GENETIC POLYMORPHISM AND EVOLUTION IN PARTHENOGENETIC ANIMALS. II. DIPLOID AND POLYPLOID *SOLENOBIA TRIQUETRELLA* (LEPIDOPTERA: PSYCHIDAE)[1]

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ABSTRACT

Genic polymorphism at sixteen enzyme loci of four different chromosomal races of *Solenobia triquetrella* (bisexual, two diploid parthenogenetic races and tetraploid parthenogenetic) has been studied by starch gel electrophoresis. Isolated small diploid bisexual populations have rather uniform allele frequencies at all loci which we have studied. Diploid and tetraploid parthenogenetic individuals of this species are in general as heterozygous as bisexual ones. All parthenogenetic local populations are different from each other in the Alps. These parthenogenetic genotypes cannot be derived from a common ancestor through single mutations but rather bear evidence for a polyphyletic origin of parthenogenesis in *Solenobia triquetrella*. In the marginal distribution areas of the species in northern Europe single genotypes are spread over far larger areas than in the mountain regions of central Europe. This may be due to the old origin of parthenogenesis and polyploidy in northern Europe. No new parthenogenetic and polyploid strains have lately arisen in the regions outside of the Alps.

SEILER (1961, 1967 and references therein) has very extensively studied the parthenogenesis and cytology of the psychid moth *Solenobia triquetrella*, the females of which are flightless. Diploid bisexual, diploid parthenogenetic and tetraploid parthenogenetic races of this bagworm moth species are known. The different races have a distinctly divergent distribution. Diploid races have thus far been found only in Switzerland, southern Germany and Austria. The diploid bisexual race lives in Switzerland only to the north of the Alps in regions which were not covered by the inland ice during the Würm Ice Age. It is also found in the Swiss Mittelland in areas raised above the Würm glaciation as nunataks. The diploid parthenogenetic race inhabits, in part, the same areas as the previous race. It is, in addition, found farther away from the glacier edge and also in the Swiss Mittelland on regions covered with ice in the Ice Age. The tetraploid parthenogenetic race is spread over the greatest part of Europe.

Both parthenogenetic *Solenobia triquetrella* races have an automictic parthenogenesis. The oocytes undergo a normal meiosis and chromosome reduction, as a result of which the zygoid nuclear phase in the eggs becomes azygoid. In the

[1] Dedicated to Theodosius Dobzhansky on the occasion of his seventy-fifth birthday in recognition of his inspiring leadership in the field of evolutionary genetics.

parthenogenetic eggs the zygoid chromosome number is restored by a fusion of the two central azygoid nuclei; this results in the formation of the so-called "Richtungs-Kopulations-Kern" (RKK). The individuals rising from parthenogenetic eggs are always females, since the fusion of the two central polar nuclei leads to heterogamy. Such an RKK is formed also in the eggs of the bisexual race, but it does not develop further when the egg is fertilized. RKK gives rise to a new embryo in the parthenogenetic eggs, the entire genotype of which is completely restored in each generation (SEILER 1963). There is no recombination due to crossing over, since chiasmata have never been observed in the meiosis of Lepidopteran females (BAUER 1939; SUOMALAINEN 1965; SUOMALAINEN, COOK and TURNER 1973).

There are local diploid parthenogenetic populations of *S. triquetrella* in which regularly a portion of the eggs do not continue to develop. In other local populations all eggs develop normally. The fact that the eggs of certain parthenogenetic populations are easily fertilized, which is not the case in others, as well as certain other results, led SEILER to conclude that the parthenogenesis of *S. triquetrella* did not arise contemporaneously in different populations—in other words that it is of polyphyletic origin. Both diploid races have two types of females, with and without the *Y* chromosome. They are designated *XY* and *XO* types. SEILER has presented evidence which indicates that the *Y* chromosome of *S. triquetrella* is genetically inert.

SEILER's interpretation of the origin of tetraploid parthenogenesis can be summarized as follows. In all parthenogenetic animals the bisexual race is the original, from which the parthenogenetic races have evolved. SEILER assumes that the bisexual race of *S. triquetrella* first gave rise to the diploid parthenogenetic race. He supposes on the basis of distribution of different races, among other factors, that the parthenogenesis in *Solenobia triquetrella* originally arose during the Ice Age. The bisexual race of *S. triquetrella* survived the Würm glaciation in the ice-free refuges. The retreat of the glaciers began about 20,000 years ago. The diploid parthenogenetic race may have originated at this time. Due to its more efficient reproduction, it began following the retreating ice.

The tetraploid parthenogenetic race of *S. triquetrella* developed from the diploid parthenogenetic race in the course of a further retreat of the glacier. This tetraploid race in its turn began following the retreating ice, thus spreading into the exposed area. Some of the tetraploid populations have originated later. The first step in the transition from bisexuality to diploid parthenogenesis is a non-stabilized parthenogenesis during which many eggs fail to develop. The next step is a stabilized parthenogenesis with normal development of all eggs. In all tetraploid *S. triquetrella* populations the parthenogenesis is stabilized.

The cortical ooplasm of diploid parthenogenetic eggs is often abnormal. In some populations the plasm containing the spindles of the meiotic divisions is absent. In certain other populations nuclei fuse at the blastoderm stage of the embryo or later. Among the new nuclear constitutions tetraploidy dominates.

We have described above what can be called SEILER's life work. His original notes on the exact location of the sampling localities exist. We have collected

samples from as many of these localities as possible. In this paper we describe the pattern of genic variation in different populations of *Solenobia triquetrella*.

MATERIALS AND METHODS

Populations studied: The localities from which *Solenobia triquetrella* moths have been analyzed are listed below. The locality names are followed first with the number of moths studied and, in italics, with the reference number "Karten-Nummer" of SEILER (1961) in cases where the population inhabiting the locality has been cytologically studied by SEILER.

Diploid bisexual Solenobia triquetrella: Fleurier, "La Caroline", Neuchâtel (1, *25*); Gurten Süd, Bern (6, *58*); Signau-Niedermatt, Bern (3, *112*); Escholzmatt-Rüttihus, Luzern (5, *114*); Albishorn, Hausen, Zürich (3, *222*); Uster, Hardwald, Zürich (2, *214*). The total number of bisexual moths collected from Switzerland is 20. We have one sample from Austria, namely Pfenningberg, Linz (29, *12*). The total number of diploid bisexual moths is accordingly 49.

Diploid parthenogenetic Solenobia triquetrella, *XY type*: Münchenbuchsee, Bern (3, *53*); Gurten Nord, Bern (2, *57*); Gurten Süd, Bern (8, *58*); Erlenbach am Zürichsee, Zürich (40, *218*); Weinfelden, Thurgau (6, *276*). All these samples are from Switzerland. Their total number is 59.

Diploid parthenogenetic Solenobia triquetrella, *XO type*: Dotzigen bei Büren, Bern (47, *50*); Weggis, Luzern (1, *178*); Lützelau bei Vitznau, Luzern (2, *180*); Rotshuh bei Gersau, Schwyz (6, *241*); Näfels, Glarus (1, *296*). The total number of these moths is 57. All of them originate from Switzerland.

Tetraploid parthenogenetic Solenobia triquetrella: Schöfflisdorf bei Bielsdorf, Zürich (2, *150*); Herrliberg am Zürichsee, Zürich (4, *221*); Uzwil, St. Gallen (9, *278a*); Netstal, Linthal, Glarus (9, *298*); Netstal, railway station, Glarus (36); Generoso, Ticino (6, *316*); Bellavista, Generoso, Ticino (1, *319*); Cozzo, Bogno, Ticino (2); Bodio, Ticino (10); Gschaid, Niederösterreich (1). With the exception of the last sample, which originates from Austria, the material has been collected from Switzerland. The total number of central European tetraploid moths analyzed is 80. The following 227 moths have been collected from Finland, namely from Storby, Eckerö, Åland Islands (7); Skag, Eckerö, Åland Islands (1); Nåtö, Lemland, Åland Islands (20); Rauma (18); Tvärminne, Ekenäs (17); Pälkäne (3); Kaarela, Helsinki (101); Askola (2); Åminsby, Porvoo (4); Asikkala (2); Lahti (17); Morovuori, Pyhtää (9); Pahalampi, Pyhtää (11); Santalahti, Mussalo, Kotka (1); Varsavuori, Mussalo, Kotka (1); Kymi (1); Mikkeli (4); Virolahti (8).

With the exception of the Cozzo and Bodio populations the Swiss samples have been collected at exactly the same locations from which SEILER's (1961) material originates. The degrees of ploidy are therefore known for the Swiss material. Extensive studies by SEILER and SUOMALAINEN (cf., e.g., SEILER 1961) have shown that the northern European populations of *Solenobia triquetrella* are tetraploid.

Laboratory procedures: In general it is difficult to ascertain the developmental status of a preimaginal bagworm moth without killing it. Accordingly, we have used spring caterpillars, pupae and adult moths in our studies. The enzyme assay and starch gel electrophoresis methods are in general use (cf., e.g., SUOMALAINEN and SAURA 1973). Consistent results for the three stages of development studied were yielded by assays for the following enzymes: adenylate kinase (Adk), esterase (Est), fumarase (Fum), α-glycerophosphate dehydrogenase (α-Gpdh), hexokinase (Hk), isocitrate dehydrogenase (Idh), malate dehydrogenase (Mdh), malic enzyme (Me), phosphoglucomutase (Pgm), superoxide dismutase (Su) (= tetrazolium oxidase) and triosephosphate isomerase (Tpi). Some enzymes, e.g. leucine aminopeptidase, were also assayed, but since they showed an apparent correlation to the age of experimental animals, the results for them are not presented.

Enzyme loci and their alleles are identified with reference to the electrophoretic migration of the corresponding enzymes and allozymes. A certain allele at a locus has been arbitrarily given the value 1.00. For a more detailed description of locus and allele identification see SUOMALAINEN and SAURA 1973.

TABLE 1

Allele frequencies at polymorphic loci in diploid bisexual populations of Solenobia triquetrella

The localities are Linz in Austria, and several Swiss populations presented here as if originating from a single population. Numbers in parentheses give the numbers of genes sampled.

Population		Alleles										Proportion of heterozygotes
		Esterase-2										
		1.00	*1.03*	*1.05*	*1.06*	*1.08*	*1.10*	*1.12*	*1.13*	*1.14*	*1.15*	
Linz	(54)	0.04	—	0.07	0.04	0.09	0.19	0.28	0.13	0.15	0.02	0.63
Switzerland	(26)	0.04	0.19	0.04	0.23	0.08	0.08	0.35	—	—	—	0.69
		Esterase-5										
					0.98		*1.00*					
Linz	(54)				—		1.00					—
Switzerland	(34)				0.06		0.94					0.12
		Hexokinase										
				1.03		*1.06*		*1.09*				
Linz	(50)			0.12		0.84		0.04				0.24
Switzerland	(28)			0.07		0.82		0.11				0.29
		Isocitrate dehydrogenase-1										
					1.00		*1.08*					
Linz	(54)				1.00		—					—
Switzerland	(40)				0.98		0.02					0.05
		Isocitrate dehydrogenase-2										
			0.98		*1.00*		*1.03*		*1.05*			
Linz	(58)		0.12		0.26		0.04		0.59			0.52
Switzerland	(38)		0.11		0.68		—		0.21			0.42
		Malate dehydrogenase-2										
			0.95		*0.97*		*1.00*		*1.05*			
Linz	(58)		0.05		—		0.67		0.28			0.45
Switzerland	(34)		0.12		0.03		0.82		0.03			0.12
		Malic enzyme										
					1.00		*1.02*					
Linz	(50)				0.80		0.20					0.24
Switzerland	(28)				0.86		0.14					0.14
		Phosphoglucomutase										
		0.97		*1.00*		*1.03*		*1.06*		*1.09*		
Linz	(30)	0.03		0.10		0.50		0.17		0.20		0.47
Switzerland	(8)	—		0.25		0.13		0.63		—		0.75
		Superoxide dismutase-1										
					1.00		*1.05*					
Linz	(36)				0.72		0.28					0.44
Switzerland	(34)				1.00		—					—
		Triosephosphate isomerase										
				0.93		*0.95*		*1.00*				
Linz	(54)			0.02		0.07		0.91				0.24
Switzerland	(38)			0.10		0.05		0.85				0.00

RESULTS

Polymorphism in diploid bisexual populations. Allele frequencies at polymorphic loci in diploid bisexual populations of *Solenobia triquetrella* are given in the Table 1. Five loci were found to be monomorphic and the allele designated *1.00* was found to be homozygous in all individuals studied. These loci are *Adk-2*, *Fum*, *α-Gpdh*, *Mdh-1* and *Su-2*. In addition to these loci, *Adk-1* is polymorphic at least in the Linz population, but no definite allele frequencies could be established. The proportions of heterozygotes indicated in the table are observed pro-

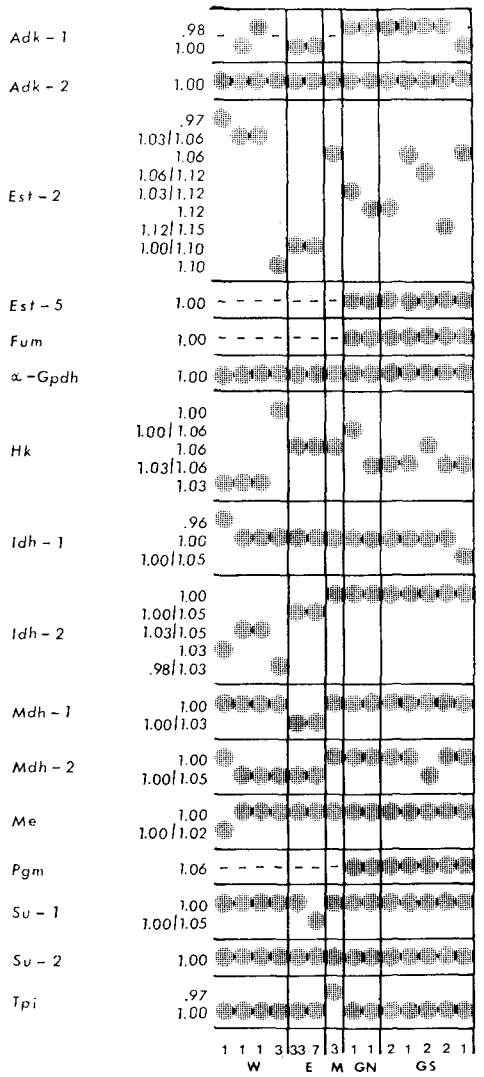

FIGURE 1.—Numbers of individuals of each overall genotype recognized in diploid parthenogenetic populations of *XY* type of *Solenobia triquetrella*. W = Weinfelden, E = Erlenbach, M = Münchenbuchsee, GN = Gurten Nord, and GS = Gurten Süd.

portions. These proportions agree well, in general, with values expected on the assumption of a Hardy-Weinberg equilibrium.

The data from six Swiss populations are treated as if they would originate from one population. The samples from any Swiss population are small indeed, but as much as we could judge, the allele frequencies seem to be uniform in the Swiss bisexual material. In any case there is no contradicting evidence. The average heterozygosity per locus per specimen of the bisexual race of *Solenobia triquetrella* is 0.23.

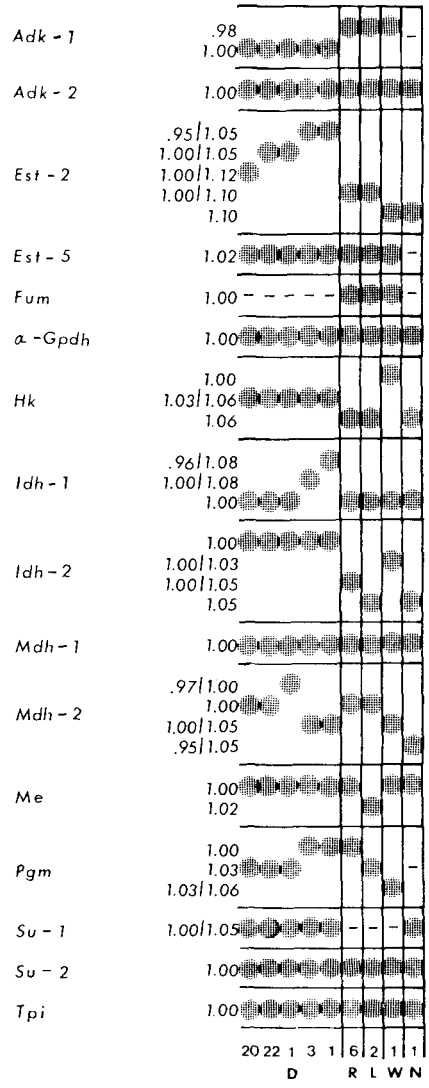

FIGURE 2.—Numbers of individuals of each overall genotype recognized in diploid parthenogenetic populations of *XO* type of *S. triquetrella*. D = Dotzigen, R = Rotschuh, L = Lützelau, W = Weggis, and N = Näfels.

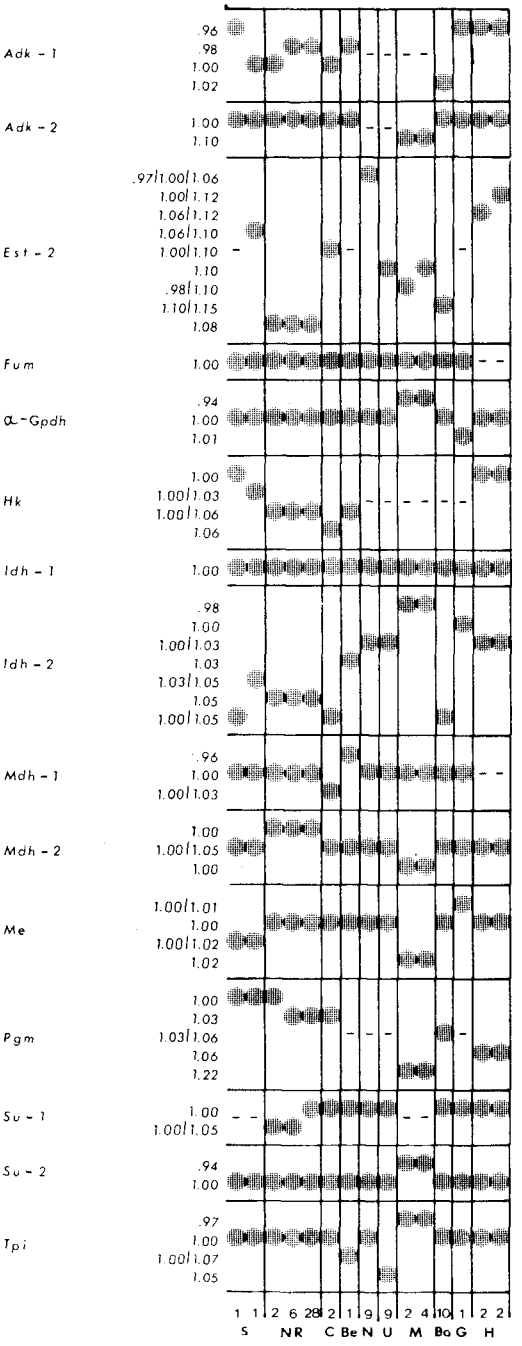

FIGURE 3.—Numbers of individuals of each overall genotype recognized in Centeral European tetraploid parthenogenetic populations of *S. triquetrella*. S = Schöfflisdorf, NR = Netstal railway station, C = Cozzo, Be = Bellavista, N = Netstal, U = Uzwil, M = Monte Generoso, Bo = Bodio, G = Gschaid, and H = Herrliberg.

Polymorphism in diploid parthenogenetic populations. Figures 1 and 2 indicate the overall genotypes for all loci studied for *XY* and *XO* type populations, respectively. The number of alleles present in diploid parthenogenetic populations is well correlated with the number of alleles at each locus in bisexual populations. However, there are alleles which have not been encountered in bisexual moths (*Est-2*$^{.95}$, *Est-2*$^{.97}$, *Est-5*$^{1.02}$, *Hk*$^{1.00}$, *Idh-1*$^{.96}$, *Idh-1*$^{1.05}$, *Mdh-1*$^{1.03}$ and *Tpi*$^{.97}$).

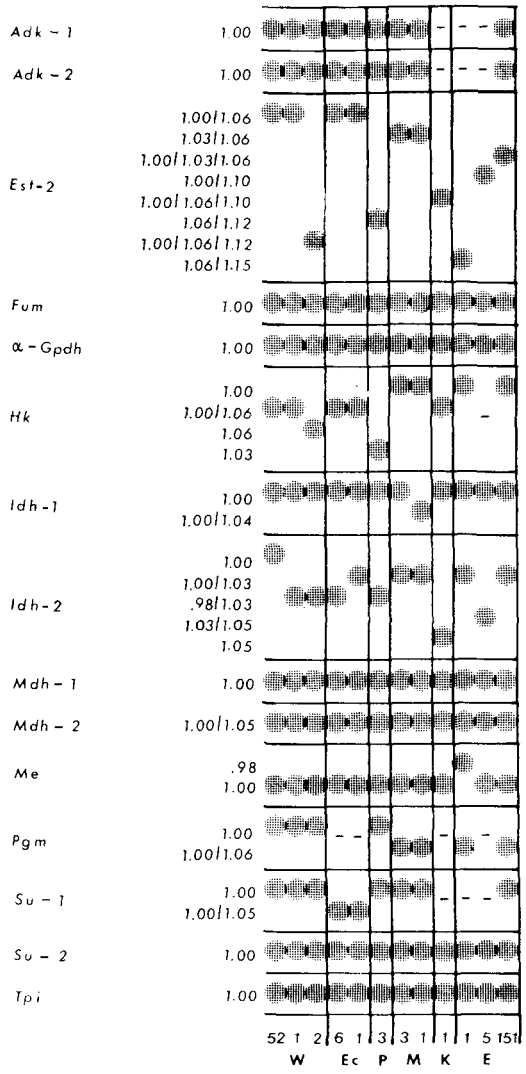

FIGURE 4.—Numbers of individuals of each overall genotype recognized in Finnish tetraploid parthenogenetic populations of *S. triquetrella*. W = Western type, comprising four populations, of which the Nåtö population contains one and the Rauma two individuals different from the main type. Ec = Eckerö, Storby, P = Pälkäne, M = Mikkeli, K = Kotka, Varsavuori, E = Eastern type, comprising ten populations, in which one individual of Pyhtää Morovuori and five individuals of Virolahti differ from the others.

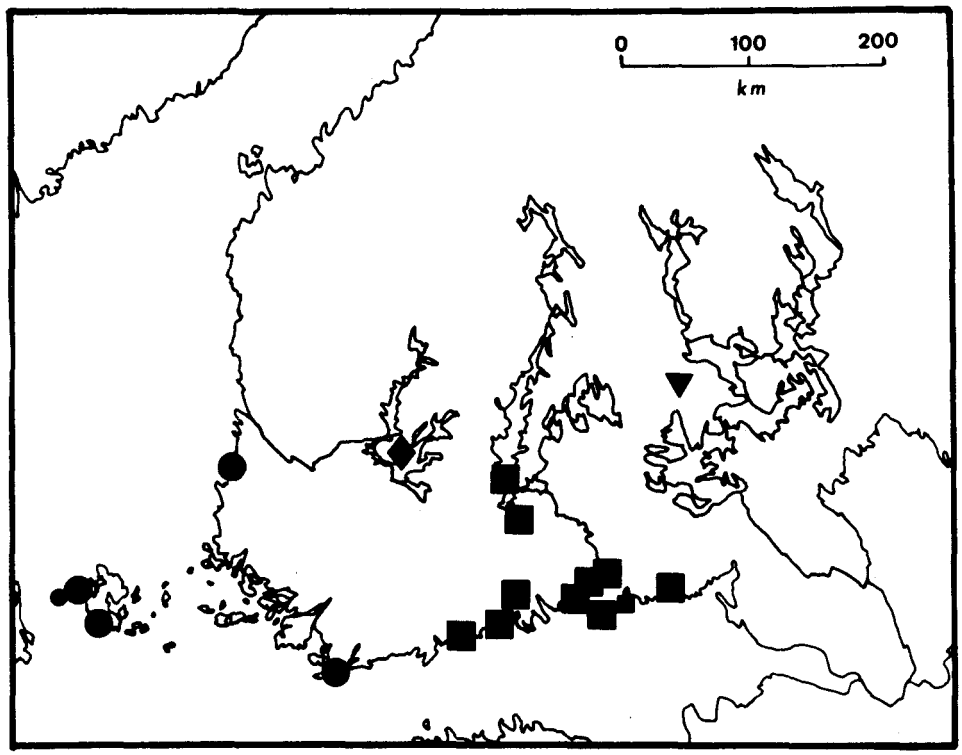

FIGURE 5.—Map of southern Finland showing the localities from which individuals belonging to different overall genotypes were found. Small circle = Eckerö Storby, large circles = western type, lozenge = Pälkäne, large squares = eastern type, small square = Kotka, Varsavuori, triangle = Mikkeli.

Considerable differences can be observed in the amount of interindividual variation between different populations. The only genotype found in more than one population is the one shared by the Gurten Nord and Gurten Süd populations, which are located about three kilometers apart. In general a single population consists of moths of rather different genotype (e.g. the Dotzigen population).

Tetraploid parthenogenetic populations: The overall genotypes observed in tetraploid populations are presented in Figures 3 and 4. It should be noted that genotypes should actually be called enzyme phenotypes rather than genotypes, since no attempt is made to indicate the dose of the allele in question (cf. SUOMALAINEN and SAURA 1973). There are thirteen alleles which have not been found either in bisexual or in diploid parthenogenetic populations. No common genotypes are found in any two populations in our central European material. None of them is identical with any Finnish population. As for the Finnish populations, four western populations (Skag, Nåtö, Rauma, and Tvärminne) contain identical overall genotypes and again moths of identical genotype have been found in ten eastern populations (Kaarela, Askola, Åminsby, Asikkala, Lahti,

Morovuori, Pahalampi, Santalahti, Kymi and Virolahti). The geographic distribution of these overall genotypes in Finland is presented in Figure 5.

In spite of the circumstance that the Finnish tetraploid material is almost three times larger than the central European, thirteen loci have been found to be variable in central Europe, with only seven in Finland.

DISCUSSION

In our previous study of genetic variation in parthenogenetic animals we compared different triploid and tetraploid individuals and populations of *Otiorrhynchus scaber* (Coleoptera: Curculionidae) with each other (SUOMALAINEN and SAURA 1973; SAURA *et al.* 1975). The variability within and between populations of these beetles can be explained by *single* mutations, which have occurred *after* the onset of parthenogenetic reproduction in these beetles. Accordingly, parthenogenesis in these beetles is very likely monophyletic.

The variability between and within populations of *Solenobia triquetrella* is clearly discontinuous. A few genotypes only can be derived from other genotypes as a result of single mutations which presumably have occurred after the origin of parthenogenesis and/or polyploidization. The simplest explanation available is the one suggested by SEILER (1961, 1963, 1967), according to which parthenogenesis and polyploidy are polyphyletic in *Solenobia triquetrella.* The peculiar cytological mechanism makes allopolyploidy improbable—furthermore, allotetraploids should be much more heterozygous than diploid parthenogenetic races, which is not the case in Solenobia.

The diploid bisexual populations are small and scattered over a wide area in the Alps. They are—and have been for a long period of time—effectively isolated from each other (cf. SEILER 1961). As evidenced by the presence of variable numbers of old bags of previous years and SEILER's and TÖPPEL's notes, the diploid bisexual populations undergo some fluctuation in numbers. The collection technique consists simply of as thorough a visual examination for bags on trees, shrubs and the ground as possible. This technique should give a rather unbiased relative—if not necessarily absolute—estimate of the size of Solenobia populations. In our opinion few Swiss bisexual populations exceed in size some tens of moths. SEILER (1961, p. 311) has very forcefully stressed the same point in predicting that bisexual *Solenobia triquetrella* very soon will die out completely in Switzerland. In any case it is evident that the Linz population from Austria is far larger than any of the Swiss populations.

The apparent similarity in allele frequencies observed between different Swiss populations and the Linz population hundreds of kilometers away is in many respects enigmatic. It is, of course, true that we have only observed a homogeneity of alleles present in the very small Swiss samples. This homogeneity may reflect frequencies as uniform as those in many Drosophila species (c.f., e.g., AYALA *et al.* 1972). The sizes of the diploid bisexual populations are so small that they should be effectively subject to random drift. The absence of any actually good evidence for random drift is, in our opinion, puzzling indeed. Active migration

cannot seriously be taken as an effective factor leveling off any of the differences arising by drift. The females of Solenobia are completely immobile and the fragile male moths living for some ten hours hardly can sustain an effective gene flow between populations isolated by vast stretches of rough terrain.

The proportions of heterozygous individuals are, on an average, equal in different diploid populations. The proportion of heterozygous loci per individual moth per locus in *Solenobia triquetrella* is 0.23 in diploid bisexual populations (calculated on heterozygosities expected on the assumption of a Hardy-Weinberg equilibrium), 0.25 in *XY* type parthenogenetic populations and 0.20 in *XO* type parthenogenetic populations. In fact, parthenogenetic populations should be more heterozygous than bisexual ones, since they can freely accumulate mutations, which are not eliminated by recombination and subsequent selection.

A correlation has been demonstrated between the physiological function of an enzyme and its amount of polymorphism in various species of Drosophila (KOJIMA, GILLESPIE and TOBARI 1970). In general enzymes involved in the primary production of energy are less variable than other enzymes. This relationship is probably not universal. In the Linz population of *Solenobia triquetrella* the proportion of heterozygotes per individual per locus coding for glucose-metabolizing enzymes is 0.25. The corresponding value for other enzymes is 0.31 in the Linz population. These figures are 0.12 and 0.13 in the Dürnstein (Austria) population of *Solenobia manni*, which is a bisexual species closely related to *S. triquetrella*.

Two alleles only ($Idh\text{-}1^{1.04}$ and $Me^{.98}$) are peculiar to the Finnish tetraploid genotypes. The Finnish tetraploid genotypes are geographically widespread in comparison with the central European genotypes—it may be noted that the area presented in Figure 5 is three times larger than Switzerland. The two major Finnish genotypes, the western and the eastern, represent probably two successful colonizing genotypes, the parthenogenesis and polyploidy of which are of different origin. The western one may have spread to Southwest Finland from Sweden over the Åland Islands and the eastern one from the east probably over the Isthmus of Karelia and the Leningrad area.

In comparison with tetraploid populations of *Otiorrhynchus scaber* (SUOMALAINEN and SAURA 1973), tetraploid *S. triquetrella* individuals have more than two alleles present at very few loci. These additional alleles could have arisen in an autopolyploid like *S. triquetrella* (cf., page 514) only after polyploidization. One reason for the low amount of additional alleles in *S. triquetrella* may be the mutation resistance of Lepidoptera—it has been established that their genes are less susceptible to mutation than usual (cf., e.g., SUGAI and MIRUMACHI 1973). Three alleles are present in single tetraploid specimens of *S. triquetrella* at one locus only, namely *Est-2*. One central European population and twelve Finnish populations have genotypes with three alleles at this locus. This may indicate that the northern European tetraploid genotypes are of older origin than the central European ones.

There are obviously very many independent parthenogenetic *S. triquetrella* populations in the central distribution area of the species in the Alps. Again the

number of different parthenogenetic genotypes is much smaller in Finland, where there are only two major types and a few minor ones in marginal areas. The degrees of genic variation are, however, quite similar in individual moths in central as well as in marginal populations. This is analogous with the situation observed in the chromosomal polymorphism *versus* genic polymorphism in several Drosophila species (e.g., AYALA *et al.* 1972). The Central European *D. subobscura* populations of the central distribution area are as polymorphic as the Scandinavian ones on the single-gene level but contain far more inversions than the latter ones (SAURA *et al.* 1973).

Bisexual and diploid parthenogenetic populations have not been found in Central Europe in the area which was ice-free during the Ice Age (between the Scandinavian and Alpine ice sheets). They have probably died out long ago. Therefore no new tetraploid populations have originated there for a rather long time. Accordingly, "strains", which have invaded northern Europe from any non-glaciated region, are old. Bisexual populations still live in the Alps and regions adjacent to them and may well continue to give rise to new diploid parthenogenetic populations. Tetraploid parthenogenetic forms originate from these diploid parthenogenetic populations. This is, in our opinion, the explanation for the great number of different parthenogenetic genotypes in the Alps and regions adjacent to them.

Collecting Solenobia is a most tedious job. Without the help of MR. KARL TÖPPEL, who kindly guided us to PROF. J. SEILER'S localities, the central European material would have been much scarcer. DR. JOSEF KLIMESCH sent us the Linz sample, for which we are most grateful. In addition to them, the following persons have helped us in the collections: JUHO ALVAS, PETER HÄTTENSCHWILER, JUHANI ITÄMIES, JAAKKO KANGAS, KALEVI KEYNÄS, MARJA-LEENA LAITINEN, HARRI LUOMA, DR. HANS MALICKY, ARTO RANTANEN, FRANZ RESSL, KAJ SAVONIUS, DR. RISTO TYNNI and PEKKA VAKKARI. PROFESSOR SEPPO LAKOVAARA has kindly criticized the manuscript. This study has been supported by grants from the National Research Council of Sciences of Finland, the Finnish Academy of Science and the Societas Scientiarum Fenniae.

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