

CYTOTAXONOMIC NOTES ON SOME GALIUM SPECIES GALIUM BOREALE L. II

(Taxonomy *G. boreale* L. and allied species)

BY

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SUMMARY

Comparative morphological investigation of *Galium boreale* L. on herbarium specimen from different parts of the area confirmed the complexity of this species as stated by others. This is discussed. Based on fruit-indument characters it is concluded that four varieties can be distinguished.

INTRODUCTION

Galium boreale L. is a polymorphic species occurring on the northern hemisphere with a circumpolar distribution. LÖVE and LÖVE (1954), after studies of comparative morphology, cytology and chorology concluded that *Galium boreale* consist of two distinct species, viz.—a tetraploid $2(n=44)$ occurring in Europe to deep in Asiatic Russia and a hexaploid $2(n=66)$ occurring on the American continent and extending to within Eastern Asia. The tetraploid would be identical with *Galium boreale* as described by LINNAEUS (1753), the hexaploid with *Galium septentrionale* as described by ROEMER and SCHULTES in 1818. URSCHLER, (1955), accepting this conclusions recognized on fruit-indument character within *Galium boreale* L. the vars. *boreale* and *hyssopifolium* (Hoffm.) D.C. and within *Galium septentrionale* R. et S. the vars. *septentrionale*, *incurvatum* Urschl. and *glabrum* Urschl. Later investigators revealed the presence of hexaploid plants also in Europe besides tetraploids (PIOTROWICZ, 1961; RAHN, 1961; KLIPHUIS, 1973). These two cytotypes are morphological inseparable when using the combinations of characters considered critical by Löve and Löve (RAHN, 1961; KLIPHUIS, 1973). More extensive research involving biometry and cultivation—and crossing—experiments equally failed to furnish reliable characters by which to distinguish the two cytotypes (KLIPHUIS, 1973). The two cytotypes in Europe clearly belong to one species. The view of Löve and Löve (1954) that there are differences in morphology which are strictly associated with the ploidy level is untenable. However, this does not immediately mean that the possible existence of two species should be rejected. One could assume that there is an European-Asiatic taxon with $2n=44$ and $2n=66$ chromosomes

and an American-Asiatic one with, as far is known, $2n = 66$ chromosomes. (Up to now only hexaploids could be demonstrated within this area, BÖCHER and LARSEN, 1950; LÖVE and LÖVE, 1954; HARA, 1956; HULTÉN, 1958; LEWIS, 1962; TAYLOR and BROCKMAN, 1966; ZHUKOVA, 1967, 1969). As a matter of fact this is also the somewhat modified opinion by LÖVE (1965) when he in spite of the results of the studies by RAHN (1961), continued to assume that the tetraploid is always the typical Eurasian *Galium boreale* and the hexaploid always the typical American-Asiatic *Galium septentrionale* despite the supported possible occurrence of boreale like taxa in Southern and Eastern Europe and Siberia in which hexaploidy may occur. Rahn (l.c.) included a study of herbarium material collected in Europe, Asia and America. Using the combinations of characters such as given by Löve and Löve, no good subdivision could be constructed. It appeared that over the whole area of the species all characters occur in almost every possible combination. Rahn, therefore, rejects the view of Löve and Löve, but is unable to offer an alternative classification.

The taxonomy of *Galium boreale*, as is clear, is still as confused as ever and this led the present author to a comparative morphological study of herbarium material from the whole area using also data obtained from experimental studies.

MATERIAL

Herbarium specimen from the following Herbaria were studied: Copenhagen (C), Leningrad (LE), Leiden (L), Michigan, Ann Arbor (AFS. Mich.), Montreal (MTMG), Stockholm (S), and Utrecht (U).

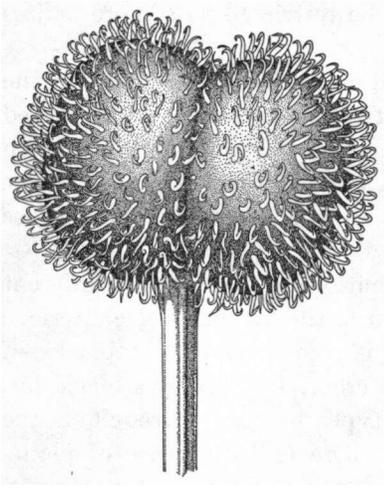
RESULTS

When comparing herbarium material of *Galium boreale*, the great variability of this species becomes obvious. It is seen in the stature, the mode of the branches, the shape of the panicle, the size of the leaves and flowers, the shape of the bracts, the indument, particularly the fruit indument.

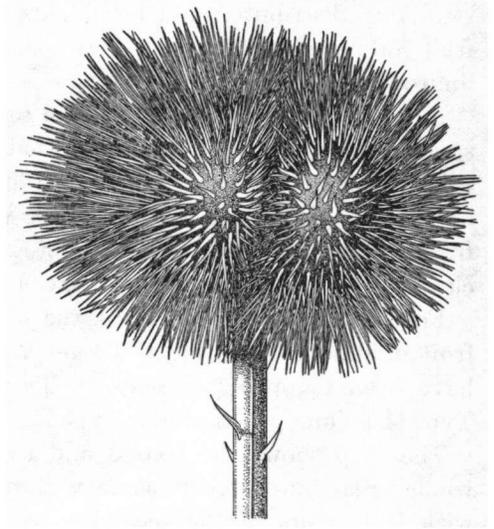
The situation is still far from clear as regards a possible correlation of any of these characters with the geography of the species. The only exception is the fruit indument. Four types of fruit indument have been observed:

1. Fruit with stiff uncinat hairs. (Type I).
2. Fruits densely covered with patent, mostly silvery hairs. (Type II).
3. Fruits with curved hairs, mostly appressed, but sometimes more or less patent. (Type III).
4. Entirely glabrous fruits. (Type IV).

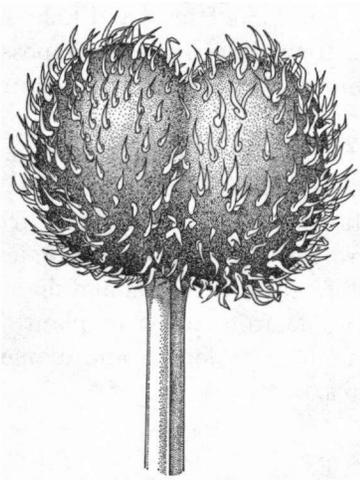
These four types are given in fig. 1: a = type I; b = type II; c = type III; and d = type IV.



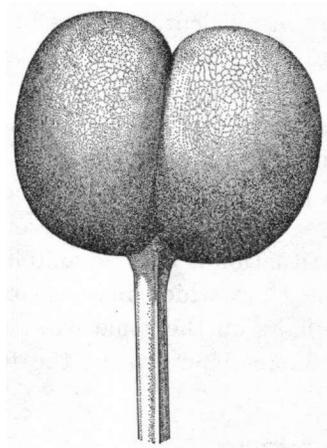
1 A



1 B



1 C



1 D

Fig. 1. Four types of fruit-indument in *Galium boreale* L: A=fruit with uncinat hairs; B=with patent, straight hairs; C=with curved hairs; D=glabrous fruit.

Fruits with hairs of the uncinat type (Type I) occur in the whole of Europe and adjacent parts of Asia to deep in Siberia. In America they are an exception (4 out of 342).

Plants with the fruit hairs of the second and third type occur on the American continent. They were also observed in plants from eastern Asia. Glabrous fruits have been found in the whole area. In Europe they are

randomly distributed and occur side by side with plants with uncinata fruit indument. In America they seem to be restricted to a more or less limited area.

A type intermediate between the second and third types occurs in the same area where those are found; hairs straight at the base and curved toward the tip, but never uncinata. These hairs can grow intermixed with ones of the second or third type, or with both of these types and vary from patent to more or less appressed. In such indument sometimes clearly uncinata hairs were observed.

For the American continent the distribution of plants with different fruit indument is not clear. To get a picture, the localities of collections have been mapped (see map 1). Type I is represented by a black —, Type II by an open triangle; Type III by a cross; Type IV by a black dot.

The map shows the second and third types to occur throughout the whole area, but there is some variation: there is an increase of plants with fruit hairs of the second type when going in west to northwest direction with a clear accumulation in Alaska, whereas type III becomes more frequent when moving in an easterly direction with a clear accumulation in the regions of the great lakes. Type IV has its greatest concentration in the area bordered by Lake Michigan, Lake Huron and Lake Erie.

The insufficient numbers of collections from Asia makes it impossible to draw conclusions on a possible distribution pattern of fruit indument types on that continent.

Not much can be stated with regard to the density of the fruit indument, particularly concerning types I and III where there is a continuous variation from plants practically glabrous to plants with very densely hairy fruits. Fruits falling under the second type are nearly always densely hairy. This situation is further complicated by differences in length and diameter of the hairs which may become considerable from plant to plant. The fruit hairs on the same plant are fairly uniform in length and diameter: they increase in size as the fruit matures.

THE PANICLE

The panicle shape is extremely variable and grows from narrowly pyramidal or almost cylindrical with flowers clustered in glomeruli to very broadly pyramidal with distinct long pedicelled flowers. Many transistors occur. The entire range of variability has been found throughout the whole area. Examples of panicle shape are given in photo 1: narrowly pyramidal a — from a plant from Denmark, (A. Lange, 1921. s.n.) (C) and b — from U.S.A., Medicine Bow, Wy. (F. Petrak, 1950 s.n.) (S); normal pyramidal c — from Denmark, (A. Hansen, 1961, D. 46) (C) and d — from Canada, Québec. (FF. Marie — Victorin et Rolland — Germain, 1944. s.n.) (S); broadly pyramidal e — from Sweden, Hålland, (C. Tillman, 1893, s.n.) (S) and f — from U.S.A., Decorah, Iowa, (E. W. D. Holway, 1884, s.n.) (S).

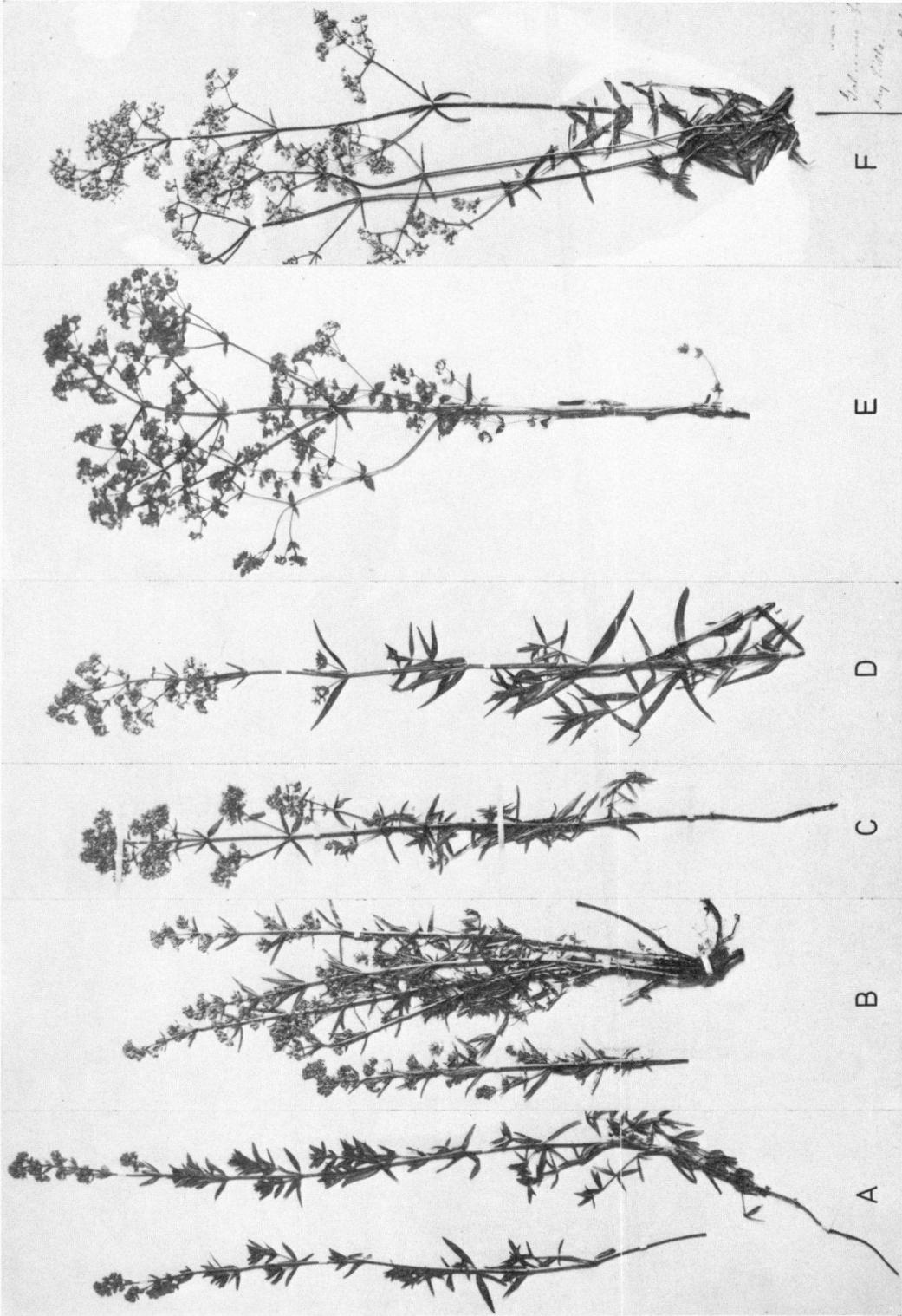


Photo 1. Example of the same variability in panicle shape of *Galium boreale* L. in Europe and North-America. Narrowly pyramidal panicle A - from a plant from Denmark, B - from Wyoming, U.S.A.; normal pyramidal panicle C - from Denmark, D - from Quebec, Canada; broadly pyramidal panicle E - from Sweden and F - from Iowa, U.S.A.

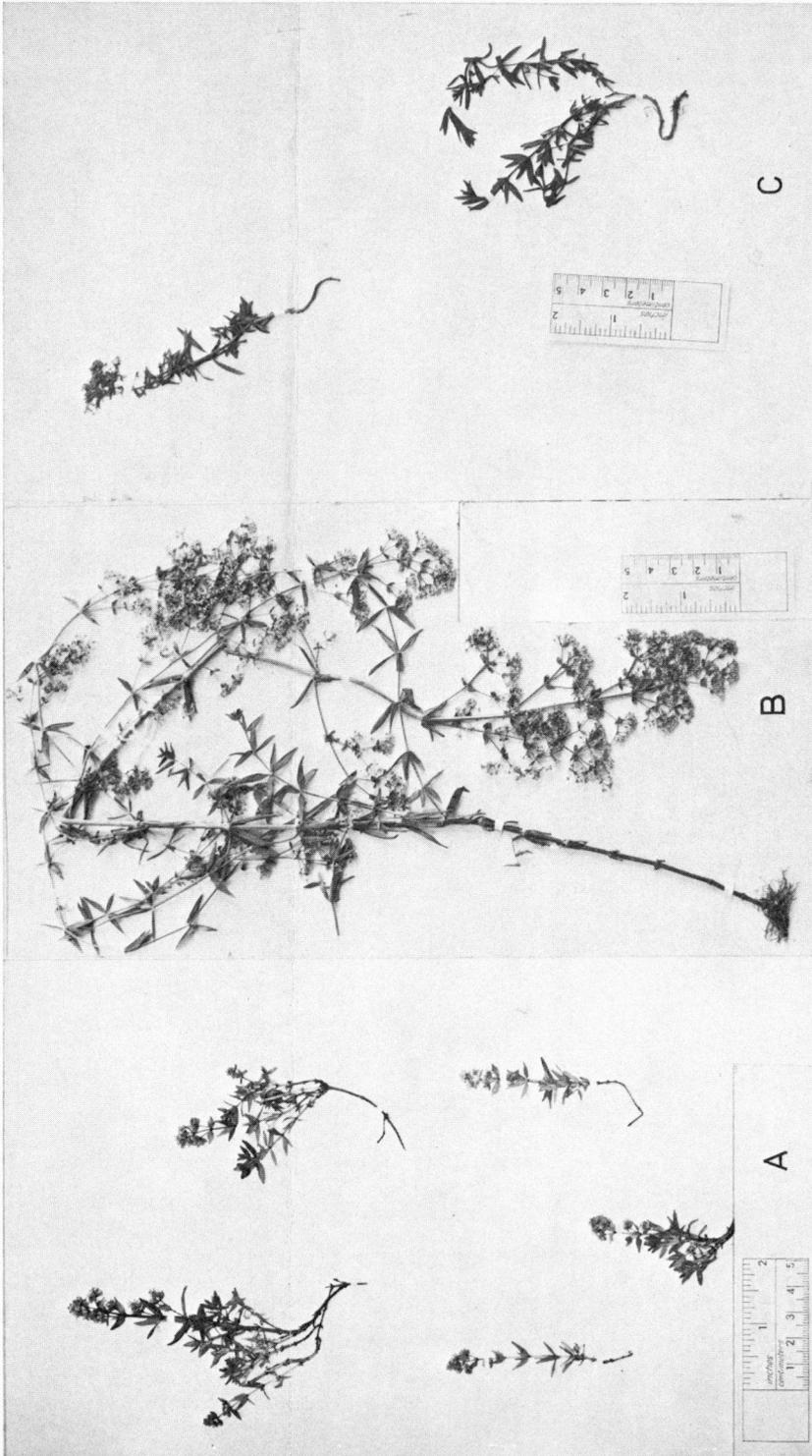
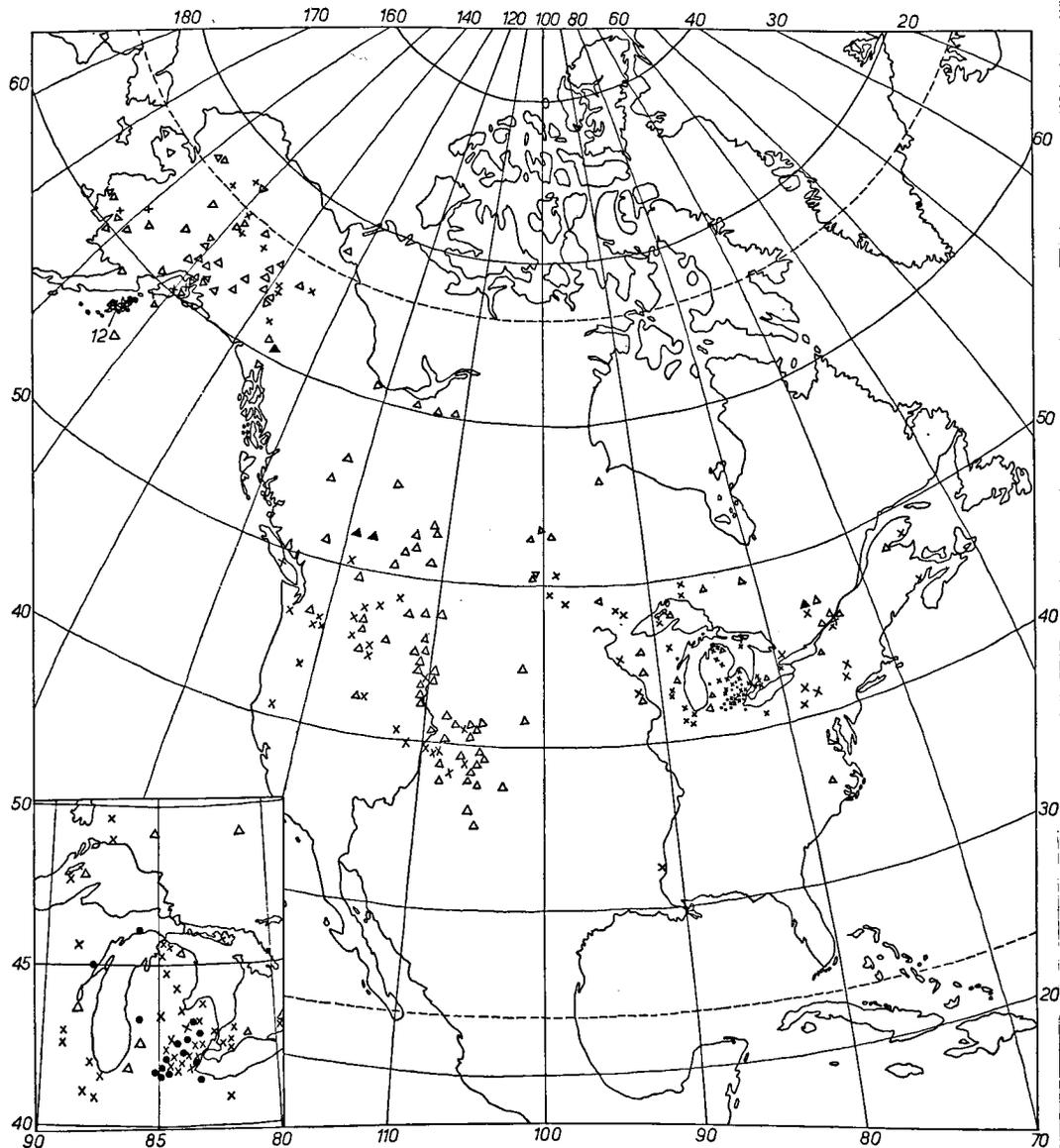


Photo 2. Phenoplasticity of *Galium boreale* L. Voucher specimen A from a plant collected in Sweden (*f. arenosum* Neum.); B. from a plant from Denmark third year of cultivation on sandy-clay; C. the same plant as B. on peaty soil, one year after transplantation (fourth year of cultivation).



Distribution pattern of *Galium boreale* on the North-American continent. ▲ plants with uncinat fruit-indument (Type I); △ with straight hairs (Type II); X with curved hairs (Type III) and ● with glabrous fruits (Type IV).

THE BRACTS

The bracts range from circular-ovate, obtuse to oblong, acute in the whole area. The two extremes even occurring sometimes on the same plant.

THE LEAVES

The leaves are in whorls of four; trinerval and highly variable in length and width. The greatest differences were observed in plants from north-east Asia where both plants with linear leaves and plants with elliptical-oval leaves occur, and also all possible intermediate forms. In other regions the extremes are much less pronounced. The general impression is that plants in America possess longer and narrower leaves than plants in Europe. Within Europe on the other hand plants from Sweden, Norway, Finland, and northern Russia seem to be longer and narrower leaved than plants from other parts, whereas plants from Iceland appear to have the smallest leaves. These distributions are vague, however, as both extremes do occur throughout the whole area.

In order to find out if length and width of the leaves could be useful as a means to separate groups statistically, the longest leaf on each herbarium specimen was measured, and the mean, the standard deviation and the standard error of the mean of the length and width values thus obtained were computed. The results are found in table Ia: first a comparison is made between America and Europe; secondly different parts of Europe are compared with each other. East-Asia could not be taken into account, as too few collections from there were available. In the first column the distributional area of the material investigated is men-

TABLE I a

Length and width of the largest leaf arranged according the origin of different parts of the distributional area of *Galium boreale*. \bar{X} =the mean, SE=standard error of the mean, SD=standard deviation, N=number of observations; Europe=Europe without Iceland; F.=Finland, N.=Norway, Swe.=Sweden and S.U.=northern parts of European Russia. All values in mm.

	Length			Width			
	\bar{X}	SE	SD	\bar{X}	SE	SD	N
America	33.44	0.51	8.43	4.39	0.10	1.56	279
Europe	24.62	0.44	6.96	4.45	0.10	1.59	251
F., N., Swe., S.U.	27.45	0.66	6.57	5.09	0.16	1.57	98
rest of Europa	22.78	0.52	6.49	4.05	0.12	1.46	153
Iceland	16.80	0.83	4.57	4.23	0.23	1.26	30

TABLE I b

Length and width of the leaves combined with fruit-indument character. For explanation see text.

	Length			Width			
	\bar{X}	SE	SD	\bar{X}	SE	SD	N
Type I	24.62	0.45	6.96	4.45	0.10	1.59	240
II	33.16	0.66	8.38	4.27	0.12	1.47	161
III	33.88	0.84	8.53	4.60	0.16	1.68	103
IV	30.31	1.63	8.30	4.22	0.39	1.53	26

tioned. In the following columns the mean (\bar{X}), and the standard error of the mean (SE), the standard deviation (SD) and the number of observations is given (N).

Computations of the standard error of difference (SED) show that American plants are longer leaved on the average than European plants. Within Europe, plants from the northern parts are again longer leaved on the average than plants from the other parts.

The leaf width gives a less pronounced picture: there is so much overlap between American and European plants that no statistical separation is possible. However, plants from Finland, Norway, Sweden and the north of European Russia on the average had broader leaves than those from the remainder of Europe and from America.

Plants from Iceland stand apart from the other groups owing to their different leaf length.

When figures for leaf length and width are combined with fruit-indument characters, (see table Ib), the average length of the leaves of type I plants appears to be significantly less than that in plants of type II and III. Types II and III cannot be separated.

No separation is possible between any two of these three types using the leaf width, due to great overlap.

The leaves of type IV plants seem to be intermediate in length between those of type I and II. Both, plants from America and Europe were used for these calculations. When arranged according to continent, the results are as follows: Plants from Europe: length: $\bar{X} = 25.45 \pm 2.34$ with SD = 7.76, width: $\bar{X} = 3.79 \pm 0.39$, with SD = 1.30, N = 11; for plants from America, length: $\bar{X} = 33.87 \pm 1.68$ with SD = 6.49 and width: $\bar{X} = 4.35 \pm 0.42$, SD = 1.64, N = 15, (values in mm).

Computations of the SED show that despite a great amount of overlapping glabrous fruited plants from America have longer leaves than those from Europe. Again it appears impossible to demonstrate differences in leaf width.

THE COROLLA

The corolla shape is very uniform: the lobes are oval and apiculate. Corolla size was recorded by measurements of the diameter of the flower and width of one lobe. The mean (\bar{X}), the SD and SE were arranged in the same way as with the leaves. (see table II).

Computation of the SED shows flowers of the American plants having larger corolla width and diameter than flowers of European plants. Within Europe, flowers of northern parts are larger both in diameter and width than flowers of other parts of Europe. The northern European flowers not being different from American flowers.

The correlation with fruit indument: flowers of type II plants are both larger in diameter and width than either those of type I or type III.

Flowers of type III are larger than flowers of type I. Type IV could

not be taken into account due to lack of sufficient material. The minimum and maximum values for this type in Europe is: diameter, 3–4.8 mm; width, 1.4–2.4 mm and for America; diameter, 3.0–5.0 mm, width 1.4–2.4 mm.

THE ANTHERS

The length of the anthers of a number of herbarium specimens was measured. See for results table III. The computed mean does not make any arrangement into groups possible.

THE INDUMENT

The indument of the stem, nodes, leaves, bracts, pedicels is variable to such an extent that there is no classification possible in anyway. Plants from East-Asia generally have more numerous and longer hairs than plants from other parts of the area.

DISCUSSION

The great variability of *Galium boreale* reported by all previous authors who studied this species is confirmed by the results of the present comparative morphological investigations. The characters studied overlap to a high extent and are found in all sorts of combinations throughout the area. The only exception is the fruit indument; here there was found a certain correlation with leaf and corolla size. Plants with fruits having uncinata hairs possess smaller leaves and flowers than plants with fruits having either straight or curved hairs. The uncinata type occur mainly in Europe and adjacent parts of Asia, the other two groups have their

TABLE II a

Flower diameter and lobe width of *Galium boreale* arranged according different parts of origin of the distributional area. See for further explanation table I.

	Diameter			Width			
	X	SE	SD	X	SE	SD	N
America	4.86	0.05	0.77	1.13	0.01	0.20	213
Europe	4.14	0.04	0.59	0.97	0.01	0.19	220
F., N., Sw., S.U.	4.32	0.07	0.70	1.05	0.02	0.19	90
rest of Europa	4.01	0.06	0.73	0.94	0.01	0.18	130
Iceland	4.18	0.13	0.58	1.00	0.04	0.18	20

TABLE II b

Diameter of flower and width of lobe combined with fruit-indument character. For explanation, see text.

	Diameter			Width			
	X	SE	SD	X	SE	SD	N
Type I	4.14	0.04	0.59	0.97	0.01	0.19	220
II	5.02	0.06	0.71	1.16	0.02	0.20	131
III	4.60	0.09	0.79	1.07	0.02	0.20	82

distribution in America and East-Asia. These differences in geographic distribution agrees with the respective areas given by LÖVE and LÖVE (1954) for what they recognized as *Galium boreale* L. and *Galium septentrionale* R. et S. Only one of Löve and Löve's differentiating characters, however, could be confirmed, namely the size of the corolla. This, on the other hand, does not agree with the results of an investigation by RAHN (1961) who was unable to find any differentiating character.

The pattern of differences in corolla size is more complicated, however, than was suggested by Löve and Löve: there are differences also within each of the two areas. In Europe plants from the north have larger corolla's than those from the rest. In America and East-Asia there is a correlation between corolla size and fruit indument type (Type II having larger corolla's).

The subdivision of *Galium boreale* into the varieties *boreale*, *intermedium* and *hyssopifolium* as encountered in European Flora's, and which is based on De Candolle's original description is also applied to *Galium boreale* in American Flora's (BRITTON and BROWN, 1952; FERNALD, 1953). According to these descriptions plants with straight fruit hairs match the concept of the variety *boreale* (= *typicum* Beck), whereas plants with curved hairs match that of the variety *intermedium* D.C. Both varieties occur throughout the area in America, but there is a clear difference between the concentration patterns of the two. The difference is not as pronounced as that what FERNALD (1928) gives, but it does largely agree with it. These descriptions, however, are not quite concordant with that in the European Flora's. DE CANDOLLE's (1830) classification is based on the indument of fruits of plants of European origin: "in uliginosis saxosis montosis Europae totius". Since this is essentially different from that

TABLE III a

Length of anthers of *Galium boreale* L. arranged according the origin of different parts of the distributional area. Values in mm. For further explanation, see table I.

	\bar{X}	SE	SD	N
America	0.81	0.01	0.15	202
Europe	0.79	0.01	0.15	220
F., N., Swe., S.U.	0.80	0.02	0.15	90
rest of Europe	0.78	0.01	0.15	130
Iceland	0.78	0.04	0.16	16

TABLE III b

Length of anthers of *Galium boreale* L. combined with fruit-indument character. For explanations see text.

	\bar{X}	SE	SD	N
Type I	0.79	0.01	0.15	220
II	0.83	0.01	0.15	120
III	0.82	0.02	0.15	82

found in American plants it is not correct to apply the names to the varieties based on this character on both sides of the Atlantic.

In view of the continuous variation in density of fruit indument and also in length and diameter of the fruit hairs among different plants it is impossible to distinguish more than two groups viz.: plants with glabrous fruits and plants with hairy fruits. This holds true for plants with uncinata hairs in Europe, but also for plants with curved hairs in America. Differences in density of fruit indument with straight hairs are also present, but a continuous variation was not observed. Consequently, the variety *intermedium* D.C. is untenable. In this respect URSCHLER's opinion can be fully supported (1955).

In Europe hairy—and glabrous fruited plants occur throughout the area or essentially so. REGEL collected a smooth-fruited plant in Turkestan 1877. This is the only collection from adjacent Asia available for the present study. The Flora of the U.S.S.R. makes mention of such plants but offers no further details neither on distribution in the European part nor on that on the Asiatic part. Perhaps this is an indication that in adjacent Asia, too, both fruit types occur intermixed with the same distribution. Contrary to Europe, var. *hyssopifolium* in America does not occur intermixed but rather concentrated in a restricted area. This could perhaps be explained by assuming that during the evolution of *Galium boreale*—which in view of the complexity and distribution certainly must be considered very old—plants with smooth fruits in Europe originated differently from those in America. The centre of distribution, in the latter case, would have to be situated in the Great Lakes region. This also means that they must stem from plants with fruits with curved hairs, rather than from plants with fruits having straight hairs. This hypothesis is supported by the fact that plants with smooth fruits in Europe and those in America differ in leaf size, just as is also seen in plants with hairy fruits. The hypothesis is not in contradiction with cytological data as far as known: smooth-fruited plants in America are hexaploid (LÖVE and LÖVE, 1954); whereas in Europe they are both tetraploid (LÖVE and LÖVE, l.c.) and hexaploid (KLIPHUIS, 1973).

Another explanation would be to assume that smooth fruited plants were introduced, probably by man, in America from Europe. Such an assumption of introduction was also made by Grøntved for *Galium boreale* collected by him in Greenland, 1953. Following the key of Gray's manual of botany (1950), GRØNTVED (1954) identified his material as var. *typicum*. Grøntved gives no description of fruit indument, but examination of his collections (Qanaisiarssat, Tunugdliarfik Fjord, nr. 2545) revealed plants with fruits with uncinata hairs in which they agree with *Galium boreale* occurring in Europe.

The results of the present investigation show that the complexity of *Galium boreale* is so great that any taxonomic treatment would seem to be extremely difficult. At any rate the strict splitting into two species

by LÖVE and LÖVE (1954) is untenable. This implies also that Urschlers treatment which distinguishes varieties and which is based on the presence of two species, cannot be maintained. HARA (1956) and also IRTIS (1957) who reduced the two species to subspecies using, however, the same character combinations as Löve and Löve: consequently these subspecies are unacceptable too. The only discriminating factor, not used as such by Löve and Löve, has proven to be the fruit indument. In spite of hybridization and hybrid fertility different taxa can be distinguished using the fruit indument, sometimes correlated with other minor morphological characters and geographical distribution. Based on these characters the subclassification in varieties seems the most reliable one, it runs as follows:

Galium boreale L. var. *boreale* – (var. *typicum* Beck, 1893; var. *scabrum* De Candolle, 1830) – fruits with uncinete hairs. Europe and adjacent Asia to deep into Siberia. Extremely rare on the American continent. $2n=44$ and $2n=66$.

Galium boreale L. var. *septentrionale* (Roemer et Schultes) Kliphuis – comb. nov. – Basonym: *Galium septentrionale* Roemer et Schultes. (*G. septentrionale* R. et S. var. *septentrionale*; URSCHLER, 1955; *G. boreale* L. var. *typicum* Fernald 1928, non Beck) – Fruits with patent straight hairs. Highest concentration in Western North-America, becoming rarer towards the East and Southeast. Also in East-Asia. $2n=66$.

Galium boreale L. var. *incurvatum* (Urschler) Kliphuis – comb. nov. (*G. septentrionale* R. et S. var. *incurvatum* Urschler, 1955; *G. boreale* L. var. *intermedium* sensu Fernald, 1950 non De Candolle) – Fruits with curved hairs (not uncinete). Highest concentration in Eastern North-America rarer towards the West. Also in East-Asia. $2n=66$.

Galium boreale L. var. *hyssopifolium* (Hoffmann) De Candolle – Fruits lacking hairs. Probably throughout the whole area (circum-polar). In Europe together with var. *boreale*; in America mainly in the Great Lake region. In Europe $2n=44$ and $2n=66$, in America $2n=66$.

The variety *hyssopifolium* (Hoffm.) D.C. may prove to be polyphyletic; its exact position in respect to the other varieties, anyhow, is not yet quite clear.

The delimitation of the varieties *septentrionale* and *incurvatum* is not always clear. The more or less intermediate fruit indument mentioned in the results given, may be explained by assuming hybridization between the two varieties. In some cases in an indument of this type also a few uncinete hairs are found. This apparently indicates certain elements from the var. *boreale*.

The delimitation may also become difficult with young fruits because those may have slightly curved and appressed hairs which, however, upon maturity become straight and patent.

In var. *hyssoipifolium* the young fruits occasionally possess a few hairs which are shed when the fruits mature. This may render the determination of this variety somewhat difficult.

Icelandic plants agree with those in Europe. Their smaller size and shorter, narrower leaves do not provide sufficient ground for recognition as a separate taxon.

In herbarium material from plants collected in Sweden there were specimens of *Galium boreale* which appear quite different in habit from the general pattern. These plants are very small, almost creeping; they were described as forma *arenosum* by NEUMAN (1901). The position of this forma is uncertain as long as no transplantation experiments have been made. It has turned out that plants from Denmark with the normal habit of *Galium boreale* var. *boreale* as known from northern Europe do not change when they are cultivated on sandy clay (KLIPHUIS, 1973). Transplantation of these plants to peaty soils produced, after one year of cultivation, plants strongly resembling the forma *arenosum*. The phenoplasticity of the species is clearly demonstrated by this example. For a picture see photo nr. 2, a—a plant from Sweden, voucher specimen of *Galium boreale* L. f. *arenosum* Neum., collected in nature; b=*G. boreale* L. var. *boreale* from Denmark, third year of cultivation on sandy clay; c=same plant on peaty soil one year after transplantation.

The delimitation of *Galium boreale* L. versus *Galium rubioides* L. is unclear, (LÖVE and LÖVE, 1954; URSCHLER, 1955). ČELAKOVSKY (1871–1872), regards *Galium rubioides* as a subspecies of *Galium boreale*. CUFODONTIS (1940) as a variety. In the experimental garden of Utrecht plants identified as *Galium rubioides* L. with Hegi's Flora of Mitteleuropa were grown from seeds collected in nature in Babadag, Dobrogea near the coast of the Black-Sea in Roumania. They are well distinct in their morphology from *Galium boreale* L. s.l. and have a chromosome number $2n=132$.

Within the genus *Galium* there is a strong reproductive barrier between various levels of ploidy, inter- as well as intraspecific, as became clear from crossing experiments. (FAGERLIND, 1934, 1937; EHRENDORFER, 1954, 1955; KLIPHUIS, 1970, 1972, 1973). This barrier becomes less effective in higher ploidy-level, (EHRENDORFER, 1954, 1955). Hybridization between representatives of the *Galium boreale* complex and *Galium rubioides*, (with $2n=44$, 66 and $2n=132$ chromosomes respectively) is not probable but not all together impossible either. The possible existence of such hybrids could be an explanation for the opinion of ČELAKOVSKY (l.c.) and CUFODONTIS (l.c.). However, in the case of Cufodontis, there is in addition probably a wrong interpretation since Cufodontis has applied the name to plants from East-Asia, notwithstanding that *Galium rubioides* must be regarded as Central-European (including central- and south Russia, extending into the Caucasus), (HEGI, 1906–1931; POBEDIMOVA, 1958).

In the Flora of the U.S.S.R. POBEDIMOVA (1958) distinguishes two subsections within the section *Platygalium* D.C. viz.: subsection *Rubioides*

Pobed. and subsection *Borealia* Pobed. The subsection *Rubioidea* is represented by *Galium articulatum* Lam., *Galium rubioidea* L., *Galium volgense* Pobed., and *Galium ussuriense* Pobed.; the subsection *Borealia* by *Galium boreale* L., *Galium amurense* Pobed., *Galium amblyophyllum* Schrenk, *Galium turkestanicum* Pobed., *Galium mugodsharicum* Pobed. and *Galium septentrionale* R. et S.

The subsection *Rubioidea* is characterized by fruits usually without hairs, the pericarp not lying against the testa. The leaves are commonly large and broad. In the subsection *Borealia* the fruits are usually setose, rarely with scattered hairs or glabrous, and the testa has coalisced with the pericarp. These fruit characters clearly separate the two subsections. The species within the two subsections are much less distinct from each other. The main discriminating characters are: stature of the plant, mode of ramification, leaf size and panicle shape. These characters tend to be variable and therefore unreliable. The species in both subsections generally have more or less separate areas, but here and there the areas overlap. In such areas POBEDIMOVA (l.c.) reports several cases of hybridization, also between species from different subsections. Whether or not these cases truly represent hybridization is not yet fully clear. This is due in part to insufficient knowledge of the cytology of the species concerned. Chromosome numbers apart from *Galium boreale* L. and *Galium rubioides* L. are only known from *Galium physocarpum* Ledeb., which has $2n=66$, (FAGERLIND, 1934, 1937). According the Flora of the U.S.S.R. this species is a pathologic forma with inflated fruits of *Galium articulatum* Lam. In Russia this species occur in an area in which also *Galium boreale* L. occurs. Hybridization with the equally hexaploid *Galium boreale* is thus possible. Interspecific hybridization between species of the same ploidy level have been reported by FAGERLIND (1934, 1937) on tetraploid level for *Galium mollugo* L. and *Galium verum* L. and by EHRENDORFER (1955) on octoploid level between *Galium pumilum* Murr. and *Galium rubrum* L.

The description of *Galium septentrionale* R. et S. in the Flora of the U.S.S.R. does not quite match as understood by LÖVE and LÖVE (1954), neither does it with the original description by ROEMER and SCHULTES (1818). The plants which I have seen from the Leningrad Herbarium and which according to the Flora of the U.S.S.R. are to be reckoned to *Galium septentrionale* R. et S. admittedly differ somewhat from *Galium boreale* L. var. *boreale* in Europe, but still fall within the variation pattern of that taxon. The same also applies to the species *Galium turkestanicum* Pobed. and *Galium mugodsharicum* Pobed. The type species of both have the characters of *Galium boreale* L. var. *boreale*. *Galium amblyophyllum* Schrenk, from West Siberia is unclear, some specimens (which have been identified as this species) are without doubt referable to *Galium boreale* var. *hyssopifolium* (Hoffm.) D.C. The isotype has sparse fruit indument in which elements of var. *septentrionale* (R. et S.) Kliph. and var. *incurvatum* (Urschl.) Kliph. can be found. Similar plants were collected in

America. *Galium amurense* Pobed. from East Siberia and North China is clearly var. *septentrionale* (R. et S.) Kliph., perhaps with somewhat narrower leaves, but this variable character is not a sound basis even for a variety.

From the foregoing it becomes obvious that the subsection *Borealia* must be regarded as a large variable group entirely falling within the limits of *Galium boreale* L. The species distinguished within this subsection in the Flora of the U.S.S.R. can all be reduced to the varieties: *boreale*, *hyssopifolium* or *septentrionale*. This is for the moment the best solution in view of insufficient cytological data especially on material from the eastern regio. Much more work in the field of experimental taxonomy within this complex has to be done to arrive at final conclusions. Probably it is built up of series of auto- and allopolyploids in the way as could be demonstrated with the polyploid-complexes within the section *Leptogalium* by EHRENDORFER (1954, 1955, 1962). With the species within the subsection *Rubioides* the picture is also uncertain. *Galium rubioides* L. as discussed before is a species of its own. *Galium volgense* Pobed. no doubt is very closely related to it, whereas the position of *Galium ussuriense* Pobed. seems to be uncertain. I have not seen any specimen of *Galium articulatum* Lam. It is not impossible that the subsection *Rubioides* is partly or wholly a very variable complex like *Galium boreale*, but this needs further investigation. The cytology of several species is unknown; for the time being it is the best to stay with the classification of Pobedimova.

On the Iberian peninsula occurs *Galium broterianum* Boiss. et Reut. This species belongs also to the section *Platygalium* and is related to *Galium boreale*. Plants collected in nature in Portugal proved to be diploid ($2n = 22$ chromosomes). Over the years of cultivation these plants remain rather uniform in their morphology, only some variation in length and width of the leaves and differences in height of the plants were observed. This diploid *Galium broterianum* has been classified as a variety of *Galium rubioides* L. by Sampaio. However, when both the chromosome number and morphology and of course also the geographical distribution are considered *Galium broterianum* can well be separated from *Galium boreale* on one side and *Galium rubioides* on the other. It, therefore merits a specific status of its own, and must be considered as the diploid southern representative of the boreale complex.

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REFERENCES

- BRITTON, N. and A. BROWN, An Illustrated Flora of the Northern United States, Canada and the British Possessions. New-York (1952).
- BÖCHER, T. W. and K. LARSEN, Chromosome numbers of some arctic or boreal flowering plants. Meddel. Grönland 147 (6), 1-32 (1950).
- ČELAKOVSKÝ, L., Prodromus der Flora von Böhmen. Prag (1870-1871).
- CUFODONTIS, G., Revision der chinesischen Galium-Arten, nebst Bemerkungen über einige ihrer Formkreise. Österr. bot. Zeitschr. 99, 211-251 (1940).
- CANDOLLE, A. P. DE, Prodromus systematis naturalis regni vegetabilis 4, Paris (1830).
- EHRENDORFER, F., Phylogeny and evolutionary mechanism in Lepto-Galium. Rapp. et Comm. VIII. Intern. Congr. Bot. sect. 4, 82-84 Paris (1954).
- , Hybridogene Merkmalsintrogression zwischen *Galium rubrum* L. s. str. und *Galium pumilum* Murr. s. str. Österr. bot. Zeitschr. 102, 195-234 (1955).
- , Die geographische und oekologische Entfaltung des europäisch-alpinen Polyploid-Komplexes *Galium anysophyllum* Vill. seit Beginn des Quartärs. Uppsala Univ. Arsskr. 6, 176-181 (1958).
- , Cytotaxonomische Beiträge zur Genese der mittel-europäischen Flora und Vegetation. Ber. Deutsch. Bot. Gesellschaft LXXV (5), 137-152 (1962).
- FAGERLIND, F., Beiträge zur Kenntnis der Zytologie der Rubiaceen. Hereditas 19, 223-232 (1934).
- , Embryologische, zytologische und bestäubungsexperimentelle Studien in der Familie Rubiaceae nebst Bemerkungen über Polyploiditätsprobleme. Acta Horti Berg. 11, 195-470 (1937).
- FERNALD, M. L., The varieties of *Galium boreale*. Rhodora 30, 106-107 (1928).
- , Gray's manual of Botany, New-York (1953).
- GRÖNTVED, J., *Galium boreale* L. new to Greenland. Bot. Tidsskr. 51, 98-102 (1954).
- HARA, H., Contributions to the study of variations in the Japanese plants closely related to those of Europe and North-America (2). Jap. Fac. Sci. Tokyo Imp. Univ. Sect. 3 Bot. 6, 343-391 (1956).
- HEGI, G., Illustrierte Flora von Mitteleuropa. München (1906-1931).
- HULTÉN, E., The amphi-atlantic plants and their phytogeographical connections. K. Sv. Vetenskapsakad. Handl. 7 (1), 1-340 (1958).
- ILTIS, H. H., Distributional and nomenclatorial notes on *Galium* (Rubiaceae). Rhodora 59, 38-54 (1957).
- KLIPIHUIS, E., Cytotaxonomic notes on some *Galium* species, *Galium silvaticum* L., *Galium aristatum* L. and *Galium schultesii* Vest., Proc. Kon. Ned. Akad. v. Wetensch. Amsterdam, Ser. C 73 (3), 271-283 (1970).
- , Cytotaxonomic studies in *Galium hercynicum* Weig. Bot. Not. 125, 487-492 (1972).
- , Cytotaxonomic notes on some *Galium* species, *Galium boreale* L. I., Proc. Kon. Ned. Akad. v. Wetensch. Amsterdam Ser. C 76, 359-372 (1973).
- LEWIS, H. W., Chromosome numbers in North American Rubiaceae. Brittonia 14 (3), 285-290 (1962).
- LINNAEUS, C., Species Plantarum, Holmiae (1753).
- LÖVE, A., The evolutionary Framework of the Biological Species concept - In Genetics To Day - Proc. of the XI Intern. Congress of Genetics, p. 415, The Hague (1963).
- and D. LÖVE, Cytotaxonomical studies on the Northern Bedstraw. American Midland Nat. 52 (1), 88-105 (1954).
- NEUMAN, L. M., Sverige Flora, Lund (1901).

- PIOTROWICZ, M. in SKALINSKA et al., Further additions to chromosome numbers of Polish Angiosperms. Acta Soc. Bot. Pol. 30, 463-489 (1961).
- POBEDIMOVA, E. G. in B. K. SCHISCHKIN, Flora S.S.S.R. XXIII, Moscow and Leningrad (1958).
- RAHN, K., Cytological and taxonomical studies of *Galium boreale* and allied species. Bot. Tidsskr. 56 (4), 351-355 (1961).
- ROEMER, J. J. and J. A. SCHULTES, Caroli a Linné Systema vegetabilum, Stuttgart (1818).
- TAYLOR, R. L. and R. P. BROCKMAN, Chromosome numbers of some Western Canadian Plants. Can. Journ. of Botany 44 (8), 1093-1103 (1966).
- URSCHLER, INGRID, Die Fruchtbehaarung des *Galium septentrionale* Roemeret Schultes. Phytion 6, 48-56 (1955).
- ZHUKOVA, P. G., Chromosome numbers in some species of plants of the north-eastern parts of the U.S.S.R. II. Bot. Zhurn. 52, 983-987 (1967).
- , Chromosome numbers in certain plants species indigenous to the north-east of the U.S.S.R. IV. Bot. Zhurn. 54, 1985-1990 (1969).