

# Aphids and a step toward the universal species concept

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Received October, 26, 1982; March 20, 1984

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**ABSTRACT:** The facts now accumulated have made some biologists revise the widely accepted "biological species concept." New data concerning structure, function, and evolution of populations and species in aphids are considered in the paper. The fact that aphids have complicated groups that are sometimes a mixture of "biospecies" and "agamospecies" belonging to the same species and even to the same population, has motivated the development of a more or less universal concept of population and species, using also data on other groups. I argue that populations and species are particular, self-regulated, dynamic and potentially eternal living systems capable of adaptations determined by the genotypes of individuals. A population is a group of individuals in a particular ecosystem whereas a species is a set of populations bound to a set of similar ecosystems (homocenoses). Hence stabilizing selection, which safeguards those adaptations common to all populations of a species, is the principal mechanism for integrating a species. Interpopulation exchange of genes is responsible not so much for integration of the species as for its dynamics and homeostasis. Isolation of populations and their groups within a species is therefore relative, whereas isolation of a species is more or less absolute. I consider the implications of this viewpoint on taxonomic, spatial and temporal parameters of species.

Various aspects of the biology of aphids are important for general questions such as regulation of populations, speciation, variation, the process of adaptation, assimilation of acquired characters, and the integration of species.

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## Introduction

The species concept presents a perennial problem and we are far from its definitive solution. Nevertheless we approach understanding of this phenomenon.

What is called "the biological species concept" (BSC) is widely accepted. The BSC is treated in books by Dobzhansky (1951, 1970), Mayr (1963, 1970), Timofeeff-Ressovsky et al. (1977), and Dobzhansky et al. (1977). Populational thinking is a virtue of modern biologists and it is natural to assume that the main merit of the BSC is to consider a species as a reproductively isolated and often polytypic group of populations having a common gene pool. Unfortunately, since the BSC has only one criterion of species (reproductive isolation), it

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Evolutionary Theory 7: 1-39 (May, 1984)

The editors thank two referees for help in evaluating this paper.

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cannot reflect the plurality of forms of species existing on Earth. No wonder that many authors consider the BSC not as the biological but as the genetical (Sinskaya, 1948; Imbrie, 1957; Simpson, 1961. etc.) or the reproductive species concept (Van Valen, 1976).

The BSC is also incapable of accounting for the history of species formation from a primitive primary clonal state to the amphimictic state and then often to secondary clonal species. Meanwhile it has been proposed that species as living systems of a certain type arose at the dawn of life, long before sexual reproduction (Polyansky, 1976; Shaposhnikov, 1976). Zavadsky (1968) assumes that "species arose at the stage of transition from eobionts to constantly self-reproducing protobionts" (p. 158) and that it represents "at present a universal form of life organization" (p. 166).

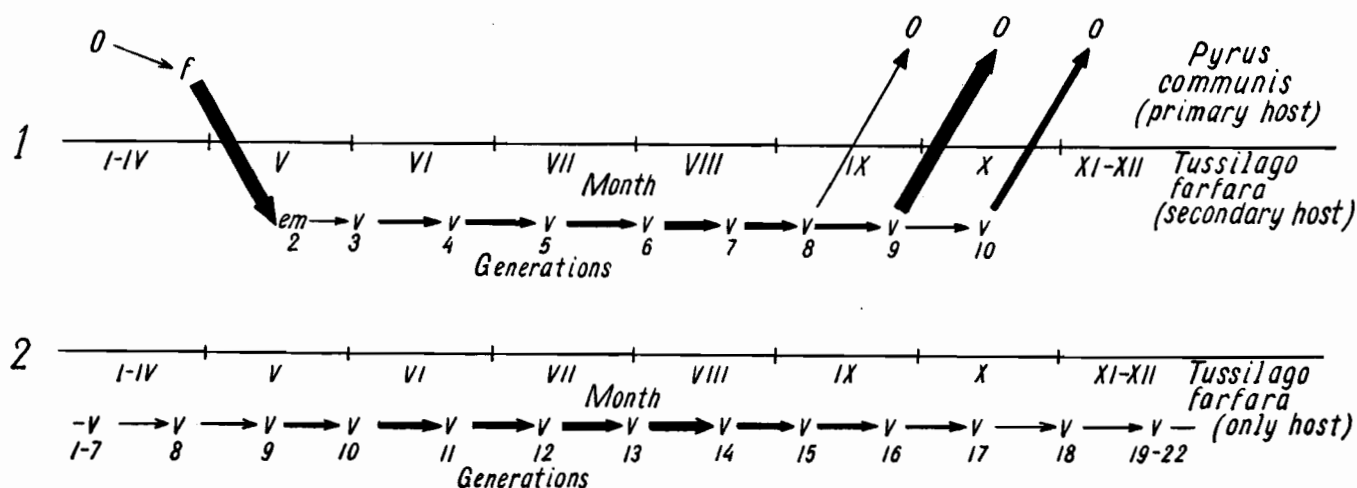
BSC not only rejects the obsolete morphological-typological species concept but at the same time rejects comparative evaluation of characters (Starobogatov, 1977), although such evaluation is indispensable. One may conclude therefore that the BSC is limited both theoretically and practically. The weaknesses of the BSC have led many scientists to dualistic ideas about biospecies and taxospecies, biospecies and agamospecies, biospecies and paleospecies, etc. Many modern authors (Jonckers, 1973; Sokal, 1973; Scudder, 1974; Krasilov, 1976), unsatisfied with the BSC, have been pessimistic as to the possibility of creating another, single and more universal species concept and assume that the "species" notion should be used as a taxonomic category only (nominalistic view).

A question discussed recently is whether species should be treated as individuals (Ghiselin, 1974; Hull, 1976, etc.) or as groups (kinds) and therefore classes (Kitts and Kitts, 1979), or both with regard to whether the species is treated as a taxon or as a category (Mayr, 1976). I (Shaposhnikov, 1974a) have taken the system approach as a basis (Bertalanffy, 1956, 1973; Blaubeurg and Judin, 1973; etc.) and thus treat the species as a historically formed living system of which populations are parts.

Most biologists treat species as a unity, as a whole, as a system, and therefore emphasis should be placed on the problem of integrating mechanisms responsible for this unity. BSC assumes as an axiom that the species as a whole is preserved due to interpopulation gene flow. Opposed to this assumption may be an ecologo-evolutionary viewpoint. To neglect the considerable differences of opinion of some authors this viewpoint can be generalized and simplified as follows: similar selection regime (Ehrlich and Raven, 1969) determines co-direction of ecological specialization of all populations of the species (Shaposhnikov, 1966) to the same unique adaptive zone (Van Valen, 1976), which results in lack of considerable divergence within a species (Wiley, 1978) and hence a unity (individuality, identity and some integrity) of a species as a whole. This concept eliminates the dualism brought about by BSC and in particular a division into biospecies and agamospecies.

Using a "morphological species concept" Gritsenko et al. (1983) define a species as a group of populations unified by identity of the epigenotypes of their individuals and incompatible with other such groups. Hence intraspecific variability of morphological and any other phenotypic characters is continuous while interspecific variability is interrupted by a hiatus. Therefore developmental homeostasis determines species integrity and the hiatus in the distribution of characters is the main species criterion.

Over the last three decades a vast body of factual evidence has been accumulated concerning structure, functioning and evolution of populations and species in aphids that is difficult to find among other living forms. Using aphids one can show more clearly than in other cases that much division into biospecies and agamospecies is unsteady and that the modes of origin of



Figs. 1, 2. Life cycles of the aphid *Anuraphis farfarae* Koch. (Crimea, 1970).

1. Holocyclic heteroecious *A.f. farfarae* Koch. 2. Anholocyclic *A.f. diana* Shap. O - overwintered ova; f, em, v - parthenogenetic viviparous females: f - apterous fundatrices, em - alate emigrants; v - aptera or alate virginoparae; O - the end of life cycle: alate gynoparae and males, apterous normal females and fertilized diapausing hibernating eggs. Thicknesses of arrows reflect very approximately the various population densities in different periods.

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secondarily clonal populations are diverse. It was probably my extensive work on aphids that led me to a revision of the problem of species as a whole. To develop a universal concept of population and species would require using all kinds of organisms from prokaryotes to vertebrates. Nevertheless it is reasonable to treat aphids as a model for this purpose. It is therefore appropriate to present data on aphids before formulating the concepts suggested by their biology. More importantly, complexity of their populations and species is insufficiently known to most biologists, and unification of fragmentary data and their interpretation from a single viewpoint are important in themselves.

This work is based on a substantial revision of my paper "Population and species in aphids and the need for a universal species concept," which was published by the Research Branch of Agriculture, Canada, Ottawa, in 1981 in a semi-official edition of 300 copies only.

#### Amphimictic and clonal populations of aphids

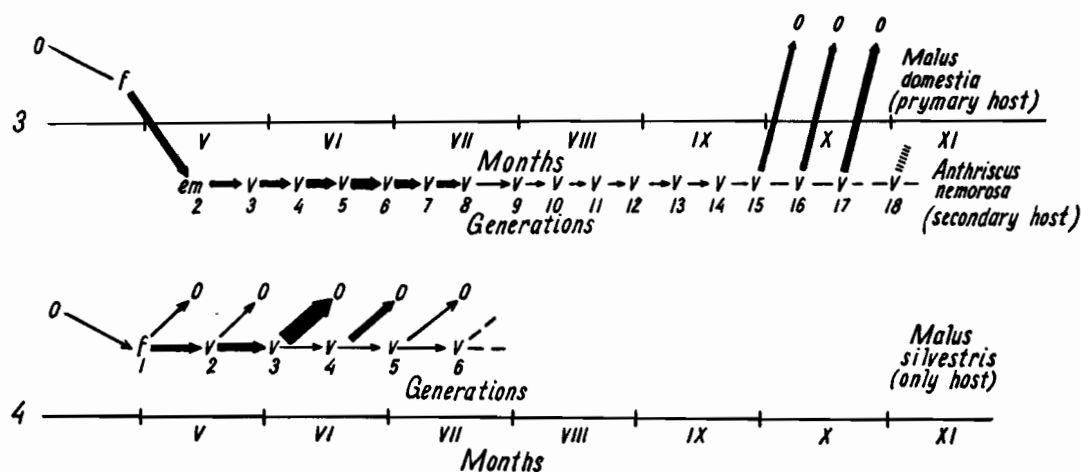
The life and evolution of aphids are influenced by adaptations to the seasonal changes of temperate or subtropical climates and, in particular, synchronization of their cycles with the seasonal cycles of their host-plants. These have led to the formation of uniquely complicated life cycles with a set of regulatory mechanisms and have resulted in a complicated seasonal structure of populations, consisting of various specialized forms, up to 8 and more. Recent aphid populations are based on cyclic parthenogenesis: amphigony in one generation is combined with diploid parthenogenesis in one or usually in several (up to 20 and more) generations per season. The seasonal transition of aphids from parthenogenetic to amphigonic reproduction occurs mainly in the autumn and is at the same time a transition to winter diapause in the state of a fertilized egg. It is controlled by a short photoperiod reinforced by a lowering of

temperature (Marcovitch, 1924; Bonnemaïson, 1951; MacGillivray and Anderson, 1964; Lees, 1966; Tsitsipis and Mittler, 1977; etc.). The effect of photoperiod is enhanced also by the increase of colony density (Bonnemaïson, 1951; Shaposhnikov, 1966), the effect of which may sometimes be independent (Judge, 1968; Swenson, 1971). Food is involved in transition to amphigony in the summer (Shaposhnikov, 1962; Dehn, 1967; Ferrest, 1970). It is customary to call forms with such a mode of life holocyclic, whether they are species, subspecies, population or clones. They form amphimictic populations. Holocyclic forms are heteroecious when they possess (1) normal females able to couple, and sometimes males, overwintering eggs, fundatrices and their progeny, developing on the primary host (woody plant), and (2) other parthenogenetic females and sometimes males developing on the secondary host (herbaceous, seldom a woody plant) (Figs. 1 and 3). In autoecious aphids the complete cycle may take place on one host, whether the aphid is monophagous or polyphagous (Fig. 4).

Along with holocyclic forms there exist different types of anholocyclic aphid forms incapable of completing their full cycle. Under the conditions provoking transition from parthenogenesis to amphigony (in closely related holocyclic forms; Fig. 1) they continue to produce parthenogenetic females (Fig. 2). Because any anholocyclic form per se can form only clonal populations, secondary clonal populations in aphids result from the change of their life cycles. I suggest that anholocyclic forms may arise in five different ways:

1. By adaptation to warm climate by natural selection. - In the northern Caucasus in 1955-1957, among three heteroecious aphid species of the genus *Dysaphis*, a small group of individuals failed to switch over to amphigony and diapause (the 18th generation on Fig. 3) and died during the winter (Shaposhnikov, 1959). In a warmer climate, such extreme cases of poor photoperiodic response might serve as the initial material for selection in favour of anholocycly. Experiments on one of these species (Shaposhnikov, 1966) and on several other species (Cognetti, 1962, 1965, 1967) have confirmed that natural selection of individuals with poor photoperiodic response under threshold conditions may lead to continuous parthenogenesis under conditions normally provoking a switchover to amphigony. New data are presented in Fig. 5.

2. By gene mutation or chromosome fragmentation (Shull, 1943; Blackman,



Figs. 3, 4. Life cycles of aphids of genus *Dysaphis* Börn. 3. *D. anthrisci majkopica* Shap. (North Caucasus, 1954-57). 4. *D. devectora* Walk. (Borisoglebsk, 1959; Leningrad, 1976). Symbols as in Figs. 1, 2.

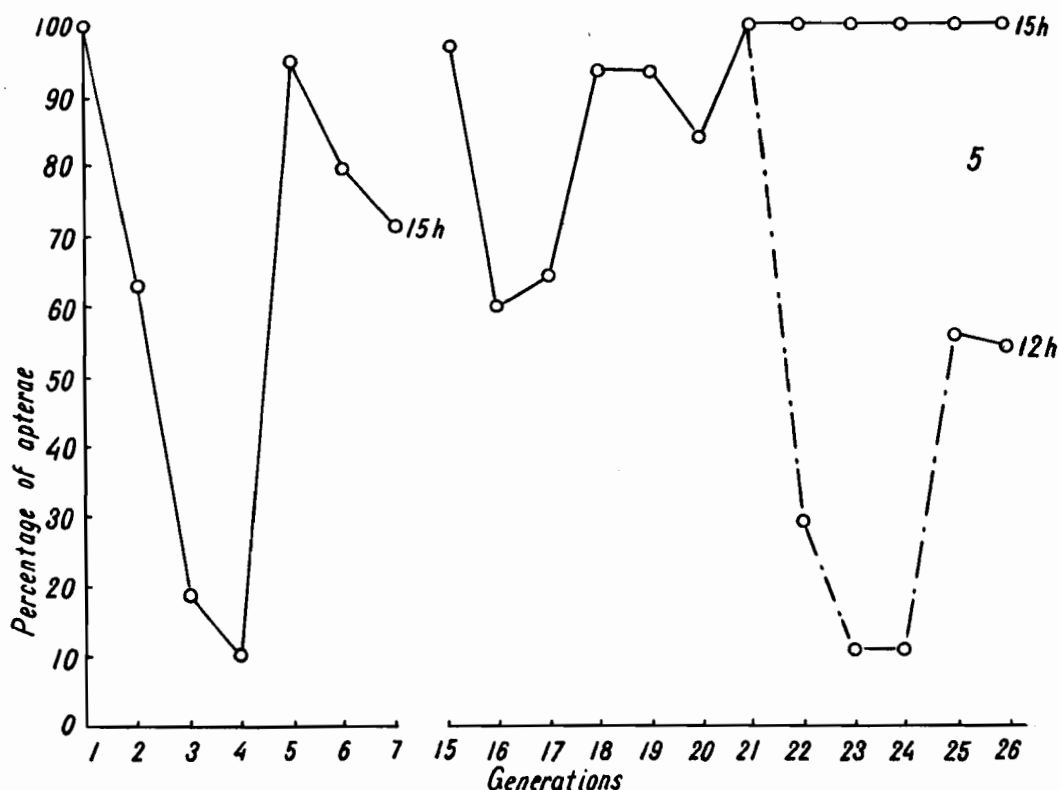


Fig. 5. The process of formation of anholocycly in heteroecious *Dysaphis anthrisci anthrisci* Börn. Under threshold conditions, alate gynoparae which had left the secondary host (*Anthriscus*) were thereby eliminated and the clone lost the ability to remigrate to the primary host (*Malus*) and to go through amphigonic reproduction. At first it was observed under natural threshold conditions (photoperiod 15 hours) and then under more severe conditions (12 hours). Rearing aphids from the eighth to the fourteenth generations under control conditions (20 hours photoperiod) shows that results achieved in threshold conditions (15 hours) are inherited and persist throughout 7 generations.

Rearings of the control lines (at 12 hours photoperiod) caused 100 percent remigration as soon as the second generation. Aphids were from a long-term rearing clone (17 generations) in the experiment in Leningrad from 16 I to 11 XI 1976, at a temperature of 20° C and 20 individuals per plant.

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1971b, 1972). - This hypothesis has no direct evidence, but it has been shown by Blackman (1980) that in obligatorily clonal species chromosome rearrangements are much more frequent (52.4% of the studied species) than in amphimictic populations (0.3%).

3. As a result of hybridization. - In natural conditions and under experimental conditions, hybrids have been observed to be fertile in parthenogenesis over many generations although incapable of switching over to amphigonic reproduction. They turned out to be anholocyclic either during the F<sub>1</sub> generation or during the F<sub>2</sub> (Dahl, 1968; Iglisch, 1968; Thomas, 1968; Müller, 1969; Müller, 1971).

4. As a result of host influence. - Some aphid species may reproduce parthenogenetically on different plant species and switch over to amphigony only

on particular plants. For example, several species of the genera *Hyalopterus*, *Aphis*, *Dysaphis* and *Myzus*, after spending the summer on their primary host, behave as anholocyclic species in autumn, whereas after colonizing secondary hosts in the summer they behave as holocyclic forms (Savary, 1953; Stroyan, 1963; Vereshchagina, 1966; Iglisch, 1972; Kolesova, 1974; Rakauskas, 1983).

5. As a result of the loss of a host, generally a primary host. - In several heteroecious species the life cycle is divided into two phases, one in which the population switches over to amphigonous reproduction and then to winter diapause on the primary host, the other in which the individuals continue to reproduce parthenogenetically, forming specialized wintering diapausing forms on the secondary host. Examples of the latter are cited in the case of Adelgidae (Cholodkovsky, 1915; Steffan, 1968) and in Pemphigidae, in particular in *Pemphigus* (Maxon and Knowlton, 1929; Zwölfer, 1957; Judge, 1967; Doroshina, 1975) and *Colophina* (Aoki, 1980). It is the second part of the cycle which serves as the basis for anholocyclic forms.

In a temperate climate with severe winters anholocyclic forms fail to lay wintering eggs and are therefore doomed to die. However, in the warm climate of the tropics, subtropics, and greenhouses, they can form clonal populations. Such populations in many aphid species exist quite independently and often prove to be more expansive forms than initial or closely related amphimictic forms and often occur as agricultural pests.

A question therefore arises. How should secondary clonal groups of individuals be regarded? What is their taxonomic status, considering that the criterion of reproductive isolation is absolutely useless here?

It should be mentioned, first of all, that most species of aphids consist of amphimictic populations and represent ordinary reproductively isolated biospecies. As for anholocyclic forms, in most cases holocyclic species from which they have originated are known.

From the holocyclic *Sacchiphantes viridis* Ratz migrating from spruce to larch, the anholocyclic species *S. abietis* L. on spruce and *S. segregis* Steff. on larch have been split off. Morphological (Philipshenko, 1916) and karyological (Steffan, 1968) distinctions between them are of subspecies rank. Cholodkovsky (1908) pointed out drastic differences in the life cycles of these forms, the impossibility of the transformation of one cycle into another, and the irreversible segregation leading to complete isolation of forms. At the same time, however, he noted great morphological similarities of the individuals. From this he suggested the idea of the "biological species," which was a novel concept in zoology at the time. An analogous term, "sibling species," was later introduced (see Mayr, 1963).

The holocyclic species *Anuraphis farfarae farfarae* Koch. alternates from *Pyrus communis* to *Tussilago farfarae* (Fig. 1). In the Crimea, in autumn and with a 14-hour day, 20°C and low colony density (20 individuals per plant), 100 per cent of gynoparae and males were formed. *A. f. farfarae* lives together with an anholocyclic subspecies, *A. f. dianae* Shap. (Fig. 2), which formed no gynoparae and no males at different combinations of 14-, 12- and 10-hour photoperiods, temperatures of 18°, 15°, 8°C, and colony density of 20 to 100 individuals per plant. In natural populations, gynoparae and males have never occurred, even when aphids reproduced in January. Both forms sometimes form mixed colonies on the same individual plant. However, morphological differences in these forms are more contrasting than in the above-mentioned Adelgidae. In particular, rostrum hairs in *A. f. dianae* are shorter than in *A. f. farfarae*. Both forms are safely isolated and could be treated as species except for two reasons: (1) *A. f. farfarae*, from which *A. f. dianae* has undoubtedly originated, may preserve the potential to produce this anholocyclic form; (2) in samples from regions with cold winters where alone or together with long-haired forms.

In addition to sympatric subspecies, many allopatric subspecies are known.



For example, the heteroecious holocyclic Dysaphis foeniculus malidauci Shap. from Middle Asia migrates from apple and probably from hawthorn to carrot and wintering anholocyclic aphids seem impossible, short-haired forms occur either some other Apiaceae, whereas in southern Europe, Africa, Australia, and North and Central America this subspecies is replaced by anholocyclic D. f. foeniculus Theob., which lives on Apiaceae. This species, as well as many other ones which lose the potentiality of amphigony, acquires the ability to greatly expand its range. Many such examples were cited in a special summary by Mordvilko (1935b).

Species that produce different combinations of holocyclic and anholocyclic forms in the same locality are of interest even though their study involves certain difficulties. Such a study has been made of Myzus persicae (Sulz.) (Daiber, Schöhl, 1959; Blackman, 1971a, 1972, 1974; MacGillivray, 1972; Kolesova et al., 1980; etc.) of Acyrtosiphon pisum (Harr.) (Meier, 1964) and of Aulacortum solani (Kalt.) (Meier, 1967; Müller, 1970).

We have seen that most aphid species form amphimictic (holocyclic) populations in which amphigonic and parthenogenetic reproduction alternate. In different ways these populations produce clones incapable of producing males or normal females or both, i.e. anholocyclic forms. Anholocyclic clones can coexist with holocyclic ones as components of a single complex population or exist as independent clonal populations. They can form clonal populations, races, and subspecies coexisting in a species with amphimictic populations and subspecies or be the only form of the species. Hence one cannot sufficiently justify a distinct division into forms capable of amphimixis (biospecies) and forms incapable of amphimixis: agamospecies, which Steffan (1968) applies to aphids, or pseudospecies (Dobzhansky, 1972). The criterion of reproductive isolation is therefore not universal enough.

#### Populations as integral self-regulated systems and their structure among aphids

By the "structure" (organization) of a population I mean a set of genetically and/or phenotypically diverse individuals and their varied interrelations within a population. Aphid populations have about three aspects of structure: temporal or seasonal, ecological-genetical, and spatial.

The temporal structure of aphid populations depends on the seasonal polymorphism, the sequence of specialized forms in the life cycle which is fixed in the genotype as a possibility. In some species this possibility is realized mainly because of external factors. For example, the emergence of fundatrices depends on the sum of effective temperatures, whereas the emergence of emigrants depends on feeding conditions or colony crowding (Bonnemaïson, 1951). The emergence of individuals of the amphigonic generation as a rule depends on photoperiod and temperature (Markovitch, 1924; etc.), both of which are inhibited by a mechanism of the "biological timer" type which prevents them from switching to amphigony and diapause in the spring (Lees, 1960; etc.). Other species have gradually elaborated the genetically fixed sequence of emergence of some specialized forms, which gives them some independence from the environment (Shaposhnikov, 1959, 1962). Entire blocks have formed, e.g. fundatrix + emigrants + exules, or gynoparae + amphigonic females, androparae + males. As a result, the population combines a firmly fixed adaptation to seasonal changes with a relative lability which allows for adaptation to sudden changes in the environment.

The obvious seasonal polymorphism of aphids, which determines the temporal structure of the population, arose due to directed evolution controlled by a complex positive feedback (Shaposhnikov, 1977). A result of this evolution was the transferring of some part of functions such as feeding, reproduction, dispersal, protection and amphimixy from an organism to a population, i.e. to a

complex of 6 to 8 types of individuals: virginiparous females such as fundatrices, emigrants, apterous and alate exules, gynoparae, androparae, sexuparae, and males and normal females.

The genetic-ecologic structure of aphid populations results from their adaptations. Specificity of aphids to host plants seems to optimize the use of food resources and it is thus reasonable that most aphid species are strictly monophagous or limited to a few host plants. For example, of the 700 aphid species in the east European fauna (Shaposhnikov, 1964), 77 per cent live on plants of a single species or of a single genus. Most of these species do not produce host races. Polyphagous species, however, commonly produce various kinds of races.

Temporary specialization on a new but somewhat acceptable host plant may result in phenotypic changes which persist during a number of parthenogenetic generations (up to 15) after returning to the initial host, a result observed in experiments on Aulacorthum circumflexus Buckt. (Smirnov and Samokhvalova, 1955; Smirnov, 1961). These temporary food preferences of Dauermodifikation type arise without elimination of individuals and are easily reversible. More profound food preferences originate in the process of adaptation to plants relatively foreign to the aphid. These in fact relate to the process of natural selection and changes take place slowly (Smirnov and Chuvakhina, 1953; Shaposhnikov, 1961). Food preferences increase the phenotypic diversity of the population.

Specialized food forms, often named as biotypes or races, are known in many aphid species. Some forms different with respect to the age of the leaves they feed on, in their ability to transmit phytopathogenic viruses, in their diet, in the ability to produce hybrids with closely related species, and in other respects as well (see reviews by Eastop, 1973; Shaposhnikov, 1974a).

In many aphid species individuals of different colors are observed in a single colony. This variation has been best studied in the autoecious species Acyrtosiphon pisum Harr. In this species green and red forms possess morphological and ecological differences and can be differentiated according to their responses to the chemical composition of their diet, to air humidity, and to colony crowding, and according to their capability of producing alate forms and developing food preferences of the Dauermodifikation type, to their fecundity and duration of life, to their capacity for colonizing papilionaceous plants and transmitting plant-pathogenic viruses, and to their response to disturbance (Markkula, 1963; Lowe and Taylor, 1964; Thottappily, 1969; Sutherland, 1969a, 1969b, 1970; Markkula and Roukka, 1970, 1971; etc.). Moreover, A. pisum consists of a number of sympatric forms which have specialized on certain species of papilionaceous plants (Medicago, Trifolium, Lotus, Sarothamnus, Ononis, Pisum), each of which carried its own combination of color morphs. The populations on all these hosts can interbreed and produce fertile hybrids, which reproduce on the host plants of the parental forms with less vigor than do the parental forms and which do not occur on these plants in nature. Müller (1962, 1971) treats them as sympatric races isolated from one another mainly by strict host preference and by hybrid inferiority. However, all these forms, and particularly hybrids among them, can normally reproduce on universally susceptible hosts (Faba vulgaris and several species of Vicia), which can serve as temporary refuges for as long as the original hosts are lacking. It is important to bear in mind that aphids can gradually change their food specialization with different degrees of reversibility during a number of parthenogenetic generations. These facts suggest that one should treat at least some of these forms as parts of a single population. Following a classification for plants (Sinskaya, 1948), one could treat them conditionally as ecoelements, a term which is more accurate for such intrapopulation forms than are the terms "biotypes" or "sympatric races." The adaptive importance of the ecoelements of



aphids may be observed in a population inhabiting diverse ecological niches yet preserving host specificity. It should be added that besides differences of the color and food morphs there are differences in the capability of producing holocyclic and anholocyclic forms in the same territory. The result is that the population, with its complicated internal structure, remains more homeostatic.

Formation of ecoelements should be treated as the last stage and the highest degree of intrapopulation genetic-ecologic differentiation. It is possible that several forms like ecoelements are so isolated that they are capable of both allopatric and sympatric existence and of forming independent populations of race status. Müller (1971) considers such intrapopulation forms as material for sympatric speciation.

The above facts show how complex can be the series of specialized forms in local aphid settlements of a single species. In such cases it is very difficult to distinguish between intrapopulation and intraspecific relations.

The spatial structure of aphid populations depends on interactions among individuals. In most aphid species their dense aggregation, the colony (or "population," as some authors call it), is the minimal and at the same time the main spatial-structural unit of the population, which usually inhabits either one single host plant or a part of it. Many aphid species change the physicochemical conditions of the part of the plant they inhabit (Nevskaya, 1945; Kennedy, 1958; Shaposhnikov and Eliseev, 1961; Sobetzky and Derzhavina, 1966; Vereshchagina, 1980; etc.) and at least some of them cannot do it alone (Nevsky, 1925; Forrest and Dixon, 1977). But this is only one of the reasons for colony formation; predators seem to be another reason (Klingauf and Sengonca, 1970). It is known, however, that aphids possess gregarious instincts (Broadbent, 1949; Kennedy and Crawley, 1967; Strong, 1967; etc.). The unusually high reproduction rate carries with it the danger of overcrowding, taking into account parthenogenesis, viviparity, and relatively complete use of food. Therefore, self-regulation of numbers is adaptive for colonies and indeed occurs in them. For example, the individuals in a colony of *Aphis fabae* Scop. stimulate their reproduction when numbers are low but suppress it when a density of about 60 reproducing individuals is attained (Way and Banks, 1967). The percentage of alate individuals increases with the density of the colony, and among the alate forms the percentage of individuals which leave the colony without producing larvae increases as well (Shaw, 1970). As a result, an equilibrium between the aphid population and food resources is attained. The aphids gain the possibility of using effectively the ephemeral conditions of existence (Mackay and Wellington, 1975; Campbell and Mackauer, 1977; Posylaeva, 1977). Such a self-regulating mechanism could arise in particular clones as a result of kin selection amongst groups of closely related individuals (Shaposhnikov, 1946b). The production of alate forms in aphid populations is induced by tactile stimulation from aphids actively searching for better feeding conditions, particularly when leaves are maturing (Bonnemaison, 1951, 1971; Johnson, 1965; Lees, 1967; Toba et al., 1967; Awram, 1968; etc.), as well as from deteriorating feeding conditions directly (Johnson, 1966; Sutherland, 1969b). Work using synthetic diets indicates that the two factors may either interact or act independently (Mittler and Kunkel, 1971, etc.). In general, the reproduction of aphid species is synchronized with the life cycle of their host-plant and is controlled by the physiological state of the plant (Mordvilko, 1901, 1935a; Shaposhnikov, 1959, 1962; Dixon, 1975, 1976, 1977; Wellings et al., 1980; Dixon and Wellings, 1982). In colonies, aphids may use either alarm pheromones (Nault and Bowers, 1974; etc.) or sound signals (Eastop, 1952) to inform their neighbours of danger so that they can avoid it by falling to the ground. Some aphid species of the families Pemphigidae and Hormaphididae develop special sterile soldier larvae to protect the colony from predators (Aoki, 1977; Aoki and Miyazaki, 1978). Ants can influence the population

regulation of aphids by improving their living conditions (Mordvilko, 1901; etc.) or by preventing the emergence of alatae (El-Ziady and Kennedy, 1956); each of these effects is apparently due in part to chemical influence (Kleinjan and Mittler, 1975).

In several heteroecious aphid species, it is common to observe aphids flying and mating only in particular places, usually isolated growing trees, even though successful development and reproduction could take place at other locations, as has been verified with field tests (Shaposhnikov, 1961). These separate growing trees seem to be mating-places, resulting in the isolation of a group of individuals. Such groups can be treated as demes (a not quite definite term) or as micropopulations, i.e. the largest spatial intrapopulation units which approximate panmixia. Some autoecious aphid species inhabit the same microstation year after year, e.g. species of Stomaphis Walk. on trunks of oaks, birchs, etc. This suggests some extent of inbreeding in such cases.

Aphid populations consist of many clones or biotypes with different features (Shaposhnikov, 1961, 1974a; Eastop, 1973). The genetic composition of a population is controlled by reproduction being mainly by those clones whose individuals are best adapted to the environment. In populations of Myzus persicae in southern England, where the primary host (peach) is rare, anholocyclic forms (which provide a higher reproduction rate) were predominant in summers following mild winters, while holocyclic forms predominated after severe winters that selected for greater ability to survive such conditions (Blackman, 1971a, 1972). The possibility of self-regulation exists even in colonies with a mixture of different clones. Thus in Pemphigus populi-transversus Ril. aphids from adjacent localities are very different from each other, whereas aphids from different trees of the same locality had almost the same variability as aphids from one tree (Rinkel, 1965). Sokal et al. (1971) explain this phenomenon by postulating that a mixture of aphid clones inhabit every tree. This assumption is confirmed by observations on Pterocomma salicis L. on willow shoots: each of the 20 newly formed colonies consisted of a moderate number of alate individuals (average number 15, maximum 54) (Shaposhnikov, 1974a). It is highly probable that the aphids, having come from different pre-existing colonies and therefore originating from different clones, formed a new colony by their gregarious instinct. As a result different clones or biotypes possessing some differences of adaptations are mixed in different proportions in a single colony. This phenomenon has been discovered also in some other aphid species. One should assume that throughout a season many clones are eliminated but some of those less adapted at any given moment persist in colonies together with better adapted ones, and thus can be mobilized during environmental changes to sustain the population (Shaposhnikov, 1966).

Therefore self-regulation of populations, of their genetic composition, of the relative proportion of morphs, and of the sequence of their emergence in the season stem from the genetic and phenotypic multiformity of individuals and from their interaction with one another and with the environment. Thus population homeostasis is realized.

#### Permanent and temporary populations

Beklemishev's idea (1960) that populations differ in their ability to reproduce themselves suggests a division of all populations into two groups (Shaposhnikov, 1974a): (1) Permanent populations are capable of indefinitely long self-reproduction, independent existence, and the ability to evolve. (2) Temporary populations cannot exist independently from one or several permanent populations for a long period of time. They can nevertheless be important to the life and evolution of the species, but always through their connection with permanent populations or the changes of them. However this does not exclude the

possibility of a temporary population transforming into a permanent one under favorable conditions. If such a transformation takes place beyond the species' range, or within it but in unusual conditions, it may promote ecological and/or geographical expansion of the species.

Temporary populations may be a mixture of members of different permanent populations of one species, temporarily functioning as a single system. For example, in mixed colonies of *Anuraphis farfarae farfarae* Koch and *A. f. diana* Shap. common self-regulation of density is suggested by experiments which show that individuals of one species and even individuals of an alien species can influence production of alate forms through tactile influence (Toba et al., 1967; Tamaki and Allen, 1969). Temporary populations may also arise from the hybridization of different species.

Although the distinction between permanent and temporary populations is not absolute, because there are many transitional states between them, the distinction is necessary because it allows for a better understanding of the species' dynamics.

Thus aphid populations consist of: (1) a set of several (usually 6-8) seasonal forms, all with the same genotype (a single clone) but with different phenotypes and with different functions in the life cycle; the sequence of their appearance is determined mainly by external factors, but some blocks of forms may be genetically fixed; (2) a set of forms which differ in their specificity to host plants and in many other ways; these forms, whether different ecoelements (biotypes) or different clones of the same ecoelement, differ phenotypically and genotypically: their proportion in different populations in different years and seasons is regulated by natural selection; (3) groups of individuals (colonies) with self-regulation, which brings aphid numbers into line with food resources and promotes dispersal of individuals to new habitats by production of alate forms; (4) localized groups (like demes or micropopulations) that apparently bring males and females together, promoting panmixia and sometimes perhaps inbreeding.

Therefore aphid populations are polymorphic systems with a complex organization that promotes self-regulation and homeostasis. However, such a complicated population structure is certainly not unique to aphids (Shilov, 1977; Schwarz, 1980; Konovalov, 1980; Gritsenko et al., 1983).

#### A universal population concept

It has been shown that aphids have both amphimictic populations and clonal populations derived from them. Among multicellular animals, clonal populations are almost always secondary, but in unicellular organisms, such as some protozoans, several algae, and all prokaryotes, they can be primary. Because the modes of existence of primary and secondary clonal populations are very different, it is wrong to unify them into a single notion of agamic forms. Nevertheless, in order to elaborate a universal concept of a population which can be used in all cases, one should try to discover the most general and important features which are typical of all populations and which at the same time distinguish them from other living systems. Five such features can be suggested.

1. A population occupies a particular place among living systems: it unites related organisms into a single system and is included in its own species and its own ecosystem and represents its species under certain conditions (Ghilarov, 1954). It should be noted here that the connection of a population with a certain ecosystem should not be conceived of in a very strict sense. For example, in heterotopic animals, and among them in heteroecious aphid and fungal species, different parts of the life cycles take part in different ecosystems though at any single time in specific conditions. Migration and geographic

remoteness of reproduction places from the sites of feeding or over-wintering do not contradict the principle of the connection of a population with its native ecosystem, i.e. to the ecosystem where the life cycle of individuals begins. For more detail see Shaposhnikov (1976).

2. A population is potentially eternal, i.e. it has a possibility of endless self-reproduction. Populations are permanent if they can realize this possibility themselves for an indefinitely long time. Populations are temporary if they can do it for only a short period or while they are connected with permanent populations of one or two species, in the latter case being hybrid populations. The permanent or temporary status of a population depends on the surrounding conditions and its position within the species' geographic range.

3. A population consists of related though diverse individuals. Genetic and phenetic diversity is attained because of indefinite variability as a result of a) new mutations, b) recombination of genetic material (crossing-over and recombinations of parental chromosomes in meiosis, chromosome rearrangements, autopolyploidy), c) assimilation of immigrants and genes entering from other populations of their own or very rarely of other species (exchange of clones, hybridization, allopolyploidy). Phenetic diversity also derives from definite variability, i.e. as a result of the environment, which invokes a particular realization of the genetic potential under one ontogeny (modifications) or under several successive ontogenies (phenomena of the Dauermodifikation type).

4. The constantly existing diversity of individuals in the population creates conditions for natural selection and thus gives the possibility of adaptive transformations. There occur both regulatory transformations, which promote stability of the population in time and space (population homeostasis) and evolutionary transformations, which change the gene pool of the population and its relation to the environment. It is natural therefore to regard a population as an elementary unit of evolution.

5. A population has its own more or less complex structure (organization), expressed in polymorphism of individuals, in their spatial and temporal distribution, and in the correlation of different forms and interactions among them. The differently directed regimes of natural selection change the structure of the population and provide for its adaptation to the changing heterogeneous habitat, its survival, and a certain stability.

In conclusion, I can suggest a general definition of the term "population". A population is a grouping of related individuals which is capable of potentially endless self-reproduction within its own species and its own biocenosis. To express it in more detail, a population is a part of a species, a local settlement connected with a specific ecosystem or ecosystems as a group of diverse, closely related individuals united into a self-regulatory system with a common gene pool and particular structure, and capable of endless self-reproduction, of adaptation, and evolution.

A population is distinguishable from suprapopulational groups mainly by its connection as a rule with only one ecosystem where reproduction takes place, while subspecies and species reproduce in several or many ecosystems. Its distinction from subpopulational groups is mainly in the impossibility for the latter of a long-term independent existence. However, in the presence of a hierarchy of groups of related individuals as in aphids (see pages 8-9), salmon (Konovalov, 1980) or lizards (Yablokov et al., 1981) it is difficult to determine which of them corresponds to the population level and which to subpopulation or suprapopulation levels. Therefore, despite a great need for the notion of population it should be realised that it has a certain vagueness.

#### The structure of aphid species

Aphid species can be separated into several categories in accordance with

the complexity of their population structure. Most aphid species are monotypic, consisting of more or less similar amphimictic populations that are not grouped into subspecies. However, more detailed studies find a greater number of polytypic species, consisting of different races and subspecies. Subspecies can be relatively homomorphic (i.e. all of them are autoecious or heteroecious) or heteromorphic (e.g. when heteroecious *Aphis frangulae frangulae* Koch., *A. f. testacea* Thom., and *A. f. beccabungae* Koch coexist with autoecious *A. f. capsellae* Kalt. and anholocyclic *A. f. gossypii* Glov.) Many heteromorphic species such as *Aphis craccivora* Koch., *Myzus persicae* Sulz., and others, consist of parmitic and clonal populations, sometimes called races, which have not differentiated enough for taxonomists to give them the rank of subspecies.

Populations of one aphid species living at different latitudes and at different altitudes above sea level possess distinct hereditary thresholds of photoperiodic response (Matinyan, 1964; Cognetti, 1965, 1967; Azaryan, 1966; Shaposhnikov, 1966).

In different geographic regions, species can be represented by different combinations of races, and subspecies can have different food specializations. Thus in *Myzus cerasi* F. in Europe three subspecies are known: in western Europe *M. c. veronicae* Walk. lives (entirely autoecious) on *Galium* whereas *M. c. cerasi* F. and *M. c. pruniavium* Börn. migrate from cherry and crab cherry to *Galium*, *Veronica*, and *Euphrasia* (Dahl, 1968; etc.). In eastern Europe *M. c. pruniavium* does not migrate to these plants (Vereshchagina, 1966) and in eastern Kazakhstan only *M. c. veronicae* is found (author). The structure of many aphid species appears to be still more complex, if we take into account the facts that in different parts of a species range its populations can consist of different sets of ecoelements, and that different relations may exist between amphimictic and clonal forms and between permanent and temporary populations.

Consider *Myzus persicae* Sulz., for example. This pest was comprehensively studied on all continents as one of the main objectives within the framework of the International Biological Programme (see summaries by van Emden et al., 1969; and Blackman, 1974). At present two subspecies are known: a polymorphic polyphagous one (*M. p. persicae* Sulz.) and one that specializes on *Licium* (*M. p. dyslycialis* Müll.)

Enzyme electrophoresis reveals both a strong interclonal variability (Baker, 1977; Takada, 1979) and a weak one (Wool et al., 1978) in which some clones are even ostensibly identical (May and Holbrook, 1978). However, the latter result lacks a good explanation. A comparative study of 13 clones both from the same and from different localities and different plants in the northern Caucasus (Kolesova et al., 1980) has shown that they differ not only in their ability to produce males and amphigonous females but also in their host relationships, in reproduction rate and in the ability to produce alate virginopara females under low or high colony density, in morphology and coloration and in the ability to change color somewhat on various host plants. Interclonal differences are sometimes revealed but only in specific conditions. These data provide evidence of interclonal differences both within and among populations. As was shown by Baker (1977), clonal composition on different plants can rapidly and considerably change during a season.

The species is subdivided into races specialized not only on different plant species but also on the same plant in different regions. Tobacco in tropical and subtropical regions (Brain, 1942; etc.) and also in Transcaucasus (Anayan, 1950) and in the northern Caucasus (Kolesova et al., 1980) is infested with the anholocyclic forms while in Middle Asia (Zagorovsky, 1947) and in southeastern Kazakhstan (Bundzhe, 1972) it is infested with holocyclic forms. In the northern Caucasus, emigrants from peach always died without producing larvae after several repeated transfers to tobacco; in the holocyclic form, only the progeny of emigrants previously reared on potatoes could survive on tobacco



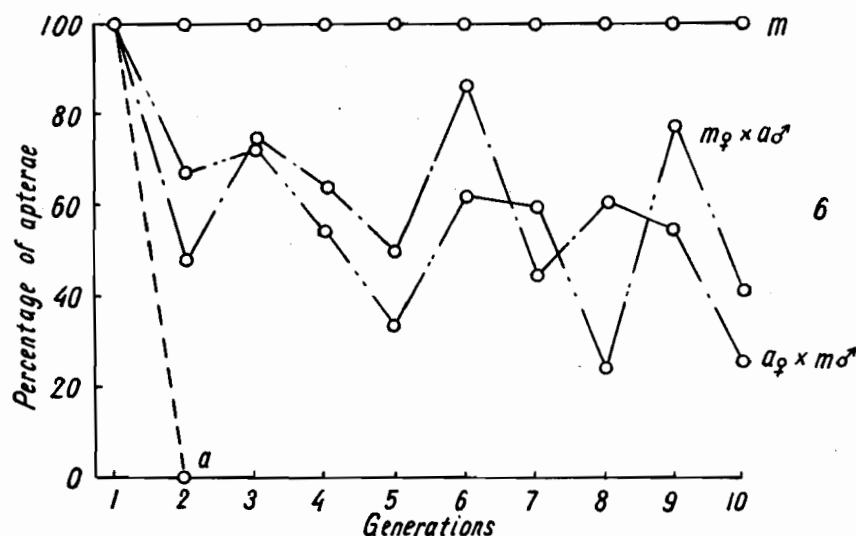


Fig. 6. Inheritance of photoperiodic reaction in hybrids between *Dysaphis anthrisci anthrisci* Börn. (a) from Leningrad and *D.a. majkopica* Shap. (m) from North Caucasus. Hybrid eggs obtained in autumn of 1962. Long-term rearing clones in the experiment from 6.XIII.1963 to 29.V.1964. Photoperiod 15 hours, temperature at scotoperiod 10° C, at photoperiod 14° C, 20 individuals per plant.

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(Kolesova et al., 1980). All the named forms are green, while aphids infesting tobacco and potatoes in Japan are dark red and are distinguished from aphids living on other plants in the same locality by different combinations of color and esterases, as has been investigated in many clones (Takada, 1979). In central and southern Europe, an anholocyclic form preferring cabbage is known in addition to the holocyclic form (Bonnemaison, 1951; Müller, 1958; Cognetti, 1967). In several places, forms have been found which differ in their ability to transmit plant viruses (Stubbs, 1955; etc.) in their resistance to insecticides (Hurkova, 1970; etc.), and in other characteristics (Tanaka, 1957; etc.).

It is therefore of great practical importance in agriculture to know the structure of aphid species and the forms that are associated with particular localities and species of plants.

#### A universal species concept

For species consisting of individuals incapable of cross-fertilization, or when the criterion of reproductive isolation cannot be applied, the "biological species concept" comes to a deadlock and species are labelled pseudospecies. In such cases, we might just as well call all unicellular organisms pseudoorganisms. However, this approach does not solve the problem. Rather, it avoids the solution.

Obviously, as in the case of a population, one ought to reveal the more general features that are true of any species, regardless of the mode of reproduction of its individuals. At the same time it is essential to find properties which characterize only species, not other living systems also. Let us discuss these features.

1. A species is primarily a system of related populations which are similarly adapted. All the populations of one species play more or less the same role in ecosystems and have a set of general obligatory adaptations



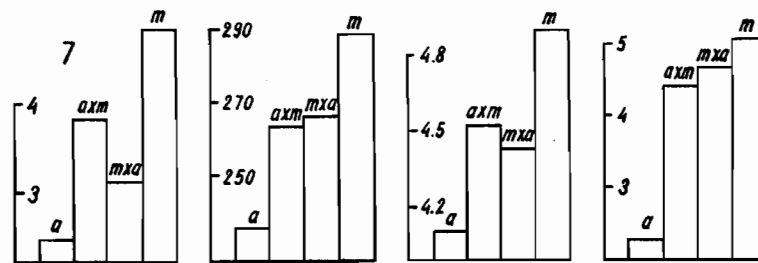


Fig. 7. Inheritance of morphological characters in hybrids between *Dysaphis anthrisci anthrisci* Börn. (a) from Leningrad and *D. a. majkopica* Shap. (m) from North Caucasus. Hybrid eggs obtained in autumn of 1962. Long-term rearing clones in the experiment from 6.XIII.1963 to 29.V.1964. Photoperiod 15 hours, temperature at scotoperiod 10° C, at photoperiod 14° C, 20 individuals per plant. For couples the order is always ♀ x ♂. Viviparae females of the fourth generation were measured. In every case 20 apterae. In the first group of columns - class of sclerotization of cuticle; in the second - length of siphunculi in μm; in the third - ratio of siphunculi length to their diameter in the middle part; in the fourth - number of secondary hairs on apical joint of rostrum.

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enabling them to survive under certain conditions. While a population is adapted usually to a particular ecosystem a species is adapted as a rule to a system of homocenoses, i.e. ecosystems of the same type (Shaposhnikov, 1976), with the exception of some eurytopic and eurytropic species. Hence we can speak of species adaptations typical of all populations of a species as well as of population adaptations promoting the well-being of the species within the limits of local conditions. When a population changes locations or when local conditions change, it is primarily the population adaptations that change, while the species adaptations, as a rule, are maintained (for evidence see below). When adaptations change in a similar way in several populations, one may speak of ecological parallelism of the changes, or of the identical trends of homeostatic or evolutionary transformations.

2. A species is a genetically unified system of populations. Genetic unity is provided mainly by stabilizing selection for species adaptations and consequently for those genetic and epigenetic mechanisms which are responsible for them. The genetic determination of species adaptations is clearly more rigid than that of population adaptations and its effects are gradually reduced in the following order of the hierarchy: species, subspecies, race, population.

Supporters of the biological species concept often claim that interpopulational gene flow is responsible for the genetic unity of a species (Dobzhansky, 1951, 1970; Mayr, 1963; etc.). However, many instances of similarity being preserved despite prolonged isolation, lead one to believe that the similarity is caused by a similar regime of selection rather than by gene flow (Ehrlich and Raven, 1969). Stabilizing selection maintaining species adaptations (Shaposhnikov, 1974a) ensures identity of developmental homeostasis and phenotypic uniformity within a species (Gritsenko et al., 1983). However, in emphasizing the integrating importance of stabilizing selection one should not overlook its differentiating role: precise conformity of each population to local peculiar features of the environment is also produced by selection, which thereby promotes a certain isolation of populations and to a certain extent prevents interpopulation gene flow.

Interdependence of common species adaptations and genetic unity can be seen from one example: The subspecies *Dysaphis anthrisci anthrisci* Börn. and *D. a. majkopica* Shap. are adapted to feeding on the same primary host (*Malus domestica* or *M. silvestris*) and both subspecies cause similar deformations of the leaves. Both subspecies migrate in the 2nd generation to the roots of the same secondary host (*Anthriscus*), in symbiosis with the same species of ants. Thus both subspecies have the same rather complex relations and play the same role in their ecosystems. All these adaptations should be regarded as specific. Nevertheless, populations of *D. a. anthrisci* from Leningrad are very different from populations of *D. a. majkopica* from North Caucasus, judging by the threshold of photoperiodic response and by their morphology. Stroyan (1963) even considered them to be different species when he knew nothing about the aphids except their morphology. Fertile hybrids between these subspecies are intermediate both in photoperiodic response (Fig. 6) and in morphology (Fig. 7). The photoperiodic response is a population adaptation; when species extend to Therefore the factors separating local populations of different subspecies (population adaptations) are less important than factors uniting them into a single species (species adaptations).

3. A species is a potentially integrated system of populations. All populations of a single species, despite their sometimes considerable isolation, the north or to the south only this adaptation is changed, whereas species-level adaptations determining the role of populations in the ecosystem are maintained.

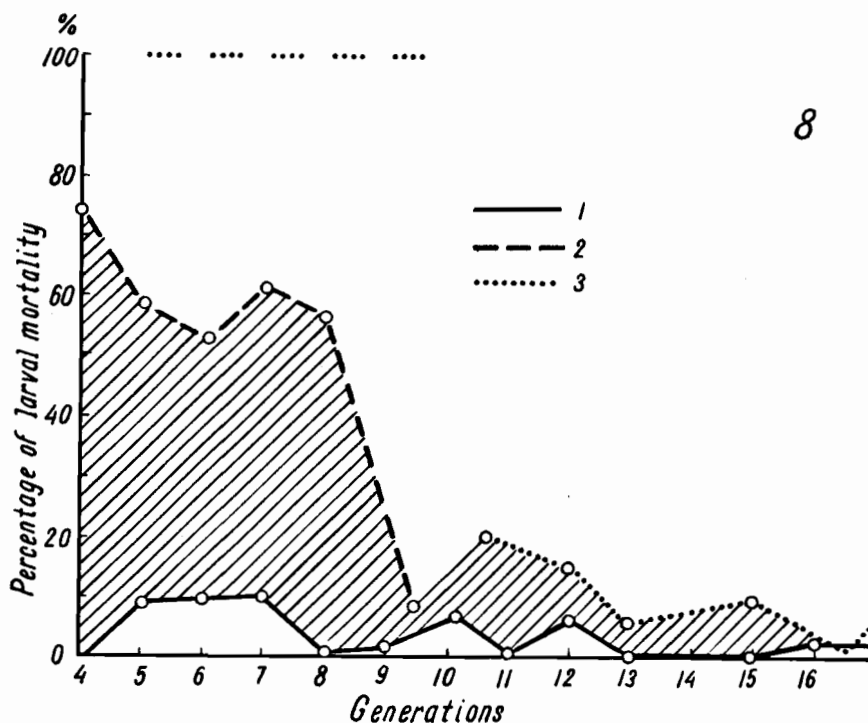


Fig. 8. Natural selection in the process of adaptation of *Dysaphis anthrisci majkopica* Shap. to new plants. Only the "obvious" selection, i.e. survival of individuals, is taken into consideration (shaded space means elimination of unadapted individuals), and "invisible" selection, i.e. differential reproduction ability, is not taken into account. All aphids after each transfer from *Ch. bulbosum* to *Ch. masculatum* died in the fifth to the ninth generations. They began to adapt to *Ch. masculatum* only in the tenth generation after complete adaptation to *Ch. bulbosum*.

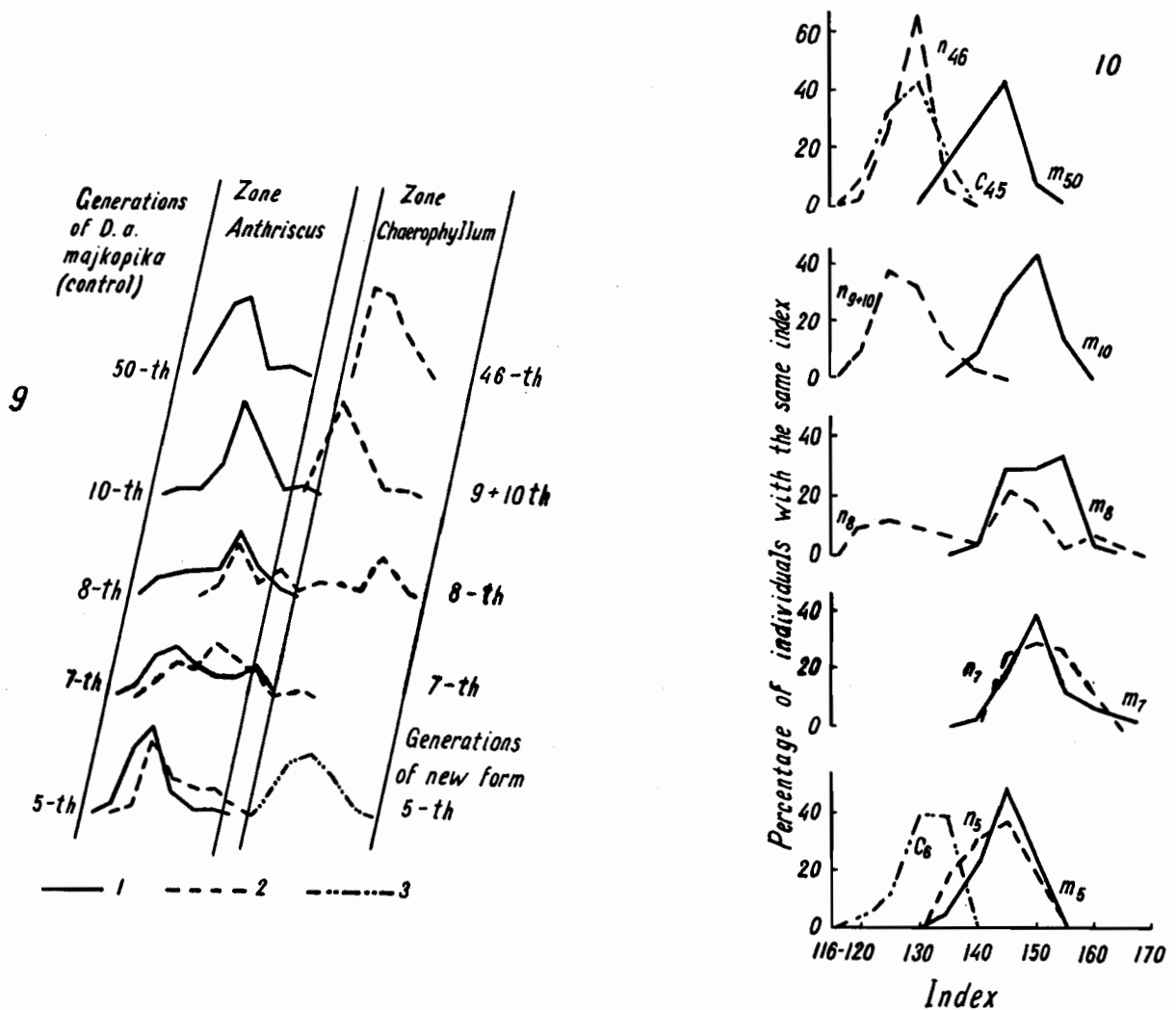


Fig. 9 (left). Change in the length of the apical joint of rostrum in apterous virginoparae females in the process of acquisition of a new adaptive zone. In every generation on the abscissa - sizes in  $\mu\text{m}$ ; on the ordinate - percentage of individuals with similar length of the apical joint of rostrum:

1 - in the clone of *Dysaphis anthrisci majkopika* Shap. on *Anthriscus*, 2 - in the same clone (transforming into new form) on *Chaerophyllum*, 3 - in *D. chaerophyllina* Shap.

Fig. 10 (right). Changes in the relative length of the apical joint of the rostrum in apterous virginoparae females in the process of adaptation to new plants.

On the abscissa is an index widely accepted in aphid taxonomy: the ratio of the length of the apical joint to the length of the second joint of the hind tarsus. m - in a clone of *Dysaphis anthrisci majkopika* Shap. on *Anthriscus*; n - in the same clone (which becomes transformed into a new form) on *Chaerophyllum*; c - in *D. chaerophyllina* Shap. on *Chaerophyllum*. Numeral by letter ( $c_6$ ,  $n_5$ , etc.) means ordinal number of generation.

preserve a potential capacity to interact because they retain a genetic unity. The interaction may be genetical and may result in complete fusion. Similar populations, e.g. those belonging to one race, can exchange immigrants and unite relatively easily, e.g. in the periods of maximal increase of species numbers. Dissimilar populations, e.g. from different subspecies, can unite only after they become similar to one another in many respects. This may be promoted by parallel evolution of ecological specialization, i.e. adaptation in the same way to similar environmental conditions, resulting in one population changing in the direction of the other or both in a new direction.

The process of acquisition of strong resemblance by reproductively isolated forms has been examined in such aphids as Dysaphis anthrisci majkopica Shap. and D. chaerophyllina Shap. The species reproduce on apple at the same time of year, when aphids can mate freely. However, they do not produce viable hybrid progeny, apparently due to the inability of spermatozoans to move through the sexual ducts of females of the other species. Both forms are heteroecious: D. a. majkopica migrates to Anthriscus nemorosa and D. chaerophyllina to Chaerophyllum maculatum, on which they are specialized. A test of the process of intense natural selection within the clone during 6 parthenogenetic generations revealed that D. a. majkopica first adapted to an intermediate host, Chaerophyllum bulbosum, which was at the beginning of the experiment rather unsuitable for the aphids. After 5 more generations, this line adapted to the previously fully unsuitable (resistant) species Ch. maculatum. Natural selection ended in the 16th generation (Fig. 8), at which point a new form had originated. By convergent evolution it acquired ecological and some morphological characters similar to D. chaerophyllina rather than to the initial form (Shaposhnikov, 1961, 1965). The process of alteration of one adaptive feature (in its absolute and relative expression) are shown in Figs. 9 and 10.

The whole genetic system of D. a. majkopica undoubtedly changed and as a result the new form lost its capability of feeding on its previous host and of crossing with the initial form; it could produce fertile progeny with D. chaerophyllina, however (Shaposhnikov, 1966), (Figs. 11 and 12), and the hybrids were normally fertile in parthenogenetic reproduction in the 6 generations studied. Many of the hybrids were essentially different not only from the parental forms but from all other 17 species of the subgenus. The total number of marginal and spinal tubercles in 75 hybrid larvae of the first instar and embryos investigated was the same as in parental forms, i.e. from 17 to 22 (within the subgenus from 14 to 33), whereas in many adult hybrids (in 65 individuals out of 120) it was sharply reduced to 0-7, with an average of 1.5. It is evident that in more than half of all hybrids the system of epigenetic transformations was disturbed, which confirms the considerable dissimilarity of the genetic systems of the new form and D. chaerophyllina. All hybrids or at least some of them would possibly be incapable of back-crossing or performing the normal transition to amphigony (as has been shown in some other aphids; Möller, 1971, etc.), which unfortunately has not been studied in this case. There is reason to assume that only ecological, morphological and physiological convergence took place, and not genetical convergence. Therefore, despite the acquired capability of interbreeding, the new form and D. chaerophyllina are evidently different species.

Three conclusions can be drawn from these phenomena: (1) Considerably different populations can become so similar by the process of selection as to lose their main differences, including reproductive isolation; (2) if these populations belong to the same species they can fuse and if they belong to different species they can form a new hybrid population (the aphids in the above experiment were capable of successful parthenogenetic reproduction); (3) Such a new hybrid form, which lacks feedback with the parental species, does not belong to either of them and should receive a taxonomic name only after it wins its

struggle for existence and acquires species rank.

Thus populations of one species, irrespective of the presence or absence of contacts between them, preserve the ability to fuse in appropriate conditions, whereas populations of different species may lose such ability if they ever had any. Hence a species should be treated as a potentially integrated system, capable of functioning as a unit but not necessarily manifesting this capacity at any one time (Shaposhnikov, 1975).

4. A species is a dynamic system capable of self-regulation. Vavilov (1931) was probably the first to indicate the necessity to take into account the dynamics of a species as a system, which bind together its "main potential," the region of highest diversity of forms, from which geographically and ecologically

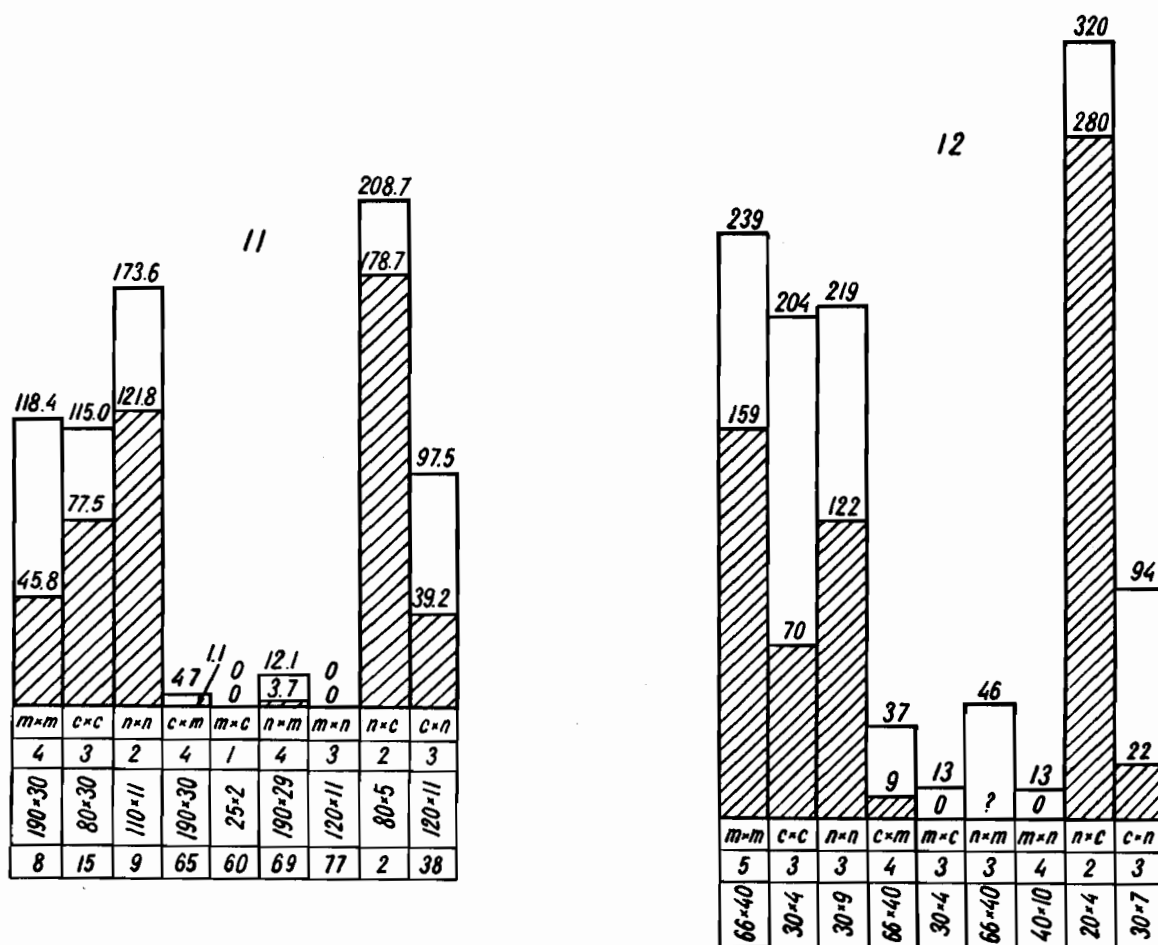


Fig. 11 (left). Results of mating of the aphids *Dysaphis anthrisci majkopica* Shap. (m), *D. charophyllina* Shap. (c), and new form (n) on leaves of apple seedlings in the spacious isolators. For couples the order is always ♀ x ♂. Figures above columns show mean number of deposited eggs calculated per 100 females; figures in the columns show the viable eggs among them; figures below: upper row - number of replications; middle - total number of females and males; lower - percentage of females feeding after mating, which indicates lack of fertilization.

Fig. 12 (right). Results of mating of the aphids *Dysaphis anthrisci majkopica* Shap. (m), *D. chaerophyllina* Shap. (c), and new form (n) without plants in the small isolators, where males encountered females very often, this increasing the chances of mating. Designated as in Fig. 11.

marginal groups segregate. It is quite logical to assume that an intensive exchange of immigrants and genes takes place between centrally converging populations, whereas the flow is reduced and becomes oriented outwards when individuals are situated near the outer limits of the range (Mayr, 1970). However, a number of facts point to the weakness or complete absence of interpopulational gene flow.

The complicated structure of some aphid species, e.g. *Myzus persicae*, and the ability of clones and populations to transform rapidly and adaptively during a single season, are the basis of species dynamics. However, let us consider some examples showing the probability of a species dynamics caused by transformations of local populations both in the same and in different directions.

Results from the aphid *Pemphigus populitransversus* Ril. in 8 localities separated by no more than 8 miles during 1961, 1964, and 1966 (Sokal et al., 1971) confirm the spatial segregation of aphid populations. Aphids from every locality always differ from aphids of other localities by a combination of several morphological characters in spite of the fact that the aphids in every locality were changing from year to year. Studies carried out for many years on the ladybird beetle *Adalia bipunctata* L. in different parts of its range have shown numerous essential changes in many populations. There are variations in the number of melanistic forms both seasonally (Timofeeff-Ressovsky and Sverizhev, 1966) and over many years. The changes are directed towards increase or decrease of the percentage of melanistic forms alternately, whereas in many other populations their number is more or less invariable (Creed, 1971; Sergievsky and Zakharov, 1981). This can be explained by flexible or rigid polymorphism in different populations (Sergievsky and Zakharov, 1981) as earlier found in *Drosophila pseudoobscura* Frol. (Dobzhansky, 1962). Observations carried out during 30 years on 22 populations of the same *Drosophila* species in the southwestern United States have revealed profound genetic changes that have proceeded in the same direction in many populations near the coast (Anderson et al., 1975). Although changes in the populations of ladybird beetles and *Drosophila* differ from each other they nevertheless indicate a complex dynamic process within the species. Of particular interest is a study of numerous fossil remains of elk and some other mammals in the eastern Baltic region (Paaver, 1976). Allometry has shown that throughout ten thousand years the directions of selection changed: during a warming period in the early Holocene animal sizes gradually decreased, while in the late Holocene sizes increased again as a result of cooling.

If one treats populations as sovereign, autonomous systems, elementary evolutionary changes probably take place in them. But if one treats species as a whole, it would be more exact to talk of their homeostatic rather than evolutionary transformations. Despite the significant local changes of, for example, elk in the Baltic region during the Holocene it remained the same European subspecies, *Alces alces alces* L. Some other mammals of this region formed chronological subspecies during that interval (Degerbol, 1933, cited after Paaver, 1976) but nevertheless remained the same species.

To better understand species dynamics it is important to estimate the role of temporary populations. They can repeatedly originate within and beyond the range of the species, e.g. as a result of transportation of insects by the wind for hundreds of kilometers (Andrewartha, 1963; Johnson, 1969), especially for cereal and grass aphids (Robinson and Hsu, 1963; Müller, 1966; Rose et al., 1975; Foot, 1977; Nikolenko and Omelchenko, 1977; Dewar et al., 1980). One can assume that the survival of such passive migrants is inversely related to distance (Shaposhnikov, 1956). However, the very high reproductive rate of aphids allows them to form new settlements of great numbers far from the one or several initial populations. In England the hops aphid *Phorodon humuli* Schr.



migrates every spring from plum trees (the primary host) to two isolated fields of hops (secondary host) to the south, and in autumn they return; the median distance travelled is 15-20 km. and the limit is 150 km. (Taylor et al., 1979).

Temporary populations of a number of aphid species are annually observed in cultivated crops. For example, *Aphis craccivora* Koch is constantly connected with alfalfa and other papilionaceous plants, although it can survive on cotton for a number of generations. Chemical control of *A. craccivora* on cotton fields may intensively select for resistance to pesticides and rearrangement of genetic structure. *M. persicae* which have become resistant to organophosphorous insecticides have changed so considerably morphologically that it is possible to recognize them visually (Eastop and Russel, 1967; Eastop and Banks, 1970). Individuals from temporary populations can probably bring new gene combinations into the permanent population and promote novel evolutionary transformations in it. However, this problem needs further investigation.

One should assume that interpopulational gene flow within a species can be controlled by natural selection, at least in some cases. Thus, gene exchange among populations can improve and increase their plasticity and adaptability to new conditions, bring about new and more advantageous gene combinations (Lewontin and Birch, 1966) and restore those lost during the period of depression (Schwarz, 1980). Clearly, in these cases, exchange is supported and accelerated by selection. In other cases gene exchange between populations\* belonging especially to different races and subspecies can disintegrate their genetic systems and reduce their adaptation. Exchange between diverging populations can slow down their further divergence (Bigelow, 1965). In most cases, as different populations are submitted to a greater variety of directions of adaptation, gene flow decreases. Both immigrants and hybrids may be eliminated, especially by indigenous homozygotes (Dubinin, 1966). It should be emphasized that gene flow between populations can occur not only from cross-fertilization, but also from exchange of clones. In general, interpopulational gene flow depends primarily on species structure and also on the migration abilities of individuals. It can be extensive in species with a small range, similar populations, and mobile individuals, insignificant in deeply differentiated species, and may be equal to zero during prolonged periods of reliable isolation.

Therefore within a species the following phenomena controlled by selection may occur: (1) adaptive transformation of different populations in the same or different directions, (2) interpopulational exchange of immigrants and genes, (3) decrease in number and complete extinction of some populations and their replacement by dispersal from other populations, (4) formation of temporary populations and their transformation into permanent populations. All these transformations can be considered homeostatic mechanisms that operate at the species level and serve as a basis for species dynamics.

5. A species is an isolated system of populations. To preserve species adaptations determined by the genomes of all individuals, the gene pool of the species needs to be protected from penetration by strange genes. In species whose individuals reproduce by cross-fertilization, the most perfect isolation mechanism is reproductive isolation. This does not mean however that "the development of reproductive isolation constitutes the essence of the process of

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\*Some authors consider the replacement of one population by another one as group selection, but it is not selection in the strict sense. Intergroup selection creates nothing new and can merely diffuse what was obtained within a population by individual selection (including kin selection) and/or by genetic drift (Shaposhnikov, 1974b). I think the term "expansion" (Van Valen, 1980) more exactly reflects the matter.

speciation" (Dobzhansky, 1951, p. 262) (see also Dobzhansky, 1970; Mayr, 1963, 1970; Ayala, 1978; etc.). Reproductive isolation is not the cause but the result of speciation: it originates either as a by-product of adaptive genetic adaptation of hybrid individuals to local conditions not being worse than that of individuals of the parental species. Because the co-existence of all these conditions is improbable, hybrid populations are rare, usually temporary, and often the result of disturbance of natural conditions usually caused by man (Mayr, 1963). It should be emphasized that with the penetration of strange elements not only hybrids are eliminated as less adapted to local conditions, but especially the immigrants themselves, including individuals of clones incapable of cross-fertilization. Hence, isolation of a species is protected not only by reproductive isolation but also by natural selection, both in biospecies and agamospecies.

This is the general situation. One should bear in mind, however, that not only species but also populations precisely corresponding to some particular conditions should preserve their adaptative structure and develop mechanisms inhibiting interpopulation gene flow that might destroy these adaptations. Among such mechanisms one can mention homing in birds and fishes. Thus in Pacific salmon (Oncorhynchus), populations are so completely disunited during the breeding season that gene flow is almost completely excluded (Konovalov, 1980). Weakness or absence of interpopulational gene flow has been noted both for invertebrates (Novozhenov et al., 1973) and for plants (Bartholomew et al., 1973). Moreover, some intrapopulation isolation is also observed as a result of positive assortative mating (Gritsenko et al., 1983) or a complicated spatial and temporary structure of populations (Konovalov, 1980; Yablokov et al., 1981).

An opposite type of phenomenon involves gene exchange between different species. Such situations are called by Van Valen (1976) "multispecies" and although they seem to occur more commonly in plants, some examples are known among animals as well. Thus some broadly sympatric species or subspecies in the northern and central parts of eastern Europe are obviously segregated by morphological and other characters, whereas in some southern regions or in the Caucasus most of the individuals are of intermediate character. This phenomenon has been studied in the mice Apodemus silvaticus L. and A. tauricus Pall. (Larina, 1965), in the mosquitos Culex pipiens pipiens L. and C. p. molestus Forsk. (Vinogradova, 1968) and in the aphids Cinara pinea Mordv. and C. curtipilosa Mordv. (Gavrilova, 1983). In the northern regions species may be more narrowly specialized ecologically and hybrids are therefore more rigidly eliminated. On the contrary, in some habitats in the southern regions hybrids appear even better adapted than the parental species. A similar picture has also been observed in gastropods (Clarke and Murray, 1969), in the water bug Notonecta (Delcourt, 1909), and in crickets (Cousin, 1964). Not in every case, however, is it clear whether intermediate forms are really hybrids rather than of some other type of origin.

Multispecies-like phenomena can naturally be treated as a result of hybridization caused by a change of local conditions (Mayr, 1963) and perhaps promoted by parallelism of ecological specialization and convergent evolution as, e.g., between Dysaphis anthrisci maijopica and D. chaerophyllina (see page 18). However, one cannot exclude the possibility that populations with individuals of intermediate type in some cases are not hybrid populations, but are incipient species, whereas distinct populations are divergent species. This suggestion can be made concrete by examples. Therioaphis trifolii Monell in Eurasia is a polymorphic species (Hille Ris Lambers and van den Bosch, 1964). Two extreme variants of this species were sequentially introduced into North America, one apparently in the last century and the other in 1953 (Dickson, 1959). After several years the latter variant developed resistance to organophosphorous pesticides and became adapted to previously resistant alfalfa

varieties (Nielson and Don, 1974); it is now distributed not only in the USA, eastern Canada, and Mexico, but also in Australia and South Africa (Wilson et al., 1981). In conformity with the "founder principle" two groups of populations evolved in America. Neither had the ability to survive on the host of the other and they are reproductively isolated (Manglitz and Russell, 1974). It is no wonder that American entomologists distinguish two species: yellow clover aphid, *Th. trifolii* Mon., and spotted alfalfa aphid, *Th. maculata* Buckt. One may agree with Blackman (1981) that we have a case of incipient speciation. *D. a. majkopica* diverged into a new form (see page 18), and had the history of origination of this new form, which is intermediate between *D. a. majkopica* and *D. chaerophyllina*, not been known it could be considered to be an incipient species, like the derivative Eurasian species *Th. trifolii*, the latter having arisen by hybridization of two American species. Therefore the multispecies phenomenon deserves a more profound and careful study.

There is always some extent of sympatry in multispecies. But many cases are known of narrow hybrid zones between allopatric species (Mayr, 1963; Endler, 1977; White, 1978). The zones possess a remarkable constancy and show a lack of reproductive isolation. There has been no satisfactory explanation of these cases by the biological species concept (Mayr, 1969a), merely the coining of the special term "semispecies."

A hybrid zone between the hooded crow and the carrion crow has remained narrow and invariable during at least 5000 years over thousands of kilometers (Mayr, 1942). It apparently consists of temporary populations that are constantly reinforced at the expense of parental forms. The narrowness of the zone suggests that the hybrids are adapted somewhat more poorly than are the parental forms and are incapable of an independent permanent existence or at least of competition with parental forms, and that therefore the hybrids cannot penetrate into the parental ranges. Sometimes individuals of hybrid populations on the boundaries of a range are even sterile, as in the case of beetles of the genus *Chilocorus* (Zaslavsky, 1966), but, despite self-destruction of the genes of each species, prereproductive isolating mechanisms have not been developed.

Why do isolating mechanisms not arise in these and many other cases? The simplest answer would be to assume that 5000 years is insufficient. However, experiments on *Drosophila* (Koopman, 1950; Thoday and Gibson, 1962; Dobzhansky and Pavlovsky, 1971, 1975) and aphids (Shaposhnikov, 1966) have shown that two or several dozens of generations are enough for reproductive isolation to arise. Alternatively, recent evolutionary geneticists think that selection is not on single loci but on genotypes as a whole, which are responsible for the adaptation of the organism (Lewontin, 1974; Ayala, 1978). Selection for isolating mechanisms could disturb the adaptive heterozygosity of both the intercrossing species. Probably temporary hybrid populations as in such cases as the crows and beetles can be treated as a "payment" for preserving intact the co-adapted genetic systems of species not isolated reproductively (Shaposhnikov, 1974a) and at the same time as an "unstable equilibrium" which until disturbed by some external factors (Rasnitsin, 1971). Similar assumptions have been made by Endler (1977) who thinks, however, that the boundary between carrion crow and hooded crow can be treated not as a hybrid zone due to secondary intergradation (Mayr, 1963), but as a steep cline due to primary intergradation, but it is difficult to accept the latter view.

Many species of plants (Zavadsky, 1968) and some of vertebrates (Borkin and Darevsky, 1980) and invertebrates, including some obligatorily parthenogenetic aphid species, have a hybrid origin. These species arise because of a lack of back-crossing (a result of allopolyploidy, parthenogenesis, etc.), so that gene flow is directed only from the parental species to the derivative one. Thus the initial species maintain their individuality and complete isolation.

In this manner species isolation can be preserved despite the absence of prereproductive isolation, the continued existence of hybrid populations in nature, and the formation of hybrid species.

In conclusion, a definition of a universal notion of species is suggested. A species is a system of related populations capable of interactions and fusion, and isolated from other such systems. A more detailed wording would be: a species is a more or less safely isolated system of related populations that, because of a set of co-occurring species adaptations and accordingly a common gene pool, and also because of a similarity of ecological specialization, are capable of interaction, fusion and replacement of one another. Moreover, a species is an integrated system, actually or potentially, and a dynamic one, capable both of evolutionary changes and homeostatic transformations and also capable of a long-term maintenance of its status quo, which makes the species potentially eternal.

A species is distinguishable from intraspecific systems by reliable isolation, from supraspecific taxa by integrity and the capacity of its parts to interact, and from synecological systems by the genetic relationship of its components. It should be emphasized that "a population is only an elementary evolving unit. The main object of historical changes is the species as a whole" (Schmalhausen, 1961 : 129). Similar ideas and facts confirming them have been adduced by other scientists (Simpson, 1961; Mayr, 1969b; Anderson et al., 1975; Shaposhnikov, 1978).

#### SPECIES PARAMETERS

By suggesting a single universal definition of species, I have attempted to define the essence of this phenomenon, the specificity of a species as a living system of a particular type.

As to applying this concept to determine species parameters and to distinguish between species and especially between species and subspecies, one must realize that a definition is not a recipe for practice. Species in different taxa are not equivalent and it is impossible to have a universal criterion for all particular cases.

Like any other living system, a species has both spatial and temporal parameters. In regarding a species as a group of populations, the biological species concept emphasizes its spatial parameters, whereas the evolutionary concept, by treating species as a lineage, i.e. as an ancestor-descendant sequence of populations (Simpson, 1961), stresses the temporal aspect. Because the evolutionary concept is applicable to organisms with bisexual, unisexual and asexual reproduction (Meglitsch, 1954; Van Valen, 1976; Wiley, 1978) it is more universal. The word "system" in my definition of the concept "species" integrates the concepts of "group" and "lineage" and thus includes both spatial and temporal parameters.

Since the concept "species" should be unitary it must be treated not only as a particular historically formed biosystem, but also as an abstract taxonomic category and as a concrete taxon. That is the starting-point.

Taxonomic parameters of the species or, more exactly, of the probability of revealing the species status (rank), are determined by a complex of criteria used practically in systematics.

Every species, like every other taxon, is in itself a hierarchy of living systems; the taxa may be distinguished on one hierarchical level and be nearly identical on the other. For example, a great similarity is observed between man and the chimpanzee at the molecular level and no common features exist in their species structure. In contrast, Anura are more different at the molecular level than at the organismic level. Many aphid species are different not so much by their morphology as by their life cycles and population structure.

Dysaphis anthrisci majkopica Shap., for example, is markedly different from D.a. anthrisci Börn (Fig. 7), but the latter subspecies is morphologically similar to D. dejecta Walk., although life cycles, seasonal structure of the populations, and position in ecosystems are very different between the species (Figs. 3 and 4). The most reliable differences between Euceraphis punctipennis Zett. and E. betulae L. are in their karyotypes (Blackman, 1976), whereas Aphis fayae Scop. and A. cirsiacanthoidis Scop. differ most in their food specialization (Iglisch, 1968, 1972) and in their enzymes (Odermatt, 1981). Many aphid species in Pemphigus and many other genera are best distinguished by the species of host plants and their organs, by gall structure, than by the morphology of the organisms themselves. Ghilarov (1974) has emphasized the necessity to take into account many other ecological characters.

Undoubtedly, the criterion of reproductive isolation is of primary importance for species reproducing by cross-fertilization. This, of course, is true of the majority of species. Furthermore, this criterion allows for the most exact evaluation of the degree of differentiation of the system of populations, taking into account the extent and mode of the reproductive isolation. An absence of fertile progeny in nature and in compulsory reciprocal crossing shows that a potential for fusion of populations is either lacking or strongly suppressed. The production of hybrids capable of parthenogenetic but not of amphigonic reproduction (in aphids, cladocerans, etc.) means that the potential for fusion can be realized to some extent only. If no crossing occurs in nature, but fertile progeny capable of backcrossing are obtained experimentally, it indicates a populational potential for fusion that can be realized easily under certain conditions. Premating isolating mechanisms retain more possibilities for hybridization than do post-mating or post-zygotic ones.

However, estimation of the whole complex of characters at all hierarchical levels is necessary for a final determination of species rank. This is necessary, since a species at least in a practical sense is a probability phenomenon. Here the experience of a taxonomist is very important, as it allows him to reveal living systems existing in nature. Adherents of a single objective criterion even as important as reproductive isolation do not take into account that evaluation of a taxon by only one criterion cannot be objective, since the very choosing of the criterion is not objective. Integrated evaluation of a taxon by all its available peculiarities diminishes the subjectivity but does not completely eliminate it.

Practice has shown that cross-breeding as well as modern methods of research (biochemical, cytological, ethological, mathematical, etc.) usually confirm taxonomists' conclusions and in some cases allow them to review the subject. This demonstrates that a taxonomist should treat the whole body of evidence and that his subjective, sometimes intuitive, solution is generally verified in the context of other science.

There are, however, clusters of sympatric, closely related forms with a complex regime of hybridization, in which species are extremely difficult to distinguish from subspecies. In such complexes of aphids these difficulties are increased by the influence of previous feeding conditions on the production of fertile or sterile (at amphigony) progeny (see page 9). Meanwhile a thorough study of such clusters using recent methods can assist in understanding the essence of species and make the revelation of its parameters more objective.

Spatial parameters of a species, i.e. boundaries of its range and distribution of its populations within its range, depend on its ecological potentials, i.e. on the ability to occupy a certain place in ecosystems and on the conditions of realization of these potentials, i.e. on the presence of suitable ecosystems and opportunities for dispersal and distribution. The spatial parameters of a species in different historic periods of its existence may vary. During a long existence of a broken range all populations can retain



a great similarity (Ehrlich and Raven, 1969) and the potential to fuse, even in cases of evolutionary transformations that are both unidirectional and weakly divergent. One should assume that the entire range can be restored under certain conditions.

In some cases boundaries of a species' range are determined by the range of contiguous closely related species, as in the case of crows among others. The spatial parameters of a species are increasingly influenced by anthropogenic factors. Thus owing to man some aphid species have realized their potentials of clonal existence and have become cosmopolitans (*Eriosoma lanigerum* Hausm., *Aphis craccivora* Koch, *Myzus persicae* Sulz., and others).

Temporal parameters of species constitute probably the most discussed problem and are closely related to the problem of phyletic and quantum transformations. In contrast to individual organisms, the duration of a species' existence has not been genetically programmed. A species is potentially eternal although its actual life duration may depend on external factors. The species exists as long as favorable conditions are preserved, or more exactly as long as the rate of change of external conditions does not exceed the capacity of the species' regulatory transformations and so allows the species to maintain its identity or individuality. According to Van Valen's picturesque expression, a species, like the Red Queen, must always run to stay in the same place (cited after Lewontin, 1978). An essential change of conditions brings about the end of the species. It dies out or else changes profoundly and transforms into a new species or, by splitting, into two or several species; the time required depends on the mode of evolutionary transformations. A quantum transformation of one species into another is a more or less easily defined shift, but gradual phyletic evolution is hard to assess, mainly because of great difficulties in determining when homeostatic changes are transformed into evolutionary changes. Starobogatov (1968), pointed out that parents and offspring cannot belong to different species. This assumption is both true and false at the same time. Transitional forms can exist in the sequence of generations which can be referred to both the initial and the descendant species. This has been shown in an experiment on aphids (Shaposhnikov, 1965): all the individuals in the experimental lineage of the clone to the fifth generation were identified, as in control lineage of the clone, as *D. a. majkopica*; in the sixth generation some individuals were of an intermediate type; in the seventh generation there were 67.5% of *majkopica*-type individuals, 32.5% of intermediate type, and 0% of the type of the new form; in the eighth generation 37.5%-20%-42.5% respectively; in the ninth and tenth generations 0%-2.5%-97.5%; in generations 11 through 46 all the individuals were identified as the new form. Such rapid changes should be treated as a typical quantum shift (Shaposhnikov, 1978) and clearly show a temporal boundary between the species. In this case the temporal boundary between the old and new forms is very narrow, occurring between the fifth and eleventh generations.

In recent years, perhaps as a consequence of discussion on punctuated equilibria, there have appeared different viewpoints on temporal boundaries of species. Willis (1981) treats species as "a part of a phylogenetic tree" (p. 84) and emphasises the phyletic continuity of the evolutionary process, whereas Wiley (1978, 1981) rejects the very possibility of non-divergent phyletic evolution. Although agreeing with the critical comments of Grant (1982) on punctuated equilibria and related questions in general, I think it appropriate to present some of my considerations.

First, evolution is always mosaic. While adaptation in particular morphological structure changes quickly by a quantum shift, another changes slowly, gradually, phyletically, or else remains the same, unaltered. Evolutionary transformations (their irreversibility proved experimentally) that arose during the adaptation of *D. a. majkopica* to new hosts of the genus



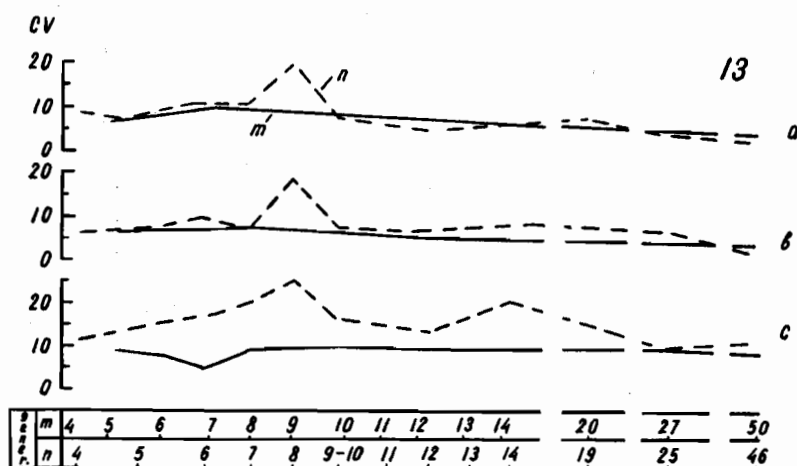


Fig. 13. Changes of coefficient of variability (CV) in the process of adaptive transformations.

a - length of apical joint of rostrum; b - ratio of the length of the apical joint of the rostrum to the second joint of the hind tarsus; c - ratio of the length of siphunculi to their diameter in the middle part; m - clone of *Dysaphis anthrisci majkopica* Shap. on *Anthriscus* (control); n - the same clone in the process of adaptation to new hosts (*Chaerophyllum*).

\* \* \*

*Chaerophyllum* and its transformation are a good illustration of this proposition. Thus the rostrum, the most significant feature from the point of view of adaptation, has changed (Fig. 9, 10) and stabilized (Fig. 13) very quickly; during 5 generations only it changed convergently and became similar to that of species inhabiting *Chaerophyllum*. Transformations of the siphunculi were stabilized much more slowly, taking more than 20 generations (Fig. 13); the pattern of cuticle sclerotization, the density of hairs on the last segment of the rostrum, and some other characters which distinguish *D. a. majkopica* from related species inhabiting *Chaerophyllum*, persisted up to the 47th generation, i.e. to the end of the experiment, and remained the same as in individuals of the initial population and in the control lineage of the clone of *D. a. majkopica*. If one determines the lineage from *D. a. majkopica* to the new form on the basis of a single character (as paleontologists sometimes do), one may conclude with regard to one character or another that the initial lineage persists, that phyletic evolution occurs, or that a quantum shift occurs.

Secondly, I must state that I understand a quantum shift (Shaposhnikov, 1978), following Simpson's logical scheme, as a "break-through from one position of stabilizing selection to another" (Simpson, 1953:391) when an old "equilibrium is lost, and a new equilibrium is reached" (Simpson, 1944:207). Instability of the system between the two equilibria is reflected in particular in an increase of morphological variability (Fig. 13). Since in the process of a quantum shift a "system is unstable and cannot long persist" (Simpson, 1944:207) it would be more correct to speak of quantum transformations occurring in populations and species than of quantum evolution in supraspecific taxa. As for phyletic evolution, one may suppose that it is at least in some cases an accumulation of small quantum shifts following one another in the same direction. Hence differences between the two modes of evolution diminish. Simpson (1953) himself pointed out the existence of transitional states between quantum and phyletic evolution.

My assumption of the accumulation of small quantum shifts (Shaposhnikov, 1978) is congenial to Grant's (1977) idea of a speciation trend of evolution,

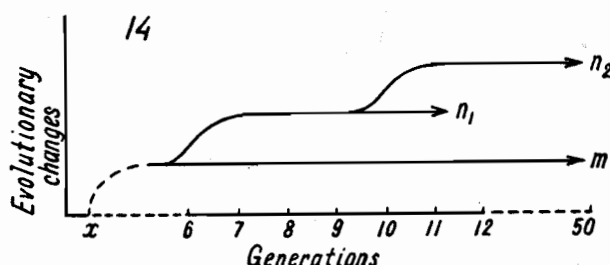


Fig. 14. Experimental model of a speciation trend of evolution (after Grant, 1977).

m - *Dysaphis anthrisci majkopica* Shap.;  $n_1$  - new form originated from m, adapted to annual *Chaerophyllum bulbosum* and died together with its host;  $n_2$  - new form originated from  $n_1$ , adapted to perennial *Ch. maculatum*.  
\* \* \*

as can be seen if the results of the experiment are depicted according to Grant's scheme (Fig. 14).

Here gradual changes indicate a sequence not of "vertical" species replacing one another like segments in an unbroken phyletic lineage (successional species of Imbrie, 1957), but of usually "horizontal" species arising in a sequence as a result of several instances of divergent evolution, the latter caused by a stepwise assimilation of a new adaptive zone. The same stepwise pattern is observed in the evolutionary transformation of the photoperiodic reaction threshold during the formation of anholocycly (Fig. 5). A stepwise pattern is observed also in nature, e.g. the well-known example of the genus *Clarkia*, which produces species that are more and more drought-resistant as it moves deeper into arid regions of California (Lewis, 1962; Raven, 1964; Bartholomew et al., 1973). The evolution of higher taxa such as mammals (Tatarinov, 1976), birds (Bock, 1965), and insects (Rasnitsin, 1976) has also been treated as a long multi-stage process of the gradual accumulation of particular adaptations.

A species as a dynamic system always undergoes some transformation, but when a new species is formed the tempo of changes increases and the transitional period is relatively short. In contrasting his theory to that of Cuvier, Darwin supported the thesis that "Natura non facit saltus," yet he did not conceive evolution as a smooth, gradual process which goes on continuously. As he mentioned more than once, "It is far more probable that each form remains for long periods unaltered, and then again undergoes modification." "... The periods during which species have undergone modification, though long as measured by years, have probably been short in comparison with the periods during which they retained the same form" (Darwin, 1873, pp. 91 and 409). Vavilov (1931) has also treated species as junctions in the infinite chain of the evolutionary process characterized by the unity of brokenness and constancy.

Practically, the problem involves difficulties in revealing and evaluating the transitional state. We encounter such difficulties in any field of biology when boundaries between phenomena become fuzzy due to the diversity of transitional states. Let us remember syncytia, siphonophores, ant colonies, lichens, etc. The probability of correct identification of both the temporal and spatial limits of extinct species and of recent species, and the very status of species as well, depends on the quantity and quality of data collected and on taxonomists' qualifications.

#### Conclusion

I am deeply convinced of the necessity for a universal species concept

applicable to every living thing present or past. One should assume that species as well as organisms appeared more or less simultaneously with the emergence of life on Earth and evolved at different rates during more than three billion years. Therefore there exist organisms and species which are primitive, highly developed, and secondarily simplified. Different types of species, e.g. agamospecies and biospecies, are no more incommensurable than are different types of organisms, e.g. unicellular and multicellular. Species, populations and organisms are adapted to perform a definite function in the biosphere, their organization being suited to the performance of that function. Like any other living system, each species seeks to preserve itself as a unique system and by all available means resists the destructive effects of the environment. It resists until external factors change so considerably as to make it either transform into a new species or become extinct if incapable of transformation.

Studies of clones, colonies, populations, and species in aphids as well as many other observations of nature force a reconsideration of the biological species concept. However, in suggesting an original concept, called universal, I treat it as being preliminary. New facts, in particular those bearing on the organization of populations and species in various sea-plankton forms, in fungi, and especially in primary clonal unicellular organisms, will make the species concept still more universal and help establish an hypothesis of the evolution of species as a living system of a characteristic type.

According to the system approach and the ideas of hierarchy, a system consists of interacting elements and is itself an element of a higher system. Therefore, in making an attempt to reveal the essence and parameters of species and population, I have taken into account both the structure of the system and its position among other systems. The main objective is to find universal properties of any species, and also to reveal features peculiar to the species alone and not found in other living systems. The universal concept of a species reveals the essence of this phenomenon and gives flexibility in the search for concrete criteria of a species in the practical study of species multiformity.

There are and there will be many difficulties on the way to a definitive solution of the species problem. It is natural that retrogressive tendencies appear time by time; one hopes that optimism will triumph over pessimism, because concepts of population and species are central to an understanding of the biology and evolution of organisms.

#### Acknowledgments

I thank Leigh Van Valen for improving the text and I appreciate the comments and suggestions of anonymous referees.

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