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Menken, S.B.J.

DOI

[10.1111/j.1570-7458.1981.tb03111.x](https://doi.org/10.1111/j.1570-7458.1981.tb03111.x)

Publication date

1981

Published in

Entomologia Experimentalis et Applicata

[Link to publication](#)

Citation for published version (APA):

Menken, S. B. J. (1981). Host races and sympatric speciation in small ermine moths, Yponomeutidae. *Entomologia Experimentalis et Applicata*, 30, 280-292.
<https://doi.org/10.1111/j.1570-7458.1981.tb03111.x>

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HOST RACES AND SYMPATRIC SPECIATION IN SMALL ERMINE MOTHS, YPONOMEUTIDAE

STEPH B. J. MENKEN¹

Division of Systematics and Evolutionary Biology, University of Leiden, The Netherlands

The amount of genetic differentiation at various levels of evolutionary divergence (con-specific populations, sibling species and non-sibling species) in *Yponomeuta* was determined. Genetic distances between siblings or non-siblings were found to cover a wide range. It is concluded that such estimates do not give much information on the speciation process itself. Inbreeding coefficients were calculated for populations of *Y. padellus* from a total of six host plants. The grand mean F_{ST} value is 0.030 ± 0.012 . F_{ST} values for populations sampled from *Crataegus*, the common food plant of *Y. padellus*, are 2–3.5 times smaller than those for populations from the other food plants taken together. Host race formation, as measured by significant differences in allozyme frequencies between sympatric populations on two or more food plants, was investigated in four areas. Host race formation seems to occur in *Y. padellus* and sympatric speciation is a likely event.

KEY WORDS: Allozyme variation — Lepidoptera — *Yponomeuta padellus* — evolutionary stages — F -statistics — panmixis.

Modes of speciation have long been a source of disagreement among evolutionary biologists. Some entomologists, such as Brues (1924), Thorpe (1930, 1945) and Smith (1941) supported the idea that in phytophagous insects adaptation to a new plant species may occur within the distribution area of the population and that the new host race may diverge to become a distinct species. This model of sympatric speciation was strongly criticised by Mayr (1942, 1947), who stressed the necessity of geographic isolation, followed by the accumulation of genetic differences, as a prerequisite for speciation in all groups of sexually reproducing animals (allopatric speciation). Although many supposed examples of sympatric host races have turned out to be cases of sibling species (possibly originating allopatrically), evidence is now accumulating that not all apparent cases of biological races are of this type. Data from a variety of taxa are most simply explained in the context of sympatric speciation (e.g. Chalcidoidea: Askew, 1968; *Rhagoletis*: Bush, 1969, 1975; *Chrysopa*: Tauber & Tauber, 1977a, b; Geospizinae: Grant & Grant, 1979; *Megarhysa*: Gibbons, 1979).

Since the study of speciation is a *post hoc* science, we have to investigate different evolutionary levels of the speciation process in extant groups of organisms. Species of the small ermine moths (*Yponomeuta*, Lepidoptera) offer the opportunity to study various steps in a speciation process (Wiebes, 1976; Herrebout *et al.*, 1976; Gerrits-Heybroek *et al.*, 1978). The five morphologically very similar members of the *padellus*-complex were considered by Friese (1960) as one polytypic species (*Y. padellus*), by Thorpe (1929) as host races and by Gershenson (1974) as full species. Studies on hybridisation levels in nature based on diagnostic allozyme characters lead to the conclusion that all are genuine biological species (Menken, 1980). Two species in the *padellus*-complex, namely *Y. padellus* and *Y. rorellus*, are oligophagous, the remaining three are strictly monophagous.

The objective of the present paper is to quantify genetic differences at various levels of evolutionary divergence in *Yponomeuta* and to investigate whether sympatric populations of *Y. padellus* on its various food plants represent freely interbreeding populations or host races *sensu* Mayr *et al.* (1953): "noninterbreeding sympatric populations, which differ in biology, but not, or scarcely, in morphology . . . prevented from interbreeding by preferences for different food plants or other hosts".

MATERIALS AND METHODS

Y. padellus was reared from *Crataegus* (mainly

¹ Present address: Department of Animal Systematics and Zoogeography, Free University, De Boelelaan 1087, 1007 MC Amsterdam, The Netherlands.

C. monogyna), *Prunus spinosa*, *P. domestica*, *P. cerasifera*, *Amelanchier* sp. and *Sorbus aucuparia*. Storage of specimens and electrophoretic methods have been described in Menken (1981) and allele (electromorph) designation in Menken *et al.* (1980).

Nei's (1971, 1972) measures of genetic identity (*I*) and genetic distance (*D*) were used to compare the genetic constitution of a pair of populations. In addition, Wright's (1943, 1951, 1965) coefficient of inbreeding (*F_{ST}*) was used as a standardised measure of the genetic differentiation of a certain number of polymorphic loci over a set of populations of *Y. padellus* (formulae in Menken *et al.*, 1980).

Only adults were used in this study, except for the computation of overall estimates of *I* and *D*, where information from larvae and adults was combined. Inbreeding coefficients were computed for the following five enzyme loci that are polymorphic in all or most of the populations studied (locus abbreviations in parentheses): hydroxybutyrate dehydrogenase (*Hbdh*), malic enzyme (*Me*), phosphoglucomutase (*Pgm*), phosphoglucose isomerase (*Pgi*) and a general protein (*Pt-1*). In addition, a maximum of another five polymorphic loci were used to quantify differences between certain sympatric populations of *Y. padellus* on different host plants: fucose dehydrogenase (*Fudh*), α -glycerophosphate dehydrogenase (α -*Gpdh*), isocitrate dehydrogenase NADP-dependent (*Idh-NADP*), malate dehydrogenase (*Mdh-1*) and glutamic-oxaloacetic transaminase (*Got-2*). These loci were used only when they were found to be polymorphic in at least one host race.

RESULTS

To measure the amount of genetic change at different stages of evolutionary divergence, Nei's (1971, 1972) estimates of genetic identity and distance were calculated for pairs of conspecific populations, sibling species and mor-

phologically well-distinguishable species (Table I). Identity for conspecific populations is high compared to several other species that have been examined (e.g. Ayala *et al.*, 1974; Ayala, 1975; Brittnacher *et al.*, 1978). Identity values range from .977 for *Y. vigintipunctatus*, which is the most locally differentiated of the nine *Yponomeuta* species studied, to 1.000 for *Y. rorellus*, which exhibits an extremely low level of allozyme polymorphism (Menken, 1981). The other two evolutionary levels cover a wide range of *I* and *D* values (Table I). There is a considerable overlap in *I* and *D* ranges between sibling and non-sibling species. For the greater part this is caused by *Y. evonymellus*, which is morphologically easily distinguished from, yet allozymically closely related to *Y. cagnagellus*, *Y. malinellus* and *Y. padellus* (Menken, 1981). The latter two species are genetically very similar to each other ($.962 < I < .989$) and their range in *I* broadly overlaps the range of conspecific populations of these two species separately ($.978 < I < .997$).

Populations of *Y. padellus* occur on various host plants (Table II); they possibly represent host races, which may be considered the first step in a sympatric speciation process. *I* and *D* estimates are based on summation over both polymorphic and monomorphic loci. When monomorphic loci predominate and are fixed for the same allele, *I* and *D* estimates are rather insensitive, as in conspecific populations of *Yponomeuta* (Menken *et al.*, 1980). In addition, due to the inability to detect all amino acid substitutions with electrophoresis, absolute *I* values are overestimates and consequently *D* values underestimates. Therefore, to study the genetic structure of the populations of *Y. padellus* (Table II), *F_{ST}* values for five polymorphic enzyme loci were computed. The results are summarised in Table III for each of the years 1976 to 1979. In these Tables *F_{ST}* values are given for all food plants com-

TABLE I

Mean and range of genetic identity (*I*) and distance (*D*) estimates for three levels of evolutionary divergence in *Yponomeuta*. Estimates for conspecific populations based on sets of 28–51 loci per comparison, those for the other two levels on 51 loci (data from Menken, 1981).

Evolutionary level	Number of comparisons	$\bar{I}$	(range)	$\bar{D}$	(range)
Conspec. populations	24	.994 $\pm$.005	1.000 – .977	.006 $\pm$.005	.000 – .023
Sibling species	10	.821 $\pm$.090	.980 – .639	.203 $\pm$.112	.021 – .447
Non-sibling species	26	.368 $\pm$.279	.864 – .080	1.331 $\pm$.875	.146 – 2.522

TABLE II

Sampling localities of *Y. padellus* per host plant species in The Netherlands (unless otherwise stated) from 1976-1979, with respective numbers of individuals investigated electrophoretically (N). ¹Combined samples (see Table VI and Discussion)

Host plant species and sampling locality	N			
	1976	1977	1978	1979
1. On <i>Crataegus</i>				
Meijendel	50	50	50	—
Vogelenzang-Zuid	50	50	25	—
Vierlingsbeek	50	50	25	40
Domat (Switzerland)	50	—	—	—
Hartheim (Germany)	—	50	—	—
Zuidoostbeemster	—	—	38	75 ¹
St. Agatha	—	—	18	—
Bayreuth (Germany)	—	—	—	20
2. On <i>P. spinosa</i>				
Lienden	17	50	25	—
Vierlingsbeek	—	—	25	34
Istein (Germany)	—	50	—	—
Bayreuth (Germany)	—	—	—	20
3. On <i>P. domestica</i>				
Domat (Switzerland)	50	—	—	—
"Valais" (Switzerland)	—	25	—	—
Wijdenes	—	—	25	—
4. On <i>P. cerasifera</i>				
Zuidoostbeemster	111	50	50	91 ¹
5. On <i>Amelanchier</i>				
Oosthuizen	—	—	25	—
6. On <i>S. aucuparia</i>				
Helsinki (Finland)	—	—	—	20

bined and for populations on *Crataegus* and on non-*Crataegus* host plants (lumped). For each locus the average sample size per collection ($\bar{n}$), the weighted mean frequency ($\bar{p}$) and the values of the standardised variance (F_{ST}) are given together with the probability levels for the individual χ^2 tests of $F_{ST} = 0$.

Considering the F_{ST} values for populations on all food plants combined, no locus is homogeneous nor significantly heterogeneous in all years. In spite of the inconsistent pattern in time for each locus the mean F_{ST} over five loci is remarkably constant for 1976-1978 ($\bar{F}_{ST} = .021, .026$ and $.025$, respectively), although the geographic range in 1978 is restricted to The Netherlands (Table II) and a lower value compared with 1976 and 1977 would be expected (Menken *et al.*, 1980). The geographic range within each year is more or less the same for populations sampled from *Crataegus* and from non-*Crataegus*, except for 1979 (Ta-

ble II). The F_{ST} for 1979, where a wide geographic area was studied, is .047; this high value is mainly due to aberrant allele frequencies in the population from Helsinki (Finland) on *S. aucuparia*.

Comparison of populations on *Crataegus* with those on the five other host plants shows that in the former, allozymes are much more homogeneously distributed than in the latter (Table III). *Pgm*, *Pgi* and *Hbdh* are all homogeneously distributed among populations sampled from *Crataegus* in the 4 years. Only *Me* in 1979 and *Pt-1* in 1977 and 1979 exhibit F_{ST} values significantly different from zero ($P < .05$, $< .01$ and $< .05$, respectively). This results in low mean F_{ST} values (.007, .012, .009 and .021, respectively; grand mean $F_{ST} = .012 \pm .006$). On the contrary, a discontinuous pattern of allozyme variation occurs in the populations sampled from non-*Crataegus* host plants. At least two out of five loci show statis-

TABLE III

Individual values of standardised variance (F_{ST}), mean sample size per collection ($\bar{n}$) and weighted mean frequency ($\bar{p}$) for five polymorphic enzyme loci in populations of *Y. padellus* for samples from all food plants combined, from *Crataegus* and from non-*Crataegus*, respectively. Probability levels for individual χ^2 tests of $F_{ST} = 0$ also given * $P < .05$, ** $P < .01$, and *** $P < .001$.

a. Populations sampled in 1976: *Crataegus* (4), *P. spinosa* (1), *P. domestica* (1) and *P. cerasifera* (1).

Locus	$\bar{p}$	F_{ST}
1976 (7 collections); $\bar{n} = 54$, except <i>Pt-I</i> , $\bar{n} = 47$		
<i>Pgm</i>	.542	.011
<i>Pgi</i>	.639	.019*
<i>Hbdh</i>	.810	.041***
<i>Me</i>	.758	.015
<i>Pt-I</i>	.925	.019*

Mean: $.021 \pm .012$

Crataegus (4 coll.); $\bar{n} = 50$,
except *Pt-I*, $\bar{n} = 49$

<i>Pgm</i>	.575	.010
<i>Pgi</i>	.625	.000
<i>Hbdh</i>	.767	.005
<i>Me</i>	.750	.017
<i>Pt-I</i>	.953	.003

Mean: $.007 \pm .007$

Non-*Crataegus* (3 coll.); $\bar{n} = 59$,
except *Pt-I*, $\bar{n} = 44$

<i>Pgm</i>	.506	.002
<i>Pgi</i>	.655	.038**
<i>Hbdh</i>	.859	.064***
<i>Me</i>	.767	.012
<i>Pt-I</i>	.886	.006

Mean: $.024 \pm .026$

b. Populations sampled in 1977: *Crataegus* (4), *P. spinosa* (2), *P. domestica* (1) and *P. cerasifera* (1).

1977 (8 collections); $\bar{n} = 47$		
<i>Pgm</i>	.473	.013
<i>Pgi</i>	.711	.031**
<i>Hbdh</i>	.787	.017
<i>Me</i>	.721	.014
<i>Pt-I</i>	.877	.057***

Mean: $.026 \pm .019$

Crataegus (4. coll.); $\bar{n} = 50$

<i>Pgm</i>	.475	.004
<i>Pgi</i>	.692	.008
<i>Hbdh</i>	.797	.015
<i>Me</i>	.727	.005
<i>Pt-I</i>	.933	.030**

Mean: $.012 \pm .011$

Non-*Crataegus* (4 coll.); $\bar{n} = 44$

<i>Pgm</i>	.471	.024*
<i>Pgi</i>	.731	.056***
<i>Hbdh</i>	.744	.016
<i>Me</i>	.714	.023*
<i>Pt-I</i>	.814	.024*

Mean: $.029 \pm .016$

c. Populations sampled in 1978: *Crataegus* (5), *P. spinosa* (2), *P. domestica* (1), *P. cerasifera* (1) and *Amelanchier* (1).

1978 (10 collections); $\bar{n} = 31$		
<i>Pgm</i>	.472	.032*
<i>Pgi</i>	.670	.017
<i>Hbdh</i>	.799	.033*
<i>Me</i>	.718	.021
<i>Pt-I</i>	.888	.021

Mean: $.025 \pm .007$

Crataegus (5 coll.); $\bar{n} = 31$

<i>Pgm</i>	.426	.016
<i>Pgi</i>	.667	.007
<i>Hbdh</i>	.776	.017
<i>Me</i>	.707	.005
<i>Pt-I</i>	.854	.002

Mean: $.009 \pm .007$

Non-*Crataegus* (5 coll.); $\bar{n} = 30$

<i>Pgm</i>	.520	.030
<i>Pgi</i>	.673	.028
<i>Hbdh</i>	.823	.046**
<i>Me</i>	.730	.038*
<i>Pt-I</i>	.923	.021

Mean: $.033 \pm .010$

d. Populations sampled in 1979: *Crataegus* (3), *P. spinosa* (2), *P. cerasifera* (1) and *S. aucuparia* (1).

1979 (7 collections); $\bar{n} = 29$, except *Pt-I*,
 $\bar{n} = 27$

<i>Pgm</i>	.472	.042**
<i>Pgi</i>	.692	.055***
<i>Hbdh</i>	.767	.035*
<i>Me</i>	.700	.062***
<i>Pt-I</i>	.890	.039*

Mean: $.047 \pm .011$

Crataegus (3 coll.); $\bar{n} = 28$

<i>Pgm</i>	.423	.001
<i>Pgi</i>	.758	.000
<i>Hbdh</i>	.706	.017
<i>Me</i>	.759	.041*
<i>Pt-I</i>	.876	.047*

Mean: $.021 \pm .022$

Non-*Crataegus* (4 coll.); $\bar{n} = 29$, except
Pt-I, $\bar{n} = 27$

<i>Pgm</i>	.509	.060**
<i>Pgi</i>	.644	.064**
<i>Hbdh</i>	.813	.023
<i>Me</i>	.656	.056**
<i>Pt-I</i>	.901	.028

Mean: $.046 \pm .019$

tically significant variation per year; no single locus, however, is heterogeneous in all years studied. Mean F_{ST} values are 2—3.5 times as large as those for populations feeding on *Crataegus* ($\bar{F}_{ST} = .024, .029, .033$ and $.046$, respectively; grand mean $F_{ST} = .033 \pm .009$). The grand mean F_{ST} over all populations and all years for *Y. padellus* equals $.030 \pm .012$, very similar to *Y. cagnagellus* ($.027 \pm .013$; Menken *et al.*, 1980).

Four areas with sympatric populations of *Y. padellus* on two different food plants were investigated for host race formation, as measured by differentiation of allozyme variation, using the *G*-test for homogeneity (Sokal & Rohlf, 1969; Menken *et al.*, 1980). Two such areas are located in The Netherlands and were studied over a period of several years, namely Vierlingsbeek (populations on *Crataegus* and *P. spinosa*) and Zuidoostbeemster (populations on *Crataegus* and *P. cerasifera*). The results are shown in Tables IVa and b, respectively. In Vierlingsbeek only one locus out of seven studied shows statistically significant heterogeneity (*Pt-1* in 1978). In Zuidoostbeemster, however, four loci (*Pgm*, *Pgi*, *Idh-NADP* and α -*Gpdh*) in 1978 and two loci (*Pgi* and *Hbdh*) in 1979 out of eight are significantly heterogeneous.

The two other areas are located in Switzer-

land (Domat, sampled in 1976, with populations on *Crataegus* and *P. domestica*) and Germany (Bayreuth, sampled in 1979, with populations on *Crataegus* and *P. spinosa*). From Table V it can be seen that half the loci show significantly different allozyme frequency distributions for the two populations in both localities. Most conspicuous is the absence of allele *Hbdh*¹⁰² from the population on *P. domestica* in Domat.

DISCUSSION

Genetic differences accumulate as speciation proceeds as a consequence of adaptation to different environments together with chance factors (Zouros, 1973; Avise & Smith, 1977). However, the bulk of genetic divergence that is observed between both sibling and non-sibling species appears through phyletic change only after reproductive isolation has been as-

TABLE IVa

Allele frequencies at 7 enzyme loci in 2 sympatric populations of Y. padellus collected from Crataegus and P. spinosa in Vierlingsbeek. Probability levels (G-test) for homogeneity in 1978 (G⁷⁸) and 1979 (G⁷⁹) with numbers of degrees of freedom in parentheses. Significance levels as in Table III.

Locus	Year No. moths	<i>Crataegus</i>					<i>P. spinosa</i>		G ⁷⁸	G ⁷⁹
		1975 50	1976 50	1977 50	1978 25	1979 40	1978 25	1979 34		
<i>Pgm</i>	Allele									
	94		.03	.01	.02	-	-	-		
	97		.14	.10	.06	.10	.08	.03		
	98.5		.03	.02	.10	.09	.06	.20		
	100		.53	.50	.38	.44	.40	.37	.06	3.62
	101.5		.08	.11	.08	.14	.06	.24	(2)	(2)
<i>Pgi</i>	103		.15	.26	.32	.22	.30	.14		
	105		.04	-	.04	.01	.10	.02		
	90		.01	-	-	-	-	-		
	93		.34	.28	.34	.24	.36	.35	.05	2.37
	100		.61	.72	.66	.76	.64	.65	(1)	(1)
	103.5		.04	-	-	-	-	-		
<i>Hbdh</i>	98		.02	-	-	-	.02	-		
	100		.79	.75	.80	.74	.80	.75	1.59	.03
	102		.19	.25	.20	.26	.14	.25	(1)	(1)
	104		-	-	-	-	.04	-		
<i>Me</i>	98	.22	.22	.30	.28	.25	.38	.26	1.13	.16
	100	.76	.78	.70	.72	.75	.62	.72	(1)	(1)
	102	.02	-	-	-	-	-	.02		
<i>Pt-1</i>	98	.90	.95	1.00	.86	.92	1.00	.90	5.45*	.36
	100	.10	.05	-	.14	.08	-	.10	(1)	(1)
<i>Idh-NADP</i>	98		.10	.07	.02	.04	-	-	1.09	.77
	100		.90	.93	.94	.96	1.00	1.00	(1)	(1)
	104		-	-	.04	-	-	-		
α - <i>Gpdh</i>	95		.05	.04	.08	-	-	-	2.02	
	100		.95	.96	.92	1.00	1.00	1.00	(1)	

TABLE IVb

Allele frequencies in two sympatric populations of *Y. padellus* sampled from *Crataegus* and *P. cerasifera* in Zuidoostrbeemster. *G*-tests as in Table IVa.

Locus	Year No. moths	<i>Crataegus</i>		<i>P. cerasifera</i>					<i>G</i> ⁷⁸	<i>G</i> ⁷⁹
		1978 38	1979 75	1975 50	1976 111	1977 50	1978 50	1979 91		
<i>Pgm</i>	Allele									
	97	.04	.01		.06	.06	.08	.02		
	98.5	.07	.13		.08	.04	.08	.09		
	100	.42	.43		.52	.52	.56	.54	15.28**	7.80
	101.5	.22	.21		.07	.09	.16	.12	(3)	(3)
	103	.24	.19		.27	.29	.06	.21		
<i>Pgi</i>	105	.01	.01		-	-	.06	.02		
	85	-	-		.03	-	-	-		
	93	.36	.29		.23	.15	.22	.46	3.91*	10.78**
	100	.64	.71		.72	.85	.78	.54	(1)	(1)
<i>Hbdh</i>	105	-	-		.02	-	-	-		
	95	-	.02		-	-	-	-		
	98	-	-		.02	.01	.01	-	2.59	6.41*
	100	.80	.71		.80	.84	.89	.83	(1)	(1)
<i>Me</i>	102	.20	.27		.18	.15	.10	.17		
	98	.33	.35	.35	.26	.25	.31	.29		
	100	.67	.65	.64	.74	.75	.69	.71	.07	1.17
<i>Pt-1</i>	102	-	-	.01	-	-	-	-	(1)	(1)
	98	.84	.90		.87	.85	.89	.88	.86	.36
<i>Idh-NADP</i>	100	.16	.10		.13	.15	.11	.12	(1)	(1)
	98	.07	.03		-	-	-	.01		
	100	.93	.97		.99	1.00	1.00	.99	4.26*	2.01
<i>Got-2</i>	102	-	-		.01	-	-	-	(1)	(1)
	92	-	.02		-	-	-	-		
	95	-	-		.01	-	-	-		1.49
<i>α-Gpdh</i>	100	1.00	.98		.99	1.00	1.00	1.00		(1)
	93	-	-	.02	-	.02	.02	.01		
	95	-	.03	.07	.06	.08	.06	-	4.65*	2.01
	100	1.00	.97	.91	.94	.90	.92	.99	(1)	(1)

sured ("the point of no return"). Dependent on their "age", good biological species within a genus cover a wide range of genetic distances: from .035 in the pupfish genus *Cyprinodon* (Turner, 1974) to 2.522 in *Yponomeuta* (Menken, 1981) and 2.816 in Hawaiian *Drosophilids* (Ayala, 1975). As was found with a number of organisms such as *Drosophila* (Ayala *et al.*, 1974) and *Peromyscus* (Zimmerman *et al.*, 1978), sibling species in *Yponomeuta* are more alike than are non-siblings (Table I). On the contrary, *Capitella capitata* (Polychaeta) appears to be a complex of as many as six sibling species that have almost no allozymes in common (Grassle & Grassle, 1976). Calculation of genetic divergence at several evolutionary stages does not give much insight into the amount of change during the speciation pro-

cess itself (Bush, 1975; White, 1978).

Studies of allozyme variation have not confirmed the theory of a "genetic revolution" accompanying speciation (Mayr, 1963; Dobzhansky, 1970). For instance, probably all five species belonging to the *padellus*-complex of the small ermine moths represent genuine biological (sibling) species (Menken, 1980), yet their genetic distances range from as low as .021 to .447 (Table I). Mayr's theory of a "genetic revolution" was a logical consequence of the way he thought about speciation: in geographically isolated populations genetic differences accumulate up to the point where they have developed sufficiently strong genetic isolating mechanisms to keep them apart when contact is re-established (allopatric or geographic speciation). So populations will evolve

TABLE V

Allele frequencies in sympatric populations of Y. padellus. Left: collected from Crataegus and P. domestica in Domat (Switzerland) in 1976. Right: collected from Crataegus and P. spinosa in Bayreuth (Germany) in 1979. G-tests as in Table IVa. ¹ Sex-linked: numbers of alleles 84 and 80, respectively.

Locus	No. moths	Domat (Switzerland)			Bayreuth (Germany)		
		<i>Crataegus</i> 50	<i>P. domestica</i> 50	G	<i>Crataegus</i> 20	<i>P. spinosa</i> 20	G
<i>Pgm</i>	Allele						
	94	.01	.04		-	-	
	95.5	-	-		.05	.10	
	97	.08	.06		-	-	
	98.5	.05	.06	4.69	.13	-	2.70
	100	.62	.47	(2)	.40	.42	(2)
	101.5	.01	.07		.35	.20	
	103	.23	.30		.07	.13	
<i>Pgi</i>	105	-	-		-	.15	
	93	.35	.47		.25	.53	
	100	.63	.51	3.03	.75	.47	6.48*
	103.5	.02	-	(2)	-	-	(1)
<i>Hbdh</i>	106.5	-	.02		-	-	
	95	-	-	23.09***	.08	-	1.91
	100	.80	1.00	(1)	.60	.75	(2)
<i>Me</i>	102	.20	-		.32	.25	
	98	.33	.16	7.95**	.10	.38	8.78**
<i>Pt-1</i>	100	.67	.84	(1)	.90	.62	(1)
	98	.97	.93	1.73	.75	.87	2.08
<i>Idh-NADP</i>	100	.03	.07	(1)	.25	.13	(1)
	98	.11	.02	3.66	.03	.20	6.89**
	100	.89	.96	(1)	.97	.80	(1)
<i>Mdh-1</i>	103	-	.02		-	-	
	100	1.00	.94	4.09*			
<i>Fudh¹</i>	106	-	.06	(1)			
	95.5	-	.02				
	97	.85	.95	5.09*			
	98.5	.10	-	(1)			
	100	.05	.03				

into different species when the period of isolation is long enough (Mayr, 1963). In contrast, there is now good evidence that new host races of phytophagous insects have arisen sympatrically on introduced and native plants in the United States (Bush, 1969; Phillips & Barnes, 1975). The importance of sympatric speciation is difficult to estimate at the moment, because of the paucity of detailed studies on phytophagous and zoophagous parasites and parasitoids. If it is important, we should be able to find significantly different allele frequencies for one or a number of enzyme loci in sympatric populations on different food plants. This will indicate that gene flow is reduced or even absent, especially when discontinuities continue to be found over a number of years. In localities

where the two host races are fixed for different alleles (a diagnostic locus), complete absence of gene flow is likely to occur and we can consider them as two separate species.

Y. padellus is associated with various host plants (Table II) and the properties of its genetic system indicate that it is a candidate for sympatric speciation (Bush, 1975; Herrebut *et al.*, 1976). Using inbreeding coefficients (F_{ST} ; Table IIIa, b, c and d) it was found that per year the mean F_{ST} over five loci was 2—3.5 times as large for *Y. padellus* feeding on plants other than *Crataegus* as for those feeding exclusively on *Crataegus*. Although mean F_{ST} values are quite constant, single locus values do not show consistent patterns in time in all populations of *Y. padellus* together, nor in

populations on *Crataegus*, nor on non-*Crataegus*. Such inconsistent patterns were also observed for *Y. cagnagellus* (Menken *et al.*, 1980). Single locus F_{ST} has a large variance due to genetic drift, when the number of subpopulations is small (Nei & Chakravarti, 1977). Therefore, it is necessary to study population differentiation by means of a F_{ST} averaged over a number of loci.

There are at least five, mutually not exclusive, reasons that can account for the higher degree of differentiation in populations on non-*Crataegus* host plants. 1) Gene exchange may be more restricted between non-*Crataegus* feeders and hence more differences are allowed to accumulate between them. Since very little is known of migration in *Yponomeuta* this cannot be tested with the data available. 2) Populations on *Crataegus* have in general large

er population sizes, so less genetic drift will occur. However, populations on *P. spinosa* and *P. domestica* often seem to be as large as those on *Crataegus*. 3) All non-*Crataegus* hosts were colonised very recently. After such a bottleneck heterozygosity (H) levels are greatly reduced on the new hosts and genetic divergence increases (Chakraborty & Nei, 1977). No significant differences in H levels were observed, but the smallest H values belong to populations on non-*Crataegus* food plants. It is, however, unlikely that populations on non-*Crataegus* represent only recent colonisations. 4) Co-adapted gene complexes differ on different food plants (see Menken *et al.*, 1980 for a discussion on the influences of gene flow and selection on patterns of allozyme distribution). 5) Differential survival on different host plants leads to differences in allozyme frequencies in

TABLE VI

Allele frequencies in two Y. padellus samples collected from Crataegus and P. cerasifera (Zuidoostrbeemster) and reared on different food plants to test whether differences in allele frequencies occurred due to differential survival (G-test for homogeneity).

Locus	No. moths Allele	Collected from <i>Crataegus</i> Reared on			G	Collected from <i>P. cerasifera</i> Reared on			G
		<i>Crat.</i> 25	<i>P. cer.</i> 25	<i>S. auc.</i> 25		<i>P. cer.</i> 41	<i>P. dom.</i> 25	<i>Crat.</i> 25	
<i>Pgm</i>	97	.02	-	.02	3.24 (6)	.04	.02	-	2.46 (4)
	98.5	.10	.16	.14		.07	.10	.10	
	100	.42	.48	.40		.57	.56	.48	
	101.5	.28	.16	.20		.09	.08	.20	
	103	.16	.18	.24		.21	.24	.20	
	105	.02	.02	-		.02	-	.02	
<i>Pgi</i>	93	.24	.28	.34	1.24	.39	.48	.54	2.97
	100	.76	.72	.66	(2)	.61	.52	.46	(2)
<i>Hbdh</i>	95	-	-	.06	.45 (2)	-	-	-	1.62 (2)
	100	.74	.68	.72		.87	.78	.84	
	102	.26	.32	.22		.13	.22	.16	
<i>Me</i>	98	.34	.38	.32	.41	.27	.24	.38	2.69
	100	.66	.62	.68	(2)	.73	.76	.62	(2)
<i>Pt-1</i>	98	.90	.86	.94	1.82	.86	.88	.92	1.06
	100	.10	.14	.06	(2)	.14	.12	.08	(2)
<i>Idh-NADP</i>	98	.10	.08	.02	3.29	.01	-	.04	1.05
	100	.90	.92	.98	(2)	.99	1.00	.96	(2)
<i>Got-2</i>	92	-	.02	.04	.48	-	-	-	
	100	1.00	.98	.96	(2)	1.00	1.00	1.00	
α - <i>Gpdh</i>	93	-	-	-	1.54 (2)	.02	-	-	.04 (2)
	95	-	.06	.02		-	-	-	
	100	1.00	.94	.98		.98	1.00	1.00	
% survival		73.2	92.7	85.5		92.7	86.3	91.8	

an effectively panmictic population. To investigate this, samples of L_4 and L_5 larvae from *Crataegus* and *P. cerasifera* (both originating from Zuidooostbeemster in 1979) were each divided into three groups of 110 larvae, reared on their own food plant and two other food plants and allele frequencies of the emerging adults were tested for homogeneity (Table VI). None of the G values approaches significance and therefore mean frequencies over the three food plants are given in Table IVb. Percentage survival of the cross-reared samples (Table VI) are similar. The low value of 73.2% for *Crataegus* larvae reared on their own food plant is exceptionally low; normally this value is about 90% (T. van der Water, pers. comm.). It can be seen that in the life stages examined no differential selection occurred on *Crataegus* and *P. cerasifera*. It is possible, however, that selection takes place in earlier life stages. T. van der Water (pers. comm.) did not find viability differences between specimens, originating from several food plants and reared on the various food plants. Moreover, it is feasible that adults differ in fitness (e.g. mating success or fecundity). Remarkably *P. spinosa* seems to be the optimal food plant for *Y. padellus* (as measured by pupal weight and % of moths emerging: Gerrits-Heybroek *et al.*, 1978). Whether *P. spinosa* is the host-of-origin instead of *Crataegus* is not testable here.

Detection of host races at localities where allozyme differentiation is not very pronounced (Vierlingsbeek and to a lesser extent Zuidooostbeemster) is more conclusive when differences continue to be found over a number of genera-

tions (i.e. years in *Y. padellus*). Alleles specific for the population on one host are especially useful in giving information on the amount of gene flow between the hosts. As host-specific alleles always occur in low frequencies in Vierlingsbeek and Zuidooostbeemster, such an allele may be apparently absent from the population simply due to sampling error. Table VII lists the probabilities of not detecting a rare allele due to sampling error for the instances discussed below, assuming that the two host races are simply groups within an interbreeding population. For example, in Vierlingsbeek allele α -Gpdh⁹⁵ only occurs on *Crataegus* (1976–1978); unfortunately this allele is absent from the 1979 sample (Table IVa). *Idh-NADP*⁹⁸ is completely restricted to *Crataegus*. Differential survival is possible, although this allele normally occurs elsewhere on *P. spinosa* (Table V) and is present in most populations of *Y. padellus* studied so far. Allele α -Gpdh⁹³ is specific for the population on *P. cerasifera* in Zuidooostbeemster (Table IVb) and has never been found elsewhere in *Y. padellus*. It occurs at a very low frequency and appears to be absent in 1976, possibly due to sampling error ($P = .011$, if the real frequency is .02). The absence of α -Gpdh⁹⁵ in 1979 from *P. cerasifera* is less easily to explain by sampling error, in view of the sample size ($N = 91$) and the frequencies in the other years (.06–.08; $P < .001$, if the real frequency is .07). *Idh-NADP*⁹⁸ in Zuidooostbeemster occurs only on *Crataegus* and not on *P. cerasifera* until 1979 where it appears at a very low frequency (Table IVb). The reverse situation holds for α -Gpdh⁹⁵,

TABLE VII

Probability (P) of not detecting a rare allele in one host race with given sample size (n : twice the number of moths), assuming the rare allele frequency (q) is the observed frequency in the other host race in the same generation, for the four localities studied, with $P = (1 - q)^n$.

Locality	Year	Allele	n	q	P
Vierlingsbeek	1978	α -Gpdh ⁹⁵	50	.08	.015
	1978	<i>Idh-NADP</i> ⁹⁸	50	.02	.364
	1979		68	.04	.062
Zuidooostbeemster	1978	α -Gpdh ⁹³	76	.02	.215
	1979		150	.01	.221
	1978	α -Gpdh ⁹⁵	76	.06	.009
	1979		182	.03	.004
	1978	<i>Idh-NADP</i> ⁹⁸	100	.07	.001
Domat	1976	Hbdh ¹⁰²	100	.20	<< .001
Bayreuth	1979	Pgm ^{98.5}	40	.13	.004
		Pgm ¹⁰⁵	40	.15	.002

which possibly cannot survive on *Crataegus* (see above; Table VI). The lower degree of substructuring and the appearance of *Idh-NADP*⁹⁸ on *P. cerasifera* in 1979 warrants the supposition that at present the two host races are fusing in Zuidoostbeemster.

These data are in accordance with the findings of Gerrits-Heybroek *et al.* (1978), who found that specimens reared from *Crataegus* and *P. cerasifera* differed in their host preferences; T. van der Water (pers. comm.), however, did not observe such differences between individuals sampled in 1979. It seems that isolation is breaking down. The lack of statistically significant heterogeneity in allele frequencies in Vierlingsbeek as opposed to Zuidoostbeemster is not due to the smaller sample sizes in the former. The genetic distance between the host races, based on an identical set of 21 enzyme loci, in Vierlingsbeek is half that in Zuidoostbeemster in 1978 (.003 and .006, respectively) and two-thirds in 1979 (.002 and .003, respectively).

There is some circumstantial evidence that presence of the host plant is connected with sexual activity in the female, suggesting that mating takes place exclusively upon the actual host plant (W. M. Herrebout, pers. comm.).

Genetic subdivision of the populations in the two localities outside The Netherlands (Table V) is much more pronounced; the populations were sampled only once. Apart from statistically significant frequencies, some alleles occur on one host plant in appreciable frequencies, but are absent from the other. Most conspicuous in this respect are allele *Hbdh*¹⁰² in Domat which occurs with a frequency of .20 on *Crataegus*, but is absent from *P. domestica*, and alleles *Pgm*^{98.5} and ¹⁰⁵ in Bayreuth which each occur only in one population (frequencies .13 and .15, respectively). It is highly improbable ($P < .001$) that allele *Hbdh*¹⁰² will not be detected in the sample from *P. domestica* in the absence of host-specific selection, assuming that individuals on *Crataegus* and *P. domestica* comprise a panmictic unit. Even if the real frequency is .10 or .05 it remains highly improbable that this allele will not be detected ($P < .001$ and $P = .006$, respectively).

It can be concluded that sympatric specimens of *Y. padellus* on different food plants do not always comprise a panmictic unit, that is to say they form host races. Host races are not to be regarded as species, although they may be incipient ones, since they have not yet reached

the "point of no return". Sympatric speciation by host race formation is a likely event in *Y. padellus*. All other *Yponomeuta* species from Western Europe are strictly monophagous (Gerrits-Heybroek *et al.*, 1978), with the exception of *Y. rorellus* which attacks a number of *Salix* species. Studying host race formation with allozymes is, unfortunately, very difficult in this species as *Y. rorellus* is almost completely monomorphic (Menken, 1981). Only one locus (glyceraldehyde-3-phosphate dehydrogenase) differs markedly from population to population. Strictly speaking, allozyme analysis as employed in this study provides little information on host race formation, but rather host race existence: it describes the current state of a dynamic process without explaining the driving forces behind the process.

Several examples of host races are known from the literature. Host range evolution and consequently speciation may proceed very rapidly in insect pest species (Zimmerman, 1960; Bush, 1974). Gould (1979) found that rapid adaptation to a new host occurred together with a reduction of fitness on the host to which it was previously well adapted. Host race formation has probably occurred many times in certain groups within the Tephritidae (Bush, 1969, 1974, 1975). Phillips & Barnes (1975) found host-determined races in populations of *Laspheyresia pomonella* on three host plants. More examples are given in White (1978). On the other hand, among sexually reproducing species of some forest Lepidoptera no host race formation was observed, but some evidence of genetic substructuring was found in the moth *Melanolophia canadaria* (Mitter & Futuyma, 1979) and in the parthenogenetic forms of *Alsophila pometaria* (Mitter *et al.*, 1979). Also the red-headed form of *Hyphantria cunea* is not composed of host races (Jaenike & Selandier, 1980) and Sluss and Graham (1979) could not identify host races of *Heliothis virescens* on three host plants.

No host-specific alleles were found in *Y. padellus*, except for α -*Gpdh*⁹³, unique for the population on *P. cerasifera*. The appearance of alleles *Got*-2⁹² and *Hbdh*⁹⁵ in 1978 on *Crataegus* in the Zuidoostbeemster (Tables IVb and VI), is probably due to new mutations, since they have never before been observed in a population of *Y. padellus* or possibly to sampling error.

Within the small ermine moths species studied, no correlation was found between hetero-

zygosity (H) and breadth of diet (Menken, 1981). *Y. evonymellus*, strictly monophagous, exhibits a slightly higher H level (.111—.136) than *Y. padellus* (.091—.128), while other monophagous species have mostly much lower H values (.047—.129); *Y. rorellus*, although feeding on various *Salix* species has the lowest values (.000—.009). The finding of Mitter & Futuyma (1979) that H and diet-breadth are negatively correlated is at variance with that of Berlocher (1976) and Sluss & Graham (1979) who found a positive correlation.

Differences in sexual pheromones may act as a primary isolating factor in Lepidoptera (e.g. Roelofs & Comeau, 1969; Roelofs and Cardé, 1974; for *Yponomeuta* see Van der Pers & Den Otter, 1978; Hendrikse, 1979), although Shorey (1970) considered it more likely that changes in pheromone specificity would follow speciation rather than take part in it. Sympatric populations of *Ostrinia nubilalis*, the European corn borer, represent two pheromone strains that differ significantly in allele frequencies at four enzyme loci (Harrison & Vawter, 1977). They evidently do not form a panmictic unit (Cardé *et al.*, 1978).

In conclusion, it is thought likely that populations of *Y. padellus* are broken up into host races. Host race formation occurs on trees (e.g. *Crataegus* and *Prunus* species); this seems to be an essential factor as the high level of resource predictability ensures utilisation by the insect each generation (Jaenike & Selander, 1979).

I thank G. Heusinger (Bayreuth, Western Germany), E. Junnikkala (Helsinki, Finland), H. Pschorn-Walcher (Délémont, Switzerland) and Th. Wildbolz and collaborators (Wädenswil, Switzerland) for supplying material; M. den Boer, G. Bryan, W. van Delden, W. M. Herrebout, J. T. Wiebes for criticism and J. Jong for advice on statistics.

Supported by grants from the Netherlands Organization for the Advancement of Pure Research (Z.W.O.)

RÉSUMÉ

Races écologiques et spéciation sympatrique dans le complexe Yponomeuta padellus

Le degré de différenciation génétique en allozymes à des niveaux divers de divergence évolutive (populations conspécifiques, sibling species et non-

sibling species) d'*Yponomeuta* a été déterminé. Les distances génétiques entre des sibling species ou des non-sibling species sont très larges. Il en est conclu que de telles estimations ne fournissent pas beaucoup d'informations sur le phénomène de spéciation même. Des coefficients de reproduction consanguine (F_{ST}) ont été calculés pour des populations d'*Y. padellus* provenant de six plantes-hôtes. La valeur moyenne F_{ST} est $.030 \pm .012$. Les valeurs de F_{ST} des populations recueillies sur *Crataegus*, (plante-hôte habituelle d'*Y. padellus*), sont inférieures 2 — 3.5 fois à celles des populations de l'ensemble des autres plantes-hôtes. L'apparition de races en fonction de l'hôte, mesurée par les différences importantes dans de fréquences des allozymes entre populations sympatriques sur plusieurs plantes-hôtes, a été examinée dans quatre régions. Il apparaît ainsi que la formation de races en fonction de l'hôte se produit chez *Y. padellus* et que la spéciation sympatrique est un événement très vraisemblable.

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