CYTOTAXONOMIC NOTES ON SOME GALIUM SPECIES

GALIUM SILVATICUM L., GALIUM ARISTATUM L. AND GALIUM SCHULTESII VEST.

BY

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INTRODUCTION

Galium silvaticum L., *Galium aristatum* L. and *Galium schultesii* Vest are closely related species belonging to the section *Eugalium* DC.. The three species are more or less distinct from each other in their geographical distribution.

Galium silvaticum is a Central European sub. atlantic species (MEUSEL, 1943). It is a common plant in Germany, Switzerland, Austria and the western parts of Poland, Czechoslovakia and Hungary. (BINZ, 1927; DUFTENSCHMIDT, 1883; FIEK, 1881; HADAC, 1969; HEGI, 1906–1931; HERMANN, 1956; REICHENBACH, 1885; ROTHMAHLER, 1958; WAGNER, 1905; ZAHRADNIKOVA, 1967).

In France it is known from the eastern parts of this country extending to the South into the Provence and to the South-West into Les Landes. (BONNIER, 1911–1935; COSTE, 1903; ROUY, 1903). In Belgium it occurs mainly in the Ardennes. (GABRIELS, 1965). The species is rare in Spain, only scarcely distributed in the North: Navarra, Aragon and Catalonia. (WILLKOMM and LANGE, 1870). In the Netherlands it is only known from one locality near Nimeguen.

Galium aristatum is a Southern European species, mainly distributed in the Balkan Peninsula, Italy, Southern Switzerland (Tessin) and Southern France. (BINZ, 1927; BONNIER, 1911–1935; COSTE, 1903; HEGI, 1906–1931; SAVULESCU and NYÁRÁDY, 1960).

The species occurs also in Austria and Bavaria (BRESINSKY, 1965; HERMANN, 1956; VOLLMANN, 1914).

Galium schultesii is a plant from Central and Eastern Europe. It occurs in Poland, large parts of Roumania, the eastern parts of Hungary and Czechoslovakia and in the European parts of Russia. It is also known from the North of Yugoslavia and Western Bulgaria (FIEK, 1881; HADAC, 1969; HEGI, 1906–1931; HERMANN, 1956; POBEBIMOVA in Shiskin: Flora of U.S.S.R., 1958; SAVULESCU and NYÁRÁDY, 1960; ZAHRADNIKOVA, 1967).

The three species are very similar in their morphology. In parts of the distribution area where *Galium silvaticum* and *Galium schultesii* occur

sympatrically the species are often confused. (KERNER, 1876; ZAHRADNIKOVA, 1967).

This is also true for *Galium silvaticum* and *Galium aristatum*. (BRIQUET et CAVILLIER, 1913–1915). Also hybridisation between these two species seems to occur. (BONNIER 1911–1935; BRESINSKY, 1965; BUTTLER and BRESINSKY, 1966).

Galium silvaticum and *Galium aristatum* were already recognized as two seperate species by Linnaeus, (Species Plantarum, third edition, 1764). *Galium silvaticum* is distinguished particularly by the shape of the stem. (Caule tereti fulcrato). *Galium aristatum* owes its name to the shape of the corolla (Corolla apice aristatae).

SCHULTES (1814) reported a plant from Eastern Europe which did not match the description of *Galium silvaticum* to which he thought it belonged. This plant was recognized as a separate species by VEST and named by him *Galium schultesii* in 1821. (Caule tetragono erecto laevi, foliis subseptenis oblongo, lanceolatis, margine scabris, glaucescentibus, paniculae subcorymbosae, pedicellis subcapillaribus, corollis subcampanulatis muticis).

An outstanding study and description of the three species concerned was published by KERNER (1876). However, his opinion that *Galium aristatum* is a synonym of *Galium laevigatum* is based on a wrong interpretation of the description in the Species Plantarum, sec. ed. On the contrary *Galium laevigatum* is synonymous with *Galium aristatum*.

Cytotaxonomic investigations showed *Galium silvaticum* to be a diploid with $2n = 22$ chromosomes. (FAGERLIND, 1937; POUQUES, 1949; KLIPHUIS, 1962; GADELLA and KLIPHUIS, 1963).

Galium aristatum is a tetraploid with $2n = 44$ chromosomes. (POUQUES, 1948; KLIPHUIS, 1962), but also diploids are reported from Bavaria, Southern Germany, by BUTTLER and BRESINSKY (1966). This cytotype is found together with *Galium silvaticum* and according to these authors hybrids between this cytotype and *Galium silvaticum* are met with in this area. Before this was known, these hybrids were considered to be the species *Galium schultesii*. Combined cytological and morphological studies on material gathered in nature showed that these hybrids have $2n = 22$ chromosomes and that in their morphology, they are intermediate between *Galium silvaticum* and *Galium aristatum*, rather than matching the description of *Galium schultesii*. (BUTTLER and BRESINSKY, l.c.).

Galium schultesii is a hexaploid with $2n = 66$ chromosomes. (FAGERLIND, 1934, 1937; PIOTROWICZ, 1958; KLIPHUIS, 1962; BUTTLER and BRESINSKY, 1966). Tetraploid plants are also reported by BUTTLER and BRESINSKY in their study: "Beitrage zur Zytologie von Galium ser. Silvatica", (1966), from localities in Slovenia and Croatia.

Galium schultesii and *Galium silvaticum* are also different in their ecology, at least in Czechoslovakia. (HADAC, 1969). *Galium silvaticum* is a plant of the communities *Galio-Carpinion* and *Fagion*. Vertically it

occurs between 150 – and 850 m. and the populations are located on limestone, basalt, sandy marlstones and gneisses. *Galium schultesii* has a wider amplitude. It belongs to the communities *Tilio-Carpinion, Fagion, Quercion pubescentipetreae, Alnion incanae, Abietion, Calamagrostidion variae, Seslerion tatrae* and *Petasition officinalis*. It has a vertical distribution from 80 – to 1720 m. and it grows mainly on limestone, andesites, basalt, sandstone, gneisses and granite, (HADAC, 1969).

In spite of the fact that several botanists paid attention to the species *Galium silvaticum, Galium aristatum* and *Galium schultesii*, combined comparative morphological and cytological investigations on the three species were never made.

As part of an investigation program on some species of the genus *Galium*, *Galium silvaticum, Galium aristatum* and *Galium schultesii* were studied. Plants of these species were cultivated in an experimental plot under uniform conditions during several years. Cytological and morphological investigations as well as crossing experiments were done. Also times of flowering were recorded during three successive years. The results of these studies are described and discussed below.

MATERIAL AND METHODS

Living plants as well as plants grown from seeds, collected in localities in the wild were cultivated under uniform conditions during six years in an experimental plot of the Botanical Garden of the State University of Utrecht.

Chromosome counts are based on the study of roottip mitoses. For these purposes the roottips were fixed in Karpechenko's fixative, embedded in paraffine, sectioned at 15 micron and stained according to Heidenhain's haematoxylin method.

Voucher specimens as well as microscopical preparations have been deposited in the Botanical Museum and Herbarium of the State University of Utrecht.

Methods used in crossing experiments are dealt with under that chapter.

RESULTS

I. Cytology

The results of the chromosome counts are given in table I. In the first column the species, in the second the plant number, in the third the chromosome number determined and in the fourth the place of origin are mentioned respectively.

In the table it may be observed that all plants of *Galium silvaticum* turned out to be diploids with $2n=22$ chromosomes, those of *Galium aristatum* tetraploids with $2n=44$ chromosomes and those of *Galium schultesii* hexaploids with $2n=66$ chromosomes.

TABLE I

In the first column the species investigated, in the second the plant number, in the third the chromosome number determined and in the fourth the place of origin. All material investigated was collected in the wild. Asterisk means precise locality not known.

Species	Plant number	2n	Origin
Galium silvaticum	K 69	22	Netherlands, St. Jansberg, Nimeguen
	K 70	22	idem
	K 71	22	idem
	K 112	22	idem
	K 346	22	France, Vosges.
	K 494	22	Germany, Harz
	K 524	22	Yugoslavia, North of the country
	K 542	22	Germany, near Weimar
	K 599	22	France, Vosges, Hohenwald
	K 604	22	Czechoslovakia, Bohemen
	K 1086	22	Austria, Mount Leitha
Galium aristatum	K 216	44	Switzerland, near Lugano
	K 218	44	Switzerland, San-Dominico
	K 219	44	Switzerland, near Gandria
	K 221	44	Switzerland, Castagnola
	K 429	44	Switzerland, Gandria, near frontier with Italy
Galium schultesii	K 113	66	Czechoslovakia *
	K 305	66	Czechoslovakia, Tatra
	K 325	66	Czechoslovakia, Tatra
	K 441	66	U.S.S.R., Carpathian
	K 445	66	Poland *
	K 509	66	Hungary, East of Budapest
	K 532	66	Poland, Zakopane
	K 582	66	Yugoslavia *
	K 595	66	Poland *

II. Morphology

Morphological characters of the three species were studied during the period of cultivation. Continuous observation over this period of several years made clear that the characters for each species remained very constant.

Although the species resemble each other very much, there are demonstrable differences. In the plants investigated these were found in the stem, the leave, the pedicel and the corolla.

Galium schultesii has a sharply quadrangular stem nearly from the base, with incrassate nodes.

The stem of *Galium silvaticum* is terete, with four, usually faint, but sometimes slightly more pronounced ribs in the upper part. The nodes

are thickened (much more so than in *Galium schultesii*), often coloured by anthocyanine.

The stem of *Galium aristatum* is terete below, becoming clearly quadrangular above. The nodes are thickened, but not as much as those of *Galium schultesii*.

The three species are also different from each other in length and width of the leaves and also in their foliar shape.

Galium aristatum appears to have the longest leaves, up to 4.5 cm., these being comparatively narrow, i.e. 3–7 mm. wide. The leaves are lanceolate, broadest just below the middle, gradually narrowing towards both ends, passing into the petiole at the base and with a tiny mucro at the top.

Galium silvaticum has the widest leaves, 4–10 mm., but also have the shortest in comparison, up to 3.5 cm. long. Leaves oblong lanceolate to oblanceolate, widest just above the middle, gradually passing into the petiole, rounded at the apical part, mucronate. The leaves of *Galium schultesii* are up to 4 cm. long, and 4–9 mm. wide, being widest at the middle in contrast to those of the other species, narrowed to both ends, apiculate at the top.

The respective leaves of the three species are shown in fig. 1.

The pedicel is geniculate in *Galium silvaticum* before anthesis, as opposed to both *Galium aristatum* and *Galium schultesii* which have a straight pedicel before anthesis.

Galium schultesii has the largest flowers, measuring up to 3 mm. in diameter. The corolla lobes are ovate, acute, finely pointed at the top. *Galium silvaticum* and *Galium aristatum* have flowers about equal in size, measuring up to 2 mm. in diameter. The coralla lobes are merely acute in

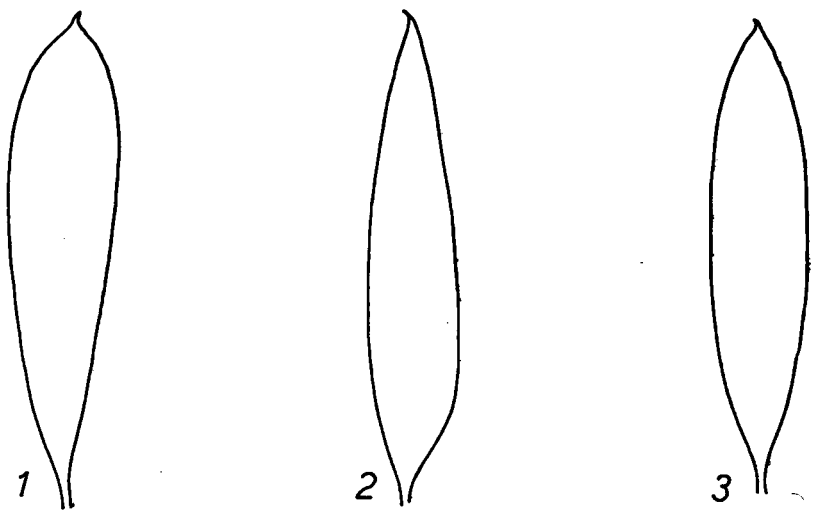

Fig. 1. Shape of the leave of *Galium silvaticum* L. (1), *Galium aristatum* L. (2) and *Galium schultesii* Vest (3).

Galium silvaticum, but in *Galium aristatum* they terminate in a solid mucro.

The morphological differences observed are summarized in table II.

Plant nr. 524 is distinct from other plants of *Galium silvaticum* by its more delicate habit, deep greyish-green leaves, by its stem colored red by anthocyanine, and deep violet buds.

The form agrees with var. *atropurpureum* Woerlein.

III. Flowering periods

During three successive years, the period of flowering of the plants in the experimental garden was recorded. The flowering period was considered as having started with the opening of the first bud of the inflorescence. Full flower means that the whole inflorescence of the plant has open flowers. In the species studied the main flowering period was followed at the end by a more irregular second flowering period due to the development of additional inflorescences and lasting till the end of the season.

Galium silvaticum L.

The beginning of the flowering period varies among the individual plants and also varies from one year to the next. Over a period of three years, the earliest beginning of flowering noted was in the first week of June. The other extreme was a plant which did not start flowering until the first week of August. Both cases are exceptions, flowering in general starting in the second and third week of June to the first week of July. Full flowering usually is reached after one week to ten days and often lasts until in the first week of August; thereafter flowering comes to an end.

Galium aristatum L.

Flowering in this species started in the first week of August, a plant flowering in the last week of July was observed as an exception. The flowering period is short, most plants having finished by the end of August. Occacionally a plant still flowered in early September.

Galium schultesii Vest

This species is somewhat irregular in the start of its flowering period. The second week of June has been noted several times. Other plants, however, started much later, in the last week of June and the first two weeks of July. Full flowering comes one to two weeks after the beginning and the flowering period may last till the end of August.

IV. Grossing experiments

Crossing experiments were done in order to gain more insight into the interspecific relationships of *Galium silvaticum*, *Galium aristatum* and *Galium schultesii*.

TABLE II

Survey of the main morphological differences of *Galium silvaticum*, *Galium aristatum* and *Galium schultesii*

	GALIUM SILVATICUM L.	GALIUM ARISTATUM L.	GALIUM SCHULTESII Vest
Stem	Terete, with four faint ribs. Nodes thickened, often coloured by anthocyanine.	Terete below, becoming quadrangular above. Nodes thickened.	Sharply quadrangular, nearly from the base, with incrassate nodes.
Leave	Oblong lanceolate to oblanceolate. Widest just above the middle, gradually passing into the petiole. Rounded at the apical part. Mucronate.	Lanceolate, broadest just below the middle, narrowing to both ends, passing into the petiole at the base, tiny mucro at the top.	Lanceolate oblong. Widest in the middle, narrowed to both ends. Apiculate at the top.
Pedicel	Geniculate before anthesis.	Straight before anthesis.	Straight before anthesis.
Corolla	Acute	Lobes terminate in a solid mucro	Ovate, acute, finely pointed at the top.

Inflorescences in a number of plants were enveloped by paper bags just before the flower buds opened. In these plants fruits were never formed.

Fruits were always formed, however, when two panicles of neighbouring plants belonging to the same species and having the same chromosome numbers were enveloped in one bag together. Seeds from these fruits produced normal plants with, as could be expected, have the same chromosome number as the parent plants. If this experiment was done with two plants belonging to different species (and with different chromosome numbers), only a very few seeds were produced, varying from four to ten in one experiment. Plants from these seeds always proved to be identical, both in morphology and in cytology, with the plants from which the seeds had been harvested, and presumably were not hybrids. In order to eliminate this source of error an other method was introduced, i.e. the method described by FAGERLIND (1937).

The corolla together with the stamens attached to it, was removed just before opening, with the aid of a pair of tweezers. By the time the flower would have opened normally, ripe pollen was brought on the stigmas. This procedure was repeated after one or two days, with flowers developing later. To keep out unwanted pollen from other plants, the whole inflorescence was enclosed in a paper bag.

On each experiment were on each plant fifty flowers treated in this way. The experiments were repeated during three years.

The survey of the crossing experiments is given in table III. A + symbol means a successful cross, resulting in fruit setting; a − symbol an unsuccessful one. The table showes that active cross pollination in all species was followed by setting of fruits. Active self pollination always remained without results. In all other crossing experiments too the result was negative, with the exception of crosses between *Galium schultesii* and *Galium aristatum* and between *Galium aristatum* and *Galium schultesii*. In the first case one experiment resulted in seven mericarps and one in three mericarps. In the second case one crossing experiment gave two mericarps. The seeds matured, but they could not germinate, so that no F_1 generation could be obtained.

DISCUSSION

The three species *Galium silvaticum* L., *Galium aristatum* L., and *Galium schultesii* Vest, are very similar in their habitat. Differences in morphology, however, can be demonstrated.

The morphological characters, including the differential ones, remained constant throughout the years the plants were grown in the experimental garden. This indicates that the differences have a genotypical basis. The cytological investigations showed that the morphological characters observed belong to *Galium silvaticum* with $2n = 22$, *Galium aristatum* with $2n = 44$ and *Galium schultesii* with $2n = 66$ chromosomes.

TABLE III

Schedule I. Crossing experiments between *Galium silvaticum* (2n=22), *Galium aristatum* (2n=44) and *Galium schultesii* (2n=66). —=no fructification; +=fructification.

♀ \ ♂	A. G. silvaticum 2n=22	B. G. silvaticum 2n=22	C. G. aristatum 2n=44	D. G. aristatum 2n=44	E. G. schultesii 2n=66	F. G. schultesii 2n=66
A. G. silvaticum 2n=22	—	+	—	—	—	—
B. G. silvaticum 2n=22	+	—	—	—	—	—
C. G. aristatum 2n=44	—	—	—	+	+ 7 mericarps	—
D. G. aristatum 2n=44	—	—	+	—	—	+ 3 mericarps
E. G. schultesii 2n=66	—	—	—	—	—	+
F. G. schultesii 2n=66	—	—	—	+ 2 mericarps	+	—

Diploids of *Galium aristatum* L. are mentioned by BUTTLER and BRESINSKY (1966). From the description provided by these authors it appears that there are no differences in morphology with the tetraploids, with the exception of the stem, which is in *Galium aristatum* 22, sharply quadrangular. This is not in agreement with the present observations on *Galium aristatum* 44. The stem of *Galium aristatum* 44 is ascendent, terete in the lower parts and becoming quadrangular in the upper parts. This is also in agreement with other literature on the subject.

A stem which is sharply quadrangular, nearly from the base, occurs in *Galium schultesii*. The stem of *Galium schultesii* described by BUTTLER and BRESINSKY (l.c.) agrees with that of *Galium aristatum* 44. ("Dem Galium silvaticum ähnlich, aber oben mit vierkantigem Stengel").

In view of the cytological data published by these authors, it is unlikely that the chromosome numbers should be incorrect. This means that within *Galium aristatum* there are two cytotypes, with $2n = 22$ and $2n = 44$ chromosomes, with perhaps a difference in the morphology of the stem.

The distribution of the cytotypes within the area of the species is not known exactly. The diploids may be common, the tetraploids being limited to a more restricted area, but the reverse might be also true, or that possibly both cytotypes occur throughout the whole area of the species, for material of each cytotype was collected in a small part of the whole area only. The diploids came from Bavaria in Southern Germany (BUTTLER and BRESINSKY l.c.), the tetraploids grew at the border of Lake Lugano in Switzerland.

BRESINSKY (1965), points out that the plants of *Galium aristatum* growing North of the Alps perhaps are glacial relicts. According to FAVARGER (1967), occupy diploid taxa, in a given systematic group, frequently refugial localities or non glaciated regions, while the polyploids are found on territories that were covered by Quaternary glaciers.

If this is true, it is not clear how the spread of the polyploids occurred after this period. Only extensive cytological investigation of material out of the whole area of the species can give a solution of this problem.

The case of *Galium aristatum* is even more confused because in literature under the synonym of *Galium laevigatum* L. tetraploids and octoploids are mentioned (FAGERLAND, 1934; 1937). This author assigns both *Galium aristatum* and *Galium polonicum* to *Galium laevigatum*.

Galium polonicum, however, is quite distinct from *Galium aristatum*. It was first described by BLOCKI in 1886. It is a typical species of Eastern Europe, (POBEBIMOVA, 1958), whereas *Galium aristatum* is a typical southern European plant.

PIOTROWICZ (1958), showed that *Galium polonicum* is a tetraploid with $2n = 44$ chromosomes. BUTTLER and BRESINSKY (l.c.) think that Fagerlind had material of *Galium polonicum*, rather than of *Galium aristatum*. To this should be added that Fagerlind's material probably was collected in Tartu (Estonia).

If the material studied by Fagerlind belongs to *Galium aristatum* and not to *Galium polonicum*, that, however, would mean that *Galium aristatum* has a polyploid series with 2n = 22, 2n = 44 and 2n = 88 chromosomes.

Galium schultesii Vest is a hexaploid. This could be confirmed by the present investigation. BUTTLER and BRESINSKY (l.c.), also make mention of tetraploids from Slovenia and Croatia. The only information provided on this cytotype is that it has narrow leaves and, since other data are not available, it is not possible to determine the taxonomic position more accurately now.

Up until recently *Galium schultesii* was to be assumed to be indegenous to Bavaria and Southern Germany. BUTTLER and BRESINSKY (l.c.) on the other hand think that these plants do not belong to *Galium schultesii*, but are hybrids between *Galium silvaticum* and *Galium aristatum* 22. In their morphological characters they are intermediate between *Galium silvaticum* and *Galium aristatum* as reported by these authors. As mentioned before, *Galium aristatum* 22 should have a sharply quadrangular stem, *Galium silvaticum* a terete stem. The hybrid has a stem which is terete below and quadrangular above. This stem type matches well that of *Galium aristatum* 44 as described in the present study. The other characters described by BUTTLER and BRESINSKY (l.c.) are characters also intermediate between *Galium silvaticum* and *Galium aristatum* 44.

In "Flore des Alpes Maritimes" (BRIQUET et CAVILLIER, 1913), plants are described matching neither *Galium silvaticum* nor *Galium aristatum*, but obviously intermediate between the two.

These plants originated from the Bois de Sanson and from Mont Cheiron, regions where both species occur. BRIQUET (l.c.) states that this material should undergo an extensive study in order to clarify this. ("L'étude sur le vif de cette variété qui est, au point de vue des caractères foliaires, intermédiaire entre les Galium aristatum et G. silvaticum, doit être recommandée").

According to KERNER (1876), hybridization between *Galium silvaticum* and *Galium aristatum* in nature is unlikely, because, they do not flower simultaneously and are asyngamous. This is not confirmed by the present observations made during the flower seasons in three successive years. It is true that the respective peaks do not coincide, but there are certainly still flowers of *Galium silvaticum* present when *Galium aristatum* is in full flower. It could hardly be conceived that this is different in wild growing plants.

The respective areas of *Galium silvaticum* and *Galium aristatum*, though largely allopatric, may be partially sympatric, and hybridization between the two closely related species with identical chromosome numbers should not to be excluded. The results of the crossing experiments by FAGERLIND, (1934; 1937) on *Galium verum* and *Galium mollugo*, both with 2n = 44 chromosomes, support such an assumption. So there are indications that *Galium silvaticum* and *Galium aristatum* do hybridize in nature, perhaps

giving rise to an hybrid which might easily be mistaken for *Galium schultesii*. However, as long as crossing experiments between *Galium silvaticum* and *Galium aristatum* 22 are not made and no artificial hybrid has been obtained, it is impossible to arrive at final conclusions.

Still the possibility of the occurence of a polyploid series with $2n = 22$, $2n = 44$ and $2n = 66$ chromosomes within *Galium schultesii*, with slight differences in morphology, should not be excluded.

The crossing experiments between the species with different chromosome number have shown the existence of a barrier between such species. This seems to be common within the genus *Galium*. This barrier may be less effective at higher ploidy level as indicated by the fact that fruits were obtained from crossing experiments between *Galium aristatum* 44 and *Galium schultesii*. However, it should be reminded that the seeds obtained from such crossings were not able to germinate.

From the results of the present investigation and from the discussion it is clear that *Galium silvaticum*, *Galium aristatum* and *Galium schultesii* must be considered as separate species.

Summary

The three species *Galium silvaticum* L., *Galium aristatum* L. and *Galium schultesii* Vest show differences in morphology, cytology and geographical distribution. These differences are described and discussed.

Crossing experiments between the three species were without results. No hybrid could be obtained.

Galium silvaticum, *Galium aristatum* and *Galium schultesii* must be considered as separate species.

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REFERENCES

Binz, A., Schul- und Exkursionsflora der Schweiz, Basel 1927.

Bonnier, R., Flore complète de France, Suisse et Belgique, Paris 1911–1913.

Bresinsky, A., Ber. Bayer. Bot. Gesellsch., 38, 55–56 (1965).

Briquet, J. and Fr. Cavillier in E. Burnet, Flore des Alpes Maritimes, V, Genève, Bâle, Lyon 1913–1915.

Buttler, K. P. and A. Bresinsky, Ber. Bayer. Bot. Gesellsch., 39, 25–28 (1966).

Coste, H., Flore de la France, Paris 1903.

Duftenschmidt, J., Die Flora von Oben-Oesterreich, Linz 1883.

Fagerlind, F., Hereditas, 29, 223–232 (1934).

————, Acta Horti Berg., 11, 195–470 (1937).

Fiek, E., Flora von Schlesien, Breslau 1881.

GABRIELS, J., Bull. du J. Bot. de l'Etat, Bruxelles, XXXV, 109–167 (1965).
GADELLA, TH. W. J. and E. KLIPHUIS, Acta Bot. Neerl., 12, (1963).
HADAC, E., Preslia, 41, 39–60 (1969).
HEGI, G., Illustrierte Flora von Mitteleuropa, München 1906–1931.
HERMANN, F., Flora von Nord- und Mittel Europa, Stuttgart 1965.
KERNER, A., Oesterreich. Bot. Zeitschr., 26, 109–120 (1876).
KLIPHUIS, E., Proc. Roy. Neth. Acad. Sc. Ser. C 65, 279–285 (1962).
LINNAEUS, C., Spec. Plant. ed III, Vienna, 1764.
MEUSEL, H., Vergleichende Arealkunde, Berlin 1943.
PIOTROWICZ, M., Acta Biol. Cracov., 1, 159–169 (1958).
POBEBIMOVA, E. G. in B. K. SHISKIN, Flora S.S.S.R., 25, Moskva, Leningrad 1958.
POUQUES, M. L. Mlle., Rev. gen. Bot., 56, 5–138 (1949).
REICHENBACH, H. G. L., Deutschlands Flora, 16, Leipzig 1885.
ROTHMAHLER, W., Exkursionsflora von Deutschland, Berlin 1958.
ROUY, G., Flore de France, Paris 1903.
SAVULESCU, T. and E. J. NYÁRÁDY, Flora Republicii Populare Romine, Bucaresti 1960.
SCHULTES, J. A., Oesterr. Flora, 1, (1814).
VEST, L. C., Flora, 4, 526–531 (1821).
VOLLMANN, F., Flora von Bayern, Stuttgart 1914.
WAGNER, H., Illustrierte deutsche Flora, 3, Stuttgart 1905.
WILLKOMM, M. et J. LANGE, Prodr. Florae Hispanicae, Stuttgartiae 1870.
ZAHRADNIKOVA, K., Biológia (Bratislava), 22, 132–142 (1967).