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THE ECOLOGICAL SIGNIFICANCE OF CORRELATION PLEIADES¹

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The concept of correlation pleiades was originally advanced by Terentjev (1931). It is based on the presence of correlations between some quantitative characteristics, e.g., between dimensions of certain parts of an organism (or between different measurements within one part), and, at the same time, on the absence of correlations between these and other parts. The existence of correlation pleiades leads to theoretically important conclusions.

The presence of correlations between, for instance, the dimensions of some parts of an organism and the absence of correlations between the dimensions of these and the other parts of the same organism indicate the independence of certain developmental processes with respect to other processes within the organism. The pleiades are thus a manifestation of differentiation.

With respect to a given part, other parts of the same organism basically constitute its environment. The origin of correlation pleiades in the course of evolution is an indication of the increasing independence of certain developmental processes with respect to environmental factors, including the influences exerted by the other parts of the same organism. The study of correlations makes it possible to establish the degree of independence reached. The adoption of such a quantitative criterion provides an adequate basis for the introduction of the comparative method in the study of the process by which this independence is attained. Investigation of correlation

pleiades has a considerable practical importance in science, as well as in agriculture and medicine.

The application of statistical methods to the solution of some taxonomical problems depends entirely on the success in the choice of non-correlated characters (Heincke, Fisher; see Lubishchev, 1959, and Terentjev, 1959). The general theory of the correlation pleiades, including their ecological interpretation, provides the pattern for selection of the non-correlated characters or "indicator-characters," as Terentjev has termed them.

In agricultural practice, especially in the industrial processing of the products of plant and animal husbandry, ever increasing practical importance is played by the standardization of raw agricultural materials. But a standard, or norm, is merely the expression of autonomy of characters, i.e., of their independence from the fluctuations of environmental factors during the development of these characters. The principle of correlation pleiades brings us close to the controlling of the process of standardization. To know how pleiades arise, is to know the mechanism of the origin of independence from environmental variability.

The general theory of correlation pleiades must obviously answer such questions as why correlation pleiades exist, and why it is a given part and not another one that escapes from the network of correlations within the organism, and either retains constant quantitative characteristics or varies according to its own principles more or less independently from the variation of other parts?

The general theory of correlation pleiades can be formulated only if some

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general principle were established, which would make it possible to consider any instance of presence or absence of the pleiades as some particular manifestation of that principle. The establishment of such a principle would enable us to predict the existence of correlation pleiades. It is obvious, however, that this task has to be confined in each specific instance to the particular branch of science involved. Each branch of biology is capable of solving problems concerning living organisms, but the answer will always be restricted to those aspects of the object that this particular branch is investigating. However, any principle, expressed in terms of a strictly defined branch of science, would, nevertheless, be a general principle, since it will allow the discovery of all the features common to the diverse

elements of the phenomenon considered from a certain viewpoint.

The purpose of the present paper is to give an ecological interpretation of the phenomenon of correlation pleiades extending the previous report on this subject (Berg, 1959b). Consequently, the focus of attention in the discussion is provided by the principle of adaptation.

There are two aspects to this problem. Firstly, the adaptive significance of the correlation pleiades must be established. For this, the variability of the very phenomenon of correlation pleiades must be investigated to start with. That is to say that it is necessary to find instances of presence as well as of absence of correlation pleiades, or that a difference in the degree of correlation between analogous characters in different species

TABLE 1. *Ecological and morphological description of the plants studied*

Species	Number of plants studied	Mode of pollen transfer	Type of floral symmetry	Position of the flower on the plant	Presence or absence of tubular parts
1. <i>Triticum aestivum</i>	100	self-pollinated	dorsiventral	lateral	lacking
2. <i>Elymus arenarius</i>	50	wind-pollinated			
3. <i>Hordeum vulgare</i> var. <i>pallidum</i>	100	self-pollinated			
4. <i>H. vulgare</i> , var. <i>nudum</i> (hulless)	100				
5. <i>Anemone nemorosa</i>	65	pollinated by unspecialized insects	radial	terminal	
6. <i>Fragaria collina</i>	50				
7. <i>Papaver</i> sp.	45				
8. <i>Cosmos bipinnata</i> (inflorescence)	150				
9. <i>Lychnis viscaria</i> *	40	pollinated by butterflies	radial	lateral and terminal	present
10. <i>L. chalcedonica</i> *	30				
11. <i>Melandrium silvestre</i> *	50		dorsiventral	lateral and terminal	
12. <i>Nicotiana glauca</i>	40				
13. <i>Phlox divaricata</i> †	50				
14. <i>Geranium pratense</i>	65	pollinated by bees and bumblebees	radial structure functioning as dorsiventral as the result of lateral position	lateral	lacking
15. <i>Chamaenerium angustifolium</i>	50				
16. <i>Linaria vulgaris</i>	30		dorsiventral	lateral	present
17. <i>Delphinium elatum</i>	53				
18. <i>Digitalis ambigua</i>	75				
19. <i>D. purpurea</i>	50				
20. <i>Tropaeolum majus</i>	150				

* In *L. viscaria*, *L. chalconica* and *M. silvestre* the false tube of the corolla is formed by laminar petals. The calyx is tubular.

† In *P. divaricata* the flower is bilateral in consequence of the position of stamen.

TABLE 2. *The measurements studied and the symbols used for them in tables 3-7*

Vegetative parts	{	Stem	Height.....	A
		Leaf	{Length.....	B
			{Width.....	C
			{Number.....	D
Reproductive parts	{	Inflorescence	Length.....	F
			Number of florets..... (or of spikelets)	G
		Corolla	{Flower diameter.....	I
			{Petal length (length of flowering glume).....	J
			{Length of tubular parts.....	K
		Calyx	{Sepal length (glume length).....	M
			{Calyx length.....	N
		Flower	{Stamen length.....	O
			{Pistil length.....	P
		Grain	Grain length.....	L

must be established. Next, it should be determined what complex of ecological relationships is associated with the presence or absence of a particular pleiad. In the course of such investigation, the adaptive significance of the presence or absence of a correlation pleiad should be revealed and the selective factor responsible for the origin of this pleiad identified. The second aspect, that dealing with the general principle of the origin of correlation pleiades, can be attacked only after this operation is applied to at least one specific case. This general principle may be sought from comparisons of mechanisms of initiation of a variety of pleiades, for the purpose of identifying features common to all of them.

MATERIAL AND METHODS

Nineteen species of herbaceous plants have been studied in order to determine the variability in the degree of dependence between the dimensions of different parts of an organism. One of the species studied, viz. barley (*Hordeum vulgare*) is represented in our study by two varieties: *pallidum*, Pushkinsky ozi-myi, no. 1, and the hullless variety *nudum*.

The wheat used in this study, *Triticum aestivum* (variety *diamant*) was studied both by Krasnovidova in 1956 and by the present author in 1957. Only the results of the second series of investigations are given in this paper. The list of the species investigated as well as the number of the specimens studied for each species is given in table 1. The list of characteristics of plants and a key to the letter symbols denoting them in the following tables are given in table 2. Not all the species were studied with respect to all characters listed, the range of the number studied for a species being from three to ten.

The plant parts investigated were classified into vegetative and reproductive according to the specific significance of form and dimensions for the process of reproduction. Stems, leaves and inflorescences are vegetative parts; stamen, pistil, corolla and calyx are reproductive parts. All the organs, the shape and dimensions of which are important in determining the success or failure of pollen transfer are thus denoted as reproductive. Hence, the inflorescence of *Cosmos bipinnata*, analogous in its function to radial flowers is regarded as

TABLE 3. Correlation coefficients between the dimensions of vegetative and reproductive parts of *Chamaenerium angustifolium* Scop.

	A	B	C	D	F	G	I	M	O
B	0.82 ± 0.05								
C	0.70 ± 0.07	0.84 ± 0.04							
D	0.78 ± 0.05	0.66 ± 0.08	0.41 ± 0.12						
F	0.85 ± 0.04	0.77 ± 0.06	0.74 ± 0.06	0.55 ± 0.10					
G	0.89 ± 0.03	0.90 ± 0.03	0.69 ± 0.07	0.56 ± 0.10	0.88 ± 0.03				
I	0.05 ± 0.14	0.20 ± 0.14	0.44 ± 0.11	-0.03 ± 0.14	0.16 ± 0.14	0.07 ± 0.14			
M	0.09 ± 0.14	0.24 ± 0.13	0.39 ± 0.12	-0.10 ± 0.14	0.13 ± 0.14	0.08 ± 0.14	0.70 ± 0.07		
O	-0.09 ± 0.14	0.08 ± 0.14	0.24 ± 0.13	-0.22 ± 0.13	-0.13 ± 0.14	-0.12 ± 0.14	0.50 ± 0.11	0.49 ± 0.11	
P	0.32 ± 0.13	0.48 ± 0.11	0.47 ± 0.11	0.08 ± 0.14	0.29 ± 0.13	0.29 ± 0.13	0.57 ± 0.09	0.50 ± 0.11	0.44 ± 0.11

a reproductive part, while the inflorescences of all the other species studied are classified as vegetative parts. The outer parts of the perianth of different species (sepal, empty glume), as well as the inner parts (petal, flowering glume) are respectively denoted by the same symbols. Analogy rather than homology was deemed to be of significance. The resemblance in function of the outer parts of the perianth of different plants justified the search for pleiades involving their dimensions. This also holds for inner parts. Minor differences in functioning of parts justify the hope that the reasons for the presence or absence of a correlation pleiad could be understood and that an ecological interpretation of pleiades may be obtained.

The dimensions of different parts were in all cases measured and analyzed within the same group of specimens. Correlations as expressed by correlation coefficients were computed for the dimensions of all parts studied within each species.

It may be seen from table 1 that the diversity of the material involved in this study afforded the possibility of comparison of plants widely differing in both

their ecological characters (e.g., the mode of pollen transfer) and their morphology (the structure and position of flowers as well as the type of their symmetry). Among the plants studied there are self-pollinators (*T. aestivum*, *H. vulgare*), anemophiles (*E. arenarius*), entomophiles having no specific insect pollinators (*A. nemorosa*, *F. collina*, *Papaver* sp., *C. bipinnata*), entomophiles pollinated in their native habitats either now or in the past by butterflies (*L. viscaria*, *L. chalcadonica*, *M. silvestre*, *N. alata*, *Ph. divaricata*) and, finally, plants having such specialized pollinators as bees and bumble-bees (*G. pratense*, *Ch. angustifolium*, *L. vulgaris*, *D. elatum*, *D. ambigua*, *D. purpurea* and *T. majus*). Our material includes plants with flowers having tubular parts (*L. viscaria*, *L. chalcadonica*, *L. vulgaris*, *D. elatum*, *Ph. divaricata*, *T. majus*), and plants with flowers completely transformed into a tube (*D. ambigua*, *D. purpurea*), as well as plants whose flowers are devoid of tubular parts (*G. pratense*, *Ch. angustifolium*), all of them possessing specialized pollinators. Plant species selected for this study vary also with respect to

TABLE 4. Correlation coefficients between the dimensions of vegetative and reproductive parts in *Delphinium elatum* L.

	A	B	G	H	K
B	0.53 ± 0.10				
G	0.67 ± 0.08	0.59 ± 0.09			
H	0.45 ± 0.11	0.57 ± 0.09	0.49 ± 0.10		
K	0.22 ± 0.13	- 0.10 ± 0.14	0.12 ± 0.14	- 0.03 ± 0.14	
M	0.16 ± 0.13	- 0.10 ± 0.14	- 0.13 ± 0.14	- 0.08 ± 0.14	0.40 ± 0.12

TABLE 5. *Correlation coefficients between the dimensions of vegetative and reproductive parts in Triticum aestivum, variety diamant*

	A*	F	G	M	I ₁ †	I ₂ †
F	0.73 ± 0.05					
G	0.61 ± 0.06	0.79 ± 0.04				
M	0.60 ± 0.06	0.69 ± 0.05	0.51 ± 0.07			
I ₁	0.57 ± 0.07	0.70 ± 0.05	0.54 ± 0.07	0.69 ± 0.05		
I ₂	0.67 ± 0.06	0.69 ± 0.05	0.59 ± 0.07	0.71 ± 0.05	0.87 ± 0.02	
L	0.43 ± 0.08	0.45 ± 0.08	0.36 ± 0.09	0.47 ± 0.08	0.61 ± 0.06	0.58 ± 0.07

* Length of the upper internode.

† I₁—length of lemma; I₂—length of palea.

the degree of oligomerization and fixation of the number of parts of the flower and the perianth.

RESULTS

It has been established that, among the nineteen species studied, twelve species have correlation pleiades, involving dimensions of some parts investigated (*L. viscaria*, *L. chalconica*, *M. silvestre*, *N. alata*, *Ph. divaricata*, *G. pratense*, *Ch. angustifolium*, *L. vulgaris*, *D. elatum*, *D. ambigua*, *D. purpurea* and *T. majus*), while seven species have no correlation pleiades with respect to the dimensions of the analogous parts (*T. aestivum*, both varieties of *H. vulgare*, *E. arenarius*, *A. nemorosa*, *F. collina*, *Papaver* sp., and *C. bipinnata*). In the former twelve species the parts studied form two groups, within each of which all the dimensions are positively correlated with each other, while bearing no

or very little correlation with the dimensions recorded in the other group. Such grouping of characters indicates, following Terentjev, presence of correlation pleiades.

In the latter seven species no correlation pleiades were observed. The dimensions of all the parts investigated were closely intercorrelated, thus forming, as it were, a single correlation pleiad. Such a phenomenon is regarded as indicating absence of correlation pleiades, since only the absence of correlations between the dimensions of certain groups of characters delimits the pleiades and thus makes it possible to distinguish between the presence of correlation pleiades and the mere existence of correlations.

Only representative data are given in the present article. The species with correlation pleiades are represented by *Chamaenerium angustifolium* (table 3) and *Delphinium elatum* (table 4), while

TABLE 6. *Correlation coefficients between the dimensions of vegetative and reproductive parts in Hordeum vulgare, var. pallidum, Pushkinsky ozimyi, No. 1*

	A*	B	F	G	M	I ₁ †	I ₂ †
B	0.65 ± 0.06						
F	0.38 ± 0.09	0.56 ± 0.07					
G	0.37 ± 0.09	0.58 ± 0.06	0.93 ± 0.01				
M	0.46 ± 0.08	0.54 ± 0.07	0.68 ± 0.05	0.66 ± 0.06			
I ₁	0.38 ± 0.09	0.43 ± 0.08	0.60 ± 0.06	0.58 ± 0.06	0.52 ± 0.07		
I ₂	0.28 ± 0.09	0.44 ± 0.08	0.66 ± 0.06	0.66 ± 0.06	0.66 ± 0.06	0.57 ± 0.07	
L	0.34 ± 0.09	0.47 ± 0.08	0.59 ± 0.06	0.62 ± 0.06	0.50 ± 0.08	0.52 ± 0.07	0.58 ± 0.06

* Length of the upper internode.

† I₁—length of lemma; I₂—length of palea.

TABLE 7. *Correlation coefficients between the dimensions of vegetative and reproductive parts in Anemone nemorosa and Geranium pratense*

Species		A	B
<i>Anemone nemorosa</i>	B	0.75±0.05	
	J	0.79±0.05	0.77±0.05
<i>Geranium pratense</i>	B	0.71±0.06	
	I	0.01±0.13	-0.05±0.13

the species having no pleiades are exemplified by *Triticum aestivum* (table 5) and *Hordeum vulgare* (table 6). Correlation coefficients between the dimensions of all the parts studied are shown for these four species. Correlations between the dimensions of vegetative and reproductive organs are indicated within the frame, shown on the table; those between the dimensions of different vegetative parts are shown above the frame, and correlations between the dimensions of different reproductive parts are to the right of the frame. As it may be seen from tables 3 and 4, in both *Ch. angustifolium* and *D. elatum* the dimensions of vegetative organs are closely correlated with one another, as are the dimensions of reproductive organs, but the correlation between dimensions of vegetative organs on the one hand and those of reproductive organs on the other hand is low or, in fact, in most cases, there is no correlation. As shown in tables 5 and 6 in wheat and barley all the dimensions studied are correlated. Correlation coefficients between the dimensions of grains (denoted by L) and those of other parts of the organism are somewhat smaller than all other correlation coefficients. This might well be expected, the grain being essentially an organism of the next generation with a genotype of its own, and not a part of the parent organism. In wheat and in barley there are no correlation pleiades with respect to the characters studied.

As shown by table 7, in *Geranium pratense* the size of the corolla is not correlated with the dimensions of the

stem and leaf, whereas in *Anemone nemorosa* such a correlation does exist.

Thus, variation, or the existence of correlation pleiades, has been established. In all instances in which pleiades were present, it was the flower that had become independent of the correlations within the plant organism.

DISCUSSION

The next step of the analysis deals with the determination of the complex of associated traits which governs the presence or absence of correlation pleiades. As shown in table 1, neither floral symmetry of the position of the flower on the plant have a bearing on whether pleiades are present or absent. But the method of pollen transfer is indeed linked with this factor. All plants with specific insect pollinators, be they butterflies or bees, have correlation pleiades. All plants lacking specific pollinators, be they self-pollinated, anemophiles or entomophiles without specialized insect pollinators, lack correlation pleiades. Presence of correlation pleiades involving the characters studied indicates a certain degree of independence of the flower dimensions. The adaptive significance of this autonomy is perfectly evident. The dimensions of the flowers of plants having specific insect pollinators are not only independent from the dimensions of the plant, but also, as it has been shown by our previous investigations (Berg, 1956, 1958), they are more stable than the dimensions of stems, leaves and inflorescences. Such stability of dimensions of zygomorphic flowers and their independence from the variation of environmental conditions including organ interactions are the indispensable conditions of successful pollen transfer. All this refers in the first place to the dimensions of stamen filaments and of the tubular parts of flowers.

Some parts of the flower act as distance and orienting signals for the pollinating insect (laminal parts of the perianth), others help to deposit the pol-

len on some definite part of the pollinating insect's body (the tubular parts of the perianth and the stamen filaments). The strict localization of the deposition of the pollen on some definite part of the body of a specialized pollinating insect was already discovered by Darwin (1862) in *Orchidaceae*. Recently Shvanvich (1952, 1956) also observed it and studied it in detail in *Papilionaceae*. The structure of some flowers, the pollen of which is transferred by specialized pollinating insects, is adapted for the precise deposition of the pollen on a definite part of the body of the pollinating insect.

Our investigation shows the remarkable stability and independence of the parts of the flowers specialized to deposit the pollen on a definite point of the body of the pollinator. The biological function of the adaptations to localize the pollen deposit on some definite part of the body of the pollinating insect is probably to reduce the wastage of the pollen. This is especially true if the pollen is deposited in a location of the insect's body which is out of reach of its pollen-removing organs. Now, the precise localization of the pollen deposit is functionally effective only if the flowers of the species have all approximately equal dimensions. The size of every flower must, thus, be adapted not only to the dimensions of the specialized insect pollinators, but the flowers of different individuals in a cross-pollinating population must also be rather uniform. A flower which locates its pollen on the insect's body in a wrong way is likely to have no progeny. The existence of correlation pleiades with respect to the characters studied is thus inevitably concomitant to the adaptations to localize the pollen deposit on some definite part of the body of the pollinating insect. The adaptations to localize the pollen deposit involve: the acquisition in the process of evolution of zygomorphic flower structure reducing to the minimum the number of possible positions on the flower of such a bilaterally symmetrical creature

as an insect pollinator; the development of tubular parts, reducing the arena where the critical events take place; the reduction in number (oligomerization) and the rigid fixation of the number of homologous parts; and, finally, lateral position of flowers on the plant, which even when radially-symmetrical, function as if bilaterally-symmetrical. Each of the twelve species possessing specific insect pollinators has at least one of these evolutionary adaptations (see table 1). The presence of correlation pleiades is thus associated with the mode of pollen transfer, involving specific insect pollinators, with adaptations to localize the pollen deposit on some definite part of the body of the pollinating insect, and with, at least, one of the structural features, providing for localization. The absence of correlation pleiades is associated with absence of specific insect pollinators, as well as with absence of structural features providing for pollen localization. In this manner the nature of the complexes of regularly interdependent characters which involve presence or absence of correlation pleiades can be said to have been established.

GENERAL CONCLUSIONS

What is then the mechanism of selection, which leads to correlation pleiades involving reproductive and vegetative organs in entomophilous plants pollinated by a limited number of specialized insect species? In this particular instance this mechanism is perfectly obvious. The advantage of the independence of dimensions of reproductive organs as well as the disadvantage of the dependent type of their development are self-evident, the plants with dependent flowers being eliminated, since their pollen could not be delivered to the stigma of another flower, while the plants exhibiting independence had a much greater chance to leave progeny. Pollinating insects were, then, selective agents for the dimensions of the floral parts, and for their standardization, which removed these

parts from the developmental interrelations and created independent correlation pleiades for reproductive organs, as well as for vegetative parts of the same organism. Standardizing selection of dimensions can be accomplished only by insect species that have themselves uniform dimensions, i.e., bees and bumblebees whose development takes place in cells of standard size. Pollinating insects take no part whatever in the formation of flowers in the course of development. Their function is only to test fitness. The discrepancy between the factors participating in the formation of the character and the selective forces determining its function is apparently a general ecological principle of making the dimensions of some parts independent of those of others, of some traits from others, that is, the general principle of the origin of correlation pleiades.

In this instance, the accomplishment of a certain function requires the precise correspondence of dimensions in organisms incapable of exerting any direct influence upon each other during their ontogeny. Such a situation is by no means unique. The biotic components of the environment taking no part whatever in the development of the individuals of a certain species frequently are of decisive significance as selective agents within the species. This is just the case in the interrelation between predators and prey, males and females, the animals dispersing the seeds of plants and such plants themselves. It is the characters and the organs accomplishing the function of communication with the biotic components of the environment that acquired independence from random environmental variations and form correlation pleiades. These organs and characters, namely, flowers, fruit and seed coats and leaves involved in the process of reproduction in plants, the nervous system, sex organs, the digestive system, behavior associated with reproduction and social instincts in animals, and so forth, are the vast field, where the proc-

esses of increased autonomy are likely to take place and where, consequently, correlation pleiades are to be sought. In all these instances the general principle underlying the origin of correlation pleiades is the discrepancy between the agencies participating in the formation of the character and the selective forces determining its function.

As it has been shown in the frog, *Rana ridibunda* Pall., by Terentjev (1931), the dimensions of sense organs and of organs participating in reproduction are characterized by the least dependence on the dimensions of the other parts of the organism. Bertalanffy and Pirozynski (1952) discovered the disproportionality of growth of brain and liver in rat embryos. The allometric growth of just these organs is in agreement with our hypothesis.

The autonomy of vital processes of a given species is based on homeostatic mechanisms of cytological, developmental (ontogenetic) and populational levels. The significance of developmental and genetic homeostasis has been recently emphasized by Lerner (1954). The genotype as a whole is a homeostatic mechanism, acting on the cellular, developmental and population levels of organization of the species. The hereditary factors play the role of stabilizers, being present in the cells of the developing organism. The origin of autonomy in the course of evolution is accompanied by the increase in the relative importance of internal factors of development, as compared to the external or environmental factors (Kamshilov, 1939, 1946; Schmalhausen, 1938, 1939, 1946). It should be clear that the dimensions of an autonomous flower are controlled by some factors, internally located, most probably by means of some intracellular mechanism.

In our example, the increased significance of internal developmental factors is the result of the distinctness of the formative and the selective factors. In higher organisms formative and selective

factors rarely coincide. Suffice it to point at the alternation of generations. The formation of an organism proceeds under one set of external conditions; its life under another. Parents engender offspring which are to live in conditions which cannot be identical with those in which they existed themselves, let alone, in conditions of their early ontogeny. Only in the course of ontogeny does the progeny begin to assume a resemblance to the parents. The organism thus does not inherit from its parents its traits and characteristics but simply an arrangement which contains in coded form a program for development. The totality of hereditary potentialities ensures a certain autonomy of the vital processes vis-a-vis the factors of the environment. The programming of development is of significance only in forms which have alternation of generations, individual development or both. The whole sense of the hereditary code lies in the discrepancy between the formative and the selective factors. This discrepancy is thus responsible for the initiation of all kinds of autonomy and of all the mechanisms ensuring independence, including the origin of the coding itself.

What then is the practical significance of the general ecological principle underlying the origin of correlation pleiades? The answer is that this principle gives us assurance that the selection of stabilized states of any character, the kind of selection that has been accomplished by insect pollinators with respect to flower dimensions, can be an effective means for breaking undesirable correlations and therefore for the creation of the required stabilized state of a given character independent from the fluctuations of environmental factors.

SUMMARY

The phenomenon of correlation pleiades, i.e., the presence of correlations between some quantitative characteristics of certain parts of an organism and at the same time by the absence of correlations

between these and the other parts demonstrates the independence of certain developmental processes with respect to other processes within the organism. The study of correlation sets makes it possible to establish the degree of such independence. The adoption of a quantitative criterion provides an adequate basis for the comparative method in the study of stabilizing selection.

Nineteen species of herbaceous plants have been studied in order to determine the variability in the degree of dependence between the dimensions of different parts of an organism. It has been established that twelve species have correlation pleiades, while seven species have no correlation pleiades with respect to the dimensions of analogous parts. In all the instances of existence of pleiades it was the flower that had become free of the correlation interdependences within the plant organism. Existence of correlation pleiades is associated with the mode of pollen transfer, involving the presence of specific insect pollinators, with adaptations to localize the pollen deposit on some definite part of the body of the pollinating insect, and with at least one of the structural features providing for such localization (zygomorphism, presence of tubular parts, lateral position of flowers, oligomerization and a rigid fixation of the number of homologous parts of a flower).

Insects were the selective factor stabilizing the dimensions of those parts of flowers which participate in the process of the precise localization of pollen on the insect body. Stabilizing selection of flower dimensions created correlation pleiades for reproductive organs, as well as for vegetative parts of the same organism. The general principle underlying the origin of developmental homeostasis in the process of evolution is the discrepancy between the agencies participating in the formation of the character and the selective forces determining its function. The same principle is responsible for the origin of correlation pleiades.

LITERATURE CITED

- BERG, R. L. 1956. Standardizing selection in the evolution of the flower. *Bot. Zhurn.*, **41**: 318-334.*
- . 1958. Further investigations of stabilizing selection in the evolution of the flower. *Bot. Zhurn.*, **43**: 12-28.*
- . 1959a. A general evolutionary principle underlying the origin of developmental homeostasis. *Amer. Nat.*, **93**: 103-105.
- . 1959b. The ecological significance of correlation pleiades. Leningrad State University, *Vestnik*, **9**: 142-152.*
- BERTALANFFY, L. VON AND W. S. PIROZYNSKI. 1952. Ontogenetic and evolutionary allometry. *Evolution*, **6**: 387-392.
- DARWIN, C. R. 1862. On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects, and on the Good Effects of Intercrossing. London.
- KAMSHILOV, M. M. 1939. Selection as a factor altering the dependence of the character from environmental condition. *Acad. Sci. URSS, Compt. rend.*, **23**: 362-365. .
- . 1946. The primary divergence of the norm of reaction depending on environmental variation. Doctorate thesis. *Acad. Sci. USSR, Moscow*.*
- KRASNOVIDOVA, S. S. 1957. The comparison of the variation of vegetative and reproductive organs in the light of the theory of stabilizing selection. Undergraduate thesis. Leningrad State University.*
- LERNER, I. M. 1954. Genetic Homeostasis. Edinburgh.
- LUBISHCHEV, A. A. 1959. Use of mathematical statistics in practical taxonomy. Leningrad State University, *Vestnik*, **9**: 128-136.*
- SCHMALHAUSEN, I. I. 1938. The Organism as a Whole in the Process of Individual and Evolutionary Development. Moscow.*
- . 1939. The Paths and Laws of the Evolutionary Process. Moscow.*
- . 1946. Factors of Evolution. Moscow.* (English translation, 1949, Philadelphia.)
- SHVANVICH, B. N. 1952. On the mechanism of red clover pollination by the honey-bee. *Lenin All-Union Akad. Agr. Sci. Dokl.*, **17**(8): 33-36.*
- . 1956. On the work of the honey-bee on hairy vetch and birdsfoot trefoil. Leningrad State University, *Vestnik*: **11**(9): 55-61.*
- TERENTJEV, P. V. 1931. Biometrische Untersuchungen über die morphologischen Merkmale von *Rana ridibunda* Pall. (Amphibia, Salientia). *Biometrika*, **23**: 23-51.
- . 1959. The method of correlation pleiades. Leningrad State University, *Vestnik*, **9**: 137-141.*

* indicates that the reference is in Russian.