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Chemotaxonomic studies in the family *Rosaceae* and the evolutionary origins of the subfamily *Maloideae*

K chemotaxonomii čeledi *Rosaceae* a k vývoji podčeledi *Maloideae*

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The hypotheses of botanical taxonomy and cytology relating to the evolutionary origins of the subfamilies of the *Rosaceae* have been briefly reviewed and a tentative scheme of phylogenetic relationships has been produced. The scheme is based upon the supposition that evolution proceeded from a spiraeoid-like ancestral group of x = 9 which gave rise to a group of x = 8 (*Prunoideae* ancestor). Allopolyploidy then took place between these two closely related groups to give an ancestral group of x = 17 with free carpels which eventually evolved into the present-day *Maloideae* (Sax, Stebbins and Gladkova). The *Spiraeoideae* arose directly from the ancestral group of x = 9 without any change in basic chromosome number but the *Rosoideae* genera of x = 7 derived from ancestors of the present-day *Rosoideae* genera of x = 9 which in turn derived from the spiraeoid-like ancestral group (Gajewski). The affinities of aberrant genera such as *Dichotomanthes, Quillaja* and *Exochorda* have been considered. All available chemotaxonomic evidence which has significance within the *Rosaceae* (principally phenolic constituents) has been collated and shown to be generally consistent with the evolutionary scheme which is presented. Although many taxonomists consider that *Maloideae* could have arisen directly from primitive *Spiraeoideae* without the involvement of primitive *Prunoideae,* the chemotaxonomic evidence clearly shows that *Maloideae* has strongest affinities with *Prunoideae,* and then (to a lesser extent) with *Spiraeoideae*. There is no chemotaxonomic evidence which indicates any exclusive affinity between *Maloideae* and *Rosoideae* (x = 7).

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INTRODUCTION

The *Rosaceae* is a family of exceptional horticultural significance, containing many economically important fruit-bearing plants, ornamental trees and shrubs. The chemotaxonomic aspects of this subject were last reviewed some years ago (CHALLICE 1974) and the present paper[1]) updates this review, an updating which is particularly necessary because of a number of important developments in this subject area.

The family is generally sub-divided into four subfamilies (e.g. REHDER 1940, MELCHIOR 1964): *Spiraeoideae*, *Rosoideae*, *Prunoideae* and *Maloideae* (formerly known as *Pomoideae*). Two former subfamilies, *Neuradoideae* and *Chrysobalanoideae* are no longer included in the *Rosaceae* but are each given separate familial status (MELCHIOR 1964).

The *Maloideae* itself is a group extremely well-defined and standing apart from the rest of the family and may be worthy of family status. *Prunoideae,*

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[1]) Based upon a lecture given to the Czechoslovak Botanical Society at the Charles University, Benátská 2, Prague, on 10th November, 1977.

Tab. 1. — Basic chromosome numbers in the tribe *Quillajeae* (*Spiraeoideae*)

Genus	n	suggested re-assignment
Lindleya	17	→ *Maloideae*?
Vauquelinia	15	
Kageneckia	17	→ New subfamily collateral with *Maloideae*?
Quillaja	14	
Exochorda	8	→ *Prunoideae*?
Lyonothamnus	27 (triploid)	→ *Spiraeoideae*?

Spiraeoideae and *Rosoideae* are also treated as separate families by some authors. The *Spiraeoideae* is undoubtedly the least important from a horticultural point of view; a few ornamental shrubs (notably *Spiraea*, *Sorbaria* and *Exochorda*) are the only representatives normally encountered horticulturally.

Inevitably this means that the *Spiraeoideae* has received least attention from natural product chemists, which is a pity because the limited phytochemical data which is available indicates that this subfamily is of considerable chemical interest.

CYTOLOGY

The basic chromosome numbers of the subfamilies are: *Maloideae* (x = 17), *Prunoideae* (x = 8), *Spiraeoideae* (x = 9) and *Rosoideae* (x = 7) (SAX 1931, 1932, 1933) but the basic chromosome numbers of the *Spiraeoideae* and *Rosoideae* are subject to certain exceptions. Table 1 shows some recent chromosome counts in the tribe *Quillajeae* of the subfamily *Spiraeoideae* by GOLDBLATT (1976), together with his suggestions for the re-assignment of the genera to other subfamilies.

The diversity of chromosome numbers in the tribe *Quillajeae* has led Goldblatt to suggest that this taxon is not a natural alliance and should be dispersed as indicated. The count of n = 17 for *Quillaja* by BOWDEN (1945) has now been shown to be in error. ROWLEY (1978) has recently referred *Quillaja* to the *Maloideae* but presumably this was due to the erroneous chromosome count of n = 17; following DARLINGTON et WYLIE (1955) who

Tab. 2. — *Rosoideae* genera with basic chromosome numbers higher than 7

Tribe *Kerrieae* (monotypic genera)	
Kerria	
Rhodotypos	n = 9
Neviusia	
Coleogyne	
Tribe *Dryadeae* (part)	
Dryas	
Fallugia	
Cowania	n = 9
Purshia	
Cercocarpus	
Tribe *Potentilleae* (part)	
Alchemilla	n = 8 (?)
Aphanes	
Tribe *Adenostomeae* (monotypic)	
Adenostoma	n = 9

did the same. Later in this review it will be seen that the chemotaxonomic data to some extent supports the suggested transfer of *Lindleya* to the *Maloideae* and the removal of *Quillaja* from the *Spiraeoideae* but not the transfer of *Exochorda* to the *Prunoideae*. On morphological grounds, the transfer of *Exochorda* to the *Maloideae* is impossible, however, because its fruit is a capsule; in fact *Exochorda* is aberrant in any of the subfamilies on account of the nature of its fruits.

Table 2 shows some chromosome numbers in the *Rosoideae* which are higher than 7 (DARLINGTON et WYLIE 1955; GAJEWSKI 1957, 1959; FEDOROV 1969).

The genus *Dichotomanthes* (n = 17) has been considered by different authorities as belonging to the subfamilies *Maloideae*, *Prunoideae* and *Spiraeoideae* in turn, and separate subfamilial status has been proposed by GLADKOVA (1969).

PHYLOGENETIC ORIGINS OF THE *MALOIDEAE* AND OTHER SUBFAMILIES

The *Rosaceae* is a family whose existence poses some interesting phylogenetic problems and the chemotaxonomic data now available would seem to be of some relevance in the consideration of these problems. However, before discussing the chemotaxonomic evidence, the hypotheses of non-chemical botanical taxonomy will be briefly discussed.

A number of conflicting hypotheses have been advanced to account for the origins of the *Maloideae* (recently reviewed by KOVANDA 1965, GLADKOVA 1972), but the one which has found most favour recently was first formulated by SAX (1931, 1932, 1933) and subsequently elaborated by STEBBINS (1950, 1958). Here, the *Maloideae* are postulated to have arisen by allopolyploidy between different primitive forms of *Rosaceae*, one of x = 8 (a prunoid ancestor) and the other of x = 9 (a spiraeoid ancestor). It is a necessary part of this hypothesis that the respective primitive forms (in the Cretaceous era) were more alike than are the present-day forms, natural allopolyploidy between contemporary members of the subfamilies *Prunoideae* and *Spiraeoideae* would be unthinkable. Whether the recently developed techniques of genetic engineering and protoplast fusion could achieve this task would appear to be an intriguing, if remote, possibility.

It is worthy of note that STEBBINS (1958) had *Exochorda* in mind as a possible living relict of the primitive prunoid ancestor, although traditionally this genus has been placed in the *Spiraeoideae*. It will be recalled that GOLDBLATT (1976) suggested the transfer of *Exochorda* to the *Prunoideae*. GLADKOVA (1972) has maintained that it is unnecessary to postulate a prunoid ancestor, because the basic chromosome numbers of x = 8 and x = 9 exist in the *Spiraeoideae* already; here *Exochorda* is considered as a member of *Spiraeoideae*. GLADKOVA goes on to suggest that the apocarpous *Quillaja* could be a living relict of a precursor of primitive *Maloideae*.

Taxonomists generally consider now that the *Spiraeoideae* include the most primitive living forms of the *Rosaceae*²) and that the *Prunoideae* and

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²) It is of interest to note that the most ancient fossil forms of the *Rosaceae* are a couple of extinct *Prunus*-type species of lower Cretaceous origin. Since early Tertiary fossil forms of all 4 subfamilies are known, it seems quite certain that the family is of Cretaceous origin at the latest (KIRCHHEIMER 1940, 1942, GAJEWSKI 1957).

Rosoideae are somewhat specialized evolutionary offshoots from a basically spiraeoid-like rosaceous stock (GAJEWSKI 1957, 1959; GLADKOVA 1972; KALKMAN 1965; TAKHTAJAN 1969; EYDE 1975; STERLING 1964a, b). It is the *Spiraeoideae* that have retained some primitive morphological characters, such as the apocarpic gynoecium not coalesced with the receptacle.

DARLINGTON (1963) has maintained that the most primitive form of the *Rosaceae* had $x = 7$ (a rosoid ancestor) and that higher chromosome numbers arose later by stepwise addition in the *Prunoideae* and *Spiraeoideae* and by unequal reduplication ($7 + 7 + 3 = 17$) in the *Maloideae*. However, GAJEWSKI (1957, 1959) has convincingly argued that because of the specialized herbaceous nature of most *Rosoideae* ($x = 7$), and the generally shrubby nature of the few small *Rosoideae* genera of $x = 9$, it is most likely that $x = 7$ was derived from a more primitive $x = 9$.

Thus, Darlington's hypothesis has fallen from favour and even the recent finding of $n = 14$ in the primitive spiraeoid *Quillaja* seems unlikely to revive it. The contention by GOLDBLATT (1976) that the *Maloideae*, $x = 17$, is a palaeotetraploid group, arrived at by the doubling of $x = 9$ and an aneuploid loss of one chromosome is an interesting suggestion. Perhaps at some future time a critical morphologist will be able to say something authoritative on the subject (GOLDBLATT, personal communication). However, it does appear at first sight that morphology neither supports nor contradicts Goldblatt's hypothesis (KOVANDA, personal communication). The finding of $n = 14$ in *Quillaja* is difficult to explain, except by a stepwise aneuploid loss from $x = 17$ or a stepwise gain from $x = 9$. GOLDBLATT (1976) himself admits that a concurrence with the most common base number of $x = 7$ in the *Rosoideae* must be regarded as coincidental, and of no phylogenetic significance.

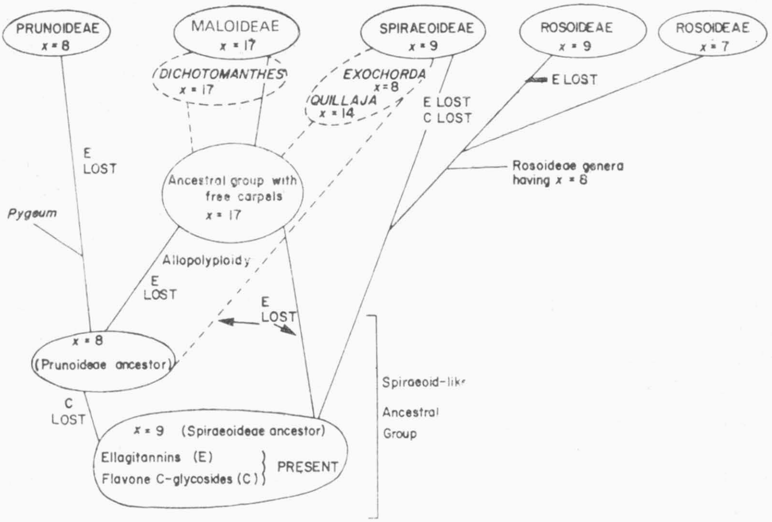

Fig. 1. — Hypothetical scheme for the evolution of *Rosaceae* subfamilies. Reproduced, with modifications, from J. Linn. Soc. — Bot. 64 : 239—259 (1974).

Fig. 1 shows an attempted synthesis of the phylogenetic views just outlined. It should be emphasised that such a scheme can only represent an approximation to what must have been in reality an exceedingly complex nexus of evolutionary relationships. It is quite common to represent such relationships by means of a tree-type diagram as in Fig. 1, and as long as it is realised that all present-day taxa are at the tips of the branches of this "tree" and the inner parts are hypothetical entities, we may perhaps be excused for attempting such exercises. However, an additional complication is that in reality our "tree" extends into a phenetic hyperspace of as many dimensions as there are characters which serve to differentiate the taxa. Only the time element may accurately be represented by one single dimension, although even this is subject to the complication that not all taxa have evolved at the same rate: some taxa (or some characters associated with these taxa) must have changed very little, whilst other taxa (or some of their characters) must have changed to a considerable extent during the course of evolution. Nevertheless, there are mathematical techniques available for projecting diagrams in multidimensional phenetic hyperspace onto spaces of reduced dimensionality and tests for determining the extent of information lost in the process e.g. GOWER (1966, 1967), GOWER et ROSS (1969); mathematical procedures which have been used in investigations of the genus *Pyrus* (CHALLICE et WESTWOOD 1973) so the exercise undertaken in Fig. 1 (albeit speculative) is not entirely without meaning.

CHEMOTAXONOMIC EVIDENCE – FLAVONE C-GLYCOSIDES

Until comparatively recently, *Crataegus* was the only genus of *Rosaceae* known to contain the distinctive flavone C-glycosides (FISEL 1965) as opposed to the more common flavone O-glycosides and to the even more common flavonol O-glycosides, but chemotaxonomic surveys (CHALLICE 1974, 1975; CHALLICE et KOVANDA 1978, 1980; KOVANDA et CHALLICE 1981) have now shown that these flavone C-glycosides have a much wider occurence within the *Rosaceae*, especially within the *Maloideae*. Table 3 gives the distribution within the *Maloideae*.

Flavone C-glycosides are a class of flavonoid in which the glycosidic moiety is attached directly to the flavonoid skeleton by a carbon-carbon bond, rather than by the more usual carbon-oxygen-carbon linkage, as in the more common flavone and flavonol O-glycosides. These O-glycosides are readily hydrolysed to flavonoid + sugar by hot acid or by enzymic action, whilst C-glycosides under these conditions remain intact. It is generally considered that these C-glycosides are biosynthetically and phylogenetically more primitive than O-glycosides; hence we have here a chemotaxonomic character of considerable potential usefulness in the *Rosaceae*.

A convenient procedure has been devised for screening large numbers of leaf samples (both fresh and herbarium specimens) for the presence or absence of these flavone C-glycosides (CHALLICE 1974; CHALLICE et KOVANDA 1978). The basic flavone C-glycosides so far encountered in the *Rosaceae* are:

vitexin (apigenin 8-C-glucoside)
iso-vitexin (apigenin 6-C-glucoside)
orientin (luteolin 8-C-glucoside)
iso-orientin (luteolin 6-C-glucoside).

Tab. 3. — Distribution of flavone C-glycosides in the subfamily *Maloideae*

Present

*Crataegus** (V + O)
Pyracantha (V + O)
Dichotomanthes (V)
Osteomeles (V)
*Hesperomeles** (V + O)

Chamaemeles (V)
*Aronia** (V)
Malacomeles (V)
*Micromeles** (V)
Sorbus subgenus *Torminaria** (V)
Sorbus subgenus *Aria** (V)
Sorbus subgenus *Sorbus** (V)
Sorbus subgenus *Chamaemespilus* (V)

Absent

Sorbus subgenus *Cormus*
Cotoneaster
Mespilus
Photinia
Heteromeles

Stranvaesia
Eriobotrya
Rhaphiolepsis
Amelanchier

Peraphyllum
*Malus**
Docynia
*Chaenomeles**
Cydonia
*Pyrus**

* Flavone O-glycosides also present
V = vitexin (apigenin 8-C-glucoside)
O = orientin (leteolin 8-C-glucoside)
N.B. The occurrence of orientin and iso-orientin in *Crataegus* (*C. monogyna* and *C. pentagyna*) has been definitively demonstrated by NIKOLOV (1977).

It has been found that under conditions of hot acid treatment, some interconversion between vitexin and iso-vitexin and between orientin and iso-orientin takes place, so under the experimental conditions used the isomeric forms cannot be accorded separate chemotaxonomic status.

It is interesting to note from Table 3 the following points:

(i) Both *Malus* and *Pyrus* (apples and pears) are −ve, yet the closely related *Sorbus* (all subgenera except *Cormus*) and *Micromeles* are +ve.

(ii) There is no apparent correlation between the presence of flavone O-glycosides and the presence/absence of flavone C-glycosides.

(iii) The distribution of flavone C-glycosides supports the hypothesis that the endemic South American *Hesperomeles* (the only naturally occurring representative of *Maloideae* in that subcontinent) evolved from primitive North American *Crataegus*, the two small endemic genera *Aronia* (North America) and *Malacomeles* (Mexico and Guatemala) representing surviving relicts of the evolutionary line as it moved southwards.

(iv) *Malacomeles* has been said to have affinities with *Malus*, *Pyrus*, *Amelanchier* and *Peraphyllum* (JONES 1945); doubt must be cast upon this statement since flavone C-glucosides, although present in *Malacomeles*, are absent from the other four genera.

(v) KOEHNE (1890, 1891), on the basis of reproductive morphology, divided the *Maloideae* into *Crataegeae* and *Sorbeae* (*Maleae*), a division supported by a study of the distribution of stone cells in the fruit (REMER 1905) as pointed out by HUCKINS (1972). It is interesting to note that the group of *Maloideae* which contains flavone C-glycosides to some extent corresponds with Koehne's *Crataegeae*. If *Cotoneaster* and *Mespilus* contained flavone C-glycosides (which they do not), and all subgenera of *Sorbus* (except *Cormus*), *Micromeles* and *Aronia* lacked flavone C-glycosides (they do in fact contain them), then the Present/

Absent division in Table 3 would correspond with Koehne's *Crataegeae* and *Sorbeae* (*Maleae*). However, it is important to note that none of these genera just mentioned can be transferred because it would not be morphologically feasible. Apparently the chemotaxonomic data are inconsistent with classical methods and any compromise appears impossible. Perhaps a morphological expert might find it worthwhile to attempt to reconcile the flavonoid data with the grouping of *Maloideae* genera into *Crataegeae* and *Sorbeae* – an apparently natural division, recently well supported by Kovanda (1965) and Kalkman (1973).

(vi) As mentioned earlier, the taxonomic position of the monotypic *Dichotomanthes* has been in dispute; the occurence of flavone C-glucosides indicates strong affinity with the *Maloideae*. *Dichotomanthes* could be a relict from some primitive group, ancestral to the *Maloideae*, exhibiting, as it does, certain morphological characteristics of the postulated ancestors to a greater extent than the other *Maloideae* genera (Gladkova 1969).

(vii) It is assumed that the genera containing both vitexin and orientin are, in a chemical sense, more primitive and that the loss of orientin is indicative of a more advanced state. Similarly, the retention of flavone O-glycosides represents a primitive character which has been lost in some genera. The evolutionary sequence seems to be (1) loss of orientin, (2) loss of vitexin and finally (3) loss of flavone O-glycosides.

At this stage perhaps a note of warning should be made: the presence of a chemical character might indicate some particular evolutionary origin but the absence of a chemical character could mean one of two situations – either it was lost at some earlier evolutionary stage or it was never there in the first place. Thus more significance is generally given to the actual presence of a particular chemical character, than to its absence.

Table 4 includes the remaining occurrences of flavone C-glucosides in the *Rosaceae*; it will be seen that they are not many. *Spiraeoideae*: *Quillaja* only, *Prunoideae*: nil, *Rosoideae*: *Adenostoma* (x = 9) and *Agrimonia* (x = 7). The restriction of flavone C-glycosides within *Spiraeoideae* to *Quillaja* alone, supports the opinion that this genus is not easily accommodated within the *Spiraeoideae*. Darlington et Wylie (1955) have placed *Quillaja* in the *Maloideae*, but this was done solely on the basis of a wrongly determined chromosome number (n = 17). In fact neither *Quillaja* nor *Dichotomanthes*

Tab. 4. – Indicators of phylogenetic affinities between subfamilies of *Rosaceae* (Flavones)

Subfamily	Flavone C-glycosides	Chrysin 7-O-glucoside	Flavone 6-O-substitution	Isoflavones	Flavone 5-O-glycosides
Maloideae	10 genera[1]	*Malus*[2]	0	*Cotoneaster*[6]	***Malus***[7]
Spiraeoideae	*Quillaja*[1]	0	*Sorbaria*[4]	0	***Spiraea***[8]
Prunoideae	0	*Prunus*[3]	0	*Prunus*[3]	***Prunus***[9]
Rosoideae (x = 9)	*Adenostoma*[1]	0	*Kerria*[5]	0	0
Rosoideae (x = 7)	*Agrimonia*[1]	0	0	0	0

[1] Challice 1974, Challice et Kovanda 1978, 1979, 1980; [2] Williams 1967, 1979; [3] Hasegawa 1958; [4] Arisawa et Nakaoki 1969, Arisawa et al. 1970; [5] Harborne et Williams 1971; [6] Cook et Fletcher 1974; [7] Hirose 1909, Williams 1968, 1969; [8] Chumbalov et al. 1975; [9] Hattori 1962, Harborne et Williams 1975.

fit readily into any of the four subfamilies of *Rosaceae* and it is perhaps to aberrant genera such as these that we should look for phylogenetic clues. In this connection it is of great interest that Basinger (1976) has discovered permineralized flowers, from the Eocene of British Columbia, of *Paleorosa similkameenensis* (*Rosaceae*), which he considers to combine more primitive features than any living member of the *Rosaceae*. He comments that *Paleorosa* probably represents an early group of rosaceous plants that preceded the tribes *Quillajae* and *Sorbarieae* of the *Spiraeoideae* and may signify the incipient development of the *Maloideae*.

CHEMOTAXONOMIC EVIDENCE – OTHER PHENOLIC COMPOUNDS

Tables 4–8 list the occurrence of certain other classes of phenolic compounds (together with the non-phenolic cyanogenic glucosides and sorbitol) which appear to indicate affinities between the subfamilies of *Rosaceae*. Tables 9–12 list classes of phenolic compounds which appear to be restricted to particular subfamilies: it would appear that these phenolics are generally later evolutionary elaborations of more primitive chemical structures. Of particular note is the interesting degree of apparent specialization in the *Spiraeoideae*. The presence of delphinidin in *Quillaja*, a phenolic cyanogenic glucoside in *Sorbaria*, a glycosylated catechin and complex diterpenoid alkaloids in *Spiraea*, all combine to make this a most chemically distinct subfamily. It will be of interest to note if any of these unusual substances are subsequently found elsewhere in the *Rosaceae*. The *Rosoideae* is also of particular interest in its apparent degree of chemical specialization, notably the presence of myricetin in *Potentilla* and the general loss of sorbitol and cyanogenic glucosides.

All of the compounds listed in both sets of tables have been selected for their potential chemotaxonomic usefulness. There is a vast array of phenolic compounds which occur throughout the *Rosaceae* in all subfamilies, though not necessarily in all genera or species: there are phenolics such as the various substituted cinnamic acids, C_6-C_1 phenolic acids, common catechins, leucoanthocyanidins and anthocyanidins, common flavones such as apigenin and luteolin 7-glycosides and common flavonols such as kaempferol, quercetin and isorhamnetin 3 and/or 7-glycosides (Challice 1972). These are

Tab. 5. – Indicators of phylogenetic affinities between subfamilies of *Rosaceae* (Miscellaneous flavonoids)

Subfamily	Dihydrochalcones	Flavanones	Leuco-pelargonidin	Leuco-delphinidin
Maloideae	*Malus*1) *Docynia*2)	6 genera1),2),3),4),5)	*Crataegus*7)	0
Spiraeoideae	*Sorbaria*2)	0	0	*Quillaja*10)
Prunoideae	0	*Prunus*6)	0	0
Rosoideae (x = 9)	0	0	*Dryas*8) *Kerria*9) *Neviusia*9)	0
Rosoideae (x = 7)	0	0	0	*Potentilla*9),10)

1) Williams 1966; 2) Challice 1973; 3) Paris et Etchepare 1965; 4) Williams 1962; 5) Kowalewski et Mrugasiewicz 1971; 6) Hasegawa 1958, Hergert 1962; 7) Lewak et Radominska 1965; 8) Pangon et al. 1964; 9) Bate-Smith 1961; 10) Bate-Smith 1965.

Tab. 6. — Indicators of phylogenetic affinities between subfamilies of *Rosaceae* (Substituted Flavonols)

Subfamily	Flavonol 3-O-methylation	Flavonol 8-O-methyl ethers	Flavonol 5-O-glycosides	Flavonol 6-O-substitution	Quercetin 4′-O-glucoside
Maloideae	*Crataegus*1)	*Crataegus*3) *Sorbus*4)	*Malus*7)	0	*Malus*10) *Sorbus*11),12)
Spiraeoideae	0	0	0	*Vauquelinia*9)	0
Prunoideae	*Prunus*2)	*Prunus*5)	0	*Prunus*2)	*Prunus*13)
Rosoideae (x = 9)	0	*Dryas*6)	*Rhodotypos*8)	0	0
Rosoideae (x = 7)	0	0	0	0	*Filipendula*14) *Rosa*15) *Geum*16)

1) NIKOLOV et al. 1973; 2) WOLLENWEBER et al. 1972; 3) BYKOV et GLYZIN 1972; 4) JERZMANOWSKA et KAMECKI 1973; 5) NAGARAJAN et SESHADRI 1964; 6) PANGON et al. 1974; 7) WILLIAMS 1968; 8) PLOUVIER 1967; 9) BATE-SMITH 1965; 10) WILLIAMS 1969; 11) BORISOV et ZHURAVL'OV 1965; 12) CHALLICE 1973; 13) SHRIKHANDA et FRANCIS 1973; 14) HÖRHAMMER et al. 1956; 15) HARBORNE 1961, 1967; 16) KAMINSKA 1971.

sometimes of value at lower taxonomic levels such as that of particular genera or species, but generally their usefulness is somewhat limited and for the purposes of this review they can be disregarded.

Returning to the chemotaxonomically significant substances, it should be remembered that it is far easier to report a presence than to report an absence of any particular substance. Sometimes the zero, as recorded in the tables 4—8, means that a survey of varying comprehensivenes has failed to detect the particular substance; other times the zero merely means that there are no records of the subfamily having been screened for the particular substance. To some extent this is a fault of the literature itself — all too often, negative results are not reported; in fact papers which report purely negative results are rarely, if ever, published!

Tab. 7. — Indicators of phylogenetic affinities between subfamilies of *Rosaceae* (Miscellaneous phenolics)

Subfamily	4-Allyl phenol	Protocatechuic acid 3-O-glucoside	Arbutin	p-hydroxybenzoyl-vanilloyl-protocatechuoyl-calleryanin (3 compounds)	Isochlorogenic acid	Ellagitannins
Maloideae	*Pyrus*1)	*Pyrus*1)	*Pyrus*2)	*Pyrus*1)	many genera4)	0
Spiraeoideae	0	0	*Sorbaria*3) *Exochorda*4)	0	*Lindleya*4)	0
Prunoideae	*Prunus*1)	*Prunus*1)	0	*Prunus*1)	0	*Pygeum*5)
Rosoideae (x = 9)	0	0	0	0	0	0
Rosoideae (x = 7)	0	0	0	0	0	many genera6)

1) CHALLICE et WILLIAMS 1968a; 2) CHALLICE et WILLIAMS 1968b; 3) PLOUVIER 1971; 4) CHALLICE 1973; 5) BATE-SMITH personal communication; 6) BATE-SMITH 1961.
N.B. *Pygeum* has now been incorporated into *Prunus* subg. *Laurocerasus* by KALKMAN (1965).

Tab. 8. — Indicators of phylogenetic affinities between subfamilies of *Rosaceae* (Non-phenolic compounds)

Subfamily	Cyanogenic1) glucosides	Sorbitol2)
Maloideae	16 genera	14 genera
Spiraeoideae	6 genera	9 genera
Prunoideae	4 genera (incl. *Prunus*)	*Prunus*
Rosoideae (x = 9)	*Kerria*	*Kerria*
	Neviusia	*Neviusia*
	Rhodotypos	*Rhodotypos*
	Cercocarpus	
Rosoideae (x = 7)	0*	0

1) Hegnauer 1973, Gibbs 1974, Gerstner et al. 1968, Conn et Butler 1969.
2) Plouvier 1963, Gibbs 1974.
* The isolated report of cyanogenesis in *Geum* (x = 7) by Gibbs 1974 should be checked.

However, the format of occurrences in tables 4—12 should enable the chemotaxonomic significance of any subsequently reported phenolic in the *Rosaceae* to be immediately assessed. For example, although flavanones are generally correlated with woodiness rather than the shrubby or herbaceous habit, there are invariably exceptions and it is quite possible that a detailed survey of the *Spiraeoideae* and *Rosoideae* subfamilies would reveal the presence of some type of flavanone in these subfamilies. Nevertheless, it is interesting that there does not appear to be even a single report of any flavanones from the *Spiraeoideae* or *Rosoideae* in the literature: if they are present they are probably only rarely present, in contrast with the *Maloideae* and *Prunoideae*. Thus, the situation as indicated in Table 5 is probably indicative of a general trend, if not of a clear-cut distribution. The same type of argument could apply to most of the substances which are listed.

It appears to be fairly obvious that when the tribe *Kerrieae* of *Rosoideae* (x = 9) evolved from *Rosoideae* (x = 7) as proposed by Gajewski (1957, 1959), ellagic acid, sorbitol and cyanogenic glucosides were generally lost. There may be a few exceptions yet to be discovered, but the general trend seems quite clear. The presence of arbutin in *Exochorda* indicates that this genus should perhaps remain in the *Spiraeoideae* and not be transferred to the *Prunoideae* (where arbutin is absent), just because *Exochorda* has

Tab. 9. — Chemotaxonomic specialization in subfamilies of *Rosaceae* (*Maloideae*)

Flavone 4′-O-glycosyation: Luteolin and apigenin 4′-O-glucosides in *Pyrus*1) and *Sorbus*2)
Vitexin 4′-O-rhamnosylglucoside in *Crataegus*3)
Flavone 5-O-methylation (?): suspected luteolin 5-methylether in *Pyrus*4)?
Caffeoylcalleryanin in *Pyrus*1),5)
2,4,6-trihydroxydibenzoylmethane 2-glucoside in *Malus*6)
Leucocyanidin 3-O-arabinoside in *Eriobotrya*7)

1) Challice et Williams 1968b; 2) Challice et Kovanda 1978, 1979; 3) Fisel 1965, Lewak 1966; 4) Challice 1972, 1973; 5) Challice et al. 1980; 6) Williams 1967a, 1979; 7) Agarwal et Misra, 1980.

Tab. 10. — Chemotaxonomic specialization in subfamilies of *Rosaceae* (*Prunoideae*)

Flavanone O-methylation: sakuranetin in *Prunus*1)
Isoflavanones: padmakastein in *Prunus*2)
O-methylated coumarins: herniarin3) and 5-OH 6,7-di MeOH coumarin4) in *Prunus*

1) Hasegawa 1958; 2) Hergert 1962; 3) Bate-Smith 1961; 4) Hasegawa 1969.

a prunoid chromosome number of n = 8. Stebbins (1958) has speculated that *Osmaronia* and *Exochorda* could be relicts of the original prunoid ancestor of the *Maloideae*; chemical evidence for such a relationship exists only in the case of *Exochorda*. It appears that there are no genera which embody strong morphological and chemical affinities with the postulated ancestors of the *Maloideae*; isolated characters, distributed amongst the present-day genera, are all that survive from the ancestral genera in question.

Tab. 11. — Chemotaxonomic specialization in subfamilies of *Rosaceae* (*Spiraeoideae*)

3′,4′,5′-trihydroxylated anthocyanidin: delphinidin in *Quillaja*1)
Phenolic cyanogenic glucoside: 2-β-D-glucopyranosyloxy 4-p-hydroxybenzoyl-3-methylenbutyronitrile in *Sorbaria*2)
Glycosylated catechin: Catechin 7-O-rhamnoside in *Spiraea*3)
Complex (diterpenoid) alkaloids*: e.g. Spiradin G and Spiradin F in *Spiraea*4)

* N.B. Trace amounts of the much simpler pyridine alkaloid, nicotine in *Prunus cerasus*4) ?
1) Bate-Smith 1965; 2) Nahrstedt 1976; 3) Chumbalov et al. 1976; 4) Hegnauer 1973 and references therein.

Returning to the evolutionary scheme in Fig. 1 it will be noted that supposed losses of the ability to synthesize ellagitannins (E) and flavone C-glycosides (C) are indicated here. It is certainly of some significance that the primitive ellagitannins have been found in *Pygeum* (now transferred to *Prunus* subg. *Laurocerasus* by Kalkman 1965); the evidently primitive p-hydroxybenzoyl-, vanilloyl- and protocatechuoyl—calleryanin esters are restricted, within the *Prunoideae*, to *P. lusitanica* which also belongs to the subgenus *Laurocerasus*.3)

The remaining chemotaxonomic data are generally consistent with this scheme of relationships. It has already been indicated that there is a tendency amongst taxonomists now to discount or minimize affinities between

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3) Two calleryanin esters (caffeoyl- and protocatechuoylcalleryanin) have also been found in the gymnosperm *Podocarpus andina* (Poyser et al. 1973): it would thus appear that these particular chemotaxonomic markers are of considerable phylogenetic age, pre-dating the rise of the angiosperms from their putative gymnospermous ancestors. The relatively rare dihydrochalcones also provide a similar link: Bhakuni et al. (1973) have found α-hydroxyphloretin (nubigenol) in *Podocarpus nubigena*. Cronquist (1968) has suggested the following evolutionary sequence of dicotyledonous plant orders: *Rosales* → *Myrtales* → *Proteales*; interestingly, derivatives of calleryanin provide a common connecting link between these three orders. Calleryanin + four phenolic acid esters in *Rosaceae* (*Rosales*), calleryanin 3-methyl ether in *Daphne mezereum*, *Thymelaeaceae* (*Myrtales*) (Kosheleva et Nikonov 1968) and p-hydroxybenzoylcalleryanin in *Protea cynaroides*, *Proteaceae* (*Proteales*) (Van Wyk et Koeppen 1974).

Tab. 12. — Chemotaxonomic specialization in subfamilies of *Rosaceae* (*Rosoideae* x = 7)

3′,4′,5′-trihydroxylated flavonol: myricetin in *Potentilla*[1])
Flavan 4-ol: luteoforol in *Fragaria*[2])
Isosalicin (salicylalcohol alcoholic glucoside) in *Filipendula*[3])
Loss of sorbitol and cyanogenic glucosides[4])

[1]) BATE-SMITH 1965; [2]) BATE-SMITH et CREASY 1969; [3]) THIEME 1966; [4]) PLOUVIER 1963, HEGNAUER 1973, GIBBS 1974*
* The isolated occurrence of cynogenesis in *Geum* (x = 7), reported here, should be checked.

Maloideae and *Prunoideae*, and to regard the *Maloideae* as a specialized development from *Spiraeoideae* alone. This is not supported by the chemotaxonomic evidence which establishes strong affinities between *Maloideae* and both *Spiraeoideae* and *Prunoideae*. On reproductive morphology, however, the *Maloideae* are most closely related to the *Prunoideae*. Affinities to the *Spiraeoideae* appear less distinct.

Table 13 represents an attempt to summarize the evidence from 24 chemotaxonomic indicators of various affinities between the subfamilies of *Rosaceae*. It will be seen that chemically the *Maloideae* shows most affinity to *Prunoideae*, with *Spiraeoideae* taking second place; we have already mentioned that this is supported by morphological evidence. The affinity between *Maloideae* and *Rosoideae* (x = 9) is not surprising, because the latter group of genera are known to be spiraeoid-like and the chemical data supports the contention of some taxonomists that the monotypic genera of the tribe *Kerrieae* (x = 9) should perhaps be transferred to the *Spiraeoideae* (e.g. BATE-SMITH 1961). The discrepancies between "simple affinities" and "exclusive affinities" are regarded as indication of a degree of reticulate evolution in the *Rosaceae*. The fact that there are no chemotaxonomic characters which indicate any exclusive affinity between *Maloideae* and *Rosoideae* (x = 7) is taken to be a clear refutation of the hypothesis, mentioned earlier in this paper, that *Maloideae* did not evolve from primitive *Rosoideae* of x = 7, the previously regarded ancestral basic chromosome number for the *Rosaceae*.

Tab. 13. — 24 chemotaxonomic indicators of affinities between subfamilies of *Rosaceae*

	Number of + ve matches	
Subfamilies	Simple affinity	Exclusive affinity
Maloideae → *Prunoideae*	14	9
Maloideae → *Spiraeoideae*	7	3
Maloideae → *Rosoideae* (x = 9)	6	2
Maloideae → *Rosoideae* (x = 7)	2	0
Spiraeoideae → *Prunoideae*	4	1
Spiraeoideae → *Rosoideae* (x = 9)	4	1
Spiraeoideae → *Rosoideae* (x = 7)	2	1
Prunoideae → *Rosoideae* (x = 9)	3	0
Prunoideae → *Rosoideae* (x = 7)	2	1
Rosoideae (x = 9) → *Rosoideae* (x = 7)	1	0

Simple affinity: characters which in some instances are also shared by a subfamily other than the two subfamilies being compared.
Exclusive affinity: characters restricted to the two subfamilies being compared.

The investigation of phylogenetic interrelationships within the *Rosaceae* is a fascinating subject and it is hoped that this review of the chemotaxonomic data which is available will not only serve to pinpoint the areas which merit more detailed chemical study, but will also encourage plant morphologists, geographers and geneticists to give further attention to the many phylogenetic problems which remain within this important family.

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SOUHRN

Autor v práci kriticky hodnotí hypotézy o vzniku a vývoji podčeledí čeledi *Rosaceae*, založené především na morfologických znacích a základních chromosomových počtech, a předkládá schéma vývoje přihlížející také k chemotaxonomickým znakům. Evoluce patrně postupovala od ancestrální spiraeoidní skupiny s x = 9 k vývojovým předchůdcům podčeledi *Prunoideae* (x = 8). Aloploidií mezi těmito vývojovými větvemi vznikla skupina s x = 17 a volnými karpely, z níž se vyvinuly dnešní jabloňovité (*Maloideae*) s x = 17; to je v souladu s názory cytologů, genetiků i systematiků. Tavolníkovité (*Spiraeoideae*) vznikly přímo z výchozí skupiny s x = 9, kdežto rody podčeledi *Rosoideae* (x = 7) vznikly z vývojových předchůdců současných růžovitých s x = 9, odvozených z výchozí spiraeoidní skupiny. Přihlíží se také ke vztahům izolovaných rodů *Dichotomanthes, Quillaja* a *Exochorda*. Chemotaxonomické doklady jsou v souladu s tímto vývojovým schématem. I když morfologicky je možno *Maloideae* odvozovat přímo od podčeledi *Spiraeoideae*, chemotaxonomické znaky ukazují, že *Maloideae* jsou nejblíže příbuzné s podčeledí *Prunoideae*, v menší míře s podčeledí *Spiraeoideae*. Chemotaxonomicky nejsou *Maloideae* bezprostředně příbuzné s podčeledí *Rosoideae* (x = 7).

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