained and possibly unhelpful analogy, the process of acquiring a new host-at the level of species, genus, or family-can be likened to filling a straight at draw poker. Five cards in numerical sequence are needed to win, but rarely does one pick up the cards in sequence. Moreover, there is no real penalty for picking them up out of sequence, just so long as all five are in the hand when all the bets have been called. Similarly, to acquire a new host, behavioral adaptations, metabolic competence, ecological (habitat) compatibility, and relative immunity from predators and parasites must also be acquired (to an extent that permits successful establishment). If each factor depends ultimately upon random genetic events (e.g. evolution of oviposition preference or biochemical resistance), there is no reason to expect any one event to initiate the process in all (or even most) cases. To do so is like expecting every royal flush to start by drawing a ten. While it's not a certainty that the acquisition of new hosts and subsequent specialization can occur via a multitude of pathways depending on both preadaptations and random mutations, it is nonetheless a fairly safe bet, and it is worth wagering time and money testing all reasonable hypotheses without excluding any one out of hand.

ACKNOWLEDGMENTS

This review is affectionately dedicated to Paul Feeny. I thank A. Zangerl and a host of graduate students (M. Cohen, J. Nitao, and S. Passoa, in particular) for insights, data, and forbearance, Olle Pellmyr and David Voegtlin for taxonomic insights, and R. Leskosky for poker tips. This work was supported by NSF BSR 88-18205.

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