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SMALL ERMINE MOTHS (*YPONOMEUTA*): Their Host Relations and Evolution

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OVERVIEW AND HISTORY

The genus *Yponomeuta*, or small ermine moths, forms a rather small genus of the family Yponomeutidae (Lepidoptera, Ditrysia). It contains some 30 species, and has a wide palearctic distribution (37, 108; G. D. E. Povel, personal communication). The present review almost entirely focuses on West European taxa.

Nine well-defined species occur in western Europe (Table 1) (115). Six of these are monophagous on shrubs or trees of the families Celastraceae, Rosaceae, and Salicaceae. *Yponomeuta vigintipunctatus* is restricted to the forb *Sedum telephium* (Crassulaceae). *Yponomeuta malinellus* can be found on *Malus* and *Pyrus* species, whereas *Yponomeuta padellus* feeds on plants from various genera of the Rosaceae. Related to *Y. padellus* is a complex of five taxa, often referred to as the "*padellus*-complex," the taxonomic and

evolutionary status of which has long been a matter of dispute because of the close morphological similarity, largely overlapping distribution ranges, and ability to interbreed in the laboratory that are shared by these moths (57, 98, 153). Evaluations of the complex have varied from five different species (50, 157) or five incipient species (142, 143) to one polyphagous and polytypic species (37).

The association with the Celastraceae is striking for the West European species of *Yponomeuta* (Figure 1), and even more so when the genus as a whole is considered. Except for 6 of the 9 species mentioned in Table 1 and *Yponomeuta gigas*, which feeds on *Salix* and *Populus*, all other 23 or so described taxa feed on Celastraceae (37, 108); in western Europe these include *Yponomeuta cagnagellus*, *Yponomeuta irrorellus*, and *Yponomeuta plumbellus* (all on *Euonymus europaeus*, spindle tree). On the other hand, outside the genus *Yponomeuta* (but within the family Yponomeutidae), only 3 of over 100 species, namely *Euhypnomyetoides trachydelta*, *Zelleria melanopsamma*, and *Xyrosaris lichneuta*, use Celastraceae as food plants (38, 48, 108). Overall, the spindle tree has an impoverished entomofauna, most likely because of the presence of toxic alkaloids and butenolides (39). This observation led to the following working hypothesis: the present affiliations in *Yponomeuta* evolved from an ancestral association with Celastraceae through allopatric speciation, mostly on *Euonymus*, and through sympatric host shifts to other food plant genera [following the scenario of host race formation (12)].

Table 1 *Yponomeuta* species and their host plants

Species ^a	Host Plant ^b	Abbreviation ^c
<i>Y. evonymellus</i>	<i>Prunus padus</i> (R)	evon
<i>Y. cagnagellus</i>	<i>Euonymus europaeus</i> (C)	cag
<i>Y. mahalebella</i>	<i>Prunus mahaleb</i> (R)	mah
<i>Y. malinellus</i>	<i>Malus domestica</i> , <i>M. sylvestris</i> , <i>Pyrus communis</i> (R)	mal
<i>Y. padellus</i>	<i>Crataegus</i> spp., <i>Prunus spinosa</i> , <i>P. domestica</i> , <i>P. cerasifera</i> , <i>Sorbus aucuparia</i> , <i>Amelanchier lamarckii</i> (R)	pad
<i>Y. rorellus</i>	<i>Salix</i> spp. (S)	ror
<i>Y. irrorellus</i>	<i>Euonymus europaeus</i> (C)	irror
<i>Y. plumbellus</i>	<i>Euonymus europaeus</i> (C)	plum
<i>Y. vigintipunctatus</i>	<i>Sedum telephium</i> (Cr)	vig

^a The second through sixth species form the *padellus*-complex.
^b Abbreviations in parentheses are: C, Celastraceae; Cr, Crassulaceae; R, Rosaceae; S, Salicaceae.
^c Equivalent to those used in Figure 1.

Figure 1 Phylogenetic tree of the nine West European *Yponomeuta* species based on allozyme data and their host affiliations. Regions are defined as: Black, Celastraceae; white, Rosaceae; shaded, Salicaceae. The black and white area in the lineage to *Y. vigintipunctatus* (on Crassulaceae) indicates that its sister species *Yponomeuta yanagawanus* feeds on *Euonymus*. For abbreviations see Table 1.

Since the early 1970s, *Yponomeuta* has been multidisciplinarily studied as a model system for evolution and speciation in which insect–host plant relationships are thought to have played—and are still playing—a key role (63, 64, 156). The main objectives of studying this model were to obtain insights into the phylogenetic relationships among taxa, the evolution of their host relations, and the speciation processes that have led to the present-day associations. This review aims to integrate the data from the constituent projects.

GENERAL LIFE CYCLE

Except for *Y. vigintipunctatus*, all *Yponomeuta* species are univoltine. Adults fly in late spring; females deposit their eggs in one or a few clusters of up to 100 eggs each on the branches of the specific food plant, often near a bud or side branch (115). Eggs hatch some three weeks later, except that for *Y. plumbellus*, eggs are laid singly and development does not start before the next spring. The larvae remain aggregated under a protective shield (the hibernaculum) until the following spring when they start to feed on the

developing foliage. First-instar larvae of *Y. irrorellus* bore into a twig of the host plant before they enter diapause. Larvae are mostly external leaf feeders, although some early stages mine inside leaves. They tie leaves together in loose webs and feed within or in the neighborhood of these communal webs, extending them as the leaves are consumed. Trail-marking pheromones are probably used for finding their way back to the webs after feeding outside of them, as well as during the process of web migration (125). After four (*Y. vigintipunctatus*) or five instars, the larvae pupate in groups within the communal web or in the understory nearby. Approximately two weeks later the adults eclose. *Y. vigintipunctatus* is bivoltine in western Europe, but univoltine in mid-Scandinavia. In southern Europe, more than two generations a year may be completed (130). In western Europe, pupae of the spring generation of *Y. vigintipunctatus* hibernate and diapause (84, 85). All nine species have broadly overlapping periods of adult activity, both in terms of time of the year and circadian rhythm (54).

Yponomeuta species may defoliate entire trees during severe infestation and thus cause economic losses. Outbreaks occur in apple [*Y. malinellus* (144)] and plum as well as ornamentals (*Euonymus*, *Crataegus*, *Sorbus*, etc). Most plant species recover fairly quickly, however, even when such infestations continue to occur for some years.

Natural Enemies

Yponomeuta species are attacked by some 20 hymenopterous and dipterous endoparasitoids (29, 32, 101). A survey of 10 years in western Europe shows that in most species of *Yponomeuta* the same parasitoid species occur but in different ratios; only *Y. plumbellus* and *Y. vigintipunctatus* each harbor a specific set of parasitoid species (29). These include strictly monophagous parasitoids (e.g. *Triclistus yponomeutae*) as well as species that are either confined to the genus *Yponomeuta* or have much broader host ranges, in some instances even spanning various insect orders (32). The ability among *Yponomeuta* species to encapsulate *Diadegma armillata* eggs, a major mechanism for preventing successful parasitization by this ichneumonid, is positively correlated with percentages of parasitization in natural populations (30, 101). Dijkerman (31) studied in some detail the synchronization of the life cycles of *Y. vigintipunctatus* and three of its important parasitoids, i.e. *D. armillata*, *T. yponomeutae*, and *Trieceles tricarinatus*, as well as of *Mesochorus vittator*, a secondary parasitoid of *D. armillata*.

Although the impact of parasitoids on *Yponomeuta* population numbers has been studied little, birds may be the major natural enemies of *Yponomeuta* (7, 69, 111). Starlings especially feed on *Yponomeuta* larvae, and in one case some 95% of an outbreak of mainly *Y. padellus* was killed in this way, but it was also noticed that starlings did not feed at all on caterpillars (7, 111). Our

own observations support the contention that caterpillars as well as moths are unpalatable, yet not aposematic, so that only experienced birds refuse to eat them. We have observed that birds appear to become drowsy if force fed. Butenolides; isosiphonodin in particular, appear to be important compounds that confer repellency (43). Such substances were detected in *E. europaeus* and *S. telephium*, and in larvae, pupae, and adults of *Y. cagnagellus* and adult *Y. vigintipunctatus*. Because adults of other *Yponomeuta* species also possess butenolides not present in their food plants, synthesis of these compounds in adult moths and/or larvae probably takes place. The presence of butenolides in some endoparasitoids can similarly be explained by synthesis or by transfer from insect host to parasitoid (40). Apparently, sequestration of secondary plant compounds does not generally add to the unpalatability of *Yponomeuta* species (40, 43; but see 41).

Some Diptera (e.g. *Agria mamillata*), Dermaptera, Hemiptera, Coleoptera, and Hymenoptera (ants) have also been observed as predators (32, 69, 78, 111). Other natural enemies include *Nosema* and *Gregarina* species (Protozoa), fungi, and viruses, some of which have been applied to control small ermine moths (96, 36). Despite this assortment of natural enemies, outbreaks regularly lead to complete defoliation. Some parasitoid species (e.g. the encyrtid *Ageniaspis fuscicollis*) are currently under study on the west coast of Canada and the USA as biological control agents of *Y. malinellus*, one of the palearctic *Yponomeuta* species that was introduced into North America (65, 70, 144).

SYSTEMATICS AND PHYLOGENY

Within the small ermine moths, there are well-differentiated species as well as (groups of) morphologically similar taxa (Table 1) (50, 108, 116). Each species has its specific group of host plant species, which in some instances led to the description as well as to the coining of the specific epithet (or name) of the insect. Incorrect food-plant labeling has resulted in some nomenclatorial confusion. *Yponomeuta evonymellus*, for instance, does not consume *Euonymus*, but rather feeds on *Prunus padus*, whereas *Y. padellus* occurs on quite a number of Rosaceae, yet never on *P. padus*.

Identification of adult moths using morphological characters alone sometimes appears inconclusive, owing to variation within characters and overlapping character states (37, 115). Many single morphological characters or ratios of measurements that are used in keys to the species (49, 111) turned out to be unreliable. Therefore, identification has long been necessarily based on the food plant from which the insects were collected as larvae. Contrary to earlier reports, *Yponomeuta* species are cytogenetically very similar (110).

All taxa listed in Table 1 are now firmly established as genuine biological

species that have diagnostic enzyme loci (4, 98, 100), differences in the morphology of larvae, pupae, and imagines (116), and differing pheromone systems (55, 92, 93). The close sibling species *Y. malinellus* and *Y. padellus* appear to be almost identical genetically. Their genetic identity (109) amounts to either 0.98 [based upon 51 allozyme loci, none of which is diagnostic (100)] or 0.92 (4) [calculated from a set of 32 loci broadly overlapping with those surveyed by Menken (100), including one diagnostic and two highly differential loci]. Statistically significant differences in allele frequencies and the presence of rare, taxon-specific alleles also hint at valid biological species, assuming that selection is negligible; such variation patterns appear to be highly constant in space and time and to hold under sympatric conditions (99, 103). With very few exceptions, populations with genetic identities of 0.95 or higher are conspecific (104, 105, 141). Thus, one might conclude that *Y. padellus* and *Y. malinellus* speciated recently.

Povel (116–118) phenetically analyzed all *Yponomeuta* taxa using numerical taxonomy and morphological characters. Moreover, unweighted pair group mean averaging (UPGMA) dendrograms based on allozyme data were constructed (100) as was a phylogenetic tree by means of a modified version of Rogers' HAP algorithm (Figure 1) (93, 126). The tree was rooted using the outgroup method; *Y. vigintipunctatus* served as the outgroup (157; see 137 for a discussion on phylogenetic analyses from allozyme data). Dendrograms based on the entire set of allozyme loci and those based on loci that are exclusively expressed in either the larval stages or the adult stage were all highly congruent (8, 100), whereas biochemical trees were less congruent than morphological ones (100, 116, 118), an observation that is not uncommon (8).

Additional species may potentially corroborate or falsify a particular phylogenetic tree. The Japanese species *Y. yanagawanus* from *Euonymus japonica* appears to be related more to *Y. vigintipunctatus* than to *Y. plumbellus* (66) (see legend to Figure 1); *Y. gigas* collected from *Populus alba* in Tenerife (Canary Islands) is very closely related to *Yponomeuta rorellus* (119). Both species fit in well with and conform to the postulated transformation series of allelic composition at the malate dehydrogenase locus, based on the nine West European representatives (S. B. J. Menken, unpublished data).

The ability among *Yponomeuta* species to encapsulate eggs of *D. armillata* parallels the phylogenetic relationships: it is superior in species that diverged early in the evolution of the genus (*Y. vigintipunctatus*, *Y. plumbellus*, *Y. mahalebells*, and *Y. cagnagellus*) and falls to intermediate levels (*Y. padellus*) or to zero in species that share recent ancestors (*Y. evonymellus*, *Y. rorellus*, and *Y. malinellus*) (30). Apparently, after *Y. cagnagellus* branched off, *Yponomeuta* species became increasingly more suitable as hosts of *D. armillata*. Below, we also relate sex pheromone composition and host plant

associations with the provisionally accepted phylogenetic relationships as depicted in Figure 1.

MATING SYSTEMS, COMMUNICATION, AND REPRODUCTIVE ISOLATION

In members of most insect orders, sex pheromones play a role in mate location and courtship behavior. Sex pheromone communication, its evolution, and the role of pheromones in reproductive isolation and speciation in insects were recently reviewed (14, 15, 88, 89; for *Yponomeuta*, see 93). Chemical communication is involved in resource partitioning, which is a major force in structuring communities (52). Insects use chemical communication channels that are usually species-specific, allowing them to function as premating isolation mechanisms. Species distinctness is maintained through differences in composition and/or in ratios of the constituents, as well as in time of pheromone release (diel and seasonal); these chemical and temporal axes can be viewed as dimensions in a multidimensional ecological niche (24, 52). Because related species possess common synthetic pathways, their pheromones often exhibit unique ratios of common components. Families often have different pheromone components (10).

The evolution of pheromone communication systems is still poorly understood (88, 89). Successful transmission of information relies both on the pheromone-emitting female (the sender) and the receiving and responding male (the receiver) (150). Divergence in pheromone systems can proceed by parallel selection on female and male traits, provided these traits possess enough heritable variation within the population. One can predict, based on the common asymmetry of sexual selection (25, 88), that the variance among males in their pheromone response is smaller than the variance among females in their pheromone production. Emittance ratios of (Z)- and (E)-11-tetradecenyl acetate (Z11-14:OAc and E11-14:OAc), two major components of *Yponomeuta* pheromones, do significantly vary among individual *Yponomeuta* females (93), and the high level of repeatability for this character in *Y. padellus* indicates that this variation is under genetic control (33). As expected, the male-response component shows no evidence for heritable variation (25).

Field observations show that *Yponomeuta* females rapidly acquire mates (25; see also section on population structure). As they mate only once or twice, attractive females quickly disappear from the mating pool; females that produce less attractive pheromones then stand a relatively better chance to obtain males, which can mate several times. This system maintains variation in pheromonal production, despite the fact that some less attractive females may remain unmated [the wallflower paradox (26)]. Variation in males

approaches zero as they are selected to respond to the mean blend composition. Thus in a random mating population, sexual selection leads to a low male-to-female variance ratio and this in turn leads to the absence of runaway selection (cf. 77, 86). Sexual selection itself may lead to speciation, but in a different way from what has been previously thought (26). Because females vary but males do not, a founder population probably would contain deviating females. Sexual selection might then lead to a steady state that is different from the source population; as a result, after some period of separation opposing sexes from the source and the derived population do not respond to each other any more, and reproductive isolation is complete.

Courtship Behavior

Most if not all *Yponomeuta* species can come into contact in the field; thus ethological premating or postmating reproductive isolation must be responsible for maintaining species distinctness in nature. Only once were hybrids (i.e. between *Y. malinellus* and *Y. padellus*) observed in nature (4, 100). Male and female *Yponomeuta* are sexually active during the end of the scotophase and at dawn; *Y. vigintipunctatus* and *Y. plumbellus* show an earlier period of activity entirely restricted to the scotophase (54). These data result from laboratory and field trap experiments in which both sexes were kept from mating; the actual activity period is likely to be much shorter as males and females cluster together in the field, and most if not all matings probably take place shortly after calling begins [*Y. padellus* females need an average of 25 minutes to attract a male (25)]. Upon eclosion, species of *Yponomeuta* are not yet sexually mature. The age at which calling starts to be effective (measured as 30% of females that are calling) varies among species from 1 day for *Y. plumbellus* to 10 days in *Y. malinellus* and *Y. cagnagellus*. Male responsiveness is also age dependent (54).

Although intraspecific attraction always exceeded interspecific attraction for any of the eight species tested in the wind tunnel, some species displayed interspecific attraction (55). For example, *Y. evonymellus* males showed strong responses to female *Y. padellus*, *Y. irrorellus*, and *Y. vigintipunctatus*, whereas *Y. vigintipunctatus* females substantially attracted *Y. evonymellus* as well as *Y. irrorellus* males. The similarity of pheromone composition corroborates these findings in almost every detail (see below). Among the climatic factors examined, wind velocity has a major impact on behavior, especially that of males; above velocities of 2 m/s the number of responding males drastically declines (59). Both sexes prefer a species-specific height in the vegetation; the height at which trapping is maximal is the one at which most oviposition takes place and most nests are encountered (68).

Hendrikse (56) described the courtship behavior of *Y. padellus* in detail. Similar patterns appear in *Y. cagnagellus*, *Y. evonymellus*, *Y. malinellus*, and

Y. rorellus, whereas *Y. plumbellus* and *Y. vigintipunctatus* exhibit a less elaborate behavior (58). Even if interspecific attraction occurs, opportunities for maintaining species distinctness are present through differences in courtship behavior such as the timing and expression of mechanical touching with antennae, acoustic or vibratory signals from wing fanning, male pheromones from abdominal brushes, or (chemo)tactile stimuli received during clasping. Male pheromone and possibly wing fanning do prevent interspecific mating after a heterospecific male has arrived at an *Y. padellus* or, to a lesser extent, at an *Y. evonymellus* female (60). In these two species as well as in *Y. cagnagellus*, wing fanning alone or in combination with the male pheromone inhibits the activation of any, including conspecific, individual males.

Host selection is of prime importance in models of sympatric speciation through host race formation (12) because disruptive selection for genes that determine host-plant choice leads pleiotropically to assortative mating. Results from electroantennograms (EAG) suggest that females and males can detect a wide variety of plant volatiles by olfaction (145). However, total response spectra are not significantly different among *Yponomeuta* species, nor do they significantly differ between *Yponomeuta* and *Adoxophyes orana*, a polyphagous tortricid that shares many food plants in common with *Yponomeuta* species. Behavioral studies indicate females do discriminate among plant species: they are attracted by the host plant, prefer to call in areas containing host-plant odor, and the presence of the host plant stimulates calling behavior (61, 67). Thus, one can assume that females generally call from their typical host plant. The reason why we do not find a relation between EAG spectra and host-plant binding might be that no biologically relevant combinations of odors were tested. Alternatively, other sense organs such as olfactory sensilla on the palpus labialis or, more likely, contact chemosensory sensilla on the tarsi may serve as detection organs, but these have not been studied. Discrimination may also take place at a higher integration level in the nervous system.

Except for those of *Y. cagnagellus*, males are not attracted by host plants alone (58). Host-plant odors, however, do appear to have a strong effect in combination with pheromones: traps in host plants usually catch significantly more males than those placed in nonhosts (61), which is in agreement with electrophysiological experiments showing that male response to sex pheromones is modified by plant volatiles (145, 149). Rendezvous on different hosts might lead to assortative mating in nature. The preceding account only pertains to monophagous *Yponomeuta* species. It discloses little about host fidelity within the oligophagous *Y. padellus*. In fact, no evidence was found for an influence of the original host on female calling behavior or male searching time (58). However, in wind-tunnel experiments in the absence of host plant odor, males of some host-associated populations were significantly

more attracted by their own females than by females from other host plants; in part these results could be attributed to differences among geographic populations.

Sex Pheromones

PERCEPTION The distribution of sense organs on male antennae has been the subject of various studies (21, 147). All *Yponomeuta* species examined possess the same types of sensilla, and the number and distribution of these do not differ significantly among the species with the exception of the sensilla trichodea. All species exhibit sexual dimorphism for these two characteristics, *Y. vigintipunctatus* excepted (19). The ultrastructure of the sensilla trichodea, sensilla basiconica, and sensilla coeloconica, the so-called wall-pore sensilla, indicates that they might be involved in chemoreception (3, 20).

The first field trapping experiments as well as EAG recordings were carried out when the composition of the actual sex pheromones was still unknown. Field and laboratory experiments showed that virgin females attracted almost exclusively their conspecific males and that EAG profiles of compounds known to be active as components of pheromones in other Lepidoptera differed among *Yponomeuta* species (54, 55, 64). For these same compounds, the more sensitive procedure of single-cell recordings of the sensilla trichodea showed that response spectra in males differed among the five species tested, indicating differing responsiveness to and probable use of different sex pheromones (148). Further refinement and extension to all nine West European representatives of *Yponomeuta* confirmed these earlier findings and suggested that Z11-14:OAc and E11-14:OAc are important components of the pheromones of most species (146).

COMPOSITION Many of the actual pheromone components of *Yponomeuta* species have been predicted using electrophysiological screening (146), although the predictive value of this technique is hampered by our poor understanding of the perception of multicomponent pheromones (93, 94). The pheromonal composition of all *Yponomeuta* species has been elucidated successively, and in subsequent tests, synthetic blends competed with those emitted by virgin females. The data almost fully agree with patterns of cross-attraction as revealed by wind tunnel and field trap experiments (55, 68, 93).

The majority of *Yponomeuta* pheromones conform to the pattern observed in many other Lepidoptera in that pheromones have unsaturated components with double bonds in particular positions and a dominance of Z-geometry desaturation (5): *Y. cagnagellus*, *Y. evonymellus*, *Y. irrorellus*, *Y. padellus*, *Y. plumbellus*, and *Y. vigintipunctatus* all use Z11-14:OAc as a primary component, together with differing amounts of the E-isomer (93, 94). *Y.*

cagnagellus has by far the lowest amount of E11-14:OAc. Niche separation of all six species requires consideration of at least one additional pheromone component or temporal aspect. In *Y. padellus*, for instance, Z11-16:OAc forms a third major component. This compound serves as a behavioral antagonist for *Y. evonymellus* and *Y. vigintipunctatus*. Thus the attraction between *Y. padellus* females and *Y. evonymellus* males in the wind tunnel (55) does not logically follow from the pheromone composition (93, 94). *Y. evonymellus* and *Y. vigintipunctatus*, although genetically far apart (Figure 1) (100), share the same pheromone system, which may indicate the primitive state in *Yponomeuta* (93, 94). In nature, interspecific matings between *Y. evonymellus* and *Y. vigintipunctatus* are simply impossible because of asynchronous occurrence, as well as several other differences in life history characteristics (68).

Pheromone analysis of the three *Yponomeuta* species that sympatrically occur on *Euonymus* revealed differing mixtures of seven compounds, two of which (Z11- and E11-14:OAc, see above) are primary pheromone components, with tetradecyl acetate (14:OAc) serving as synergist in *Y. cagnagellus* (91). Removal of the alcohols changes the attractiveness of the mixture for this species, but has no effect on the other two. Premating reproductive isolation among these species is achieved by differences in time of sexual activity, rate of pheromone emission, height of flight, and possibly male pheromones.

The remaining three West European species, *Y. rorellus*, *Y. malinellus*, and *Y. mahalebells*, possess radically different pheromonal blends, both in qualitative terms and in the reduced number of compounds. *Y. rorellus* is very distinctive; it has the most simple pheromone and uses 14:OAc as the major component (92). A comparably simple situation is found in *Y. gigas*, a species that is closely related to *Y. rorellus*. (119; S. B. J. Menken, W. M. Herrebout & C. Löfstedt, unpublished data). Z11-14:OAc, the primary pheromone component of many *Yponomeuta* species, acts as a behavioral antagonist for *Y. rorellus* (90). A combination of only two components (Z11-14:OH and Z9-12:OAc) of the multicomponent sex pheromone of *Y. malinellus*, which was elucidated recently (97), is highly effective in field traps and results in even better catches than traps baited with live females. Z11-14:OH elicits a negative behavioral reaction in *Y. padellus*. Finally, *Y. mahalebells*' pheromone glands produce three 16-carbon acetates and 14:OAc only (93). We may conclude that niche separation among *Yponomeuta* species is complete in the natural habitat.

Now the pheromonal compositions can be related to the presumed evolution of *Yponomeuta* (Figure 1) (93). The similarities in the pheromones of six of the nine *Yponomeuta* species, those between the distantly related species *Y. vigintipunctatus* and *Y. evonymellus* in particular, make it plausible that the

primitive ermine moth pheromone consisted of a mixture of 14-OAc, Z11- and E11-14:OAc, and their corresponding alcohols. The loss of pheromone components in the remaining three species agrees with Kaneshiro's argument (76) that in general derived species should have simpler species-recognition mechanisms than ancestral ones (see also 92). Because of the postulation that data on biosynthetic routes to pheromones are more useful for the elucidation of evolutionary relationships than composition per se (124), Löfstedt et al (93) analyzed the occurrence of fatty-acid pheromone precursors in the pheromone glands of the small ermine moths. The results underline the biochemical similarity of *Yponomeuta* pheromones, but the limited number of differences in distinct biochemical reaction steps unfortunately provides low resolution for phylogenetic analyses.

INSECT-HOST PLANT INTERACTIONS

A large proportion of insect species are monophagous (120) and many polyphagous species exhibit local specialization for specific hosts (136). Variation of diet breadth among insect species results from differences in either adult behavioral responses to attractants or deterrents (i.e. the failure of an ovipositing female to recognize certain plant species as suitable hosts) or physiological adaptation (genetically based constraints) of the larvae (e.g. phagostimulants versus deterrents and the ability to tolerate chemical and physical plant features).

The relationship between adult oviposition preference and larval performance is a central problem not only in debates about the evolution of host specificity, but also in studies of selection for enemy-free space and of allopatric or sympatric host shifts onto new food plants in connection with models of speciation (138, 139). Trade offs in fitness associated with host-plant shifts are often assumed in the evolution of host specificity (46). The results in many such studies are quite dissimilar, ranging from good to poor (73, 140). Consequently, because such a trade off is generally thought to be an important basis for genetic polymorphism in host utilization, a change in host specificity is said to most likely take place in geographical populations (13, 46), minimizing the likelihood of host race formation and sympatric speciation. However, when making such assumptions, researchers can overlook important indirect effects, e.g. performance is only studied in the absence of predators, parasitoids, and the like. The interaction effects (enemy-free space) as well as competition for food might be considerable (e.g. 2, 23, 123). Thus, because compensation for lowered fitness on a new host caused by allelochemicals or poor food quality has hardly been considered, the conceptual framework is too limited for one to draw firm conclusions (73; see also 122 for criticism of the biological relevance of the performed tests).

Oviposition

The studies on *Yponomeuta* have focused little on oviposition. Since newly hatched larvae cannot migrate long distances and therefore have a limited capacity for host selection, gravid females make the critical host choice during oviposition. Generally, females discriminate between host and nonhost plants (80). When females were forced to oviposit on a nonhost that is a host plant for other *Yponomeuta* species, the resulting larvae survived in a few host-insect combinations (e.g. *Y. padellus* on *P. padus*, and *Y. evonymellus* on *Crataegus* but not on *Prunus spinosa*) (83; see also next section). However, the larval food never induced oviposition preference for that resource.

Y. padellus exhibits interpopulation variation in host-plant use (i.e. regional polyphagy) (136). For example, in Finland *Y. padellus* mainly infests *Sorbus aucuparia*; the other normal host plants, *Crataegus* and *P. spinosa*, do not occur there, and these Finnish *Y. padellus* clearly preferred *S. aucuparia* for oviposition (151). Such situations might lead to allopatric speciation (136, 151). *S. aucuparia* is also attacked in the eastern but not in the western part of the Netherlands, although Finnish *Y. padellus* happily eats from the western Dutch form. Dutch *Y. padellus* that feed on *Sorbus* do not prefer *Sorbus* as host plant in choice experiments with *Crataegus*, and *S. aucuparia* is otherwise a rather unattractive host for *Y. padellus* oviposition (80). In general, *P. spinosa* is the most preferred host of West European *Y. padellus*, irrespective of the original host plant. Attempts to establish differences in oviposition behavior among supposed host races of *Y. padellus* had negative results [with a few exceptions, e.g. a locality with *Y. padellus* populations on *Prunus cerasifera* and *Crataegus*; these populations were genetically differentiated as indicated by allozyme analysis (99)].

Food Acceptance and Performance of Larvae

Caterpillars perceive plant chemicals that are cues for the initiation and maintenance of feeding with a few contact chemoreceptors in the lateral and medial sensilla styloconica (95, 128, 152). Successful colonization of new hosts often requires evolutionary changes in the perception of novel plant odors and tastes and in behavioral responses (28, 45). Changes might be minor if a new host shares major chemical properties with the original one. Thus, host plants of related species of insects are often chemically similar, although the plants might be unrelated taxonomically. However, to test the likelihood of a host-shift scenario, one must document correspondence between chemosensory capabilities of related insect species and the shared chemical properties of their hosts (27, 75, 107).

The balance between positive and negative inputs perceived from complex chemical plant signals likely governs feeding behavior (129, 152). Among the many potentially important chemical signals are some of particular interest in *Yponomeuta*. Electrophysiological experiments revealed a remarkable corre-

spondence between chemosensitivity to and presence in the food plant of certain primary plant compounds, especially sugar alcohol isomers. The predominant sugar alcohol in Celastraceae, dulcitol, acts as a phagostimulant to all *Euonymus*-feeding *Yponomeuta* species, whereas sorbitol, predominant in Rosaceae, does so for all Rosaceae feeders. Species feeding on *Prunus* (Rosaceae) also react positively to dulcitol, at first considered an enigmatic result until low quantities of dulcitol were encountered in *Prunus* (42). The behavioral threshold of *Y. evonymellus* for dulcitol response, for example, is about an order of magnitude lower than that of *Y. cagnagellus* (113), which closely corresponds with the actual concentration of dulcitol in their respective food plants. Feeding in *Y. evonymellus* was even more enhanced by dulcitol than by sorbitol. A similar situation was observed for *P. spinosa* and *Prunus mahaleb* (42, 152). As expected, *Y. cagnagellus* is not responsive to sorbitol, which is absent from *Euonymus*.

Interspecific comparisons show that, without exception, larvae perform best on their own food plant, but under laboratory conditions performance is also normal on several hosts that are never selected for oviposition in the wild (80, 81). In *Y. padellus*, patterns of larval preference and performance appeared to be fairly consistent, showing a hierarchy similar to the oviposition preference: almost all prefer and perform best on *P. spinosa*, no matter what their host of origin is; next come *Crataegus* and *P. cerasifera*, which in turn are more suitable than *Prunus domestica*, *Amelanchier lamarckii*, and *Sorbus* (80). Earlier data from larval food preference (48) and larval taste sensitivity experiments (152) also suggest that *P. spinosa* is the optimal host for *Y. padellus*. Intraspecific differences in host suitability were occasionally observed for *Crataegus monogyna*: larvae forced to complete their development on trees that were uninfested in nature reached one time low, another time normal, pupal weights (80).

Inheritance of gustatory sensitivity to dulcitol, phloridzin (see below), and sorbitol was studied in F1 progenies from crosses between *Y. cagnagellus* and *Y. malinellus* (153) (the parental species display clearly different neural and behavioral responses to these three compounds). The results indicated that sensitivity to a particular compound is dominant or at least semidominant over nonsensitivity.

PHYLOGENY OF HOST ASSOCIATIONS If, as we have argued before, *Euonymus* spp. (Celastraceae) served as host plants of the common ancestor of *Yponomeuta*, then the following shifts could explain the present-day host affiliations (Figure 1).

1. A shift to Rosaceae has occurred at least twice, one shift leading to *Y. mahaleb* and one to the ancestor of *Y. evonymellus*, *Y. padellus*, and *Y. malinellus*. Despite considerable differences in secondary plant chemistry

between Celastraceae and Rosaceae, some commonalities in their chemistry might have facilitated the host shifts. A scenario is feasible in which perception of the dulcitol present in Rosaceae was the basis for the repeated shift from Celastraceae to the phytochemically radically different Rosaceae; this shift did not require extensive modifications in the overall neural perception of the groups that switched (113). This scenario was shown to be plausible by an experiment in which *Y. cagnagellus*, normally strictly monophagous on *E. europaeus*, readily and successfully accepted *P. padus* (the food plant of *Y. evonymellus*) that was impregnated with dulcitol (82). The reverse is not true. *Y. evonymellus* rarely accepts *Euonymus* (48), and *Y. padellus* and *Y. malinellus* absolutely refuse *Euonymus* even after impregnation with sorbitol (80); apparently unknown compounds of *Euonymus* act as strong feeding deterrents. Similarly, *Y. cagnagellus* larvae could not be forced to accept *P. mahaleb* (82), probably because this plant species contains coumarin and herniarin, which play an important role in its chemical defense against insect herbivores (41). Whether *Y. mahaleb* will accept *E. europaeus* has not been tested.

2. A shift to Crassulaceae might have been facilitated by the presence of butenolides in Celastraceae and Crassulaceae (44). Larvae of *Y. cagnagellus* and *Y. vigintipunctatus* detect butenolides, and preliminary data show that these chemicals can act as phagostimulants (L. M. Schoonhoven, unpublished data). *Euonymus* is unsuitable as host for *Y. vigintipunctatus* (81), although some have claimed just the opposite (1).

3. Insensitivity to salicin [a deterrent for non-*Salix* feeders (152)] presumably supported a shift from Rosaceae towards Salicaceae. Such a shift does not seem to require many adaptational changes as representatives of several families of Macro- and Microlepidoptera feed on both plant families (62). *Y. rorellus* is not sensitive to dulcitol and sorbitol (152).

4. The evolution of insensitivity to the otherwise strong antifeedant phloridzin probably assisted in the shift from an ancestral association with *Prunus* to *Malus* (79, 152). *Y. malinellus* rarely accepts other Rosaceae host plants, whereas *Y. padellus* accepts, even in choice experiments, and survives on *Malus*, albeit with difficulty (79).

All in all, these data lend much more support to the hypothesis that the genus evolved from an ancestral association with Celastraceae than to the alternative explanation of an association with Rosaceae. In six out of nine cases, speciation has involved a host shift, and most shifts have occurred between Celastraceae and Rosaceae or within the Rosaceae. Usually, *Yponomeuta* species did not retain the ability to respond and develop on the ancestral host plant, *Euonymus*.

Clearly, *Yponomeuta* radiation postdated the divergence of their host plants. The conclusion that colonization rather than coevolution explains host

associations in *Yponomeuta* also may apply to many other phytophagous insects (47, 75, 100). The fact that *P. spinosa* seems to be the original food plant of *Y. padellus*, which experienced further shifts onto, for instance, *Crataegus* and *S. aucuparia*, which do not contain dulcitol, further endorses this host-shift scenario.

POPULATION STRUCTURE

General Aspects

Whether a species is genetically fragmented or coherent depends on the balance between gene flow, genetic drift, and natural selection as well as on historical events. Broadly speaking, little gene flow, small population size, and differing selection pressures promote population differentiation (i.e. closed population structure), while extensive gene flow, large population size, and geographically uniform patterns of selection result in spatially homogeneous arrangements of genetic variation (i.e. open population structure). Among these stochastic and deterministic forces, gene flow is of prime importance; even small amounts counteract the diversifying effects of genetic drift and weak selection pressure (34, 127, 158). Only if the selection coefficient is greater than the migration rate does selection cause divergence (131). If gene flow is restricted between populations, geographic differentiation could result from genetic drift and/or spatial variation in selection regimes. However, low-frequency alleles occurring throughout a species' range indicate that gene flow among populations is substantial because the stabilization of selection over temporally and spatially diverse habitats is not a likely alternative (22, 112, 132). Indeed, the same species-specific, low-frequency alleles show up in nearly all populations of *Y. cagnagellus*, *Y. padellus*, and *Y. malinellus* (4, 99, 103), suggesting that populations of these three species possess an open population structure.

Population structure and indirect estimates of levels of associated gene flow can be investigated using gene-frequency data in at least two different ways: inbreeding coefficients (F_{ST}) and private alleles (for a comparison of these and other methods, see 134). In both models, a simple relation between gene frequency data and levels of gene flow has been found. Gene flow estimates are calculated as $N_e m$, where N_e is the effective population size and m the migration rate; $N_e m$ is the average number of migrants exchanged between populations per generation (159). Information on inbreeding coefficients in *Yponomeuta* was averaged over loci, years, and populations that covered approximately the same geographic area for four of five *Yponomeuta* species. Population differentiation is generally low for *Y. cagnagellus*, *Y. rorellus*, and *Y. padellus* (F_{ST} ranges from 0.027–0.030; corresponding $N_e m$ values

range from 8.1–9.0) and is appreciable in *Y. vigintipunctatus* ($F_{ST} = 0.092$, $N_e m = 2.5$), especially if one considers the smaller geographic area from which samples were taken. *Y. malinellus* occupies an intermediate position ($F_{ST} = 0.057$, $N_e m = 4.1$) (99, 102, 103, 106).

The private allele (i.e. alleles that occur in only one population) method (133) yields very similar results (103). Estimated values of $N_e m$ vary from 7.1 to 7.3 for *Y. cagnagellus*, *Y. rorellus*, and *Y. padellus*, whereas the value for *Y. vigintipunctatus* is a low 1.9, and *Y. malinellus* again occupies an intermediate position: populations on apple exchange an average number of 3.4 individuals per generation. Differences among species in estimated levels of gene flow are congruent with our general knowledge of the biology of the various species (103). For instance, dispersal of *Y. cagnagellus* was observed on a lightship some 50 kilometers off the coast (51). Moreover, observations of mass migration in the Rhine valley and of infestation patterns of isolated spots support the idea that species often disperse over considerable distances. On the other hand, *Y. vigintipunctatus* is a much more sedentary species, a view supported by the very local occurrence of a recessive mutant that lacks the characteristic black spots on the wings (W. M. Herrebout & S. B. J. Menken, unpublished data).

Mark-release-recapture data suggest that most males and females do not disperse farther than some 10 meters from the release site (M. Brookes & R. Butlin, personal communication). Occasionally a moth is caught about 100 m from the point of release. Such direct ecological means of estimating dispersal cannot track long distance dispersal, whereas indirect genetic means integrate historical levels of gene flow that might be sometimes totally irrelevant to present-day levels (18). Furthermore, even small amounts of gene flow can effectively keep populations homogeneous, at least at neutral loci (158). Therefore, the results of the indirect and direct approaches are quite complementary: most adults stay on the trees where they eclose, so that calling females readily find a mate, yet long-distance dispersal is enough to keep geographic populations genetically similar. Given the fact that both sexes need a period of sexual maturation and the fact that mating is likely to take place shortly after the start of pheromone emission, it is necessary to know when and how widely dispersal occurs in order to gain insight into effective levels of gene flow.

The closely related species *Y. padellus*, *Y. malinellus*, *Y. cagnagellus*, and *Y. evonymellus* share major allozyme polymorphisms at many loci (100, 103). *Y. rorellus* lacks these polymorphisms most probably because of a genetic bottleneck at the origin of the common ancestor of this species and *Y. gigas*, and possibly because of additional bottlenecks in *Y. rorellus* evolution in particular (92, 102). At each such locus, allelic variation within the four species is large compared to variation between them. Apparently, the daugh-

ter species inherited many of the polymorphisms present in their common ancestors (Figure 1), and these polymorphisms still persist after speciation. A comparable situation has been found in species of *Ectoedemia* (Lepidoptera, Nepticulidae) (104). Similar patterns of shared variation have also been observed in *Drosophila* spp. at the DNA level (6). If ancestral polymorphism is indeed passed on to daughter species, the size of the new founder populations was probably not small or did not remain small for very long. In case of a small founder event, either monomorphic or essentially diallelic loci are expected in newly formed species because of the almost complete loss of low-frequency alleles during a severe genetic bottleneck (16, 105). Overall heterozygosity substantially declines only if small population sizes persist for some time. Mutation pressure is insufficient to restore the original heterozygosity level in the short time elapsed since the origin of *Y. padellus*, *Y. malinellus*, *Y. cagnagellus*, and *Y. evonymellus* and is certainly not able to produce similar electromorphs in similar frequencies. Alternatively, introgression between species may also contribute to these patterns of polymorphism (6).

At least for the glucosephosphate isomerase (*Gpi*) locus, another explanation of the genetic variation patterns is possible. Various studies (e.g. 53, 71, 155) produced evidence that patterns of variation at this locus might be explained by some form of natural selection. Therefore, at this and other such loci, selection regimes common to the four similar *Yponomeuta* species might cause their similar allozyme composition to be retained following speciation. The essentially diallelic *Gpi* locus in these species conforms to variability patterns along the major polymorphism axis (87), comparable with, for example, the alcohol dehydrogenase polymorphism in *Drosophila*, thus hinting at a locus at which variation is likely to be maintained by natural selection.

Host-Race Formation and Speciation

Host-plant shifts might occur for several reasons. First, a female may mistakenly lay her eggs on a nonhost. Adult conditioning to the new host, especially when adults emerge from their host material, could predispose later generations to stay on this host (17, 121). However, little evidence supports larval conditioning, i.e. the propensity of females to lay eggs on the same species of food plant they fed on as larvae (72). Second, intraspecific competition for food may exist. Although entomologists generally believe that community structure of phytophagous insects is not determined by intraspecific competition (136), evidence is now accumulating that indicates its potential importance (73). Third, there may be selection for enemy-free space (73, 74); the study of host shifts is thus related to the question of whether empty niches are available in a community.

Earlier reports on putative host races of *Yponomeuta* include those by

Thorpe (142, 143) and Pag (111), who both observed in choice experiments an oviposition preference for the original host plant by *Y. padellus* taken from *Prunus spinosa* and *Crataegus*. Given the percentages of preference and variability of their data, however, not much can be concluded from their results. Host shifts, especially after introduction of new plant species, are commonly observed in many phytophagous insects (136). Petrof (114) found a shift of *Y. padellus* from native *Prunus sogdiana* and *Crataegus* to introduced *P. domestica* and *P. spinosa* in southern USSR. Furthermore, *Y. gigas* must have shifted from *Salix canariensis* to introduced *Populus alba* in the Canary Islands. Finally, we collected *Y. cagnagellus* from several exotic *Euonymus* species in some Dutch botanical gardens (82, 106).

The idea that host races may appear from adaptation to a new host plant within the distribution area of the population and subsequently may diverge to become a distinct species dates back to over a century ago (154; see also 11, 135, 143). A basic general model for the origin of host races is that of Bush (12), which describes the recombination of a host-selection gene (which pleiotropically acts as an assortative mating gene if mating takes place on the host) and of a host-survival gene that produces new genotypes that can shift to new plant species. Recently, various population-genetics scenarios have been proposed, including single and multiple origins of the host race combined with differing ways of dispersal (9). In theory, the conditions under which host-race formation and sympatric speciation can occur are far less restrictive than previously thought (for an overview, see 138); but additional data from natural populations are needed. The most detailed example of the existence of host races comes from the very same group of insects for which this scenario was originally proposed: true fruit flies of the genus *Rhagoletis* (35).

In *Y. padellus*, statistically significant differences in allele frequencies at particular loci were found among sympatric populations on various food plants (99, 103). In addition, some low-frequency alleles were restricted to populations on one food plant only, and the pattern was consistent over two years of study. Differences could not be explained by sampling error or host-specific selection against certain alleles at these loci or at loci closely linked to and in linkage disequilibrium with them (99). Therefore, the patterns are most easily explained by a reduced level of gene flow. The two indirect means of estimating gene flow levels produce results that corroborate the suggestion that fewer individuals on the average are exchanged between sympatric populations on different hosts than between geographic populations on the same host (103). A comparable investigation in Italy failed to find genetic differentiation between sympatric populations on different hosts (4), but these findings can be partly attributed to a less elaborate statistical analysis (99). Similar to what has been found among closely related *Yponomeuta* species, host races in *Y. padellus* do not exhibit significant reductions in

average heterozygosity or in the effective numbers of alleles (103). Thus, the origin of *Y. padellus* host races shows no sign of severe bottlenecking, a pattern comparable with the one encountered in *Rhagoletis pomonella* (35).

CONCLUDING REMARKS

Evidence is accumulating, particularly in insects, indicating that sympatric speciation through host-race formation explains, in part, the large numbers of species (35, 136, 138). Conspecific, sympatric populations of *Y. padellus* use different host plants. Allozyme data suggest that some of them are partially reproductively isolated host races. However, the results from mate preference, oviposition behavior, and performance studies of these supposed host races are ambiguous. Sometimes a strong mate preference was observed but no oviposition preference was found; other times the reverse situation was encountered. In nearly all cases, performance was best on *P. spinosa*. The data do not consistently support the conclusion from population-genetics evidence that the characters varying between hosts are genetically determined and not environmentally induced. These discrepancies and inconsistencies can have two causes, assuming host races are real: (a) experiments were executed under laboratory or greenhouse conditions, and (b) the analyses were not sensitive or complete enough to reveal consistent differences. Our handling of the insects, for example, prevented early adult experiences that normally might occur in nature because *Yponomeuta* species predominantly eclose in close contact with their host material (17). Also feasible is that both sexes perfectly smell their host plants and are attracted to them only prior to mating. All in all, natural effects may be encountered only under field conditions where an insect is fully exposed during its entire lifetime to relevant abiotic and biotic variables such as normally growing host plants, conspecifics, competitors, parasitoids, predators, pathogens, and the like. Although such conditions are experimentally quite inaccessible, it is evident that all evaluations must finally be made under natural conditions.

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