Phytospreading as a factor of biological evolution (revising of the idea of S. V. Meyen)

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Abstract

One of the main unsolved problems of theoretical biology is the search for a mechanism of progressive evolutionary transformations. Neo-Darwinism could not explain morphophysiological complication of organisms, and, moreover, the cause of this complication. Palaeobotanist S.V. Meyen suggested the hypothesis of phytospreading, according to which new "advanced" high rank taxa appear in the equatorial belt. Later, the representatives of these taxa migrate to the middle latitudes during warming. If to supplement this hypothesis with the inverse process, which is caused by cooling, then the new hypothesis of reversible or repeated phytospreading (biospreading) can bring us closer to an understanding the mechanism of progressive evolutionary changes. The main role in this case is played by heterochrony and hybridization as a result of convergence of ancestral equatorial species and their changed descendants, which have "returned" from the middle latitudes.

Key Words: biological evolution, phytospreading, biospreading, heterochrony, hybridization.

1. Introduction

The creators of Neo-Darwinism (Synthetic Theory of Evolution) believed that genetics in the near future will provide answers to the principal questions of theoretical biology. Indeed, the first decades of development of genetics gave rise to such optimism. However, already in the 1960s, some biologists began to question the realism of the method of speciation, which was described by the genetics of populations. For example, one of the founders of the STE E. Mayr at the end of his life came to the conclusion that macroevolution cannot be explained by changes in the frequency of genes [1]. Macroevolution in general was overboard Neo-Darwinism, because by the end of the twentieth century, the impossibility of implementing macroevolution through microevolution became obvious. STE was unable to explain the phylogeny and to predict any act of progressive biological evolution.

Non-Darwinian hypotheses explaining the essential and direction of evolution are known to have appeared before Charles Darwin. However, the alternative to Neo-Darwinism in the form of a number of reasoned hypotheses began to be formed only in the second half of the twentieth century. The most popular non-Darwinian ideas, which had the internal consistency and the potential for further development, were the hypotheses of Saltationism and Macro-Mutationalism. There are no clear semantic boundaries between them. These hypotheses are not as alternative, but as complementary to each other. Geneticist R. Goldschmidt [2] proposed an interesting version of the mechanism of progressive evolution - the hypothesis of systemic mutations. Its meaning lies in the fact that the source of macroevolutionary changes are system mutations, which realize radical transformations of the internal structure of chromosomes and lead to the emergence of a new phenotype and a new species. Thus as a result of mutations there is a mass of anomalous forms, among which there may be single individuals (“hopeful monsters”). It is they who, under favorable circumstances, can give rise to a new macroevolutionary branch. The paleontologist O. Schindewolf [3] brought to his hypothesis the idea of the cyclicity of the evolutionary process and its stages. He believed that macromutations are due to external (cosmic) factors.

New advances in molecular biology and paleontological data did not refute the hypothesis of R. Goldschmidt, but did not provide conclusive evidence for its favor. Later, on the basis of these ideas, the theory of punctuated equilibrium [4] was formed. The theory is considered the most authoritative alternative to STE, although, in fact, it does not contradict it. However, the process of evolution and its direction remain unresolved problems. There is no conclusive evidence of the existence of systemic macromutations. There is no explanation for the irreversibility of the morpho-physiological complexity of organisms. The theory of punctuated equilibrium did not give a single answer to these questions.

2. S.V. Meyen and his idea of phytospreading

An important role in the study of the mechanism of biological evolution belonged to paleobotanist S.V. Meyen. The most important of his achievements are the introduction of the concepts of meron and refrain, the creation of meronomy as a section of taxonomy, and the hypothesis of phytospreading. He could not completely abandon the postulates of Neo-Darwinism, and, perhaps, because of this conciliatory position, did not create a holistic concept. Nevertheless, he came closest to understanding the mechanism of evolution.

S.V. Meyen showed that almost all the higher taxa of higher plants appear in the equatorial belt at a lower stratigraphic level than outside of it [5]. In other words, they have equatorial origin. During warming periods, representatives of these taxa migrate from the equatorial belt to higher latitudes. This is the essence of phytospreading, or "equatorial pump". As the distance from the equator increases, the macroevolutionary activity of the higher plants decreases, and in the Arctic zone, only speciation occurs. A more successful macroevolution of higher plants in the equatorial zone can be associated not with the strengthening but rather with the weakening of natural selection. Generally, the role of natural selection in the early days of taxon formation at the family level or higher apparently is not predominant, but rather is episodic. According to S.V. Meyen, a crucial role in evolution is played by selectively neutral saltations. Earlier, a similar thought was expressed by K. Darlington [6], however, without sufficient factual justification.

At the next cold snap, in the middle and high latitudes, settlers either disappear or persist at the new location but with a slight change in their overall organization, giving rise to new species, genus, and, to a lesser degree, higher rank taxa, but not with higher orders.

The hypothesis of phytospreading has not been unambiguously assessed by biologists. However, S.V. Meyen found followers who tried to correct the hypothesis and give it the status of a universal mechanism of florogenesis and faunogenesis [6, 7, 8].

3. The process of "reversible" or "repeated" phytospreading and its phases

The process described by S.V. Meyen, is typical for the epochs of global warming. What will happen at a cold snap?

Obviously, the reverse process will not be symmetrical to the direct process. According to S.V. Meyen, during a cold snap, entire ecotopes (relatively homogeneous environments with the appropriate biocenosis), not separate forms, shift from high latitudes to low. Traces of the introduction of boreal species into the tropical flora have not been recorded. However, the ecotope shifts, and in its biocenoses there will necessarily be representatives of the flora, whose ancestors during warming were brought out by phytospreading in the middle latitudes. At the peak of cooling, this rhythmic process (we call it reversible phytospreading), when the areas of the ancestral (near-equatorial) species and the species "modified" in the mid-latitudes, will join together. The process depends entirely on climatic rhythm.

There is an alternative (or complementary) version of the full phytospreading cycle. Once the species brought by the "first wave" of phytospreading consolidates at the new location in the middle latitudes is forced to undergo some phenotypic and genetic changes due to subsequent cooling, a new warming period will occur. The "second wave" of phytospreading will bring the new portion of ancestor species to the same middle latitudes. A possible, but not obligatory, result of both phytospreading variants is hybridization.

Analyzing the behavior and transformation of lower taxa in the process of "reversible" or "repeated" phytospreading, it is possible to construct a basic model for the formation of a new, more highly organized lower taxon (probably a species). Let us trace the "mechanism" of the reversible phytospreading process.

Phase 1: relatively warm climatic era with a weakened zonal (latitudinal) stratification. Representatives of equatorial species freely migrate and settle within a wide belt up to the modern temperate zone. Individuals of species that have gone particularly far will undergo certain morphological and functional changes of an adaptive nature. However, these changes do not yet affect the principal organization of the species.

Phase 2: the completion of the warm era, the beginning of cooling and the strengthening of zonal climatic stratification (and consequently latitudinal geographical belts). For a long time, estimated in hundreds of thousands or millions of years, the marked group of individuals (species) undergoes various changes. In fact, these changes are also adaptive, but already more significant. However, they do not lead to fundamental (progressive) changes of this species. The group of individuals in the middle latitudes belt is exposed to two natural factors. The first is a general lowering of the air temperature. The second is the uniqueness of the thermal and insolation regime of the atmosphere. If the first factor is more or less clear, then the second requires explanations.

The life activity of organisms living in the equatorial zone is governed primarily by the daily rhythm. Seasonality, of course, manifests itself in one form or another, but it does not dominate. In latitudes corresponding to present subtropics, the determining rhythm of many natural processes is the annual (seasonal). In particular, the reproduction of the offspring will be largely reoriented to the annual rhythm. This phenomenon and the beginning of cooling will lead to a change in the character of ontogenesis. This process will manifest itself in the form of changes of morphological features and sizes of individuals and their allometric modifications. There will be a genetic adjustment in the form of fixing in the genotype of the usual adaptive mutations caused by an unfavorable environment. (We can say that we are talking about idioadaptations or allomorphosis rather than about aromorphosis in Severtsov's view [9].) There are many written works about the unfavorable climatic conditions affecting the vital activity of organisms. It is important that these climatic conditions are the cause of mass heterochronies [10, 11]. As expected, the most significant evolutionary role is played by neoteny and accompanying progenesis. It must be emphasized that heterochrony also manifests itself in a certain increase in the duration of the reproductive process. As a confirming example, one can recall one of a number of well-known facts, which, however, has no direct relation to botany: the duration of pregnancy among African women is one week less than for Caucasoid women. Since this is a slow process of adaptive type, these heterochronies become the norm and are fixed in the genotype. One can assume that by the end of this stage the difference between the ancestral group and the mid-latitude group will reach the level of two species of the same genus. This is a divergent process, conditioned by the adaptive rearrangement of the genotype. It is possible (but not necessary) that by this time the whole range of the species will be divided. This can happen, for example, as a result of the appearance of a tropical deserts zone.

Phase 3: the maximum stage of cooling and the maximum strengthening of zonal climate and stratification. Part of the middle latitude species begins to shift toward the equator in the composition of the ecotope that includes it. In the process of “reversing”, the individuals of this group (species) will undergo further phenotypic and genotypic changes, but not essential. The output of reversible phytospreading and the final of the third phase is a compound (convergence) in the low latitudes of areas of the two related plant groups (species) and subsequent hybridization.

What is the level of phylogenetic difference between these convergent related groups? There isn't a certain answer because both the "species" and the "subspecies" do not have absolutely clear criteria. One can say that the optimal level is the level of closely related species of the same genus. The necessary condition is the ability to cross and create hybrid progeny. The third phase is completed by the appearance of hybrids, capable, in turn, to give offspring.

To explain the present act of evolution, it is necessary to resort to contemplative modeling, which cannot be left behind by theoretical biology.

4. Contemplative modeling of reversible phytospreading (biospreading) and forming of evolutionary "advanced" species

For this procedure, it is preferable to use the representatives of those species (genera, families), which, according to palaeobotanists, are the most probable ancestors of the "evolutionary advanced" high-ranking taxa. However, the model of "biospreading hybridization" should be workable for all raw materials, so the choice of objects can be quite arbitrary.

4.1 Example 1: homosporous bracken.

Its developmental cycle consists of two states. The first is the sporophyte, and the second is the gametophyte. These formations cannot be combined. On the underside of some leaf plates of sporophyte sporangia, bracken spores, resulting from meiosis sporulation, appear. Bracken spores germinate on the ground in a small prothallus, such as in the case of Prothallia dioecious. On the bottom side of the prothallia, the genitals are formed - archegonia (female) and antheridia (male), where the fixed egg and sperm (mobile in water) are developed and insemination takes place with the participation of water. After insemination of the egg, leaf-shaped body sporophytes begin to grow and the cycle is completed.

By the beginning of the second phase, plants will have virtually no differences from their subequatorial ancestors. They will most likely form a continuous area that can be ruptured afterwards. Further, as a result of initial cooling, the zonal stratification is enhanced. Bracken individuals, which are already in the middle latitude (now subtropical) zone, undergo significant adaptive changes, including a form of heterochrony. At the start of the third phase this modified species (subspecies) begins to spread in an equatorial direction. As the geographical areas of the ancestral and modified species (subspecies) converge, a convergence of their morphological traits, caused by the increasing similarity in climatic conditions, will appear, and subsequently, it could facilitate cross-fertilization and the formation of hybrids capable of producing offspring.

To the end of the phase, gametes of individuals of the subequatorial species participate in the insemination of the eggs from individuals of the modified species. Notably, the reproductive cycle of the first group is <u>shorter</u> and the sporulation velocity is higher. In this case, the new hybrid may have a peculiar neoteny, such as accelerated sporulation and more high speed development of sporangia (typical for subequatorial individuals) at the normal speed of vegetative growth corresponding to maternal modified (subtropical) individual.

One can draw the following conclusion: **the formation of the hybrid may proceed in accordance with the formula: the velocity of the development of the vegetative part corresponds to the**

maternal, the rate of sporangia development is higher compared with the vegetative part, and the maturation rate of sporules is higher than the rate of the development of the sporangia.

There is no direct confirmation of the reality of this type of neoteny in the natural environment, and in the laboratory, it is impossible to artificially recreate the conditions of phytospreading hybridization. However, there is an indirect confirmation. Biologists are familiar with genomic imprinting, an epigenetic process by which the expression of certain genes is dependent on the parent sex that provided the allele. For example, the representatives of mammalian paternal genes are responsible for the formation of the placenta and female genes for the differentiation of embryonic cells [12]. This effect is also observed in insects and in flowering plants. It is reasonable to assume that this phenomenon has a certain “fundamental” genomic basis, which is not yet entirely clear. To a certain extent, it is common to a wide range of species. V.A. Geodakyan [13] defines this effect (in relation to placental mammals) in the following manner: in the beginning of embryogenesis, only the genes of the mother “work”, then the father genes step in and gradually progress, and in the final phase of embryogenesis, only the father genes “work”.

One can say, this is a classic neoneny, but as a result of hybridization. In the case that this scenario develops, instantaneous changes of the morphophysiological organization of the resulted hybrids will appear in comparison with both of the ancestral forms. First, there will be certain changes in leaf plates with sporangia on them. They will take the form of strobila. The separation (or even split) of microsporocytes and macrosporangia are likely to take place. Second, the sporules will germinate without leaving a sporophyte. The gametophyte phase of plant development sharply reduces. The outcome: a completely new species, reminiscent of a highly organized heterosporous fern-moss selaginella or a primitive gymnosperm appears. This is the result of the heterochrony that, according to R. Goldschmidt, affects the course of individual development and leads to the emergence of a new phenotype and a new species. However, its source is not a random systemic macromutation, rather a systemic hybridization. If hybrids maintain the ability to interbreed with each other in the favorable conditions of equatorial climate, they will have a real chance of survival. Ecological and evolutionary advantages of the new species will manifest themselves afterwards. The genetic consolidation of this natural finding is a different issue. It can be solved in agreement with the traditional notions of STE.

A similar simulation can be carried out with gymnosperms with the purpose of obtaining angiosperms. However, it is no coincidence that the origin of flowering plants is recognized as one of the greatest mysteries of biology. A flower is not constructed as a result of such simulation. More accurately, it is possible to generate a monosexual male flower from the male cones. To do this, it is necessary to assume that the maturation of gametes (pollen) is not accelerated, but is rather delayed (this effect is called retardation), and that the micro-strobilus, due to such a delay, will have no additional development, as is “prescribed” by the genome. It will appear as the outrunning growth of scales and sprouts, connecting the pollen sacs with an axis.

Subsequently, these sprouts with the pollen sacs become stamens, while the scales become carpels. It is clear that such a scheme is too rough and primitive; nevertheless, its logical basis gives hope for detailing and elucidating the specific mechanisms for the conversion of strobili into flowers. Interestingly, S.V. Meyen, based on the rich fossil material, analyzed in detail possible ways of appearance of flowering [14]. He came to the conclusion: male sporangia gymnosperms (presumably, Bennettitales) could mutate into ovule simplest flowering. As can be seen, the solution is close, but we can't take into account some unknown factor.

4.2 Example 2: nimble or sand lizard.

Selection of the object, as in the first case, is random. For the third phase (now, of reversible zoospreading or biospreading), the areas of subequatorial and former mid-latitude species converge. The process of hybridization involves female individuals of the subequatorial species and subtropical male individuals. Delayed expression of male genes in the final stages of embryonic development results in the incomplete formation of the hard shell of the embryo at the time of its full maturity; this is how the viviparity appears. Because the newborn hybrid organism is under stressful conditions, the hypothesized transformation of some of the sebaceous or perspiratory glands into the lactescent glands seems very plausible. The body of the female must learn a new function – the search for a special liquid to save the life of the newborn. This new function requires an appropriate organ. It had been forming for long enough. Next, the adjustment and polishing of the new form goes through selection, where it will have one distinct potential advantage: the better preservation of offspring in unfavorable conditions. It is interesting that in this case, there is no need for the hypothesis of "hopeful monsters", as proposed by R. Goldschmidt. Hybridization is going to be massive, and the problem of finding reproductive partners is not going to be as sharp as in the "monsters" hypothesis.

According to the results of contemplative modeling under such hybridization, there is the almost instantaneous and radical redesign of the process of reproduction and reproductive organs. Vegetative parts of the plants and animal soma are changing afterwards (it may be said "get adjusted"). In other words, the process of the shaping of a fundamentally new type, as a consequence of a heterochrony and hybridization, initiates with the reproductive organs, and gradually extends to the rest of the body. It does not happen in a single generation, but will be fast enough to regard the process of species emergence as a saltation.

Palaeoclimatic data generally does not contradict the hypothesis of biospreading. The authenticity of the stratigraphic determination of gymnosperms, angiosperms and mammals is that it is possible to "adapt" to the cold climate stage (reversible biospreading) and/or the warm stage (repeated biospreading) [15, 16].

5. Evolutionary implications of biospreading hybridization

Reversible or repeated biospreading doesn't always lead to progressive development, that is, to morphofunctional complication of organisms. Inadequate or, conversely, excessive genetic differences of the two species to the third stage are very likely. In addition, even in the case of achieving the first positive effect of the biospreading hybridization, further progressive evolution can be disrupted by external factors.

According to speculative modeling, such hybridization predetermines a sharp functional rearrangement of a large group of individuals. The restructuring inevitably requires appropriate compensation in the form of the same scale morphofunctional rearrangement of organs, or the emergence of new ones. Apparently, in emergencies, the creation of new organs seems to be the best solution. The structure of the body responds to sudden functional dissonance by its own complication with the help of meta-morphosis of tissues.

From all that has been said, one can draw another important conclusion. There is a possibility that the "advanced" species will give a phyletic line, which will later branch and, thus, become the ancestor of a number of new related species. However, many species can be involved in biospreading, including species of the same genus and even of a higher rank taxon. Thus, this number of new hybrid species can form a community that biologists will consider to be one genus, family, etc. The appearance of a new high-ranking taxon will most likely be monophyletic, but such an assertion cannot be considered unconditional. The ancestors of a new, morphophysiologically progressive high-ranking taxon (family and upper) may be one species (later divergent), and different species of the genus, and also species forming taxa of a higher rank.

6. Conclusion

The weakness of the proposed hypothesis, like any other hypothesis, lies in the absence of irrefutable evidence. Everything begins with the hypothetical nature of the original process, i.e. the phytospreading itself. It cannot be observed and cannot be modeled. True, the first step on the path to phytospreading was made by A. Wallace [17]. He noted the following trend: relics, i.e. remnants of ancient groups tend to occupy the outskirts of the former ranges of their groups (deciduous forests are occupied by warm countries, and conifers are pushed into the temperate zones). After the works of S.V. Meyen, K.Yu. Eskov [6], D. Jablonski et al. [18] and other authors, the mechanism of biospreading has acquired specific outlines. Moreover, the evidence of the zoospreading reality was practically confirmed [19].

The idea of reversible or repeated biospreading suggested in this paper is even more hypothetical. This hybridization cannot be simulated. It cannot be verified on the basis of known fossil material. However, this idea logically follows from the nature of the change in the paleoclimate. For example, L.S. Berg used glacial theory to explain the existence of bipolar species (living in temperate belts of both hemispheres) of marine biota [20]. In fact, he proceeded from the assumption of the reversibility of biospreading.

Finally, the question of why the morphophysiological complication occurs is quite insoluble. We are confident that the modeling methodology will be improved, and therefore we can hope for the appearance of a rough imitation of biospreading in the near future. We are confident in the appearance of new paleontological data. However, the reason for the complication refers to fundamental philosophical problems. S.V. Meyen considered himself an adherent of nomogenesis (evolution based on regularities). The mechanism for regularities realizing is the problem that can be solved theoretically. Nevertheless the causal aspect of nomogenesis ("why" and "for what") is hidden so deep that it can be revealed only on the basis of the synthesis of biology, chemistry, physics (including cosmology) and philosophy.

7. References

1. E. Mayr. The growth of biological though. Diversity, evolution and inheritance. (1982) Cambridge (Mass.) Belknap press of Harvard Univ. Press, London.

2. R. Goldschmidt. The material basis of evolution. (1940) Yale Univ. Press, NY, London.

3. O. H. Schindewolf. Neokatastrophis-mus? Ztschr. Dt. Geol. Ges. Bd. 114 (1963) 430-445.

4. S.J. Gould. 1982. Evolution now. In: A century after Darwin. San Francisco, Freeman. (1982) 129-145.

5. S.V. Meyen. Geography of macroevolution in higher plants. J. Gen. Biol., 3 (1987) 291-310.

6. K.Yu. Eskov. History of the Earth and Life on it. From Chaos to Mankind. (2000) MIRos-Nauka, Moscow.

7. V.V. Zherikhin. Selected Works. (2003) KMK, Moscow.

8. Yu.V. Tchaikovsky. Active Coherent World. Experience of the Theory of Life Evolution. (2008) KMK, Moscow.

9. A.N. Severtsov. Morphological Pattern of Evolution. (1939) Publishing House of the Academy of Sciences, Moscow-Leningrad.

10. V.S. Kirpichnikov. The significance of adaptive modification in evolution. J. Gen. Biol. 1 (1940) 121-152.

11. P.K. Anokhin. Selected Works. Philosophical aspects of the theory of functional systems. (1978) Nauka, Moscow.

12. D. Haig, M. Westoby. Parent-specific gene expression and the triploid endosperm. Am. Nat. 134 (1989) 147-155.

13. V.A. Geodakyan. Riddle of genomic imprinting – myth and reality. In the World of Science 3 (2012) 74-79.

14. S.V. Meyen. 1986. The hypothesis of the origin of Angiosperms from Bennettitales by means of gamoheterotopy (transfer of features from one sex to another). J. Gen. Biol. 3 (1986) 291-308.

15. V.A. Krasilov. The Origin and Early Evolution of Flowering Plants. (1989) Nauka, Moscow.

16. V.N. Konischev. Cryosphere in the history of the Earth. Vestn. Mosk. Univ., Ser. 5 Geogr. 1 (2005) 65-73.

17. V.I. Nazarov. Evolution is not Darwinian: Change the Evolutionary Model. (2007) LKI, Moscow.

18. D. Jablonski, K. Roy, J.W. Valentine. Out of the Tropics: Evolutionary Dynamics of the Latitudinal Diversity Gradient. Science 314 (2006) 102-106.

19. Yu.I. Chernov. Phylogenetic level and geographical distribution of taxa. Zool. Zhurnal 10 (1988) 1445-1457.

20. L.S. Berg. Climate and Life. (1922) Gosizdat, Moscow.

