ISSN : 0974 - 7532 Volume 11 Issue 1

Research & Reviews in

BioSciences

Regular Paper

RRBS, 11(1), 2016 [047-061]

Evolutionary analysis of long structured phylogenetic branches in angiosperms

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ABSTRACT

We concentrate on the idea of the neontologic chronicles of evolution, anizotomy of philogenetic process, cryptaffine taxa and cryptaffine transition in angiosperm's phylogeny, complex structure of phylogenetic branches. We noted that macroevolutionary process's mechanism in angiosperms is not limited to random mutations and selection. The intracellular processes and mechanisms must be at the basis of the major macroevolutionary transformations. Phylogenetic process in general is naturally determined and nomogenetic. © 2016 Trade Science Inc. - INDIA

KEYWORDS

Neontological chronicle;
Structured phylogenetic branch;
Cryptaffine taxa;
Cryptaffine transition;
Nomogenesis;
Homo sapiens evolution;
Quantum evolution;
Punctuated-equilibrium.

NEONTOLOGICAL CHRONICLES OF EVOLUTION

In our previous papers we formulated the evolutionary concept of cryptaffinic transition in Angiosperm's phylogeny. Principally it concerns macroevolutionary problems starting at taxonomic level of families and higher. The formulation was finalized[1, 2]. During the construction of the concept we applied many of the new or rarely used terms and definitons. These can prove themselves useful while conduction evolutionary research and are essential for the understanding of shown view on the evolutionary process in plants. Below we will describe the processes and explain the terms used. More dietailed description of the fundamentals of this concepts could be found in the articles mentioned above.

Graphically evolutionary process could be described as a variable slope curve with evolutionary stage on the horizontal axis and time on the vertical axis. The closes match to this scheme is found in the punctuated equilibrium concept based on paleontological material[3, 4, 5]. However, molecular analysis of recent material allows us to consider deeper the idea of the punctuated equilibrium.

We consider sufficiently developed macro system of modern plant organisms as a neontological chronicle of the evolution. A.Elenkin[6] referred to the system of modern organisms as living chronicle of the evolution. At the same time we assume that several ancestral groups in a little degree modified forms exist simultaneously with their descendants, but direct descendants may differ significantly from their ancestral groups.

Consideration of the system as a chronicle or as an equivalent fossil stratigraphic sequence is traditional in biology. All comparative morphology, anatomy, embryology and biochemistry in their evolutionary interpretation based on the idea that the system is the chronicle of evolution. Charles Dar-

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win noted: «The Natural System is a genealogical arrangement, with the acquired grades of difference maked by the terms, varites, species, genera, families, & c; and we have to discover the lines of discent by the most permanent characters whatever they may be and of however slight vital importance» [7: 399]. E. Haeckel formulated the rule of "triple parallelism"[8] based on detailed analysis of chronicles. Codes of primitive and advanced characteristics in modern taxonomy also include historical component[9]-[12]. R. Thorne: "Ancestral characteristics and the direction of trends of specialization can often be recognized in existing angiosperms"[13: 37]. A. Takhtajan noted: "As the whole history of biology after Darwin shows zoologists and botanists are well able to make definite conclusions about the phylogenetic relationships of... systematic groups already only on the basis of a comparative study of living organisms"[14: 12].

Consideration of the system of modern organisms as neontological chronicles of the evolutionary process is in a certain contradiction with well established notions of synthetic theory of evolution (STE). In general, according to STE, there are two sister branches with approximately equal evolutionary potential at the bifurcation point. They can develop in different directions, but in equal taxonomic categories. Phylogenetic process is conceived as isotomic divergence corresponding to dichotomous branching diagrams illustrating the phylogeny in the academic literature. The equality of sister branches is especially emphasized in cladistics, although the rule of nonequivalent branching (Deviationsregel) was noted[15]. It is very important that according to STE modern taxa should not be considered as ancestors and descendants originating from one another. Otherwise, paleontological observations and practice of macro taxonomy demonstrate that modern taxa differ by the level of evolutionary advance and some of them are in the relationship of phylogenetic kinship, i.e. relations of ancestors and descendants.

Our comparative morphological and serological studies of the orders Liliales and Asparagales show several proteins to be acceptable markers of the chronicle of evolutionary events. Indeed, ancestral clades consist from taxa having a set of more primitive characteristics and the top of the system proved to be taxa rich by apomorphies[16]. Of course, neontological chronicle fixes characteristics not so strictly as paleontological chronicle, but it has its own advantages, because it is based on characteristics not remaining in a fossil state. The reconstruction of neontological chronicle requires special approaches partially outlined below.

ANISOTOMIC BRANCHING OF PHYLEM

The key notion of neontological chronicle is the assumption that organisms belonging to the ancestral and derived phylogenetic branches differ by evolutionary potentialities. It was demonstrated that while in evolutionary static ancestral groups species and genera form, in a sister evolutionary active groups arise new families[17] and even taxa of higher rank. For example, the formation of several genera and species inside Tofeldiaceae correspond to the formation of subclass Alismatidae inside the sister evolutionary active branch[18]. Thus, probably, series of slow (stasis) and fast (quantum) evolution events form a long phylogenetic branch. Well known paleontologist O. Abel[19] denoted evolutionary unequivalent sister branches as Ahnereihe and Stufenreihe, i.e. ancestral branch and a number of step-branches from it. The taxa of ancestral branch survived to the present day preserve characteristics more or less close to bifurcation point, the taxa of another branch accumulates apomorphies.

In recent decades, influenced by the latest versions of STE, the idea that modern taxa not characterize particular ancestral groups and have only "common ancestor" is actively promoted in taxonomy. Otherwise, the problem of the distance between existing taxa and this hypothetical ancestor is often beyond the scope of the general theory of evolution.

We believe that there should be no difficulties in deducing modern genera and families from each other. Several modern taxa of high rank may be derived from taxa very close to modern taxa of lower taxonomic rank. For example, the family Trilliaceae is possible to deduce from Zigadenus, one of the genera of the family Melanthiaceae, family Agavaceae from genus Hosta, representative of monotype family Funkiaceae, etc[1], [20].

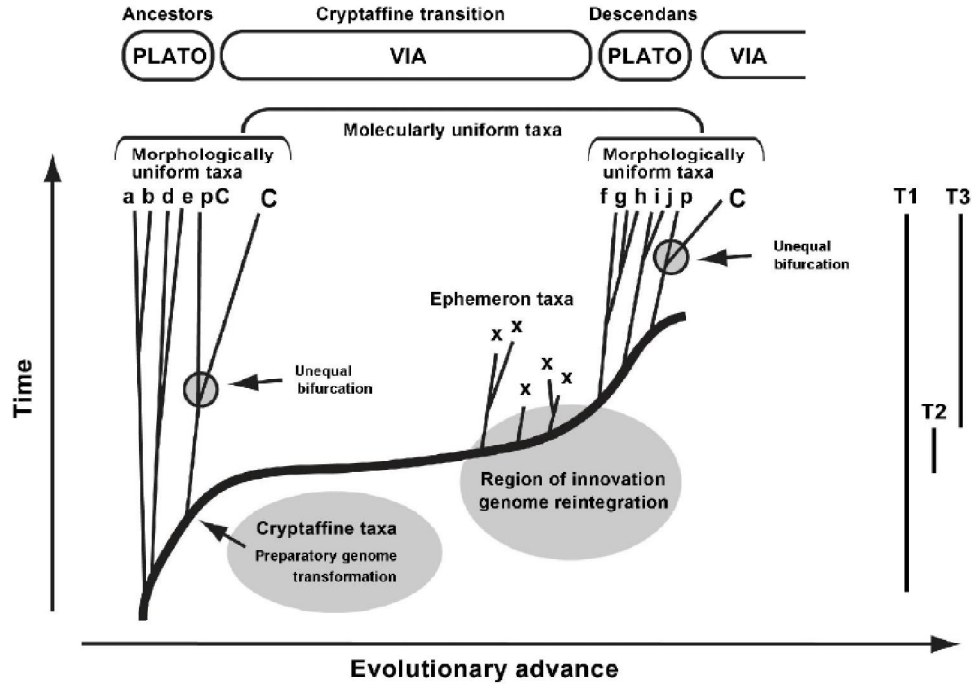

Figure 1 : The model of an element of long structured phylogenetic branch include: modern taxa of PLATO ancestors (a, b, c, d, e); modern taxa of PLATO descendants (f, j, h, i, j); cryptaffine taxa (C); precryptaffine taxa (pC); suppositional extinct ephemeron taxa not represented in neonthological chronicle (x); points of considerable unequal bifurcations; the time of existence of PLATO ancestors (T1), PLATO descendants (T3) and the time of evolutionary transformations (T2). slightly larger slope of the phylogenetic line of cryptaffine taxa (C) correspond to the Pavlov-Berg's phenomenon

The establishing of phylogenetic relationships of morphologically differing taxa is related with the notion of unequal bifurcation dividing evolutionary stasis and the evolutionarily much more active branches. Evolutionary stasis branch preserve to our time characters close to the time of bifurcation. In contrast, evolutionary active branch accumulate a significant set of apomorphies. This bifurcation (Figure 1) divides precryptaffine (kriptaffin-passive) and true cryptaffine (kriptaffin-active) taxa.

CRYPTAFFINE TAXA

For the first time we are faced with a hidden related taxa during comparative serological study of seed proteins of Liliaceae s. l. [20 and earlier]. It was found that for the majority of taxa the serology data support well grouping based of the morphological (s. lato) data. However several genera were closer to the morphologically dissimilar representatives of other families. For example, the genera *Clintonia* and *Medeola* (Melanthiaceae) serologically converging with Liliaceae. *Convallaria majalis* (Convallariacea) turned out to be the closest relative of the family Ruscaceae. *Hemerocallis* and *Simethis* (Asphodelaceae) serologically were close to Phormiaceae, genus *Hosta* (Funkiaceae) turned out to be the closest relative of the family Agavaceae and so on. Such unusual convergence received further confirmation based on DNA sequencing[21]. We designated these taxa as "cryptaffine" (hidden-related), i.e. morphologically similar to one group and according to molecular data similar to another one. Detailed studies have shown that in some cases, but not always, cryptaffine taxa have very specific morphological characteristics indicating the same relations as serological and other molecular data. For example, the genera *Hemerocallis* and *Phormium* have the same branched nectaries, the genus *Simethis* and Phormiaceae resemble in the structure of pollen grains and the type of microsporogenesis, the genus *Hosta* has a specific 60-chromosomal karyotype, as well as representatives of the family Agavaceae. *Clintonia* and *Medeola* are similar to Liliaceae according to its embryological characteristics[20].

It is important that according to the complex of morphological characters taxa, which approached

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to cryptaffine taxa by molecular data, are more evolutionarily advanced as compared with themselves and their "morphological" relatives. Therefore, probably, the morphological relatives of cryptaffine taxa are ancestors. Cryptaffine taxa themselves are intermediate groups. Molecular relatives of cryptaffine taxa are descendants[22], [23].

PHYLOGENETIC TAXA PLATO AND VIA

Thereby, it was possible to distinguish two groups of taxa: PLATO (lat. flat, wide), taxa uniform in their morphological and molecular characteristics and VIA (lat. path), taxa gravitating to ancestor groups by morphological characters and to descendant groups by molecular data[24]. These terms emphasize the role and place of these taxa in the evolutionary process. Taxa PLATO are large families of modern genera and species retaining morphological and molecular homogeneity. Taxa VIA are mono- or oligotype genera or families connecting PLATO of ancestors and PLATO of descendants (Figure 1).

In almost all studied cases of cryptaffine transitions the number of species in cryptaffine groups is rather small in comparison with the groups of ancestors and descendants: Melanthiaceae (90) – *Zigadenus* (1) – Trilliaceae (70); Uvulariaceae (30) – Medeolaceae (2-6) – Liliaceae (500-600); Asphodelaceae (800-900) – Simethidaceae (1), Hemerocallidaceae (15-20) - Phormiaceae (30-35); Anthericaceae (600-700) – Funkiaceae(15), Camassiaceae(20-23) – Agavaceae (300-400); Asparagaceae (300-400) - Convallariaceae s.str (10) - Ruscaceae-Dracaenaceae (250-300); Restionaceae (400) – Flagellariaceae (3), Joinvilleaceae (2), Ecdeiocoleaceae (3) – Poaceae (8000-10000)[1]. In parentheses is the number of species in the broad sense of cryptaffine groups.

In some cases cryptaffine transitions between genera may be revealed: *Mahonia* (110) – sec. Horridae from genus Mahonia (9) – *Berberis* (500). At the same time, the transition between the genera *Vancouveria* and *Epimedium*, belonging to the same family, has not cryptaffinic characteristics.

PRECRYPTAFFINE TAXA

Phylogenetically cryptaffine taxa and their closest relatives (precryptaffine taxa) form a single group (Figure1), but differ sharply in their evolutionary role. The genome of cryptaffine taxa has a number of features such as a significant increase in the number of chromosomes, high G+C, CpG and CpNpG content in rDNA, a frequent presence in their morphology of several characteristics typical to PLATO descendants (Pavlov-Berg phylogenetic anticipation), that can be considered as a indication of subsequent morphological transformations. Precryptaffine taxa morphologically close to PLATO ancestors and phylogenetically to cryptaffine taxa do not posses such characteristics. Precryptaffine taxa belong wholly to PLATO ancestors. Cryptaffine taxa carry in their genome traces of the processes resulting in genome reintegration and morphological changes after bifurcation.

RECIPROCATING MUTATIONAL PROCESS

An important tool for the study of the evolutionary process could be the study of nucleotide composition of several DNA regions that vary correlated with the process of morphological evolution such as nuclear ribosomal DNA of angiosperms, including spacers ITS1, ITS2 and coding region 5.8S rDNA. Particularly the analysis of total C+G content of guanine (dG) and cytosine (dC) and correlated indices CpG and CpNpG proved to be informative.

Dinucleotides CpG and trinucleotides CpNpG in plants play an important role in the functioning of the genome and its mutation activity. The interest in the frequency of occurrence dC, CpG and CpNpG sequences in DNA of different organisms is considerably related with exposure to cytosine methylation at these sites because methylation of cytosine in CpG is a key regulatory mechanism in ontogenetic development, apoptosis, cell differentiation, regulation of transcription and proliferation, genome protection against the introduction of mobile elements[25]-[30].

Thus methylated 5mC can be readily deaminated,

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TABLE 1 : The percentage of nucleotides, the numbers of CpG and CpNpG sequences, total dG+dC and CpG+CpNpG content per 100 b.p. in ITS1 5.8S rDNA[41] with additions*

N	Taxa	N species	dA	dT	dG	dC	dG+dC	CpG	CpNpG	CpG+CpNpG
Order Melanthiales										
Family Melanthiaceae										
1	Anticlea	3	26	25	26	23	49	6	3	9
2	Toxicoscordion	8	25	23	28	24	53	7	5	12
3	Veratrum	5	26	28	25	21	46	5	2	7
4	Melanthium	4	25	29	26	21	47	6	3	9
5	Stenanthium	4	26	25	26	23	49	6	3	9
6	Amianthium	1	28	31	22	20	42	5	1	6
7	Schenocaulon	2	26	25	24	25	49	7	5	12
	Average		26.0	26.5	25.3	22.4	47.8	6.0	3.1	9.1
	σ		1	2.8	1.9	1.8	3.6	0.8	1.5	2.3
8	Zigadenus	1	21	16	34	29	63	13	9	22
Family Trilliaceae										
9	Kinugasa	1	27	23	29	21	51	7	4	10
10	Daiswa	4	27	22	31	20	51.0	7	3	10
11	Paris	3	25	23	32	21	52	6	3	8
12	Trillium	18	23	20	33	24	58	9	5	15
	Average		25.5	22.0	31.3	21.5	53.6	7.3	3.8	10.8
	σ		1.9	1.4	1.7	1.7	2.9	1.3	1.0	3.0
Order Liliales										
Family Liliaceae										
13	Cardiocrinum	1	23	19	28	30	58	8	10	18
14	Lilium	53	20	20	29	28	58	11	8	19
15	Nomocharis	1	19	20	32	29	61	12	8	21
16	Gagea	7	18	19	33	30	63	9	9	18
	Average		20.0	19.5	30.5	29.3	60.0	10.0	8.8	19.0
	σ		2.2	0.6	2.4	1.0	2.4	1.8	1.0	1.4
Order Asparagales (xerocarpous)										
Family Amaryllidaceae										
17	Crinum*	4	19	23	35	24	59	6	6	12
18	Lycoris*	1	17	16	34	33	67	13	11	24
19	Pancratium*	1	15	15	36	33	69	15	9	24
20	Ungernia*	1	19	16	33	32	65	13	7	21
21	Narcissus*	2	15	15	36	34	70	16	9	25
Family Asphodelaceae										
22	Bulbine	1	19	14	31	36	67	15	8	23
23	Kniphofia*	5	21	15	30	34	64	12	8	20
24	Aloe	6	22	17	29	32	61	12	7	19
Family Camassiaceae										
25	Camassia	1	17	16	34	32	66	13	10	23
Family Funkiaceae										
26	Hosta	1	12	11	41	36	77	17	13	30

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N	Taxa	N species	dA	dT	dG	dC	dG+dC	CpG	CpNpG	CpG+CpNpG
					Family Agavaaceae					
27	Agave	7	17	17	36	30	66	11	10	21
28	Manfreda	2	16	19	36	30	65	10	10	20
29	Hesperaloe	2	18	19	34	29	63	10	9	19
30	Yucca	2	17	18	34	31	65	10	8	18
	Average (excl. Hosta)		17.8	16.9	33.7	31.5	65.2	12.0	8.6	20.7
	σ		2.1	2.4	3.0	3.0	3.1	2.7	1.4	3.4
					Order Asparagales (juicycarpous)					
					Family Asparagaceae.					
31	Asparagus	3	19	18	31	32	63	13	9	22
					Family Convallariaceae					
32	Aspidistra*	1	16	10	34	40	74	17	12	29
					Family Dracaenaceae					
33	Dracaena	1	18	12	34	36	70	13	12	25
34	Calibanus	1	18	16	34	32	66	14	9	23
35	Nolina	3	15	13	36	36	72	16	10	26
36	Sansevieria	2	15	11	36	38	74	15	11	26
					Family Polygonataceae					
37	Polygonatum	2	16	10	35	39	74	17	12	29
38	Maianthemum*	2	19	11	34	37	71	14	12	26
	Average		17.0	12.6	34.2	36.2	70.5	14.9	10.9	25.8
	σ		1.7	2.9	1.6	2.9	4.1	1.6	1.4	2.5

Big karyological sequence. Reciprocating evolution of karyotype

converting it in thymine (dT). If we carry on the analysis of noncoding strand, complementary to the coding sequence will be replaced by dG/dA. Appropriate mutations in the coding strand reflect in noncoding one in the same way. As a result of subsequent cycles of replication TpG and CpA may be formed instead of CpG. This is the nature of the evolutionary changes of DNA is described by several researchers on a variety of objects from plants to humans[31]-[40].

In plants, due to chromometilase (additional methyltransferase) that methylates dC also in CpNpG[39] one can expect more intensive elimination of dC and decreasing of CpG and CpNpG content.

The following are the main conclusions concerning the analysis of nucleotide and dinucleotide composition of rDNA in several groups of plants[22], [23], [41]. TABLE 1 shows the distribution of the number of nucleotides, CpG and CpNpG elements in ITS1 rDNA. There is a more or less uniform decrease of adenine (from 26 to 17%) and more significant decrease of thymine (26 to 13%) from the representatives of the primitive family Melanthiaceae to highly evolutionarily advanced representatives of the families of the order Asparagales. The content of guanine and cytosine increases from 25 to 34% and from 22 to 36% respectively. Evenly from 47 to 70.5% is an increase in the total content of cytosine and guanine. In two and a half (from 6 to 15 per 100 b.p.) increases the content of CpG and almost four times (3 to 11) CpNpG.

Similar changes we observe in ITS2. The content of adenine slightly decreases from 17 to 13.9%. The content of thymine decreases more significant from 29 to 11%. The content of guanine and cytosine increases approximately to the same extent from 29 to 38% and from 24 to 36% respectively. Also approximately 2.5 - 3.0 times the content of CpG and CpNpG increases.

Perhaps the stabilizing effect of selection for the coding region 5.8S rDNA is much higher and the amount of change is correspondingly less. The change in the content of adenine is doubtful and in-

crease of guanine is on the verge of reliability only in dry-fruited Asparagales. However, reducing the content of thymine and cytosine, and increase of C+G are valid according to the second significance level, which may indicate a same trend of mutational changes in coding and non-coding regions of rDNA[22], [23], [41].

At the same time, it has attracted attention that the content of CpG and CpNpG elements in the coding region is slightly higher in the order Liliales as compared with Melanthyaceae and further has not increased, remaining at 10 and 5 respectively, while as in the spacers it has increased to 15 and 10 per 100 b.p. This might indicate the existence of limits of CpG and CpNpG saturation in coding regions.

As we pointed out above, the interest to dC content in different organisms from evolutionary point of view is due to the fact of exposure of these sequences to methylation and subsequent conversion of cytosine to thymine decreasing the content of cytosine and cytosine-containing CpG and CpNpG.

Analysis of nucleotide substitutions in taxa PLATO of Angiosperms revealed the "burnout" of guanine and cytosine. The number of substitutions C/T in any adjacent positions can be 3-5 times higher than the number of any other substitutions. In CpG such excess is up to ten times higher[24].

However, our data do not show a decrease or even preserve the original amount of cytosine, CpG and CpNpG sequences, and vice versa significant increase in evolutionarily advanced groups of monocots. These data indicate that exactly inside cryptaffine taxa the saturation of rDNA by dG and dC can occur. The genera *Zigadenus* and *Hosta* confirm this assumption demonstrating considerable higher C+G content[41].

Preliminary analysis of zoological data in the primate clade indicates the similar trend of C+G content in rDNA. Noteworthy is a very high value of this index in higher primates and humans. This may indicate that these groups of organisms are close to the point of evolutionary saltation[42].

Thereby the general trend of the changes in the nucleotide composition of rDNA in a long structured phylogenetic branch can be described as follows. There are two processes creating mutational pressure of different directions. The first one is the saturation by cytosine and guanine resulting in an increase of easily converted CpG and CpNpG sequences. This process is prevalent in VIA and probably related with features of replication/reparation apparatus, especially replicases "working with errors»[43]-[45] or by GC-biased gene conversion[46], [47]. In evolutionary stasis taxa PLATO dominates another process of "burnout" of cytosine, especially in methylated CpG sequences resulting accumulation of TpG and CpA elements. The content of G+C, CpG and CpNpG decreases in evolutionary stasis taxa PLATO and increases in taxa VIA. Thus, in a long branch the mutation process is bidirectional, or reciprocating.

It is well known that both basic (x) and diploid (2n) numbers of chromosomes change in evolution[48]-[50]. However, this conclusion was based mainly on a study of short evolutionary periods corresponding to genera or families. The analysis of the longer phylogenetic branches reveals new patterns of evolution of karyotypes (TABLE 2, Figure 2).

The generalized sequence of events in a long structured branch can be represented as follows[1]. Primary sector of PLATO in the considered group of angiosperms monocot Melanthiaceae (TABLE. 2) is characterized by taxa often with low basic chromosome number x=7, rarely 8, 10 or 11 and polyploid series multiples of the low basic number.

Next sector is a cryptaffine transition group VIA. Karyotype of previous sector is usually preserved in precryptaffine taxa, but inside true cryptaffine taxa the chromosome number is skyrocketing. For example, in Melanthiaceae - Trilliaceae precryptaffine genus *Shoenocaulon* (2n=16) – cryptaffine genus *Zigadenus* (2nH"52). In PLATO descendants Trilliaceae the basic number decrease up to 5 (2n=10) and arise correspondent polyploids with 2n=20, 30 and 40.

As can be seen from the TABLE, the basic number of chromosomes in PLATO descendants not always immediately drops to a low x=5-8. In most cases it stabilizes first around 10-12 and only gradually lower to 7-2.

In this respect the distribution of basic chromosome numbers inside the family Poaceae is indicative (Figure 2). The direct ancestors of the family Poaceae have been identified recently. They were

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representatives of the family Ecdeiocoleaceae[51].

The closest low chromosome number ancestor of this clade is probably the cluster Haemodoraceae - Philydraceae - Pontederiaceae - Lowiaceae – Dasypogonaceae[52] with x = 7, 8; 2n = 14, 16 and polyploids on this basis.

The Grass Phylogeny Working Group (GPWG) is conducting a wide study of the phylogeny of cereals using molecular techniques. They were allocated 12 subfamilies[53] and subfamily Micrairoidea added later[54]. We have adhered to the phylogenetic system of cereal based on a study of three regions of the chloroplast genome: rbcL, matK and trnL-F[55], which is largely a continuation of GPWG (TABLE. 2, Figure 2).

Evolutionary dynamics of chromosome numbers in this long phylogenetic branch is following (Figure 2). As mentioned above the basic group is a low-chromosome (x=7, 8) group of families Haemodoraceae - Philydraceae - Pontederiaceae - Lowiaceae – Dasypogonaceae. It remains unknown whether there high-chromosome transition group between these families and the subsequent phylogenetic branch Rapateaceae – Restionaceae with x=10-12. Near the family Poaceae we can observe three oligotype families with the increased basic chromosome number: Flagellariaceae (2n=38, x=19), Joinvilleaceae (2n=36, x=18) and Ecdeiocoleacea (2nH"48, 2nH"64-66). It is most likely that the basic chromosome number in Joinvilleaceae is x=n=18 because there are no any triploids neither in previous group nor in Poaceae (tetraploids in Poacea are based on n=9). Ecdeiocoleacea can be regarded as paleopoliploids based on x=12 or 11, but assuming the reality of x=18, 19 in the previous taxa, a higher base number of chromosomes can be expected also in this family. In any case a high value 2n throughout the transition group to the family Poaceae is well expressed.

Thereby we can see that Rapateaceae - Restionaceae (x=10-12) diverges from low-chromosome number group Haemodoraceae – Dasypogonaceae (x=7-8). Apparently in several side branches, such as the family Anarthriaceae, x is reduced to 6. There are no species with a high number of chromosomes between these two groups of taxa. The next group consists from high-chromosome number olygotype families Flagellariaceae, Joinvilleaceae, Ecdeiocoleaceae (x=18, 19 and more).

The next evolutionary step is the emergence of the family Poaceae. The primary taxa of this family are subfamilies Anomochlooideae and Pharoideae characterized by reduced basic chromosome number (x=12). Further the branch splits into two clades known by major subfamilies: BEP (Bambusoideae, Ehrhrartroideae, Poooideae) and PACMAD (Panicoideae, Aristidoideae, Chloridoideae, Micrairoideae, Arundinoideae, Danthonioideae). In both clades a gradual decrease of x from 12 to 10, 9 and below can be observed. In PACMAD clade x=8, 7, 6 are rare, but in BEP clade the largest subfamily Pooideae almost entirely is represented by the species with x=7. A number of species of this subfamily's probably just continue to drop to x=2, and then, on the basis of this chromosome number a hybridogenic series of polyploid taxa with 2n=8, 16 arise[1].

Let us note that in a long branch the chromosome number not always again falls to low x=5-8 inside PLATO descendants. It can be assumed that in these cases, for example, families Agavaceae and Ruscaceae, karyotype evolution is not yet complete. Also one can note another kind of deviation. There are no taxa with considerable high chromosome number in cryptaffine transition Medeolaceae - Liliaceae. At the same time in the family Liliaceae species with x=12 dominate. It can be assumed that the genus *Medeola* is precryptaffine taxon and hypotetical high-chromosome cryptaffine taxon has not been preserved in the neontological chronicle of this long phylogenetic branch. In this way the sequence of karyological events in a long phylogenetic clade can be represented as follows (Figure1).

Primary taxa PLATO ancestors have a low basic chromosome number x=7-8 and correspondent neopolyploid series. Precryptaffine taxa usually preserve karyotypes of previous section. This is followed by cryptaffine VIA transition taxa with high-chromosome number.

The next group is PLATO descendants represented by morphologically and physiologically apomorphic taxa. It can be divided into two subgroups. In the first one the basic number of chromosomes (x=11-13) is significantly lower than in

cryptaffine taxa VIA, but higher than in PLATO ancestors. In the second group chromosome number drops to the ground level of PLATO ancestors and in some cases even lower.

Thus, we observe a periodic process repeated in different groups and at different levels of monocotyledonous angiosperms: (x=6-8) – (x>18-30, 2n=38-60) – (x=6-8). It can be denoted as a *big karyological sequence*. Well known polyploid series in species and genera with following polyploid drop can be denoted as a *small karyological sequences*.

CRYPTAFFINE TRANSITION

We have already used the term cryptaffine transition. Let us discuss it in more detail. It can be the area of phylogenetic clade or taxon VIA. It connects phylogenetically PLATO ancestors and PLATO descendants. It is characterized by active evolutionary changes and consists of a preliminary transformation and innovative genome reintegration.

Preliminary transformation. It is almost not detected at the morphological level (except phylogenetic phenomenon of Pavlov-Berg, see below) and therefore is not reflected in the phylogenetic system based on the concept of the identity of morphological similarities and genealogical kinship. This stage is characterized by an increase in G+C, CpG and CpNpG content in ITS1-5,8S-ITS2 rDNA region and a significant increase in the number of chromosomes. Probably these processes initiate the cryptaffine transition.

Innovative genome reintegration. As shown above, the karyotypes of first representatives PLATO descendants are characterized by considerably low number of chromosomes (x=11-12 and lower) as compared with cryptaffine taxa. It seems to be very important that the transition from high chromosome numbers in cryptaffine taxa to low chromosome numbers in first groups of PLATO descendants correlate with arising of new morphological characteristics and new families. This correlation can be considered as *the innovative reintegration of genome*[1].

EPHEMERON TAXA

First steps of the emergence of new morphological taxa are not represented in neontological chronicles of the evolution of the plants, also no any fossil paleobotanical data on any transitional forms. Yet the existence of transitional taxa in the evolutionary process is very likely and their absence is related probably with a short periods of their existence. Provisionally we denote such transitional forms on the Figure 1 as *ephemeron taxa.*

Phylogenetic phenomenon of pavlov-berg anticipation

When analyzing cryptaffine transitions between families and orders of angiosperms one can often observe the phenomenon of phylogenetic anticipation. L. S. Berg[56], [57] described this phenomenon on the basis of Pavlov's[58] ideas of the phylogenetic acceleration, consisting in the manifestation of characteristics of adult stages of derivative groups in the juvenile stages of their phylogenetic ancestors. L. Berg expanded the understanding of the phylogenetic acceleration shifting its effect on adult stages of ancestral taxa. He writes: "... we consider the phylogenetic acceleration or anticipation of characteristics not only the appearance of characteristics of the higher forms in young animals of lower, but also the appearance of characteristics of higher forms in adults of the lower groups, i.e. we denote by this term all cases, when the organism, still young or old, is ahead of its time, or the average level of the group"[56: 50].

Our research on the phylogeny of modern taxa indicates that phylogenetic anticipation exists inside the cryptaffine taxa. Thus in the cryptaffine transition *Hemerocallis, Simethis* - Phormiaceae one can find in the genus *Hemerocallis* specific branched septal nectaries, characteristic to genus *Phormium* and to a lesser extent *Dianella* (Phormiaceae). Trichotomsulcate pollen grains and simultaneous microsporogenesis are rare in monocots but typical for Phormiaceae and monotype genera *Simethis*.

In the transition *Hosta* - Agavaceae in species of the genus *Hosta* a rare 60-chromosomal bimodal karyotype is typical, as well as inside the family

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TABLE 2 : Chromosome numbers in long structured phylogenetic branch of several monocots[1]

Region	Number genera/ species	2n (n species)	Expected basic chromosome number x (rare)
Melanthiaceae – Zigadenus – Trilliaceae			
PLATO ancestors Melanthiaceae	6/55	16 (11); 32 (20); 20 (2); 22 (8)	8 (10-11)
Precryptaffine Shoenocaulon	1/up to 25	16 (11)	8
Cryptaffine Zigadenus	1/1	˜ 52	˜ 26
PLATO descendants Trilliaceae	4/˜ 70	10 (44); 20 (4); 30 (2); 40 (1)	5
Uvulariaceae – Medeolaceae - Liliaceae			
PLATO ancestors Uvulariaceae	3/˜ 30	14 (6); 16 (17); 12 (2); 18 (2); 22 (1);32 (1)	7, 8
Precryptaffine Streptopus, Scoliopus, Clintonia	3/ 20	14 (1); 28 (5); 16 (3); 32 (3);	7, 8
Cryptaffine Medeola	1/1	14 (1)	7
PLATO descendants Liliacea	10/˜ 500	24 (276); 22 (1); 26 (2); 14 (3), 18 (3); 36 (13); 48 (32)	12, (9, 7)
Asphodelaceae – Hemerocallidaceae, Simethidaceae – Phormiaceae			
PLATO ancestors Asphodelaceae	13/˜ 900	14 (300); 28 (15); 42 (3); 12 (40); 42 (3); 56 (4)	7 (6)
Precryptaffine Hemerocallis	15 - 20	22 (22); 33 (2); 44 (1)	11
Cryptaffine Simethis	1/1	48 (1)	24
PLATO descendants Phormiaceae	6/ 30-35	20 (3), 18 (1); 16 (4); 32 (5)	10, 9, 8
Anthericaceae – Camassiaceae, Funkiaceae – Agavaceae			
PLATO ancestors Anthericaceae	22/˜ 600	22 (30); 24 (5); 44 (3); 56 (2); 14 (14); 28 (10);16 (33); 32 (8); 8 (9)	12, 11, 7, 8, 4
Precryptaffine Camassiaceae	5/ 19	30 (5); 36 (1); 34 (1); 24 (2); 60 (1)	12, 13, 15, 17
Cryptaffine Funkiaceae	1/ 23	60 (17); 48 (1); 90 (1); 120 (1)	30
PLATO descendants Agavaceae	8/350-400	60 (60); 24, 36, 90, 120, 180 (1-5)	30
Anthericaceae – Convallariaceae, – Ruscaceae, Dracaenaceae			
PLATO ancestors Anthericaceae	22/˜ 600	22 (30); 24 (5); 44 (3); 56 (2); 14 (14); 28 (10);16 (33); 32 (8); 8 (9)	12, 11, 7, 8, 4
Precryptaffine and cryptaffine Convallariaceae s. str.	10/100-110	36 (16)38 (39); 40 (4)	18, 19, 20
PLATO descendants Ruscaceae, Dracaenaceae		40 (7); 60 (1) 40 (21); 38 (14); 36 (16); 30 (4); 28 (2); 22 (5); 20 (21); 18 (18); 14 (1); 16 (1)	20, 19, 18, 11, 10, 9, (8, 7)
Lowiaceae, Haemodoraceae, Dasypogonaceae – Flagellariaceae, Joinvilleaceae, Ecdeiocoleaceae – Poaceae			
PLATO ancestors Lowiaceae, Haemodoraceae, Dasypogonaceae	1/16; 15/101; 4/16	Dominate 2n = 14, 16, Rare corresponding polyploids	7, 8, (9)
Cryptaffine Ecdeiocoleaceae	2/3	˜ 48 (1); ˜ 64-66 (1)	24?, 32-33?
PLATO descendants Poaceae	˜ 800/ ˜ 11000	Except species with variable 2n 24 (87); 48 (138); 22 (40); 44 (37); 20 (224); 40 (276); 18 (211); 36 (228); 72 (49); 16 (13); 32 (6); 14 (685); 14, 28 (58); 56 (181); 28 (473); 42 (254); 12 (27); 24 based on x=6 (4–5); 10 (44); 8 (4); 4 (3); 2 (1).	12, 11, 10, 9, (8), 7, 6 (4, 2)

Agavaceae. In the transition *Medeola* - Liliaceae a number of the embryological characteristics of the family Liliaceae can be found inside the genus *Medeola* and precryptaffine taxa *Clintonia* and *Scoliopus*[20]. In the cryptaffine transition Tofieldiaceae - Alismatidae[59] a specific 3-circular 9-staminate androecium is characteristic for the genera *Pleea* (Tofieldiaceae, Lilianae) and *Butomus* (Butomaceae, Alismatanae). For other Lilianae 3-6 staminate 1-2-circular androecium is typical.

Cryptaffine transitions also can be observed at the genera level, for example, the transition between the genera *Mahonia* and *Berberis* (Berberidaceae). In this case the cryptaffine taxa are the section Horridae of genus *Mahonia*. According to molecular data[60] nine species of this small section of the group Occidentales of the genus *Mahonia* are closer to genus *Berberis* as compared with "morphological" relatives from the group Occidentales. These species are separated from the group Occidentales by the group Orientales.

L. Ahrendt[61], the monograph of genera *Berberis* and *Mahonia*, notes that characteristics of a young shoot have diagnostic significance. «Smoother, dark red stems, such as are familiar in Berberis, appear in the few Mahonia species of the unusual section Horridae; this being one of several characters which place these *Mahonia* nearer to *Berberis* then the others.»[61: 2])

The notion of phylogenetic anticipation usually causes objections from supporters of strict selection adaptogenesis. A. Severtsov[62], [63] notes that phylogenetic anticipation can be explained by an independent parallel development, based on a similar effect on the selection of the genomes of related organisms. With regard to our material we believe that it is consistently developing taxa and most of considered characteristics have not an adaptive significance. A detailed analysis of problems related with parallelisms and phylogenetic anticipation one can found in the publication of I. J. Popov[64].

Long structured phylogenetic branch

Thus we can assume that certain structure exists in the phylogenetic branch. One taxon (in our case family) flows into the other (other family) not di-

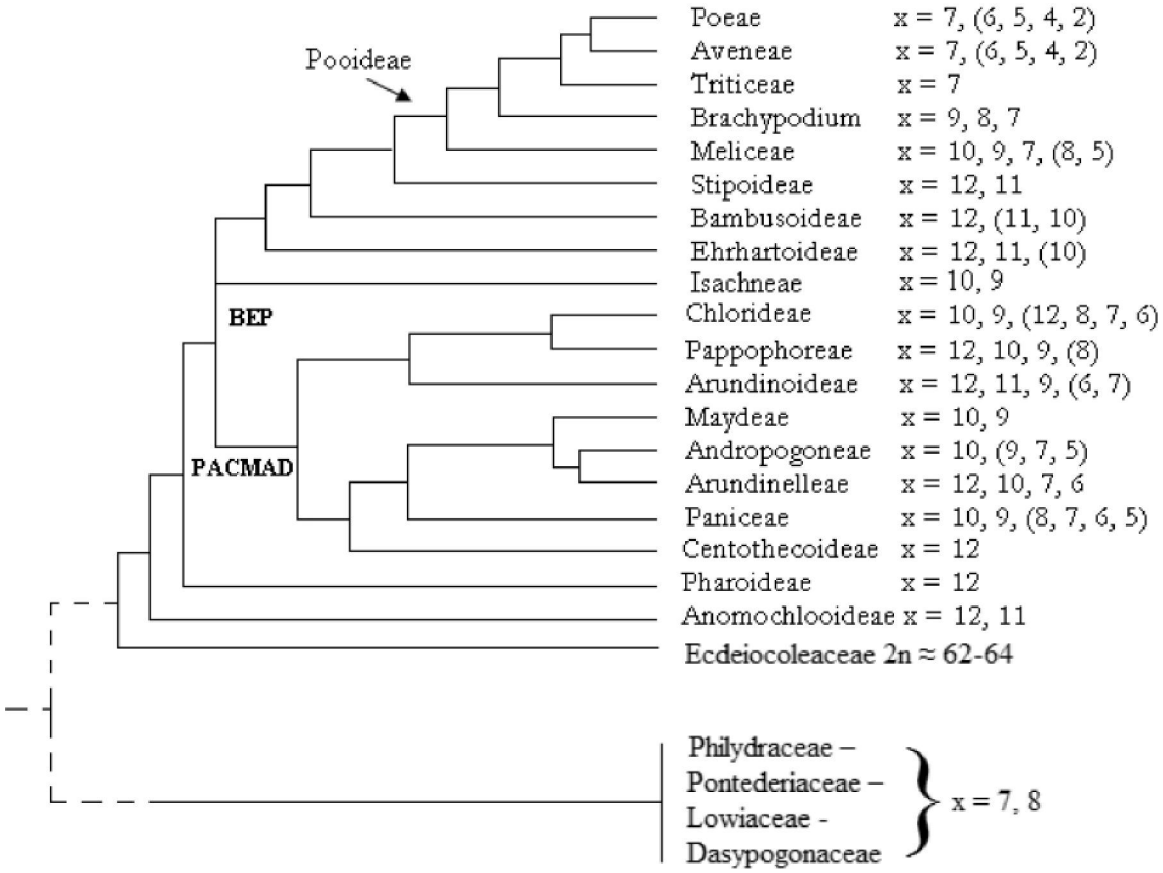

Figure 2 : Basic chromosome numbers (x) in phylogenetic tree of monocots including poaceae

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verging gradually but via the specific intermediate section, marked by cryptaffine and, supposedly by ephemeron taxa. These taxa are characterized by specific features. Among them we can convey molecular (the nucleotide composition of the certain genome sites), carpological (determined change in the basic number of chromosomes), morphological (the accumulation of apomorphies, cases of Pavlov-Berg anticipation), and statistic (different numerical representation of taxa on the different phyleme regions) features. This kind of structuring was revealed on the level of the highest rang taxa, we use the term "long structured phylogenetic branch". Figure 1 demonstrates the fragment of long structured phylogenetic branch, containing two consecutive PLATO regions and the connecting VIA region[1].

As we have said, our evolutionary reconstructions apparently are corresponding to the theory of punctuated-equilibrium[3]-[5] and every cryptaffine transition is similar to the element of quantum evolution[65]. However, both Simpson and supporters of punctuated-equilibrium theory believed that saltations can be explained by random changes and gradual selection. Our model of structured branch and cryptaffine transitions is based on the notion that the similar complex transformations occur multiple times in different parts of phylogenetic tree. Therefore, it is more consistent with the nomogenesis[56], [57].

CONCLUSION

Consideration of taxonomical system as a neontological chronicle of the evolution is an important background for evolutionary findings based on taxonomical studies. The existence of hidden-related (cryptaffine) taxa is revealed by comparison of molecular and morphological data within the macro system of angiosperms. Phylogenetically their morphological characteristics bring cryptaffine taxa closer to a group of ancestors and molecular – to descendants. Cryptaffine taxa possess a number of specific features: high basic and diploid chromosome numbers, high G+C, CpG and CpNpG content in 5,8S rDNA and phenomenon of phylogenetic anticipation. Probably cryptaffine taxa represent first steps of the evolutionary saltation. Long phylogenetic branches of angiosperms are naturally structured and consist of sections corresponding to slow (taxa PLATO) and fast (taxa VIA) evolution. Basically, macroevolutionary process in Angiosperms is nomogenetic. Preliminary molecular comparison of nucleotide content in rDNA of several animal species and *Homo sapiens* indicate a certain similarity of evolutionary processes in plants and animals[42].

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