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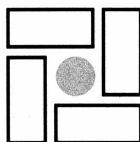
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Member of the Russian Academy of Sciences
Director of the Institute of Plant and Animal Ecology,
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The Ecological Dependence of Ontogeny and Phylogeny in Mollusks

I. M. Khokhutkin

*Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences,
ul. Vos'mogo Marta 202, Ekaterinburg, 620144 Russia*

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Abstract—Population polymorphism was studied in terrestrial mollusks of the order Geophila. Polymorphism patterns were analyzed in species from closely related higher taxa. Biological characteristics of the studied species, as well as the literature data on terrestrial gastropods, indicate that *K*-selection occurred in their populations. This type of selection determines a higher functional efficiency of populations in a biogeocenosis. In this case, the population gene pool accumulates, in the course of stabilizing selection, the genes improving fitness, which results in the formation of an integrated phenotype displaying the maximum possible adaptation. Thus, a colonial system of population complexes develops. A sustainable functioning of the population is ensured by maintaining the constancy of its characteristics, i.e., the population homeostasis. The corresponding characters and properties are formed and preserved in the course of phylogeny on the basis of morphological and physiological characteristics that are genetically determined and expressed during ontogeny of the given form.

The problem indicated in the title is complex, has no unambiguous solution, and has not been sufficiently covered in the literature. In our opinion, two studies contain the most important conclusions.

The importance of any given form of variation differs according to the environmental conditions. I.I. Schmalhausen (1968) considered this subject in detail. Stable organisms, including animals with autonomous morphogenesis, display a considerably higher individual stability of forms than labile organisms. In the course of phylogeny, stability is determined by a higher importance of variation in the factors of homogeneous environment rather than regular factors of heterogeneous environment. The latter factors (which are either temporary or local) determine a labile organization. This is especially true for animals with mosaic development, such as mollusks. However, sedentary marine mollusks exhibit a wide skeletal modification. Variation in the mosaic organisms is characterized by the occurrence of pronounced mutation-dependent differences, whose discrete nature is more or less obvious.

The biological importance of stability is determined by the fact that the ecologically limited, homogenous environment imposes stringent requirements. The organizational stability as a consequence of autonomous development implies a complex regulatory mechanism, which protects normal morphogenesis against possible disturbances caused by random deviations of environmental factors. As morphogenetic processes are integral and depend primarily on the intrinsic developmental factors, the same regulatory mechanism also protects normal morphogenesis against some random changes in these factors, i.e., against mutations. In this case, ecological polymorphism is expressed as genetic

polymorphism or heteromorphism. In other words, it is based on a continual segregation of stable forms adapted to specific ecological conditions. At the genus level, adaptations to the types of ecosystems (biogeocenoses) are formed; these adaptations are considerably restricted by environmental conditions. At the species level, adaptations to specific physical and chemical conditions, primarily to temperature, arise. While the formation of adaptive morphological characteristics is based on selection of phenotypes with adaptive advantages, the ecological and physiological properties of the genotype are determined by the ecological and physiological adaptation and translation of selection to the cellular and molecular levels in the course of speciation (Golikov, 1973).

Consider the polymorphism of a "mosaic" organism in terrestrial mollusks of the order Geophila as an example. For this consideration, we will choose only one type of discrete variation. In terms of genetics, the continuous intraspecific variation, which has been repeatedly discussed in literature, has no fundamental differences from the discrete variation; however, it requires a separate analysis. Consider the discrete variation at the population level and analyze its patterns in species belonging to closely related higher taxa.

THE GENERAL CHARACTERISTICS OF VARIATION IN MOLLUSKS

The elementary traits of the shell color form two phenotypic systems: the overall background and the presence or absence of spiral or transverse colored bands on the shell (banding). In genetically studied species, these traits characterize the population polymor-

phism. In a polymorphic population, the most frequent phenotype is not necessarily determined by dominant genes. In populations of some species, recessive alleles may be more frequent than dominant (Komai and Emura, 1955; Cain, 1958). Polymorphism has only been studied comprehensively in a few cases; 14 species of terrestrial mollusks were analyzed in this respect (Clarke *et al.*, 1978). Note that in all studied species of terrestrial mollusks, shell banding is inherited as a monogenic trait. In quantitative studies of polymorphism, the numbers of animals without bands (morph 0) and with one or several bands on the shell (morphs I, ..., n) are recorded. The ratio between the frequencies of morphs is usually expressed as the frequency of the recessive gene (q) (Li, 1978) or, if the inheritance of the morphs is unknown, as the proportion or percentage of one of the morphs. The pattern of shell coiling (clockwise or counter-clockwise) is another polymorphic character. This study does not deal with the latter type of polymorphism.

Phenotypes in General As an Object of Natural Selection

The phenotype as an integral system experiences interrelated transformations. Populations of many mollusk species are strictly localized; i.e., their population and even species ranges are restricted. In these species, various aspects of speciation have been studied. One field of research is the phylogenetic importance of geographic isolation in terrestrial mollusks. Gulick (1905) considered geographic isolation the main factor of speciation; this author emphasized the differentiating role of random isolation of small animal groups. Crampton (1916) analyzed this problem using mollusks of the genus *Partula* as an example. In all early studies, the role of natural selection was, to a certain extent, underestimated in favor of isolation. All authors emphasized that polymorphic traits were neutral, and that differences between populations were random. Schmalhausen (1968) noted that, although isolation is important for intraspecific differentiation, it is not a necessary condition for evolution. Some authors attach more importance to the spatial isolation, compared to the degree of isolation of individual colonies and populations. In widespread species, the spatial isolation of peripheral populations from "central" ones protects new genetic complexes from the destructive effect of panmixia (Cain, 1958; Clarke and Murray, 1969).

ORGANIZATION AND VARIABILITY OF THE SPECIES POLYMORPHIC STRUCTURE

The methodological approaches to estimating color polymorphism have been described above. It is difficult to compare the adaptive values of different morphs, because they differ in many characteristics important for selection, including reproduction rate, fecundity, metabolism, survival under unfavorable conditions,

behavior, etc. Polymorphism is polyfunctional; i.e., it depends on various factors (Sheppard, 1970). Some authors (Lamotte, 1951; Komai and Emura, 1955; Goodhart, 1962) concluded that the population polymorphism is unrelated to the biogeocenotic factors; i.e., polymorphic variants are indistinguishable from one another in terms of selection. In later studies, the same authors eventually decided that different forms of selection interact with one another and with the founder effect. It has been demonstrated that a balanced polymorphism in natural populations is stable; in this case, the distribution of color types may remain unchanged for a long time. In such populations, stabilizing selection occurs (Kalabushkin and Altukhov, 1974).

Although the polymorphism of shell color and pattern is characteristic of many mollusk species, they are not universal: related species are often monomorphic with respect to these traits. However, many of them are polymorphic with respect to the isozyme composition and other traits that are not revealed visually. Goodhart (1987) supposes that all species possess the genetic basis of the exterior diversity; however, in the majority of species, a single phenotype or a small number of phenotypes are adaptively favorable. In these species, the external expression of genetic diversity is suppressed by selection for epistatic genes.

The Genetics of Shell Banding

Cross-fertilization prevails in natural populations of many hermaphroditic species of terrestrial univalves, with rare exception (Murray, 1964; McCracken and Brussard, 1980). Earlier, others and I demonstrated that shell banding was inherited as a monogenic trait in the snail *Bradybaena fruticum* with the dominant absence of the bands; the morph I was homozygous for the recessive allele. In the colonies of this species living near Sarapul (the Pre-Ural region), the variations of the polymorphic structure are less pronounced than those expected under the constant pressure of inbreeding characteristic of self-fertilization. It may be safely suggested that a considerable panmixia occurs in the colonies of an integrated population complex. Taking into account certain mechanisms inherent in gastropod populations, the effective population sizes should be assumed to be at least 1.5–2 times larger than the observed values. These mechanisms, which are also characteristic of the given species, include multiple mating and long-term storage of sperm by the animals (Murray, 1964; Clark, 1978). These are adaptations to a drastic decrease in the size of the reproductive group.

The Intrapopulation Variation of Shell Banding

Polymorphic species are a suitable model for studying many aspects of microevolution. Species of the suborders Achanatini and Helicina (order Geophila) have been most comprehensively studied in this respect. The data on these species have been reported in single stud-

ies and reviews (Jones *et al.*, 1977; Clarke *et al.*, 1978; Matekin and Makeeva, 1977). Although population structures have been adequately addressed in the literature, many problems are far from being definitely solved. The difficulties are accounted for by the fact that many studies were relatively short-term and, hence, could not take into account temporal variations of some parameters that might substantially affect the original characteristics of the given structures.

The studied colonies of the different *Br. fruticum* population from Sarapul inhabit sites of a floodplain mixed forest. The studied area extended for 4 km in a north-south direction. A smaller northern plot of the forest (about 10 ha) was separated from a larger forest by a meadow and a bog, where this species did not occur. Although the larger forest had a heterogeneous microrelief, it was almost entirely populated by colonies of the studied snail. Between these plots, at a distance of 3 m from each of them, a forest island (200 m²) was located. A path rounded the island on both sides. In rainy seasons, the path overgrew with nettle; in some years, the smaller plot and the island extended to touch each other. Therefore, the isolation between the plots was incomplete.

In all the colonies, the studied parameter exhibited pronounced fluctuations. The comparison of colonies confirmed that differences between them were significant and, hence, the colonies' specificity was preserved. However, relatively small and often unidirectional fluctuations of the parameter studied suggest that this habitat contained an integrated population system in the form of semiisolated panmictic colonies. Therefore, we may suggest that large populations of *Br. fruticum* exist in the form of subdivided populations consisting of semiisolated panmictic colonies.

Interpopulation and Interspecific Variation of the Polymorphic Structure

In population genetics, the concept of "breeding size" is accepted. This term refers to the number of individuals that are actual ancestors of the next generation. In other words, they actually contribute to the genetic composition of the next generation (Li, 1978). There are three distributions of q that correspond to a given effective population size. The empirical distributions of q in the reproductive and crossing groups of *Br. fruticum* from the Sarapul population were close to the theoretical distribution that corresponded to a large effective size. In the given case, this is an l -shaped normal distribution with a very narrow base and a high peak (Li, 1978). Gene frequencies are grouped around the point of stable equilibrium, which is determined by counteracting systemic pressures of mutations, selection, and migration. A population comes to such a state if the biogeocenotic factors are dynamically constant.

In the Sarapul population, as well as in a population living near Talitsa (the Trans-Ural region), the propor-

tion of each homozygote increased by the value of the q variance at the expense of the decreasing proportion of heterozygotes. This indicates that the population was subdivided with respect to the given set of traits. The variance of q in different groups was a measure of differentiation (heterogeneity or variability); it may also be used to estimate differentiation in a large population uniformly distributed over its range. The inbreeding coefficient (F) is directly proportional to the q variance. If F is equal to or less than 0.005, the differentiation is insignificant, as was the case in the studied population. In a large population continuously distributed over a wide area, crossing is confined to a "neighborhood," so that crossing between two distant animals is almost impossible. Such populations exhibit an implicit form of subdivision known as isolation by distance.

To compare the variation in total populations, I analyzed the distributions of q in them. In the Sarapul population, q varied from 0 to 0.6; in the Talitsa population, from 0.2 to 0.8; the weighted average values were 0.4 and 0.5, respectively. Notwithstanding the large overlapping, the difference between the populations was significant. Thus, the difference in polymorphic structure of populations from geographically close areas was revealed.

The results of ANOVA in the corresponding pooled samples indicated that the levels of variation within the groups and in the entire sample were almost the same. The intergroup differences in this value were the most significant. Variations between colonies of the subdivided population and between populations of different geographic regions were of the same order of magnitude (0.02–0.07), whereas the variation between all populations of the species was an order of magnitude higher, approaching the interspecific differences in the studied order (0.26–0.29).

The range of the microgeographic variation in *Br. fruticum* was relatively small; the q value varied from 0.42 to 0.60 for different biotopes. This was most likely due to a similarity between microstations. Typically, biotopes differed considerably from one another in the frequencies of different morphs in populations. In the biotopes that were the least favorable for the given species, q was the highest. In the entire species range, q exhibited a clinal variation. Data on the microgeographic (biotopic) variation of shell banding were analyzed. As a rule, the proportion of shells with few or no bands increased with the absolute altitude of the habitat. In open habitats, this proportion was higher than in forests.

POLYMORPHISM AND STRUCTURE OF HIGHER-RANK TAXA

Superspecific variation is determined by complex relationships. These are interactions between populations of phylogenetically related or distant species in biogeocenoses, environmental differences or similari-

ties of biogeocenoses, and epigenotypic "restrictions" imposed on the phenotype. It is generally accepted that the majority of genetic differences between closely related species are accounted for by the existing polymorphism. Ecologically and phylogenetically similar species usually have similar variation patterns. In many species, variation had "parallel" trends, so that their traits copy each other. In general, related species display allopatric convergence and sympatric divergence (Solem, 1985). This confirms the concept of biological interaction between related species (Schindel and Gould, 1977). In other words, the original genetic information is preserved, which determines the continuous succession of taxon development. However, regarding the divergence, we may regard higher-rank taxa formed by certain groups of species as adaptive types. The hierarchical succession of taxa may be described by the exponential function. This structural pattern is related to the considerably higher number of monotypical groups and groups comprising fewer subordinate taxa, compared to polytypic groups.

Differences in significant phenotypic variables make it possible to estimate with sufficient certainty the differences between species that emerged in the course of their development, when each species occupied a new ecological niche. To date, the genetics of shell-color patterns of four species from the suborder Achatinina, as well as one Pupillina and nine Helixina species, have been studied. Most species are polymorphic for one elementary system of color pattern, namely, the shell banding pattern. Most likely, the original variant was a shell without bands or, to be precise, a dark gray shell with a light margin. A possible direction for future change in color pattern is the general lightening of the background and the secondary emergence of a pattern formed by spiral bands and spiral rows of color spots (Shileiko, 1978).

Regarding different types of the distribution of bands over the shell, note that all these morphs belong to the same system of traits forming the parallel variation series. Shells of some species have a slanting or transverse band instead of a spiral one. In some species, the number of bands on the shells is considerable. There are various types of fusion and division of the bands; these patterns are under polygenic control. The genes of the background color are known to be linked to the genes of the shell banding pattern; they are often considered supergenes. Now consider these patterns only in several representatives of the studied suborders.

In the suborder Achatinina, the absence of bands is a dominant trait; in the suborder Helixina, dominance is variable—the unbanded morph is dominant in five species and recessive in four. In *Brephulopsis bidens*, the unbanded morph is dominant. In terms of morphology, the species *Br. fruticum* is most similar to the original form of the entire family Bradybaenidae (Shileiko, 1978). In this species, the unbanded morph, which is dominant, is most frequent. Almost all remaining

Br. fruticum have one band on the shell. There are also two mutant forms with two or three bands and four bands, respectively; their frequencies are about 0.02%. Species *Br. schrenki* and *Br. transbaicalia* originated from the species *Br. fruticum*. It is most likely that in the former species, the unbanded morph is recessive; it is observed in 9% of the animals. In *Br. transbaicalia*, the inheritance of the banding pattern has not been studied; the frequencies of the two morphs do not differ significantly. *Bradybaena lantzi* is closely related to the aforementioned species. In this species, the three-banded morph is prevalent, with all other morphs been found only as "relicts," i.e., reverse mutations. In *Br. almaatini*, which is close related to the latter species, the frequency of the unbanded morph is 13%; the mode of its inheritance is unknown. In populations of *Br. similaris*, an eastern Asian species of this genus, most animals have a recessive unbanded morph (the species average frequency is 88%). In *Cepaea vindobonensis*, the main color patterns are two-banded morphs. In two other *Cepaea* species, the five-banded morph is prevalent, whereas the dominant morph is the unbanded one. In *Cochlicella acuta*, the two-banded morph is prevalent and the unbanded one is recessive.

Species of different superfamilies of the infraorder Helixinia are abundant in the Holarctic and even outside it (Shileiko, 1979). The distribution of species of the superfamily Helicoidea by groups of characters is the same in America and other regions. On average, it is drastically different from this distribution in the superfamily Hygromioidea. The difference in distributions of unbanded species is pronounced, whereas the difference between unbanded Helicoidea species from America and other regions is considerably smaller (26.2 and 4.1%, respectively).

Based on the phylogeny and the history of species expansion, species from the studied superfamilies may be assumed to be parts of biotic communities in the following regions: North and South America, West Europe, the former Soviet Union (the European part, the Carpathians, the Caucasus, the Crimea, Central Asia, Altai, Siberia, and the Far East), the Philippines, and Australia. Each region is characterized by a certain number of species with a certain set of characters forming a system. Species of the studied taxa are abundant in the Palearctic. In many regions, they constitute a considerable part of biotic communities, or associations outside the communities. To estimate phenetic similarity, I used the method of calculating the resemblance function based on binary ratios. The main results of this analysis are the following. In the course of speciation in the superfamily Helicoidea, North America became the center of taxon formation; the association between traits of different species regularly decreased with an increase in the distance from this center. In this region, the proportion of polymorphic species was maximal. This indicates that polymorphism is adaptive; it is only formed in the course of a long-term interaction of a species with the factors of the

corresponding biogeocenosis. The widest genetic variation and the greatest number of polymorphic species were found in the families that comprised the greatest number of polytypic species. The method of data analysis that I suggest in this study is based on the notion that the entire evolution may be described as a biogeographic whole (Grehan, 1988); each biota may be regarded as an integrated set of morphologically and geographically differentiated taxa.

CONCLUSION

Evolution is based on variation. Individual variability is the basis of the historical changeability of organisms. Studying evolutionary changes in organisms, phylogenetics analyzes the temporal series—or, to be precise, the evolutionary development—of living organisms (Skarlato and Starobogatov, 1974). Responses of an organism to environmental factors are originally functional irritants that, in turn, induce a morphogenetic reaction. The pattern of the latter is primarily determined by the organism itself (rather than the environment) and, in particular, by the ontogenetic stage at which the organism is exposed to external factors. Most probably, the organism has not been affected by the given factors at the same rates, if at all, in the course of evolution. The effects of these factors depend on the nature and strength of their action, as well as individual characteristics of the organism, primarily, its physiological state (Schmalhausen, 1968).

Analysis of biological features of the studied species and published data on terrestrial gastropods indicate that their populations experience *K*-selection. This type of selection increases the functional efficiency of populations in given biogeocenoses. In the course of stabilizing selection, the population gene pool accumulates the genes that improve fitness. This yields an integrated phenotype adapted to its environment to the highest possible extent. Ultimately, a colonial system of population complexes develops. The sustainable functioning of a population is ensured by maintaining its parameters at a constant level, i.e., by population homeostasis. The corresponding traits and properties are formed and preserved in the course of phylogeny on the basis of morphological and physiological characteristics that are genetically determined and expressed during ontogeny of the given form. The integrity of a species is accounted for not only by the gene flow, but also by the fact that all its populations possess the same homeostatic systems, with this species-specific canalization ensuring a sufficient stability.

Interaction between species takes forms of competition and coevolution. In general, evolutionary processes in related species are interconnected. Only a few possible genetic combinations are actualized in macroevolution, so that the whole process is directional. The directions of macroevolution are determined by natural selection on the basis of diverse variation at the population level. This makes it possible to reveal the impor-

tance of genotypic determination for macroevolution. The rates of the previous evolution of traits are reflected by the existing differences between taxa.

Adaptation of biological systems of a certain rank is based on the structural and functional diversity of genetically variable elementary systems of traits. Selection is directed to coadaptation of structures in integrated biological systems. All structures are based on the same elementary systems of traits, which determine functional characteristics of populations and cenoses as integral systems. Genetically related species are interconnected and behave as a single object in the course of evolution. This indicates that higher taxa are also integral. Homeostatic mechanisms manifest themselves at structural levels.

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