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The Origin and Distribution of Clonal Diversity in *Alsophila pometaria* (Lepidoptera: Geometridae)

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The Origin and Distribution of Clonal Diversity in *Alsophila pometaria* (Lepidoptera: Geometridae)

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Summary

A survey of spatial and temporal variation in the frequency of electrophoretically defined genotypes in the geometrid moth *Alsophila pometaria* revealed a high diversity of uncommon or rare asexual genotypes and clinal distributions of two of the more common clones. There was substantial year-to-year variation in genotype frequencies in seven of eleven sites. Progeny tests have revealed that sexual reproduction is uncommon in two populations and that new asexual genotypes arise from the sexual population. The recurrent origin of asexual genotypes is likely to account for the high genetic and ecological diversity of the asexual contingent of this species' populations, in contrast to the lower genetic diversity in some obligately asexual species in which such recruitment does not occur.

Recent studies have established that asexual populations are often genetically heterogeneous (e.g., Suomalainen et al., 1976; Parker, 1979; Vrijenhoek, 1979). In addition, the presence of geographic variation in asexual taxa indicates that they have considerable capacity to evolve (Suomalainen and Saura, 1973; Atchley, 1977). Parker (1979) has pointed out that the adaptive potential of asexual genotypes can depend on the mechanism that produces them. Asexual lineages that are generated by mutation may have considerably less variation in fitness than those arising independently (polyphyletically) from a sexual population. *Solenobia triquetrella* is a good example of polyphyletic origin of asexual lineages. This moth has extensive clonal diversity that arose from relict sexual populations (Lokki et al., 1975; Suomalainen et al., 1976). In other species, new asexual genotypes may arise by diverse means. For example, the results of Parker and Selander (1976) implicate mutation,

recombination, and hybridization in generating new clones of the lizard *Cnemidophorus tesselatus.*

In the present study, we have examined the sexual and asexual modes of reproduction of *Alsophila pometaria*, the fall cankerworm, in order to infer the mode of origin of the asexual genotypes which predominate in most populations of this species (Mitter et al., 1979). We have also surveyed temporal and spatial patterns of clonal variation in populations to evaluate the possible role of selection in changing asexual genotype frequencies.

The fall cankerworm is a univoltine defoliator of various deciduous trees and shrubs. Winter is spent in the egg stage, and hatching occurs approximately at the time that trees break bud in the spring. Dispersal of hatchling larvae by ballooning on silk threads may be extensive (Futuyma et al., 1981). The larvae feed for about four weeks and then drop from the vegetation to the ground. They burrow in a few inches, pupate, and spend six to seven months in an obligate summer diapause. Adults eclose in the late fall and early winter. The females, all of which are wingless, may be found on tree trunks until they mate. Immediately after mating, they climb up into the trees and deposit an egg mass.

Both asexual and sexual reproduction are present in populations of *Alsophila pometaria*. The asexual females are apparently gynogenetic, for they must mate with a conspecific male in order to reproduce. The cytological mechanism of asexual reproduction is not known, but it is observed that progeny typically inherit the maternal genotype (Mitter and Futuyma, 1977). Sexual females are also present, and they produce offspring with approximately a 1:1 sex ratio. Electrophoretic surveys have determined that populations of the fall cankerworm are composed of numerous asexual genotypes (here termed "clones") and a smaller contingent of sexual individuals (Mitter et al., 1979).

Materials and Methods

Clonal Variation

In order to study temporal and spatial variation, late instar larvae were taken from 22 locations on Long Island, New York. Eleven localities, shown by open circles in figure 1, were sampled in late May in both 1979 and 1980; these paired samples were taken at almost exactly the same sites. In 1980, eleven additional localities, shown by closed circles, were included. In each site, collections were made by beating vegetation of ten to fifty host trees over a rectangular cloth. Larvae were put in plastic bags and placed on ice until they were frozen at –70°C the same day.

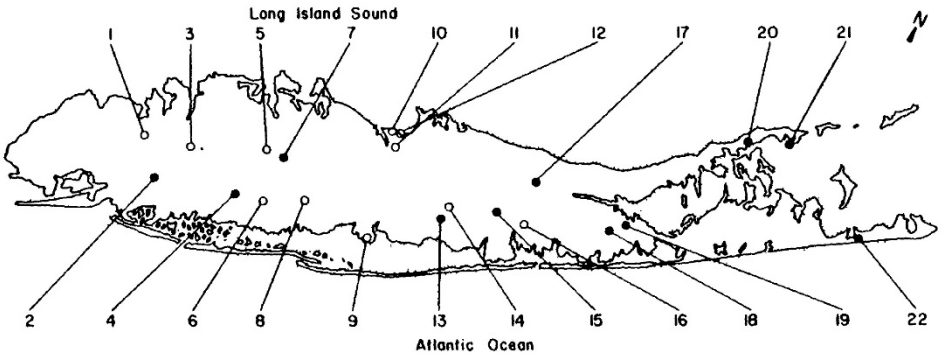

Figure l. Collection sites of *Alsophila pometaria* in 1979 and 1980. Open circles designate sites sampled in both years; filled circles indicate those sampled only in 1980.

Electrophoresis was carried out as described by Mitter et al. (1979) and Futuyma et al. (1981). Our electrophoretic surveys routinely assay four polymorphic enzymes for each individual. An electrophoretic phenotype was considered to represent an asexual genotype if it corresponded to a previously identified clone or appeared more than once in a sample (Mitter et al., 1979). This is a reliable procedure because allele frequencies from the males indicate that the most probable four-locus genotype in the sexual population will appear twice in a sample of one hundred individuals with a probability of less than one in ten thousand. Clones are identified in this paper by a number-letter code (table 1), with the letter part of the code corresponding to the designations of Mitter et al. (1979).

Table 1. Rank abundance of asexual genotypes in Long Island samples

Samples[a]	Asexual genotypes[b]	Sample size[c]
1A	l(C), 27, 26(A), 10, 4, 55, 70, 6, 22, 56, 58	104
1B	l(C), 27, 8(Y), 10, 26(A), 22, 58, 21, 32(K), 33, 41, 55, 56, 57, 59	102
2B	6, l(C), 31, 32(K), 34, 27, 33, 35	98
3A	1(C), 26(A), 8(Y), 3(X), 21, 22, 5, 13, 40, 41, 42	98
3B	1(C), 8(Y), 21, 26(A), 13, 22, 33, 43, 44	94
4B	6, l(C), 27, 2(B), 10, 26(A), 13, 20,	59
5A	l(C), 2(B), 13, 23, 11, 53, 5, 26(A)	96
5B	l(C), 2(B), 13, 8(Y), 3, 7, 45, 46, 47	92
6A	l(C), 2(B), 8(Y), 6, 13, 25, 3(X), 10, 26(Z), 20, 29, 39	99
6B	l(C), 2(B), 8(Y), 6, 10, 21, 13, 25, 20, 26(A), 30, 38	99
7B	13, l(C), 2(B), 20, 26(A), 8(Y)	82
8A	13, 2(B), 8(Y), 18, 5, 15, 17, 19, 26(A), 7, 37	101
8B	2(B), 13, l(C), 7, 5, 15, 16, 8(Y), 18, 19, 37	104
9A	l(C), 2(B), 20, 26(A), 10	64
9B	2(B), l(C), 13, 19, 23, 51, 52, 53, 54	80
10A	l(C), 2(B), 3(X), 26(A), 10, 13, 20, 48(Z)	89
10B	2(B), l(C), 13, 23, 3(X), 26(A), 5, 8(Y), 20, 49, 50	94
11A	l(C), 2(B), 26(A), 5, 3(X), 7, 8(Y), 42, 67	85

11B	2(B), l(C), 18, 12, 26(A), 3(X), 8(Y), 11, 14	107
12A	l(C), 2(B), 5, 3(X), 26(A)	53
12B	l(C), 2(B), 5, 3(X), 6, 7, 8(Y), 9, 26(A), 68	101
13B	2(B), l(C), 11, 7, 12, 13, 69	86
14A	2(B), l(C), 7, 11, 5, 6, 60, 61, 62	94
14B	l(C), 2(B), 11, 13, 5, 20, 63	97
15B	2(B), l(C), 13, 12, 7	69
16A	2(B), l(C), 11, 13, 12, 7, 19, 16, 64, 65, 66	93
16B	2(B), l(C), 11, 13, 6, 8(Y)	66
17B	2(B), l(C), 11, 7, 13, 18, 5, 8(Y), 26(A)	83
18B	l(C), 7, 8(Y), 2(B), 11, 13	67
19B	2(B), l(C), 8(Y), 13, 6, 7, 11, 22	56
20B	l(C), 2(B), 30	68
21B	2(B), 36	18
22B	2(B), 28, 12, 32	44

a. The numbers correspond to locations shown in figure 1; A and B denote samples collected in 1979 and 1980, respectively.
b. In each location, clones are listed in decreasing order of abundance. See Materials and Methods (Clonal Variation) for a description of clonal nomenclature. Singleton genotypes are not listed.
c. Total sample size includes asexual larvae and singleton genotypes.

Patterns of geographic variation can be evaluated by spatial autocorrelation techniques that rely on the calculation of covariation of a variable, in this case clone frequency, over distance classes (Sokal and Oden, l978a, l 978b; Sokal, 1979). Distance classes are derived from a connected graph of an interpoint distance matrix. Locations are assigned to distance classes so that the first class includes nearest-neighbor populations, and the last class includes those locations farthest removed from a particular site. All distance classes have approximately the same number of locations. Only in 1980 was a sufficient number of locations sampled for spatial autocorrelation analysis. As a measure of spatial covariation, we have used Moran's *I* (Sokal and Oden, l 978a), which ranges from + 1 (complete positive autocorrelation) to –1 (complete negative autocorrelation). We have relied on the GEOVAR program developed by Neal Oden to evaluate patterns of spatial variation. This program is available at the State University of New York at Stony Brook.

Mode of Reproduction

Genotypes appearing only once in a sample were assigned to the sexual population by Mitter et al. (1979); yet these genotypes may be uncommon asexual lineages. To determine the prevalence of rare clones, we collected mating pairs from two field locations to directly identify sexual and asexual reproduction by electrophoresis of parents and progeny.

Mating pairs were collected in the Ashley Schiff (AS) site on the campus of the State University of New York at Stony Brook and in the Village Wood (VW) site, three kilometers away in the village of Stony Brook (adjacent to locations 10 and 11 in fig. 1). Collections were made in the evening during the first week in December 1980, which was the peak

period for mating that year. Moths were transferred with soft forceps to a half-liter cardboard container, often remaining in copula. A record was kept of the order in which they were taken in the Ashley Schiff site. The containers were left overnight in the woods to allow females to deposit their eggs, which 90% did by the next morning. The moths were frozen at –70°C for electrophoresis, and each egg mass was placed in an unheated shed for most of the winter.

After two months of exposure to winter temperatures, a segment of each egg mass was broken off and gradually brought up to room temperature (24°C). Because first instar larvae are small, they were assayed only for the most easily visualized of the enzymes (PGM and PHI). Each larva was homogenized in 12 to 14 μl of the grinding buffer used by Mitter et al. (1979), and the homogenate was placed on gels without centrifugation. The electromorphs were well stained with appreciable separation, and it was possible to determine accurately the genotype of almost every individual.

In order to classify the mode of reproduction of mated females, we assumed that sexual reproduction was indicated by a pattern of syngamy and recombination of adult markers. In no case were both parents homozygous for the same alleles at *Pgm* and *Phi*; thus it was possible to determine the mode of reproduction in all matings. The worst case for the detection of sexual reproduction occurs when the parents differ by only one allele at one locus. In this event, the probability of not detecting syngamy in the progeny and misclassifying the mode of reproduction is $(0.5)^n$, where n is the number of larvae scored. When ten larvae were typed, the probability of missing sexual reproduction was approximately one in a thousand. The basis for identifying asexual reproduction was the presence of a genetically homogeneous sibship which had the maternal genotype.

Additional information on the mode of reproduction and on the origin of asexual genotypes has been obtained by progeny-testing two generations of several lineages that were classified as sexual. In February and March of 1980, a collection of egg masses was taken from the woodlots around Stony Brook. Each discrete egg mass presumably represented the reproductive effort of one female. Some of the first instar larvae from the egg masses were electrophoresed, and two progenies (HL75 and VW139) were classified as sexually produced. The siblings of these sexually derived larvae were reared on foliage in the lab and then placed on a mixture of sand and potting soil for pupation. After the summer diapause, adults eclosed in the fall of 1980. The surviving females were mated to wild-caught or labstock males and after oviposition were frozen for electrophoresis. The offspring from these crosses were examined by electrophoresis, and the observation of recombination among siblings was used to identify sexual reproduction by their mothers. The data were originally collected for stock-keeping purposes, and usually the male genotype was not determined. Nevertheless, it was possible to obtain preliminary information on the fidelity of sexual reproduction in the females.

Results

Clonal Variation

A multi-locus genotype was determined for each of 2,778 wild-caught larvae. Many genotypes were found only once in a sample and may have belonged to either the asexual or sexual contingent. However, 79.0 percent of the larvae had a profile that appeared at least twice and thus were classified as members of asexual lineages. The number of identified clones (table 1) ranged from 2 to 15 with an average of 8.4 per sample. The number of clones detected is correlated with sample size ($r_s = 0.79$, $P < 0.01$); nevertheless, it is clear that populations of the fall cankerworm are quite polymorphic when compared to those of many other asexual species (Parker, 1979). A total of 70 clones were identified in this survey. Many are rare endemics found in only one site and represented by only two or three individuals. Only 14 clones were represented by more than 30 individuals. Two clones, l(C) and 2(B), were extremely common and composed over 50% of the asexual larvae.

In order to analyze temporal changes, each genotype was assigned to a separate class if it appeared at least five times in a sample, and the remainder were pooled. A test of independence revealed that seven of eleven sites had significant changes in genotype composition from 1979 to 1980 (table 2). These changes were not primarily caused by shifts in the frequency of uncommon genotypes, nor did it appear that the habitat at sites with substantial changes in genotype frequency differed in an obvious way from those with small changes.

Table 2. Change in genotype composition, 1979 to 1980

Location number	*G*	*d.f.*	
1	14.858	6	$P < 0.025$
3	10.870	5	n.s.
5	8.414	5	n.s.
6	15.502	9	n.s.
8	34.596	12	$P < 0.001$
9	26.288	5	$P < 0.001$
10	24.010	7	$P < 0.005$
11	21.218	8	$P < 0.005$
12	10.092	5	n.s.
14	25.646	6	$P < 0.001$
16	14.544	6	$P < 0.025$

Most of the common clones collected in 1980 showed no statistically significant spatial covariation (table 3). Clone 11 is an exception, with significant positive autocorrelation in the first two distance classes and significant negative autocorrelation in two classes further removed. This pattern is typical of clinal variation, and accordingly the frequency of clone 11 progressively drops to the north and east of site 13, where it is most abundant. This clone has not been found to the west of site 13.

Table 3. Values of *I* (Moran's autocorrelation coefficient)

	Distance class[a]					
Clone	1	2	3	4	5	6
l(C)	–0.374	0.077	–0.076	–0.016	–0.063	–0.011
2(B)	0.498**	0.239*	–0.113	–0.014	–0.239	–0.224
3(X)	0.505**	–0.105	–0.255	–0.262	0.000	–0.151
5	–0.026	0.016	–0.075	–0.187	–0.303	–0.096
6	–0.210	0.188*	–0.080	–0.111	–0.123	0.024
7	0.072	0.089	–0.141	–0.161	0.050	–0.172
8(Y)	–0.031	0.102	–0.382**	–0.251	0.010	0.323
10	–0.018	0.220**	–0.181	–0.107	–0.110	–0.159
11	0.343*	0.313**	–0.244	–0.329*	–0.693**	–0.359
12	0.037	–0.009	–0.060	–0.108	–0.194	0.310**
13	0.121	–0.138	–0.001	0.056	–0.215	–0.062
20	–0.018	–0.084	–0.016	–0.059	–0.025	–0.010
26(A)	0.293	–0.183	0.401**	–0.126	–0.078	–0.233
27	–0.096	0.236**	–0.070	–0.100	–0.160	–0.155

*($P < 0.05$)

**($P < 0.01$)

a. See text for a description of how locations are assigned to distance classes.

Clone 2(B) shows a pattern of spatial autocorrelation that indicates clinal variation even though the negative values of *I* in the third through sixth distance classes are not significant. This clone is not found in the westernmost two sites on Long Island. Toward the east there is a steady rise in frequency to the middle of the island where clone 2(B) composes between 25% and 30% of the samples. Thereafter, the relative frequency fluctuates, with the largest drops occurring in sites such as 18, which have plant assemblages that are typically more mesic than those found in surrounding locations. Generally, mesic habitat tends to be more common in western Long Island, while the eastern portion is typified by extensive areas of well-drained sandy soil which supports scrub vegetation dominated by *Pinus rigida* and *Quercus ilicifolia*. There is an indication that the frequency of clone 2(B) is correlated with increasing aridity of the collection sites.

Mode of Reproduction

An example of sexual reproduction is presented in table 4, in which the alleles are designated by letter. Syngamy and recombination of adult markers suggest typical sexual reproduction (part A of the table). An insufficient number of progeny were typed to make an argument for deviations from Mendelian expectations. Part B of table 4 presents two cases of a phenomenon we interpret as "male allele inclusion." In these cases, an allele present only in the male parent appeared in a larva. These anomalous fertilization events occurred once in a female of a common genotype, 8(Y), and once in a female with an uncommon genotype. In each case, nine of the ten larvae sampled had the maternal genotype, but one larva had an allele possessed by the father. These occurrences are not likely to be an artifact because the electrophoretic profiles of all the progeny were unambiguous. These

were the only observed aberrations in otherwise clonal reproduction; in every other case, the maternal genotype was transmitted intact.

Table 4. Examples of sexual reproduction in the Ashley Schiff population of *Alsophila pometaria*

	Pgm	*Phi*	*N*
A. Typical sexual reproduction			
♂	AB	CC	
♀	BC	CC	
Progeny:	AC	CC	0
	AB	CC	4
	BC	CC	1
	BB	CC	7
B. Male allele inclusion			
♂	AB	AB	
♀	AB	CC	
Progeny:	AB	CC	9
	AB	AC	1
♂	AC	CC	
♀	AA	BC	
Progeny:	AA	BC	9
	AC	BC	1

Progenies produced by 90 females collected in copula in the Ashley Schiff site and by 27 such females from the Village Wood site were analyzed by electrophoresis of an average of 9.4 larvae per sibship. Only one typically sexual female was found in each site. The estimated percentages of sexual females, with 95% confidence limits, are 1.11 (0.03–6.04) and 3.70 (0.09–18.97) for the Ashley Schiff and Village Wood samples, respectively. The confidence limits are broad, but it does appear that sexual reproduction was uncommon in these populations.

The Ashley Schiff and Village Wood females whose complete four-locus genotype was determined can be compared to clones collected elsewhere on Long Island. Most females had genotypes that matched that of one of the previously identified clones (table 5). In the Ashley Schiff sample there were six unique genotypes not found elsewhere in our study. One was the sexual female, one was not progeny tested, and four proved to be asexual when their offspring were electrophoresed. The sequence in which all genotypes were collected was known, and scrutiny of the data indicated that the unique genotypes were collected together. A runs test ($t_s = -6.036$, $P < 0.001$) confirms that the unique genotypes were clumped, which suggests that there was a concentration of reproductive instability associated with sexual reproduction. Three unique genotypes were found in the Village Wood sample. One female was not progeny tested, one was sexual, and one was asexual. In general, it appears that populations of the fall cankerworm are characterized by an abundance of uncommon or rare asexual genotypes.

Table 5. Females collected in the Ashley Schiff and Village Wood populations

Electrophoretic identity[a]	Number in Ashley Schiff[b]	Number in Village Wood[c]
8(Y)	22	4
2(B)	16	9
26(A)	8	3
48(Z)	8	0
71	5	0
3(X)	4	1
l(C)	3	2
73(Q)	2	0
13	2	0
72	2	1
6	1	0
7	1	0
45	1	1
62	1	0
12	0	1
—	1	0
—	1	0
—	1	0
—	1	0
—	1	0
—	0	1
—	0	1
—	0	1

a. Dashes indicate a unique electrophoretic profile.
b. $N = 82$
c. $N = 25$

Further insight into the mode of reproduction of *Alsophila pometaria* was obtained by testing the progeny of females from two field-collected egg masses, HL75 and VW139. Table 6 shows the letter-designated four-locus genotypes of most of the females and their offspring, independently for *Pgm* and *Phi*. Recombination among progeny indicates that five females (A, B, C, F, G) from egg mass HL75 were sexual. The genotype of the male and a relatively large number of tested progeny were available from cross F. In this case at neither *Pgm* nor *Phi* was there a significant deviation from Mendelian expectations *(Pgm*: $\chi^2 = 3.62$ n.s., *Phi*: $\chi^2 = 4.29$ n.s.). Two females (D, E) from egg mass HL75 were clearly asexual because all of their offspring were heterozygous at one locus and had the maternal genotype. The multilocus genotypes of females D and E differ and do not correspond to any clone identified in the Stony Brook area. Thus, it does not seem likely that eggs from other asexual females contaminated egg mass HL75. Sexual and asexual reproduction were also observed among daughters of VW139 (table 6). Female H produced a three-banded larva with one allele presumably coming from the male. This larva was probably

a newly generated triploid. Three-banded late instar larvae and adults have been observed in electrophoretic surveys of natural populations (Harshman, 1982), but they are rare. No three-banded sibships have been discovered, which suggests that triploids do not persist as asexual lineages. A definitive interpretation of three-banded individuals awaits a cytological analysis of the reproductive mode of *Alsophila pometaria*. The rest of the progeny from female H were all heterozygous at one locus and must have been produced asexually. Females I and J were classified as sexual. The progeny analysis of daughters from egg masses HL75 and VW139 suggests that sexually reproducing females can produce daughters that reproduce asexually.

Table 6. Progeny tests of females from egg masses HL75 and VW139

	Pgm	*Phi*	*Ap*	*G6Pdh*
HL75				
♀(A)	—	—	—	—
progeny:	AB(9)	BC(4)		
	BB(2)	CC(7)		
♀(B)	BC	BC	AB	BC
progeny:	BC(4)	BC(7)		
	AB(3)	BB(2)		
	AC(5)	CC(4)		
	BC(2)			
♀(C)	AB	CC	AB	AC
progeny:	AA(1)	BC(8)		
	AB(6)	CC(4)		
progeny:	AA(1)	BC(8)		
	BB(2)			
♀(D)	AB	CC	BC	CC
progeny:	AB(8)	CC(8)		
♀(E)	AB	CC	BC	AC
progeny:	AB(l2)	CC(l2)		
♂	AB	BC	AA	AC
♀(F)	BC	BC	AB	AC
progeny:	BC(8)	BC(l2)		
	BB(4)	CC(6)		
	AB(3)	BB(1)		
	AC(4)			
♀(G)	BC	BC	AA	AC
progeny:	—	BC(3)		
		CC(6)		
VW139				
♂	AB	BC	AB	AC
♀(H)	—	—	—	—

progeny:	AC(9) ABC(1)	CC(10)		
♀(I)	AA	CC	AA	CC
progeny:	AB(3) AA(3)	CC(5)		
♀(J)	AA	CC	AA	CD
progeny:	AB(5) AA(4)	CC(10)		

Discussion

Temporal variation in the frequency of asexual genotypes has been well documented in *Daphnia* spp. (Hebert, 1974; Hebert and Ward, 1976; Hebert and Crease, 1980) and in *Lonchoptera dubia* (Ochman et al., 1980). Selection could be playing a role in producing the changes observed in these taxa and in temporal changes observed in *Alsophila pometaria*. In the fall cankerworm, variable patterns of dispersal could also be a factor in year-to-year changes. Another possibility is the presence of very small scale spatial differences in the collection sites, which may have been sampled in a slightly different manner each year; however, the considerable capacity for larval dispersal in this species (Futuyma et al., 1981) makes this an unlikely explanation. Certainly, the year-to-year differences in genotype frequency were pronounced and warrant further investigation.

Local geographic variation in the frequency of asexual genotypes is present in the fall cankerworm and in a number of other species, in which variation can occur over a matter of meters or across hundreds of kilometers (Saura et al., 1977; Christensen, 1979; Mitter et al., 1979; Vrijenhoek, 1979; Jaenike et al., 1980). In the tetraploid apomictic weevil *Otiorrhynchus scaber* extensive electrophoretic surveys have detected over 70 asexual genotypes, and, as in *Alsophila pometaria*, only a few genotypes are widespread and abundant (Suomalainen et al., 1976).

In *Alsophila pometaria*, host plants can affect the distribution of clones (Mitter et al., 1979; Futuyma et al., 1981). Clone 2(B) has been observed to be associated with oak stands (Mitter et al., 1979), and the predominance of oak in drier sites may explain the spatial distribution of 2(B) observed in this study. Moisture may play an additional role since fall cankerworm larvae spend a long summer diapause in the soil. (Dessication is a critical source of mortality for subterranean pupae and other insects, such as *Glossina* [Glasgow, 1963].) In the present study, it was observed that most clones were not clinally distributed, and few showed any significant autocorrelation. The frequency of these clones could be a result of mosaic selection patterns or of random fluctuations in relative abundance.

The high diversity of rare asexual genotypes in *Alsophila* in itself suggests that asexual females arise polyphyletically and frequently from the sexual population, and this supposition is supported by our finding several such originations in the limited progeny testing we have performed. It is quite possible that the sexual population harbors considerable genetic variation affecting the mechanism of meiosis; a genetic basis for apomixis versus sexual reproduction has been determined for some plants (e.g., Muntzing, 1958; Savidan,

1980), and it is possible to select parthenogenetic lines from sexual populations of *Drosophila mercatorum* (Carson, 1967; Annest and Templeton, 1978). It is intriguing that a single female may yield both sexually and asexually reproducing progeny, suggesting that the mechanism of meiosis may involve the production of reduced gametes, some of which are susceptible to fertilization while others form reconstitution nuclei. Although we have not undertaken a cytological analysis of meiosis in *Alsophila*, a possible model consistent with our observations is that described by Seiler (1961, 1967) for the psychid moth *Solenobia triquetrella*. In *Solenobia*, centric fusion of non-sister nuclei reestablishes the ploidy of the mother and will reestablish the maternal genotype if, as is generally thought to be the case in Lepidoptera, there is no crossing over in females. Our observations of "male allele inclusion" in some offspring in otherwise parthenogenetically produced broods would conform to this model if some eggs are fertilized rather than undergoing restitution by centric fusion. Fertilization in combination with centric fusion could account for the triploids that electrophoresis occasionally reveals.

The apparently frequent origin of asexual lineages from the sexual population in *Alsophila* doubtless accounts for the high genotypic diversity in the asexual contingent. There surely must be considerable scope for interclonal selection, which can act effectively on the whole field of recombinant genotypes that are generated by sexual reproduction and then "frozen" by parthenogenesis. Ecological differences among such genotypes may account for their coexistence with each other and with the sexual population (Maynard Smith, 1978) and may expand the ecological amplitude of the population beyond that attainable in an entirely sexual population (Roughgarden, 1972). This "frozen niche variation" model of genotypic diversity, as Vrijenhoek (1979, 1984) has described it, is supported by observations of pronounced ecological differences among sympatric parthenogenetic genotypes of *Poeciliopsis* (Vrijenhoek, 1979, 1983) and *Alsophila* (Mitter et al., 1979; Futuyma et al., 1981). This model also appears to apply to *Daphnia*, in which there are substantial ecological differences among asexual genotypes (Lynch, 1983); in this species the great diversity of asexual genotypes generated periodically by sexual reproduction declines as interclonal selection proceeds. In *Alsophila*, ecological differences among some of the clones undoubtedly contribute to their persistence, but the high diversity of uncommon genotypes may be a result of frequent origination of clones compensating for loss from populations by chance or factors such as competition.

In all the above examples, when the genetic and ecological diversity of asexual genotypes is high, they appear to arise polyphyletically from sexual populations at moderate to high frequency. In contrast, the earthworm *Octolasion tyrtaeum* is obligately parthenogenetic and, judging from the high genetic distances among clones, has been so for a considerable time (Jaenike et al., 1980; but see their caveat about this interpretation). Compared to *Alsophila*, the genotypic diversity in this earthworm is very low; electrophoresis of ten variable enzymes revealed only eight clones among 2,197 individuals taken from numerous habitats throughout North Carolina, Tennessee, and New York. Moreover, Jaenike et al. (1980) could discern almost no indication of ecological differences among any of the genotypes, the two most common of which have indistinguishable, broad, ecological distributions.

The contrast between *Alsophila*, *Poeciliopsis*, and *Daphnia* on the one hand and *Octolasion* on the other suggests that the diversity of asexual genotypes, and consequently their ecological diversification and response to selection, is considerably greater when asexual lineages are recurrently recruited from a sexual population than when parthenogenesis is obligate and mutation is the sole source of genetic variation (Maynard Smith, 1978). If so, the numerous parthenogenetic forms in which abundant genetic diversity has been found may constitute evidence against the supposition that parthenogenesis dooms a population to early extinction, for, in many such instances, genetic diversity may be replenished repeatedly by the origin of new asexual genotypes.

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