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The Divergence Law of Charles Darwin as one of the foundations of geographic-morphological method in taxonomy

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Dedicated to 200 anniversary of the birth of Charles Darwin (12.02.1809 – 12.02.2009)

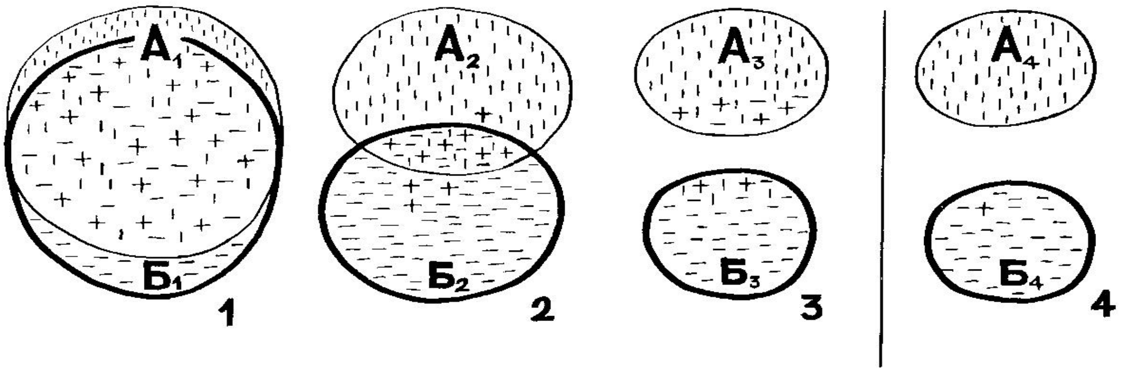
Annotation

At present taxonomy of plant and animal world endures an impasse situation, consisting in the absence of discriminated signs between geographical and numerous ecological races, which are peculiar to only a small fraction of all species (15-20%) under stage of the formation of species. As a result, some botanists describe, at the best, numerous subspecies, aggregates and micro-species in the system of species, while others consider them in the rank of species. Taxonomists try to distinguish species by inexhaustible biological properties of the form and protein, yet classical taxonomy is developed simple concepts as the law of divergence of Charles Darwin, the rule of R. Wettstein and specific series of V.L. Komarov, who make up the classic geographical-morphological method of systematics. Diagnostic indicators of geographical and ecological races, including their differences from the species were exposed on the basis of deep monographic study of genus Rhaponticum Ludw., Calligonum L. and a number of individual species, using a geographic-morphological method of systematics and methods of intra-specific taxonomy of N.I. Vavilov. Development of knowledge about the law of divergence of Charles Darwin put forward by A.P. Khokhriakov whereby one taxon in the process of divergence may occur at the same time not more than two new taxa. This idea is developed in our investigation and it is shown that the dichotomy is manifested only in the basic taxonomic levels, such as species and subspecies (geographic race). Do not obey the law of divergence ecotype (variety), row (seria), subsection (subsectio) and section (sectio), which are secondary taxonomic levels in relation to the principal - the species and subspecies. The impossibility of simultaneous formation in the system of the polytypic species more than two subspecies is proved. Thus, one of the polytypic species can form only two subspecies, but the number of ecotypes (varieties) - 2-3 and more. These findings are consistent with the law of A.N. Severtsov and speciation diagram of Ch. Darwin, which include alternated polytomic and dichotomous ways of variety formation in geological time.

Keywords: the law of divergence of Charles Darwin, the law of alternation of the main directions of evolution A.N. Severtsov, polytomic and dichotomous ways of taxa formation, subspecies, geographical race, ecotype, ecological race, geographic-morphological method of taxonomy.

Content

Hitherto diagram divergence of Charles Darwin in his book "The Origin of Species ..." (Darwin, 1937, 1939) continues to attract the attention of scientists of various disciplines. Work of Charles Darwin attached great importance to the founders of theoretical taxonomy of two schools in the USSR, academician V.L Komarov, and N.I. Vavilov, under the editorship of which came first edition of “The Origin of Species". N.N. Vorontsov (2004, p. 40) reproduces in the original figure of divergence of Darwin, but does not analyze it A.P. Khokhryakov (1986, 1990) and others justify the divergence law of Darwin, in which each parent taxon (class. subclass, order, family) is divided (diverged) in the development of only two sibling taxa. It was made based on the principle of dichotomous diagrams of cladistic method taxonomy of W. Henning (1950). Previously, we have come to the same conclusion at the level of species when have analyzed polytypic species, containing subspecies. Property to form only two subspecies in the divergence was confirmed when monographic study of genus Rhaponticum Ludw. and Calligonum L. (Soskov, 1959, 1963, 1989, 1991, 2007, 2007a), species Trigonella foenum-graecum L. (Soskov, Bayramov, 1990) and Bromopsis inermis (Leys.) Holub (Soskov, Sinyakov, 1990), in the processing of 14 genera for the "Flora of the Tajik Soviet Socialist Republic”, 3-4 vols., when analyzing polytypic species in desert perennial forage plants (Ivanov, Soskov, Buhteeva, 1986) and books by other authors. Thus, in the monograph of A.G. Yelenevskiy (1978) for the genus Veronica L. within the USSR and adjacent countries of the 30 polytypic species, only 4, not yet sufficiently studied species, as expressed by the author himself, contain more than two subspecies. Analysis, for example, polytypic species Veronica spicata L. s.l. with 6 subspecies and V. anagallis-aquvatica L. with 5 subspecies showed that several subspecies in the volume of these types of Veronique were not geographical races, i. e., subspecies. On the basis of comparison and study of cross-pollinated polytypic species areas in the genera Calligonum and Rhaponticum, caught in different phases of divergence, we have been drawn up a tentative scheme of micro-accumulation speciation in these genera. Consider the scheme **(Fig. 1).**



. **Fig. 1.** Scheme of the process of micro-accumulative speciation in genera Calligonum L. и Rhaponticum Ludw.: position 1 - polytypic species with subspecies of the young age, 2 - polytypic species with subspecies of the middle age, 3 - polytypic species with subspecies in the final stages of speciation, 4 - two newly emerged young species," I "- individuals A subspecies, “–” individuals B subspecies, "+" – hybrids between subspecies A and B.

According to the **figure 1 (1),** in the area of one species, there are two morphologically very similar populations, which we define as subspecies (A_1 and B_1). The population of the A_1 tends to the north, the population of B_1 - to the south. In pure form (without any hybrids) both populations are represented only at the edges of area. In most part of the range one and the other populations overlap each other and hybridize. The number of non-hybrid individuals is much smaller than the number of hybrids. This fact leads to the assumption that the first phase of divergence should be preceded by a massive hybridization of some environmental forms located in the area of species. Otherwise, how can take so many hybrids? Thus environmental form standing in the subordination below the subspecies is the ecotype or ecological race. We know several examples of mass hybridization of ecotypes Kochia prostrata (L.) Schrad. and other perennial forage crops in the cultivated together ecotypes (Soskov, 2007). Such hybridization may occur each time on Earth with the periodicity 18,5 centuries, which corresponds to detected by A.V. Shnitnikov (1957) period of the total wetting of the Earth, which periodically shifts and leads to hybridization and the restructuring ecotypes and plant communities. According to N.N. Tsvelev (1975) for the beginning of specialization requires de-specialization taxa through distant hybridization. In our case, despecialization of the first subordinate in rank form till the elements of the population takes place, of which over tens of thousands of generations are formed subspecies and species.

The initial phase of divergence with the formation of geographical races (subspecies) is described above, marked by us in the form south- turanic Calligonum leucocladum (Schrenk) Bunge (Musaev, Soskov, 1977). The subspecies in this form in the early stages of divergence differ only by one character. Population of A_1 C. leucocladum (subsp. leucocladum) with yellow fruits tends toward the north, and the population (subsp. persicum (Boiss. et

Buhse) Sosk.) with red fruits tends toward the south. At the initial stage of subspecies formation **(Fig. 1, 1)** divergent signs are few and they are expressed very poorly, so that in some cases difficult to record the transition between the subspecies forms.

Figure 1(2) is just the same, but only populations A_1 and B_1 have less overlap each other. The number of individuals with transient signs is decreasing, while the number of individuals typical for each population is increasing. This level of divergence is close to the middle, marked by us in the kazakh-siberian mountain species Rhaponticum carthamoides (Willd.) Iljin (Soskov, 1959, 1963) and the kyzyl-kum, kara-kum species Calligonum eriopodum Bunge (Musaev, Soskov, 1977). East kazakhstan subspecies R. carthamoides subsp. carthamoides differs from the southern siberian subsp. orientalis (Serg.) Sosk. by shape and texture, leaves envelope, width of leaf blades and xeromorphyc degree of the whole plant. Karakum subspecies C. eriopodum subsp. turkmenorum Sosk. turkmenorum Sosk. et Astan. differs from kyzylkum subsp. eriopodum by presence of pubescence on the green twigs. Divergence signs in this middle stage of divergence already appear as a clear marker signs, well preserved in any phase of development. The number of distinguishing features between the subspecies is also increasing. Not only quantitative changes occur in this stage of divergence, but also notable qualitative ones, which indicate the series of small jumps in the system of high jump, marking the transition from one species into two new ones.

In **figure 1 (3)** is the same as in positions 1 and 2, only the ranges of populations A_1 and B_1 are disconnected. In each, or one of them on the periphery of the close neighboring populations of plants another population is found, as well as a few hybrids between diverging populations. Populations are close to transform them into separate species with mutually exclusive ranges. This final stage in the divergence of the form marked by us in respect of the ancient species with a relict habitat - turan- ili -djungarian C. junceum (Fisch. et Mey.) Litv. and arabia - indian C. crinitum Boiss. The northern subspecies of C. junceum subsp.

junceum clearly differs from the widespread southern subsp. ludmilae Sosk. by the presence scarious ochreas and prostrate form of a bush (Musaev, Soskov, 1977). C. crinitum subsp. arabicum (Sosk.) Sosk. differs from rajasthan subsp. crinitum absence of wings in the law of the nut, three-row bristles and straight nut (Soskov, 1975). These two ancient species in the near geological time may lose rare subspecies - subsp. junceum and subsp. arabicum. Morphological hiatuses (gaps) between subspecies are much greater than that of subspecies in the middle stage of divergence. With all of this morphological and biological affinity populations of A_1 and B_1 can not be denied. Leap for them greatly delayed and perhaps even wouldn't lead to the formation, for each of them, two new species. Species will remain monotypic, but would have still, in some new capacity.

Thus, in the first three positions **(Fig. 1)** the process of speciation through divergence across subspecies is shown. The lowest level of divergence is represented in position 1, the greatest - in position 3.

In **figure 1 (4)** population A_1 and B_1 have been purified from the plants of neighboring populations, as well as from the hybrids. If hybrids remain, the number of them does not exceed 1-3%. The process of speciation is completed, polytypic species becomes in two close monotypic species with disparate ranges. Shift of the quantitative to qualitative changes took place by a large jump. The old species vanished. Instead, within the limits of its range there are two young, close to him, neighboring species, which for most features are similar to extinct species. As we studied in genus Calligonum and Rhaponticum, process of speciation always ended this way through the subspecies, even if it was preceded by introgression, or distant hybridization between species of different sections. Neighboring formed two new species with disparate ranges form a new row (series), or supplement the number of species in an old row of V.L. Komarov (1908, 1934).

Meanwhile, according to N.N. Tzvelev (1979, pp. 24-27) in the family of cereals (fam. Poaceae) the population of initial species on the part of the area remains almost unchanged, that is "almost does not evolve". In monographic study of genus Calligonum, having the Tertiary age, despite of predictions I.T. Vasilchenko (1959) about the wide dissemination in this highly polymorphic genus gregarizm kind of phenomena, that is sympatric closely related species, all species without exception were grouped by us the best manner only in the rows (Soskov, 1989).

An interesting fact noted by us that wild and cultivated species have the ability to share only two subspecies, and no more than two new species are formed at once from one polytypic species. From classical genetics is well known that the gene is always manifested in only two alleles, regardless of how many alleles present (Lobashev, 1967). Initially, the divergence is carried out by fixing in opposite parts of the range of alternative alleles (Mettler, Gregg, 1972; Lewontin , 1978). We don't know of any cases to within the range of one species divergence occurred simultaneously on two, three or more pairs of alternative characters. Obviously, a species in a state of subspecies divergence of one gene does not allow for divergence in another gene, the more that the process of divergence according to Komarov (1901) and Pachosky (1925) takes place in the entire range of the species with the participation of all its individuals, even if the species is represented by isolated populations. An example is the process of divergence Calligonum junceum with huge diffusely relict area dissected dozens of isolated populations (Musaev, Soskov, 1977).

The **figure 1** shows that the newly emerged two new species have the same age, are most close to each other, and at the same time, they have mutually excluding ranges. If the ranges of subspecies are not separated in the process of divergence, then they will never reach the species level. For the normal development process of divergence and isolation of subspecies and new species do not require any physical barriers, as it is evidenced by the careful study of habitat polytypic species. All forms of the species participate in the formation of two new subspecies and species. The formation of two new species ranges in the first stage of speciation is in place without migration, within the range of the old species, and that was reflected in the literature before us (Komarov, 1901; Pachosky, 1925).

Separation of subspecies (homo-zygotes) is carried out using hybrids between subspecies (hetero-zygotes). Homo-zygotes are more adapted to the polar parts of the area, and the hetero-zygotes to the middle of the range. With the development process of divergence and increasing disparities between homo-zygotes, hetero-zygotes are becoming decreasingly vital, and are gradually replaced homo-zygotes. Finally, there comes a state when in the middle of the range, none of the homo-zygotes (subspecies) due to an advanced divergence can no longer exist, and hetero-zygotes (hybrids between subspecies) become weak vital and uncompetitive and die out, as a result a gap arises between the ranges close neighboring, just emerging species. That is, in our opinion, the most likely process of speciation in cross-pollinating plants.

The number of polytypic plant species is usually more or less constant in different genera and families and is 15-20%. So, according to our data, in genus Calligonum there are 15% of polytypic species, in genus Rhaponticum - 18%, genus Hordeum L. -11% (Luk'yanova & etc., 1990), genus Avena L. (Rodionova & etc., 1994) - 17 %, in genus Melilotus Mill. (Suvorov, 1950) - 25 %, genus Triticum (Dorofeev & etc., 1979) - 15%, genus Veronica L. of flora USSR (Yelenevskiy, 1978) - 16%, in genera of a family of cereals USSR (Tzvelev, 1976) - 23%, in the subarctic flora of Eurasia - 18% (Kuvaev, 2006), genus Lathyrus L. North America (Hitchcock, 1952) - 20% etc. The number of polytypic species (in average 15-20%) corresponds to the number of gametes (19%) with mutations in one plant generation (Timofeev-Resovskii, Vorontsov, Yablokov, 1977), the frequency of mutations (0.1411) on chromosome per generation (Lewontin, 1978), the number of natural hybrid samples (15%) in the herbarium specimens of the genus Calligonum, stored in herbaria of the world, with the number of hybrids from beet (18%) with the heterotic effect (Goodwill, 1929).

It seems that there is the optimal level of hetero-zygotes for the plants in the nature of which in turn depends on the optimal level of mutation frequency. Such wise, the number of polytypic species in plants is small, varies in different taxonomic groups within the 11 - 30%, and apparently is supported by natural selection at an average of 18%. Genera in which there are a large number of polytypic species spend more energy than the last ones with their small number. They in the process of evolution can not compete and die, so a certain optimal percentage of the polytypic species is established in the nature, which also supported by the natural selection.

At the same time it comes off to note that not all examined levels of taxa appear the law of divergence, but only the main. Taxa variety, row and section are secondary taxonomic levels and do not obey the law of divergence. Within the limits of some species or subspecies (geographic races) there are numerous environmental race, such as ecotypes or groups of ecotypes (Sinskaya, 1948; Dzyubenko, Soskov, Khusainov, 2007, etc.), which also do not obey this law.

Charles Darwin (1937, 1939: 353-359) in the well-known figure of divergence examined the formation of varieties by 11 start species of (A, B, C, D, E, F, G, H, I, K, L) for the period 10000 generations **(Fig. 2)**. The outcome of the alleged signs of differences, the survival of the fittest and the extinction of the extreme varieties of intermediate varieties can not compete are considered after every 1000 generations. Only two species of E and F went all the way in 1000 generations without the formation of new species. Species A and I gave birth to new species. Other species die. For the species A and I on the diagram of divergence Ch. Darwin **(Fig. 2)** the number of cases of dichotomous division within 10000 generations and loss of one of the two dichotomous branches was calculated.

It is observed 25 cases (100%) dichotomy and 18 cases (72%) loss of one of the two dichotomous branches in species A, a species I, respectively, 15 (100%) and 12 (80%). Consequently, Darwin assumed that the dichotomous branching with the formation of two new "species" (species, genera, families ...) one of the branches as a result of the struggle for existence could disappear. Thus, according to the diagram, of the newly formed taxa may disappear during the evolution of 72-80 taxa (table).

Table. Dichotomic divergence characteristics (species) in two species A and I in the scheme of divergence of Charles Darwin **(Fig. 2)** and the origin of new species from the old to the hypothetical period of 10 thousand generations (Darwin, 1939, pp. 353-359).

Generation	Species A, the number of cases		Species I, the number of cases	
	dichotomy	disappearing of one of the branches	dichotomy	disappearing of one of the branches
10000	3	2	2	2
9000	3	3	2	2
8000	3	3	2	2
7000	4	3	2	1
6000	3	2	2	2
5000	2	1	1	0
4000	2	1	1	1
3000	2	1	1	1
2000	2	2	1	0
1000	1	0	1	1
The number of cases	25	18	18	12
%	100	72	100	80

A careful analysis of Darwin's scheme of divergence **(Fig. 2)** in two species (A, I) were found two types of varieties. The first type formed varieties is presented in the form of numerous short dashed twigs that die before reaching the next mark in 1000 generations. The second type of varieties associated with dichotomous branching, is represented by two branches, which usually reach to the next mark in 1000 generations with the formation of two new species.

The diagram **(Fig. 2)** shows that the first type of varieties over 10000 generations, 10 times was alternating with the second type of varieties. There is a sequential change of these two basic types of variability. The first type of varieties (polytomy) does not give rise to new species, but, apparently, facilitates to enhance the range and prosperity of species, and thus prepares species for the divergence. There are clearly visible ecotypes (Sinskaya, 1948; Dzyubenko, Soskov, Khusainov, 2007) in the first type of varieties, while the second type (dichotomy) - subspecies. The alternation of these same two types of variability (ecotypes and subspecies) is consistent with the law of A.N. Severtsov (1967) on the alternation of the main directions of the evolutionary process at the higher taxonomic levels in animals – idioadaptation and aromorphose. A.N. Severtsov and B.S. Matveev (1967) have repeatedly emphasized that the rule change the main directions of the evolutionary process must occur also at lower taxonomic levels, such as species, genus, family. N.N. Vorontsov (2004) examined the effect of Severtsov's law at the molecular level.

By A.L. Takhtajan (1951) and A.I. Tolmachev (1951) in plants are viewed as two main lines of the progressive development - ideoadaptations, the same allogenez and aromorphoses, the same arogenez (Timofeev-Resovskii, Vorontsov, Yablokov, 1977).

Charles Darwin (1937, 1939) considered that did not necessarily to consider the outcome of divergence for adopting him period during 10 000 generations. This may be a longer period of time. Based on the diagram of divergence of Darwin, we have compiled more understandable diagram **(Fig. 3)** during a time interval of 1.8 million years of the Quaternary period (600 000 generations) for perennial plants that bear fruit from the third year (600 000 generations, reproductive × 3 years / generation = 1 800 000 years).

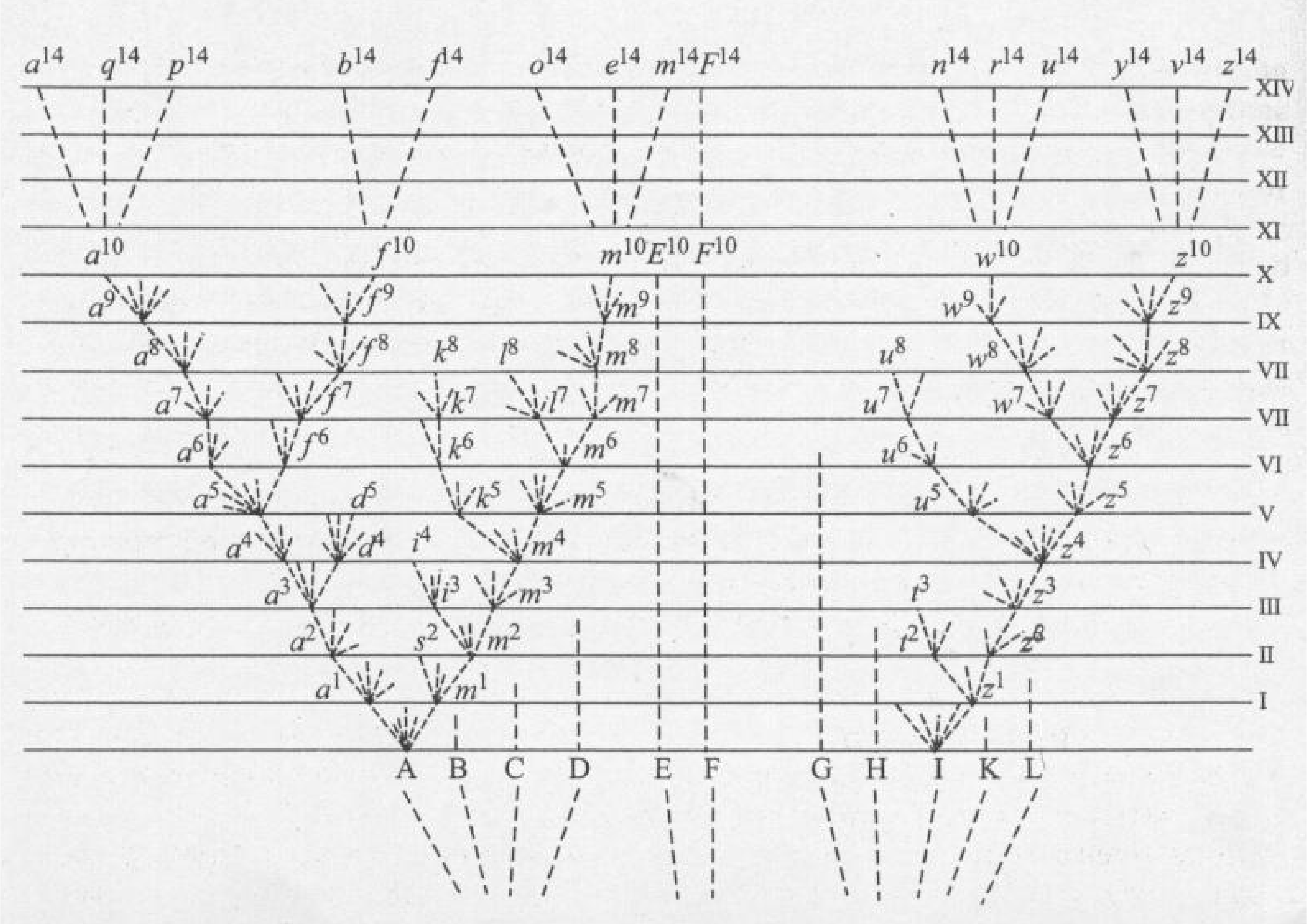


Fig. 2. Diagram of divergence of Ch. Darwin (Darwin, 1939).

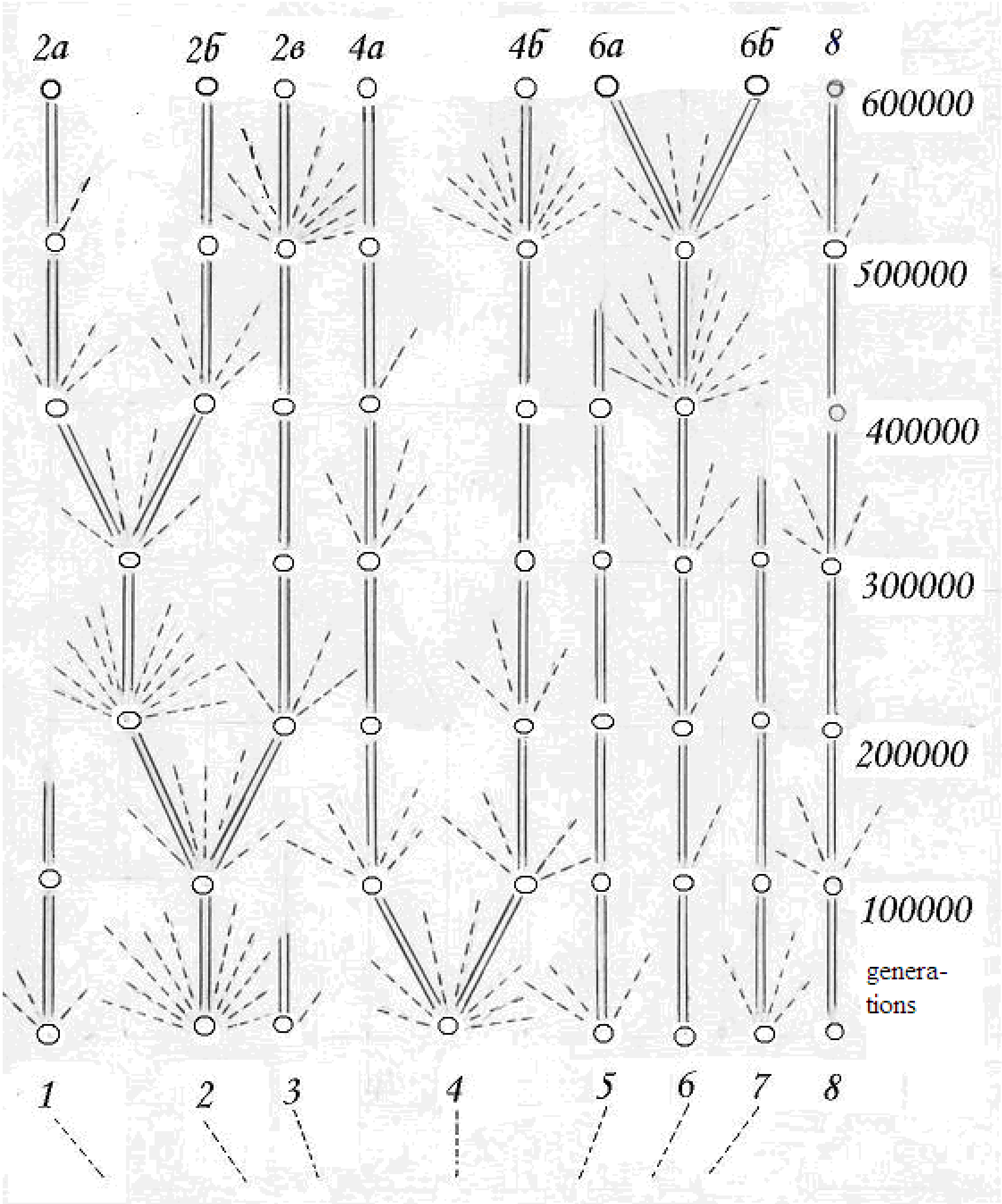


Fig. 3. Diagram of divergent development of species genus «n» in the Quaternary period of 600 000 generations, according to the ideas of Charles Darwin (1939) on the divergence in our option, bearing in 3rd year of life: 1-8 - species of the genus «n» in start position to 1,8 million years ago; ○ - species of the genus «n» and their descendants in every 100 000 generations, 2a, 2б, 2в, 4a, 4б, 6a, 6б, 8 - a new kinds of the genus «n» by 600 000 generations, or 1.8 million years ago (600 000 generations × 3 years / generation), the dashed thin twigs - ecotypes and groups of ecotypes (ideoadaptation), dichotomous branching - the formation of two new species through a subspecies, that is itself the divergence of Ch. Darwin (aromorphose).

In the section, or genus «n» 1,8 million years ago **(Fig. 3)** 8 species have started (1-8). The results of divergence are considered in every 100 000 generations. Species first has finished its development and has died before reaching the second mark of 200 000 generations. Species second with numerous varieties (ecotypes) has prepared a framework for the divergence and at the first mark of 100 000 generations has diverged, i.e., two of the six varieties have been most favorable for the species. They at first have transformed into two subspecies, and at the second point - in two new species: one with 11 varieties and another - with 4. The first of them at the third mark again has diverged across subspecies and has transformed to the fourth mark in close neighboring two new species, closely related to their original form. Soon both species (2a and 2б) have finished at the sixth mark through 600 000 generations. Return to the second branch of the dichotomous twig of the second species at the second point where we have left it with four varieties. Further it uniformly developed, successfully reached the sixth grades and formed a new species 2в. At the penultimate mark of 500 000 generations, it produced nine varieties and one must assume that in the near future geological time, probably, would be diverged. Thus, species second has finished in the form of three new species (2a, 2б, 2в), which can be combined into a new independent row (series), and maybe even a new section. Species third with two varieties did not reach the first mark and became extinct. Species forth immediately has diverged into two species, which were not sharing with a small number of species, has changed little, reached the finish line in the form of two new closely related species (4a, 4б). Species fifth has started with four varieties, immediately lost them and did not reach their fifth grades extinct. Species sixth gradually gained variability, at the fourth mark it suddenly got a lot of varieties and already at the fifth mark, it was transformed through two new subspecies of closely related species (6a, 6б). Species seventh has extinct before reaching the fourth mark. Little changed never diverged species eighth has reached the finish line almost without change **(Fig. 3)..**

L.N. Gumilev (1989) as a result of syntheses of ethno-development of the world for three thousand years, came to the conclusion that the new closely related peoples (ethnic groups), according to Semenov-Tian-Shansky (1910) - nationality (ecological races) come into being quite rapidly, in average of 300 years, i.e. for 15 reproductive generations (300 years: 20 years / generation = 15 generations), reaching a peak in its development 600 years after birth and after 600 years complete development, passing the whole cycle at average for 1200 years or 60 generations (1200: 20 = 60). While, in the absence of other data, we can tentatively accept the lifetime of ecotype within an average of 1200 years.

Thus, the diagram and above the data show that the ecotype (ecological race) and subspecies (geographical race) are quite different intraspecific subordinate categories that differ in life expectancy, formation methods, and resistance to environmental factors, role in the evolutionary process and other properties. This fact has been reflected repeatedly in the literature and not refuted (Mayr, Linsley, Yuzinger, 1956; Davis, Heywood, 1963, p.100-101, 423; Ivanov, Soskov, Buhteeva, 1986, pp. 15; Soskov, 1991, pp. 128; Dzyubenko, Soskov, Khusainov, 2007; Soskov, 2007, 2007a, etc.). Differences between ecotypes and subspecies are reflected in two laws - the law of divergence of Charles Darwin and the law of A.N. Severtsov, which are the essence of geographical-morphological method of systematics, together with the rule R. Wettstein (Wettstein, 1898) and species rows V.L. Komarov (Komarov, 1908).

As it turned out "split" or dichotomy, more properly called a "divergence", manifests itself in nature everywhere, but our data shows that only basic levels of organization of matter, such as: an atom (protons and electrons), power (+ and -), a charge of the molecule in inorganic chemistry (cation and anion), the spatial isomerism of molecules (left - and right) gene (two alleles), chromosomes (meiosis and mitosis), cell (divided into only two new ones), sex of the organisms (male and female), species (2 subspecies); philosophical categories and dialectical opposition (always paired), computer (0 and 1), etc. Close binary stars and close binary galaxies recently discover in the field of astronomy, but there are no a close triple, five fingers ... etc. close stellar systems (Kiselev, 1996; Karachentsev, 1996; Kosinov, 2000; Surdin, 2001). Thus, the law of divergence of Darwin is a part of the common law - "the fundamental duality", as it is justified and called by N.V. Kosinov.

Conclusions

1. In the diagram of divergence of Charles Darwin there are two types of varieties. Numerous, short-lived varieties, not giving rise to new species are ecotypes or groups of ecotypes (ecological races), and dichotomous branching, long-living, giving rise to new species are subspecies (geographical races).

2. The law of divergence of Darwin appears not at all taxonomic levels, but only the main (in spite of A.P. Khokhryakov) - subspecies and species ones. Taxa variety (varietas), seria (series), section (sectio) and subsection (subsectio) are secondary taxonomic levels and not obey the law of divergence.

3. In the diagram of divergence of Charles Darwin are clearly visible two laws - the law of divergence of Charles Darwin and the law of A.N. Severtsov about alternating the main directions of evolution - ideoadaptations (allogenez) and aromorphose (arogenez).

4. Most likely scheme of micro-accumulative species formation was given, which supported the law of divergence of Charles Darwin and was based on the analysis of areas polytypic species in the studied worldwide genera Calligonum L. and Rhaponticum Ludw.

5. The impossibility of simultaneous formation in the system of polytypic species more than two subspecies is proved.

6. Conclusion of V.L. Komarov (1901) is confirmed, that in the process of formation of new species and subspecies the entire populations on all the area of species are involved.

7. Conclusion of I. Pachosky (1925) is confirmed, that the process of areas formation of two new species in the first stage of species formation is in place, without migration, within the range of an old species.

8. It is found that in the process of divergence with the formation of two new related species the former species disappears as a result in some variation of all its individuals (i.e. according to the philosophical category of negation).

9. Geographic isolation of subspecies (homozygotes) in the process of divergence is made using the heterozygotes (divergent hybrids) and does not require physical barriers - mountains and water spaces.

10. The law of divergence of Charles Darwin is a part of a more general law of N.V. Kosinov, the fundamental law of duality, which manifests on the main levels of organization of matter.

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