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Non-equivalency of genera in *Angiospermae:* evidence from DNA hybridization studies

A. S. Antonov, K. M. Valiejo-Roman, M. G. Pimenov, and N. A. Beridze

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Abstract: The problem of taxa equivalency in phylogenetically distant groups can hardly be solved by comparing morphological differences alone. An attempt is made to approach the problem by means of DNA comparisons, e.g., DNA hybridization. Data obtained for *Compositae, Umbelliferae* and *Iridaceae* indicate that both unique and repetitive DNA sequence comparisons lead to the conclusions that genera within these families are not equivalent, e.g., the differences in the DNA among the species of *Iris* are much more pronounced than among those of *Achillea*; some genera of *Umbelliferae* occupy an intermediate position.

The problem of taxa equivalency (i.e., of the volume of taxa of one rank* in different phyla of the organic world) is among the most complex ones in modern systematics. This question has not received due consideration in taxonomic and phylogenetic studies, possibly, because its solution on the basis of morphological criteria becomes increasingly problematic with the transition to higher rank taxa. It is generally accepted that there exist no objective criteria for the rank of suprageneric taxa, including the genus (which holds a special place only because the proper name of a species depends on its generic position). Taxonomic ranks reflect only relative similarity (and thus affinity). In practical terms, newly established taxa are given a definite rank in conformity with the empirical standards applied in the systematics of their proper group, a practice going back to the early days of scientific systematics. With the specialization progress in systematics, the criteria of taxonomic rank in different groups of plants and animals have become quite different.

It is common knowledge that the conventional genera, tribes, subfamilies and even families of *Angiospermae* are non-equivalent, some are clearly distinct, others are connected by transitions, some have much "cohesion" (or "compactness"), others less. However, since different characters are predominantly used in the systematics of different taxa (e.g., fruit structures in the *Umbelliferae,* flower structures in the *Leguminosae* and *Labiatae*, synflorescence characters in the *Compositae*,

* Of the same category within the hierarchy of taxonomic categories.

etc.), it is difficult to prove the equivalency or non-equivalency of genera and other taxa (e.g., see the discussions for *Compositae:* TURNER 1985, CRONQUIST 1985). However, it is essential for phytogeographic, phylogenetic and evolutionary comparisons that the taxa of the same rank should at least be approximately equivalent, a necessity also acknowledged by SOKAL & SNEATH (1973) for phenetic criteria. According to these authors, taxa of the same rank should be characterized by an equal level of phenetic variability among their species; the phenetic distances between taxa of the same rank should be comparable. For the reasons outlined above such standards are applicable to limited groups of organisms only. It is impossible to make such phenetic comparisons for phylogenetically distant groups.

Molecular biology makes it possible to attack the problem of taxa equivalency by studying similarities and differences in the nucleic acid and protein structures, comparable even among phylogenetically distant organisms. This approach opens up entirely new prospects, because it is applicable to large phyla, not only to *Angiospermae* but to all land plants. Although the molecular methods used are not new, they are important for plant systematics and evolution and should be tested in respect to their advantages and limitations, particularly as their use has been challenged.

Methods

Molecular biology has advanced a number of approaches to the taxa equivalency problem. The most wide-spread among these is based on the DNA hybridization methods applied to repeated (rs) and single copy (sc) sequences. These methods allow to determine experimentally the degree of homology in DNA primary structures as a yardstick of taxa evolutionary divergence. On the other hand, the degree of divergence, alongside with discreteness, may be applied for obtaining an objective evaluation of a taxon rank (ANTONOV 1974).

In higher plant studies, DNA hybridization methods may be used within relatively narrow limits: with their aid, one may confidently determine DNA homologies in species only within a single family. Hence the taxa equivalency problem on the basis of DNA hybridization data can be considered mainly at the generic level.

The application of the DNA hybridization method in systematics was the target of moderate criticism (see, e.g., TAKHTAJAN 1974) because at an earlier stage, one used it for studying only a part of plant genetic material (rs) and not the entire set of DNA sequences. Subsequently attempts were made to premise this criticism on the peculiarities of DNA reassociation in higher eucaryotes, on the high lability and the complex organization of their genomes (CRAWFORD & GIANASSI 1982, DOVER 1980, EHRENDORFER 1983). Even though DNA hybridization investigations are aimed at resolving a variety of taxonomic and phylogenetic problems (and by no means the rank problem alone), it appears necessary to consider these critical remarks. Thus, it was recommended that one should work with sc DNA exclusively (MURRAY & al. 1981), but this recommendation is in contradiction with the results obtained at the same laboratory (MURRAY & al. 1981) from which it follows that a major part of sc (the so-called "fossil" rs) originated as a result of rapid rs evolution. Consequently, there is no qualitative difference between rs and sc, and for this reason both may be used a priori in DNA hybridization experiments with an equal measure of success. For that matter the results of the early experiments which, for technical reasons, were carried out only with rs DNA, are quite reliable. Thus, according to these first experiments, the share of homologous DNA sequences varied in representatives of different genera – sometimes to such an extent that it was suggested that some genera should be regarded as a conglomerate of genus rank taxa (SLUSARENKO & al. 1973). It was in this work that

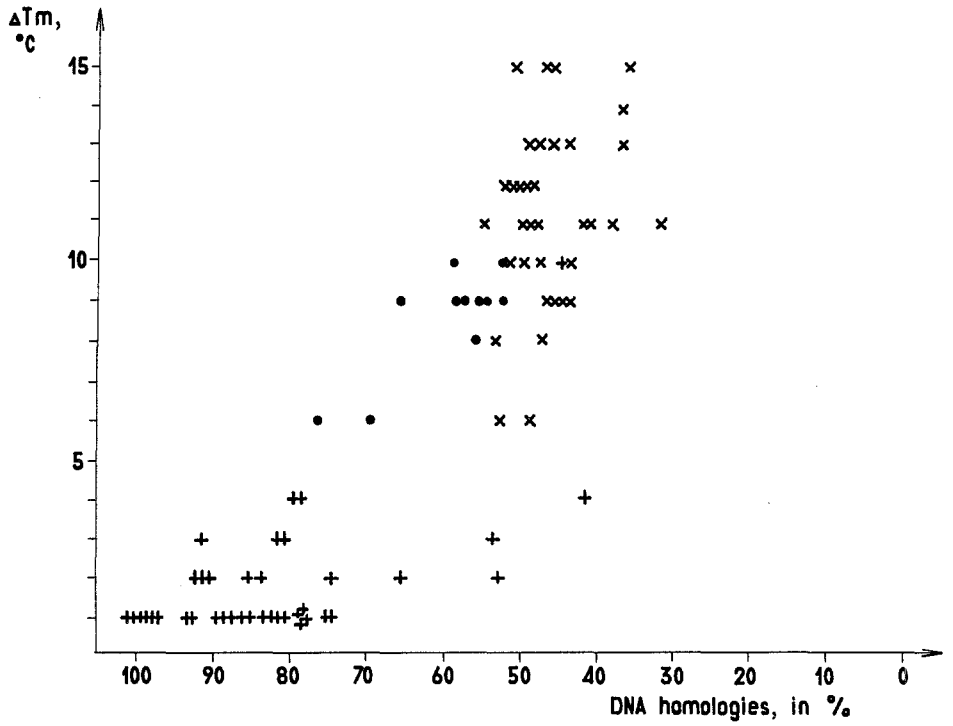

Fig. 1. Interrelationships between the rate of rs DNA homology losses and the accumulation of nucleotide substitutions. × *Umbelliferae*, + *Compositae*, ● *Iridaceae*

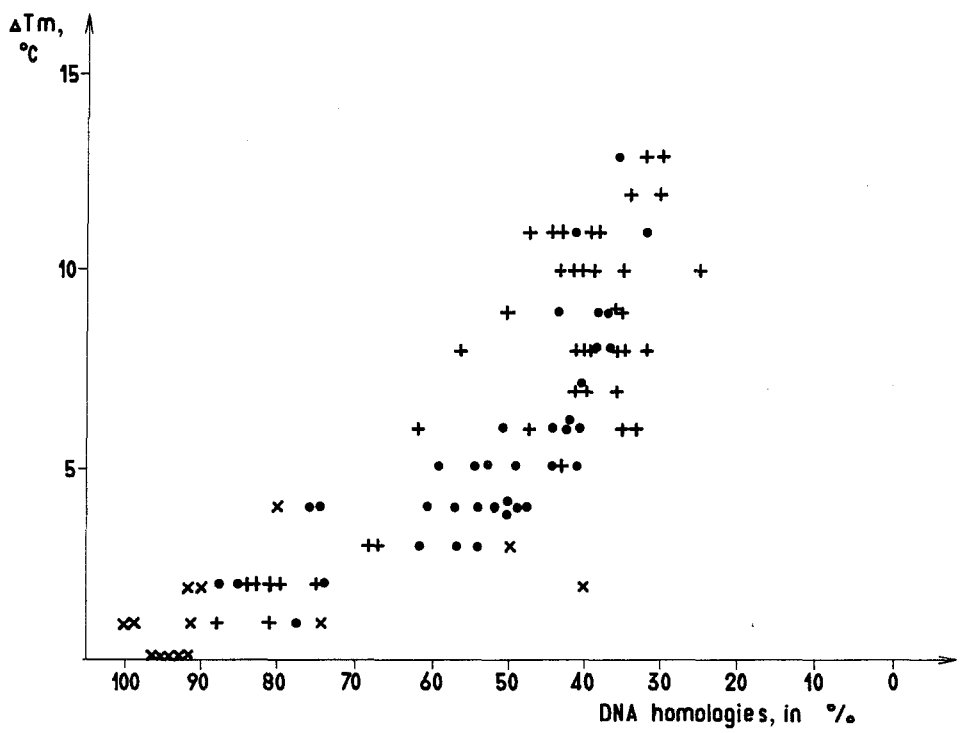

Fig. 2. Interrelationships between the rate of sc DNA homology losses and the accumulation of nucleotide substitutions. + *Umbelliferae*, × *Compositae*, ● *Iridaceae*

a suggestion was first advanced to the effect that such data may be used for resolving the taxa equivalency problem in *Angiospermae*. Our new evidence (KASHEVAROV & ANTONOV 1982; VALIEJO-ROMAN & al. 1979, 1982) confirms the assumption that analysis of both rs and sc leads practically to identical conclusions.

For the reasons mentioned above the following methods were used in this study:

DNA extraction and labelling has been described earlier (VALIEJO-ROMAN & al. 1982).

DNA reassociation was carried out at a labelled : unlabelled DNA ratio = 1 : 2 500. Various concentrations of phosphate buffer (PB) were used and all the values corrected to the Cot value equivalent to criterion conditions (BRITTEN & al. 1974). Thermostability of hybrid duplexes was determined by melting the reassociated DNA at 5 °C intervals (40–80 °C) in 0.2 M PB with 8 M urea.

Rs and sc DNA separation was made as described earlier (VALIEJO-ROMAN & al. 1979, 1982, KASHEVAROV & ANTONOV 1982).

Phenogram construction was made by UPGMA method (SNEATH & SOKAL 1973) with minor modifications due to non-linearity of DNA changes (see Figs. 1, 2). DNA characteristics analysed were the homology percent and the thermostability of hybrid duplexes standardized in such a way that they varied from 0 (complete identity) to 1 (maximum dissimilarity).

Results

Certain regularities of DNA evolution in *Angiospermae*. We have used two parameters – the share of homologies and thermostability of hybrid duplexes – as criteria of DNA divergence.

Let us look into the correlation of these parameters (percentage of homologies and ΔT_m values) which characterize the results of rs and sc DNA heterologic hybridization. As it follows from Figs. 1 and 2, a distinct interrelationship exists between the rates of DNA homology losses and the accumulation of "nucleotide substitutions" (or rather small changes in the primary structure) – something we should have expected. At the same time, as it follows from the plots, divergent evolution of rs DNA sequences at the initial stage is accompanied by a more rapid loss of homologous sequences and by a relatively low rate of nucleotide substitutions accumulation in the homologous sequences of the compared species genomes. This must be the stage at which the results of active amplification-deletion changes appear to be most pronounced (FLAVELL 1980); these changes, as it seems to us, affect but a part of this plant genome fraction (judging by Fig. 1, about 50 – 60%). The other part of the genome is less subject to quantitative changes and evolves chiefly by accumulation of nucleotide substitutions; this follows from the fact that at small changes in the level of DNA homologies (20–40%), we discover a relatively fast accumulation of nucleotide substitutions in these sequences.

Possibly it is this DNA fraction that contains sequences the very existence of which in the genome is under strict selection control. Although by modern data the share of expressed DNA sequences in plant genomes is low (a few per cent or even less, GOLDBERG & al. 1978), proceeding from our present knowledge about the complex structure of eucaryote genes and about the significant role of some long but non-coding sequences in their expression, we may assume that they constitute the groundwork of the slowly evolving fraction of DNA in *Angiospermae*.

A comparison of Figs. 1 and 2 shows that rs accumulate substitutions faster than sc, but on the whole their divergence takes a similar course as in sc. One

possible reason is that sc may comprise sequences which have a definite role to play in genome functioning (for review, see ANTONOV 1986).

The most surprising part of our results is that the quantitative interrelationships between thermostability changes and homology losses revealed in heterologic reactions of hybridization have a similar pattern in such distant *Angiospermae* families as *Apiaceae, Iridaceae* and *Asteraceae* (the results of their DNA hybridization are plotted on the same curve). We may presume therefore that the established regularities of rs and sc evolution are proper to all *Angiospermae*. If this is so, these observations create a solid basis for investigations into the problem of *Angiospermae* taxa equivalency.

Therefore the previous results of homology studies in rs of *Angiospermae* (BENDICH & BOLTON 1967, MARINOVA & al. 1969, SLUSARENKO & al. 1973, SCHNEJER & ANTONOV 1975, YANEVA & ANTONOV 1977) may well be used for correlation with data obtained by more up-to-date methods. Needless to say, one should take into account the peculiarities of the DNA hybridization methods used and compare the results with respect to the identical conditions of hybridization.

Taxa equivalency. The aim of our experiments was to elucidate inter-species and intergeneric relationships in three taxa of *Angiospermae* – fam. *Umbelliferae* (*Apiaceae*): genus *Seseli,* fam. *Compositae* (*Asteraceae*): genus *Achillea* (including *Ptarmica*) and fam. *Iridaceae:* genus *Iris*. Naturally we were clearly aware of the fact that the prevailing notions on genus volumes in these taxa are different (for instance, the traditional interpretation of *Iris* is wider than that of *Achillea*); however, this belongs to the realm of intuition and does not involve any quantitative assessment (TURNER 1985). For this reason competitive hypotheses on generic volumes coexist in the systematics of as good as any major taxon, as manifested in frequent revisions of taxa volumes and/or ranks. For instance, this is characteristic both of *Umbel-*

Table 1. Homologies in rs and sc DNA of some *Seseli* species (*Apiaceae*). [1, 2] Two different diploid populations. [3, 4] Diploid and hexaploid populations. *a* Nucleotide substitutions in %. *b* Homologies in DNA fractions in %

Plant species	Labelled DNA of					
	Seseli mucronatum		*Seseli condensatum*			
	SC		RS		SC	
	a	*b*	*a*	*b*	*a*	*b*
Seseli condensatum (L.) REICHNB.[1]	3.5	76.0	0.0	100.0	0.0	100.0
Seseli condensatum[2]	2.5	87.0	1.0	73.0	0.5	88.0
Seseli mucronatum (SCHRENK) M. PIMEN. & SDOBN.[3]	0.0	100.0	2.0	70.0	3.0	70.0
Seseli mucronatum[4]	0.0	91.0	3.5	64.0	8.5	78.0
Seseli nemorosum (KOROV.) M. PIMEN.	4.0	88.0			3.5	78.0
Heracleum lehmannianum BUNGE	6.0	47.0			9.5	46.0
Paraligusticum discolor (LEBEB.) V. TICHOMIROV	7.0	54.0			10.5	39.0
Peucedanum latifolium BIEB.	7.0	57.0			12.5	30.0

Table 2. Homologies in rs and sc DNA of some *Compositae* spp. *a* Nucleotide substitution in %. *b* Homologies in DNA fractions in 1

Plant species	Labelled DNA of											
	Achillea setacea						*Achillea taurica*					
	Cot 0–1		Cot 1–100		Cot 100–10 000		Cot 0–1		Cot 1–100		Cot 100–10 000	
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
Achillea setacea Waldst. & Kit.	0.0	100	0.0	100	0.0	100	2.0	74	2.0	83	2.0	81
A. millefolium L.	0.5	98	0.5	99	0.5	93						
A. inundata Kondr.	1.0	100	1.0	100	1.0	100						
A. pannonica Scheele	1.0	100	1.0	100	1.0	100						
A. nobilis L.	1.0	97	1.0	93	1.0	91	1.5	86	1.4	85	2.0	84
A. euxina Klok.	1.0	98	1.0	83	1.5	74						100
A. taurica Bieb.	1.5	91	1.5	87	2.0	80	0.0	100	0.0	100	0.0	87
A. micrantha Willd.	1.5	89	1.0	80	2.0	81	1.0	78	1.0	81	2.0	91
A. micranthoides Klok.	1.5	98	1.0	88	2.0	83	1.0	78	2.0	91	2.0	91
A. birjuczensis Klok.	1.0	93	1.0	82	1.0	77	1.5	75	2.0	91	2.0	80
A. ochroleuca Ehrh.	3.0	91	2.0	85	3.0	67	4.0	77	3.0	81	4.0	
Ptarmica borysthenica (Klok.) & Sakalo	4.0	78	2.5	65	3.0	50	4.0	71	—	61		
Tanacetum odessanum (Klok.) Tzvel.	2.5	53	2.0	52	2.0	40						
Anthemis spec.	2.9											

Table 3. Homologies in rs and sc DNA of some *Iridaceae* spp. * Two different populations of one and the same species. *a* Nucleotide substitutions in %. *b* Homologies in DNA fractions in %

Plant species	Labelled DNA of									
	Iris pumila		*Iris carthaliniae*		*Iris imbricata*		*Iris pseudacorus*			
	Cot 100–10 000		Cot 100–10 000		Cot 100–10 000		Cot 100–10 000		Cot 0–100	
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
Iris ensata THUNB.	3.0	57.0								
I. pseudacorus L.	4.0	50.0	3.5	54.0	5.0	44.0	0.0	100.0	0.0	100.0
I. lactea PALL.	3.5	52.0					2.5	68.0	6.0	76.0
I. ruthenica KER-GAUL.	4.5	59.0								
I. carthaliniae FOMIN.	3.5	54.0	0.0	100.0	3.5	57.0	4.5	53.0	8.5	65.0
I. colchica KEM.-NATH.	4.0	49.0	1.5	75.0	3.5	54.0	5.5	51.8	9.8	57.0
I. hungarica WALDST. & KIT.							5.5	42.0	9.5	52.0
I. imbricata LINDL.*	2.0	81.0	4.5	54.0	0.0	100.0	4.5	49.8	9.5	58.0
I. alberti REGEL	3.5	76.0					5.0	43.0	8.0	55.0
I. pumila L.	0.0	100.0	4.0	50.0	1.0	74.8	4.0	48.0	9.5	58.0
I. imbricata LINDL.*	1.5	85.0					5.5	41.0	9.0	54.8
I. iberica HOFFM.	3.5	75.0	5.5	42.0	2.5	62.0	5.0	41.0	8.5	54.0
Siphonostylis lazica (ALBOV) W. SCHULZE	6.0	44.0	4.8	49.0	6.5	41.0	3.5	61.0	6.0	69.0
Juno caucasica (HOFFM.) KLATT			8.0	36.0	8.5	37.0				
Xiphium vulgare MILL.	8.5	43.0	12.5	35.0	11.0	32.0	9.0	35.0	10.0	44.0
Iridodictyum reticulatum (BIEB.) RODION.	12.8	41.0								

Table 4. Homologies in rs and sc DNA of some *Apiaceae* spp. *a* Nucleotide substitutions in %. *b* Homologies in DNA fractions in %

Plant species	Labelled DNA of									
	Anthriscus glacialis				*Prangos pabularia*				*Seseli nemorosum*	
	Cot 1, 0		Cot 100–10 000		Cot 1, 0		Cot 100–10 000		Cot 140–10 000	
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
Anthriscus glacialis Lipsky	0.0	100.0	0.0	100.0	10.7	30.6	6.5	33.8	6.5	35.5
Anthriscus ruprechtii Boiss.	4.0	79.0	–	–	13.5	36.0	–	–	–	–
Elaeosticta hirtula (Regel & Schmalh.) Kljukov, M. Pimen. & V. Tichomirov	8.0	53.0	–	–	10.7	46.5	–	–	–	–
Siella erecta (Huds.) M. Pimen.	9.0	55.0	–	–	13.0	47.5	–	–	–	–
Seseli libanotis (L.) Koch.	10.5	49.0	–	–	13.5	43.0	–	–	1.0	81.0
Seseli nemorosum (Korov.) M. Pimen.	12.5	48.0	–	–	13.5	46.0	7.5	40.5	0.0	100.0
Seseli condensatum (L.) Reichnb.	–	–	–	–	–	–	–	–	1.5	88.0
Seseli condensatum (L.) Reichnb.	–	–	–	–	–	–	–	–	2.5	87.0
Seseli mucronatum (Schrenk) M. Pimen. & Sdobn.	–	–	–	–	–	–	5.8	43.0	3.0	82.5
Pimpinella anthriscoides Boiss.	11.5	51.0	10.1	43.0	11.0	40.5	11.0	40.5	7.0	40.5
Ferula kokanica Regel & Schmalh.	8.9	46.0	9.7	40.7	11.5	41.8	12.8	32.3	11.8	29.9
Peucedanum latifolium Bieb.	9.1	42.6	–	–	12.3	49.5	7.9	31.6	12.5	30.2
Angelica komorovii (Schisch.) V. Tichomirov	12.2	48.0	8.0	35.2	13.4	46.7	11.6	33.5	10.8	47.1
Prangos pabularia Lindl.	8.7	43.9	9.9	40.6	0.0	100.0	0.0	100.0	8.4	39.6
Smyrniopsis aucheri Boiss.	10.3	43.4	10.1	35.0	6.4	52.2	6.4	42.2	6.4	50.3
Lecokia cretica DC.	11.3	48.8	10.2	38.6	5.7	48.3	6.4	35.0	8.4	35.9
Laserpitium latifolium L.	8.8	57.5	–	–	10.7	57.2	–	–	7.5	38.8
Bupleurum aureum Fisch.	9.6	47.1	–	–	14.9	34.6	8.1	35.0	6.0	47.1
Conioselinum latifolium Rupr.	11.3	47.6	11.2	43.2	14.8	49.8	11.5	38.4	7.7	56.2
Paraligusticum discolor (Ledeb.) V. Tichomirov	11.2	53.6	–	–	11.9	51.0	10.8	43.9	8.9	36.4
Heracleum lehmannianum Bunge	12.6	44.5	–	–	13.0	35.8	9.6	25.1	6.9	39.7
Eryngium giganteum Bieb.	17.3	19.0	–	–	17.2	18.4	–	–	–	–

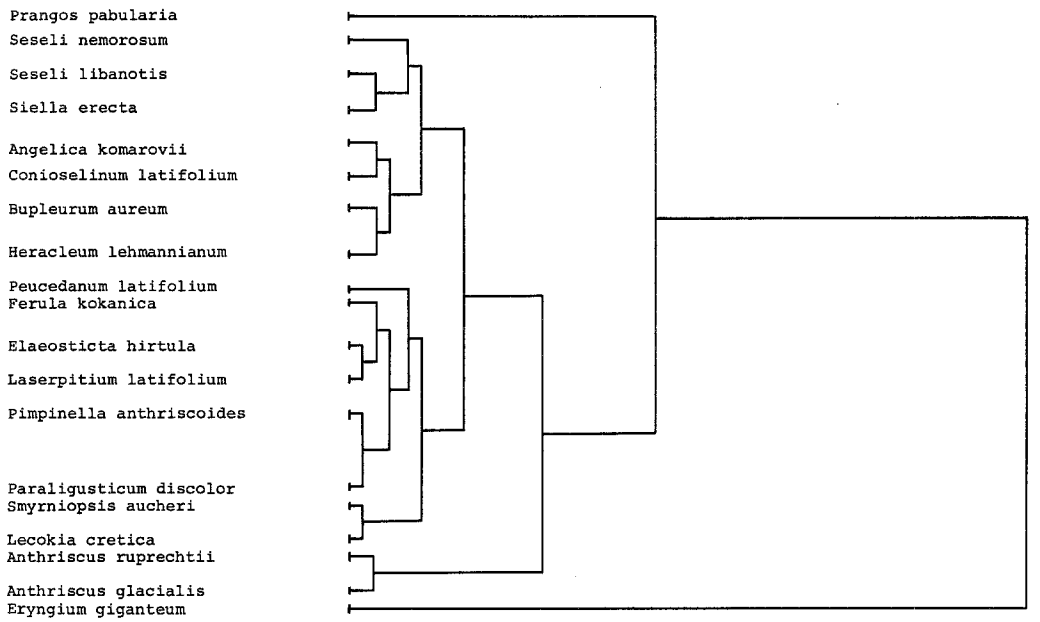

Fig. 3. Phenogram of interrelationships between *Umbelliferae* taxa based on DNA : DNA hybridization data

liferae and of the tribe *Anthemideae* of the family *Compositae* (*Asteraceae*) to which *Achillea* belongs; in the family *Iridaceae*, along with the broad concept of *Iris* (RODIONENKO 1961), there has been a clear trend to isolate smaller but natural genera from this genus (DYKES 1913).

The difficulties of the problem of rank are reflected in the ongoing struggle between the "splitters" and the "lumpers". Overall, the taxonomic rank inflation trend prevails (DAVIS 1978). Thus, whereas 90 genera of *Compositae* (*Asteraceae*) were described in 1753, their present number amounts to 1 200. This mammoth growth has occurred not only owing to the discovery of hitherto unknown groups (CRONQUIST 1985).

So, how should we assess the DNA hybridization results for the plants we have studied (Tables 1–4) and the phenograms drawn with the aid of cluster analysis (Figs. 3 and 4).

Analysis of the DNA of *Achillea* spp. reveals their very high homology, i.e., attests to the close relatedness of species even belonging to different sections (*Millefolium* and *Filipendulinae*). In some cases not only the species rank but the level of ploidy as well affects the differentiation of DNA primary structures, which is consistent with cytogenetic findings (EHRENDORFER 1953).

As far as intra-generic comparisons are concerned, despite the limited amount of material (a single species for *Ptarmica, Anthemis* and *Tanacetum,* respectively), we may point to the *Achillea* relatedness to these genera being at approximately the same level as in the general *Triticum* and *Aegilops* (YANEVA & ANTONOV 1977) but at much higher level than in the genera of *Iridaceae* (SCHNEJER & ANTONOV 1975). The results of intrageneric comparisons of DNA in *Anthemideae* do not quite coincide with the prevalent interpretation of their interrelationships by sys-

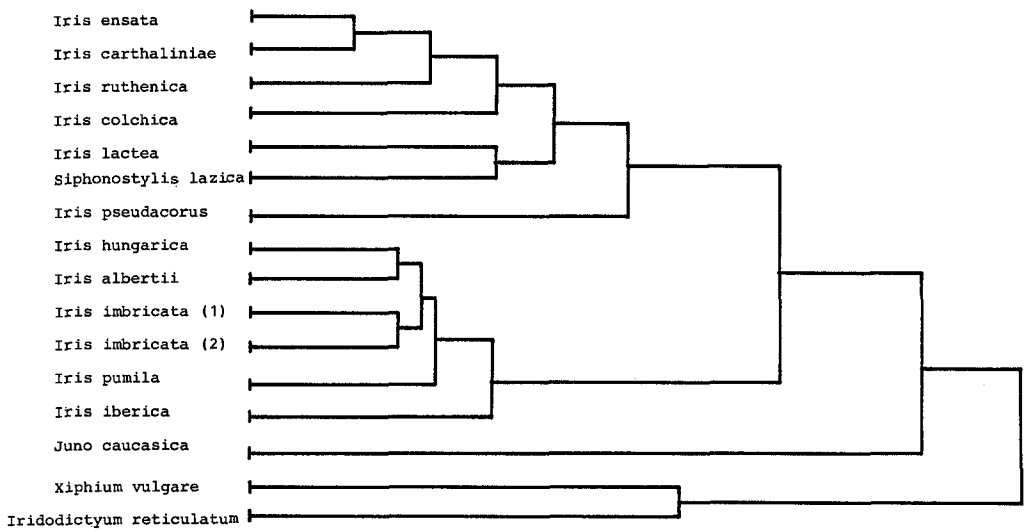

Fig. 4. Phenogram of interrelationships between *Iridaceae* taxa based on DNA : DNA hybridization data

tematicians. The distinctions of *Ptarmica* and *Tanacetum* from *Achillea* in the percentage of nucleotide substitutions are not higher than those of *A. ochroleuca* from the other species of the latter genus; besides, % of substitutions revealed in hybridization studies with *Achillea* species is smaller for *Tanacetum* than it is for *Ptarmica*. Yet *Ptarmica* is viewed as a genus closest to *Achillea* or even as a section of the latter (BOCHANTSEV 1961), while *Tanacetum* – as a genus close to *Pyrethrum*. In this case the results of homology percentage are in better correlation with the existing systems of *Anthemideae* and , if we are to judge by them only, confirm the genus rank of *Ptarmica,* not to speak of *Tanacetum*.

Let us now collate these results with the evidence of DNA hybridization in *Iridaceae* species. As it follows from Table 3, the genus *Iris* is a taxon which has diverged much more than the genus *Achillea* has, for the differences in rs and sc DNA sequences are far more distinct in it. This is especially apparent from a dendrogram constructed on the data of hybridization of sc DNA from *Iridaceae* (Fig. 4).

Even within each of the two groups of *Iris* species DNA sequences exhibit greater differences than in the *Achillea* genus. Also, the genus *Siphonostylis* differs significantly less from some of the irises than the latter do among one another and thus does not deserve the genus status. The genera *Xiphium* and *Iridodictyum* are considerably isolated from the other investigated taxa, but reveal smaller differences between each other than the two groups of irises do, i.e., there is no ground for singling out two taxa of the generic rank. On the whole these conclusions agree well with the results of the earlier work performed in our laboratory (SCHNEJER & ANTONOV 1975).

With respect of *Umbelliferae,* the rank problem had a different scale, though generic rank equivalency was also dealt with (the genus *Seseli*). The latter proved to take an intermediate position between *Iris* and *Achillea* in DNA variability (VALIEJO-ROMAN & al. 1979).

Classical approaches applied to the problem of suprageneric taxa, especially of the tribe rank, have not yielded satisfactory results in the systematics of *Umbelliferae*. At present there is not clear understanding of taxa interrelationships (genera, tribes) within the *Umbelliferae* family. The existing classifications (DRUDE 1898, KOZO-POLJANSKY 1916, CERCEAU-LARRIVAL 1962) built on a purely morphological basis furnish a contradictory interpretation of these relationships, while tribes singled out within these systems do not coincide either in volume or in content. Proceeding from the most popular system of DRUDE (1898), we selected our objects in such a way that different subfamilies and different tribes of the subfam. *Apioideae* were represented. The results of hybridization are shown in Table 2. We studied these data by cluster analysis and thus built a dendrogram of DNA relatedness for the investigated *Umbelliferae* species. The results obtained (Fig. 3) show that the investigated material falls into two distinct and unequal parts: one comprises all the genera of the *Apioideae*, and the other – the only representative of the *Saniculoideae, Eryngium giganteum*. The latter has only 18 – 19% rs DNA homologies with *Apioideae* spp. at $\Delta T_m = 17\,^{\circ}C$, whereas the lowest homology ratio in the same fraction within the subfam. *Apoideae* is not below 35%.

On the other hand, one does not observe a clear-cut division of *Apioideae* genera into tribes. The obtained groups do not coincide with (or at least approach) any of the existing *Umbelliferae* systems. The distances between the genera referred to a single tribe are often no smaller than between the genera of different tribes. Compared with the distances of *Eryngium giganteum* from another subfamily, the distances in the subfam. *Apioideae* show relatively small differences. In other words, the degree of genetic material relatedness proves practically identical when one compares representatives of genera from one and the same and different tribes in a single subfamily. If the rate of nucleotide substitutions in the evolution of a given phylum has been more or less constant, this means that the phylogenetic tree of this group of *Umbelliferae* genera is bush-like; the branches coming off from the common stem have about the same length.

This is not the first evidence for the saltatory nature of taxa formation obtained by molecular biology methods (ANTONOV 1974), which accords with the punctuated equilibrium evolutionary hypothesis (GOULD & ELDRIDGE 1977) devised mainly from paleontological data. Such a concurrence of conclusions drawn on the basis of different material appears highly promising for the further development of the evolutionary theory.

Thus, of the genera we have studied *Achillea* belongs to the most homogeneous and *Iris* – to the most heterogeneous ones: among *Iridaceae* species of one section may differ more than species of different genera of *Anthemideae* (*Compositae*): the fact which should interest systematicians. A similar conclusion was made by WILLIAMS & HARBORNE (1985): analysing data on *Iridaceae*, he points to a greater variety of phenolic compounds in this family than in the closely related families of *Liliaceae* and *Amaryllidaceae*. One cannot escape the impression that among the *Iridaceae* systematicians the "splitters" appear to take a more correct stand, while among the *Achillea* systematicians these are the taxa "lumpers". It will be observed here that the results of DNA homologies agree well with some biological properties of the investigated species: thus, *Achillea* spp. readily form hybrids in natural conditions, which is less typical of *Umbelliferae* and *Iridaceae* with their more pronounced inter-species reproductive isolation. Just as few sc DNA ho-

mologies have been found among species of the genus *Atriplex* which exhibit considerable phenotypic divergence (BELFORD & THOMPSON 1981 a, b) and which are well reproductively isolated.

In contrast to the wide-spread views on the continuous and uniform increase in taxa difference levels with a higher rank (according to the majority of classical and numeric systematicians), it was shown in works on DNA hybridization (VALIEJO-ROMAN & al. 1982) that homology of plant DNA changes in a discrete or graduated pattern. The distribution patterns of DNA homologies represented in this work are polymodal: peak I refers to the results of hybridization of species from the same genus, peak II – species from different genera, and peak III – from different subfamilies.

In the course of earlier investigations in our laboratory (MEDNIKOV & al. 1973), discrete levels of homology were discovered in animal DNA. It is noteworthy that the degree of relatedness among plant species which systematicians refer to different genera of a single subfamily proves to be roughly equal to that among animals from different families of the same order of *Vertebrata*. Yet no matter how tempting, the problem of taxa equivalency at such a rank is not the subject of our consideration.

Possibly, with a wider range of *Angiospermae* families studies and more comprehensive DNA hybridization results, discreteness in DNA homology may become marred: the evolutionary history of species taxa and genomes takes a wide variety of forms. Nevertheless, we find it advisable to use even the available assessment of DNA homology within taxa of different ranks for revising the systems. From the results of statistical processing of the information obtained via DNA hybridization it follows that species of one *Angiospermae* genus have, as a rule, no less than 60% DNA homologies (and no more than 6% nucleotide substitutions in homologous sequences). These values are 20% and 16% respectively for different genera of one family.

Thus, it becomes possible to arrive at a more objective solution of the rank criteria problem.

How is this problem tackled in contemporary numeric taxonomy which seeks to overcome the limitations of the intuitive approach? By means of drawing what is called "phenon lines", i.e., by referring each of the taxonomically known hierarchic ranks to a definite level of phenetic relatedness. Phenon lines are drawn arbitrarily, but in such a way that taxonomic changes are minimal, i.e., with due account of the previous experience of systematics. Our data make it possible to correlate each of the DNA homology distribution maxima with a definite taxon; the presence of hiatuses (or minima) creates a more reliable basis for this.

We are fully aware that an attempt to unequivocally determine the taxon rank according to the degree of DNA structure divergence would be a clear manifestation of reductionism predicated on the "molecular clock" concept, a theory which has not been proved and which is becoming the target of mounting criticism (ANTONOV 1986, WILSON & al. 1977). Yet we learn by comparison. The advantage of our approach over others (for instance, determination of ranks on a purely morphological basis) is based on lower possibility of convergence and parallelism at the molecular level, especially in detecting genotype similarities and distinctions by the method of DNA molecular hybridization or by analyzing DNA expression products: mRNA or a set of synthesized proteins.

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Address of the authors: A. S. ANTONOV, K. M. VALIEJO-ROMAN, M. G. PIMENOV, and N. A. BERIDZE, A. N. Belozersky Laboratory of Molecular Biology and Bioorganic Chemistry, Moscow State University, Moscow 119899, U.S.S.R.