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Biochemical and systematic study of the genus *Betula* L.

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Abstract

The division of the genus *Betula* L. accomplished on the basis of the flavonoid composition characteristic for the particular species; the proposed systematic classification also takes the chromosome number and geographical distribution into account. It showed the best agreement with the classification system suggested by Natho.

Key words: Betula L., Betulaceae, flavonol glycosides.

INTRODUCTION

The genus *Betula* is numerously represented in the Northern Hemisphere. The number of its taxa is now estimated as about 80 (Rehder 1974) to 100 (Natho 1976), but not further back than 75 years ago Winkler (1904) distinguished only 47.

The first more comprehensive systematic classification of this genus was presented by Regel (1868), and modified by Winkler (1904). Nevertheless, since the publication of Winkler's system a very large number of papers have appeared which describe new birch species from nearly all territories where the genus *Betula* occurs (Gunnarsson 1925, Vassilev 1963, 1965, 1969, 1970a, b, Dugle 1966, Brittain and Grant 1965a, b, 1966, 1967a, b, 1968a, b). As the new species were distinguished and described according to various criteria, the elaboration of an up-to-date system presented considerable difficulties. Although attempts were made by Sukachev (1911), Lindquist (1945, 1947), and others, to classify birches anew, they were limited to taxa occuring only in part of areas occupied by this genus. It was Rehder (1956, 1974) who first proposed a new approach to the genus *Betula* distin-

guishing 80 taxa and classifying them in 4 series and 28 main species. Natho (1976) presented a different classification based on his own studies and on those of Vassilev (1963, 1965, 1969, 1970a, b).

MATERIAL AND METHODS

The description of the material and of the methods of isolation, identification, and analysis of the flavonoid composition in the leaves of all specimens is given by Pawłowska (1980a, b, c, 1982a, 1983).

RESULTS

Examination of about 80 birches representative of 20 taxa (Table 1) and their hybrids, showed that their mature leaves contain flavonol, flavone, dihydroflavonol and flavanone, mono- and diglycosides as well as flavonol methyl ethers, and polyphenol acids. Flavonol and luteolin glycosides were most abundant. At the same time the set of the last-mentioned compounds was found to be generally stable and characteristic for every species (Pawłowska 1982b). Although only individual specimens of a few species were studied, nevertheless it was possible to make classification on the basis of just that characteristic qualitative composition.

DISCUSSION

Hänsel and Hörhammer (1954) carried out the first comparative studies of flavonoids in the family *Betulaceae* classified in accordance with the system of Prantl (i.e. comprising the genera *Betula, Alnus, Carpinus, Corylus, Ostrya* and *Ostryopsis*), the genus *Betula* including 14 taxa presumably by single specimens.

Hegnauer (1964), on the basis of the above findings, included the species of this family into 3 tribes, according to the flavonol glycoside predominant in their leaves:

1) with hyperoside (together with quercitrin and myricetin 3-digalactoside or rutin);
2) with myricitrin (as well as quercitrin and myricetin 3-digalactoside or rutin);
3) with rutin and additional hyperoside.

Consequently, it would be necessary to include the European species of the genus *Betula*, such as *B. pendula* Roth., *B. pubescens* Ehr., and

Table 1

Flavonol and some flavone glycosides of the genus *Betula* L.

Symbol of compound Taxon	grL	gK	grQ	gQ	g'Q	rQ	aQ	g'M	g_2'M	rgK	rM	g'R'	gL		
Sect. 1. *Acuminatae*															
B. maximowiczii (1)	+	—	++	negl.	++	negl	++	—	—	+	—	+	++	—	—
Sect. 2. *Betulenta*															
B. lenta (4)	++/[d]	—	++	+	++	+	+/[c]	+/[c]	—	+	++	—	+/[d]	—	—
B. lutea (4)	++/[d]	—	++	++	++	++	tr.	0	+/[d]	+	++	+/[c]	++	—	—
B. potanini (1)	—	—	++	negl.	++	+	+	—	—	++	++	—	++	—	—
B. grossa (1)	—	—	+++	+	+	+	negl	0	+	+	+++	—	+	—	—
B. albo-sinensis /[a]	?	?	+	?	—	+	?	?	—	?	+++	?	?	?	?
Sect. 3. *Albae*															
Subsect. *Verrucosae*															
B. pendula (11)	—	negl	—	—	++++	++	negl	0	+	—	—	+	—	—	—
ssp. *obscura* (4)	—	+	—	—	++++	++	negl	0	+	—	—	+/[d]	—	—	—
B. oycoviensis (12)	—	negl	—	negl/[d]	+++	+	+	0	+	negl/[d]	++	negl/[d]	—	—	—
B. japonica (2)	—	tr/[d]	—	—	++	++	negl	0	+	+	++	negl	+	—	—
B. "nova" (3)	—	—	—	+	++	+	++	0	++	++	+++	—	—	—	—
B. fontinalis (1)	—	—	—	—	–	+	negl	0	tr.	++	+++	negl	++	—	—
B. coerulea-grandis/[a]	?	?	—	?	—	+	?	0	+	?	+++	?	?	?	?
Subsect. *Betula*															
B. papyrifera (1)	—	—	—	—	—	+	negl	negl	+	+	+++	+	+	—	—
B. koehnei/[a]	?	?	—	?	—	+	?	0	+	?	+++	?	?	?	?
B. neoalascana (2)	—	—	—	++	++	+	negl	negl/[d]	+	+	+	+/[d]	+	—	—
B. papyrifera															
var. *commutata* (1)	—	—	—	negl	+++	+	tr.	0	+	+	++	+	+	—	—
B. turkiestanica (1)	—	tr.	—	—	+++	+	negl	0	+	—	—	+	+	—	—
B. pubescens															
ssp. *pubescens* (8)	—	negl	—	+/[c]	+++	+	+	0	+	—	—	+	+	—	—
ssp. *tortuosa*															
var. *tortuosa* (2)	—	tr.	++	++	+++	+	+	negl	+	—	—	negl	+	—	—
var. *carpatica* (5)	—	tr.	negl	+	+++	++	negl	0	++	—	—	negl	+	—	—
Sect. 4. *Neurobetula*															
B. utilis /[a]	?	?	—	?	+++	+	?	0	+	?	?	?	?	?	?
B. ermani /[a]	?	?	—	?	+++	+	?	0	+	?	?	?	?	?	?
B. insignis /[a]	?	?	—	?	+++	+	?	0	+	?	?	?	?	?	?
Sect. 5. *Nanae*															
B. nana (2)	—	negl	+	+	+++	+	negl	negl/[d]	—	—	—	—	—	—	—
B. humilis (5)	—	tr.	++++	+/[d]	negl	—	negl	—	—	—	—	—	—	—	—
B. middendorffii /[b]	?	?	?	?	+	—	?	?	?	?	?	?	?	+++	+

r. — trace amount; negl. — negligible amount; /[a] studied by Hänsel and Horhammer (1954); [b]/ studied by Glyzin and Bańkovskiy (1971); /[c] occurs only in some spacimens; /[d] occurs in the majority of specimens; 0 — as an intermediate metabolite; A — isohyperoside; B — myricetin 3-arabinoside. grL — luteolin 7-rutinoside; gK — kaempferol 3-glucoside; grQ — rutin; gQ — isoquercitrin; g'Q — hyperoside; rQ — quercitrin; aQ — quercetin 3-arabinoside; g'M — myricetin 3-galactoside; g_2'M — myricetin 3-digalactoside; rgK — kaempferol 3-rhamno-7-glucoside; rM — myricitrin; g'R' — isorhamnetin 3-galactoside; gL — luteolin 4'-glucoside; ( ) — number of studied specimens

B. nana L. besides other species and taxa of lower order closely related with them (e.g. *B. pubescens* ssp. *tortuosa)* into tribe 1, and *B. humilis* Schrk. into tribe 3. On the other hand, tribe 2 would comprise the taxa occurring in East-Central Asia and North America, such as *B. albo-sinensis* Burk., *B. coerulea-grandis* Blanch., *B. papyrifera* Marsch. and *B. fontinalis* Sarg. However, some doubts arise in the classification of *B. "nova"* containing the highest amount of myricitrin and at the same time a rather large amount of hyperoside. This problem would also concern e.g. *B. japonica* Sieb. and *B. oycoviensis* Bess. Likewise a large number of glycosides newly detected by Glyzin and Bańkovskiy (1971) and by Pałowska (1980a, b, c, 1982a) in the leaves of more numerous trees representing some other taxa additionally complicates the original system of classification introduced by Hegnauer (1964). Besides, his system does not correspond to any of the classification systems for the genus *Betula.*

In order to simplify the nomenclature of the compounds detected as biochemical characters, the present investigator introduced some letter symbols in a further part of this study, small letters denoting sugars and capital ones aglycones: a — arabinose, g — glucose, g' — galactose, r — rhamnose, K — kaempferol, Q — quercetin, M — myricetin, L — luteolin, R' — isorhamnetin, and d — methyl radicals.

Owing to the constancy and frequency of their occurrence and their high content the above-mentioned flavonol glycosides were adopted as diagnostic biochemical characters for the unit higher than a species. Quercitrin was left out, as it occurred in all taxa studied except *B. humilis.* Combinations of monoglycosides i.e. myricitrin (rM), or hyperoside (g'Q) with diglycosides: myricetin 3-digalactoside (g'_2M) or rutin (grQ) results in the following classification of the species in question:

a) g'Q and grQ — such a set occurred in *B. nana* and *B. humilis;*
b) g'Q and g'_2M — this group comprised *B. pendula, B. p.* ssp. *obscura, B. turkiestanica,* and *B. pubescens* s.s.;
c) rM and g'_2M — occurred in *B. fontinalis* and *B. papyrifera;*
d) rM and grQ — such a set was only characteristic of B. *albo-sinensis* studied by Hänsel and Hörhammer (1954).

Group **a** did not include *B. maximowiczii,* though it contained g'Q (hyperoside) and grQ (rutin) in approximately balanced amounts, as the specimen of this species had ten quite different but unidentified flavonoids (for this reason they are not listed in Table 1). Group **c,** on the other hand, might comprise *B. coerulea-grandis, B. andrewsii,* and *B. koehnei,* which have been investigated by Hänsel and Hörhammer (1954). However, it should be noted that the composition of flavonoid glycosides for the taxa studied by Hänsel and Hörhammer (1954) requires corroboration at least by the method of two-dimensional chromatography.

Nevertheless, the above-given scheme does not cover a large number of taxa which contain some other combinations of flavonol glycosides. In view of this, the scheme was modified, references being made to the classification systems, based on morphological similarity. Taking into account the division systems of Regel (1868), Winkler (1904), Rehder (1974), and Natho (1976), groups **b** and **c** were treated jointly. The joining of these groups was also justified by the homology of the genomes of *B. pendula* and *B. japonica*, and *B. pubescens* with *B. papyrifera*, this having been proved on the basis of experimental hybridization (Johnsson 1945, 1949, Klaehn 1950, Clausen 1966, 1970). At the same time it should be emphasized that isorhamnetin 3-galactoside (g'R') occurred in all studied specimens of *B. pendula*, *B. pubescens*, and *B. turkiestanica* as well as in *B. japonica*, *B. fontinalis*, *B. papyrifera*, *B. neoalascana* and *B. species nova* (= *B. papyrifera* var. *commutata*) — further on provisionally called *B. commutata* (Table 1). Compound g'R' (isorhamnetin 3-galactoside) can be recognized as characteristic of a group of taxa of the composition g'Q (hyperoside) and/or rM (myricitrin) and g'$_2$M (myricetin 3-digalactoside). In *B. pubescens*, *B. japonica*, *B. fontinalis*, *B. papyrifera*, *B. neoalascana*, and *B. commutata* also luteolin 4'-glucoside (gL) was detected, whereas the leaves of *B. pubescens*, *B. turkiestanica*, and *B. japonica* under study exhibited the presence of kaempferol 3-glucoside (gK). This modified, newly formed group comprised *B. oycoviensis*, *B. "nova"*, *B. japonica*, *B. commutata*, and *B. neoalascana*, until then remaining outside all former groups. With respect to the biochemical characters studied these species form an intermediate group between group **b** (*B. pendula*, *B. turkiestanica*, and *B. pubescens*) and group **c** (*B. fontinalis* and *B. papyrifera* — Table 1), however, this group is not morphologically uniform and requires further comparative studies.

In the former scheme, group **b** would also embrace *B. utilis*, *B. Ermani*, and *B. insignis* studied by Hänsel and Hörhammer (1954), this nevertheless, not seeming logical in view of the classification systems adopted hitherto. These three species belong together with *B. lenta*, *B. lutea*, *B. potanini*, *B. albo-sinensis*, and *B. grossa* to the same subsection (according to Winkler) or series (according to Rehder) *Costatae*. But *B. utilis*, *B. Ermani*, and *B. insignis* vary from *B. lenta*, *B. lutea*, *B. potanini*, and *B. albo-sinensis* in that they lack not only monoglycoside rM (myricitrin) but also diglycoside grQ (rutin). The schematic formula for *B. utilis*, *B. Ermani* and *B. insignis* may be g'Q (hyperoside) and g'$_2$M (myricetin 3-digalactoside), and for *B. lenta*, *B. lutea*, *B. potanini*, *B. albo-sinensis*, and *B. grossa* — g'Q and/or rM and grQ.

In 1976 Natho, on the basis of his own findings and these of Vassilev, taking as a criterion the similarity of hulls and drupels of and the structure of the pericarp, divided the taxa of the genus *Betula* into 5 sub-

genera, which, with certain modifications, conform to the here-distinguished groups. This classification is as follows:

1) g'Q and grQ and g'R' — *Acuminatae* (Spach.) Reg. — *Betulaster* Natho;
2) rM and/or g'Q and grQ — *Betulenta* Natho;
3) rM and/or g'Q and g'$_2$M and g'R' — *Albae* Reg. — *Betula* Natho;
4) g'Q and g'$_2$M — *Neurobetula* Natho;
5) g'Q and grQ — *Nanae* Reg. — *Humiles* Koch — *Chamaebetula* Natho.

Within the subgenus *Betula* Natho (1976), he distinguished three sections: *Fruticosae*, *Verrucosae*, and *Betula*, including *B. humilis* and *B. fruticosa* in the first of these sections. However, the flavonoid composition in *B. humilis* is quite different from set 3., whereas it is identical with set 5. (cf. Table 1 and the above scheme). Besides, *B. humilis* similarly as *B. nana*, contains quercetin 7-rhamnoside which is absent from specimens of the section *Betula*. In view of this *B. humilis* ought to be transferred to the section *Nanae*, the more so that this species was already included in the subsection *Nanae* (Regel 1868, Winkler 1904) or in the series *Humiles by* Vassilev (1969) and Rehder (1974). The remaining taxa of the subgenus *Betula* Natho are distinguished by the presence of isorhamnetin 3-galactoside (g'R' — Table 1). They vary in the number of chromosomes amounting to 2n = 28 or 2n = 56 to 84 (Table 2). In the present author's opinion this can serve as a basis for differentiation within the section *Betula* of two subsections *Verrucosae* and *Betula*, the classification of which is largely in accordance with the division proposed by Natho (Tables 1, 2). As consequence of the adoption of the chromosome number as basis the subsection *Verrucosae* will embrace the species which are phylogenetically older than those in the subsection *Betula*.

The difference between these two subsections lies in the frequency of occurrence of luteolin 4'-glucoside (gL), which is present in all taxa of the subsection *Betula* and in only some of the subsection *Verrucosae* (Table 1).

Both the proposed subsections exhibit two conspicuous "phylogenetic lines" of biosynthesis of glycosides: hyperoside (g'Q) and myricitrin (rM). Compound g'Q is the main glycoside in *B. pendula* of the subsection *Verrucosae* and in *B. pubescens* of the subsection *Betula*. On the other hand, monoglycoside rM predominates in *B. fontinalis* and *B. coerulea-grandis* which belong to the subsection *Verrucosae*, and in *B. papyrifera* of the subsection *Betula*. The species containing hyperoside occur in Europe and those containing myricitrin — in America. It follows from the above description that the "phylogenetic lines" are conditioned by the geographical distribution of birches.

Dugle (1966), while studying the karyology and morphology of the leaves of many American birches, among them *B. fontinalis* and *B. pa-*

Table 2

Chromosome numbers in some taxa of the genus *Betula* L./[a]

Taxon	2n/[b]
1. *Costatae* Reg.	
B. utilis D. Don	28
B. ermanii Cham.	56
B. lenta L.	28
B. albo-sinensis Burk.	56
B. lutea Michx.	84
B. grossa Sieb. et Zucc.	84
2. *Nanae* Reg.	
B. humilis Schrk.	28
B. nana L.	28
3. *Albae* Reg.	
B. pendula Roth.	28
B. oycoviensis Bess.	28
B. "nova"	28/[c]
B. japonica Sieb.	28
B. coerulea-grandis Blanch.	28
B. fontinalis Sarg.	28
B. pubescens Ehrh.	56
var. *tortuosa* Ledeb.	56
var. *carpatica* Walds. et Kit.	56
B. papyrifera Marsh.	56, 70, 84
var. *commutata*	56, 70, 84/[d]
4. *Acuminatae* Reg.	
B. maximowiczii Reg.	28

/[a] — in Winkler's (1904) classification; /[b] — in Vaarama and Valanne (1967); /[c] — Szwabowicz (1972); /[d] — Brittain and Grant (1966).

pyrifera, modified the classification system proposed by Rehder, distinguishing a separate series of *Fontinales*. Taking her suggestions and the findings of the present studies into account, it would be possible to distinguish in the subsection *Verrucosae* the series *Pendulae* (*B. pendula* and others of similar morphology, biochemical traits, and 2n = 28) and the series *Fontinales* (*B. fontinalis* and others of similar morphology, with 2n = 28 chromosomes, containing myricitrin as a dominant flavonol glycoside, with no hperoside), and consistently, in the subsection *Betula* the series *Papyriferae* (*B. papyrifera* and other birches resembling it with respect to the above-mentioned traits) beside the series *Pubescentes*.

Among the remaining taxa of the section *Betula*, three species, i.e. *B. oycoviensis*, *B. japonica*, and *B. "nova"* should be included in the series *Oycovienses* within the subsection *Verrucosae*, and two species, i.e. *B. commutata* and *B. neoalascana*, in the subsection *Betula* as a separate series which has been provisionally called *Commutatae*. The proposed division of the genus *Betula* is presented in Table 3, but this proposition should be regarded with great caution until comparative

Table 3

Division of the genus *Betula* L. on the basis of biochemical characters and the chromosome numbers

Sect. 1. *Acuminatae* Reg.	g'Q and grQ and g'R'
B. maximowiczii	
Sect. 2. *Betulenta* Natho	rM and g'Q and grQ
B. lenta	
B. albo-sinensis	
B. potanini	
B. lutea	
B. grossa	
Sect. 3. *Betula*	rM and/or g'Q and g'_2M and g'R'
Subsect. *Verrucosae* Natho	2n=28
Ser. *Pendulae*	g'Q and g'_2M and g'R' (Europe)
B. pendula	
ssp. *obscura*	
Ser. *Oycovienses*	rM and g'Q and g'_2M and g'R' (Europe, Asia)
B. oycoviensis	
B. japonica	
B. "nova"	
Ser. *Fontinales* Dugle	rM and g'_2M and g'R' (North America)
B. fontinalis	
B. coerulea-grandis	
Subsect. *Betula* Natho	2n=56 to 84
Ser. *Pubescentes*	g'Q and g'_2M and g'R' (Europe, Asia)
B. pubescens	
ssp. *pubescens*	
ssp. *tortuosa*	
var. *tortuosa*	
var. *carpatica*	
B. turkiestanica	
Ser. *Commutatae*(?)	rM and g'Q and g'_2M and g'R'gQ and gQ (Asia?, North America)
B. commutata	
B. neoalascana	
Ser. *Papyriferae*	rM and g'_2M and g'R' (North America)
B. papyrifera	
Sect. 4. *Neurobetula* Natho	g'Q and g'_2M
B. utilis	
B. ermani	
B. insignis	
Sect. 5. *Nanae* Reg.	g'Q and grQ
B. nana	
B. humilis	
(?) *B. middendorffii*	

g'Q — hyperoside; grQ — rutin; g'R' — isorhamnetin 3-galactoside; rM — myricitrin; g'_2M — myricetin 3-digalactoside; gQ — isoquercitrin.

morphological studies have been carried out. Such studies are particularly necessary for the species of the series *Commutatae*.

Among 27 taxa of birches subjected to chemotaxonomic examinations only *B. middendorffii* showed the qualitative composition of its flavonol glycosides, ascertained by Glyzin and Bańkovskiy (1971) to depart from the above norm (Table 1). Therefore the systematic position of this species remains problematic. It should noted that *B. middendorffii* is a Siberian endemic form (Oguryeyeva 1974), and that, according to Regel (1868), this birch belongs to the subsection *Fruticosae* beside *B. fruticosa*, and according to Winkler (1904) it is among the species *Albarum forsan* hybride beside *B. microphylla*, whereas Rehder (1974) places it in the series *Humiles* beside *B. humilis* and *B. fruticosa*, while Vassilev (1969) and Natho (1976) include it in the subgenus *Chamaebetula*, in series *Middendorffii*.

The absence of quercitrin (quercetin 3-rhamnoside) in the leaves of *B. humilis* (Hänsel and Hörhammer 1954, Pawłowska 1976) even in the initial period of vegetation (Pawłowska, unpublished data) indicates the lack of activity of transglycosidase quercetin: UDP-rhamnose. Since the absence of activity of this transglycosidase is demonstrated by all specimens of this species independently of environmental conditions, this may testify to the genetic conditioning of this absence, e.g. by mutation in the dominant gene, as this species has been found to contain a vestigial amount of presumably quercetin 7-rhamnoside (Table 1).

If in both of these quercitrin-free species the same type of mutation is proved by means of recombination, this will indicate that they are related. It will then be possible to include *B. middendorffii* in the section *Nanae*, in accordance with the proposition put forward by Vassilev (1969) and Natho (1976). The fact that quercitrin does not occur in only two species under discussion out of the total number of 27 taxa of the genus *Betula* hitherto subjected to chemotaxonomic analysis may indicate that it was only in the post-glacial period that this mutation process took place.

PHYLOGENETIC ASPECTS

A relationship between the genera *Alnus* and *Betula* which form the family *Betulaceae* (Walters 1964) may be demonstrated not only on the basis of the occurrence of flavonol glycosides (Fig. 1) but also by the presence of numerous flavonol methyl ethers (Wollenweber 1975). At the same time, taking as a basis the frequency of occurrence of betuletol (kaempferol 6-methoxy-4'-methyl ether) in particular, it may be supposed that the genus *Alnus* is older than *Betula*.

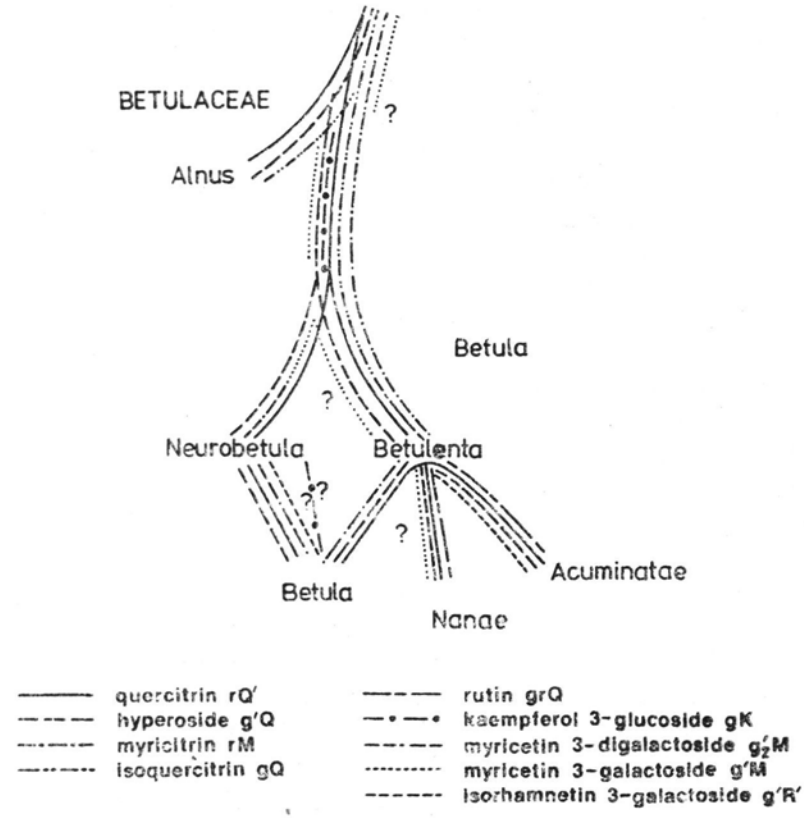

Fig. 1. Hypothetical schematic diagram of phylogenetic correlations on the basis of the occurrence of flavonol glycosides

The presence of flavonol glycosides rM (myricitrin) and especially of diglycosides grQ (rutin) and g'$_2$M (myricetin 3-digalactoside) points to a phylogenetic correlation between sections of the genus *Betula*: rM — between sections *Betulenta* and *Betula;* grQ — of the section *Betulenta* with *Nanae* and *Acuminatae;* and g'$_2$M — of the section *Betula* and *Neurobetula* (Fig. 1). According to Natho (1976), anatomical an morphological characters of the hulls and drupels also indicate a similar relationship. The most extensive correlations of *Betulenta* with other sections are evidence of its essential position in the phylogenesis of the genus *Betula*.

B. brongniartii is one of the oldest of the genus *Betula* and also most frequently found in fossil localities throughout Northern Hemisphere (i.e. in areas now occupied by the genus discussed), resembling most of all contemporary *B. lenta* or *B. lutea* (Koch 1963, Tanai and Suzuki 1963, Axelrod 1964, Wolfe et al. 1966, Celyabaeva 1971, Zhilin and Tokar 1971, and others). This concurrence en-

courages the supposition that at least some taxa of the section *Betulenta* are older than those of the sections *Betula, Nanae,* or *Acuminatae.* The rich qualitative composition of flavonol glycosides in the section *Betulenta* permits the supposition that during the process of speciation of the taxa of the remaining sections some biochemical characters studied, e.g. rM or g'Q underwent reduction in the section *Betula.*

Another example of a fossil taxon is *B. prisca* of very frequent occurrence in the Tertiary deposits throughout the Northern Hemisphere. This taxon is usually compared to the contemporary *B. utilis* included in the section *Neurobetula,* the only one manifesting no relation with the section *Betulenta* (Fig. 1). In recent years an interesting discovery has been made, i.e. a new chromosome number 2n = 14 has been found for *B. utilis* var. Pratti (Mehra and Sareen 1973, cf. Table 2). It would thus follow therefrom that among the species of the section *Neurobetula* there are also some of the oldest taxa of the genus *Betula.*

The origin of *B. "nova"* presents a very interesting and so far unsolved problem. The question aroused even more interest when this species was found to contain some compounds which did not occur in any Polish taxon (Pawłowska 1980b), except *B. oycoviensis* which is a hybrid of *B. "nova"* × *B. pendula* (Jentys-Szaferowa 1967 and others). Jentys-Szaferowa (1967), taking as basis the resemblance of some morphological characters of this species to those of the taxa belonging to the subsection *Nanae* (in Winkler's classification, 1904), advanced the hypothesis that *B. "nova"* may have arisen in the late glacial period by the crossing of some taxon resembling a modern *B. humilis* with an arborescent specimen representative of the subsection *Albae.*

However, the biochemical characters of *B. "nova"* differ so much from those of *B. humilis* as to exclude the possibility of *B. "nova"* arising in this way. On the other hand, it follows from studies on flavonoids carried out hitherto that, with respect to these biochemical characters, *B. "nova"* resembles most of all *B. commutata* (North America), *B. neoalascana* (North-West America), and *B. lenta* (North-East America — Table 4). Thus, one may wonder the cause of the occurrence of numerous traits in common in the birches from geographically so distant localities.

The already mentioned *B. brongniartii* was found in Tertiary deposits from the Eocene to the Pliocene in: the south-western part of the Soviet Union (Jakubovskaya 1955, Krishtofovich and Baykovskaya 1965, Baykovskaya 1974), southern Poland (Menzel 1910), western Germany (Mädler 1939), Czechoslovakia (Knobloch 1961), and Hungary (Andreánszky 1963). According to these investigators, this fossil species is like *B. lenta* or rather *B. lutea.* But *B. lutea* is hexaploid (Table 2) and perhaps a hybrid of *B. lenta* × *B. papyrifera* (Pawłowska 1983), hence the resemblance of a Tertiary

Table 4

Biochemical characters studied in some species of the sections *Betula*, *Betulenta*, and *Nanae*[a]

Compound / Species	aQ	rQ	rM	g'Q	g'M	g'_2M	gQ	grQ	g'R'	gK	rgK	Qd	Kd	Kd'	gAd	gL	grL	Ratio of similar and different traits in comparison with *B.* "*nova*" (percent of similarity)
B. lenta	+	+	+	+	+	—	+	+	—	—	+	+	—	—	—	+	+	13:4 (76.5)
B. lutea	+	+	+	+	0	+	+	+	+	—	+	+	—	—	+	+	+	12:5 (70.6)
B. pendula	+	+	—	+	0	+	—	—	+	+	—	—	+	+	+	—	—	8:9 (47.0), 13:4[b] (76.5)
B. "*nova*"	+	+	+	+	0	+	+	—	—	—	+	+	—	—	—	—	—	
B. oycoviensis	+	+	+	+	0	+	+	—	+	+	+	+	+	+	+	—	—	12:5 (70.6)
B. japonica	+	+	+	+	0	+	—	—	+	+	+	—	—	+	—	+	—	11:6 (64.7)
B. fontinalis[c]	+	+	+	—	0	+	—	—	+	—	+	+	—	—	+	+	—	12:5 (70.6)
B. commutata[c]	+	+	+	+	0	+	+	—	+	—	+	—	—	—	+	+	—	13:4 (76.5)
B. neoalascana	+	+	+	+	0	+	+	—	+	—	+	+	—	+	+	+	—	13:4 (76.5)
B. humilis	+	—	—	+	—	—	0	+	—	+	—	—	+	—	—	—	—	8:9 (47.0)

[a] — the list does not include compounds of no taxonomic value, compounds unidentified or those whose identification is not quite certain; [b] — ratio of characters studied in *B. pendula* to those of *B. oycoviensis*; [c] — symbols +, —, and 0 refer only to single specimen of this species under study; "—" — denotes the lack of expressivity of a particular gene in the studied specimens of a given species; aQ — quercetin 3-arabinoside, rQ — quercitrin, rM — myricitrin, g'Q — hyperoside, g'M — myricetin 3-galactoside, g'_2M — myricetin 3-digalactoside, gQ — isoquercitrin, grQ — rutin, g'R' — isorhamnetin 3-galactoside, gK — kaempferol 3-glucoside, rgK — kaempferol 3-rhamno-7-glucoside, Qd — quercetin 3,7,4'-trimethyl ether, Kd — kaempferol 3,4'-dimethyl ether; Kd' — kaempferol 6-methoxy-4'-methyl ether; gAd — acacetin 7-glucoside; gL — luteolin 4'-glucoside; grL — luteolin 7-rutinoside.

B. brongniartii to *B. lutea* seems to be rather accidental. To be sure, some fossil leaves resembling modern *B. papyrifera* have been discovered in the Miocene and Pliocene deposits but only in Poland and Rumania (Kräusel 1918, Givulescu and Ghiurca 1969).

When compared with the recently discussed contemporary species as regards the chromosome number, *B. "nova"* exhibits the closest resemblance to *B. lenta*. The two species have 2n = 28 chromosomes, whereas *B. papyrifera* 2n = 56, 70 or 84, and *B. lutea* 2n = 84 chromosomes (Table 2). Thus the demonstrated similarity of *B. "nova"* to *B. lenta* is the most conspicuous example of phylogenetic correlations between the sections *Betula* and *Betulenta*.

On the other hand, *B. "nova"* differs from *B. lenta* in the occurrence of flavonol diglycosides: the former contains myricetin 3-digalactoside (g'_2M) and the latter rutin (grQ). None the less, the leaves of *B. "nova"* were found to contain isoquercitrin (gQ) which in all likelihood was a substratum for the biosynthesis of rutin. Furthermore, two specimens of *B. lenta* contained trace amounts of probably myricetin 3-galactoside (g'M — Table 1), thus, it would be a substratum in the biosynthesis of g'_2M. Besides, unlike *B. lenta*, *B. "nova"* was not found to contain luteolin glycosides (Table 1). In addition, the two species vary considerably in their morphology. To be sure the sites of a fossil taxon resembling *B. lenta* overlap those of contemporary *B. oycoviensis* (Korczyk 1967) which is the hybrid of *B. "nova"* × *B. pendula*, nevertheless, the survival of this fossil taxon till the post-glacial period and, consequently, a direct descendance from it of *B. "nova"* is rather unlikely. It seems more probable that the genes conditioning the capacity for the biosynthesis of flavonol glycosides rM (myricitrin), and rgK (kaempferol 3-rhamno-7-glucoside) and of quercetin trimethyl ether (Qd) have been transferred from the gene pool of European but other than Polish taxa.

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Badania biochemiczno-systematyczne rodzaju Betula L.

Streszczenie

W pracy zaproponowano system klasyfikacyjny rodzaju *Betula* L. w oparciu o przeprowadzone badania składu jakościowego flawonoidów. W proponowanym podziale uwzględniono także liczby chromosomów i występowanie geograficzne ujmowanych taksonów. Podział ten jest bardzo podobny do systemu klasyfikacyjnego wymienionego rodzaju wg Natho, który przyjął za kryterium podziału cechy morfologiczne i anatomiczne nasion oraz liści. W niniejszej pracy przedyskutowano również niektóre aspekty filogenetyczne rodzaju *Betula*.