Genetic Structure and Climatic Correlates of Desert Landsnails

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Summary. Allozymic variation in proteins encoded by 20 loci was analyzed electrophoretically in 126 adult specimens representing 4 populations and 2 species of the desert landsnail Trochoidea, subgenus Xerocrassa, in a variable desert background of temperature and water factors. In addition, geographic variation in 3 morphological body variables of these snails was also studied. The results indicate that: (i) Most loci (55%) were strongly polymorphic; (ii) A large proportion of the polymorphic loci (55%) displayed fixation of alternative alleles either within or between species; (iii) Most of the variant alleles (75%) were not widespread, indicating sharp local and regional geographic differentiation; (iv) Southward progressive trends were found in genetic diversity, some allele frequencies, shell banding and body characters. (v) The mean estimates of genetic indices are: no. of alleles per locus, A = 1.69; proportion of polymorphism per population P = 0.41, and proportion of heterozygosity per individual, H = 0.07; (vi) The level of P increases and that of H decreases southward; (vii) The amount of variation in different functional classes of enzymes follows the Gillespie-Kojima and partly the Johnson hypotheses; (viii) Coefficients of genetic distance, D, between populations are high, D = 0.14, range 0.05-0.26. D's within species may be higher than between species. Likewise, D's from the northernmost population increase progressively southwards; (ix) Significant gametic phase disequilibrium occur in several populations in both species; (x) Deviations from Hardy-Weinberg equilibrium were found in several loci in some populations in both species; (xi) A statistically significant (P<0.001) amount of morphological variation of all 3 body variables occurs within and between species. Body diameter decreases with evaporation. (xii) P, H, and allozymic variation in several gene loci are significantly correlated with climatic variables, primarily related to some water factors and secondarily to temperature; (xiii) Shell banding was negatively correlated with solar radiation; and (xiv) Few correlations between allozymic and morphological variations were revealed.

The pattern of genetic variation of Trochoidea (Xerocrassa) seetzenii and T. (X) erkelii suggests that (a) climatic selection plays a major role in allozymic (and morphological) population structure and differentiation; (b) variation in allozyme and visual polymorphisms may provide the genetic basis for the complex physiological adaptations of landsnails enabling them to survive in hostile, hot and dry deserts, and is therefore partly adaptive rather than neutral.

Introduction

The debate whether allozyme variation in natural populations is selectively meaningful or adaptively neutral is still going on (Lewontin 1974; Kimura 1979). Direct correlation between allozyme variation and the environment is one promising avenue to elucidate the riddle, since it emphasizes the role of ecology in population genetics. Likewise, if allozymic variation is shown to be associated with locus function (Gillespie and Kojima 1968; Johnson 1974) its supposed neutral nature may be challenged.

Molluscs are suitable for testing evolutionary genetics theories due to their largely sedentary nature which results in marked differentiation of populations to local conditions. Previous studies of landsnails suggest that climatic selection affects shell (Bar 1978; Bar and Nevo 1976; Jones et al. 1977) as well as allozymic polymorphisms (Nevo and Bar 1976; Nevo et al. 1981a), on both the macro- and microgeographical (Nevo et al. 1981b) levels. We have tested in this study the genetic structure of 4 populations and 2 species of the desert snail Trochoidea (Xerocrassa) seetzenii and T. (X) erkelii in Israel in a search for climatic correlates; and compared it to the genetic patterns found in other desert snails, genus Sphincterochila (Nevo et al. 1981a).

Materials and Methods

Systematics, Distribution and Ecological Background. The taxonomy, morphology, anatomy, distribution and habitats of the members of the subfamily Helicellinae of Israel and Sinai, including all 20 xeric species of Trochoidea subgenus Xerocrassa in Israel and Sinai, have been described in detail (Forcart 1976). Trochoidea (Xerocrassa) seetzenii was studied extensively by Yom-Tov (1970a) in terms of predation and population density (1970b), thermoregulation (1971a), water balance (1971b), feeding patterns (1971c), general biology (1971d) and reproductive strategy (1972). In this article we refer to the 2 species as Xerocrassa seetzenii and X. erkelii.

Xerocrassa seetzenii is a habitat generalist species living in dry steppes from Iraq to the Negev and northern Sinai. Its main range in Israel is from the Dead Sea basin through the Judean desert to the central Negev. It ranges altitudinally from -380 to 1,035 m, and under rainfall regimes from below 50 up to 700 mm, involving primarily xeric habitats but extending also northward into Mediterranean biota. Relative to the former species the second species studied, Xerocrassa erkelii, is a habitat specialist species, living primarily in extreme desert environments in the Sinai desert from Cairo in the west to the Israeli Negev in the East. It ranges altitudinally from 0 to 900 m, and under rainfall regimes from below 100 up to 200 mm living exclusively in desert habitats.

Sampling. A total of 126 adult specimens representing 4 populations and 2 species were sampled in Israel involving 3 populations of Xerocr-
Fig. 1. Geographic distribution of sampling localities of Xerocrassa in Israel

rassa seetzenii and 1 population of Xerocrassa erkelii. Sampling in all localities was conducted on 1 January 1976, during the winter breeding period. Data on localities and ecogeographical parameters are given in Table 1; distribution is shown in Fig. 1. Each of the 4 samples was collected in an area of about 100 m. The 4 populations are distributed largely along a southward transect from the Judean desert to the Negev desert.

Electrophoresis. Live specimens were homogenized in the laboratory after recording morphometric and shell-banding data. Allozymic variation of enzymes and other proteins encoded by 20 gene loci was studied by standard starch gel electrophoresis with procedures described in Selander et al. (1971). The 20 loci coding for soluble proteins studied are given below. Isozymes and alleles were designated numerically and alphabetically, respectively, in order of decreasing mobilities of their allozymes. The 20 loci are classified according to function, following Gillespie and Kojima (1968):

Group 1: Glucose Metabolizing Enzymes, malate dehydrogenase (E.C. 1.1.1.37) (Mdh-1), alpha glyceraldehyde dehydrogenase (E.C. 1.1.1.37) (αGpdh); isocitrate dehydrogenases (E.C. 1.1.1.42), 2 loci (Idh-1,2); phosphoglucomutase (E.C. 2.7.5.1) (Pgm); phosphoglucone isomerase (E.C. 5.3.1.9) (Pgi); hexokinase (E.C. 2.7.1.1) (Hk). Group

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Table 1. Ecogeographical data for populations of 2 species of Trochididae (Xerocrassa) in Israel

<table>
<thead>
<tr>
<th>Species</th>
<th>Population No.</th>
<th>Locality</th>
<th>Long. (°E)</th>
<th>Lat. (°N)</th>
<th>Mean Temp. (°C)</th>
<th>Rainfall (mm)</th>
<th>Humadity (%)</th>
<th>Evaporation (mm)</th>
<th>Clouds (°N)</th>
<th>No. of Days with Rain</th>
<th>No. of Days with Snow</th>
<th>Inter. border</th>
<th>Xerocrassa seetzenii</th>
<th>Xerocrassa erkelii</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trochididae</td>
<td>1</td>
<td>Qumran</td>
<td>35.45</td>
<td>31.87</td>
<td>15</td>
<td>24.7</td>
<td>100</td>
<td>90</td>
<td>0.3</td>
<td>12</td>
<td>1</td>
<td>0</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>(Xerocrassa</td>
<td>2</td>
<td>Meitar-El-Shalem</td>
<td>34.67</td>
<td>31.66</td>
<td>15</td>
<td>24.8</td>
<td>100</td>
<td>90</td>
<td>0.3</td>
<td>12</td>
<td>1</td>
<td>0</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>seetzenii</td>
<td>3</td>
<td>Yeroham</td>
<td>34.30</td>
<td>31.98</td>
<td>15</td>
<td>24.8</td>
<td>100</td>
<td>90</td>
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<td>12</td>
<td>1</td>
<td>0</td>
<td>0.3</td>
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</tr>
<tr>
<td>erkelii</td>
<td>4</td>
<td>Mitzpe Ramon</td>
<td>34.80</td>
<td>30.60</td>
<td>15</td>
<td>24.8</td>
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<td>1</td>
<td>0</td>
<td>0.3</td>
<td>0.3</td>
</tr>
</tbody>
</table>

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* Plant community according to Plant Communities Map by Danin A. & M. Nadmore: 10 = Artemesia herba-albae, 12 = Zeyherophyllum damasii

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* Soil type: 1 = Desert soil, 2 = Loess

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