INTRASPECIFIC VARIABILITY AND SPECIES-FORMATION: EVOLUTIONAL AND GENETICAL ASPECTS OF THE PROBLEM

SCHWARZ S.S.
The Institute of Plant and Animal Ecology of the Urals Research Centre of the USSR Academy of Sciences, Sverdlovsk, USSR

1. Intraspecific variability is a form of adaptation of a species to the conditions of existence and a requisite of evolution. Its most important manifestations include individual (variability within the confines of single settlements in a given time interval), chronographic (variation of the mean norm of variability at different stages of a population's life cycle and in different years), micropopulational (differences between chronological subdivisions of a common population), interpopulational, geographical. The unity of all manifestations of intraspecific variability.

All signs and characteristics of animals are subject to variability: from body size and proportions to tissue biochemical peculiarities and molecular structure of intracellular proteins. The part of genomic and ergonic correlations in the manifestation of variability; variability of basic and related characteristics. Body size, growth rate and morphological peculiarities which determine the conditions of maintaining the energy balance — the most important of the essential characteristics which determine the general manifestation of variability of concrete populations.

Homeostatic reorganisation of the generic structure of a population and microevolution. Similar to macroevolution, microevolution is
irreversible. The initial stage of a microevolutional process—variability of characteristics and properties of animals, which determine the character of their relationships with environment.

2. Morphophysiological and genetic distinctions between intra-specific forms of different ranks. Immunogenetic studies which substantiate notions on the dissimilarity of the extent of morphophysiological differentiation and genetical distinctions. The particular importance of genetic distinctions, between close morphophysiologically identical populations. Developing in identical conditions the genetically non-identical populations, which are governed by the laws of stabilizing selection and the principle of optimum phenotype preserve their morphological similarity against the background of increasing genetic distinctions (a result of different forms of genetico-automatic processes). The basic possibility of accumulating genetic distinctions among non-distinct populations up to the level of a "species rank" and the emergence of the incompatibility of genomes of undistinguishable populations; the origination of twin-species—a consequence of stabilizing selection.

3. The immunological unity of a species. Experiments into the study of the transplantation immunity indicate that any population (including a population of sharply differentiated subspecies) distinguishes a population of its own species from any other population. It has been found by experimentation that extreme immunological distinctions among animals belonging to one and the same population, most cases surpass the average differences among sharply differentiated intraspecific forms. Taking into consideration the relation of genetic peculiarities in a population to their morpho-physiological properties, the results of these observations should be viewed as proof of the fundamental impossibility of a chiasm even among sharply differentiated subspecies. The empirical criterion of a species that has been elaborated by specialists in taxonomy is substantiated by biochemical investigations.

4. Any intrapopulation grouping of animals (chorological or functional) is genetically unique. The dissimilar genetic structure of different age groups, seasonal generations and micropopulations of animals indicate directly to the dependence between the ecologic and genetic structure of populations. The change in the ecological structure of a population entails without fail a change in its genetic composition; an induced change in the ecological structure is the basic ecological mechanism of evolution.

5. Intraspecific variability and species formation. Intraspecific
variability—a prerequisite of species-formation; the formation of differentiated intraspecific forms and species, however, follows different pathways. In the first case, adaptation to the conditions of existence occurs through an intensification of the functioning of individual physiological systems (hypertrophy of the heart and lungs, increased hemoglobin concentration in the blood of mountain populations of widespread species; similar changes and a sharply increased fertility related to increased energy consumption in the arctic forms, etc.). During the assimilation of a new environment of habitation by intraspecific forms the natural selection which in the first stage of a population reorganisation operated mostly on the functional basis begins to operate in keeping with the system of energy appraisals. The animals which are characterized not by morpho-physiological (functionally perfect but unprofitable in terms of energy) but biochemical tissue adaptation in settling the ecological tasks facing the specific populations with the least expenditure of energy gain definite advantage. The first pathway of adaptation is characteristic of specialized intraspecific forms, the second—of species. An object confirmation of these views: upon the macrophysiological level closely related species differ by infinitely smaller distinctions than the clearly differentiated subspecies. This makes it patent that the "species or not" dilemma is settled by no means on the morphological level.

6. The notion of different animal adaptation ways which characterize the two most important trends of initial stages of the evolution (intraspecific differentiation and species-formation) is corroborated by comparing close forms on the genom level (the structure of DNA molecules, molecular hybridization). The studies on close forms of voles have made it clear that the extent of genetic distinctions between differentiated intraspecific forms (subspecies) might be greater than among species. The gen-specific material of Microtus oeconomus oeconomus Pall. has greater similarities with the DNA of M. arvalis Pall. than with the DNA of M. oe. chahlovi Seal. Morphological DNA-coded peculiarities of the arctic form of M. oeconomus required greater changes on the genom level than the distinctions between the initial (forest-steppe) form of M. oe. oeconomus and M. arvalis (the genetic value of the subspecific distinctions proved to be greater than the specific differences). This means that the noted most important evolutional dilemma (species or not?) is resolved not on the strength of the volume of genetic distinctions but by their substance, by the ecological consequences to which these distinctions lead. This gives
us the right to take our conclusion a step further: the question: "species or not?" is resolved neither on the physiological or the genetical level, but on the ecological level: a species is characterized by the unique type of its association with the environment, it occupies a unique and unrepeatable place in the biosphere and in a concrete biocenosis. The genetic isolation is a consequence rather than the cause of species-formation. It is only natural that the trunk-line of initial stages of the evolution which creates the requisites for subsequent macro-evolutionary reorganisations does not preclude some or other partial and peculiar ways of emergence of new species (species-formation on islands, in the circumstances of impoverished biocenoses and weakened struggle for existence; the genetical isolation of related forms which have not reached the level of species differentiation, as a result of accidental, ecologically avoidable changes in the chromosome apparatus, etc.) but the general course of the evolution of individual groups, accompanied by the morphophysiological progress and the evolution of communities (progressing effectiveness in utilization of environmental resources) testifies in favour of the ecological determination of intra-specific differentiation and species-formation.