Absence of isozyme variation in geographically isolated populations of the land snail *Chondrina clienta*

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Genetic differentiation of the rock-dwelling land snail *Chondrina clienta* was examined by enzyme electrophoresis in five isolated populations of an outlying area (the Baltic island of Öland, Sweden), and in one population from the species' main range (eastern Alps, Austria). Patterns of allelic variation were compared for 17 putative gene loci involving ten protein systems. All individuals from the five isolated populations on Öland were identically homozygous at all gene loci assayed. Snails from the eastern Alps were homozygous and allelically identical, but they differed by one isozyme band that was absent in animals from Öland and by different alleles fixed at three loci. The absence of isozyme variation and anatomical evidence indicate that self-fertilization may be the prevailing type of reproduction in *C. clienta*. The allelic identity of the five populations on Öland suggests that they were derived from a single strain, the origin of which probably consisted of one or few self-fertilizing individuals which colonized the island.

INTRODUCTION

The genetic differentiation of island populations is affected by propagule size, arrival time of founders, genetic structure, breeding system, reproductive rate, generation time, and rate of gene flow and selection (Baker and Stebbins, 1965; Endler, 1977; Berry, 1986). Theoretical and empirical evidence suggest that genetic bottlenecks over several generations and the mating system are the most important factors for differentiation among populations (Nei *et al.*, 1975; Williamson, 1981; Wool, 1987). It is often assumed that founder events can lead to a substantial reduction of genetic variation in island populations, and that changes in allelic frequencies provide opportunities for speciation (Mayr, 1963; Carson, 1984). However, it is still not clear how important founder events are in real populations (Barton and Charlesworth, 1984). Determining the impact of founder events is difficult, because the dynamic process of genetic differentiation can rarely be followed in nature and only the present level of differentiation of island populations can be examined and compared with that of putative source populations.

Chondrina clienta (Westerlund) is a rock-dwelling land snail which has a disjunct distribution as

it occurs far from its main range in central and southeastern Europe on the Baltic islands of Öland and Gotland and at one site on the Swedish mainland (fig. 1) (Kerney *et al.*, 1983; Gittenberger, 1984; Waldén, 1984). It has been surmised that *C. clienta* colonized these remote areas in Scandinavia from continental sources during the Boreal or Subboreal warm periods (8800–7500 and 4700–2800 years B.P., respectively) (Proschwitz, 1977; Waldén, 1986). On the island of Öland, the present-day distribution of *C. clienta* is patchy: changes in agricultural methods over the last century have fragmented the habitat of the species (heathlike grassland with exposed rock surfaces), and thereby increased the isolation of snail populations (Königsson, 1968; Rosén, 1982; Baur, 1988).

Here we compare genetic variation in five isolated populations of *C. clienta* from the island of Öland with that from a population of the eastern Alps (the species' main range) by assaying electrophoretic variation of enzymes.

MATERIALS AND METHODS

The species

Chondrina clienta has a cylindro-conical shell with an adult height ranging from 5.5 to 7.0 mm

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Figure 1 Distribution of *C. clienta* and sampling sites of our study. Hatching indicates the recent range of *C. clienta* (the occurrence in the Caucasus is beyond the eastern limit of the map) (after Kerney *et al.*, 1983; Gittenberger, 1984; Waldén, 1984). S₁–S₅ refer to the sampling sites on Öland (Sweden) and A to that in the eastern Alps (Austria).

(Kerney *et al.*, 1983; Baur, 1988). Confined to very special environment, it occurs in open limestone habitats, such as exposed rock-surfaces, stone walls and piles of stones (Kerney *et al.*, 1983; Gittenberger, 1984; Baur, 1987). The snails are particularly well adapted to rocky habitats; they exhibit a high resistance to drought (cf. Neuckel, 1981), and a specialized radula enables them to graze lichens from rock-faces (Schmid, 1929; Gittenberger, 1973; Breure and Gittenberger, 1982). The type of reproduction in *C. clienta* is unknown.

Specimens were collected from five sites (referred to as S₁–S₅) on the Baltic island of Öland (Sweden) in April 1987 and from one site (site A) in the eastern Alps (Austria) in August 1987 (fig. 1): S₁: Sandvik. Weathered limestone rocks at the edge of a quarry.

S₂: Gullehamn. Calcareous stone pile adjacent to a water-filled quarry, 20 km south of S₁.

S₃: Frösslunda. Stone wall made of flat pieces of lime stone, in the heath-grassland of Stora Alvaret, 45 km south of S₂.

S₄: Frösslunda. Stone pile, consisting mainly of calcareous rocks, separated by a 10 m belt of grass and herbs from the stone wall making up site S₃.

S₅: Enetri. Stone pile, consisting mainly of calcareous rocks, surrounded by arable land, 35 km south of S₃ and S₄.

A: Near Villach (Austria; 46°36'N, 13°50'E). South-facing dolomite rocks in a spruce forest (1100 m a.s.l.). Approximately 1200 km south of the sites on Öland.

At each site 70–100 fully-grown *C. clienta* were collected from an area of 5–30 m².

Electrophoresis

Individual snails were homogenized in cooled (4°C) 1.5 ml Eppendorf tubes containing 30 µl homogenization buffer (20 mM Tris-HCl pH 7.4, 2 mM EDTA, 2 per cent Triton-X-100, 2 mM Dithiothreitol (Schlegel, 1985)). After 20 min. lysis at 4°C the homogenate was centrifuged at

Table 1 Enzymes assayed and buffer systems used in the study of isozyme variation in *Chondrina clienta*

Enzyme	E.C. no.	Electrophoretic buffer*
Cytochrome-b ₅ -reductase (<i>Dia</i>)	1.6.2.2	TEB 8·2, TM 8·0
Esterase (α -Naphthylacetate) (<i>Est</i>)	3.1.1	TEB 8·2, TP 7·0
α -Glycerophosphatedehydrogenase (α - <i>Gpdh</i>)	1.1.1.8	TM 8·8
Hydroxybutyrate dehydrogenase (<i>Hbdh</i>)	1.1.1.30	TM 7·4, TM 8·8
Isocitrate dehydrogenase (<i>Idh</i>)	1.1.1.42	TC 6·3, TC 8·6, TEB 8·2, TM 8·8
Malic enzyme (<i>Me</i>)	1.1.1.40	TM 8·2
Peptidase (1-Leucyl-L-Leucine) (<i>Pep</i>)	3.4	TEB 8·2, TP 7·0
Phosphoglycoisomerase (<i>Pgi</i>)	5.3.1.9	TC 6·3, TC 8·6, TM 8·8
Phosphoglucomutase (<i>Pgm</i>)	2.7.5.1	TC 6·3, TM 8·8
Superoxide dismutase (<i>Sod</i>)	1.15.11	TC-LiOH 8·2

* TEB 8·2 = 0·5 M tris - 0·02 M EDTA - 0·65 M boric acid, pH 8·2, Gel 1:9; TC 6·3 = 0·223 M tris - 0·086 M citric acid, pH 6·3, Gel 1:27; TC 8·6 = 0·094 M tris - 0·0235 M citric acid, pH 8·6, Gel 1:5; TM 7·4/TM 8·0/TM 8·2/TM 8·8 = 0·1 M tris - 0·1 M maleic acid - 0·01 M EDTA - 0·01 M MgCl₂, pH adjusted with 1 M NaOH, Gel 1:9; TP 7·0 = 0·09 M tris - 0·12 M NaH₂PO₄, Gel 1:10; TC-LiOH = 0·19 M boric acid - 0·03 M LiOH, pH 8·2, Gel 0·045 M tris - 0·0072 M citric acid - 0·019 M boric acid - 0·003 M LiOH.

10,000 g for 15 min. The supernatant was immediately used for electrophoresis or stored at -70°C. Electrophoresis was carried out at approximately 5°C using horizontal 12 per cent starch gels (220 × 150 × 10 mm, Sigma-Starch and Connaught-Starch in proportions of 1·46:1) with an electric output adjusted to 10-12 Watt (for buffer systems see table 1). Techniques of starch gel electrophoresis and enzyme staining are as described by Shaw and Prasad (1970), Selander *et al.* (1971), Schlegel (1985) and Klemm (1988).

Fifteen enzyme systems were tested; ten systems representing 17 putative gene loci were stainable (table 1).

RESULTS

All individuals in the samples from the five populations on Öland were homozygous and allelically identical at all putative gene loci assayed (table 2). This suggests that all populations of *C. clienta* investigated on Öland represent a single strain.

Similarly, no electrophoretic variation could be found in individuals from the Austrian population; all snails were homozygous and allelically identical (table 2). However, snails from this population were characterized by the fast migrating isozyme *Dia*-2 absent in animals from Öland and by different alleles fixed at the *Dia*-1, *Est*-2 and *Pep*-1 loci.

Since there was no variation within populations, the mean heterozygosity was zero in all six populations. The mean genetic identity (I) between snails on Öland and those in the eastern Alps was 0·813 (according to Nei (1972); calculation based on the 16 loci in common).

DISCUSSION

Our study shows no electrophoretic variation within and among five populations of *C. clienta* on Öland. Although only 30 to 50 per cent of the variation at the DNA level can be detected by enzyme electrophoresis (Lewontin, 1974; Johnson, 1977; Selander and Whittam 1983), it does appear that the level of genetic variability in *C. clienta* is low.

Table 2 Distribution of genotypes in *C. clienta* from five populations on Öland (Sweden) (S₁-S₅) and from one population in the eastern Alps (A). The figures give the number of individuals assayed for each enzyme loci

Enzyme	Genotype*	Population					
		S ₁	S ₂	S ₃	S ₄	S ₅	A
<i>Dia</i> -1	100	25	25	31	17	33	0
	20	0	0	0	0	0	27
<i>Dia</i> -2	100	0	0	0	0	0	27
<i>Est</i> -1	100	20	20	26	15	33	27
<i>Est</i> -2	100	20	20	26	15	33	0
	95	0	0	0	0	0	27
<i>Est</i> -3	100	20	20	26	15	33	27
<i>Est</i> -4	100	20	20	26	15	33	27
α - <i>Gpdh</i>	100	10	10	10	10	18	10
<i>Hbdh</i> -1	100	10	10	15	15	18	10
<i>Hbdh</i> -2	100	10	10	15	15	18	10
<i>Hbdh</i> -3	100	10	10	15	15	18	10
<i>Idh</i>	100	28	28	31	12	33	24
<i>Me</i>	100	5	5	5	5	13	10
<i>Pep</i> -1	100	20	20	20	20	20	0
	80	0	0	0	0	0	27
<i>Pep</i> -2	100	20	20	20	20	20	27
<i>Pgi</i>	100	28	28	25	10	25	24
<i>Pgm</i>	100	18	18	22	22	31	24
<i>Sod</i>	100	20	20	20	10	10	24

* Designation of genotypes relative to the fastest band front.

Of all the factors determining the genetic structure of a population, none has a more profound effect than the breeding system (reviewed by Mather, 1973). Gastropods display a great variety of breeding systems, ranging from obligate outcrossing to frequent (if not obligate) self-fertilization and including parthenogenesis (Duncan, 1975; Fretter, 1984; Geraerts and Joosse, 1984; Tompa, 1984). The degree of allozyme variation is a strong indicator of the type of breeding system employed (e.g., Selander and Ochman, 1983; Brown and Richardson, 1988). Anatomical investigations indicate that *C. clienta* is aphillic in Austrian populations (Gittenberger, 1973, personal communication). In samples collected on Öland most of the individuals were aphillic (Klemm, unpubl. data). The absence of male copulatory organs in stylommatophoran snails indicates self-fertilization (or, alternatively, some type of parthenogenesis) as the exclusive breeding system (Duncan, 1975; Tompa, 1984). Is the absence of heterozygosity in *C. clienta* a result of obligate self-fertilization? Although we cannot rule out the possibility of an occasional outcrossing event, our evidence indicates that the amount of outcrossing in this species is very low.

Dispersal in *C. clienta* averaged 1 to 3 m per year, depending on type of habitat (stone pile or limestone pavement) (Baur, 1988). The five populations on Öland are spread over 100 km and thus are geographically isolated from each other. Since dispersal is restricted to stony habitats (Baur, 1988), even the two populations at Frösslunda might be isolated from each other. Owing to the low vagility of *C. clienta*, the present-day distribution of the species on Öland cannot be explained by subsequent active dispersal. It is likely that the foundation of new populations has been facilitated by accidental transport, by wind, water, birds or humans (cf., Rees, 1965). The genetic structure of the Öland populations suggests that they all derive from a single strain. Supralittoral deposits give evidence that *C. clienta* originally occurred also at the Estonian coast of the Baltic, where the species is now extinct (Schlesch, 1958). However, our data allow no conclusions about the origin of the Öland populations.

The lack of within-population heterozygosity in *C. clienta* is consistent with its probable breeding system. Nevertheless, the fact that five populations of *C. clienta*, separated by as much as 100 km, are identically monomorphic at 16 putative loci is a problem. We might expect mutation, natural selection, and drift to have fixed different alleles in isolated populations. Nei and Li (1975) developed

a method for estimating the probability of allelic monomorphism under the neutral mutation hypothesis. Using their model and assuming initial gene frequencies of one, population sizes of 10,000, and a mutation rate of 10^{-7} , which seems reasonable for electrophoretically detectable variation (Nei 1987), the probability of five isolated populations remaining identically monomorphic at 16 loci after 2500 generations is 0.30 (generation time of *C. clienta* is assumed to be three years; cf. Baur 1988). Thus, identical monomorphism among the five *C. clienta* populations on Öland is not unlikely. Empirical data also indicate that differentiation of isolated populations may require many thousands of generations. For example, Fowler and Morris (1977) were unable to detect any genetic variation in four widely separated populations of *Pinus resinosa* and postulated that mutation has not had sufficient time to reestablish heterozygosity in the approximately 20,000 years since an assumed bottleneck. Similarly, the populations of *C. clienta* on Öland have probably not had enough time since separation to incorporate different alleles. Due to the Pleistocene glaciation, populations on Öland cannot have existed for more than about 8000 years (Proschwitz, 1977; Waldén, 1986).

The apparent absence of genetic variation is unusual. For example, of 178 vascular plant species surveyed, only four (2.2 per cent) completely lacked genetic variation (Hamrick *et al.*, 1979; Hamrick, 1983; Ellstrand and Roose, 1987; Lesica *et al.*, 1988). By contrast, of 57 species of terrestrial gastropods surveyed, nine (15.8 per cent) completely lacked genetic variation, namely six slug and three snail species (Foltz *et al.*, 1982, 1984; Selander and Ochman, 1983; Boato, 1988; Brown and Richardson, 1988; this study). One of the snail species, *Rumina decollata*, is an obligate self-fertilizer, and a very successful immigrant in the southern United States (Selander and Kaufman, 1973; Selander *et al.*, 1974; Selander and Hudson, 1976), whereas *C. clienta*, another snail species with no enzyme variation, has narrow habitat requirements and a restricted range of distribution (cf., Kerney *et al.*, 1983).

Attempts to relate the frequency of selfing to factors such as niche breadth, habitat complexity and stability have been relatively inconclusive (e.g., Foltz *et al.*, 1984; Loveless and Hamrick, 1984; Nevo *et al.*, 1984; Lavie and Nevo, 1986). However, self-fertilizing species are likely to have an enhanced probability of colonization success and are able to reproduce even in absence of mating partners (Baker and Stebbins, 1965;

Tomlinson, 1966; Ghiselin, 1969; Baur and Bengtsson, 1987).

Snails from the Austrian population were also homozygous and allelically identical, but differed from the snails on Öland in three out of the 17 putative loci assayed. Inclusion of populations from the Baltic island of Gotland and of further populations from the species' main range (eastern Alps) would be particularly interesting in future studies of the possible path of colonization of *C. clienta*. Furthermore, a thorough study of the species breeding system, using cytological methods and breeding experiments is needed. While this study provides only an introductory look at the genetic variation in *C. clienta*, it shows that more detailed studies are warranted for determining the geographical scale and connectedness of the distinct strains within this species.

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