

Flavonoids as markers of taxonomic relationships in the genus *Sorbus* in Europe

Flavonoidy jako ukazatelé taxonomické příbuznosti evropských druhů rodu *Sorbus*

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CHALLICE J.¹) et M. KOVANDA²) (1978): Flavonoids as markers of taxonomic relationships in the genus *Sorbus* in Europe. — Preslia, Praha, 50 : 305—320.

The European species of the genus *Sorbus* L. em. CRANTZ have been surveyed for the presence of flavone O-glycosides and flavone C-glycosides. Within the primary sexual species, vitexin (apigenin 8-C-glucoside) is restricted to *Sorbus torminalis* (L.) CRANTZ and *S. chamaemespilus* (L.) CRANTZ, both of which represent separate subgenera, *Torminaria* (DC.) C. KOCH and *Chamaemespilus* (DC.) C. KOCH, respectively. Four different flavone O-glycosides are restricted to *S. torminalis* alone, of the primary sexual species. The occurrence of these flavonoids in certain hybrids and hybridogeneous species has proved of value in the diagnosis of their parentage. The subgenera *Aria* PERS., *Cormus* (SPACH) DUCHARTRE and *Sorbus* completely lack flavone O- and C-glycosides. The phylogenetic implications of the results are discussed and the possibility is considered that the subgenera of *Sorbus* represent lines of polyphyletic evolution.

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INTRODUCTION

Sorbus L. em. CRANTZ has long been recognized as a taxonomically difficult genus in Europe (WARBURG et KÁRPÁTI 1968). The genus, whose present principal source of diversity lies in Europe, is still apparently in an active state of speciation. A prominent factor in its continuing evolution is interspecific hybridization, combined with polyploidy and apomixis (LLJEFORS 1955, KOVANDA 1961a, b); this produces the intricate variation pattern which is primarily responsible for the taxonomic complexity of the genus.

All primary species of *Sorbus* are diploid and sexual with the basic chromosome number of $x = 17$ which is common to all *Maloideae*. The great majority of hybridogeneous species are apomictic tetraploids with a few apomictic triploids. Here, *Sorbus* is more akin to *Crataegus*, *Malus* and *Cotoneaster* than to *Pyrus* where polyploidy and apomixis are unknown in the natural state (ZIELINSKI et THOMPSON 1967). Indeed, *Pyrus* is no longer in an active state of speciation and, in further contrast to *Sorbus*, its principal source of diversity lies in the region of Eastern Asia; in Europe *Pyrus* is poorly represented.

It now seems clear that *Sorbus* s. l.¹) consists of five easily recognizable

¹) The Asian genus *Micromeles* is sometimes described as a subgenus of *Sorbus* (e.g. REHDER 1940) but in our opinion *Micromeles* is sufficiently distinctive in its morphology and geographic range to be separated from *Sorbus*. The endemic N. American genus *Aronia*, although particularly closely related to *Sorbus*, is now universally considered as a separate genus on the basis of similar criteria.

groups treated as sections (FRITSCH 1898—99) or subgenera (KOVANDA 1961a): the polymorphic *Aria* and *Sorbus* s. str. and the monotypic *Torminaria* [*S. torminalis* (L.) CRANTZ], *Chamaemespilus* [*S. chamaemespilus* (L.) CRANTZ] and *Cormus* (*S. domestica* L.)²) This pattern of primary sexual species is relatively a simple one, contrasting with the complex range of apomictic and hybridogeneous species which exists throughout Europe. The subgenera of *Sorbus* are connected by many hybrids and hybridogeneous species (e.g. KÁRPÁTI 1960, KOVANDA 1961b); it is interesting to note that all hybrids so far recognized involve a member of the subgenus *Aria*, which seems to occupy a key position in the hybridization process. Of the five subgenera, all except *Cormus* are known to produce hybrids. The remaining four subgenera do not interbreed freely: *Sorbus* s. str., *Torminaria* and *Chamaemespilus* are able to hybridize with *Aria* (and vice versa) but *Sorbus* s. str., *Torminaria* and *Chamaemespilus* are unable to hybridize with each other.

The five subgenera differ by leaf shape, vernation of leaves, reproductive morphology and floral biology. They have often been treated as separate genera (see e.g. MEDICUS 1793, ROEMER 1847, DECAISNE 1874, KOEHNE 1890, BECK 1892) or merged as subgenera or sections with *Pyrus* or *Crataegus* (see e.g. WILLDENOW 1809, DECANDOLLE 1825, FOCKE 1892). The present circumscription of the genus did not become established until FRITSCH (1898—99). The subgenera may be briefly described as follows:

subg. *Torminaria* (DC.) C. KOCH

Trees, rarely shrubs. Leaves simple. Vernation plicate. Flowers protogynous. Calyx teeth erect, entire, glandular, dying after florescence. Petals white, patent. Ovary inferior. Carpels 2, coalescent up to 1/2 of styles. Styles glabrous at base. Fruits brown, densely dotted. Mesocarp homogeneous. Sclereids present, rarely almost missing. Endocarp thick, tough.

Torminaria occupies a rather isolated position not only within *Sorbus* but even within the *Maloideae* as a whole (see DECAISNE 1874, KOEHNE 1890, KOVANDA 1961a). By the structure of the endocarp it approaches *Crataegus* but it differs considerably by the coalescent styles and the absence of calyx in fruit. It cannot be derived from any other subgenus of *Sorbus*. The subgenus is European in its distribution, extending to SW. Asia and N. Africa.

subg. *Chamaemespilus* (DC.) C. KOCH

Shrubs. Leaves simple. Vernation involute. Flowers homogamous. Calyx teeth erect, entire, glandular, persistent in fruits. Petals red, erect. Ovary almost inferior. Carpels 2, rarely 3, coalescent nearly to top of ovary cells. Styles free, lanuginous at base. Fruits brownish-red, sparsely dotted. Mesocarp heterogeneous. Sclereids absent. Endocarp cartilaginous.

The anatomical structure of the mesocarp suggests relationships to *Aria*. It is important to note that a heterogeneous mesocarp (that is one containing groups of large cells with tannins and chromoplasts, see DECAISNE 1874, KOVANDA 1961a) is found only in the subgenera *Aria* and *Chamaemespilus* and in the Asian genus *Micromeles*. By the homogamous flowers and erect petals, however, *Chamaemespilus* differs from all other subgenera. ROEMER (1847) first classified it as a separate genus. The subgenus is confined to the mountains of W., C. and S. Europe.

²) The nomenclature of these subdivisions is arbitrary and liable to change.

subg. *Aria* PERS.

Shrubs or trees. Leaves simple. Vernation plicate. Flowers proterogynous. Calyx teeth patent to reclinate, entire, eglandular, persistent in fruit. Petals white to yellowish, patent. Ovary semi-inferior. Carpels 2-3, coalescent by their basal parts (up to 2/3 or 3/4 of ovary cells). Styles free, lanuginous at base. Fruits red, rarely orange or brownish, dotted. Mesocarp heterogeneous. Sclereids absent. Endocarp cartilaginous.

Aria is a relatively primitive group. A certain progress is seen in the reduction of the number of carpels. The evolutionary ancestors of *Aria* are likely to have had a pentamerous gynoeceium. Morphologically, *Aria* cannot be derived from *Chamaemespilus*, the latter being a rather specialized group (possibly a blind alley of evolution). It could possibly be derived from an ancestor of *Torminaria* but its origin from *Crataegus* appears more likely. The subgenus contains a number of species widely distributed in Europe and Asia.

subg. *Cormus* (SPACH) DUCHARTRE

Trees. Leaves pinnate. Vernation conduplicate. Flowers proterogynous. Calyx teeth patent, entire, eglandular, persistent in fruit. Petals white or rarely pinkish, patent. Ovary semi-inferior. Carpels 5, coalescent up to top of ovary cells. Styles free, lanuginous at base. Fruits yellow or reddish, dotted. Mesocarp homogeneous. Sclereids present. Endocarp thin, membranous.

A subgenus closely resembling *Sorbus* s. str. in its vegetative parts but differing principally by the morphology of fruit and flower. The gynoeceium is pentamerous and syncarpic (with free styles). It would appear that *Cormus* originated from the same stock as *Sorbus* s. str. but prior to it (that is, prior to the reduction of the number of carpels). The similarity of the leaf-shape may be due to convergent evolution. Alternatively, both *Cormus* and *Sorbus* s. str. may have evolved directly from *Crataegus*. It seems impossible for them to have arisen from *Torminaria* or *Chamaemespilus*. The only species, *S. domestica* L., is south European, extending to C. Europe, N. Africa and Asia Minor.

subg. *Sorbus*

Trees or shrubs. Leaves pinnate. Vernation conduplicate. Flowers proterogynous. Calyx teeth erect, finely toothed, glandular, persistent and often pulpose at base in fruit. Petals white, rarely pink, patent. Ovary semi-inferior. Carpels 3, rarely 2 or 4, coalescent by their basal parts only. Styles free, lanuginous at base. Fruits red, rarely yellow, smooth. Mesocarp homogeneous. Sclereids present. Endocarp thin, membranous.

It seems certain that *Sorbus* s. str. originated from primitive *Aria*, before the process of coalescence of carpels had begun. The extent to which the ovary is united with the receptacle and the structure of the endocarp are very much the same. A primitive character is the almost apocarpic gynoeceium. In both *Aria* and *Sorbus* s. str. the number of carpels is subject to variation. The subgenus is widely distributed in the temperate zone of the northern hemisphere. The type species is *S. aucuparia* L.

WARBURG et KÁRPÁTI (1968) in *Flora Europaea* provide a very full listing of the European species of *Sorbus*, belonging to the five subgenera as listed above.

It is the purpose of the present investigations to survey the flavone O- and C-glycosides of the European³⁾ *Sorbus* species in order to gain further

³⁾ In *S. domestica* and *S. graeca*, specimens from the Asian part of Turkey were also included.

insight into the evolutionary relationships between the various species and hybrid complexes and to reconsider the many taxonomic treatments previously proposed.

Earlier chemotaxonomic surveys (CHALLICE 1972, 1974) revealed the presence of flavone O-glycosides in the leaves of *S. torminalis* and in the hybridogeneous *S. intermedia* but did not reveal the presence of flavone C-glycosides⁴) in *Sorbus*, although they were found in the closely related *Aronia*. In this same survey, quercetin 4'-glucoside was detected in trace amounts in the leaf of *S. aucuparia* L., *S. decora* C. K. SCHN. and *S. commixta* HEDL. Flavanone glycosides appeared to be restricted to *S. commixta* HEDL., *S. tianshanica* RUPR., *S. vilmorinii* C. K. SCHN. and *S. koehneana* C. K. SCHN. (all belonging to the subgenus *Sorbus* s. str.). A glycoside of the rare flavonol, 8-methoxykaempferol, has been found in *S. aucuparia* by JERZMANOWSKA et KAMECKI (1973) and work is currently in progress by us to find a chromatographic system which is able to resolve this new flavonol and its glycoside(s) from the more common flavonoids present. It is possible that this new flavonoid will be of value as an additional taxonomic indicator. A preliminary account of the investigation described in this paper has already been published (CHALLICE et KOVANDA 1978).

MATERIALS AND METHODS

Extraction of flavonoids

Specimens were received as either fresh leaf or dried herbarium leaf; the sources are indicated in Table 1. The procedures for the extraction and subsequent acid hydrolysis of the flavonoids are basically as described in CHALLICE (1974). Dried herbarium leaf (0.2 g) was moistened with 0.2 ml distilled water, 4 ml ethanol was added and this was boiled for a short time in a 2.3 cm × 5 cm specimen tube. The leaf was cut into small pieces and the extraction completed by leaving the stoppered tube to stand for at least a week. Fresh leaf (2 g) was extracted with 10 ml ethanol in a similar manner.

Acid hydrolysis

1 ml of the above ethanol leaf extract (= 200 mg fresh leaf or 50 mg dried herbarium leaf) was pipetted into a 15 cm × 0.7 cm tube and 1 ml 4N hydrochloric acid added. After sealing, the contents were mixed and the tubes placed in a boiling waterbath for 6 hours. The tubes were then cooled, opened and the contents evaporated to near-dryness in vacuo at 50° C, taken up in 2 ml water and the flavonoids extracted with 0.4 ml amyl alcohol.

Paper chromatography

Portions of the original unhydrolysed leaf extracts, and of the hydrolysed leaf extracts (each equivalent to 50 mg fresh leaf or to 25 mg dried herbarium leaf) were examined separately by two-dimensional paper chromatography. Whatman No. 1 chromatography paper, sheets 36 cm square, were used, run in the first direction with sec-butanol : acetic acid : water (70 : 2 : 28) for 17 hours, and in the second direction (at right angles to the first) with acetic acid : water (2 : 98) for 20–30 hours, over-run with the end of the sheet serrated. Spots of flavonoid glycosides

⁴ Flavone C-glycosides (where the glycosidic moiety is directly attached to a carbon atom of the flavonoid) are biosynthetically and phylogenetically quite distinct from the more common flavone O-glycosides (where the glycosidic moiety is attached to a carbon atom of the flavonoid via an oxygen bridge). Similarly, the flavone O-glycosides are also biosynthetically and phylogenetically distinct from the almost ubiquitous flavanol O-glycosides (i.e. 3-hydroxyflavone O-glycosides). For further information on flavonoid chemistry, see, for example, HARBORNE, MABRY et MABRY (1975). Chemical formulae of the flavone glycosides which have been found in *Sorbus* are given in Figs. 2 and 3.

Tab. 1. — *Sorbus* specimens examined

| Species | Specimen no. | Locality |
|---|--------------|---|
| (1) <i>S. domestica</i> L. | 1 | Br: Arley Castle Arbor, Worcs., HUTCHINSON 1943 (K) |
| | 2 | Gr: Greece, ATCHLEY 939, 1931 (K) |
| | 3 | Ju: Bosnia, GOFAZDA, VANDAS 1896 (PR) |
| | 4 | Tu: Molbai, A. CALLIER 1900 (PR) |
| | 5 | Tu: Paphlagonia, Karkün, P. SINTENIS 1892 (PR) |
| (2) <i>S. aucuparia</i> L. subsp. <i>aucuparia</i> | 1 | Br: Kew Arboretum, Roths |
| | 2 | Cz: Plešivec Hill, near Jince, WC. Bohemia, MK 1976 (PR) |
| | 3 | Cz: Vej Hulce Wood near Březina, distr. Jindřichův Hradec, MK 1976 (PR) |
| | 4 | Cz: On road from Račín to Velké Dářko, Žďárské vrchy Mts., MK 1977 (PR) |
| | 5 | Cz: Hutě near Přibraz, distr. Jindřichův Hradec, MK 1977 (PR) |
| | 6 | Cz: Summit area of Mt. Králický Sněžník (1426 m), E. Sudeten Mts., MK 1976 (PR) |
| | 7 | Cz: Near Pančice Waterfalls, Krkonoše Mts., MK 1976 (PR) |
| subsp. <i>glabrata</i> (WIMM. et GRAB.) HAYEK | 6 | Cz: Summit area of Mt. Králický Sněžník (1426 m), E. Sudeten Mts., MK 1976 (PR) |
| | 7 | Cz: Near Pančice Waterfalls, Krkonoše Mts., MK 1976 (PR) |
| (3) <i>S. torminalis</i> (L.) CRANTZ | 1 | Ge: Tübingen, DÜLL 1959 (K) |
| | 2 | Br: Portishead Wood, N. Somerset, J. W. WHITE 1923 (BRIST) |
| | 3 | Br: Kings Wood, Yatton, N. Somerset, D. FRY 1888 (BRIST) |
| | 4 | Cz: Nižbor, woodland on road to Dřevíč, distr. Beroun, MK 1976 (PR) |
| | 5 | Cz: Hradiště Hill, České středohoří Mts., N. Bohemia, MK 1976 (PR) |
| | 6 | Cz: Bílá stráň, České středohoří Mts., N. Bohemia, MK 1968 (PR) |
| | 7 | Cz: Homole Hill, near Vrané nad Vltavou, C. Bohemia, MK 1976 (PR) |
| | 8 | Cz: Štěpánovská hora Hill, near Štěpánov, České středohoří Mts., N. Bohemia, MK 1977 (PR) |
| | 9 | Cz: Kalvárie Hill, near Litoměřice, České středohoří Mts., N. Bohemia, MK 1977 (PR) |
| | 10 | Cz: Bořeň Hill, near Bílina, České středohoří Mts., N. Bohemia, MK 1977 (PR) |
| | 11 | Cz: Dražovka Wood, near Hořovice, WC. Bohemia, MK 1977 (PR) |
| (4) <i>S. chamaemespilus</i> (L.) CRANTZ | 1 | Cz: Summit of Mt. Salátin (1631 m), Nízke Tatry Mts., MK 1965 (PR) |
| | 2 | Cz: Summit of Mt. Tanečnica (1678 m), Nízke Tatry Mts., MK 1965 (PR) |
| | 3 | Cz: Summit of Mt. Kraková hoľa (1753 m), Nízke Tatry Mts., MK 1965 (PR) |
| | 4 | Au: Tirol, Schönberg near Luttach, G. TREFFER 1895 (PR) |
| | 5 | Ju: Crna Gora, Durmitor Mts., Lokva Lake, near Žabljak, P. SILLINGER et M. DEYL 1933 (PR) |
| (5) <i>S. aria</i> (L.) CRANTZ | 1 | Br: Kew Arboretum, GILMOUR 1933 |
| | 2 | Cz: Plešivec Hill, near Jince, WC. Bohemia, MK 1976 (PR) |

Tab. 1 (contd.)

| Species | Specimen no. | Locality |
|---|--------------|--|
| | 3 | Cz: Summit area of M. Klak (1395 m), Velká Fatra Mts., MK 1967 (PR) |
| | 4 | Cz: On road from Počůvanské jazero to Mt. Sitno, Štiavnické pohorie Mts., MK 1966 (PR) |
| | 5 | Cz: Lipská hora Hill, near Medvědice, České středohoří Mts., N. Bohemia, MK 1977 (PR) |
| | 6 | Cz: N. slope of Střev Hill, near Karlštejn, C. Bohemia, MK 1977 (PR) |
| | 7 | Cz: Raštún Hill, Malé Karpaty Mts., W. Slovakia, MK 1977 (PR) |
| (6) <i>S. graeca</i> (SPACH) KOTSCHY | 1 | Ju: Crna Gora, Njeguš, J. ROHLENA 1903 (PR) |
| | 2 | Tu: Paphlagonia, Küre-Nahas, P. SINTENIS 1902 (PR) |
| (6) <i>S. porrigentiformis</i> E. F. WARBURG | 1 | Br: Bracken Hill, Bristol, JC 1977 |
| (6) <i>S. eminens</i> E. F. WARBURG | 1 | Br: Leigh Woods, Bristol (type locality), JC 1977 |
| (6) <i>S. wilmottiana</i> E. F. WARBURG | 1 | Br: Sea Mill, Bristol (type locality), JC 1977 |
| (6) <i>S. porrigens</i> HEDL. | 1 | Hb: Scalp, Co. Wicklow, J. P. BRUNKER 1932 (PR) |
| (7) <i>S. rupicola</i> (SYME) HEDL. | 1 | Br: Burrington Combe, N. Somerset, J. W. WHITE 1902 (BRIST) |
| (8) <i>S. danubialis</i> (JÁV.) KÁRPÁTI | 1 | Cz: Plešivec Hill, near Litoměřice, České středohoří Mts., N. Bohemia, MK 1976 (PR) |
| | 2 | Cz: Bořeň Hill, near Bílina, České středohoří Mts., N. Bohemia, MK 1977 (PR) |
| | 3 | Cz: Bezděz Hill, near Doksy, N. Bohemia, MK 1977 (PR) |
| (8) <i>S. umbellata</i> (DESF.) FRITSCH | 1 | Gr: Ajon Oros, Athos, J. WAGNER 1934 (PR) |
| (9) <i>S. minima</i> (A. LEY) HEDL. | 1 | Br: Near Crickhowell, Brecon, H. J. RIDDELSDELL 1900 (BRIST) |
| (11) <i>S. austriaca</i> (G. BECK) HEDL. | 1 | Cz: Summit area of Mt. Klak (1395 m), Velká Fatra Mts., MK 1967 (PR) |
| | 2 | Cz: Vyšná Revúca, on road to Čierny kameň, Velká Fatra Mts., MK 1964 (PR) |
| | 3 | Cz: Summit area of Mt. Rozsutec (1606 m), Malá Fatra Mts., MK 1965 (PR) |
| | 4 | Au: Lichtenstein near Judenburg, E. PREISSMANN 1897 (BRIST) |
| (11) <i>S. anglica</i> HEDL. | 1 | Br: Leigh Woods, Bristol (type locality), JC 1977 |
| | 2 | Br: Nightingale Valley (N. side), anon. 1964 (BRIST) |
| (12) <i>S. thuringiaca</i> C. K. SCHN. | 1 | Br: Kew Arboretum, KNAPHILL N. 895 - 37 |
| | 2 | Br: VC 100, gorge off Glen Cateol, Arran, anon. 1895 (BRIST) |
| | 3 | Br: near Gogar Station, anon. 1910 (BRIST) |
| (13) <i>S. hybrida</i> L. | 1 | Br: Kew Arboretum, BUTCHER 400 - 26 |
| (14) <i>S. meinichii</i> (LINDEB.) HEDL. | 1 | No: Holmestrand, J. DYRING 1909 (PR) |
| (15) <i>S. intermedia</i> (EHRH.) PERS. | 1 | Br: Kew Arboretum, 103.27 AA |
| | 2 | Br: Wood to the west of Griccieth, N. Wales, J. W. WHITE 1895 (BRIST) |
| | 3 | Cz: 3, Řičanská Street, Prague, MK 1976 (PR) |
| | 4 | Su: Glasbacken near Skara, E. ALMQVIST 1911 (PR) |
| | 5 | Su: Berg, O. BÖKMAN 1931 (PR) |
| | 6 | Rs(B): Saaremaa Island, K. R. KÜFFER 1902 (PR) |

Tab. 1 (contd.)

| Species | Specimen no. | Locality |
|---|--------------|--|
| (16) <i>S. latifolia</i> (LAM.) PERS. | 1 | Cz: University Botanic Garden, Prague, MK 1977 (PR) |
| (16) <i>S. devoniensis</i> E. F. WARBURG | 1 | Br: Near front entrance to Bracken Hill, Bristol, JC 1977 |
| (16) <i>S. decipiens</i> (BECHST.) IRM. | 1 | Ge: Thüringen, Waltershausen, J. BORNMÜLLER 1907 (PR) |
| (16) <i>S. multicrorenata</i> J. BORNM. ex DÜLL | 1 | Ge: Thüringen, Greifenstein near Blankenburg, J. BORNMÜLLER 1911 (PR) |
| (16) <i>S. subcordata</i> J. BORNM. ex DÜLL | 1 | Ge: Arnstadt, REINECKE et RUDOLPH 1884 (PR) |
| (16) <i>S. bakonyensis</i> (JÁV.) KÁRPÁTI | 1 | Hu: Vanyarc near Keszthely, S. JÁVORKA 1927 (PR) |
| (16) <i>S. bohémica</i> KOVANDA | 1 | Cz: Hradiště Hill, České středohoří Mts., N. Bohemia, MK 1976 (PR) |
| | 2 | Cz: Boreč Hill, České středohoří Mts., N. Bohemia, MK 1976 (PR) |
| | 3 | Cz: Plešivec Hill, near Litoměřice, České středohoří Mts., N. Bohemia, MK 1976 (PR) |
| (16) <i>S. bristoliensis</i> WILMOTT | 1 | Br: Clifton Down, Bristol, J. W. WHITE 1909 (BRIST) |
| | 2 | Br: Leigh Woods, Bristol (type locality), JC 1977 |
| | 3 | Br: Church Road, outside Bracken Hill, Bristol (No. 4), JC 1977 |
| | 4 | Br: Nightingale Valley, N. Somerset, J. W. WHITE 1890 (BRIST) |
| (16) <i>S. pseudosemiincisa</i> BOROS | 1 | Hu: Szappanos-völgy Valley, near Csákberény, A. BOROS 1934 (PR) |
| (16) <i>S. pseudovertesensis</i> BOROS | 1 | Hu: Csatorna-völgy Valley, near Csákberény, A. BOROS 1935 (PR) |
| (16) <i>S. semiincisa</i> BORB. | 1 | Hu: Between Piliszentiván and Piliscsaba, J. B. KÜMERLE 1909 (PR) |
| (16) <i>S. slovenica</i> KOVANDA | 1 | Cz: Valley of Hrabutnica, near Nové Mesto nad Váhom (type locality), MK 1958 (PRC) |
| (16) <i>S. vertesensis</i> BOROS | 1 | Hu: Meszes-völgy Valley, near Csákberény, A. BOROS 1934 (PR) |
| (17) <i>S. sudetica</i> (TAUSCH) FRITSCH | 1 | Cz: Near Pančice Waterfalls, Krkonoše Mts., MK 1976 (PR) |
| (18) <i>S. margittaiana</i> (JÁV.) KÁRPÁTI | 1 | Cz: Summit area of Mt. Suchý (1468 m), Malá Fatra Mts. (type locality), MK 1964 (PR) |
| (18) <i>S. hostii</i> (JACQ. f.) C. KOCH | 1 | Cz: Summit of Mt. Salatín (1631 m), Nízke Tatry Mts., MK 1965 (PR) |
| (18) <i>S. ambigua</i> (DECAISNE) NYMAN | 1 | Cz: Summit area of Mt. Čierny kameň (1481 m), Veľká Fatra Mts., MK 1964 (PR) |

Key to abbreviations: MK — collected by M. Kovanda in Czechoslovakia, JC — collected by J. Challice in England.

were visualized on the dried sheets by ultraviolet absorption, yellow fluorescence in the presence of ammonia fumes (and after dipping in an ethanolic solution of aluminium chloride), green, violet or blue colours with Gibb's reagent and brown colours with diazonium reagent as described in previous papers (CHALLICE et WILLIAMS 1968a, b). Under the hydrolysis conditions employed,

all flavone C-glycosides remain intact, whilst all flavonoid O-glycosides are hydrolysed to the flavonoid aglycone + sugar. Comparison of chromatograms of hydrolysed leaf extracts with those of unhydrolysed leaf extracts made it possible to locate the flavone C-glycoside spots on the latter chromatograms. Fig. 1 illustrates the paper chromatographic separation of flavone glycosides.

Sorbus material

For convenience the *Sorbus* specimens examined are listed in Table 1, in the order in which they are listed in *Flora Europaea*. The number immediately before each species name refers to the section number in *Flora Europaea*.

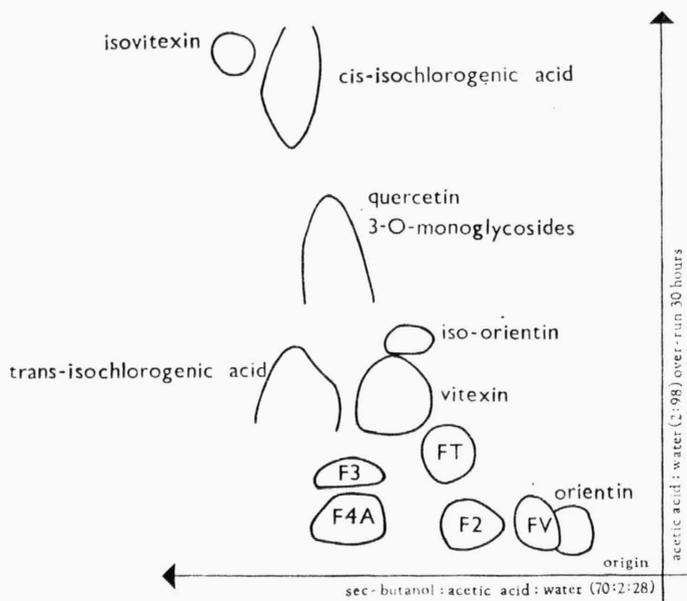


Fig. 1. — Composite two-dimensional paper chromatographic map of some flavone C- and O-glycosides of *Sorbus*. The spots representing the *trans*- and *cis*-isomers of isochlorogenic acid and the complex of quercetin 3-O-monoglycosides (which are present in most species of *Sorbus*) are included for reference purposes. Orientin (luteolin 8-C-glucoside) and iso-orientin (luteolin 6-C-glucoside) have not been found in *Sorbus*, but since they occur in related genera of the *Maloideae* (CHALLICE 1974) they also are shown for reference purposes. Full details of the various colour reactions used in the detection of these phenolics are given in CHALLICE et WILLIAMS (1968a, b) and CHALLICE (1972, 1973, 1974). After acid hydrolysis the flavone C-glycosides alone remain unchanged on the chromatogram.

RESULTS AND DISCUSSION

The results of the paper chromatographic survey for the occurrence of certain flavone glycosides of known taxonomic significance in European *Sorbus* species are given in Table 2. Vitexin (apigenin 8-C-glucoside) has previously been found in certain other genera of the *Rosaceae* (CHALLICE 1974); related flavone C-glycosides such as isovitexin (apigenin 6-C-glucoside), orientin (luteolin 8-C-glucoside) and iso-orientin (luteolin 6-C-glucoside) could not be found in any of the *Sorbus* specimens which were examined. The five flavone O-glycosides which were found in the present *Sorbus* specimens have all previously been detected elsewhere and their chemical structure determined: F2

Tab. 2. — Occurrence of vitexin (apigenin 8-C-glucoside) and five flavone O-glycosides in *Sorbus*

| Species | Specimen no. | Vitexin | Flavone O-glycosides | | | | | |
|--|------------------------|---------|----------------------|-------|----|-------|----|---|
| | | | FT | FV | F2 | F4A | F3 | |
| <i>S. domestica</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 5 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. aucuparia</i> subsp. <i>aucuparia</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 5 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | subsp. <i>glabrata</i> | 6 | 0 | 0 | 0 | 0 | 0 | 0 |
| | 7 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. torminalis</i> | 1 | t | + (+) | + | 0 | 0 | 0 | |
| | 2 | ++ | 0 | + | 0 | 0 | 0 | |
| | 3 | ++ | 0 | ++ | 0 | + (+) | 0 | |
| | 4 | ++ | (++) | + | 0 | 0 | 0 | |
| | 5 | ++ | (++) | + | t | 0 | 0 | |
| | 6 | ++ | (++) | + (+) | 0 | + | 0 | |
| | 7 | ++ | (++) | + (+) | 0 | 0 | 0 | |
| | 8 | + | ++ | ++ | 0 | 0 | 0 | |
| | 9 | (+) | ++ | ++ | 0 | 0 | 0 | |
| | 10 | + | ++ | ++ | 0 | 0 | t | |
| | 11 | t | ++ | + | 0 | 0 | 0 | |
| <i>S. chamaemespilus</i> | 1 | ++ | 0 | 0 | 0 | 0 | 0 | |
| | 2 | ++ | 0 | 0 | 0 | 0 | 0 | |
| | 3 | ++ | 0 | 0 | 0 | 0 | 0 | |
| | 4 | ++ | 0 | 0 | 0 | 0 | 0 | |
| | 5 | ++ | 0 | 0 | 0 | 0 | 0 | |
| <i>S. aria</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 5 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 6 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 7 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. graeca</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. porrigentiformis</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. eminens</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. wilmottiana</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. porrigens</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. rupicola</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. danubialis</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. umbellata</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. minima</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. austriaca</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 4 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. anglica</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | |
| <i>S. thuringiaca</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 2 | 0 | 0 | 0 | 0 | 0 | 0 | |
| | 3 | 0 | 0 | 0 | 0 | 0 | 0 | |

Tab. 2 (contd.)

| Species | Specimen no. | Vitexin | Flavone O-glycosides | | | | |
|-----------------------------|--------------|---------|----------------------|-------|-----|-------|----|
| | | | FT | FV | F2 | F4A | F3 |
| <i>S. hybrida</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>S. meinichii</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>S. intermedia</i> | 1 | t | + (+) | + | t | 0 | 0 |
| | 2 | t | (+) | + (+) | 0 | 0 | 0 |
| | 3 | 0 | (+) | + | t | t | 0 |
| | 4 | (t) | + | + | 0 | 0 | 0 |
| | 5 | t | + | + | 0 | 0 | 0 |
| | 6 | t | + | + | 0 | 0 | 0 |
| <i>S. latifolia</i> | 1 | t | + | + | t | ++ | t |
| <i>S. devoniensis</i> | 1 | t | + | + | 0 | 0 | t |
| <i>S. decipiens</i> | 1 | (+) | ++ | + | 0 | + | t |
| <i>S. multirenata</i> | 1 | t | + | ++ | (+) | + (+) | t |
| <i>S. subcordata</i> | 1 | (+) | + | ++ | t | 0 | t |
| <i>S. bakonyensis</i> | 1 | 0 | + | + | t | 0 | 0 |
| <i>S. bohemica</i> | 1 | 0 | 0 | + (+) | t | + (+) | 0 |
| | 2 | 0 | (+) | ++ | t | + (+) | 0 |
| | 3 | 0 | (+) | + | t | + (+) | 0 |
| <i>S. bristoliensis</i> | 1 | t | 0 | ++ | t | + (+) | 0 |
| | 2 | t | + | ++ | (+) | 0 | t |
| | 3 | t | ++ | ++ | (+) | 0 | t |
| | 4 | (+) | ++ | ++ | t | 0 | 0 |
| <i>S. pseudosemiincisa</i> | 1 | t | + | ++ | t | 0 | t |
| <i>S. pseudovertesensis</i> | 1 | t | + | ++ | (+) | 0 | t |
| <i>S. semiincisa</i> | 1 | 0 | + | ++ | 0 | 0 | 0 |
| <i>S. slovenica</i> | 1 | 0 | t | ++ | t | + | 0 |
| <i>S. vertesensis</i> | 1 | (t) | + | ++ | (+) | 0 | 0 |
| <i>S. sudetica</i> | 1 | ++ | 0 | 0 | 0 | 0 | 0 |
| <i>S. margittaiana</i> | 1 | ++ | 0 | 0 | 0 | 0 | 0 |
| <i>S. hostii</i> | 1 | + (+) | 0 | 0 | 0 | 0 | 0 |
| <i>S. ambigua</i> | 1 | ++ | 0 | 0 | 0 | 0 | 0 |

Key to Table 2:

vitexin = apigenin 8-C-glucoside
 FT = luteolin 7-O-rhamnosylglucoside
 FV = luteolin 7-O-diglucoside
 F2 = luteolin 7-O-glucoside
 F4A = luteolin 4'-O-glucoside
 F3 = apigenin 7-glucoside

Scoring code: 0 = absent
 t = trace amount only
 + = small amount
 ++ = moderately strong spot
 () = reservations, score on low side

(luteolin 7-O-glucoside), F4A (luteolin 4'-O-glucoside) and F3 (apigenin 7-glucoside) in *Pyrus* (CHALLICE et WILLIAMS 1968a, b, CHALLICE 1973, CHALLICE et WESTWOOD 1973); FT (luteolin 7-O-rhamnosylglucoside) and FV (luteolin 7-O-diglucoside) in *Exochorda*, *Aronia* and *Sorbus* (CHALLICE 1972, 1973). Chemical formulae are given in Figs. 2 and 3. The present survey of European *Sorbus* has indicated that the flavone C-glycoside vitexin is restricted, within the primary sexual species, to *S. torminalis* and *S. chamaemespilus*, both of which represent separate subgenera, *Torminaria* and *Chamaemespilus*,

respectively (KOVANDA 1961a). The flavone O-glycosides appear to be restricted, within the primary sexual species, to *S. torminalis* alone. The finding of luteolin 4'-O-glucoside is of some interest since within the family *Rosaceae* it was previously known only in *Pyrus* (CHALLICE 1973, 1974). The remaining primary sexual species of *Sorbus*, *S. domestica* (subgenus *Cormus*), *S. aria* (subgenus *Aria*) and *S. aucuparia* (subgenus *Sorbus*) all completely lack both flavone C-glycosides and flavone O-glycosides. Thus the presence of

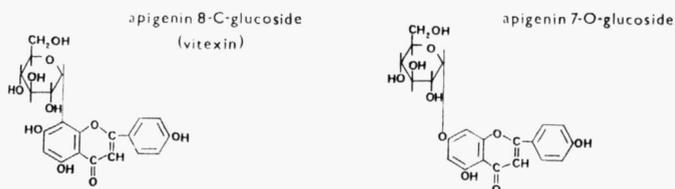


Fig. 2. — Chemical formulæ of the *Sorbus* flavone C-glycosides, vitexin, and the related apigenin 7-O-glucoside.

vitexin alone in a hybridogeneous species is indicative of the involvement of *S. chamaemespilus* and the presence of both vitexin and flavone O-glycosides is indicative of the involvement of *S. torminalis*.

Hence the presence of vitexin (unaccompanied by flavone O-glycosides) in *S. sudetica*, *S. margittaiana*, *S. hostii* and *S. ambigua* is indicative of the presence of *S. chamaemespilus* in each of these four hybridogeneous species, as previously suggested by KÁRPÁTI (1960) and KOVANDA (1965). Flavone O-glycosides (unaccompanied by vitexin) are also present in *S. bakonyensis*, *S. bohémica*, *S. semiincisa* and *S. slovenica*, which confirms the supposed involvement of *S. torminalis* in these hybridogeneous species (KOVANDA 1961b). It is unclear why vitexin is not present; possibly these taxa represent the result of back-crossing in which the genes for flavone C-glycosylation have become segregated from the genes for flavone O-glycosylation.

Both flavone O-glycosides and vitexin are found in *S. intermedia*, *S. latifolia*, *S. multicrenata*, *S. decipiens*, *S. subcordata*, *S. pseudosemiincisa*, *S. pseudovertesensis*, *S. vertesensis*, *S. bristoliensis* and *S. devoniensis* which supports the involvement of *S. torminalis* in their parentage. One doubtful specimen of *S. bristoliensis*, growing in the University of Bristol Botanic Gardens, was found to lack both vitexin and flavone O-glycosides which are clearly present in the tree from which the original type specimen was taken; here again the doubtful specimen is probably the result of back-crossing with the non-*S. torminalis* parent (i.e. *S. aria* s.l.). Unfortunately, the subgenera *Aria*, *Cormus* and *Sorbus* were not found to be sufficiently distinctive in their phenolics patterns for the facile detection of their members in hybrids to be possible. As intimated in the introduction to this paper, it is hoped that further investigations will reveal some chemotaxonomic markers for these subgenera.

The controversial apomictic species *S. intermedia* merits some further discussion here. Its hybrid nature was clearly recognized by early authors who invariably considered it to be *S. aria* × *S. aucuparia*. An analysis of

reproductive morphology (see KOVANDA 1961a) confirmed the involvement of these two species in its parentage. However, LILJEFORS (1955) observed that certain characteristics of *S. intermedia*, such as the yellowish-grey indumentum of the leaves, shape of the terminal tooth of the leaf-lobe, the extent to which the carpels are joined together and the brownish tinge of the fruit, were reminiscent of *S. torminalis* and went on to substitute this

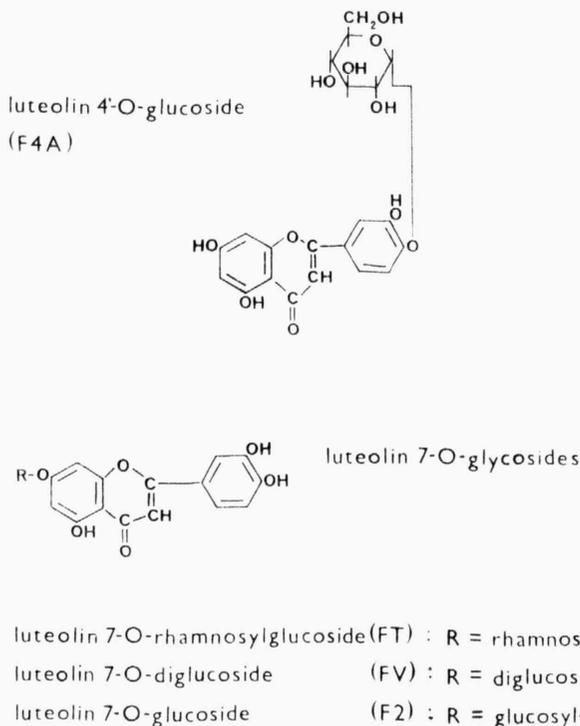


Fig. 3. — Chemical formulae of the *Sorbus* flavone O-glycosides, F4A, FT, FV and F2.

species for *S. aucuparia* in the parentage of *S. intermedia*. Of the characters listed by him, only the high degree of the coalescence of the carpels may be accepted as an argument for *S. torminalis*. It should be pointed out, however, that the same extent of coalescence is found in *S. mougeotii* (see KOVANDA 1961a) which even Liljefors himself recognized as a hybrid *S. aria* × *S. aucuparia*. The yellowish-grey indumentum of leaves is also known to occur in *S. aria* and the dentation of leaves is the same as in other *S. aria* × *S. aucuparia* hybrids, as is also the colour of fruit. All *S. aria* × *S. torminalis* hybrids and hybridogeneous species differ considerably from *S. intermedia* in having triangular leaf-lobes, ovary almost completely inferior, calyx teeth dry, often missing in fruit and densely dotted fruits. Characters like calyx teeth persistent and pulpose at the base in fruit and almost complete absence of lenticels on the fruits of *S. intermedia* clearly indicate the involvement of *S. aucuparia*. The discovery of flavone glycosides in *S. inter-*

media is most surprising therefore and difficult to account for on the basis of the present knowledge. A possibility would be that *S. intermedia* is a triple hybrid, combining the characters of *S. aria*, *S. aucuparia* and *S. torminalis*, or that it is a hybrid of *S. aucuparia* and a member of the subfamily *Maloideae* which is now extinct.

Phylogenetically it would not appear unreasonable, on the basis of both morphological and chemical evidence, to speculate that all five subgenera of *Sorbus* evolved as separate lines from primitive *Crataegus*. If this was in fact so, i.e. that *Sorbus* is of polyphyletic origin, then the genus *Sorbus* (as presently known) would have to be split into five separate genera. The

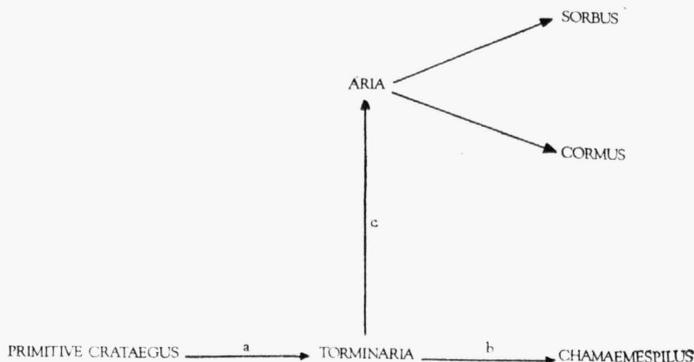


Fig. 4. — Phylogenetic scheme for the origins of the subgenera of *Sorbus* (A).

presence of distinctive phenolics such as arbutin in all species of *Pyrus* and dihydrochalcones in all species of *Malus* (see CHALLICE 1973, 1974) can be regarded as good evidence for the monophyletic nature of these genera but there does not appear to be any distinctive phenolic compound present in all species of *Sorbus* which would indicate a monophyletic origin for this genus. From a biochemical viewpoint the phylogenetic scheme for the origins of the subgenera of *Sorbus* seen in Fig. 4 would seem more satisfying and could involve the splitting of *Sorbus* into three genera only: (1) *Torminaria*, (2) *Chamaemespilus* and (3) *Aria* + *Cormus* + *Sorbus* s. str. This scheme would involve three distinct loss-mutations, i.e. (a) loss of orientin but retention of vitexin, (b) loss of flavone O-glycosides but retention of vitexin, and (c) loss of both flavone O- and C-glycosides. It is a well-known chemotaxonomic principle that once the genes for the biosynthesis of a particular compound are lost from a particular evolutionary line, then these genes will never re-appear in that line and hence the compound, once lost, will never again re-appear in that line. Thus, although it might be morphologically possible to derive the subgenus *Chamaemespilus* from *Aria*, this derivation is chemically impossible since a primitive taxonomic marker as significant as the flavone C-glycoside vitexin, once lost from a phylogenetic line, could never be regained. On the same principle, the chemotaxonomic evidence would also exclude the following derivations:

Chamaemespilus → *Torminaria*
Aria → *Torminaria*

| | | |
|-----------------------|---|-----------------------|
| <i>Cormus</i> | → | <i>Torminaria</i> |
| <i>Cormus</i> | → | <i>Chamaemespilus</i> |
| <i>Sorbus</i> s. str. | → | <i>Torminaria</i> |
| <i>Sorbus</i> s. str. | → | <i>Chamaemespilus</i> |

It is of some significance that none of these derivations are morphologically feasible.

Morphologically, it appears more likely that *Chamaemespilus* was derived from primitive *Crataegus* rather than from *Torminaria*. The latter has coalescent styles and could not possibly give rise to a group with free styles,

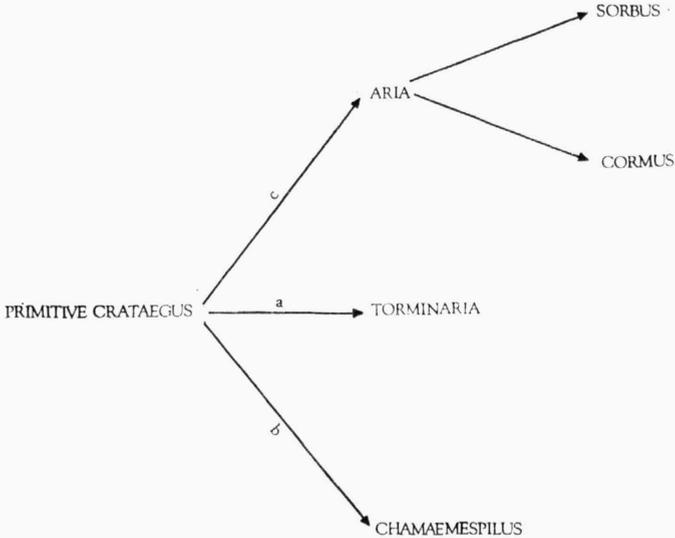


Fig. 5. — Phylogenetic scheme for the origins of the subgenera of *Sorbus* (B).

unless the concept of retrograde evolution is adopted. Thus it is possible that a phylogenetic scheme such as in Fig. 5 might have to be adopted, where the loss-mutations are as in the previous scheme. As previously, this scheme could involve the splitting of *Sorbus* into three genera only. The subgenera *Cormus* and *Sorbus* can both, on morphological grounds, be derived from *Aria* but as yet there is no positive chemical evidence to support this derivation.

It should be remembered that both the schemes are overall summaries of views given in the text and that they can only be very rough approximations to what in reality must have been a complex nexus of evolutionary relationships.

It is hoped that subsequent investigations will disclose the existence of additional flavonoid markers which will help to determine exactly to what extent the genus *Sorbus* is polyphyletic. In addition it is hoped to extend the survey to include non-European species of *Sorbus* and the related Asian genus *Micromeles*, and to consider the place of *Sorbus* in the overall phylogeny of the subfamily *Maloideae*.

ACKNOWLEDGEMENTS

Thanks are due to Dr D. Gledhill and Dr M. Smith, University of Bristol, and to Dr J. Soják, National Museum of Prague, for their kind co-operation in providing herbarium and/or fresh leaf specimens of some of the *Sorbus* species which were examined. Thanks are also due to the British Council and to the Czechoslovak Academy of Sciences for financing visits to Prague by Dr Challice, which have greatly facilitated these investigations.

SOUHRN

U evropských druhů jeřábů (*Sorbus* L. em. CRANTZ) bylo sledováno zastoupení flavonoidních O- a C-glykosidů. Z primárních, pohlavně se rozmnožujících druhů [*S. torminalis* (L.) CRANTZ, *S. chamaemespilus* (L.) CRANTZ, *S. aria* (L.) CRANTZ, *S. domestica* L. a *S. aucuparia* L.] se flavonoidní C-glykosid vitexin (apigenin 8-C-glukosid) vyskytuje jen u prvních dvou, tj. u břeku (*S. torminalis*) a mišpulky (*S. chamaemespilus*), které patří do samostatných podrodů *Torminaria* a *Chamaemespilus*. Výskyt flavonoidních O-glykosidů (luteolin 7-O-rhamnosylglukosid, luteolin 7-O-diglukosid, luteolin 7-O-glukosid a luteolin 4'-O-glukosid) je z primárních druhů omezen na *S. torminalis*. Pozoruhodné je zjištění luteolin 4'-O-glukosidu, který byl v čeledi *Rosaceae* až dosud znám jen u rodu *Pyrus* L. U podrodů *Aria*, *Cormus* a *Sorbus* nebyly flavonoidní O- a C-glykosidy zjištěny. Výskyt vitexinu (při absenci flavonoidních O-glykosidů) u *S. sudetica* (TAUSCH) FRITSCH, *S. margittaiana* (JÁV.) KÁRPÁTI, *S. hostii* (JACQ. f.) C. KOCH a *S. ambigua* (DECAISNE) NYMAN je důkazem přítomnosti mišpulky (*S. chamaemespilus*) v těchto hybridogenních druzích. Jak flavonoidní O-glykosidy, tak vitexin byly nalezeny u *S. intermedia* (EHRH.) PERS., *S. latifolia* (LAM.) PERS., *S. decipiens* (BECHST.) IRM., *S. bristolensis* WILMOTT, *S. devoniensis* E. F. WARBURG, *S. multicrenata* J. BORNM. ex DÜLL, *S. subcordata* J. BORNM. ex DÜLL, *S. pseudosemiincisa* BOROS, *S. vertesensis* BOROS a *S. pseudovertesensis* BOROS, což dokládá přítomnost břeku (*S. torminalis*) v jejich rodičovské kombinaci. Výskyt flavonoidních O-glykosidů (při absenci vitexinu) u *S. bakonyensis* (JÁV.) KÁRP., *S. bohémica* KOVANDA, *S. semiincisa* BOROS a *S. slovenica* KOVANDA potvrzuje rovněž podíl břeku (*S. torminalis*) na jejich vzniku. Absence vitexinu u těchto hybridogenních druhů ukazuje, že vznikly pravděpodobně zpětným křížením s některým druhem ze skupiny *Aria*. Výsledky studia naznačují, že z pěti podrodů rodu *Sorbus* (*Torminaria*, *Chamaemespilus*, *Aria*, *Cormus* a *Sorbus*) nejméně první tři reprezentují samostatné vývojové linie, dobře charakterizované i morfologií a geografickým rozšířením.

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Received December 28, 1977