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FLAVONOIDS AS TAXONOMIC MARKERS IN FLOWERING PLANTS

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A review of the flavonoids as taxonomic markers in flowering plants is given. Flavonoids are the most important group of plant pigments and secondary compounds generally, from chemotaxonomical point of view. Chemistry and structural variation of anthocyanins, yellow flavonoids and colourless flavonoids and their significance as taxonomic markers is reported. It has been shown that flavonoids, especially colourless fraction can be used as taxonomic parameters at various taxonomic levels (species, genus, tribe, family). The present evidence indicates that colourless flavonoids are most useful at the generic level. They will undoubtedly continue to be extensively studied by plant systematists. In addition, according to the composition of these compounds it is possible, in some cases, to document hybrids between certain crossbred species. Flavonoids can also be of interest in comparison at high taxonomic levels, showing phylogenetic implications. There is a general evolutionary trend towards complex structures and the diversity of highly substituted flavonoids are present in advanced and specialised families of flowering plants.

Key words: flavonoids, diversity, flowering plants, taxonomic significance, phylogenetic implications.

Ključne reči: flavonoidi, raznovrsnost, cvetnice, taksonomski značaj, filogenetske implikacije.

INTRODUCTION

The pigmentation of flowers and other tissues has limited application in comparative morphology and classical systematics in general. However, scientists from many different disciplines, particularly plant biochemists, have for many years been attracted by the investigation of plant pigments.

In higher plants a number of various pigments has been identified. Plant pigments are conventionally divided into four groups: flavonoids, carotenoids, quinonoids and betalains. Flavonoids are further divided into anthocyanins, yellow flavonoids and colourless flavonoids. In the last three decades all of these groups have been broadly investigated from different aspects. One of the very interesting aspect is the one dealing with systematic problems. Chemotaxonomy or Biochemical systematics has become one of the most important discipline within Plant systematics. Plant pigment investigation, especially flavonoids, are of great importance.

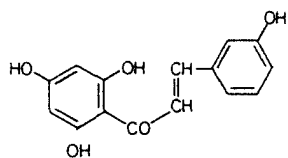
The purpose of this text is to review published data, including our results, dealing with flavonoids as taxonomic markers. The aim is, also, to review state and potential of this approach to plant systematics and phylogeny especially of flowering plants.

CHEMISTRY AND STRUCTURAL VARIATION

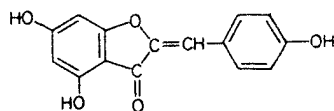
Anthocyanins

Anthocyanins are the most important group of chemical compounds responsible for the colour of certain plant tissues and organs. This group of pigments is water soluble and various shades of blue, violet and red, found on flowers, fruits and leaves originate from it. Anthocyanins, as their name suggests, are based on cyanidin. Cyanidin is an aromatic compound out of which all other derivatives are obtained by adding different functional groups (Fig. 1). Anthocyanin aglycones are formed after an acid hydrolysis - thus forming anthocyanidins. There are six common or basic anthocyanidins: cyanidin, which is certainly the most frequent, then pelargonidin, delphinidin, paeonidin, petunidin and malvidin. Sugar molecules are very often connected with the mentioned anthocyanidins (1, 2 or 3). The most frequent sugars which are connected are glucose, galactose, rambnose and others.

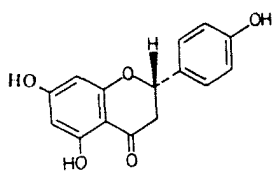
Anthocyanins are very widespread among plants. They can be found in most primitive higher plants - mosses and ferns but are particularly represented with gymnospermae and flowering plants. Only in a few families from the subclass Caryophyllidae anthocyanins are replaced by betacyanins. The taxonomic significance of these two pigment groups will be considered later. There are many books dealing with the distribution and variety of anthocyanins in plants but it is particularly summarized in a few outstanding works (Harborne, 1963, 1967a; Timberlake & Bridle, 1975; Hrazdina, 1982).



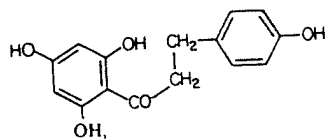
Chalcone



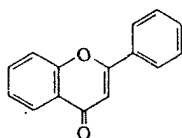
Aurone



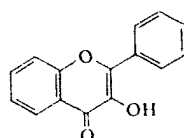
Flavanone



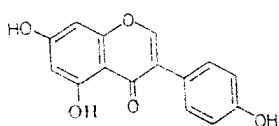
Dihydrochalcone



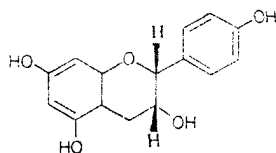
Flavone



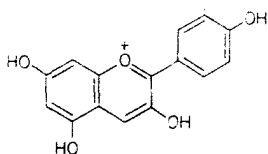
Flavonol



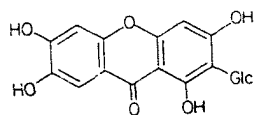
Isoflavone



Dihydroflavonol



Anthocyanidin



Xanthone: Mangiferin

Fig. 1. - Structures of flavonoid groups

Yellow flavonoids

This fraction of flavonoids is responsible for the yellow colour in a series of plant species. It is a complex group of pigments which is further divided into following groups: yellow flavonols, yellow flavones, chalcones and aurones. The last two groups are usually known as anthochlors. Yellow flavonols are based on two fundamental components - gossypetin (8-hydroxyquercetin) and quercetagetin (6-hydroxyquercetin). Up till now the presence of gossypetin and its derivatives has been found in more than 12 flowering plant families and they have even been detected in horsetails (*Equisetum*). Quercetagetin has a somewhat smaller distribution (in about 8 families). Both types of yellow flavonols are present with two big and important dicotyle families - Asteraceae and Fabaceae. Otherwise they are seldom found together within a family (H a r b o r n e, 1975).

The best known yellow flavones which respond to the above mentioned flavonols are hypolaetin (8-hydroxyluteolin) and 6-hydroxyluteolin. However, they are more often found in leaves than in a flower.

Colourless flavonoids

The majority of plant flavonoids are not directly coloured, though they often influence flower or fruit colour. The most frequent colourless flavonoids are flavonols and flavones. With some authors, they are marked together as anthoxanthines (i.e. yellow flower pigments) though the term is rather seldom used nowadays. Flavonols and flavones are important anthocyanin copigments, necessary in many flowers for the full anthocyanin colour expression in mild acid pH cell sap of a corolla tissue. If there is a surplus of them, they can also change the purple and red anthocyanin into blue region.

As far as distribution of flavanones, dihydroflavonols, biflavonyls, dihydrochalcones, isoflavones and proanthocyanidins in nature is concerned, they are hardly of any importance.

Flavonols are widespread among plants both in flowers and in leaves. The basic structure of the flavonol is given in (Fig. 1). More than 150 flavonols are known but only three are frequent: kaempferol (which corresponds to anthocyanidin pelargonidin), quercetin (corresponds to cyanidin) and myricetin (corresponds to delphinidin). Other known flavonols mainly have a simple structural variations of these flavonols (Fig. 2). More than 500 flavonol glycosides have been detected so far, a hundred of which refer to glycosides quercetin. The most frequent quercetin 3-O rutinoside, better known as rutin.

Unlike flavonols, flavones do not have a hydroxyl group in 3-position (Fig. 1). Flavones often replace flavonols in the herbaceous plant leaves. There are only two frequent flavones: luteolin and apigenin. According to structure they correspond to flavonols quercetin and kaempferol. Flavone tricetin, which corresponds to flavonol myricetin, is very rare in nature. Very often there are two methyl ethers in nature: luteolin 3-methyl ether (chrysoeriol) and tricetin (3, 5 dimethyl ether tricine).

Flavones very often appear in nature united with sugars in the form of O-glycosides. The frequent type is 7-O-glycoside, as for exemple luteolin 7-O-glycoside. Unlike flavonols, flavones often appear united with sugars in the form of C-glycosides. The so-called series of those glycosylflavones is known. One example is luteolin 8-C-glycoside (orientin).

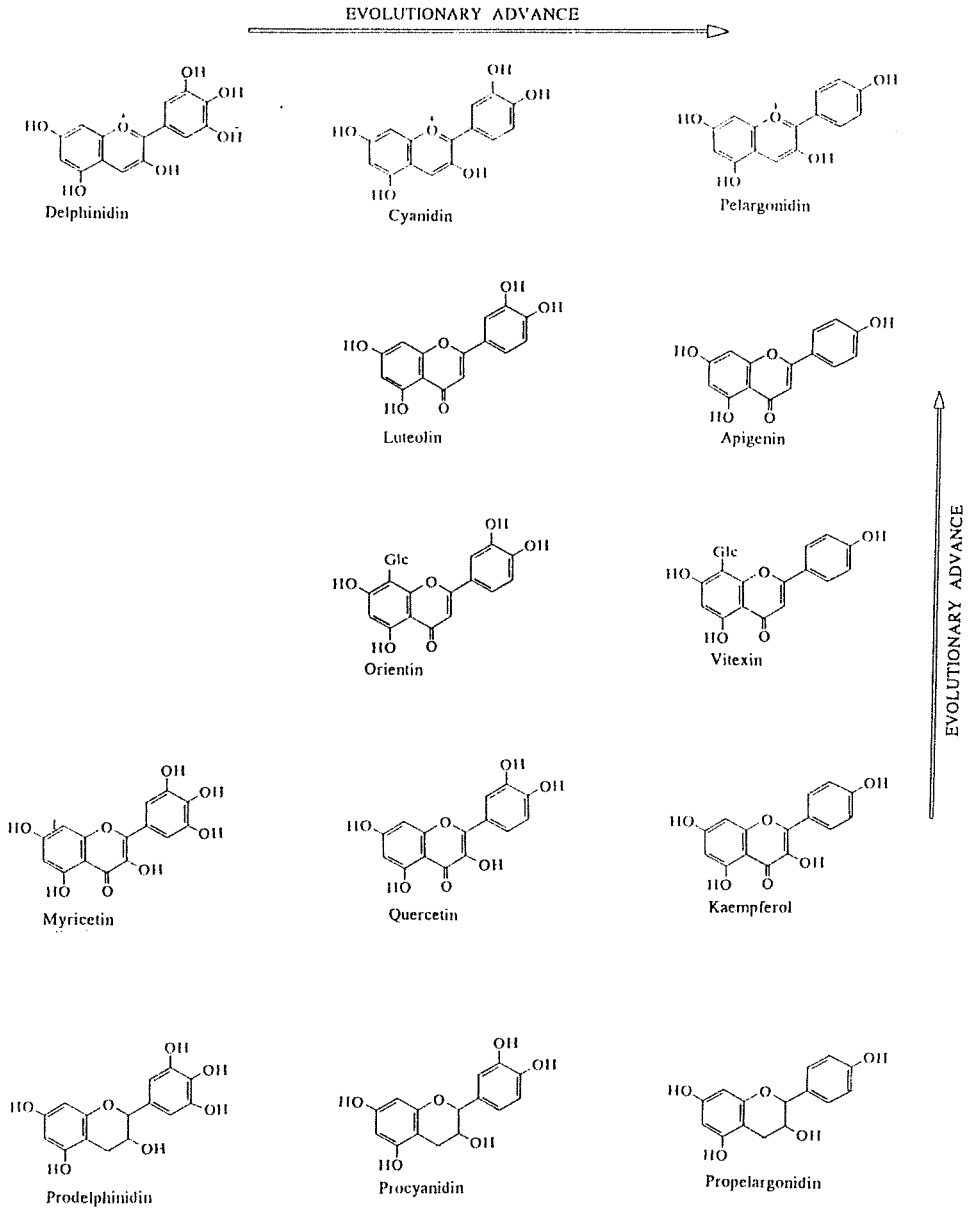


Fig. 2. - Some common flavonoids in plants

DETECTION AND IDENTIFICATION OF FLAVONOIDS

Some of flavonoid types are detectable in visible spectrum. Thus, the anthocyanins are most widespread group of colouring compounds in plants. Some of flavonoid groups are invisible (colourless flavonoids). These flavonoids *sensu lato* have a characteristic maxima of absorbance in UV spectrum (250-450nm).

Flavonoids are mainly water-soluble compounds. They are usually very stable compounds, being unchanged even for a 100 years in herbarium specimens (Harborne, 1984).

They can be extracted with ethanol or methanol and remain in the aqueous layer, following partition of this extract with petroleum ether. After extraction flavonoids can be separated by PC, 2DPC, TLC in different solvents. The flavonoids can be identified by means of UV, NMR and MS procedures.

General procedures for flavonoid detection, separation and identification can be found elsewhere (Harborne, 1967a, 1984; Harborne & Turner, 1984; Mabry et al., 1970; Markham, 1982).

TAXONOMIC SIGNIFICANCE

Before the start of a detailed chemical researches concerning plant pigments, the colour itself of flowers or other organs in taxonomic literature, has been relatively little used as a reliable taxonomic character. Despite a huge variety of colour shades, one of the reasons for that is probably the fact that the colour faded even in the herbarium specimens, and on the other hand, it is well known that flower colour may considerably vary with many species because of the differences regarding ecological conditions. At the same time, it is known from numerous literary sources, that completely different pigments may give the same flower colour. This may even refer to the same family, eg. Asteraceae, various pigments may be responsible for the yellow flower colour. Flower colour description of some plant species may also mean similarity. However, it can at the same time lead to a completely wrong conclusion. If reliable conclusions are to be obtained, it is necessary to perform a detailed chemical pigment and copigment characterization responsible for certain flower colour or some other organ. In each coloured flower, fruit or other organ, there is almost exclusively a pigment mixture. Their potential taxonomic significance will be presented further in the text.

Variability

One of the first steps in chemotaxonomy, as well as in systematics in general, is the establishing of certain character variability under the influence of ecological factors. If certain factors considerably vary due to ecological factors influence, their taxonomic value is very much diminished or even neglected. It is well known that many chemical compounds in plants vary, both qualitatively and quantitatively. Secondary metabolites, to whom flavonoids also belong may vary depending on the plant development phase, as well as on tissues and organs which are being analysed. Therefore, likewise researches must take care always to analyse plants that are in the same developing phase, that if possible, plants are grown under the same ecological conditions, to perform adequate material sampling and that absolutely identical methods (under the same controlled conditions) for analysing flavonoids (or other components) are used. Most qualitative differences, if such in the case exist, will be the result of genetic factor differences.

Thus flavonoids, as a fairly uniform group, have been intensively researched from a physiological-genetic aspect (H a r b o r n e, 1967a; K i b r y & S t y l e s, 1970). Variability of flavonoids under various strictly controlled conditions, has been analysed with some species from Lemnaceae (M e C l u r e & A l s t o n, 1964; M e C l u r e & A l s t o n, 1966). It was established that all of 186 clones, that had been analysed, contained all of the 47 flavonoid components if grown under the same conditions. Only in the case of *Lemna perpusilla* a qualitative difference of a flavonoid profile was found which meant that there was no infraspecific variability. Comparative analyses of flavonoids with four species of cotton (*Gossypium*) were also performed and the plants were grown experimentally (H a r b o r n e, 1967b; P a r k s et al. 1972). It was shown that there was greater flavonoid variability in leaves than in flowers. It is very likely that the reason for it must have been the stadium development difference (particularly in leaves). Flavonoids are generally considered not to show a considerable quantitative variability. However, in the anthocyanin analysis at *Matthiola incana*, in the lines with a common genetic base, it was shown that phenotypes with nine possible genotypes may differ qualitatively with considerable quantitative differences (J a n a & S e i f f e r t, 1971). They concluded that the quantitative differences are the result of genetic factor differences.

At any rate, flavonoid variability under the influence of ecological factors is not expressed in such a degree to enable diminishing their application in systematics. It was thus shown that sample species of *Mentha* genus demonstrate the same flavonoid profile although they were collected on different localities in Serbia (M a r i n, 1989). The differences which may be established in the qualitative structure can also be explained by insufficient method sensitivity and the instruments used within the analysis.

Hybridization

Hybridization among more or less similar plant species is a relatively rare phenomenon in nature, regardless of the fact that there is a whole series of literary data which document the hybridization (K n o b l o c h, 1972; S t a c e, 1975). Morphologists are very often capable of recognizing hybrides between certain cross-bred species. However, caryological methods were used for the sake of a detailed hybride analysis. These methods are not always capable of reliably showing certain hybride origin due to the complexity of hybridization as a phenomenon. Phytochemists tried to document hybridization relatively a long time ago. As for flavonoids, one of the first works on the theme was a whole series of hybrid analysis regarding species of *Baptisia* genus (T u r n e r & A l s t o n, 1959). These works and the later ones of the mentioned authors, greatly influenced the researchers who dealt with chemotaxonomy. Therefore, flavonoids of the various genera have been investigated from that aspect. These results were reviewed elsewhere (H a r b o r n e, 1984).

Flavonoids as secondary metabolites may be very good parameters for the confirmation of a sympatric hybridization (A l s t o n & H e m p e l, 1964; A l s t o n, 1965; A l s t o n & T u r n e r, 1962; B a e t c k e & A l s t o n, 1968; H e s s, 1971; M u r r a y et al., 1972; W o l l e n w e b e r, 1975 etc.).

The existence of sympatric interspecific hybrids *Sideritis serrata* Cav. ex Lag. x *S. bourgaeana* Boiss. by means of HPLC analysis of flavonoid glycosides and external methylated flavonoid aglycones (F e r r e r e s et al., 1989). In some individual plants

hybrids have produced compounds characteristic for parental taxa. This fact has enabled a relatively easy detection of F1 hybrids. Generally speaking, a clear correlation between biochemical results and the results of the morphological analysis has been noticed.

It has also been shown that polyploidy which is otherwise very much represented in plants, influences the flavonoid profile. It is known that polyploids are more robust than the diploids, which enabled the supposition that the chemical components return also has to be larger. It has thus been shown that natural autotetraploids of *Briza media* among other flavonoids contain iso-orientin, iso-orientin 4 - glucoside and orientin 4' - glucoside, which have not been detected in diploids (W i l l i a m s & M u r r a y, 1972). However, it is not excluded that diploids have produced the above quoted components, but they may have been in small concentrations and thus not detected. At any rate it did not diminish the significance of polyploidy in the increased production of flavonoids. This would likely be explained by doubling up genomes. M u r r a y & W i l l i a m s (1976) have further artificially induced polyploids of this species ($2n \times 4n$). However, the difference among flavonoid profile analysed samples has not been noticed. Further more, multiplication of genomes did not influence the flavonoid content. A considerable difference regarding flavonid structure was found neither in the six polyploids nor in their precursor structure. Only in one of them it was noticed that triclin 5- glycoside, which is otherwise a very frequent component of grass, was present in diploids and not in polyploids. Flavonoids can be very useful both in documenting hybridization and in some cases where they can indicate the level of ploidy.

The flavonoids as markers at lower taxonomic levels

Polymorphism is universal in flora on a macromorphological level while the same phenomenon is present on a chemical level as well. As for flavonoids as secondary metabolites, it is necessary to analyse the variability within and among populations in order to approach a detailed analysis regarding the species and higher taxa. Polymorphism of chemical characters some authors called dpolychemism (T é t é n y i, 1968, 1970). Authors came to similar results even earlier when within morphological, more or less the same populations, they were able to recognize different dchemical races (A l s t o n & T u r n e r, 1963a,b). The question put forward was whether there is any necessity of an independent nomenclature as T é t é n y i (1968) suggested. Such nomenclature usage would certainly arouse confusion in taxonomy. On the other hand, the existence of such dchemical races is reality, regardless of the fact that generally they cannot be morphologically distinguished. One of the classic examples is analysis of the 22 population of the *Chenopodium fremontii* in western parts of the USA (C r a w f o r d & M a b r y, 1978). The existence of at least four chemical races which differed by the derivative structure of isorhamnetin, kaempferol and quercetin was established. It should be pointed out that it is not a question of individuals as chemotypes, but of populational chemotypes. Intraspecific variability is not equal in all plant species, neither when flavonoids are in question nor other secondary metabolites (H a r b o r n e & T u r n e r, 1984). Chemical, genetical as well as morphological structure of population are very complex. Factor influencing population structure are: population size, ecological position, migration, variation, selection and reproductive mechanisms (E h r e n d o r f e r, 1968). Nowadays knowledge about population differentiation is mainly based on morphological and karyological characters. The data referring to macromolecules, in this case to flavonoids, are still sparse.

Flavonoids as taxonomic markers have very often been used at generic level. Regardless of the intrapopulational and interpopulational variability, described earlier, a series of works on chemosystematics were published in the last thirty years. In most of the works, variability (lower or higher) among the analysed samples was very well documented. Variability under the influence of different ecological and genetic factors was analysed. The main thing the authors clung to was the rule of sampling. Before beginning research work on certain species, abundant sampling was performed in order that variability of the samples could be established.

Since morphological variability of plants is an universal phenomenon, variability in secondary metabolites is expected. It was thus shown that some plant groups may be rather uniform, while a considerable variability of secondary metabolites was noticed with others. With the species of *Baptisia* genus, for example, some compounds appeared in about 80% of individuals that were examined, others had a smaller percentage and some compounds were rarely present (in less than 5% of individuals) (Horn, 1965; Alston, 1967). It is certain that it cannot be absolutely claimed that these compounds were absent. It is possible that they were present in small quantities which were not detected by the used techniques.

In their earlier works the authors tried to express their qualitative and quantitative differences either among populations or individuals, in various ways. Thus for example, Greger (1978) analysed the species of *Anacyclus* (Asteraceae). Each species was collected from a number of different localities. Various individuals of certain species were examined according to the qualitative and quantitative structure. However, absolute amount of certain components was not given and the presence (smaller or larger) of these components was marked by different symbols (such as: a large amount, small in traces, and so on). In the analysis of the genus *Helenium* (Asteraceae) similar methodology was also applied (Bierer, 1973). Alike data were given by Valant (1978) in the analysis of number of samples within *Achillea* genus (Asteraceae).

At any rate, in the above quoted examples, it can be noticed that regardless of certain quantitative and somewhere qualitative variability within a species, flavonoids may be taxonomic characters. In the quoted examples either individual species or group species may be differentiated within the appropriate genera.

One of the very illustrative examples is the analysis of a species from the *Baptisia* genus, though made as far as the middle sixties by a few authors, which even today represents a classic example of the correct approach to some chemotaxonomic problem (Horn, 1965; Brehm, 1966; Alston, 1967).

Horn (1965) firstly analysed 32 populations of *Baptisia nuttallina* by means of two-dimensional chromatography. Twenty individuals from each population were analysed. It was shown that certain spots (components) appear in every individual and all populations, while in most populations and individuals the spots appear in a smaller percentage than a 100%. A few years later a more detailed study of flavonoids species *Baptisia* genus (Markham et al., 1970) was performed. In the study the distribution of 62 main flavonoid components was shown and some minor ones were neglected. Regardless of the fact that some of the components were species specific, it was shown that flavonoid profile may be useful when similarities of certain species are being established. Later on, a similar analysis was performed with another north-american *Thermopsis* genus, which is considered to be very much alike the genus *Baptisia*, even its ancestor (Dement & Mabry, 1972, 1975). According to flavonoid profile, it was shown that *Baptisia* is a more advanced genus than *Thermopsis*.

A very illustrative study concerning flavonoids is connected to genera *Lemna*, *Spirodela*, *Wolfia* and *Wolffiella* (Lemnaceae) (McCure & Alston, 1966). It is known that these are water plants, believed to have come into being from those land ones. Though it is a question of morphologically very reduced plants, it is noticed that in morphological sense there is a gradual reduction from *Spirodela*, through *Lemna* to *Wolfia* and *Wolffiella*, an attempt was made to prove or refute such a phylogenetic series through flavonoid profile. It was really demonstrated that flavonoid profile results are correlated with morphological reduction. Concretely, concerning flavonoids, *Spirodela* contains flavones, flavonols, glycoflavones and anthocyanins; *Lemna* flavones, glycoflavones and anthocyanins; *Wolfia* flavones and glycoflavones, and *Wolffiella* only flavonols. According to a detailed analysis of flavonoids of the genus *Wolfia*, it was noticed that two very distinctly separated groups of species can be made as well. One group species shows similarity to *Lemna* genus and directs to the origin of the genus, while other group is more similar to *Spirodela* genus. The question is whether it is an independent, byphyletic origin of the two groups of *Wolfia* genus. The problem that it could even be the matter of different genera, lies in the absence of exomorphological differences, bearing in mind that species whose vegetative and generative organs are much reduced are in question. It would certainly be desirable to perform the analysis of some other chemical compounds so that more reliable conclusions could be drawn.

Some authors have put forward a thesis that flavonoid reduction is a rule within many plant groups (Mabry, 1973). It was shown in a few genera that such reductions exist in many closely related plant groups. In this sense it seems most convenient to analyse closely related genera since it is not possible to claim for sure which groups are more primitive and which more derived on the level of family, subfamily and tribe. The thesis has in a certain way been confirmed in the genera study of Dilleniaceae family (Gurni & Kubitski, 1981). In this study the authors were not able to recognize any taxon between genus and family (according to flavonoids, of course). It is considered that a compound or a group of compounds, which can be found in a hypothetically primitive group, are also primitive and that the specialized compounds having limited distribution, are advanced. It has for example been proved that flavonol glycosides are with *Degeneria* and primitive characteristics of magnoliids (concretely family Degeneriaceae and that C-glycosyllavones are advanced (more progressive) characters which are met with *Idiospermum* (Idiospermaceae). From the comparative-morphological aspect it is also considered that Idiospermaceae is a more advanced family in relation to Degeneriaceae (Young & Sterner, 1981). Besides following the reduction and specialization of flavonoids, some authors have tried to evaluate the relation between oxidation and methylation of flavonoid types in order to indicate primitivity or advancement concerning a plant group (Gomes et al., 1981). The mentioned authors have analysed the genera *Deris* et *Lonchocarpus* (Fabaceae). It was concluded that there was not a distinct correlation between a classic morphological and chemical cladogram. Naturally, it is not possible to expect that morphological changes will always be parallel with the chemical structure changes. It should be understood that morphological, chemical and other characters are exposed to unequal selectional pressures and that such correlations may but need not appear in analyses.

Based on the researches of species *Teucrium* (Lamiaceae) genus, the authors have concluded that chemical results are generally correlated with infrageneric classification (at the sectional level) (Harborne et al., 1986). More recent, micromorphological investigation concerning this interesting and taxonomically difficult genus,

have shown the correlation with obtained results, on flavonoid basis (Marin et al., 1994). Apart from this, both chemical and micromorphological analysis of the genus indicate that section *Teucrium* is a phylogenetically the basic group of the genus *Teucrium*.

The analysis of flavonoids of species from the *Mentha* genus, regardless of the species complexity themselves, indicates that these components may to a certain extent be useful in the infrageneric classification (Marin et al., 1990).

One of the new and interesting examples of flavonoid use at the generic level is the distribution of methylated flavones in the family Lamiaceae (Tomás-Barrán et al., 1988). It was also shown that flavonoids are good taxonomic markers in the delimitation of closely related species *Micromeria*, *Calamintha*, *Clinopodium*, *Acinos* and *Satureja* (Saturejaceae, Lamiaceae) (Marin, 1989).

Use of flavonoids at the suprageneric levels

Though it has up till now been shown that flavonoids as taxonomic markers are of the greatest importance at the generic level, many authors have tried to establish the significance of such compounds on higher levels (tribes, subfamilies, families and so on), trying above all to detect phylogenetic connections among the analysed taxa in these analyses.

The problem of limitation referring to secondary metabolite application on higher taxonomic levels, might be in a way compared to the same problems also met in comparative-morphological studies. Namely, by comparing leaf and stem hairiness, toothiness or leaf divisions or other characters, it would be difficult to make a cladogram appropriate to the similarities of higher taxa. In other words, such morphological characters may appear among a number of taxa (eg. families) which are not even alike. If a distribution example of cyanidin, pelargonidin, myricetin and other compounds in a families of flowering plants is taken into account, it can be noticed that these compounds are present (or absent) independently, both in close and in phylogenetically unrelated families. To use likewise compound types reliably, on high taxonomic levels, it would be desirable to be acquainted with biosynthetic and alternative pathways of all such compounds as well as enzymes which are included in the given processes. In other words, without knowing biosynthetic pathways it is very difficult to establish if some similarities in a chemical structure mean a relation or a convergent evolution, i.e. the phenomenon of the same substances in given plants. Of all secondary metabolites found in flowering plants, flavonoids are being researched most intensively (on higher taxonomic levels as well) (Gornal et al., 1979; Harborne, 1977a,b, 1984). According to the analysis regarding the presence of different flavonoids in flowering plants, Gornal et al., (1979) it is concluded that many flavonoid structural classes are polyphyletic and that their significance above family level is being considerably reduced. Crawford (1979) also came to similar conclusions.

Regardless of the above quoted problems, a large number of authors have made a survey of flavonoids on suprageneric levels. In such analyses, flavonoids are often used because only herbarium material is quite enough for them. It is a question of stable compounds which do not change their structure for a many years. Some analyses of herbarium material a hundred years old, have shown that flavonoid structure has not essentially changed (Harborne, 1984).

We shall give a review of some interesting works referring to flavonoid application on higher taxonomic levels.

Anthocyanins, which are considered to be better taxonomic markers at lower levels, have also been analysed at higher levels. It was, for example, shown that presence/absence of a relatively rare and unusual anthocyanin group (3-desoxyanthocyanins) within a family Gesneriaceae was in correlation with infrafamilial classification (H a r b o r n e, 1966, 1967a; L o w r y, 1972). In other words, 3-desoxyanthocyanins are present in subfamily Gesnerioideae, unlike subfamily Cyrtandrioideae. Another illustrative example is the analysis of distribution regarding different anthocyanidin glycosides in the tribes Viciaceae and Trifolieae (H a r b o r n e, 1971).

A very interesting group of secondary metabolites - betacyanins, which however does not belong to flavonoids *sensu lato*, but is indirectly connected with anthocyanins, showed itself to be a very good taxonomic parameter on the family level. Namely, it is known that within the order of Centrospermae (= Caryophyllales) there are two suborders: Chenopodiinae, into which the so called betalain families are classified and Caryophyllinae in which anthocyanin families exist (M a b r y, 1977). Betalains are nitrogen pigments, giving a similar colour to that of anthocyanins. However, according to the present results, those two types of pigments absolutely exclude each other, in other words, their mutual presence has not been confirmed in any of the species within the order Caryophyllales. Some authors consider that betalains have through evolution replaced anthocyanins with the so called betalain families (M a b r y, 1976; C r o n - q u i s t, 1977).

According to recent analyses it has been shown that the type of glycolysation and acylation of anthocyanins separate the Lamiaceae family from the neighbouring families (eg. Boraginaceae) (H a r b o r n e, 1992). It has been established that there is a connection with Verbenaceae family on the similarity basis of some anthocyanins.

As for the yellow flavonols, the presence of gossypetin otherwise present in numerous plant groups, is interesting and is considered to be of a polyphyletic origin in Primulaceae family. Namely, this compound is present only in the genera from Primuleae tribe (H a r b o r n e, 1968). Then, for example, quercetagenin is characteristic as a taxonomic marker within Asteraceae family (H a r b o r n e, 1975).

One of the earlier works deserving attention is the isoflavone research in Fabales order (= Leguminosae) (H a r b o r n e, 1969). The only group rich in these compounds are Fabaceae (= Papilionoideae). Though isoflavones are present in all of the tribes of Papilionaceae, their presence is not equal or absolute in all species within genera. However, some particular components, as 5-methylgenistein is, can be taxonomic markers on the tribal level. The mentioned component can only be found in Genisteae tribe (but nevertheless not in all species within the tribe).

M o o r e et al., (1970) on the flavonoid bases have shown similarity between Empetraceae and Ericaceae families.

Then a few works on family Graminae ought to be mentioned (W i l l i a m s et al., 1971), Palmae (W i l l i a m s et al., 1973), Bixaceae (H a r b o r n e, 1975), Bromeliaceae (W i l l i a m s, 1978) and the others, which suggest rearrangements, that is a revision of infrafamilial classifications on the basis of the obtained results regarding the structure of the colourless flavonoids. The analysis of flavonoids of families within the order Zingiberales, is also not in harmony of valid classifications (W i l l i a m s & H a r b o r n e, 1977a). On the basis of the obtained results referring to Cyperaceae family and by comparison of the same in the families Poaceae and Juncaceae and particularly the discovery of luteolin 5-methyl ether presence within

Cyperaceae, classifies this family nearer (in the chemical sense) the family Juncaceae, out of which this compound has first been isolated (Williams & Harborne, 1977b).

In a recent study of the family Cyperaceae, it was shown that flavonoids are characteristic at the generic and specific level, however, differences can be noticed at the tribal level as well (Harborne et al., 1985).

Previous analyses above all referred to leaves or whole plants. It should be mentioned that flavonoids are present in other plant parts as well. Thus, it was shown that the flavonoid profile in fruits of Umbelliferae family (=Apiaceae) are in correlation with infrafamiliar classification (Harborne & Williams, 1972). Some components were characteristic at the level of subfamilies and some at tribal level.

On the analysis basis of 97 taxa of Oleaceae family, it was shown that there is a difference at subfamily level, which is also in correlation with the obtained research work of chromosomes (Harborne & Green, 1980).

According to some other authors who analysed particular families and orders, it was also shown that there is a need for a taxonomic revision of certain groups, which

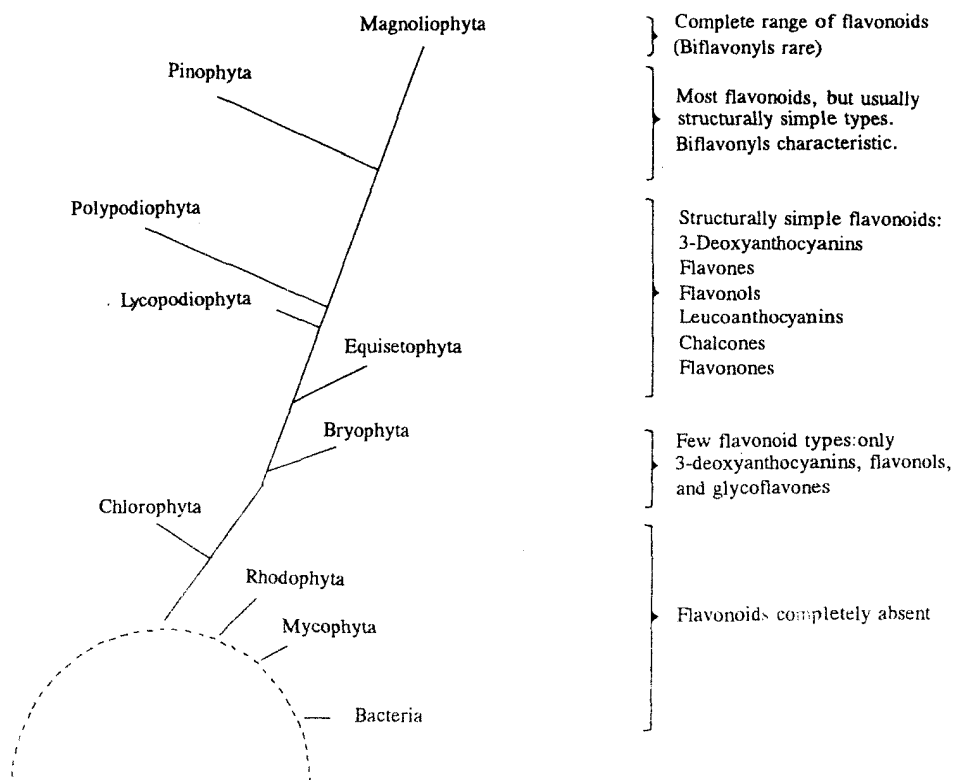


Fig. 3. - Evolution of flavonoids in plants

regarding chemical aspect show smaller or bigger distance and require status change of the researched taxa (Bate-Smith et al., 1975; Lowry, 1976; Gray & Waterman, 1978; Sterner & Young, 1980).

FLAVONOID EVOLUTION AND THEIR PHYLOGENETIC IMPLICATIONS

Flavonoid evolution in the past has been considered mainly from a chemotaxonomic aspect, based on the end products accumulated in different plant groups, particularly within flowering plants (Harborne, 1988). Chemotaxonomic studies of the distribution of flavonoids within mosses and other lower vascular plants have been summarized (Markham, 1988, 1990).

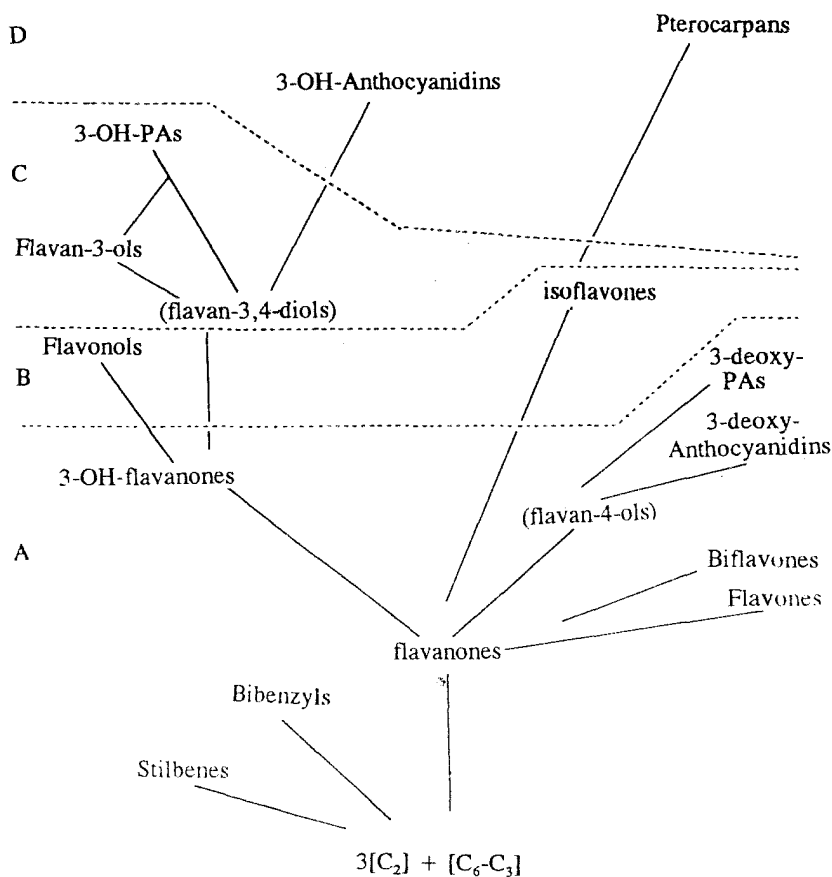


Fig. 4. - Evolutionary scheme of enzymic steps in the biosynthesis of the major subgroups of flavonoids with a 5,7-dihydroxy A-ring. Levels A, B are found in Bryophyta, C in Polypodiophyta and their allies, and D in Pinophyta and Magnoliophyta. PA=proanthocyanidin. Adapted from Stafford (1991).

In spite of some difficulties in understanding or opinion, the main concepts and trends of plant phylogeny is widely accepted. The same reason should be used to relate chemistry to phylogeny.

Flavonoids can also be of interest in comparison at high taxonomical levels. Thus, flavonoids are apparently absent in bacteria, fungi and lower plants. There are few flavonoid types in Bryophyta (Fig. 3). In Polypodiophyta, Equisetophyta and Lycopodiophyta there are structurally simple flavonoids. In seed plants more advanced flavonoid types can be found. Especially in Magnoliophyta there is a complete range of flavonoids. There is a general evolutionary trend towards complex structures and the wealth of highly substituted flavonoids are concentrated in highly specialised families (Fabaceae, Asteraceae, etc.). A simpler patterns are found in primitive families such as Magnoliaceae and Ranunculaceae.

Evolutionary status of flavonoid characters is reviewed elsewhere (H a r b o r n e, 1967a). For example, general trend is the change in flavonoid pattern in leaf (replacement flavonols by flavones) with the replacement of woody by herbaceous habit of plants.

Recently, flavonoid evolution in land plants based on the present day distribution of the major subgroups of flavonoids in Bryophyta, as well as in lower and higher vascular plants has been reviewed (S t a f f o r d, 1991).

The significance of varied functions in the origin of pathways with a series of sequential steps leading to end-products is considered. According to given results, evolutionary scheme of enzymic steps in the biosynthesis of the mayor subgroups are presented (S t a f f o r d, 1991) (Fig. 4.).

CONCLUDING REMARKS

From all groups of plant pigments, three classes of flavonoids were recognized as being of chemotaxonomic significance. From the literature data, it can be concluded that colourless flavonoids are of the highest importance as taxonomic markers. In contrast to other plant pigments, flavonoids, especially colourless flavonoids are very stable compounds. In addition, colourless flavonoids are ubiquitous and diverse in higher plants, and could be relatively easily analysed.

In comparison to other secondary metabolites, flavonoids were recived most attention in chemosystematic studies, probably because of their universal distribution and great structural variation in higher plants, especially in flowering plants.

At the present time, it can be seen that flavonoids, as well as other secondary metabolites are most useful at generic and specific levels. Flavonoid investigations at suprageneric levels (family, order etc.), in spite of some excellent examples are of less significance. Looking at the highest levels (classis, phylum) clear differences in flavonoid classes can be seen (Fig. 3). The obtainable results suggest the necessity of using chemosystematic investigation, especially based on flavonoids as additional methods in clarifying and solving taxonomic as well as phylogenetic problems. These studies are especially important in cases where comparative morphological methods are limited.

H a r b o r n e, (1967) noted that: "Nowhere is the need for such biochemical data greater than in the field of plant taxonomy, which in its broadest sense embraces every aspect of plant science and which has the task of arranging in order over a quarter of a million plants". This is especially true if a phylogenetic treatment of plants under study is sought.

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Re z i m e

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FLAVONOIDI KAO TAKSONOMSKI MARKERI KOD CVETNICA

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U radu je izvršen pregled flavonoida - jedne od najinteresantnijih grupa sekundarnih metabolita viših biljaka sa taksonomskog aspekta. Prikazana je njihova hemija i strukturna raznovrsnost, detekcija i identifikacija.

Od svih grupa biljnih pigmenata, frakcija takozvanih bezbojnih flavonoida se pokazala kao najznačajnija sa hemotaksonomskog aspekta. To je hemijski najstabilnija grupa, koja je istovremeno i jedinstvena i veoma raznovrsna u biljnom svetu i, što je takođe važno, bezbojni flavonoidi se relativno lako izoluju.

U radu je analizirana infraspecijska varijabilnost flavonoida. Pokazano je da se na osnovu njihovog sastava može dokazati hibridizacija između određenih taksona. Posebno je dat pregled dosadašnjih najznačajnijih radova koji se odnose na njihovu upotrebu kao taksonomskih markera na infraspecijskom, generičkom, kao i na suprageneričkim nivoima.

Prema dostupnim rezultatima, može se zaključiti da su flavonoidi, kao i ostali sekundarni metaboliti, najpouzdaniji taksonomski markeri na nivou roda. Na višim taksonomskim nivoima su manje pouzdani, što je i očekivano s obzirom na njihov biosintetički put. Međutim, flavonoidi imaju i određene filogenetske implikacije. Kod prokariota i nižih biljaka nisu prisutni. Kod mahovina se nalaze najjednostavniji strukturni oblici i preko prečica, paprati, golosemenica do cvetnica pokazuju trend ka uslošnjanju građe i povećanju raznovrsnosti.