Biosystematic investigations in Cardamine pratensis L.s.l : 1. Diploid taxa from Central Europe and their fertility relationships

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Biosystematic investigations in Cardamine pratensis L.s.l.
I. Diploid taxa from Central Europe and their fertility relationships

by KRYSTYNA URBANSKA-WORYTKIEWICZ and ELIAS LANDOLT

Contents

1. Introduction

The present investigations form part of a study which aim has been to obtain a picture of the speciation trends within *Cardamine pratensis* s.l. Variation in morphological and cytological characters, reproduction and breeding behaviour, isolation barriers as well as geographical distribution and ecology were investigated. *C. pratensis* frequently occurs in meadows remaining under human influence; the problem of the origin of taxa living in such biotopes has been of a particular interest for the authors.

The *C. pratensis* complex has previously been investigated from various parts of its range (SENJANINOVA cit. acc. to ILJINSKIJ 1926, LAWRENCE 1931, MANTON 1932, FLOVIK 1940, LÖVE and LÖVE 1944, GUINOCHET 1946, LÖVKVIST 1947, 1953, 1956, HOWARD 1948, HUSSEIN 1949, MATTICK cit.acc. to TISCHLER 1950, BANACH 1951, KUZMANOV and KOZUHAROV 1969, DERSCH 1969, SOUCHON 1971, SOUCHON and TOMASSONE 1971, MATTFIELD - personal communication). However, only some fragmentary reports were hitherto known from the Alps.

Our preliminary results have recently been published (LANDOLT and URBANSKA-WORYTKIEWICZ 1971). Remarkable karyological differentiation has been found in the studied material; of a particular interest proved to be the diploid taxa which showed diversified patterns of geographical distribution and different ecological requirements. It seemed advisable to pay them a special attention as the diploids apparently constitute a basis for speciation within the group of *C. pratensis*. Our collection has notably grown in the meantime; thus, we have decided to pursuit the investigations by passing successively through various levels of polyploidy represented in our material.

It should be mentioned that some diploid taxa were found quite recently; apart from the chromosome counts and preliminary morphological observations no studies could have been carried out on these plants. Hence, they are briefly mentioned in the present paper,yet will be investigated in further course of our program.

Acknowledgements

A number of persons have contributed to our collections; they have mostly sampled the polyploid populations of *Cardamine pratensis*. The authors should like to express their gratitude to Dr. F. SPETA, H. RANNER, R. STEINWENDTNER (Linz), F. GRIMS (Taufkirchen), Dr. J. PFADENHAUER (Munich), Dr. E. SULGER-BÜEL (+), PROF. Dr. H. HESS, Dr. E. LANDOLT-STADLER, W. ENGETSCHWILER (Zurich) as well as to our colleagues and friends from the Geobotanical Institute: E. BRÄM, J. BURNAND, P. BOLLIGER, E. BROUILLET, Dr. A. GIGON, Dr. F. GROSSMANN, Dr. M.HAUSER, A. HEITZMANN-HOFFMANN, PD Dr. F. KLÖTZLI, Ch. LEUTHOLD, CH. ROTH, H. SIGG and S. ZÜST.

The floristic information given to us by Dr. A. BECHERER (Lugano) has been of great benefit. Thanks are also due to the Directors and the Keepers of the Herbaria for loan of specimens.

Our ample material could not have been fully investigated without help of the technical staff of our Institute. Special attention is due to the gardener, Mr. E.BROUILLET and to Mrs M. JONSEN who have taken care of the collected plants and kept them in experimental garden. Technical assistance of Mrs M. SIEGL, Mrs A. HEGI and Miss U. BODMER is greatly appreciated. Drawings and graphs were faultlessly made by Miss E. BRÄM to whom the authors present their sincere thanks. The photos were made by Mr. H. SIGG.

2. Material and methods

Plants for the present study have been sampled in 1969 - 1974, mostly by the authors. A number of other persons have also contributed to the collection which actually comprises 900 populations. The diploids were found in 224 populations out of which 208 (1637 plants) are dealt with in the present paper, (Tables 1-6). A relatively high percentage of the diploids doesn't exactly reflect the pattern of geographical distribution of the whole group of *Cardamine pratensis*; at the present phase of our investigations a special attention has been payed to the diploid taxa.

Plants for the investigations were chosen at random within their populations. As a representative sample, 8-15 plants were collected; subsequently they were transferred to the greenhouse and, later on, into the experimental field of the Geobotanical Institute.

The studied region was principally confined to the Alps; however, for comparative purposes, the neighbouring areas were as well included in our program. In general, the boundaries of the investigated area can be traced along the following lines: Landsberg (Bavaria) - Innsbruck - Bolzano - Lecco - Turin - Chambéry - Nantua - Besançon - Epinal - Colmar - Rottweil - Landsberg. Rather intensive collections were made within this area and one can assume that a general pattern of distribution of the diploid taxa has been followed there.

As far as other parts of the Alps are concerned, some plants were sent to us from surroundings of Salzburg and from Oberösterreich; they represented higher polyploid levels and therefore are not included in the present paper. It should be noted, however, that LÖVKVIST (1956) has previously dealt with some diploid taxa from the region of Vienna and from Styria. The Swedish author has also studied an ample material of *C. pratensis* s.l. from various parts of its area of distribution.

Southwestern Alps are not represented in our collections. According to the bibliographic data, the *C. pratensis* complex is there either extremely scarce or totally absent.

Not only living plants, but also an ample herbarium material was studied in the course of the present work; numerous specimens were tested for the pollen quality. The following collections were obtained on loan;

Austria: Graz (GZU), Innsbruck (IB,IBF), Klagenfurt (KL), Linz (LI)
France: Grenoble (GR)
Germany: Munich (M)
Italy: Florence (FI), Genoa (GE), Padua (PAD), Pavia (PAV), Verona (VER)
Switzerland: Berne (BERN), Geneva (G), Lausanne (LAU), Lugano, Zurich (Z, ZT,RUEB)
Yugoslavia: Ljubliana (LJU)

As far as some herbarium collections from Vienna (W, WU) and those from Turin (T) are concerned, we refer to the data of LÖVKVIST (1956).

Figures in the description of the taxa are based upon a combination of data from measurements of the herbarium material collected in natural conditions and those of the cultivated plants. Maps and lists comprise as well the data obtained from the loan specimens.

The methods used in cytological investigations as well as technical details concerning the experimental crosses are given in the respective chapters.

3. Nomenclature problems and species delimination

Six taxa have been distinguished among the diploids occurring within the studied area: *Cardamine granulosa*, *C. Matthioli*, *C. udicola*, *C. rivularis*, *C. pratensis* and *C. nemorosa*. *C. udicola*, very rare and particularly isolated in its geographical distribution, was but partly investigated in the course of the present work.

The nomenclature used in the present paper corresponds in general to that previously accepted by LÖVKVIST (1956). However, LÖVKVIST has not distinguished *C. udicola* from other taxa; furthermore, he has considered *C. nemorosa* only as a variety and has used the name of *C. pratensis* in a more general sense than do the present authors.

In *Cardamine pratensis* s.l., as in any other critical biological complex, the delimination of taxa is to a certain extent arbitrary. The authors are fully aware of the fact that a definite taxonomical status of actually presented taxa still remains an open question. Only after having completed biosystematic study on the whole group, including all polyploid levels, a more reliable revision can be done. For practical purposes, however, provisional specific names were presently given to the resp. diploid taxa and we intend to follow them in further course of the investigations.

The name of *Cardamine granulosa* All. has appeared for the first time in 1789 in "Auctarium ad Floram Pedemontanam". The described specimens originated from the surroundings of Turin. The plants studied in the course of the present work correspond well to this original diagnosis.

Cardamine Matthioli Moretti has been described in 1847 in "Flora Comense" by COMOLLI, who distinguished this species from *C. pratensis* and referred to a very precise diagnosis by MORETTI: "Caule caespitoso ramoso; racemo composito, floribus albis". COMOLLI mentioned very small seeds occurring in *C. Matthioli* ("Semi piccolissimi"). The diagnosis of *Cardamine Matthioli* based on the data of MORETTI and COMOLLI seems to be univocal. It should be added that a name of *C. Hayneana* Welwitsch, previously reported as a synonyme for *C. Matthioli*, has been published without description and hence is not valid (see LÖVKVIST 1956).

Cardamine udicola Jord. has been described in 1860; the diagnosis of JORDAN has been based upon material from the region of Lyon, France. The plants found by the present authors in the surroundings of the Lake of Thun as well as in southern Ticino correspond rather well to the original description; however, we have not seen the type specimen.

Cardamine nemorosa Lejeune has been described in 1813 from the surroundings of Spaa, Belgium. LÖVKVIST (1956) assumed that this name corresponded to the diploid plants of the forest type. However, during our field-work in the surroundings of Spaa tetraploid plants have solely been found.

Nevertheless one might assume that the diploids remain to be found in this region.

Cardamine pratensis L. appeared for the first time in "Species Plantarum"(1753). The diagnosis of LINNEUS was probably based on tetraploid plants occurring frequently in meadows of southern Sweden. As far as the morphology of *C. pratensis* is concerned, it is virtually impossible to distinguish the plants which grow in fertilized meadows of Central Europe north of the Alps from those occurring in Sweden; the name of *C. pratensis* should be used accordingly for all various cytotypes, including the diploid one investigated in the course of the present work.

Cardamine rivularis Schur has been described in 1853 from Mt. Arpas in Transsilvania. The original specimens of SCHUR, kindly sent to us by Prof. Dr. K.H. RECHINGER (Museum of the Natural History, Vienna), represented various pollen types; it might be assumed that they comprised diploids, tetraploids as well as some hybrid individuals. Our representatives of *C. rivularis* are identical with the putative diploid herbarium specimens of SCHUR.

4. Morphology

4.1. Morphological variation and diagnostic characters

The variation pattern of the *Cardamine pratensis* group is intrinsically complex; phenotypic modifications as well as polymorphism and racial variation contribute to the taxonomic difficulty of studied diploids. Total range of genotypically and environmentally induced variation is large. Even where morphological distinctions between taxa are rather well-marked, the ranges of variation may overlap and some phenotypes of one taxon may mimic certain phenotypes of another taxon (e.g. *C. nemorosa* – *C. pratensis*). This creates difficulties for determination of herbarium specimens which do not show the whole range of variation within the population. An accurate identification may sometimes be virtually impossible in the herbarium, given an inadequate series.

Some amount of racial variation from population to population is not practicable to recognize taxonomically. On the other hand, some races which grow in isolated habitats are separated by a certain degree of morphological discontinuity from their relatives (e.g. *C. Matthioli*, *C. udi-*

cola).

In order to check experimentally some aspects of variation occurring within the *C. pratensis* group, diploid clones from various populations were kept for about six months in conditioned chambers where light, temperature and air humidity were controlled. The obtained results have not yet been wholly evaluated; however, some of them were taken into consideration when morphological characters given below and their diagnostic value were discussed.

Rhizome. In general, the diploid taxa do not manifest marked differences in morphology of the rhizome. Its volume seems to reflect the soil quality; in plants growing on humid and light soils the rhizome appears to be thicker than in the materials collected in more compact and dryer soils. The rhizomes of *C. rivularis, C. udicola* and *C. Matthioli* are rather short and not much developed. On the other hand, they are somewhat elongated in *C. granulosa.* The leaf scares are rather pronounced, especially in *C. granulosa;* they are also well-marked in *C. nemorosa* and *C. pratensis.* The granules or tubers of roots, previously described by LÖVKVIST (1956) in *C. granulosa* were not found by the present authors; however, it should be noted that we have had only a limited number of plants at our disposal.

Stem. Length and volume of the stem are very variable and again this character is subject to environmental conditions. In general, plants from fertilized meadows and those from the forests are bigger than the individuals growing in poor soils in bogs or swamps. This correlation appears rather independently of systematic affinities of given plants.

Basal leaves. Basal leaves most frequently form a rosette. Only in *C. granulosa* a typical rosette is not observable for the leaves are usually upright. In some taxa the basal leaves are often not recognizable at later developmental stages, when the plants are bearing fruit (e.g. *C. Matthioli, C. udicola, C. granulosa*).

The number and morphology of the leaflets are highly variable in relation to environmental and seasonal factors, yet seem to be as well genotypically conditioned, at least to some extent. The lowest number of the leaflets was found in *C. granulosa* (1, rarely 3), the highest one - in *C. rivularis* (7 - 31). Other diploid taxa represented intermediate values, *C. nemorosa* having 1 - 11 leaflets, *C. Matthioli* - 3 - 17, *C. udicola* - 5 - 25.

The terminal leaflet in *C. nemorosa*, *C. pratensis*, *C. udicola* and *C. rivularis* is roundish to polygonal and reniform at the base. The latter type of terminal leaflet was also frequently observed in *C. Matthioli*; however, this taxon has also terminal leaflets that are blunt at the base. In *C. granulosa* the reniform leaflets were rare; most frequently they were blunt at the base and had oblong, broad and irregular lobes.

Lateral leaflets show a similar morphology as the terminal ones, yet they are rather smaller. Differences in size between the terminal and lateral leaflets are rather pronounced in *C. nemorosa*, *C. pratensis*, *C. Matthioli* and *C. granulosa* where the lateral leaflets were less than half as large as the terminal ones. On the other hand surface of the lateral leaflet in *C. rivularis* was larger than half of that in the terminal leaflet. *C. udicola* represented intermediate proportions.

In plants collected in their natural habitats the highest value of the width of the terminal leaflets comported 1 - 3.5cm in *C. granulosa*, 1 - 5cm in *C. nemorosa*, 1 - 3.5cm in *C. pratensis*, 1 - 3.5cm in *C. Matthioli*, 0.5 - 3cm in *C. udicola* and 0.5 - 1.5cm in *C. rivularis*.

It should be added that *C. Matthioli* and, in particular, its plants growing in fertilized meadows in Piedmont, showed most frequently a notable diminution in size of the lateral leaflets towards the base of the petiole: the leaflets were partly overlaying each other. In *C. rivularis* where the basal leaves are also multifoliate, such a rapid diminishing was not observed and the marginal parts of the leaflets came only exceptionally in contact.

Gristly teeth were found in the whole studied material. On the other hand, occurrence of small hairs and their morphology proved to be a useful character for determination of particular taxa. In *C. nemorosa* and *C. pratensis* rather flat and adherent triangular hairs were observed in nearly all leaves, at least at their upper surface near the margin of the leaf blade. They measured about 0.04 - 0.08 mm of width at the base. The other studied diploids either had no hairs at all, or bore narrow (0.02 - 0.04mm), cylindrical ones.

Cauline leaves. Lower cauline leaves were often similar to the basal ones, being only smaller. The number of leaflets diminished gradually upwards and the leaflets became narrower. The morphology of the cauline leaves is extremely variable and therfore does not seem to offer any definite diagnostic value for the studied taxa. It is relatively useful in *C. granulosa* where 1 - 3 cauline leaves occur and the two uppermost ones are pinnate to pinnasect with 3 - 5 divisions. Other diploid taxa have most frequently 3 - 8 cauline leaves which are pinnate, most of them consisting of more than five leaflets. It is interesting to note that lower leaflets of lower cauline leaves in *C. Matthioli* are slightly deflexed and rounded whereas in other diploids they are mostly acute, horizontally spreading and rather ascending.

The ratio: length of the terminal leaflet/length of the rest of the cauline leaf seems to be helpful for determination of *C. rivularis*. It comports 1/4-3/4 in the second uppermost leaf of this species whereas other diploid taxa represent higher values viz. 3/4-3.0.

Flowers. So far, only recognizable differences in morphology of the flowers within the *C. pratensis* group are those in colour and size of the petals. There occur as well some slight differences in size of the anthers yet this character does not seem to have any significant diagnostic value. The petal length varied between 5 - 8 mm *(C. Matthioli)* and 8 - 12 mm *(C. granulosa, C. nemorosa)*. *C. rivularis, C. udicola* and *C. pratensis* offered intermediate values.

As far as the colour of the petals is concerned, the flowers of *C. Matthioli* and *C. granulosa* were invariably white in living plants: only in some herbarium specimens of *C. granulosa* the petals were tinged. *C. pratensis* has rather uniformly pale-violet flowers; a similar shade was found in *C. nemorosa*. On the other hand, *C. rivularis* had pinkish flowers. *C. udicola* has both white- and pink-coloured flowers.

The colour of the petals proved to be uniform in most of the studied diploid populations. In some stations, however, white-flowering plants and those with pink flowers were growing side by side. Such mixed populations were found once in *C. rivularis* (Les Diablerets) and twice in *C. udicola*. It is interesting to note that both mixed populations of the latter taxon were observed in the surroundings of the Lake of Thun whereas all plants investigated from southern Ticino had invariably white flowers.

Some diversity in the growth sequence of stamens and carpels was noted in *C. udicola* from Ticino. The anthers matured in a position above the style; as the style grew during anthesis, the stigma became receptive for pollen when it was level with upper anthers. The time lapse between the onset of anthesis and stigma receptivity was about 48 hours. It should be mentioned that these plants proved to be partly autogamous. Other diploids which are predominantly allogamous displayed usually an inverse pattern of flower development i. e. the style grew prior to the anthers. Aforementioned differences were observed in experimental material; it was rather difficult to recognize them in the herbarium specimens collected at various stages of flower development. The question, whether the observed differences stay in any relation to variation in breeding behaviour, requires further investigations.

The differences in time of flowering that occur between particular diploid taxa are apparently influenced by altitude above sea level as well as type of vegetation in which given taxon occurs. In general, plants from the forests and those from fertilized meadows *(C. nemorosa, C. pratensis)* flowered earlier than individuals inhabiting reed meadows and bogs *(C. rivularis, C. udicola)*. In Piedmont, the authors observed *C. granulosa* and *C. Matthioli* flowering at the same time, the latter taxon being apparently at the end of its flowering period.

The differences in time of flowering observed in natural conditions were accordingly found in experimental field, although the pattern was somewhat less pronounced.

Fruit. Variability in length and width of the siliques were rather well-recognizable within the *C. pratensis* group. It should be added that different proportions of length and width occured in some of the studied taxa; accordingly, one might describe the siliques in a general way as "long narrow type" (most plants of *C. Matthioli)* "long broad type" *(C. pratensis, C. nemorosa)* or "short broad type" (most frequently observed in *C. rivularis* and *C. udicola)*.

Long siliques (up to 3.5 cm) were found in most of the studied plants of *C. Matthioli*, although short siliques were sometimes observed in few populations. Siliques of *C. nemorosa* and those of *C. pratensis* represented "long type", their length corresponding to that of long siliques in *C. Matthioli*. In *C. rivularis* and *C. udicola*, short siliques (1.5 - 2.5 cm) were most frequently found ; however, these taxa were sometimes represented by individuals bearing long siliques.

The number of ovules was proportional to the length of the siliques. In *C. granulosa* 25 - 50 ovules were usually observed ; in *C. Matthioli*, their number amounted to 36 - 48. Siliques of *C. pratensis* and those of *C. nemorosa* contained 20 - 40 ovules. *C. udicola* and *C. rivularis* proved to be rather variable in this respect: number of ovules ranged from 8 to 32.

As far as the width of siliques is concerned, *C. Matthioli* represented a narrow type (0.6 - 0.9 mm). The width values for *C. rivularis*, *C. udicola*, *C. nemorosa* and *C. granulosa* comported respectively 0.9 - 1.3 mm, 0.9 - 1.5 mm, 1.3 - 1.6 mm and 0.9 - 1.1 mm.

The size of seeds appeared to be highly variable, even in the same silique. However, the differences in width of fully developed seeds corresponded in a general way to the type of the silique : *C. Matthioli* had very narrow seeds (0.5 - 0.7 mm), whereas higher values (0.8 - 1.2 mm) were found in all other diploids.

Width of the style measured in herbarium materials showed some differences. In *C. rivularis* it comported 0.25 - 0.40 mm. The resp. values for *C. Matthioli*, *C. udicola*, *C. granulosa*, *C. pratensis* and *C. nemorosa* were : 0.3 - 0.6 mm, 0.3 - 0.6 mm, 0.4 mm, 0.3 - 0.6 mm, 0.5 - 0.8 mm.

4.2. Morphological description of the studied diploid taxa

Cardamine granulosa All. (Fig. 1)

Rhizome rather thin, often elongated, loosely covered with thickened scales. Stem most frequently **simple**, erect. Plants up to 40 cm tall. *Basal leaves usually erect, long-petioled, most frequently consisting of a single terminal leaflet;* sometimes with one pair of lateral leaflets, terminal leaflet rather large, up to 3.5 cm long, *blunt* or rarely reniform at the base, often longer than broader and irregularly lobed. Leaves most frequently glabrous, only rarely with sparse thin hairs. *Cauline leaves in number 1 - 3*, the two uppermost ones pinnatisect with narrow, oval, ascending divisions which *highest number is 3 - 5*. Terminal division of the second uppermost leaf notably longer than the rest of the leaf. Inflorescence racemose, simple ; *petals white*, sometimes tinged in herbarium specimens, 8 - 12 mm long. Silique 0.9 - 1.1 mm broad with 25 - 50 ovules. Seeds

0.8 - 1.0 mm broad. Style about 0.4 mm thick.

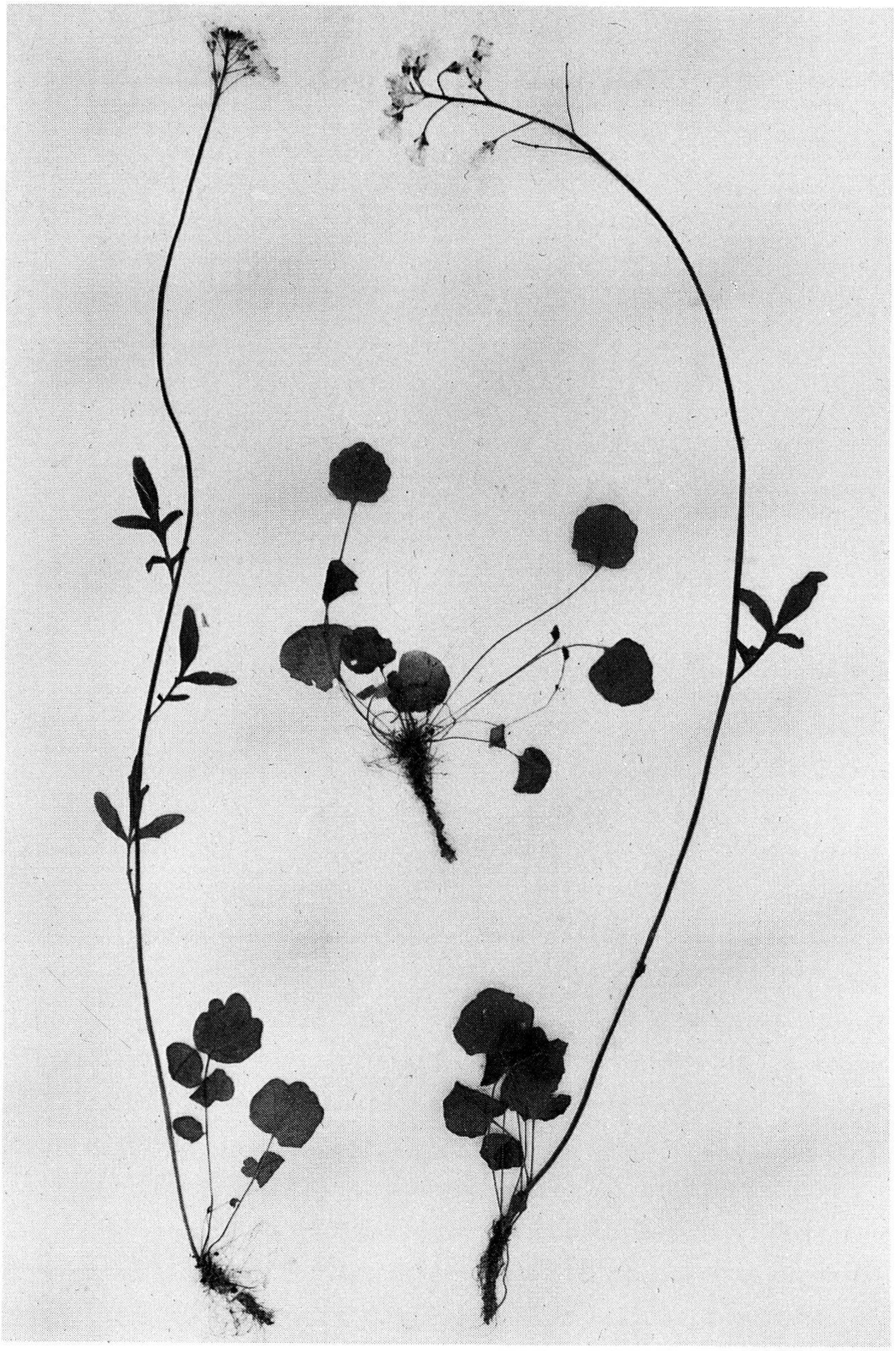


Fig. 1. *Cardamine granulosa* (560) from Avigliana, Piedmont. 1/3 natural size.

Cardamine Matthioli Moretti (Fig. 2a, b)

Rhizome thin and often short, only at the uppermost part with small thickened scales. Stem one or numerous, most frequently branched at the base and also at upper part, erect or ascending; plants up to 50 cm tall. Basal leaves usually prostrate, 3 - 17-foliolate. Terminal leaflet rather large, reniform or blunt at the base, glabrous or hairy (hairs 0.02 - 0.04 mm broad at the base). Surface of the terminal leaflet often being more than twice as large as that of the uppermost lateral leaflet. Lateral leaflets often diminishing rapidly in size towards the base of the petiole. Cauline leaves pinnate, in number 5 - 20. The second uppermost cauline leaf 5 - 11 foliolate, its terminal leaflet being about 3/4 - 1 1/2 times as long as the rest of the leaf. *Lower leaflets of lower cauline leaves rounded and slightly deflexed.* Inflorescence racemose, compound;*petals white,* 5 - 8 mm long. *Silique 0.5 - 0.9 mm broad,* most frequently 2.5 - 3 cm long, *with 36 - 48 ovules.* Seeds 0.5 - 0.7 mm broad. Style 0.3 - 0.6 mm thick.

Cardamine udicola Jord. (diploid)(Fig. 2c)

Rhizome thin and often short, only at the uppermost part with small thickened scales. Stem one or numerous, simple or branched, erect or ascending; plants up to 40 cm tall. Basal leaves usually prostrate, 5 - 25-foliolate. Terminal leaflet small to large, reniform at the base, glabrous or with thin hairs, (hairs 0.02 - 0.04 mm broad at the base). Surface of the terminal leaflet occasionally more than twice as large as that of the uppermost lateral leaflet. Lateral leaflets diminishing gradually in size towards the base of the petiole. Cauline leaves pinnate, usually in number 4 - 10. The second uppermost cauline leaf 5 - 11-foliolate, its terminal leaflet being about 2/3 - 1 1/4 times as long as the rest of the leaf. *Lower leaflets of lower cauline leaves acute,horizontally spreading or slightly ascending.* Inflorescence racemose, simple or compound: *petals white or pale violet (both types occurring often within the same population),* 7 - 11 mm long. *Silique 0.9 - 1.3 mm broad,* 1.5 - 3 cm long, with 8 - 32 ovules. Seeds 0.8 - 1.2 mm broad. Style 0.3 - 0.6 mm thick.

Fig. 2a, b. *Cardamine Matthioli:*
a. No. 569 from a wet station (Lago di Viverone, Piedmont);
b. No. 561 from a fertilized meadow (Pinerolo, Piedmont).
c. *Cardamine udicola* (137) from Lido di Ascona (Ticino). 1/3 natural size.

Cardamine rivularis Schur (diploid) (Fig. 3)

Rhizome thin and often short, only at the uppermost part with small thickened scales. Stem usually one, most frequently simple, upright; plants up to 30 (40) cm tall. Basal leaves most frequently prostrate, 7 - 31-foliolate. *The terminal leaflet rather small, rarely longer than 1.5 cm,* reniform at the base, glabrous, or with thin hairs (hairs 0.02 - 0.04 mm *broad at the base).* Surface of the terminal leaflet being not more than twice as large as that of the nearest lateral leaflet. Lateral leaflets diminishing gradually in size towards the base of the petiole. Cauline leaves pinnate, usually in number 3 - 5. The second uppermost cauline leaf most frequently 7 - 11-foliolate, *its terminal leaflet being about 1/4 - 3/4 times as long as the rest of the leaf.* Lower leaflets of lower cauline leaves acute,horizontally spreading or slightly ascending. Inflorescense simple racemose; petals pinkish, (exceptionally also white), 7 - 11 mm long. Silique 0.9 - 1.3 mm broad, 1.5 - 3 cm long, with 8 - 32 ovules. Seeds 0.8 - 1.2 mm broad. Style 0.25 - 0.40 mm thick.

Cardamine pratensis L. (diploid) (Fig. 4)

Rhizome thin or slightly thickened, with small scales, bearing one or numerous stems that are simple or branched, most frequently erect; plants up to 50 cm tall. Basal leaves usually prostrate, 1 - 13-foliolate *(most frequently more than three leaflets).* The terminal leaflet variable in size, *rarely longer than 3.5 cm,* reniform at the base, most frequently hairy at the marginal part *(hairs 0.04 - 0.08 mm broad at the base).* Surface of the terminal leaflet often more than twice as large as that of the nearest lateral leaflet. Lateral leaflets diminishing rapidly or gradually in size towards the base of the petiole. Cauline leaves pinnate, usually in number 3 - 8; the second uppermost cauline leaf frequently 5 - 11-foliolate, its terminal leaflet being about 3/4 - 2 1/2 times as long as the rest of the leaf. Lower leaflets of lower cauline leaves acute,horizontally spreading or slightly ascending. Inflorescence racemose, simple or compound; petals pale-violet, 7 - 11 mm long. Silique 1.1 - 1.3 mm broad, more than 3 cm long, with 20 - 40 ovules. Seeds 0.8 - 1.2 mm broad. *Style 0.3 - 0.6 mm thick.*

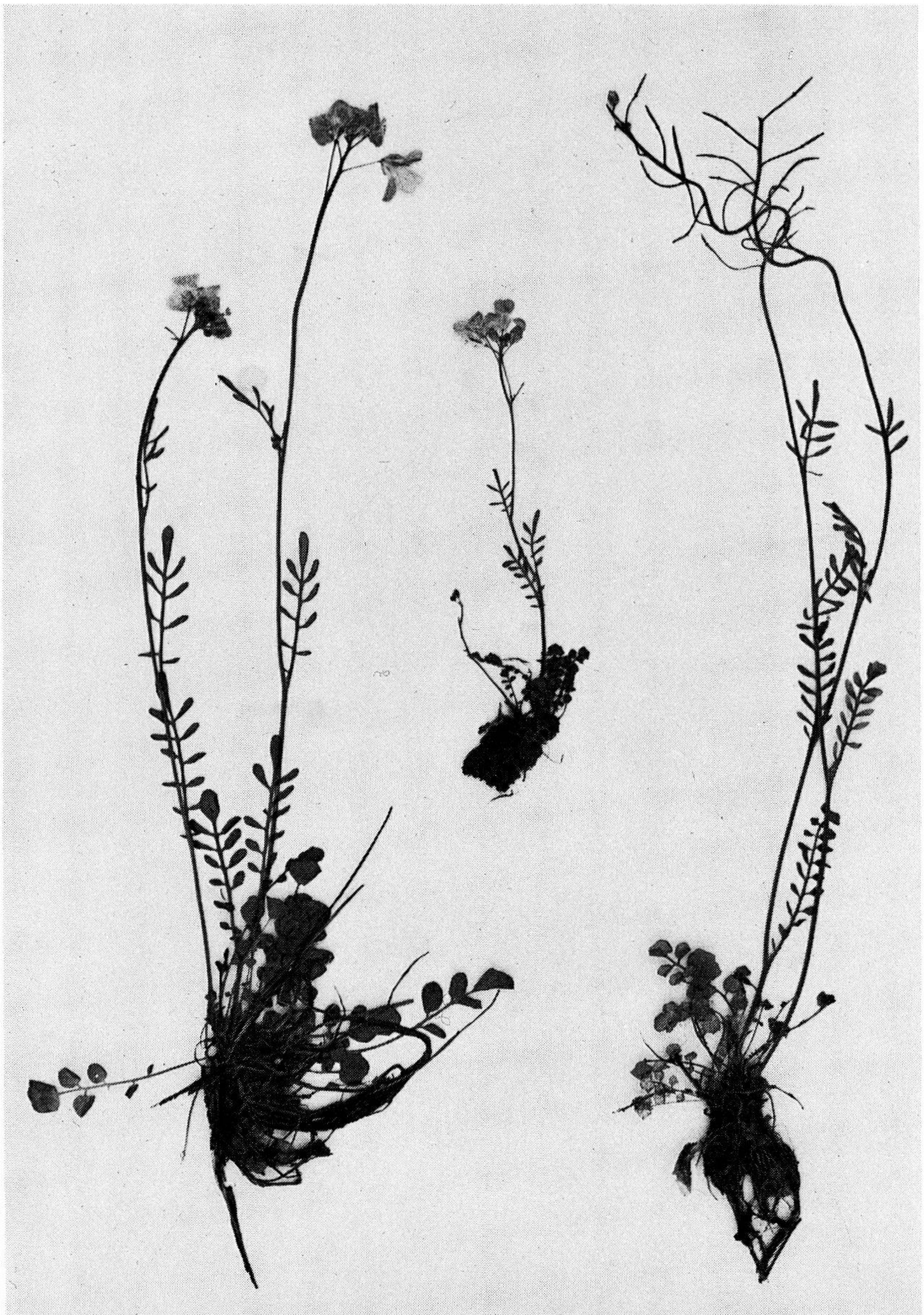


Fig. 3. *Cardamine rivularis* (33) from Valbella (Graubünden). 1/3 natural size.

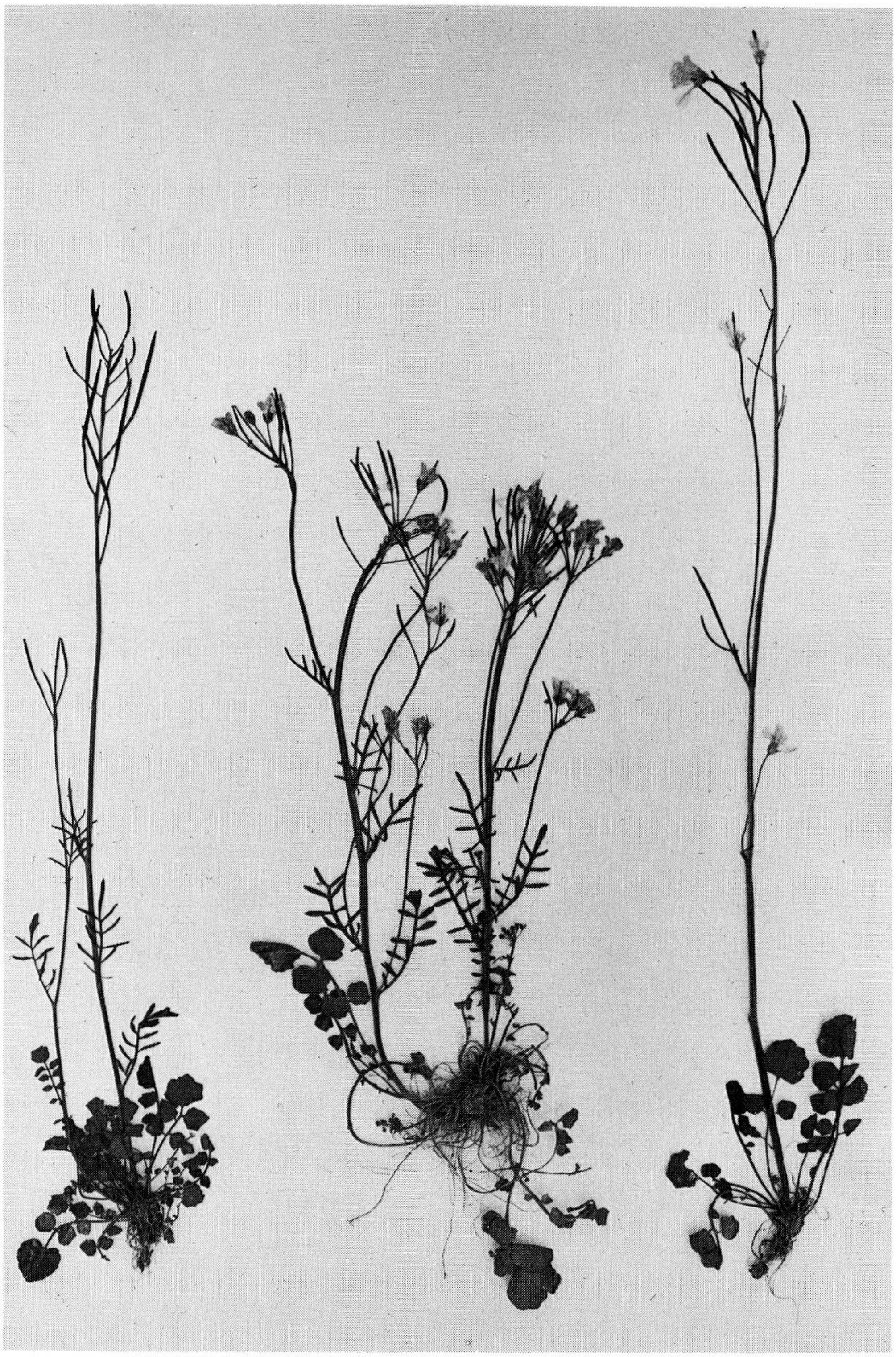


Fig. 4. *Cardamine pratensis* (38) from Gams (St. Gallen). 1/3 natural size.

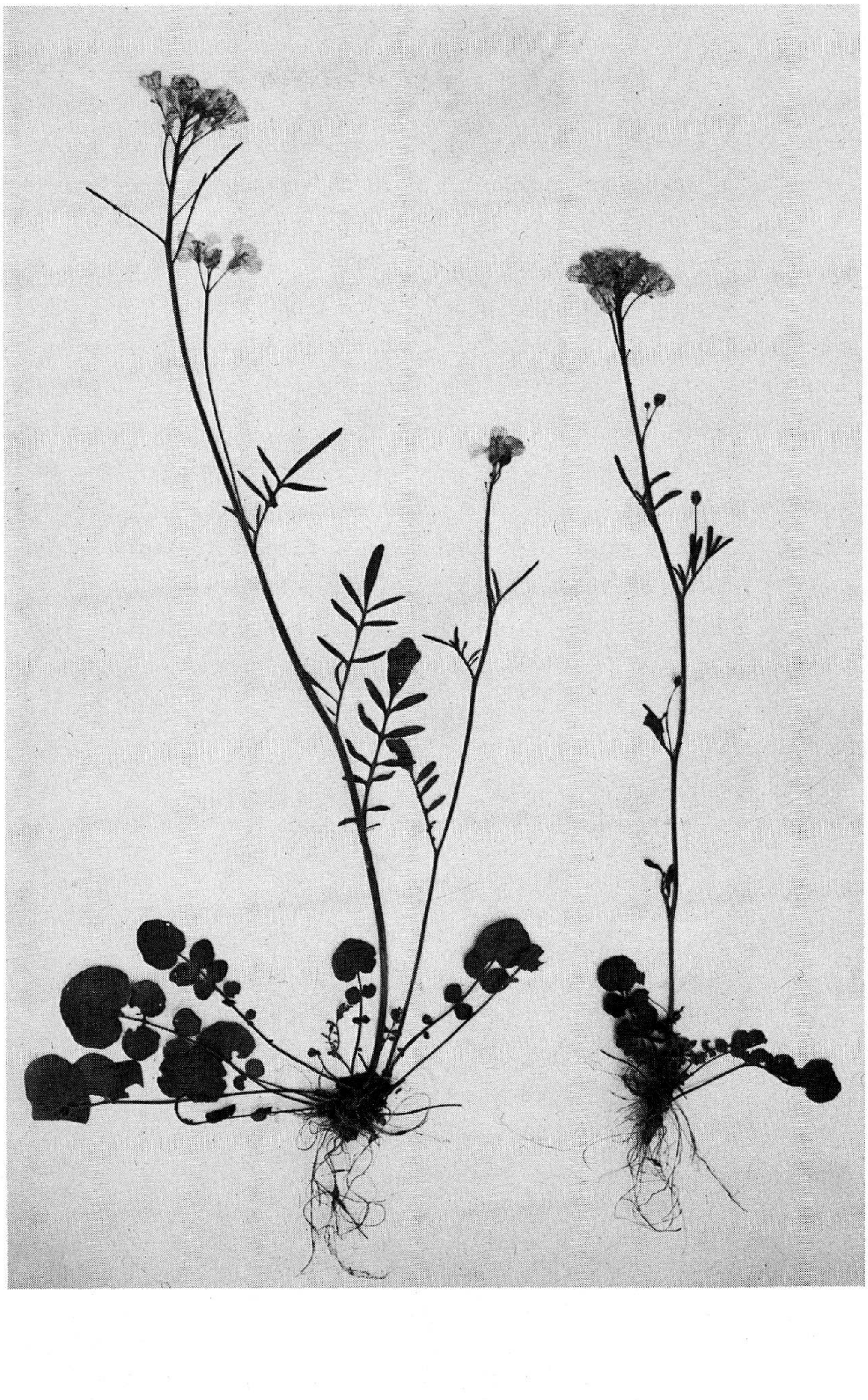


Fig. 5. *Cardamine nemorosa* (65) from Les Prēs-de-Vaire(Doubs) 1/3 natural size.

Cardamine nemorosa Lejeune (Fig. 5)

Rhizome often thick and short, with numerous thickened scales. Stem one or numerous, simple or branched, most frequently erect; plant up to 50 cm tall. Basal leaves usually prostrate, 1 - 11-foliolate *(leaves with 3 leaflets frequent)*. The terminal leaflet *often longer than 3.5 cm*, most frequently reniform at the base, hairy at least at the upper surface, in the marginal part of the leaf blade *(hairs 0.04 - 0.08 mm broad at the base)*. Surface of the terminal leaflet usually more than twice as large as that of the nearest lateral leaflet. Size of lateral leaflets diminishing gradually or rapidly towards the base of the petiole. Cauline leaves pinnate, in number 3 - 8; the second uppermost cauline leaf most frequently 5 - 9-foliolate, its terminal leaflet being 4/5 - 3 times as long as the rest of the leaf. Lower leaflets of lower cauline leaves acute horizontally spreading or slightly ascending. Inflorescence racemose, simple or compound: petals pale-violet, 8 - 12 mm long. Silique 1.3 - 1.6 mm broad, often longer than 3 cm, with 20 - 40 ovules. Seeds 0.8 - 1.2 mm broad. *Style 0.5 - 0.8 mm thick.*

4.3 Key to diploid taxa of *Cardamine pratensis* s.l. from Central Europe

1\. Numerous basal leaves with only one leaflet, leaves with more than 5 leaflets never occurring. Cauline leaves 1 - 3, the upper ones with 3 - 5 narrowly ovate divisions that are 2 - 5 times as long as broad. Petals white, in herbarium specimens occasionally tinges

C. granulosa

1*. Only very few basal leaves with one leaflet, mostly some leaves with more than 5 leaflets. Cauline leaves, at least at the middle part of stem, with more than 5 leaflets, or with very narrow leaflets (more than 7 times as long as broad). Petals pinkish, pale-violet or white.

2\. Silique 0.5 - 0.9 mm broad with 36 - 48 ovules. Lower leaflets of lower cauline leaves slightly deflexed and rounded. Petals white

C. Matthioli

2*. Silique 0.9 - 1.5 mm broad with 8 - 40 ovules. Lower leaflets of lower cauline leaves horizontally spreading or slightly ascending, mostly acute. Petals pinkish, pale-violet or white.

3\. Basal leaves in the spring time with 9 or more leaflets. Leaves without hairs or with thin ones (0.02 - 0.04 mm broad at the base). Petals pinkish or white

4\. Terminal leaflet of the second uppermost cauline leaf 3/4 - 1 1/4 times as long as the rest of the leaf. Populations uniformly white-flowering or mixed i.e. consisting of white and pinkish flowering individuals

C. udicola

4*. Terminal leaflet of the second uppermost cauline leaf 1/4-3/4 times as long as the rest of the leaf. Flowers pinkish, only exceptionally white.

C. rivularis

3*. Basal leaves in the spring time with 1 - 11 leaflets. Leaves at least at the marginal part of upper surface with relatively short and broad hairs (0.04 - 0.08 mm at the base). Petals most frequently pale-violet.

5\. Silique 1.1 - 1.3 mm broad; style 0.3 - 0.6 mm thick. Basal leaves with 3 - 13 leaflets, their terminal leaflet only rarely longer than 1.8 cm

C. pratensis

5*. Silique 1.3 - 1.6 mm broad; style 0.5 - 0.8 mm thick. Basal leaves with 1 - 11 leaflets, their terminal leaflets often longer than 1.8 cm

C. nemorosa

5. Geographical distribution

The geographical distribution of the studied diploid taxa is presented in Figs. 6 - 11.

Cardamine granulosa (Fig. 6)

The actual area of this taxon seems to be confined to the hill region in the surroundings of Turin, Piedmont. The most of other reports are rather doubtful. It can be assumed that *C. granulosa* might still occur in southern Piedmont; however, the authors have not seen any material from this region. LÖVKVIST (1956) has previously reported similar plants from the surroundings of Pisa. The authors have some diploid plants collected from three hatitats in Tuscany; they are not included into the present investigations yet at least the colour of their petals is different from that of *C. granu-*

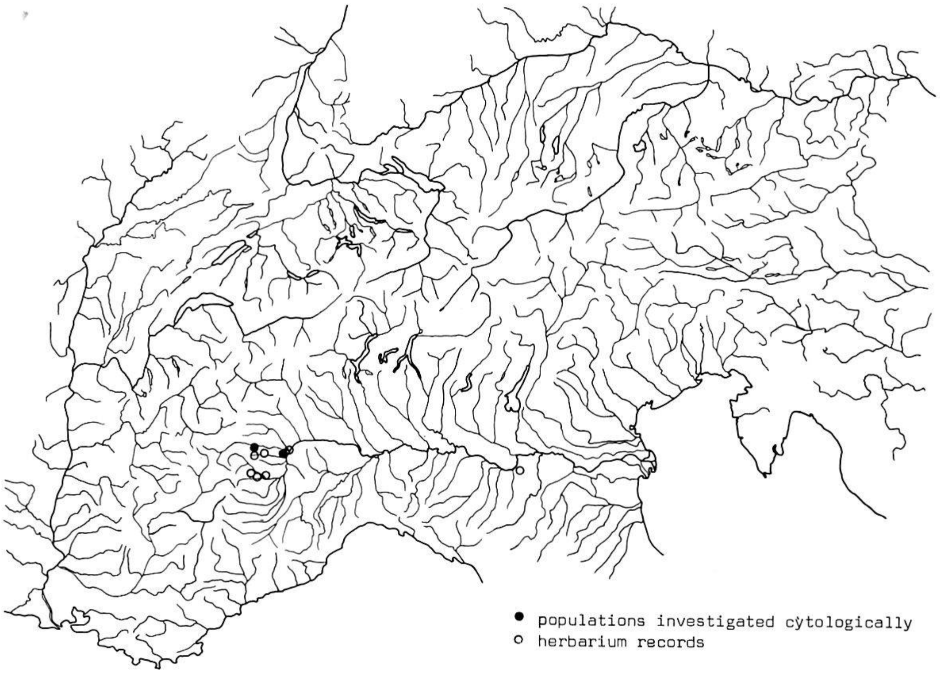


Fig. 6. Geographical distribution of *Cardamine granulosa*

losa (violet versus white). On the other hand, we have seen herbarium specimens from Guastalla (Emilia) which belong to *C. granulosa:* the plants might have arisen from seeds that were incidentally brought down from the Piedmont by the Po river.

Cardamine Matthioli (Fig. 7)

According to the bibliographical data, *C. Matthioli* has its main center of geographical distribution in the eastern part of Central Europe, being especially frequent in Hungary. It spreads from lower situated stations in Romania and Bulgaria towards the Eastern Alps and occurs south of the Alpine ridge up to the western part of the Piedmont. It should be noted that in the regions situated south of the Alps, *C. Matthioli* occurs in a series of minute, disjunct areas; in spite of numerous previous records,

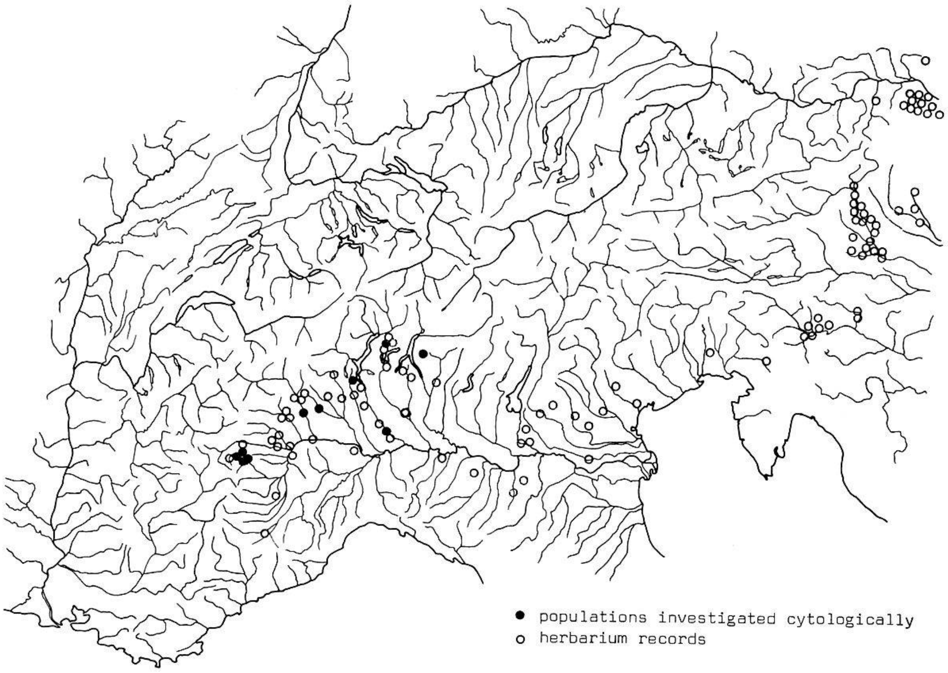


Fig. 7. Geographical distribution of diploid *Cardamine Matthioli*

the present authors found there only rare, small and isolated populations. Solely in the surroundings of Pinerolo (Piedmont) is *C. Matthioli* still relatively frequent.

Cardamine udicola (Fig. 8)

Only two regions in which diploid *C. udicola* occurs are actually known: 1) the surroundings of the Lake of Thun and 2) southern Ticino. However, the herbarium data point to a wider original distribution of this taxon. It should be added that numerous stations, ecologically similar to those of the diploids, are actually inhabited by the tetraploids (2n =32) or the pentaploids (2n =40) which have rather wide geographical distribution; it

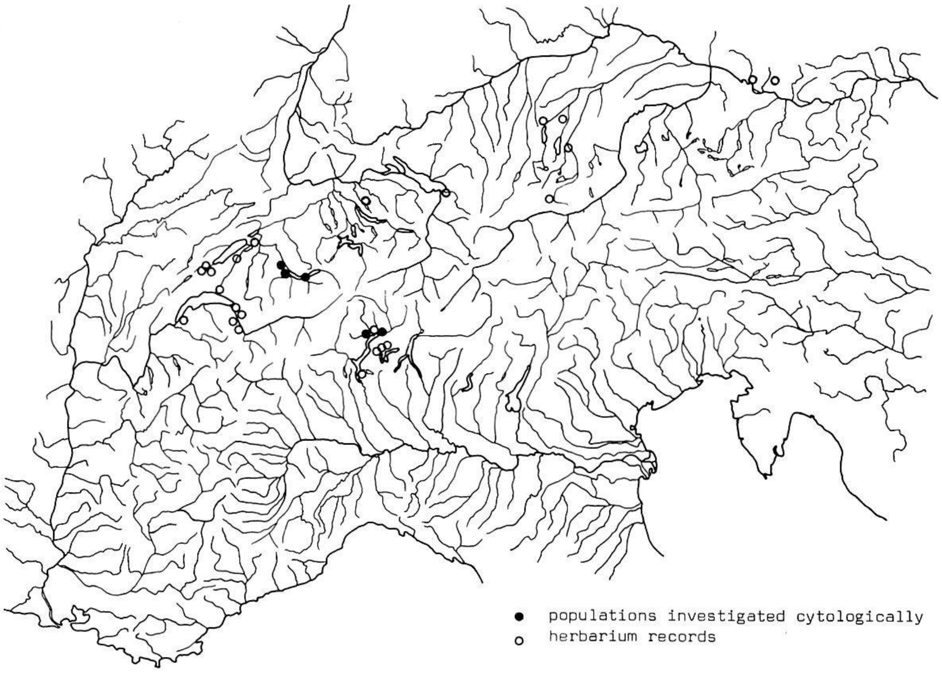


Fig. 8. Geographical distribution of diploid *Cardamine udicola*

seems rather significant that out of three stations studied by the present authors in the surroundings of the Lake of Thun, two comprised not only diploids but also numerous tetraploid plants of *C. udicola*. Morphological and genetical affinities between diploids and tetraploids remain to be further investigated.

Cardamine rivularis (Fig. 9)

Principal area of distribution of this taxon corresponds to the mountains of Central and Southern Europe. It occurs also in Bulgaria (the Rila Mts, the Rhodope Mts), in Romania (SE Carpathians) as well as in the Appenines (Emilia). There are some records of *C. pratensis* from mountains of Yugoslavia and Greece; however, the authors have not seen any herbarium material from this latter region. On the other hand, some diploid plants found in Central France (Mt. Mézenc, Mt. Aigoual) appear to be similar to *C. rivularis*. LÖVKVIST (1956) has referred to some stations of *C. rivularis* from the Pyrenees; however, the authors have neither found any plants of this taxon in nature, nor have seen them in the herbarium material. According to the recent report of BERNARD (personal communication), diploid plants belonging to *C. rivularis* occur in the Vosges (Etang Noir du Frankental).

The area of distribution of diploid *C. rivularis* within the Alps is remarkably discontinous. This taxon is rather frequent in the Eastern Alps, above all in Styria. It also occurs in numerous stations situated within the middle part of Northern Alps between Säntis and Reuss. By contrast, only a few localities of the diploid have been found hitherto in NW Alps.

It seems probable that this situation is at least partly caused by a competition from polyploid mountain types belonging to the *C. pratensis* group.

Tetraploid plants morphologically similar to *C. rivularis* were found in numerous stations. In most of the studied habitats they formed populations that were cytologically uniform; only once a tetraploid plant has been found within otherwise diploid population (see p. 81). However, the pollen tests performed on an ample herbarium material suggest an occurence of such mixed populations within rather a wide geographical range. It should be added that tetraploids are particularly frequent in the middle part of the Northern Alps, between the Glarus Alps and Haute Savoie; on the other hand, there are some large parts of the Alps, in particular in Central and Southern Alps, where no mountain plants belonging to the *C. pratensis* complex are known.

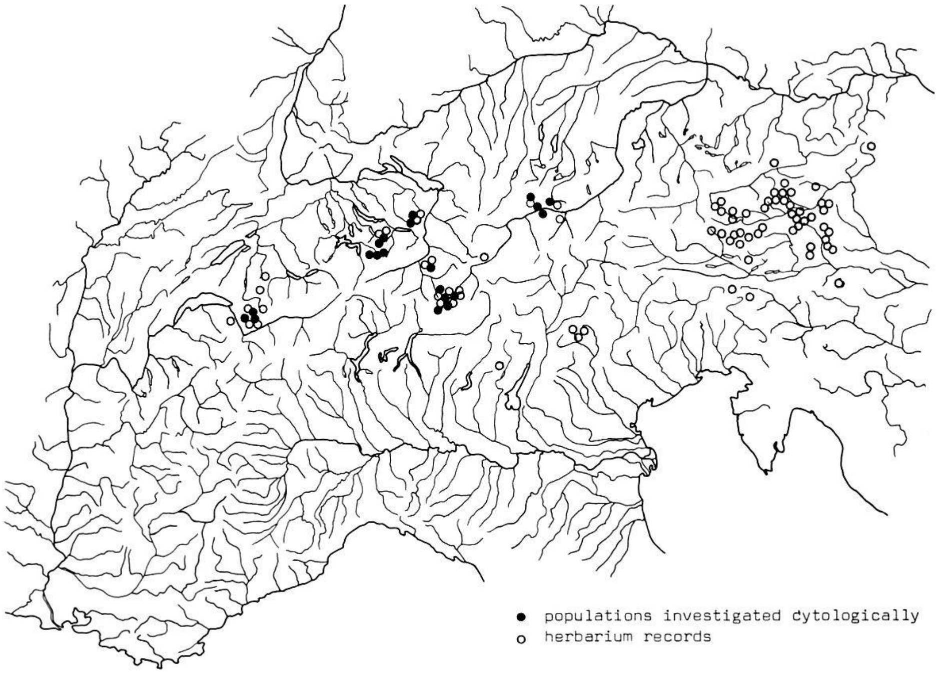


Fig. 9. Geographical distribution of diploid *Cardamine rivularis*

The plants from Tyrol, formerly assigned to *C. rivularis* (Table 4, Fig. 9), have recently been re-examined. Some of their morphological characters resemble rather *C. udicola*; on the other hand, their chromosomes represent the *C. rivularis* type. This material is to be futher investigated.

Cardamine pratensis (Fig. 10)

C. pratensis is the only diploid taxon that has rather a well-defined area of distribution. It occurs just north of the Alps having its center around the Lake of Constance. One might roughly describe the area of distribution of diploid *C. pratensis* as corresponding to the terrains covered by the glacier of the Rhine during the last glaciation. This area extends only a little further northwards through the Jura to Rottweil and eastwards to Lech and the Valley of the Inn, where diploid *C. pratensis* occurs in some isolated stations.

The area of *C. pratensis* appears somewhat fragmentated at its borders, especially in the eastern part and in the regions where the diploid comes

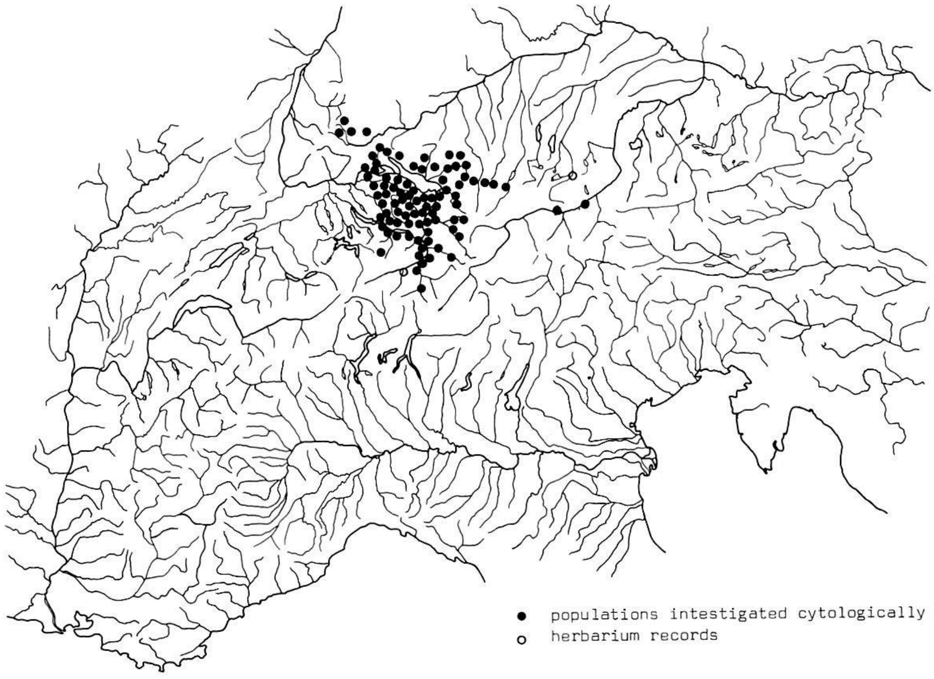


Fig. 10. Geographical distribution of diploid *Cardamine pratensis*

into contact with polyploid types, widely distributed in Europe ; however in hilly regions where not too acid soils occur, the diploid *C. pratensis* is apparently an efficient competitor towards the other representatives of the complex.

Cardamine nemorosa (Fig. 11)

The distribution of diploid *C. nemorosa* is very difficult to follow up in view of the fact that the only reliable criteria for determination of the diploid plants seem to be cytological control and the pollen test. It should be mentioned that 30 chromosomic plants, occurring sometimes in the

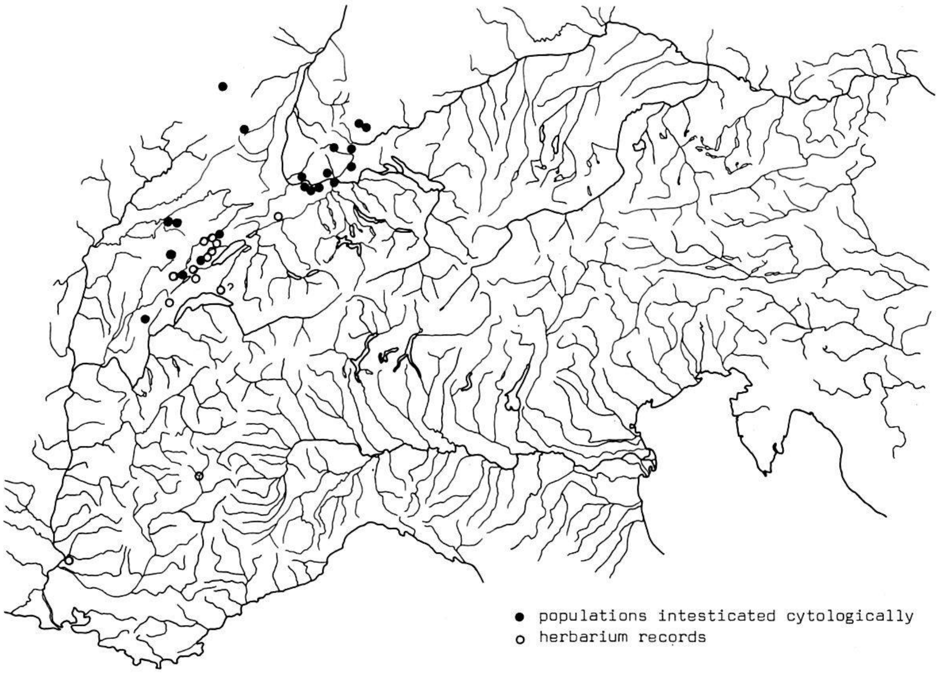


Fig. 11. Geographical distribution of *Cardamine nemorosa*

forests, have rather different ecological requirements as compared to the diploids : they usually grow in more acid and wetter soils. However, the edaphic preferences do not seem to draw sufficient distinctions between the diploids and the polyploids.

As far as the studied region is concerned, *C. nemorosa* appears to be distributed along the Jura ridge and nearly always stays out of the areas covered by the ice sheet during the last glaciation. An isolated station was found in the Vosges (Hohneck). According to rather well-documented, recent reports of DERSCH (1969), *C. nemorosa* occurs as well in Central Germany (Niedersachsen and Hessen).

The list of localities of diploid taxa belonging to *Cardamine pratensis* s.l.

The list given below comprises the authors' own collections marked by asterisks (*) as well as the loan materials. The abbreviations used in brackets correspond to those published in the Index Herbariorum (1964). Most of our specimens will be transferred to the Herbarium of the Swiss Federal Institute of Technology, Zurich.

Cardamine granulosa

Italy

Piemonte : Torino (FI,G,LAU,M,TO), Stupinigi (FI,G,GZU,PAD,TO,Z *), Cremum (TO), Trana (FI) Giaveno (PAD,TO), Venaria Reale (TO), Pinerolo (TO), San Francesco su Avigliana (M,PAD,TO,*), Sacra di San Michele (G), San Germano Chisone (G,GE,M), Pramollo (FI,G,GE,GR).
Emilia : Guastalla (FI).

Cardamine Matthioli

Austria

Niederösterreich and surroundings of Vienna: Mannersdorf (W), Mariabrunn

(GZU,LI), Purkersdorf (FI,GZU,M,W,WU,Z), Weidlingau (FI,GZU,LAU,LI,TO,W), Hainbach (FI,GZU,LAU,RUEB,W,Z), Mauerbach (FI), Wienerwald (W), Zwerndorf (W), Tulnerbach (W), Rekawinkel (W), Pressbaum (FI, GZU,LAU,LI, M, RUEB, W,Z), Altenburg (W), Pfalzau (FI), Achau (W), Breitenfurth (G,M,W,WU), Steinbach (M,W,Z), St. Poelten (VER,W), Feldsberg (WU), Oberbergen (GZU), Neuwaldegg (GZU), Penzing (GZU), Hütteldorf (GZU), Kahlenberg (GZU):

Steiermark : Ruckerlberg (FI,GZU,LAU,LI,RUEB W,Z), Ragnitztal (GZU, W), Graz (GZU), Stifting (GZU), Weinitzen (GZU), Spielfeld (GZU), Gaisberg (GZU), Drassling (GZU), Waltendorf (GZU), Gösteringertal (GZU), Andritzgraben (GZU), St. Peter b. Graz (GZU), Hartberg (GZU), Pernegg (GZU), Saggau (GZU), St. Georgen a.d. Stiefing (GZU), Stainz (GZU), Leibnitz (GZU), Fürstenfeld (GZU), Stubenberg (GZU), Niederschöckel (GZU), Gasselberg (GZU), Krems (GZU), Wenisbuch (GZU), Premstätten (GZU), Lustbüchel (GZU), Autal (GZU), Deutsch-Landsberg (GZU), Heiligenkreuz (GZU), Gleinstätten (GZU), Schönau (GZU), Maria Grün (GZU).

Yougoslavia

Slovenija * : Adelsberg (W), Ober. Radkersberg (W), Tüffer (FI,GZU, LAU,LI,RUEB,W,Z), Radizel (LJU), Ljubljana (LJU,W), Rogatec (LJU), Zavrč (LJU), Borl (LJU), Žička (LJU), Draža (LJU), Pernica (LJU), Biš (LJU), Ptuj (LJU), Hrastenice (LJU), Domžale (LJU), Klenik (LJU), Koseze (LJU), Mertui (LJU), Velika Nedelja (LJU), Celje (GZU).

Italy

Venezia Giulia : Fagagna (FI)
Veneto : Tregnago(VER), Verona (LAU,PAD,VER,W,ZT), Lugo (G,Z), San Martino (PAD), Battaglia (PAD), Castelfranco (PAD), Padova (FI,PAD), Vicenza (PAD), Mestre (PAD).
Emilia : Fontanellato (FI), Carpi (FI), San Savino (FI), Piacenza (FI).
Lombardia : Ponte di Dódici (FI,G,GE,LAU,PAD,W,Z,ZT), Castel d'Ario (VER), Mantova (PAD), San Giorgio-Mantova (FI), San Lanfranco (PAV), Bergamo (PAV), Ballabio (Z,*), Milano (FI), Pavia (FI,LAU,PAD,PAV,VER,W,*), Naviglio (PAV), S. Giuseppe in Valleggio (PAV), Lodigiano (PAV), Carbonara (PAV).
Piemonte : Borgo Ticino (PAV), Arona (*), Varallo (FI,GE), Oldenico (FI), Novarra (TO), Vercelli (FI,G), Sartirana (PAV), Crescentino (FI), Quinto(FI), Viverone (*),

* Plants from Slovenija very often have tinged petals and acute leaflets of lower cauline leaves.
They resemble in this respect *C. udicola*.

Candia Canavese (TO,*), Oropa (TO), Anzaso(FI), Ivrea (FI), Tavagnasco (FI), Cuorgné (G,Z), Torino (PAD,TO), Venaria Reale (FI), Montcalieri (PAD), Leini (TO), Druent (PAD), Front (FI), Stupinigi (TO), Castello Apertote (TO), Collegno (TO), Giaveno (TO), San Germano (FI,G,LAU,M,PAD,Z), Scalenghe (PAD), Pinerolo (FI,G,M,PAD,W,*), Villar Perosa (*), Perrero (G), Martiniana Po (FI), Valdieri (FI).

Switzerland
Ticino : Monte Ceneri (Z), Rivera (Z,*), Bironico (FI,LAU,Z), Origlio (G,LAU), Melano-Capolago (LAU).

Cardamine udicola

Austria

Oberösterreich : Hellmonsödt (LI), Neuhauserberg (LI).
Vorarlberg : Bregenz (ZT).

Germany

Bayern : Wildenroth (M), Moosach (M), Wolfrathshausen (M), Mittenwald (M).

Switzerland

Zürich : Schwerzenbach (ZT).
Bern : Fräschels (BERN), Geistsee b. Gurzelen (BERN,*), Gwatt (BERN,*), Weissenau (ZT,*).
Vaud : Entreroche(BERN,FI,G,GR,LAU,LUGANO,M,Z,ZT), Orbe (G, LAU), Bavois (G,LAU,ZT), Avenche (LAU), Vidy (BERN,ZT), Villeneuve (ZT), Roche (Z), Aigle (LAU).
Valais : Bouveret (Z), Vernayaz (Z), Massongez (Z).
Genève : Belotte (Z).
Ticino : Magadino (BERN,*), Muralto (G), Roncaccio (LUGANO), Locarno (FI,G,Z,ZT), Ascona (*), Muzzano (FI,G,LAU, LUGANO, RUEB,ZT), Ango (ZT), Ponte Tresa (LAU,ZT).

Italy

Lombardia : Angera (LAU).

Cardamine rivularis

Austria

Oberösterreich : Warscheneck (LI).
Steiermark : Schneeberge (W), Scharfes Eck (GZU,LAU,LI,RUEB,W,WU), Zirbitzkogel (GZU,W), Winterleitsee (GZU), Judenburg (GZU), Reitersee-Rottenmannertauern(W), Griesmeier Alm (GZU), Schönfeldspitze-Wözertauern(GZU), Pölsgraben (GZU), Franzstatt (GZU), Planner Alpe (GZU), Hohenwart-Niedere Tauern (GZU), Hohentauernpass (M), Schladminger Tauern (W), Stubalpe (FI,GZU,LI,M,W,WU), Almhaus Stubealpe (GZU), Koralpe (IB), Glashütten (GZU),

Grosses Kar (GZU), Weisswassergraben (GZU), Seekar (GZU), Bärental (GZU), Hühnerstützen (GZU), Reitalm (GZU), Moschkogel (W), Wolfsberg (W), Rosanintal-Gurktaler Alpen (GZU), Schilchernock (GZU), Kallwang (GZU), Obdach (GE), Griesstein (FI,W), St. Lambrecht (GZU), Kuhalpe (GZU), St. Lorenzen b. Knittelfeld (GZU), Rinseneck-Stangalpen (GZU).

Kärnten : Stangalpe (KL), Ebene Reichenau (KL), Waldkogel (KL), Wöllauer Nock (GZU), Katschtal-Hohe Tauern (GZU), Malta-Tal (KL), Himmelberg(KL), Forstalpe (KL), Rinsennock (KL), Winterleitental (KL), Saualpe (KL), Koralpe (KL,ZT), Wandspitze (KL).

Salzburg : Radstätter Tauern (GZU,WU), Passegger Alm (GZU), Taurachtal (WU).

Tirol : Obsteig (IBF), Amras (IBF), Seefeld (IB), Telfs (*), Fernsteinsee (*), Flirsch(*), Haiming (*), Silz (*).

Yougoslavia

Slovenija : Jelovica (LJU).

Italy

Veneto : Alpi Venete (PAD).

Trentino-Alto Adige: Lago di Andermole (PAD), Montalone (FI,PAD), Monti di Torcegno (FI,LAU).

Lombardia : Monte Cadi (FI).

Switzerland

Graubünden : Ftan(Z), Samaden(G,Z,ZT), Bevers (BERN,G,Z,ZT), Celerina (Z,ZT), Serlas (RUEB), Surpunt (RUEB,ZT), Lej da Staz (*), Pontresina (RUEB), St. Moritz (Z,ZT,*), Sils (G,Z,ZT), Silvaplanersee (ZT,*), Maloja (*), Tigias (*), Alp Flix (ZT), Lenzerheide Z,*), Parpan (ZT).

St. Gallen : Schönenbodensee (ZT), Schwendisee (*).

Appenzell : Schwägalp (*).

Glarus : Obersee (BERN), Oberalp (ZT).

Schwyz : Richisau (*), Pragelpass (*), Sihlseeli (ZT,*), Oberiberg (BERN).

Uri : Klausen (G,*), Urnerboden (*), Brunnital (*).

Bern : Jaunpass (BERN), Stierendungel (BERN,ZT), Lauenental (BERN).

Vaud : Bretaye (BERN,G,LAU), Chamossaire (G), Lac Chavonne (LAU,ZT), Thomalay (LAU), Saziême (LAU), Anzeindaz (LAU), Alpes d'Ollon (LAU), Le Pillon (LAU,*), Les Diablerets (*), Pierre de Moëlle (ZT,*).

France

Haute Savoie : Tourbière Autun (G).

Cardamine pratensis

Austria

Tirol : Vils (*), Innsbruck (*), Weer (*).
Vorarlberg : Nenzing (*), Braz(*), Klösterle (*), Bregenz (*), Hard (*), Dornbirn (*), Bödele (*), Vorder-Mellau (*), Schoppernau (*), St. Anton (*), St. Gallenkirch (*).

Liechtenstein : Nendeln (*), Balzers (*).

Germany

Bayern : Bad Tölz (M), Immenstadt (*), Ober Reute (*), Lindau (*), Opfenbach (*), Isny (*), Wengen (*), Nesselwang (*),Pfronten (*).
Baden-Württemberg: Degersee (*), Tettnang (*), Obereschach (*), Horgen (*), Balgheim (*), Engen (*), Schiener Berg (*), Moos (*), Stetten (*), Baindt (*), Bad Waldsee (*), Tuttlingen (*), Balsheim (*), Bohlingen (*), Allensbach (*), Liggeringen (*), Beuren (*), Feldmoos (*), Krätermühlhöfe (*), Liptingen (*), Rottweil(*), Neufra (*).

Switzerland

Thurgau : Sonnental (*), Fischingen (*), Bichelsee (*), Balterswil (*), Aadorf (*), Münchwilen (*), Bettwiesen (*), Nettlen (*), Sulgen (*), Hauptwil (*), Pfyn (*), Homburg (*), Salen (*), Matzingen (*), Stettfurt (*), Sonnenberg (*), Freudenberg (*), Thundorf (*), Wolfikon (*), Strohwilen (*), Burghof (*), Hüttlingen (*), Eschikofen (*), Hüseren (*), Mülheim (*), Unter-Hörstetten (*), Hörhausen (*), Reckenwil (*), Lören (*), Steckborn (*).
Appenzell-Ausserroden: Urnäsch (*), Bühler (*), Landmarch (*), Wissegg (*), Rehetobel (*).
Appenzell-Innerroden : Gonten (*), Pfannenstil (*), Brülisau (*).
St. Gallen : Gams (*), Ricken (*), Kaltbruner Ried (*), Bertschis (*), Trübbach (*), Grabs (*), Wildhaus (*), Stein (*), Wattwil (*), Steinach (*), Oberwil (*), Mühlrüti (*), Sirnach (*), Wil (*), Niederwil (*), Brunnardern (*), Altstätten (*), Rheineck (*), Mörschwil (*), Schänis (*), Vättis (*).
Zurich : Elgg (*).
Glarus : Bilten (*), Linthal (*).
Graubünden : Pardisla (*), Andeer (*), Bonaduz (*), Bad Ragaz (*), Bad Serneus (*), Igis (*), Untervaz (*), Chur (*), Ilanz (ZT).

Cardamine nemorosa

Germany

Baden-Württemberg: Erzingen (*), Haagen (*), Wehr (*), Wutachschlucht (*), Wutachmühle (*), Achdorf (*), Balgheim (*).

Switzerland

Aargau : Sisseln (*), Rheinfelden (*), Zurzach (*).
Solothurn : Gärisch (LAU).
Neuchâtel : La Chaux-de-Fonds (*).
Vaud : Baulmes (*), Le Sentier (*), Risoux (ZT), Pétosan (LAU), St. Cergue (LAU), Grandsonne-dessus (LAU), Mont Tendre (LAU), Feyguire (?) (LAU).

France

Vaucluse : Sorgues (M).
Hautes-Alpes : Briançon (Z).
Ain : Belleydouc (*).
Doubs : Lac de St. Point (*), Les Prés-de-Vaire (*), Marais de Saône (*), Besançon (*).
Vosges : Hohneck (*).
Meurthe et Moselle: Nancy (*) .

6. Ecology

The following ecological factors were studied:

1. *Soil humidity.* All the studied species avoid permeable and fast drying soils. Most of them grow in slightly moist sites; they can be found sometimes in wet stations where competition from polyploids does not seem to occur. *Cardamine rivularis* and *C. udicola* show a definite preference for stations characterized by rather a high water table.

2. *Nutrients content.* In general, most of the studied diploids grow in stations rather rich in nutrients. Only *C. rivularis* and *C. udicola* were most frequently found in stations where the soil was rather poor; this behaviour is probably influenced by competition.

3. *Light conditions. C. nemorosa* and *C. granulosa* represent shadow plants that pass most of their development at early spring time. Other species require most frequently open sites or places where the leaves receive the light after grazing or cutting.

4. *pH values of the soil* .(Fig. 12). Two groups were distinguished in the studied material: in the first one, represented by *C. nemorosa* and *C. pratensis*, pH values ranged most frequently from 6.5 to 7.5 and no sites with pH value lower than 5.0 were found. The second group, comprising the other taxa, showed pH values usually varying between 4.5 and 5.5. No stations with pH values higher than 7.0 were observed in this group. As far as

C. granulosa is concerned, only two measurements could have been taken, both values being 5.0.

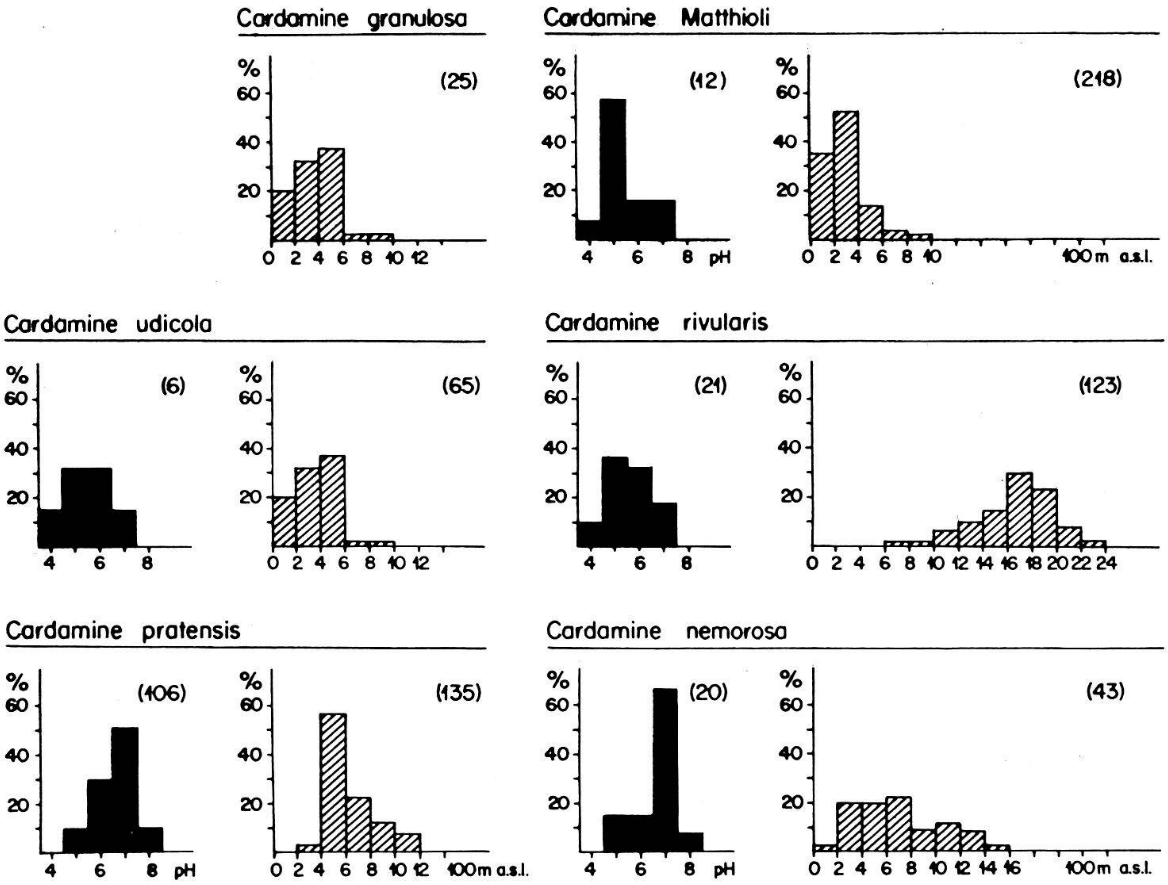


Fig.12. Ecological distribution of diploid taxa of the *C. pratensis* group. Black columns refer to pH values of the soil, shaded ones- to the altitude a.s.l.

Numbers in brackets are those of stations investigated in field; data concerning the altitude comprise as well the herbarium records.

5. *Altitude above sea level* (Fig. 12.) *C. Matthioli* decidedly is a lowland taxon that probably does not occur at altitudes higher than 850 m. a.s.l. (Perrero, Piedmont). *C. granulosa* seems to occur within similar altitude limits as *C. Matthioli;* the present investigations confirm the data of LÖVKVIST (1956). *C. udicola, C. pratensis* and *C. nemorosa* mainly occur within the colline zone and in the lower montane zone. Rare occurrence of *C. pratensis* in low situated habitats is apparently due to the fact that the stations situated lower than at 400 m.a.s.l. do not occur at all in the investigated area of distribution of the diploid taxon.

The uppermost altitude limit for the diploid *C. udicola, C. pratensis* and *C. nemorosa* comport about 1000 m.a.s.l., 1200 m.a.s.l. and 1500 m.a.s.l., respectively . The only diploid taxon occurring within the subalpine zone is *C. rivularis;* lower situated stations of this species occur within high mountain ridges (e.g. Valley of the Inn); the highest known Alpine station was recorded from Styria (Wölzer Tauern, Hohenwart, 2360 m.a.s.l. GZU).

Each of the studied diploid taxa shows its maximal frequency in different types of vegetation; they can as well enter some neighbouring associations, especially when competition is not too strong.

Cardamine granulosa. Half-shadow conditions occurred in both stations studied by the present authors. In the first site, plants of *C. granulosa* were growing in rather not too intensively managed forest meadows and were particularly frequent at the border of a mixed Castanea-forest. In the second station, *C. granulosa* grew in a moist soil, at the border of the *Populus*-plantation.

Cardamine Matthioli. Between Pinerolo and Perosa (Piedmont), *C. Matthioli* appears rather frequently in fertilized, manured meadows belonging to the *Arrhenatherion.* By contrast, all other stations studied in the course of the present work proved to be of a different type: *C. Matthioli* was found in wet meadows and swamps rather rich in nutrients and did not occur in neighbouring fertilized meadows. The vegetation within the wet sites represented no stable associations and *C. Matthioli* formed there only small and isolated populations; it can be assumed that this taxon is at the point of extinction in this part of its area. It should be added that the only forest station of *C. Matthioli* was found by the authors near Pavia: the isolated population of *C. Matthioli* was growing among poplars, in a moist soil.

Cardamine udicola occured in reed meadows or bogs where the nutrient contents were very low. Plants from the surroundings of the Lake of Thun as well as those from Magadino occured within the *Caricetum elatae* s.l.; those from Ascona were found in an open shore vegetation growing in a sandy soil.

Cardamine rivularis. Phytosociological affinities of *C. rivularis* are rather well marked: at higher altitudes it occured most frequently on lake shores or around creeks, within the *Caricion canescenti-fuscae.* Sometimes it was also observed in neighbouring, moist or mossy meadows.

Cardamine pratensis. Diploid *C. pratensis* occured most frequently in the *Arrhenatherion,* the *Triseto-Polygonion,* as well as in some associations which bridge these alliances with the *Cynosurion cristati.* It entered sometimes moist meadows in the regions where the polyploids of the group and *C. rivularis* do not occur. Very seldom one could find *C. pratensis* in forests roads or at the borders of the forests; it apparently came there from the adjacent meadows.

Cardamine nemorosa. C. nemorosa shows preference for not too dry, base rich stations inhabited by the *Fagion* and appears to avoid sunny sites. It can also be found in bushes bordering the forests and, on limestone-containing soil, under the *Picea*-trees. Single plants enter sometimes neighbouring fertilized meadows or pastures, wet meadows or the *Alnus*-shrubs. It should be noted, however, that in these untypical stations *C. nemorosa* does not seem to stand well the competition from polyploid types occurring around.

The isolated station from the Vosges (Hohneck) presents quite untypical ecological conditions for *C. nemorosa;* it grows there within tall herbs, in a place where the soil is irrigated by base rich water.

Ecological indicators and altitude zones of the diploid taxa

Ecological indicators evaluate the sites in terms of moisture, pH, nitrogen content etc. (ELLENBERG 1952, 1963). The following abbreviations are used below: F - humidity of the soil; R - pH value of the soil; N - the nitrogen content of the soil; L - the light amount. The numbers range from 1 to 5; in each case higher number represents higher indicator for the given factor. The altitude zones are specified according to Hess, Landolt and Hirzel (1967).

Cardamine granulosa: colline. F 3-4, N 3, R 37, L 3
Cardamine Matthioli: colline. F 3-4(4-5), N 3-4, R 2-3, L 4
Cardamine udicola: colline, montane. F 4-5, N 2, R 2-3, L 4
Cardamine rivularis: montane, subalpine. F 4-5, N 2, R 2-3, L 4
Cardamine pratensis: colline, montane. F 3-4, N 3-4, R 4, L 3-4
Cardamine nemorosa: colline, montane. F 3-4, N 3, R 4, L 2-3

7. Cytology

7.1 Chromosome numbers

The diploid level within the *Cardamine pratensis* group is represented by 2n=16, the primary basic number being thus x=8. The present results stay in agreement with previous data (GUINOCHET 1946, MATTICK cit. acc. to TISCHLER 1950, LÖVKVIST 1953, 1956, DERSCH 1969, KUZMANOV and KOZUHAROV 1969, LANDOLT and URBANSKA-WORYTKIEWICZ 1971). It should be mentioned that LÖVKVIST assumed an occurrence of another primary basic number viz. 7 as being of evolutionary importance for the *C. pratensis* group. However, no 14 chromosomic plants have been found in the course of the present investigations; deviating chromosome numbers at the diploid level were invariably hyperdiploid (2n=17,18,19,20) and in most of the studied cases the resp. plants apparently represented polysomic types (URBANSKA-WORYTKIEWICZ and LANDOLT 1974).

The origin of the studied material is given in Tables 1 - 6. The studied diploid populations most frequently proved to be cytologically uniform (160 populations out of 208). Cytological variation observed in 48 populations was apparently conditioned not by a single factor but represented diverse aspects. At least three phenomena contributed to the formations of mixed populations: 1) local migrations, 2) gene flow, 3) aneusomy.

Table 1. *Cardamine granulosa:* origin of material (collection numbers are those of the authors)

No of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
	Italy				
	Piedmont:				
560*	Avigliana	600 m	5.0	16	10
567*	Stupinigi	240 m	5.0	16	8

* karyotype investigated

Table 2. *Cardamine Matthioli:* origin of material (Collection numbers are those of the authors)

No.of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
	Italy				
	Lombardy:				
698	Ballabio	710 m	6.0	16	15
871	Pavia	80 m	5.0	16	14
	Piedmont:				
561*	Pinerolo I	500 m	5.0	16	14
562	Pinerolo II	500 m	5.0	16	5
564*	Pinerolo III	500 m	7.0	16	7
565	Villar Perosa	450 m	4.5	16	9
566	Pinerolo IV	530 m	4.0	16	9
568*	Lago di Candia	230 m	6.5	16	11
569*	Lago di Viverone	230 m	5.0	16	9
570*	Arona	195 m	5.0	16	8
	Switzerland:				
	Ticino				
872	Rivera	450 m	5.5	16	12

* karyotype investigated

Table 3. *Cardamine udicola:* origin of material (collection numbers are those of the authors)

No.of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
	Switzerland				
	Bern:				
860*	Geistsee	660 m	-	16,32	3,22
330 861	Unterseen	559 m	5.0	16,32	23,21
579	Gwatt	558 m	-	16	8
	Ticino:				
56	Magadino I	195 m	5.0	16	10
57	Magadino II	195 m	4.5	16	27
137	Lido di Ascona	195 m	6.0	16	7

* mixed with *Cardamine pratensis* (2n=40, 2n=48)

Table 4. *Cardamine rivularis:* origin of material (collection numbers are those of the authors)

No.of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
	Austria				
	Tyrol:				
225	Telfs	660 m	6.5	16	6
226	Fernsteinsee	1000 m	6.0	16	7
466	Flirsch	1100 m	6.5	16	1
467*	Haiming	660 m	4.5	16	15
468	Silz	650 m	5.5	16	15
	Switzerland				
	Graubünden:				
33*	Valbella I	1484 m	-	16	9
34	Valbella II	1484 m	-	16	6
36*	St. Moritz-Bad	1768 m	-	16	4
37	Lej da Staz	1790 m	-	16	6

Table 4: Continuation

No. of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
211	Tigias	1977 m	6.0	16	7
212	Maloja I	1800 m	5.0	16	9
213	Maloja II	1800 m	4.0	16	6
214*	Lej da Champfèr	1800 m	4.5	16	8
	St. Gallen:				
39*	Schwendisee I	1159 m	-	16	7
40	Schwendisee II	1159 m	-	16	6
41	Schwendisee III	1159 m	-	16	6
	Appenzell (AR):				
703	Schwägalp	1275 m	5.0	16	11
	Schwyz:				
233*	Sihlseeli I	1830 m	5.0	16	9
234	Sihlseeli II	1830 m	4.0	16	8
236**	Richisau	1130 m	7.0	16	2
707	Pragelpass	1545 m	-	16	6
	Uri:				
167*	Urnerboden I	1310 m	-	16	2
168	Urnerboden II	1310 m	-	16	1
169*	Klausenpass	1764 m	-	16	10
182	Urnerboden III	1310 m	4.3	16	7
855	Brunnital	1650 m	-	16	5
	Vaud:				
624*	Col du Pillon	1685 m	6.0	16	16
625	Les Diablerets	1180 m	6.0	16,32	12,1
627	Pierre de Moëllé	1661 m	7.0	16	13

* karyotype investigated

** mixed with *Cardamine pratensis* (2n=40)

\+ Taxonimical status of the Tyrolian plants is not definite (see p. 66).

Table 5. *Cardamine pratensis:* origin of material (collection numbers are those of the authors)

No. of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
	Austria				
	Tyrol:				
401*	Vils	820 m	5.0	16,18,21	7,1,1
461	Innsbruck	570 m	6.0	16	10
472	Weer	550 m	7.0	16,40	3,4
	Vorarlberg:				
217	Nenzing	490 m	7.0	16	8
218	Braz	700 m	8.0	16	9
219	Klösterle	1050 m	5.0	16	8
231	Bregenz	600 m	5.0	16	9
359	Hard	400 m	6.5	16	12
396	Dornbirn	437 m	8.5	16	11
397	Bödele	1146 m	7.5	16	9
398	Vorder-Mellau	670 m	8.0	16,40	3,3
399	Schoppernau	840 m	5.0	16	7
463	St. Anton i.M.	650 m	6.0	16	10
464*	St. Gallenkirch	850 m	5.0	16	14
	Germany				
	Bavaria:				
229	Immenstadt	740 m	7.0	16	8
230	Ober Reute	850 m	7.5	16	9
360*	Lindau	470 m	5.0	16	11
368	Opfenbach	580 m	5.5	16	10
369	Isny	680 m	5.0	16,17,18,19	7,1,1,1
370	Wengen	750 m	5.0	16,30	2,12
373	Nesselwang	900 m	5.5	16	12
374	Pfronten	900 m	7.0	16,17,19,24	6,1,1,1,
	Baden-Würtemberg:				
361	Degersee I	470 m	5.0	16	7
362	Degersee II	470 m	5.5	16	12

Table 5. Continuation

No.of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
363	Degersee III	470 m	6.0	16	7
364	Tettnang	470 m	5.5	16	10
507	Obereschach	750 m	6.0	16,17	6,1
508	Horgen	650 m	7.0	16,30	7,4
509	Rottweil I	600 m	5.0	16,17,18,19	10,1,2,2
510	Rottweil II	600 m	6.5	16	13
511	Neufra	600 m	7.0	16	8
514	Balgheim	700 m	-	16,17,18,19	7,1,1,1
515	Engen	550 m	7.0	16,30	1,13
518*	Schiener Berg I	650 m	6.5	16	15
519	Schiener Berg II	680 m	7.0	16	9
520	Moos	400 m	6.5	16,18,38	13,2,4
521	Stetten	420 m	6.0	16	20
525*	Baindt	500 m	7.0	16	18
526	Bad Waldsee	580 m	5.0	16,18	14,1
542	Tuttlingen	650 m	7.0	16,30	2,15
591	Balsheim	570 m	5.5	16,30	4,6
592	Bohlingen	450 m	6.0	16	5
593*	Allensbach	400 m	5.5	16	13
594	Liggeringen	530 m	5.0	16	12
597	Beuren	552 m	7.0	16	9
601	Feldmoos	550 m	6.0	16,30,38,46	2,7,3,2
606	Krätermühlhöfe ca.	650 m	7.0	16,30	2,5
607	Liptingen ca.	600 m	7.0	16	9
	Liechtenstein:				
216	Nendeln	450 m	6.5	16	4
462*	Balzers	470 m	7.5	16	10
	Switzerland:				
	Graubünden:				
75*	Pardisla	580 m	7.0	16	10
138	Andeer	985 m	7.0	16,32	6,1
141	Bonaduz	600 m	-	16	7

Table 5. Continuation

No.of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
142*	Bad Ragaz I	500 m	-	16	5
143	Bad Ragaz II	500 m	-	16	8
210	Bad Serneus	1010 m	6.5	16	6
385	Igis	535 m	6.0	16	9
386	Untervaz	540 m	7.0	16	7
645	Chur	600 m	7.0	16	12
	St. Gallen:				
15	Ricken	805 m	-	16	7
38	Gams	510 m	-	16	6
101	Kaltbrunner Ried	300 m	5.8	16	7
103*	Berschis	440 m	5.0	16	7
104	Trübbach	470 m	6.5	16	6
105	Grabs	443 m	7.0	16	8
106	Wildhaus	970 m	6.5	16	5
107	Stein	860 m	6.0	16	9
108	Wattwil	620 m	6.0	16	8
125	Steinach	440 m	6.0	16	7
127	Oberwil I	585 m	6.0	16	3
128	Oberwil II	585 m	6.0	16,32	5,1
295	Mühlrüti	760 m	6.0	16	6
308	Sirnach	530 m	6.0	16	5
309	Wil	575 m	6.5	16	7
311	Niederwil	605 m	6.0	16	8
338	Brunnadern	660 m	7.0	16	6
347*	Altstätten	480 m	5.5	16	10
358	Rheineck	410 m	6.0	16	13
704	Mörschwil	530 m	-	16	12
708	Vättis	1000 m	6.0	16	9
720	Schänis	420 m	5.5	16	9
	Appenzell-Ausserrhoden:				
339	Urnäsch	1000 m	6.0	16	13
344	Bühler	860 m	5.0	16	10

Table 5. Continuation

No.of sample	Plant of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
346*	Landmarch	1000 m	6.0	16	10
356	Wissegg	1030 m	4.5	16	5
357	Rehetobel	950 m	5.0	16	12
	Appenzell-Innerrhoden:				
340	Gonten I	900 m	5.0	16,17,18	8,1,4
341*	Gonten II	900 m	6.0	16	11
342	Pfannenstil	940 m	6.0	16	11
343	Brülisau	900 m	7.0	16	13
	Glarus:				
721	Bilten	440 m	6.0	16	9
	Thurgau:				
310	Sonnental	500 m	7.0	16	6
296	Fischingen	610 m	6.5	16	8
297	Bichelsee	585 m	6.5	16	6
307	Balterswil	570 m	6.0	16	9
316	Aadorf	538 m	7.0	17	1
317	Münchwilen	575 m	7.5	16	7
318	Bettwiesen	540 m	7.0	16	5
319	Mettlen	530 m	6.5	16	8
320	Sulgen	480 m	7.0	16	8
322	Hauptwil	570 m	5.0	16	3
352	Pfyn	565 m	5.5	16,30	5,7
588	Homburg I	615 m	6.5	16,30,38	1,10,1
589	Salen I	730 m	6.0	16,30,38	4,3,3
667	Matzingen I	465 m	6.5	16	9
668	Matzingen II	450 m	7.0	16,38	8,1
669*	Matzingen III	455 m	7.0	16	12
670	Stettfurt I	470 m	6.0	16	15
671	Stettfurt II	490 m	7.5	16,19,38,54	4,1,2,1
672	Sonnenberg	590 m	7.5	16	11
673	Freudenberg	547 m	5.5	16,18	10,1
674	Thundorf I	570 m	7.0	16,30	1,10

Table 5. Continuation

No.of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
675	Thundorf II	570 m	6.5	16,30	4,9
676	Wolfikon	625 m	5.5	16	8
677	Strohwilen	580 m	6.0	16,30,38	7,2,1
678	Burghof	555 m	7.0	16,30	9,3
680	Hüttlingen	400 m	7.5	16,30	10,2
681	Eschikofen I	410 m	7.0	16,30	7,1
682	Eschikofen II	410 m	7.0	16,30	2,12
683	Hüseren	410 m	7.5	16,30,54	6,1,3
684	Mülheim I	405 m	7.0	16,30	1,11
685	Mülheim II	450 m	7.5	16,30	1,7
686	Unter-Hörstetten	495 m	6.5	16	12
687	Hörhausen I	530 m	7.0	16,30	2,6
688	Hörhausen II	555 m	7.0	16,18,23-24,30	3,1,2,4
689	Reckenwil	575 m	7.0	16,30,38	1,6,3
691	Homburg II	600 m	7.0	16,30	6,4
692	Lören	640 m	6.0	16,30	7,1
693	Salen II	686 m	7.0	16,38	10,2
694*	Salen III	640 m	7.0	16	8
695	Steckborn	610 m	7.5	16	6
	Zürich:				
315	Elgg	630 m	6.0	16	4

* karyotype investigated

Table 6. *Cardamine nemorosa:* origin of material (collection numbers are those of the authors)

No. of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
	Germany				
	Baden-Würtemberg:				
409	Erzingen	420 m	6.5	16	12
440*	Haagen I	380 m	5.0	16	12
441	Haagen II	320 m	7.0	16	11
445	Wehr	600 m	5.0	16	12
450*	Wutachschlucht	680 m	7.0	16	11
452	Wutachmühle	580 m	7.0	16	9
501	Achdorf	600 m	7.0	16	12
512	Balgheim I	700 m	7.0	16	9
513	Balgheim II	700 m	6.0	16	10
	Switzerland				
	Aargau:				
46	Sisseln I	305 m	-	20	1
47	Sisseln II	305 m	-	16	1
50	Sisseln III	305 m	8.0	16,30	1,6
86	Rheinfelden	295 m	-	20	3
88*	Zurzach	400 m	6.0	16	6
	Neuchâtel:				
32	Chaux-de-Fonds	830 m	-	20	4
	Vaud:				
9	Baulmes I	605 m	-	20	7
10	Baulmes II	605 m	-	20	6
63	Le Sentier	1020 m	-	20	1
	France				
	Ain:				
26	Belleydoux	800 m	-	20,32	4,1
	Doubs:				
31*	Lac de St. Point	850 m	-	16	8
65*	Près-de-Vaire I	720 m	7.0	16	11

Table 6. Continuation

No.of sample	Place of origin	Altitude a.s.l.	pH	2n	Number of investigated plants
66	Près-de-Vaire II	720 m	-	16,30	3,4
67*	Marais de Saône I	390 m	5.5	16	11
68	Marais de Saône II	390 m	7.0	16	8
69	Marais de Saône III	390 m	6.5	16	7
70*	Besançon	450 m	5.0	16	10
	Meurthe-et-Moselle:				
764	Nancy	300 m	6.0	16	10
	Vosges:				
845*	Hohneck	1250 m	5.0	16	10

* karyotype investigated

The most frequent mixed populations were those obviously influenced by local migrations: 26 populations comprised not only diploids but also tetraploids (2n=30 or 2n=32), in two other stations pentaploid plants (2n=40) were growing among the diploids. Still more complex was a population of *C. udicola* from Geistsee: three diploids were accompanied by numerous tetraploids of the same taxon, but pentaploids and hexaploid belonging to *C. pratensis* occurred as well in this habitat.

11 studied populations consisted not only of diploids and tetraploids, but also of some higher polyploids (2n=38, 46, 54), that apparently were of a hybrid origin.

In 13 populations plants with hyperdiploid chromosome numbers, representing most frequently various polysomic types, were found among the diploids.

Above mentioned cytological variation was observed mostly within *C. pratensis* (42 populations), *C. nemorosa* (3 populations) and *C.udicola* (2 populations). As to *C. rivularis*, a single tetraploid plant (2n=32) was once found within otherwise diploid population from Les Diablerets (Table 4). Its occurrence might be explained by a local migration from neighbouring tetraploid populations; however, a possibility of an incidental polyploidization cannot be excluded. *C. Matthioli* and *C. granulosa* proved to be cytologically uniform.

It is interesting to note that there seems to occur a certain pattern of cytological variation within the diploid taxa of the *C. pratensis* group: deviating populations were most frequently found in the regions where the diploids came into contact with various polyploid types. One could assume that populations inhabiting the center of the distribution area of given taxon are subject to selection pressures which are different from those occurring within the marginal populations.

Cardamine granulosa All.

This taxon has not been cytologically studied hitherto. The authors investigated 18 plants from two stations in Piedmont (table 1); diploid chromosome number 2n=16 has been invariably found.

Cardamine Matthioli Moretti

Previous reports of MATTICK (cit. acc. to TISCHLER 1950) and those of LÖVKVIST (1956) dealt with *C. Matthioli* from Eastern Alps and from the surroundings of Vienna. The present results obtained on the material from 11 stations dispersed in western part of the range (Table 2) are in agreement with the previous data. No cytological variation has been observed.

Cardamine udicola. Jord.

C. udicola has been studied here for the first time. Out of six stations that have been investigated four proved to be cytologically uniform and comprised solely the diploids. (Table 3). It is interesting to note that *C. udicola* from southern Ticino was invariably 16 chromosomic whereas the populations from the surroundings of the Lake of Thun were rather differentiated. The station from Weissenau was inhabited by diploids and tetraploids, the population from Geistsee comprised not only some diploids and tetraploids of *C. udicola* but also pentaploids and hexaploids of *C. pratensis* type.

Cardamine rivularis Schur

C. rivularis has been previously studied by LÖVKVIST (1956) from Engadine and from Austrian Alps. More recently, a report from the easternmost limit of the range of this taxon i.e. from the Rila Mts has been published (KUZMANOV and KOZUHAROV 1969). The present authors studied numerous plants from 29 populations within the Alpine range (Table 4). Except for a single tetraploid plant from Les Diablerets , all the studied individuals were 16 chromosomic. Our results stay in agreement with the previous data.

It can be assumed that the tetraploid plant found within otherwise diploid population of *C. rivularis* may reflect local migrations: in the investigated area, several tetraploid populations were found in the mountains. These tetraploids remain to be investigated in detail.

Another plausible explanation for a sporadic occurrence of 32 chromosomic plants within the diploid population could be their putative autopolyploid origin. In numerous populations of the diploid *C. rivularis* unreduced pollen grains were observed in a variable frequency. The results obtained on live material corroborate with numerous pollen tests performed on herbarium specimens. The problem of karyological differentiation within *C. rivularis* requires further studies.

Cardamine pratensis L.

Diploid chromosome number for the meadow plants has been reported for the first time by the present authors in their previous publication (LANDOLT and URBANSKA-WORYTKIEWICZ 1971). Since then, numerous populations of this taxon were studied and its whole area of geographical distribution has been traced (Table 5). Out of 132 investigated stations, 90 proved to be cytologically uniform. In 42 populations various cytotypes occurred among the diploid plants: 13 populations comprised hyperdiploids (2n=17, 18, 19, 20), in 31 populations two or more different cytotypes were observed. It should be emphasized that nearly all mixed populations were found near the distribution limits of the diploid *C. pratensis*, where this taxon comes into contact with various polyploid types of the group (URBANSKA-WORYTKIEWICZ and LANDOLT 1974). Accordingly it can be assumed that this cytological variation might partly reflect local migrations from neighbouring populations; on the other hand, some higher polyploids were apparently of a hybrid origin and their occurrence was probably due to the gene flow between the populations.

Cardamine nemorosa Lejeune

The first cytological record for *C. nemorosa* has been presented by GUINOCHET (1946) from the French Jura. More recently, DERSCH (1969) has published numerous chromosome counts of diploid plants growing in deciduous forests in Central Germany. It should be noted that DERSCH was the first author who reported the occurrence of aneuploids (2n=17,18,19,20) within *C. nemorosa:* he has found 10 stations where the hyperdiploids were growing among the diploids. However, the German author neither specified the frequency of the hyperdiploids within the given populations nor has he suggested any interpretation for an origin of supernumerary chromosomes. He has solely mentioned their similarity to other chromosomes of the diploid set of *C. nemorosa*.

In the course of the present study 28 stations of *C. nemorosa* were investigated (Table 6). Most of the studied stations proved to be cytologically uniform; however, it is interesting to note that some small and isolated populations in the Jura appeared to consist exclusively of 20 chromosomic plants.

In two populations of *C. nemorosa* the diploid plants were accompanied by hypotetraploids (2n=30); in a single population, sampled in French Jura, 4 individuals of *C. nemorosa* proved to be 20 chromosomic and one plant was tetraploid (2n=32).

7.2 Analysis of karyotype

Comparative analysis of karyotype was performed on root-tips pretreated with 0.02 mol/l aequous solution of oxyquinolin and stained with lacto-propionic orcein. Populations used for this study are marked by asterisks in Tables 1 - 6.

Eight good metaphases with about the same degree of contraction of the chromosomes were selected from each sample. The measurements were taken from drawings made with LEITZ camera lucida under 3500 x magnification. Mean values of the length were subsequently worked out and used for calculations of the ratio short arm/ long arm (index). The results are presented in Figs. 13 to 18 and Tables 7 to 12.

On the whole, morphological differentiation of the chromosomes does not seem to be particularly distinct in the diploid taxa of the *C. pratensis* group. In most of the studied species the chromosome set consisted of rather small, submetacentric chromosomes, one pair bearing satelites.

On the other hand, some differences were found between the particular taxa both in total amount of the chromatine (TCL) as well as in structural arrangement of the chromosomes.

Cardamine granulosa. The chromosome set of *C. granulosa* consisted of the chromosomes that were only slightly differentiated (Table 7); the longest pair measured 1.57 µ of total length, the shortest one 1.12 µ. As to the position of centromere, one pair appeared to be metacentric; the others represented submetacentric types, the index varying from 0.55 to 0.98, respectively the SAT-chromosomes were the longest pair of the set (Fig. 13).

Total length of the karyotype (TCL) presented the lowest value of all the studied diploid taxa (i.e. 20,42 µ) (Fig. 18, Table 12).

Table 7. *Cardamine granulosa:* Analysis of karyotype (mean length values in µ)

Long arm	Short arm	Total length	Index Type
0.99±0.01	0.58±0.02	1.57±0.02	0.58 SM SAT
0.87±0.02	0.48±0.01	1.35±0.02	0.55 SM
0.78±0.02	0.56±0.02	1.34±0.03	0.72 SM
0.69±0.01	0.49±0.02	1.18±0.02	0.71 SM
0.65±0.02	0.65±0.02	1.30±0.02	1 M
0.64±0.03	0.54±0.01	1.18±0.04	0.84 SM
0.59±0.02	0.58±0.01	1.17±0.02	0.98 SM
0.58±0.01	0.54±0.01	1.12±0.02	0.93 SM

Cardamine Matthioli. The chromosome set of *C. Matthioli* was rather uniform and comprised solely submetacentric chromosomes. The length of the chromosomes presented rather low values, the longest pair measuring 1.69 µ, the shortest one - 1.13 µ. SAT-chromosomes were of a medium type for *C. Matthioli* (Fig. 14).

Position of centromere varied only slightly in the studied material; the respective values of the index ranged from 0.68 to 0.89 (Table 8).

C. Matthioli was next to *C. granulosa* as far as the total length of the karyotype is concerned (Fig. 18): it comported 22,52 µ (Table 12).

Table 8. *Cardamine Matthioli:* Analysis of karyotype (mean length values in µ)

Long arm	Short arm	Total length	Index Type
0.96±0.01	0.73±0.02	1.69±0.03	0.76 SM
0.88±0.02	0.60±0.02	1.48±0.02	0.68 SM
0.88±0.02	0.66±0.01	1.54±0.03	0.75 SM
0.83±0.02	0.64±0.03	1.47±0.02	0.77 SM
0.76±0.01	0.60±0.02	1.36±0.02	0.78 SM
0.70±0.02	0.62±0.02	1.32±0.02	0.89 SM SAT
0.69±0.01	0.58±0.01	1.27±0.02	0.84 SM
0.67±0.02	0.46±0.02	1.13±0.02	0.69 SM

Cardamine udicola. *C. udicola* remains to be investigated in details. However, preliminary observations permit to characterize its chromosome set as falling into nearly the same category as that of *C. Matthioli* i.e. the chromosomes are rather small, submetacentric and not very much differentiated.

Cardamine rivularis. The chromosomes of *C. rivularis* represented mostly a submetacentric type; however, the index values were rather variable, ranging from 0.45 to 0.99 (Table 9). In addition, one pair of acrocentric chromosomes was observed (Fig. 15). *C. rivularis* proved to be the taxon which showed the highest value of total karyotype length: it comported 25.26µ, the chromosomes being rather uniform within the set (Table 12).

The present results, obtained on pre-treated material from the Alpine range, are somewhat different from the data of KUZMANOV and KOZUHAROV. Unfortunately, the Bulgarian authors gave only a general characteristics of the chromosome complement of *C. rivularis* from the Rila Mts. It would be interesting to compare detailed measurements of the chromosomes of *C. rivularis* from various parts of its wide geographical range.

Table 9. *Cardamine rivularis:* Analysis of karyotype (mean length values in µ)

Long arm	Short arm	Total length	Index	Type
1.19±0.01	0.43±0.02	1.62±0.02	0.36	A
1.06±0.02	0.48±0.01	1.54±0.02	0.45	SM
0.94±0.02	0.49±0.02	1.43±0.02	0.52	SM
0.88±0.02	0.76±0.01	1.64±0.02	0.84	SM SAT
0.87±0.03	0.77±0.01	1.64±0.02	0.88	SM
0.83±0.02	0.81±0.02	1.64±0.02	0.97	SM
0.81±0.02	0.80±0.01	1.61±0.02	0.99	SM
0.77±0.02	0.74±0.02	1.51±0.03	0.96	SM

Cardamine pratensis. Diploid *C. pratensis* has the chromosome set that seems to be rather well-differentiated both as to the length of the respective chromosomes as well as to the position of centromere (Fig. 16). The longest pair of chromosomes measured 2.07 µ, the shortest one 0.88 µ. Most of the chromosomes proved to be submetacentric, their index values ranging from 0.41 to 0.98. The SAT-chromosomes were of a medium length (Fig. 18, Table 10).

Table 10. *Cardamine pratensis:* Analysis of karyotype (mean length values in µ)

Long arm	Short arm	Total length	Index	Type
1.38±0.02	0.69±0.01	2.07±0.03	0.50	SM
1.18±0.01	0.38±0.01	1.56±0.02	0.32	A
1.12±0.02	0.46±0.01	1.58±0.02	0.41	SM
0.97±0.02	0.65±0.02	1.62±0.02	0.67	SM
0.78±0.01	0.72±0.02	1.50±0.03	0.91	SM SAT
0.76±0.02	0.66±0.02	1.42±0.02	0.87	SM
0.64±0.03	0.63±0.01	1.27±0.03	0.98	SM
0.52±0.01	0.36±0.01	0.88±0.01	0.69	SM

Total karyotype length of *C. pratensis* amounted to 23.80 µ. (Table 12)

Cardamine nemorosa. The chromosome complement of *C. nemorosa* is notably similar to that of *C. pratensis*. Two longer chromosomes (2.12 µ) are present; one pair of very short chromosomes (0.69 µ) was also observed. On the whole, the chromosomes of *C. nemorosa* are mostly submetacentric, their centromere position being rather variable within the set (index values range from 0.44 to 0.99 (Table 11). SAT-chromosomes are of medium length. The shortest chromosomes within the set represent acrocentric type (Fig. 17). In this respect, *C. nemorosa* differs from *C. pratensis*; the shortest pair of the chromosomes of the latter taxon is submetacentric.

Total length of the karyotype represented the second highest value within the studied material (24.74 µ, Fig. 18, Table 12).

Table 11. *Cardamine nemorosa:* Analysis of karyotype (mean length values in µ)

Long arm	Short arm	Total length	Index	Type
1.31±0.02	0.81±0.01	2.12±0.02	0.62	SM
1.25±0.01	0.62±0.02	1.87±0.01	0.50	SM
1.13±0.01	0.50±0.01	1.63±0.02	0.44	SM
1.12±0.02	0.37±0.02	1.49±0.02	0.33	A
0.87±0.01	0.82±0.03	1.69±0.03	0.94	SM
0.76±0.02	0.75±0.01	1.51±0.02	0.99	SM
0.69±0.02	0.68±0.02	1.37±0.02	0.98	SM SAT
0.44±0.01	0.25±0.01	0.69±0.02	0.57	SM

Chromosome length and their structural differentiation can be employed only in a general way as criteria for classification of the diploid taxa within the *C. pratensis* group. One could distinguish two groups: 1) taxa with small, not much differentiated chromosomes (*C. granulosa, C. Matthioli, C. udicola*) and 2) taxa with more pronounced structural differentiation of the chromosomes, showing higher values of the total karyotype length (*C. rivularis, C. pratensis, C. nemorosa*).

The first group does not seem to offer any characteristic pattern of differentiation within the chromosome set. On the other hand, *C. rivularis*, *C. pratensis* and *C. nemorosa* have the same general formula of the karyotype i.e. their sets consist of one pair of acrocentric chromosomes and seven pairs of submetacentric ones, a single pair being that of SAT-chromosomes. However, one can distinguish within this group rather pronounced differences in frequency of chromosomes representing the given values of the length. This means that *C. rivularis* has rather uniform chromosomes, their length varying only slightly from 1.43 to 1.64 μ. By contrast, both *C. pratensis* and *C. nemorosa* show a well-defined chromosomes differentiation: the respective values of maximal and minimal chromosome length comport 2.07 μ - 0.88 μ in the former taxon and 2.12 μ - 0.69 μ in the latter one.

Table 12. Karyotype characteristics in five diploid taxa of the *C. pratensis* group

Taxon	TCL (in μ)	Karyotype formula
Cardamine granulosa	20.42	$2_{M}14_{SM}(2_{SM\ SAT})$
Cardamine Matthioli	22.52	$16_{SM}(2_{SM\ SAT})$
Cardamine pratensis	23.80	$14_{SM}(2_{SM\ SAT})\ 2_{A}$
Cardamine nemorosa	24.74	$14_{SM}(2_{SM\ SAT})\ 2_{A}$
Cardamine rivularis	25.26	$14_{SM}(2_{SM\ SAT})\ 2_{A}$

The particular similarity of the chromosome sets occurring between *C. nemorosa* and *C. pratensis* points to a close relationship of the two taxa. It can be assumed that *C. pratensis* and *C. nemorosa* either represent different forms derived from the same ancient stock, or one taxon might have contributed in the formation of another one. The details of the geographical distribution and ecology of the two taxa are rather in favour of the second hypothesis: it seems probable that *C. nemorosa* was one of the parent taxa for *C. pratensis*.

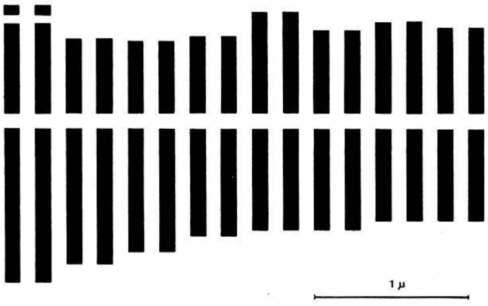


Fig. 13 Chromosome complement of *Cardamine granulosa*

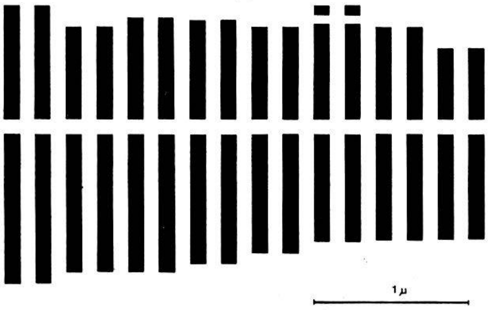


Fig. 14 Chromosome complement of *Cardamine Matthioli*

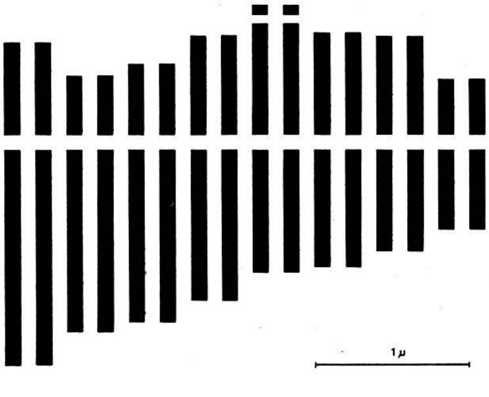


Fig. 15 Chromosome complement of *Cardamine* ~~*rivularis*~~ pratensis

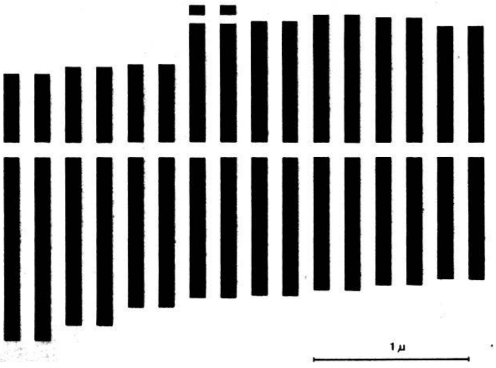


Fig. 16 Chrosome complement of *Cardamine* ~~*pratensis*~~ rivularis

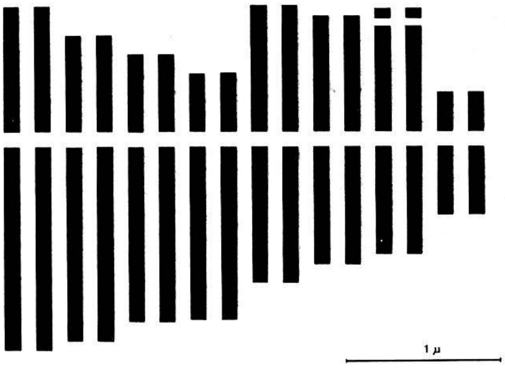


Fig. 17 Chromosome complement of *Cardamine nemorosa*

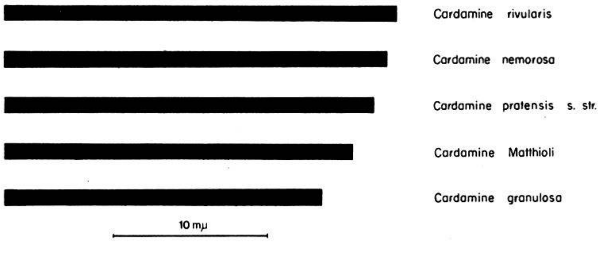


Fig. 18 Total karyotype length of five diploid taxa of the *Cardamine pratensis* group.

8. Inbreeding experiments

The *Cardamine pratensis* group manifests homomorphic self-incompatibility remaining under sporophytic control. Investigations on this problem have been carried out previously by numerous authors (HILDEBRAND 1896 cit. acc. to LÖVKVIST 1956, CORRENS 1912, BEATUS 1929, BATEMAN 1955, LÖVKVIST 1956). However, it should be emphasized that only LÖVKVIST performed his experiments on plants that were cytologically controlled.

Out of 355 plants used in LÖVKVIST's study, only 9 were diploid; no seed setting was observed after forced selfings. However, it is not quite sure which diploid taxon has been in fact represented in the material of the Swedish author .

In the course of the present study, forced selfings and control cross-pollinations were performed on 44 plants representing all the six diploid taxa. It should be mentioned that *C. udicola* from Ticino was used only in rather limited number of pollinations. In addition, some crosses were made within *C. Matthioli*.

Artificial pollinations were made in conditioned, insect-proof chambers. Four series of experiments were parallely carried out:

A - pollinations with the pollen of the same flower
B - pollinations with the pollen from other flower of the same individual
C - pollinations with the pollen from other individual of the same population
D - pollinations with the pollen from other population of the same taxon

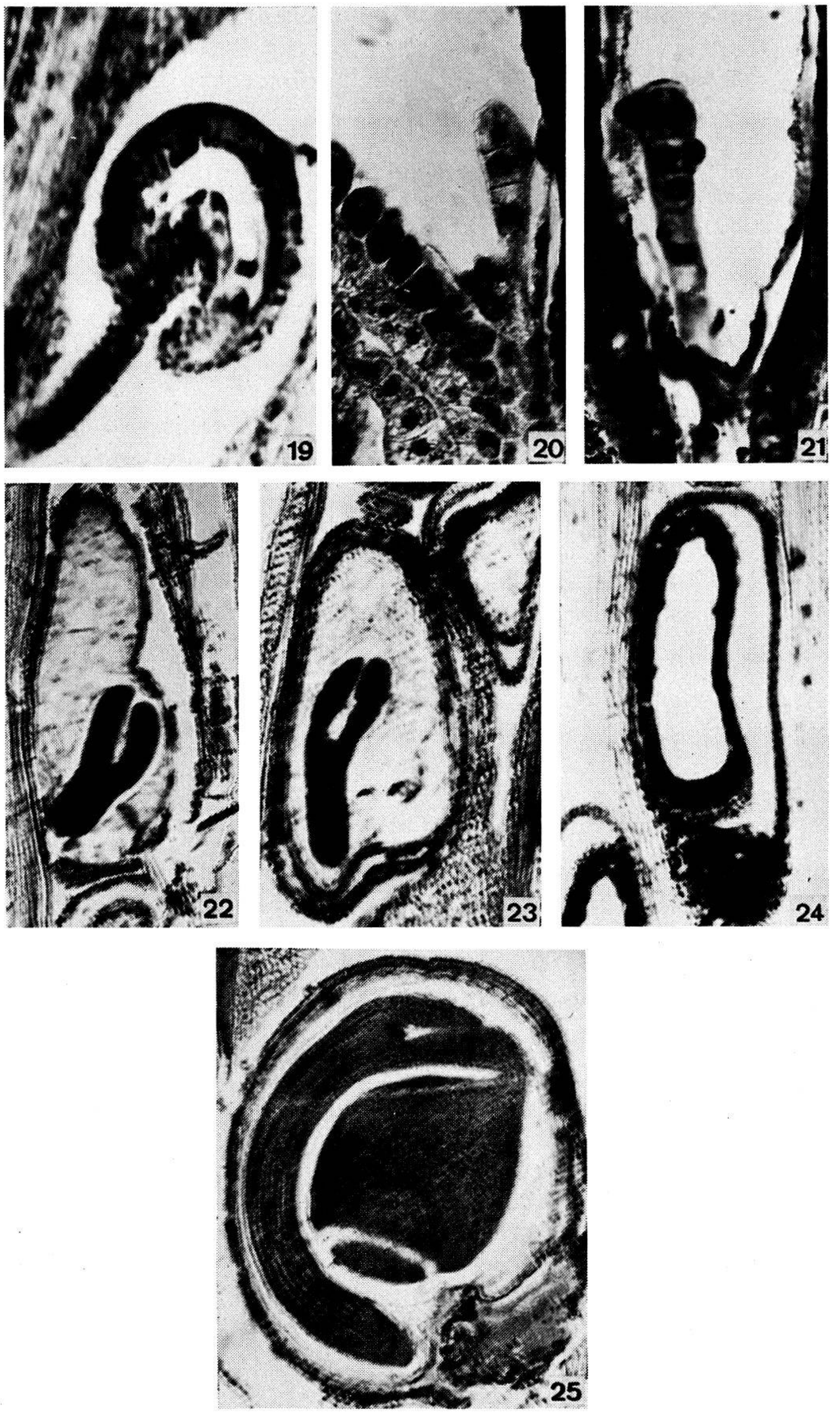
The pollinated flowers were respectively tagged; in about two and a half months the fruits were collected. Subsequently, the germination tests were made. The young plants obtained from selfings as well as some representative specimens raised from control have been kept in conditioned chambers.

For embryological investigations, materials were fixed in acetic alcohol (1:3), beginning from 48 h. after the pollination; fixations were carried on in 48 h. intervals, up to 42 days. It should be noted that some seeds maturated later i. e. in about 50 days.

Fixed flowers and siliques were dehydrated and embedded in paraffin in the usual way. Microtome sections, 10µ and 11µ thick were stained with Heidenhain's or Mayer's haematoxylin.

The structure of ovules and details of the seed development, including the observed aberrations, are alike in the whole investigated material. For that reason, descriptions given below would serve for any diploid taxon. (Figs. 19 - 25).

The ovules are campylotropous (Fig. 19). From an early developmental stage the young embryo sacs were in contact with the endothelium which consisted of a single layer of cells filled with a dense cytoplasm.



Figs.19-25. Diploid taxa of the *Cardamine pratensis* group: seed development after selfings and cross-pollinations. 19. Campylotropous ovule.c.225x. 20-21. Young embryos in endosperm.c. 720x. 22-23. Advanced development of embryo and endosperm. 24. Empty seed with developed seed-coat. 25. Normally developed seed.c.150x.

Mature ES was rather large, sometimes twisted and highly vacuolated. It contained three big, multinuclear and extremely long-persisting antipodals, a secondary nucleus and an egg-aparatus comprising egg-cell and two synergids.

The response to selfings proved to be somewhat ambiguous in the studied material. Individual as well as interpopulational variation was observed both in frequency of developed seeds as well as in their subsequent germination. The results which are presented here do no more than illustrate a general breeding behaviour of the diploid taxa within the *C. pratensis* group. For a more thorough analysis, it will be necessary not only to multiply the number of experiments but also to control them further, beyond the stage of young plants.

In most of the pollinated flowers the embryo sacs persisted for rather a long time, up to 18 to 20 days after pollination; however no observable changes in size and structure of the ovules and ovaries could be discerned. At later stages the degeneration of the ovules was observed.

In some flowers of *C. nemorosa*, siliques began to form in spite of fact that there was no seed development.

However, the seed failure after selfings was by no mean absolute. In some ovules, fixed by the 17th day after pollination, embryo sacs did not manifest any further developments, but the endothelium became hypertrophied, the whole ovule being larger than the other ones within the ovary. At later stages some empty seeds with nevertheless well developed seed-coat were found (Fig.24).

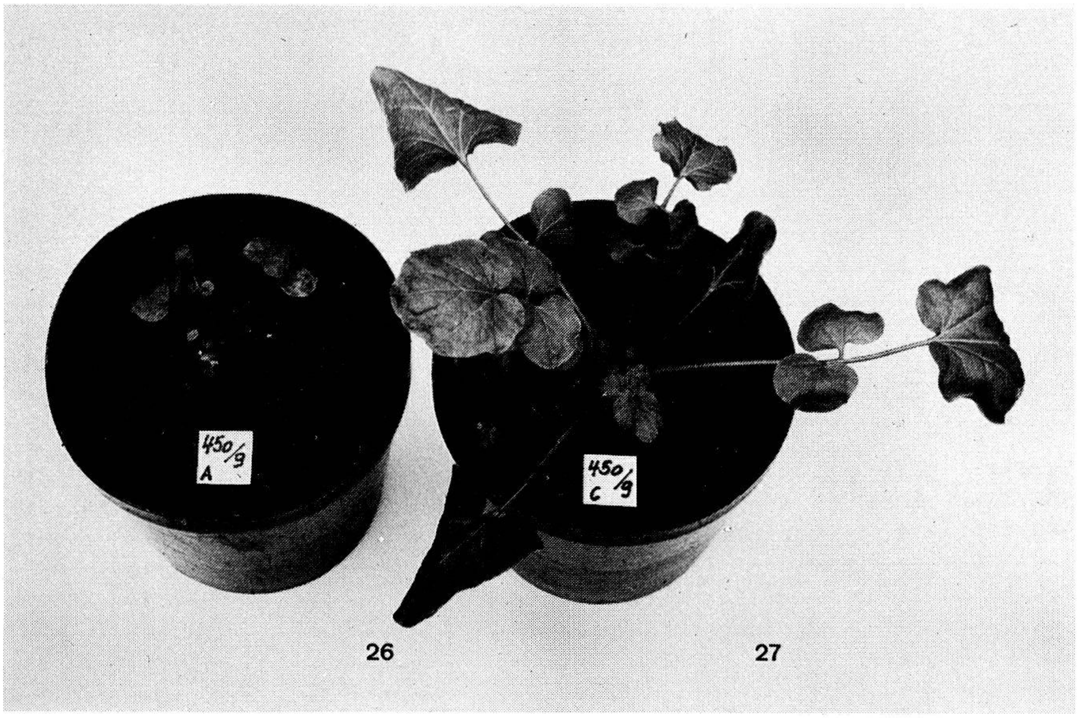
The development of embryo and endosperm presented sometimes aberrations. By 24 days after pollination, the zygote stayed undivided and only some few endosperm nuclei were visible. In some other materials fixed at the same time, a thin and elongated young embryo, most frequently two-celled, was observed. In one ovule from this series four-celled embryo was found (Fig. 20, Fig. 21). The cells of the embryo were strongely vacuolated. Endosperm nuclei in the above described ESs were few; they were rather evenly distributed within a thin layer of cytoplasm that lined the seed cavity. Only at the micropylar end was the endosperm a little better developed. In spite of apparently defective development of embryo and endosperm, the respective ovules were notably enlarged and the development of the seed-coat appeared to be rather advanced.

Normal seed development began about 7 - 9 days after pollination, both in selfings as well as in outcrosses. It was rather slow between 12 and 18 days: the embryo stayed small and spherical, its suspensor being distinctly elongated. Endosperm was multinuclear and it occurred in a larger amount at the micropylar end of the ES. Big antipodals reached deep into the seed cavity.

Between 18 and 26 days after pollination, the embryo and endosperm developed rather rapidly; by 28 days well-developed, elongated embryo surrounded by a dense endosperm was lying centrally within the seed cavity. The respective ovules were much enlarged and the seed-coat was advanced in its differentiation (Fig. 22, 23). By the 42nd day, some fully developed embryos were observed; endosperm was at that time mostly resorbed and the seed-coat presented no anomalies (Fig. 25).

Differences between selfings and control cross-pollinations occur mostly in the seed output (Tables 13 - 19). The seed setting proved to be invariably good in the latter experiments whereas the former ones yielded seeds in low and variable frequency. Only in two populations, one of *C. Matthioli* from fertilized meadow in the Piedmont, the other of *C. udicola* from Ticino, rather high percentage of apparently well-developed seeds was obtained from selfings. These results stay in agreement with embryological observations: various developmental stages of embryo and endosperm were most frequently observed in the selfed ovules of *C. Matthioli* and *C. udicola* from the stations mentioned above.

Seed germination after selfings proved to be rather erratic. In *C. pratensis* only two seeds developed in a single individual out of 13 tested ones. One seed germinated giving rise to a vigorous young plant. Selfings in *C. granulosa* yielded likewise two seeds from a single plant (10 individuals tested); however, the germination was nil (Table 13). Out of two studied populations of *C. rivularis*, only one produced seeds after selfings; three tested plants yielded no seeds at all, in one plant a single developed seed was found, in the last individual 13 seeds were collected. None of these seeds germinated. *C. nemorosa* manifested still some more variation: out of three studied populations, two yielded seeds in very variable frequency (Table 19). In addition, development of well-formed, yet empty siliques was observed. Two seeds germinated; however, the young plants were apparently affected in their development (Figs 26,27).



Figs 26,27. 14 days old plants of *Cardamine nemorosa:*
26. Plant obtained from selfings.
27. Plant obtained from cross-pollination, about 1/2 natural size.

Table 13. *Cardamine granulosa:* seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
560/2	10(-)	8(-)	16(132)	4(24)	-	-	12.1%	2.3%
560/4	11(-)	7(-)	9(40)	6(37)	-	-	11.1%	1.8%
560/5	9(2)	1(-)	8(68)	9(51)	-	-	9.8%	1.1%
560/10	9(-)	5(-)	10(97)	3(6)	-	-	14.8%	10.0%
560/14	15(-)	--	7(42)	- -	-	-	7.4%	-
567/1	17(-)	5(-)	4(13)	3(12)	-	-	5.5%	0.3%
567/4	8(-)	6(-)	4(18)	6(21)	-	-	32.2%	5.8%
567/5	2(-)	1(-)	17(67)	2(11)	-	-	28.3%	3.4%
567/7	16(-)	4(-)	1(6)	1(3)	-	-	30.0%	2.9%
567/8	7(-)	4(-)	9(57)	4(9)	-	-	8.8%	4-7%

Note. Number of sound-looking seeds is given in brackets

Table 14. *Cardamine Matthioli:* seed output after selfings and cross-pollinations

No. of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
561/1	5(32)	9(14)	6(10)	8(20)	14.2%	3.8%	23.2%	48.1%
561/3	13(116)	6(15)	14(38)	8(26)	22.4%	14.8%	31.2%	38.9%
561/4	7(36)	6(11)	7(13)	5(14)	18.6%	2.9%	41.3%	52.6%
561/5	6(18)	4(7)	8(52)	7(23)	11.1%	8.2%	12.3%	38.1%
561/8	11(56)	3(4)	8(16)	9(31)	18.1%	5.8%	33.2%	38.1%
568/9	12(-)	8(-)	8(71)	3(6)	-	-	46.3%	32.7%
568/11	10(-)	5(-)	13(126)	2(7)	-	-	52.3%	42.2%
568/12	8(-)	6(-)	7(79)	4(21)	-	-	49.8%	44.4%
569/3	13(-)	8(-)	11(116)	2(12)	-	-	29.6%	31.2%
569/7	9(-)	7(-)	7(164)	4(-)	-	-	56.3%	-
569/9	14(-)	6(-)	12(103)	6(31)	-	-	51.1%	22.8%
570/1	9(-)	6(-)	9(78)	4(30)	-	-	47.9%	36.5%
570/3	11(-)	3(-)	8(54)	5(44)	-	-	12.8%	11.3%
570/6	14(-)	7(-)	7(49)	4(38)	-	-	39.4%	41.6%

Note- Number of sound-looking seeds is given in brackets

Table 15. *Cardamine Matthioli:* crosses between two ecological races

Cross (seed parent listed first)	N of pollinated flowers	N of siliques	Total N of seeds	N of sound seeds	Germination
561 x 569	12	12	396	388	76.2%
569 x 561	11	10	389	382	82.8%

Average N of ovules in seed plants: 561 x 569 38.1
569 x 561 42.1

Table 16. *Cardamine udicola* from Ticino: seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
56/1	14(40)	8(18)	10(6)	3(16)	-	-	-	-
56/2	8(38)	3(6)	8(7)	6(18)	-	-	-	-
56/3	7(43)	4(8)	9(11)	- -	-	-	-	-
56/4	12(130)	4(9)	8(16)	8(47)	-	-	-	-
56/5	9(51)	8(28)	10(6)	7(21)	-	-	-	-

Note. Number of sound-looking seeds is given in brackets

Table 17. *Cardamine rivularis:* seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
624/2	15(13)	6(-)	9(41)	4(2)	-	-	28.1%	3.2%
624/3	10(1)	4(-)	5(38)	- -	-	-	14.6%	-
624/5	14(-)	5(-)	8(72)	4(17)	-	-	43.2%	11.1%
624/8	11(-)	5(-)	9(69)	1(3)	-	-	21.3%	4.4%
624/10	12(-)	4(-)	8(64)	4(11)	-	-	12.8%	10.2%
168/9	9(-)	6(-)	7(68)	- -	-	-	38.2%	-
169/2	11(-)	5(-)	12(97)	6(26)	-	-	48.5%	16.2%
169/3	10(-)	- -	8(32)	4(9)	-	-	41.7%	9.9%
169/5	12(-)	6(-)	11(86)	2(6)	-	-	28.3%	2.7%
169/8	10(-)	7(-)	7(41)	4(12)	-	-	51.3%	18.7%

Note. Number of sound-looking seeds is given in brackets

Table 18. *Cardamine pratensis:* seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
75/1	5(-)	3(-)	6(32)	6(58)	-	-	56.6%	51.3%
75/3	4(-)	2(-)	8(38)	2(21)	-	-	49.8%	36.6%
75/6	9(-)	1(-)	4(14)	2(9)	-	-	44.9%	28.1%
75/7	8(1)	2(-)	9(61)	4(20)	-	-	52.7%	55.4%
464/1	12(-)	4(-)	8(59)	6(31)	-	-	44.7%	28.1%
464/7	9(-)	5(-)	11(78)	4(20)	-	-	62.1%	44.5%
464/8	11(-)	6(-)	10(72)	2(13)	-	-	54.4%	50.0%
464/10	10(-)	4(-)	8(80)	3(18)	-	-	51.9%	35.4%
464/13	12(-)	8(-)	6(49)	2(9)	-	-	18.3%	11.2%
720/2	8(-)	2(-)	9(73)	5(41)	-	-	69.9%	51.4%
720/6	6(2)	3(-)	11(81)	2(16)	1 seed	-	54.8%	33.5%
720/8	12(-)	4(-)	10(78)	6(37)	-	-	31.2%	28.4%
720/11	13(-)	2(-)	12(90)	- -	-	-	47.7%	-

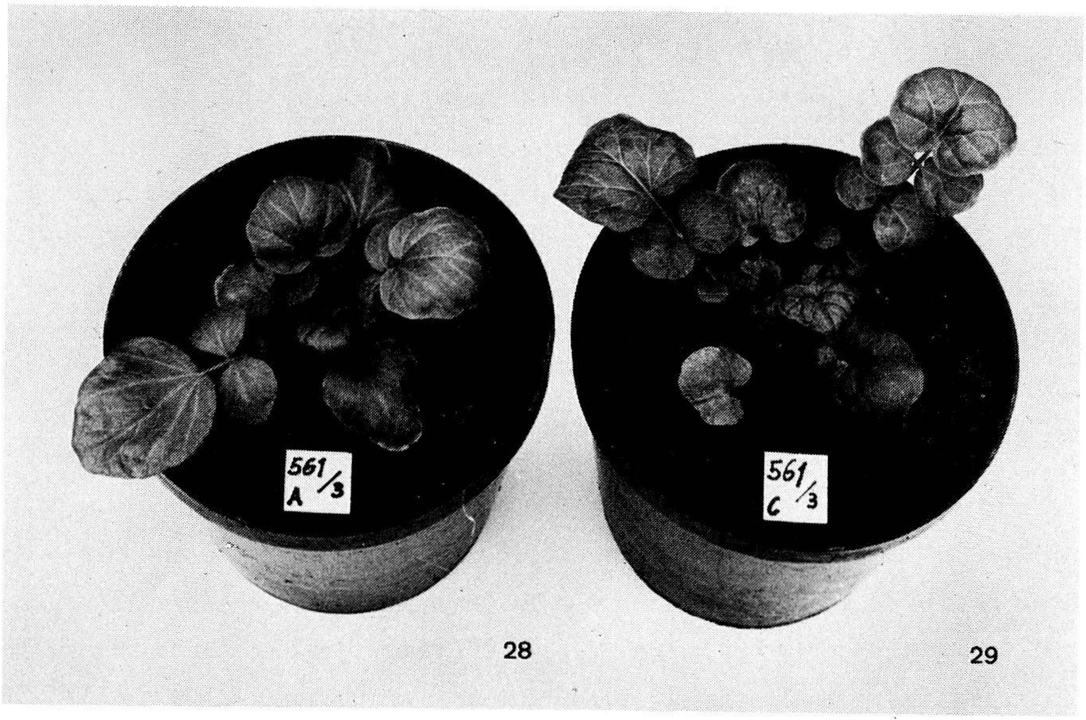
Note. Number of sound-looking seeds is given in brackets.

Table 19. *Cardamine nemorosa:* seed output after selfings and cross-pollinations

No.of plant	Total number of pollinated flowers - Series				Germination Series			
	A	B	C	D	A	B	C	D
70/2	8(-)	6(-)	6(31)	2(12)	-	-	41.2%	48.1%
70/8	12(-)	5(-)	9(21)	6(7)	-	-	54.0%	18.2%
70/13	9(-)	4(-)	12(47)	4(18)	-	-	38.6%	50.9%
440/1	11(-)**	4(-)	12(180)	3(40)	-	-	52.3%	51.7%
440/3	8(-)	2(-)	6(71)	4(36)	-	-	32.2%	30.1%
440/4	9(-)**	4(-)	18(216)	6(47)	-	-	54.4%	36.2%
440/5	14(6)	5(-)	9(104)	4(36)	-	-	30.6%	42.1%
440/9	12(21)	3(-)	8(47)	4(51)	-	-	28.3%	31.8%
450/9	8(6)	3(-)	4(36)	4(26)	1 seed	-	49.9%	38.4%
450/10	13(-)	8(1)	14(92)	10(79)	-	1 seed	48.6%	52.2%
450/11	22(-)	4(-)	9(59)	1(8)	-	-	56.4%	48.2%

** well-developed siliques containing no seeds
Note. Number of sound-looking seeds is given in brackets

C. Matthioli deserves a special mention. On the whole, 14 plants belonging to two ecological races were tested (Table 14). No seeds at all were developed from selfings in the plants originating from wet stations in northern Italy. On the other hand, the race growing in fertilized meadows in the Piedmont proved to be partly self-fertile. The five tested plants yielded seeds; however, their germination was highly variable(2.9% to 22.4% ,Table 14). The young plants raised from selfings were somewhat inferior towards the control material at very early stages of their development, but in rather a short time no difference could be discerned (Figs 28, 29).



Figs 28, 29. 14 days old plants of *Cardamine Matthioli*.
28. Plant obtained from selfings
29. Plant obtained from cross-pollination, ca. 3/4 natural size.

The control cross-pollinations resulted in rather a good seed output. However, the germination was rather low, its average value being about 54%. It should be noted that the highest germination ratio was revealed in the interracial crosses within *C. Matthioli* (82.2%, Table 15).

The evaluation of results obtained on *C. udicola* is rather difficult for only the plants from a single population in Ticino were used in the present experiments. It is interesting to note that the yield of seeds was very good yet the germination was nil (Table 14). The plants from Ticino have not produced any germinating seeds in all experimental series (selfings, cross-pollinations within the same population, interpopulational crosses as well as interspecific crosses), if they were used as female parent. This particular behaviour requires further investigations, especially those on *C. udicola* originating from the second center of its disjunctive geographical range (the Lake of Thun).

The present results permit to characterize the diploid taxa of the *C. pratensis* group as predominantly self-incompatible. It seems probable that the incompatibility blocks remain under multi-allelic control. They operate most frequently at pre-mating stages and might cause an inhibition of the pollen tube growth; on the other hand, the seed incompatibility apparently plays a complementary role resulting in seed-or germination failure. Negative response to selfings seem to appear sometimes at later developmental stages (break-down of the inbred plants); however, in most of the studied cases the self-incompatibility barrier does not seem to be complete.

9. Interspecific crosses

9.1. Seed output

Interspecific crosses between six diploid taxa belonging to the *Cardamine pratensis* group were performed in three consecutive years 1972-1974. Only the experiments from 1972 and 1973 were included into the present paper for the seeds obtained from the last series are actually being at their dormancy period.

Various strains were intercrossed on 30 combinations, 15 of which led to the production of F_1 hybrids. The results are given in Table 20.

Artificial cross-pollinations were made in insect-proof conditioned chambers where the parent plants were transferred long before their flowering. The normal precautions were taken to prevent contamination of cultures through mixing of pollen or seeds. All plants were emasculated about 48 h. before the opening of the flowers. Each pollination was repeated in 24 h. interval in order to get the stigmas at their most receptive stage.

Two and a half months after the pollinations, the siliques were collected and a score of developed fruits was made in relation to the total number of pollinated flowers. About three months later, the seeds were sown on moist blotting paper and the percentage of germinating ones was subsequently calculated. Young hybrid plants have been kept in cultivation partly in conditioned chambers, partly in a cold greenhouse. Plants obtained in 1972 were transferred into experimental field after having completed their first year of growth.

It was recently emphasized by BENTZER (1973) that an estimation of genomic relationships between taxa which is based on the ability of a particular cross to produce seeds that germinate, is only of a limited reliability. Numerous authors have shown that there was no apparent correlation between crossability and fertility (e.g. ORNDUFF 1969), nor was there any particular correlation between the germinating potential of hybrid seeds and their viability (STRID 1970). On the other hand, reciprocal differences in compabilility and pollen fertility, inversely correlated with one another, were found by GRANT (1952) in some crosses performed at homoploid level with the *Gilia capitata* group.

Not all strains of the diploid taxa within the *C. pratensis* group have been included into the present experiments. It should be also noted that the ratio of hybrid individuals to the flowers that were pollinated is not entirely reliable,for the germination of seeds was sometimes low, even in control. Another factor is that in some materials, hybrid or parental alike, seeds ranged in continuous series from obviously sound to obviously abortive and dividing line between viability and inviability, could not be traced without doubt. The result of these and other conditions is that minor differences in the degree of crossability might be obscured by incomplete data, or by experimental errors. Our experiments do, however, reveal marked differences in crossing behaviour of the respective diploid taxa and some general correlations are apparent.

The most pronounced crossability was found between *C. nemorosa* and *C. rivularis*. Both reciprocal crosses yielded a fair amount of rather well-developed seeds which manifested a definite ratio of germination (41.4%, 62.1% in the respective crosses). Plants of the first hybrid generation were growing vigorously and flowered during the first year of their growth.

Table 20. *Cardamine pratensis s.l.*: interspecific crosses at diploid level

Cross (seed parent listed first)	N of pollin. flowers	N of sili-ques	Total N of seeds	N of sound seeds	Ger-mina-tion
C. *granulosa* x C. *Matthioli*(569)	12	10	30	4(13.3%)	nil
C. *Matthioli*(569) x C. *granulosa*	18	16	170	164(96.5%)	4.2%
C. *granulosa* x C. *Matthioli*(561)	12	10	60	14(23.3%)	7.1%
C. *Matthioli*(561) x C. *granulosa*	15	12	71	29(40.8%)	nil
C. *granulosa* x C. *rivularis*	12	10	24	3(12.5%)	nil
C. *rivularis* x C. *granulosa*	12	9	84	66(78.6%)*	nil
C. *granulosa* x C. *pratensis*	13	10	63	27(42.8%)	nil
C. *pratensis* x C. *granulosa*	15	15	247	144(58.3%)	2.1%
C. *granulosa* x C. *nemorosa*	15	14	48	36(75.0%)	nil
C. *nemorosa* x C. *granulosa*	16	16	313	36(11.5%)	nil
C. *Matthioli* C. *udicola*(56)	13	12	181	163(90.0%)	nil
C. *udicola* (56)x C. *Matthioli*	12	12	46	21(45.6%)	nil
C. *Matthioli*(561) x C. *rivularis*	11	9	144	26(18.0%)	nil
C. *rivularis* x C.*Matthioli*(561)	13	11	117	84(71.8%)	nil
C. *Matthioli*(569) x C. *rivularis*	12	10	272	60(22.1%)	5.0%
C. *rivularis* x C. *Matthioli*(569)	11	11	256	80(31.2%)	nil
C. *Matthioli*(569) x C. *pratensis*	16	14	164	80(48.8%)	41.2%
C. *pratensis* x C. *Matthioli* (569)	16	14	136	120(88.2%)	5.8%
C. *Matthioli*(561) x C. *pratensis*	9	7	74	31(41.9%)	27.5%
C. *pratensis* x C. *Matthioli* (561)	8	6	53	29(54.7%)	19.3%
C. *Matthioli*(561) x C. *nemorosa*	13	10	96	34(35.3%)	nil
C. *nemorosa* x C. *Matthioli*(561)	16	13	151	51(33.8%)	nil
C. *rivularis* x C. *pratensis*	15	14	76	36(47.3%)	5.5%
C. *pratensis* x C. *rivularis*	14	13	138	90(65.2%)	32.2%
C. *rivularis* x C. *nemorosa*	18	15	78	64(82.0%)	62.1%
C. *nemorosa* x C. *rivularis*	20	18	291	291(100%)	41.0%
C. *pratensis* x C. *nemorosa*	17	15	252	234(92.8%)	33.3%
C. *nemorosa* x C. *pratensis*	18	15	248	246(99.2%)	0.4%
C. *nemorosa* x C. *udicola*(56)	14	12	197	105(53.3%)	2.9%
C. *udicola*(56) x C. *nemorosa*	20	18	214	55(25.7%)	nil

* seeds well-formed but empty under thick seed-coat.
Note. The numbers in brackets by C. *Matthioli* and C. *udicola* refer to the collections that were used in crosses (see Tables 2,3)

C. pratensis showed an interesting pattern of crossability towards *C. nemorosa* and *C. rivularis*. Both crosses with these taxa resulted in sound-looking seeds when *C. pratensis* was used as female parent. The germination ratio comported 33.3% and 32.2%, respectively (Table 20). Young hybrid plants were growing normally and no aberrations were found.

The opposite cross-direction i.e. when *C. pratensis* was used as male parent, resulted in rather a good yield of seeds; by contrast, their germination proved to be extremely low. It comported 0.4% in cross *C.nemorosa x C. pratensis* and 5.5% when *C. rivularis* was pollinated by *C. pratensis*. The viability of few obtained hybrid plants did not seem, however, to be affected in any visible way.

C. Matthioli and *C. pratensis* appeared to be partly intercompatible: two different races of *C. Matthioli* crossed reciprocally with *C. pratensis* produced variable amount of sound-looking seeds (Table 20). The percentage of young F_1 plants ranged from 5.8% to 41.2% and it appeared to follow the cross-direction: germination of seeds was better when *C. Matthioli* represented female parent.

Limited reciprocal compatibility was observed in crosses between *C. Matthioli* and *C. granulosa*. As in the formerly described cases, a marked drop between amount of sound-looking seeds and their germination was observed. The highest germination ratio observed in these crosses was 7.1%, in other combination it comported 4.2%, otherwise the germination was nil.

Very weak interfertility was found between *C. Matthioli* and *C. rivularis* out of four different crosses only one yielded seeds and 5% of hybrid plants were obtainded.

Similar results were brought about by crosses between *C. udicola* from Ticino and *C. nemorosa:* 2.9% of hybrids were obtained and that solely from the cross where *C. nemorosa* was pollinated by *C. udicola;* seeds yielded from the reciprocal cross direction did not germinate at all.

The last cross which yielded any hybrid plants was that of *C. pratensis* pollinated by *C. granulosa:* 2.1% of F_1plants obtained from this cross and nil germination found in the reciprocal one point to an extremely low intercompatibility occurring between the two taxa.

The results of the present study permit to estimate the nature of internal mechanisms preventing or limiting hybridization within the *C. pratensis* group. The number of developed siliques was most frequently slightly inferior to that of pollinated flowers. It seems probable that the incompatibility blocks limiting the formation of hybrids between the diploid taxa operate as very important sieves at later post-mating stages. In this respect the interspecific crosses bring about different results as compared to inbreeding experiments where rather a non-significant number of seeds was developed after most of the selfings (see p.103-106).Accordingly one can assume that self-incompatibility mechanisms act essentially at pre-mating stages (pollen incompatibility) whereas those separating particular taxa appear at more advanced period of the seed development (seed incompatibility). The present results stay in agreement with previous data of LÖVKVIST (1956) who obtained seeds from crosses between various cytotypes of the *C. pratensis* group; the ratio of sound-looking seeds varied remarkably in the material of the Swedish author.

It seems probable that the barriers of interspecific incompatibility act in a similar way at various levels of polyploidy within the whole group.

The seed incompatibility is a very complex phenomenon and numerous attemps were made to give the most accurate explanation for seed failure. It should be pointed out that this sort of aberration is rather well-known in crosses representing different levels of polyploidy on the other hand, seed-incompatibility appearing in crosses at homoploid level is rather rare.

Four principal theories dealing with seed incompatibility are based on the assumption of "genomic strength" or"genetic values". These terms were introduced by HOWARD (1947) and have been since utilized by numerous students. The basic of genetic values is that the interaction of different parts of the seed is assumed to require an exact balance of unknown substances essential for the development; concentration of these substances depends on genetic strength of genomes and on the number of genomes present in the respective tissues of the seed.

The most popular theory is that based on the ratio of genetic values between endosperm and embryo (HOWARD 1947). The second one shows that the ratio: endosperm/maternal tissues holds sometimes balance of the seed development. This theory has been most thoroughly tested by VALENTINE (1951, 1954, 1955, 1956, 1963) and WOODELL (1960, 1961). The importance of the relationship between maternal and paternal genomes in the endosperm nuclei was emphasized in particular by RUTISHAUSER(1969). The last theory, developed by WAGENHEIM (1962) assumed that the important ratio is between genetic values of the endosperm genomes and plasmon. Recent investigations of GYMER and WHITTINGTON (1973) point to importance of this latter mechanism.

It seems probable that discrepancies found in the course of the present investigations are largely due to the incompabitility between endosperm and the maternal tissues. In this respect, diploid taxa of the *C. pratensis* group approache the *Primula* species investigated by VALENTINE and WOODELL. Unpublished results of the present authors are in favour of this assumption: in experimental crosses between *C. rivularis* and *C. amara*, hybrid plants of the F_1 generations were growing and developing normally only after having removed their apparently too thick seed-coat; no germination has been observed in normal conditions, in spite of the fact that the embryos were well-developed.

9.2 F_1 hybrids

Vegetative development

The vegetative development proved to be quite normal in most of the obtained hybrids. Only a single plant born from cross: *C. nemorosa x C. udicola* was aberrant i.e. its leaves were malformed and its growth was very slow.

In about two months after germination, the young hybrid plants had already well-developed rosettes. Nearly all of them flowered in their first season. Only in the aberrant plant that was described above, no flowering shoots appeared. On the other hand, the two hybrids obtained from cross-direction: *C. rivularis x C. pratensis*, produced some flowering shoots that developed up to a certain point yet eventually ceased to grow before flowering.

Vegetative propagation in hybrid plants began rather early; propagules on the rosette leaves occurred sometimes already in the third month after germination. They rooted easily and some of them produced later flowering shoots.

Meiosis in anthers

The aim of the study on meiosis in anthers of the F_1 hybrids has been to test further aspects of incompatibility between diploid taxa. On the whole, meiosis was investigated in 67 plants (Table 21). At later stages, all flowering hybrid plants were tested for percentage of good pollen.

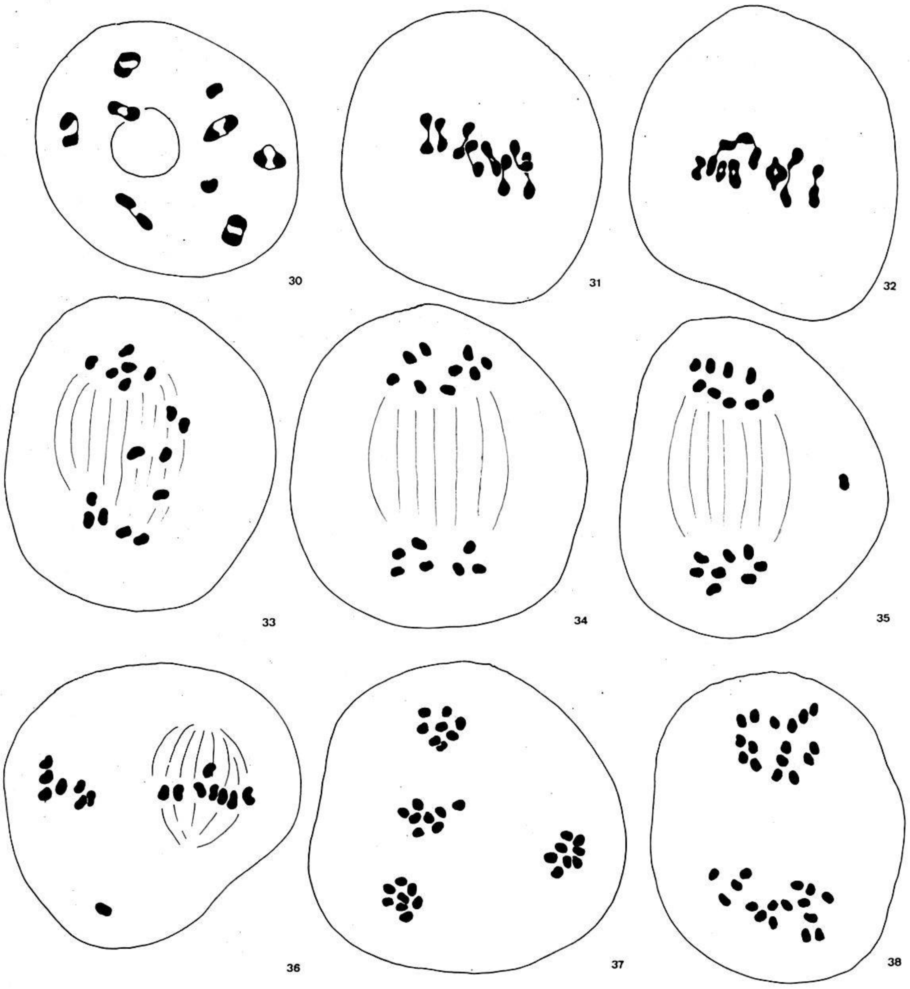
The results of these investigations are presented in Table 24.

Table 21. Experimental F_1 hybrids used for the study on meiosis in anthers

Cross type (female parent listed first)	number of studied plants
C. granulosa x *C. Matthioli* (561)	1
C. Matthioli (569) x *C. granulosa*	7
C. pratensis x *C. granulosa*	3
C. nemorosa x *C. granulosa*	2
C. Matthioli (569) x *C. rivularis*	3
C. Matthioli (569) x *C. pratensis*	5
C. Matthioli (569) x *C. pratensis*, 2n=18	1
C. pratensis x *C. Matthioli* (569)	7
C. pratensis x *C. Matthioli* (561)	8
C. pratensis x *C. rivularis*	6
C. rivularis x *C. nemorosa*	6
C. nemorosa x *C. rivularis*	7
C. nemorosa x *C. pratensis*	1
C. pratensis x *C. nemorosa*	7
C. nemorosa x *C. udicola*	3
Total	67

Normal course of microsporogenesis was observed in most of the studied PMC s (Table 22). The chromosome pairing, although somewhat variable and incomplete, resulted mostly in eight bivalents (Fig. 31). Univalents occurred in rather a low number (Fig. 30). Polyvalents were found only exceptionally, in a single hybrid plant (Fig. 32, Table 22). The congression of chromosomes in I metaphase was regular.

In I anaphase the chromosomes were most frequently distributed in a normal way towards the poles. In some PMC s, however, several chromosomes were either lagging in the equatorial plate, or remained scattered along the spindle (Fig. 33). It can be assumed that restitution nuclei might sometimes be formed as a result of such disturbances, for some unreduced PMC s were found at the second division (Fig. 38). Another aberration observed in the studied material consisted in elimination of some chromosomes, both during the first as well as the second division in the PMC s (Figs 35,36).



Figs 30-38. Experimental F_1 hybrids: meiosis in anthers.
30. *C. rivularis* x *C. nemorosa:* diakinesis with 7 bivalents and 2 unival.
31. *C. pratensis* x *C. nemorosa:* I metaphase with 8 bivalents.
32. *C. granulosa* x *C. Matthioli* (561): I metaphase with 1 quadrivalent and 6 bivalents.
33. *C. pratensis* x *C. rivularis:* I anaphase with some chromosomes scattered along the spindle
34. *C. nemorosa* x *C. pratensis:* unequal distribution (7 versus 9 chromosomes) at I anaphase.
35. *C. Matthioli* (569) x *C. pratensis,* 2n=18: unequal distribution at I anaphase accompanied by elimination of a single chromosome.
36. *C. Matthioli* (569) x *C. rivularis:* II metaphase with a single eliminated chromosome.
37. *C. nemorosa* x *C. udicola:* normal II telophase.
38. *C. granulosa* x *C. Matthioli* (561): II telophase in an unreduced PMC c.2100x.

Table 22. Experimental F_1 hybrids between diploid taxa of the *C. pratensis* group: meiosis in anthers

Diakinesis-Metaphase I	Anaphase I - Telophase I				Anaphase II - Telophase II			
Chromosome pairing	Normal	Bridges	Laggards	Elimination	Normal	Bridges	Laggards	Elimination
C. granulosa x *C. Matthioli* (561):								
$8_{II}, {}^{1}{}_{III}{}^{2}{}_{II}{}^{9}{}_{I}, {}^{1}{}_{IV}{}^{6}{}_{II}, {}^{1}{}_{VI}{}^{5}{}_{II}$	16	2	8	-	27*	4	2	-
C. Matthioli (569) x *C. granulosa:*								
$8_{II}, {}^{7}{}_{II}{}^{2}{}_{I}$	33	-	2	1	34	-	1	-
C. pratensis x *C. granulosa:*								
$8_{II}, {}^{5}{}_{II}{}^{6}{}_{I}, {}^{4}{}_{II}{}^{8}{}_{I}$	21	1	5	2	17	-	4	-
C. nemorosa x *C. granulosa:*								
$7_{II}{}^{2}{}_{I}, {}^{4}{}_{II}{}^{8}{}_{I}$	9	-	8	4	12	1	6	2
C. Matthioli (569) x *C. rivularis:*								
$8_{II}, {}^{7}{}_{II}{}^{2}{}_{I}, {}^{5}{}_{II}{}^{6}{}_{I}$	18	-	11	-	34	-	7	1
C. Matthioli (569) x *C. pratensis:*								
$8_{II}, {}^{6}{}_{II}{}^{4}{}_{I}$	26	2	2	1	14	1	2	-
C. Matthioli (569) x *C. pratensis*, 2n=18:								
$9_{II}, {}^{8}{}_{II}{}^{2}{}_{I}$	11**	-	4	3	6	7	4	3
C. pratensis x *C. Matthioli* (569):								
$8_{II}, {}^{7}{}_{II}{}^{2}{}_{I}$	39	-	2	-	54	1	2	2
C. pratensis x *C. Matthioli* (561):								
$8_{II}, {}^{6}{}_{II}{}^{4}{}_{I}$	42	3	4	-	21	1	4	2

C. pratensis x *C. rivularis:*								
8_{II}	48	-	6	-	29	1	12	-
C. rivularis x *C. nemorosa:*								
$8_{II}, 7_{II}2_{I}, 6_{II}4_{I}$	37	-	3	1	42	-	-	-
C. nemorosa x *C. rivularis:*								
$8_{II}, 7_{II}2_{I}$	67	-	4	-	43	1	2	-
C. nemorosa x *C. pratensis:*								
8_{II}	22***	-	-	-	18	-	1	-
C. pratensis x *C. nemorosa:*								
$8_{II}, 7_{II}2_{I}, 6_{II}4_{I}$	51	1	2	1	19	-	-	-
C. nemorosa x *C. udicola:*								
$8_{II}, 7_{II}2_{I}, 5_{II}6_{I}$	34	-	4	1	14	-	3	-

* in three PMCs unreduced chromosome number 2n=16 was observed (Fig. 30)

** in some PMCs unequal distribution (10/8, 9/8 + 1 elimin.) was found

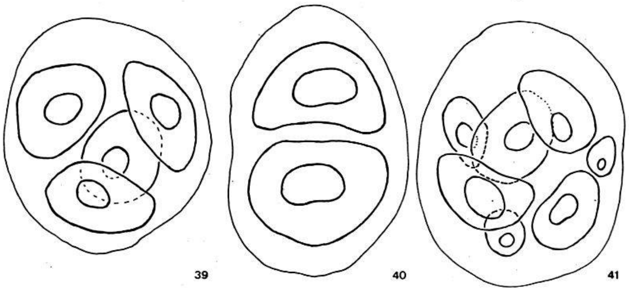
*** unequal distribution (7/9) was found in four PMCs (Fig. 34)

A particular distribution of chromosomes in I anaphase was sometimes observed. Instead of two groups, each containing eigth chromosomes, nine chromosomes gathered at one pole whereas the other group comprised only seven chromosomes (Fig. 34). Such aneuploid distribution might subsequently contribute to the formation of aneusomatic plants; it should be recalled that hyperdiploid, aneusomatic plants were found in some diploid taxa studied in the course of the present work (see p. 82-86).

Table 23. Artificial F_1 Hytrids between diploid taxa of the *Cardamine pratensis* group: tetrad stage in PMCs

Type of cross (female parent listed first)	Tetrads	Dyads	Triads	Polyads
C. granulosa x C. Matthioli (561)	32	8	-	12
C. Matthioli(569)x*C. granulosa*	43	2	1	3
C. pratensis x C. granulosa	16	1	-	2
C. nemorosa x C. granulosa	22	-	2	6
C. Matthioli(569)x*C. rivularis*	41	3	1	9
C. Matthioli(569)*x C. pratensis*	33	-	-	2
C. Matthioli(569) *x C. pratensis*, 2n=18	18	-	1	6
C. pratensis x C. Matthioli(569)	28	1	-	3
C. pratensis x C. Matthioli(561)	39	1	1	1
C. pratensis x C. rivularis	72	4	-	-
C. rivularis *x C. nemorosa*	81	-	-	6
C. nemorosa x C. rivularis	112	6	-	1
C. nemorosa x C. pratensis	61	-	-	-
C. pratensis x C. nemorosa	49	1	-	1
C. nemorosa x C. udicola	52	-	-	4

The tetrad stage was most frequently normal (Table 23). However, in some hybrid plants, dyads of apparently unreduced microspored occurred in a variable frequency (Fig. 40). Some polyads were also observed in the studied material (Fig. 41). The observations on the tetrad stage corroborate with the results obtained from investigations on microsporogenesis.



Figs 39-41. Experimental F_1 hybrids: tetrad stage
39. Tetrad.
40. Dyad.
41. Polyad. c.1000 x.

The 18 chromosomic hybrid, born from cross *C. Matthioli* (569) *x C. pratensis*, deserves a special mention. The plant was rather vigorous and flowered earlier than its siblings. The chromosome pairing in its PMCs was rather normal, yet in I anaphase uneven distribution of chromosomes was sometimes observed. As a result, gametes with 8 and 10 chromosomes, respectively, were sometimes formed. In some other PMCs, the anaphase groups comprised 8 and 9 chromosomes whereas a single chromosome was eliminated outside the spindle (Fig. 35). Tetrad stage was observed only in a limited material; normal tetrads were most frequently observed; in addition, a single triad, some dyads and several polyads occurred in the studied sample. The percentage of a good pollen was low (23%).

All flowering hybrid plants were tested for percentage of good pollen. The results are given in Table 24. It should be noted that only a general evaluation is possible, for the number of the obtained hybrids is extremely variable, ranging from a single plant up to 82 individuals. The lowest percentage of a good pollen comported 23%, the highest one 98%. The modal values corresponded to 70 - 90%.

In general, one could estimate the pollen fertility in artificial F_1 hybrids as being rather reduced; however, it should be kept in mind that the diploid taxa of the *Cardamine pratensis* group represent themselves

Table 24. Percentage of good pollen in experimental F_1 hybrids

Cross combination (female parent listed first)	number of plants 20%	30%	40%	50%	60%	70%	80%	90%	100%	Total number of plants
C. granulosa x *C. Matthioli* (561)	-	-	1	-	-	-	-	-		1
C. Matthioli(569) x *C. granulosa*	-	-	3	2	1	1	-	-		7
C. pratensis x *C. granulosa*	-	-	-	1	2	-	-	-		3
C. nemorosa x *C. granulosa*	-	2	-	-	-	-	-	-		2
C. Matthioli(569) x *C. rivularis*	-	1	2	-	-	-	-	-		3
C. Matthioli(569) x *C. pratensis*	1	-	5	-	3	5	19	-		33
C. Matthioli(569) x *C. pratensis*(2n=18)	1	-	-	-	-	-	-	-		1
C. pratensis x *C. Matthioli*(569)	-	-	-	3	2	1	1	-		7
C. pratensis x *C. Matthioli*(561)	-	-	-	1	1	1	3	2		8
C. pratensis x *C. rivularis*	-	-	7	3	3	1	14	1		29
C. rivularis x *C. nemorosa*	-	2	-	1	-	4	27	2		36
C. nemorosa x *C. rivularis*	-	4	5	1	3	47	17	5		82
C. nemorosa x *C. pratensis*	-	-	-	-	-	1	-	-		1
C. pratensis x *C. nemorosa*	-	1	3	3	4	43	16	7		77
C. nemorosa x *C. udicola*	-	-	1	1	1	-	-	-		3

as a notably variable material in this respect, the frequency of a good pollen being sometimes very low. This particular phenomenon seems to be related, at least partly, to an extensive vegetative propagation within the complex. More detailed investigations on this subject are continued.

9.3 Isolation barriers between diploid taxa of the *Cardamine pratensis* group

The factors that are relevant to the isolation of particular diploid taxa may be now summed up.

C. nemorosa and *C. rivularis* seem to keep their genetic affinities rather well. It should be noted, however, that hybridization between these taxa is actually rather impossible for they are separated by definite geographical, ecological and seasonal barriers.

Apparently unilateral crossability found between *C. pratensis* and *C. nemorosa/C. rivularis* seems to represent a factor that notably limits the possibilities for natural hybridization between these taxa. *C. pratensis* comes sometimes into contact with *C. nemorosa* and, in another part of its range, with *C. rivularis*. However, it is possible that some hybrids might be formed solely when *C. pratensis* is the recipient population.

C. Matthioli showed some intercompatibility with *C. pratensis*. However, the two taxa are separated from each other by a wide gap in their geographical distribution: the former one occurs in the Eastern Alps and south of the Alpine ridge, the latter one has its area just north of the Alps. This pattern seems to be rather sufficient for isolation.

Some limited crossability occurred between *C. Matthioli* and *C. granulosa*. These two taxa occur in the same region and were seen flowering at the same time. It appears possible that ecological differentiation might decide about a mutual isolation of these species. On the other hand, seed incompatibility could be an important factor contributing to elimination of some hybrid zygotes.

Crossing behaviour of *C. Matthioli* in relation to *C. rivularis* is apparently conditioned within the studied area by geographical, ecological and seasonal barriers; seed incompatibility seems to be as well a rather important mechanism preventing spontaneous hybridization. Similar patterns appeared in relation between *C. Matthioli* and *C. nemorosa* as well as *C. udicola* and *C. nemorosa*. However, the crossing behaviour of *C. udicola* remains still to be investigated in detail.

It can be concluded that isolation barriers occurring between diploid taxa of the *C. pratensis* group are very variable in their nature and strength. They apparently act in cooperation: the most of diploid taxa remain distinct over their range partly because of differences in geographical distribution, partly because where they occur together their habitats differ and they have different times of flowering. But in some places they meet and flower together; given that the pollen is carried by insect vectors from one species to another, seed incompabitility is likely to represent a further barrier to successful hybridization. This internal mechanism acts at various post-mating stages, not only affecting development of embryo and endosperm, but also seems to influence the strongely reduced potential of germination of the hybrid seeds.

10. Discussion

The results of the present investigations contribute to the knowledge of evolutionary mechanisms that have played rôle in the speciation at homoploid level within the *Cardamine pratensis* group.

Some aspects of the problem i.e. types of variation and isolation barriers should be characterized in a general way. One might say that interpopulational variation within the *C. pratensis* complex is to a large extent camouflaged by the intrapopulational one. Allogamy that is a predominating type of the breeding system in all studied diploid taxa, undoubtebly represents an important factor in the creation of new genotypes. On the other hand, vegetative reproduction, strongly marked within the group of *C. pratensis*, seems to neutralize in some part the effects of selection; this means that the plants which have a characteristic genotype can be preserved in population even if they are sometimes unbalanced.

Isolation barriers occurring within the *C. pratensis* group are strongly diversified. The particular taxa are not separated by a single mechanism, yet by a combination of different ones acting in cooperation. In this way, a joint effect of several incomplete isolation factors may bring about more or less effective separation of the respective species from its congeners.

The spatial isolation is rather pronounced at diploid level within the group of *C. pratensis* and rarely more than two 16chromosomic taxa occur within the same geographical area. Most of them are further separated by ecological and (or) seasonal barriers. The effects of the external barriers are more or less reinforced by internal mechanisms of isolation: in particular, seed incompatibility appearing at various post-mating stages prevents partly or totally the gene exchange between some diploid representatives of the *C. pratensis* group. A similar pattern of isolation was recently observed by GUSTAFSSON (1973, 1973a) within the group of *Atriplex triangularis* from Scandinavia. It should be pointed out that the isolation barriers occurring between diploid taxa of the *C. pratensis* complex are greatly variable as to their strength: some diploids are apparently well-separated from certain representatives of the group, whereas a different combination gives either a slight or a good chance for hybridization. The observations performed in nature are in agreement with the results of interspecific crosses.

It might be assumed that the events of speciation that marked an evolutionary divergence of *C. granulosa*, *C. Matthioli*, *C. nemorosa* and *C. rivularis* must have occurred relatively early in the phylogeny of the group. The present results concerning karyology of these diploids show small yet rather definite differences both in total amount of chromatine as well as in structural arrangement of the chromosomes. Each of these four taxa displays rather a stable set of morphological characters that permit to recognize it without difficulties. It seems probable that morphological and karyological differentiation of this sort might have gradually been achieved in rather a long time.

Cardamine granulosa is rather isolated from other diploids. It represents not only a taxon that is morphologically extreme within the group, but also has the lowest amount of the chromatine. As far as its geographical distribution is concerned, *C. granulosa* occurs within a limited area in western Piedmont, between Turin and eastern foothills of the Cotian Alps, in a few isolated stations. Only a single station of *C. granulosa* was recorded outside this area in the region of Guastalla (Emilia). It is impossible to decide whether the distribution range of *C. granulosa* was originally wider, for no data are available. However, at least part of the original area of *C. granulosa* has been destroyed by construction sites in the surroundings of Turin. This was probably the reason why LÖVKVIST (1956) has been unable to get any living plants for his investigations and wrote: "It is not certain whether this species is still among the living plants in the present flora". In the recent edition of the Flora Europaea, *C. granulosa* is also quoted as "now possibly extinct". In spite of these prognostics, *C. granulosa* has actually been found in two stations and it cannot be excluded that there are some further chances to find this taxon in some other places.

It might be assumed that *C. granulosa* was originally a forest plant growing in rather moist, humic soils; it might later colonize some shadowy meadows that got mown late in summer. Apparently *C. granulosa* does not stand well a competition in normal fertilized meadows, its flowering time being rather late. Natural or nearly natural forests within the Plain of the Po River have practically disappeared at times, being replaced by agricultural fields and the poplar plantations. It seems probable that *C. granulosa* has therefore only a limited opportunity to find a convenient type of station.

Cardamine Matthioli can usually be distinguished from other diploid taxa of the group by its very narrow and rather long siliques. As far as the cytological characters of this taxon are concerned, it stays near *C. granulosa*; however, it seems to be genetically isolated from *C. granulosa, C. rivularis* and *C. nemorosa*. This area of geographical distribution of *C. Matthioli* spreads from Transsylvania to Piedmont. Two races of *C. Matthioli* were found within the investigated area: a/ plants that inhabit fertilized meadows and b/ individuals found in wet sites, rich in nutrients. It should be noted that the stations of *C. Matthioli,* situated south of the Alps appear to be destroyed for the most part. Only local, isolated and fairly small populations were found; it is likely that they are remnants of a formerly wider and more continuous range. It is rather difficult to precise an exact type of station that might have originally been inhabited by *C. Matthioli*. The authors observed it mostly in the habitats remaining under human influence: fertilized meadows, drain ditches, open swamp vegetations in sites rich in nutrients. Only a single population of *C. Matthioli* was found in a poplar forest near Pavia (Lombardy). On the other hand, SOÒ (1968) has reported this taxon from the *Alnion*-forests in Hungary.

It might be assumed that *C. Matthioli* has arrived from the East to the West at post-glacial period and colonized in the first place the *Alnion*-forest, very frequent then and widespread in the Plain of the Po River. An alternative hypothesis might be that *C. Matthioli* migrated westwards later, after the Plain of the Po River has been cleared of forests; the spreading of *C. Matthioli* could be then influenced by human activities. However, it is impossible to decide which of these two interpretations would be correct,for too few data stay at our disposal. The *Alnion*-forest became exceedingly rare in the Plain of the Po River and only very few records of *C. Matthioli* are known from these relictic stations. The chance of surviving of *C. Matthioli* in the Plain of the Po River got still diminished during the last hundred years; meadows that were not replaced by cultivation fields are systematically ploughed and intensively grazed so that the conditions there do not seem suitable anymore for *C. Matthioli*. It seems probable that actual stations of this taxon in the Plain of the Po River are mostly confined to a few wet sites rich in nutrients, such as the localities Nos 568, 569, 570 and 698 found by the present authors (Table 2). The management of the meadows has apparently not been altered, only in the Alpine foothills situated in some marginal parts of the Plain of the Po River; it can be assumed that a frequent occurrence of *C. Matthioli* in fertilized meadows near Pinerolo (western Piedmont) is conditioned by this particular ecological factor.

Human influence apparently played an important rôle in destruction of the habitats in which *C. Matthioli* could have grown previously. On the other hand, it seems probable that *C. Matthioli* might have been eliminated from some of its former stations through competition from recently introduced, white-flowering *Cardaminopsis arenosa* (L.) Hayek. This problem requires further investigations; however, *C. arenosa* that occurs at present frequently in meadows situated south of the Alps, has not been known there in the last century. The data of *C. arenosa* given by COMOLLI in 1847 refer probably to *Cardaminopsis Borbasii* (Zapal.) Hess et Landolt, a taxon that has pink flowers. Still in 1910 CHENEVARD has not reported any stations of *Cardaminopsis arenosa* from Ticino, Actually it is very common in this region. In Valsesia, the authors could not find any *C. Matthioli*, yet *Cardaminopsis arenosa* occurred frequently in the meadows. In Grigna, near Ballabio, notably reduced population of *C. Matthioli* was confined to a wet station, but adjoining meadows were populated by *Cardaminopsis arenosa.*

Cardamine rivularis represents an opposite extreme within the *C. pratensis* group both as to morphological characters as well as to the chromatine content. The results of experimental crosses point to a complete isolation of *C. rivularis* from *C. granulosa* and to rather a pronounced interspecific incompatibility with *C. Matthioli*; on the other hand, numerous reciprocal hybrids, easily obtained from crosses between *C. rivularis* and *C. nemorosa*, suggest a close relationship between these two taxa.

C. rivularis has the widest range of geographical distribution as compared to all other diploid taxa of the group: it spreads from Eastern Carpathians to Western Alps and the Massif Central. The area of *C. rivularis* is particularly discontinous. This might be explained to some extent by ecological requirements of this mountain taxon that grows in wet stations rather poor in nutrients. On the other hand, some gaps in the distribution range of *C. rivularis* are rather obscure: in spite of apparently suitable ecological conditions, it does not occur in SW Alps as well as in some parts of Central and Southern Alps. It remains an open question whether the absence of *C. rivularis* in these regions is due to some particular migration trends, or it is merely incidental. However, it should be mentioned that some of the areas where diploid *C. rivularis* is actually missing, are being inhabited by polyploid types of the *C. pra-*

tensis group (2n=32, 2n=40) that might have proved themselves more efficient competitors.

The stations of *C. rivularis* are situated below potential timberline and distributed within the area that has been covered by the ice sheet during the glaciation period. One might suppose that *C. rivularis* has survived the glaciation in some lowland stations which were not glaciated and its area might still have been continuous at that time. After the retreat of the glaciers, *C. rivularis* might have migrated along the Alpine valleys and has maintained itself in the mountain stations while its lower situated habitats have been destroyed by growing forests. It is also possible that the disappearance of *C. rivularis* in lower stations might have been caused by competition from some other taxa of the *C. pratensis* group which were better adapted to new conditions.

C. rivularis occurs most frequently in the natural stations such as open flat shores of lakes or around creeks where the soil is turfy, base-poor and contains rather a low amount of nitrogen. Only rarely it was found in very slightly manured, humid meadows and pastures i.e. in the stations influenced by human activities.

An interesting detail should be mentioned: among the studied diploid taxa, *C. rivularis* is the only one that manifests a tendency to produce unreduced pollen grains (up to 32%). This particular character has apparently contributed to the formation of the triploid (2n=24)and hexaploid (2n=48) natural hybrids between *C. rivularis* and *C. amara* (URBANSKA-WORYTKIEWICZ and LANDOLT 1972, URBANSKA-WORYTKIEWICZ and LANDOLT unpubl.); it can also be of an evolutionary value for *C. rivularis* itself. Further investigations will be carried out on this interesting problem.

Cardamine nemorosa can be distinguished from *C. rivularis*, *C. Matthioli*, and *C. granulosa* for some of its morphological characters are rather easily recognizable (type if hairs, thickness of the style, large terminal leaflets in basal leaves). The relationship between *C. nemorosa* and *C. rivularis* manifests itself to some extent in a similar chromatine content of the two taxa as well as in their breeding behaviour; it is still more definitely marked in their fairly good crossability. By contrast, *C. nemo-*

rosa is completely isolated from *C. granulosa* and *C. Matthioli*.

The whole area of geographical distribution of *C. nemorosa* is rather difficult to trace. It is notably discontinuous and spreads at least from Niedersachsen to the southern part of the Jura. It can be assumed that *C. nemorosa* might have migrated into the studied area from two opposite directions: it might have arrived to SW Jura from the West whereas northern Jura and its surroundings might become inhabited by plants that arrived from the North. These putative migration paths have apparently stayed off the Black Forest and the Vosges; that would have accounted for the absence of *C. nemorosa* in the middle part of the Jura.

The actual stations of *C. nemorosa* are very local and most frequently isolated from each other. In spite of its apparently relic character, *C. nemorosa* does not seem to be endangered by extinction as it occurs nearly always in rather natural forest stations.

As shown above, various phenomena of *primary speciation* were involved in the evolution of the *C. pratensis* group. We are using this term as proposed recently by GRANT (1971), to include the speciation phenomena involved in primary evolutionary divergence and to exclude the hybrid speciation. However, it seems possible that *re-fusion* has also contributed to the formation of some diploid taxa within the *C. pratensis* complex: *C. udicola* and *C. pratensis* seem to be of a hybrid origin.

C. udicola is of rather an intermediate character within the group of *C. pratensis*. As to the morphology, it stays between *C. Matthioli* and *C. rivularis*, the range of variability being rather wide. The chromosome set of this taxon can be characterized in a general way as approaching that of *C. Matthioli*. On the other hand, ecological preferences of *C. udicola* are very similar to those of *C. rivularis* (wet, poor soils).

The actual geographical distribution of *C. udicola* represents rather an obscure pattern. This taxon occurs very locally in two areas, fairly separated from each other; one of them is situated in northern part of the Alps (surroundings of the Lake of Thun), the other - in southern Ticino. It is interesting to note that the populations of *C. udicola* from northern Alps comprise both the plants with white and pink petals whereas in southern Ticino only white-flowering individuals were found. According to the herbarium data, the former area of diploid *C. udicola* was wider than the actual one: numerous stations were recorded from Ticino, the Swiss Midland, Bavaria, Upper Austria, Tchechoslovakia and southern Poland. At present, diploid *C. udicola* seems to be on a verge of extinction due to human interference (draining of the reed-meadows, construction sites on the lake shores, pollution); it should be added that in numerous stations the diploids have apparently been replaced by plants representing various polyploid levels.

Only a limited material of *C.udicola* was used in the experimental crosses the present paper is dealing with. Solely the plants from Ticino were investigated; it should be pointed out that they fall outside the normal scheme of crossability. The seed setting after selfings appeared to be normal. In spite of rather a good seed output, *C. udicola* from Ticino was seed-sterile: no germination whatsoever has been observed either in selfings, or in cross-experiments of any kind. The only three hybrid plants were obtained from crosses with *C. nemorosa* where *C. udicola* has been used as male parent. It is impossible to say at present which factor has influenced an apparent seed sterility occurring in the plants described above. Only a few individuals of *C. udicola* from Ticino were investigated, so the phenomenon might be merely incidental. Further investigations are required on this subject.

Only general conclusions concerning the origin of *C. udicola* can be presented, for the study on this taxon has not yet been completed. One can assume that *C. udicola* might have arisen either through a racial differentiation from *C. Matthioli* or through hybridization between *C. Matthioli* and *C. rivularis*.

It cannot be excluded that *C. udicola* represents a specialised, isolated race of *C. Matthioli* that got stabilized through genetic drift; the cytological characters of *C. udicola* would rather support this assumption. On the other hand, the seed sterility observed in crosses between *C. udicola* and *C. Matthioli* point to rather an accentuated incompatibility between the two taxa. *C. udicola* does not fit so well within the range of morphological variation of *C. Matthioli*. Intermediate morphological and ecological characters of *C. udicola* seem to be in favour of its putative hybrid origin. This taxon might have arisen from crosses between *C. Matthioli* and *C. rivularis*; it is possible that these taxa were wider distributed at the post-glacial time and they could incidentally get into contact with each other through a random migration. It should be noted, however, that a possibility of a successful hybridization between *C. Matthioli* and *C. rivularis* is actually very difficult to verify as both taxa show a mutual incompatibility, at least in the experimental conditions. Further investigations, including *C. Matthioli* and *C. rivularis* from various parts of their distribution range, would be advisable.

Cardamine pratensis is of rather intermediate character within the studied group. Its origin could be alternatively explained in two ways: 1/ through a racial differentiation or 2/ through hybridization.

It might be assumed that *C. pratensis* has originally derived, through a racial differentiation from an ancient stock that has also given rise to *C. nemorosa*; only later it might have acquired genes from *C. rivularis* or, perhaps, from *C. udicola* and its competitive abilities became improved in this way. Morphological and cytological charaters of *C. pratensis* do not exclude such a hypothesis. However, a limited, apparently unilateral intercompatibility of *C. pratensis* and *C. nemorosa* as well as the data concerning geographical distribution of *C. pratensis* and its particular vigour, are rather in favour of its hybrid origin.

C. pratensis presents a somewhat complicated problem as far as one of its putative parent form is concerned. The relationship between this taxon and *C. nemorosa* is clearly evident; on the other hand , it is a little difficult to decide about the other parent.

Most likely, *C. pratensis* could be placed as an intermediate taxon between *C. rivularis* and *C. nemorosa*. The latter taxon apparently has more influence upon the characters of *C. pratensis*; this affinity appears not only in morphology but also in structural differentiation of the chromosome set. As to its ecology, *C. pratensis* occurs in stations that are intermediate between those of *C. nemorosa* and *C. rivularis*, the altitude zone and type of soil resembling rather *C. nemorosa*, yet the type of vegetation (meadows and pastures) showing more affinities with *C. rivularis*.

As far as the geographical distribution is concerned, *C. pratensis* is the only diploid taxon within the group which has a well-defined and rather a compact area; it stays between discontinuous areas of *C. nemorosa* and those of *C. rivularis*. In some regions *C. pratensis* comes into contact with *C. nemorosa* and was observed flowering simultaneously with the latter taxon. Only exceptionally was *C. pratensis* entering the area inhabited by *C. rivularis*, but then flowering time of these two taxa overlapped, at least partly.

The results of interspecific crosses bring an interesting information about the fertility relationships occurring between *C. nemorosa*, *C. rivularis* and *C. pratensis*. In spite of their geographical, ecological and seasonal isolation, *C. nemorosa* and *C. rivularis* appear to be intercompatible and rather easily produce reciprocal hybrids in experimental conditions. On the other hand, *C. pratensis* shows certain compatibility with *C. nemorosa* and *C. rivularis*, but solely when these two taxa are used as male parents. An opposite cross-direction revealed a pronounced seed-incompatibility that manifested itself mostly in very low percentage of germinating seeds.

It could be assumed that *C. pratensis* has arisen from spontaneous crosses between *C. nemorosa* and *C. rivularis*, at times when these two taxa were still in contact; subsequently, repeated backcrosses with *C. nemorosa* might have affected both visible traits and structural arrangement of the chromosomes of *C. pratensis*. Similar cases were reported by GRANT and GRANT (1960) in *Gilia cana* and *G. ochroleuca vivida*, both representing diploid taxa within the sect. *Arachnoides* of the genus *Gilia*.

The pattern of the geographical distribution of *C. nemorosa* does not permit to postulate that this taxon might have formerly occurred in the Alps. More probable would be the assumption that *C. rivularis* has maintained itself for a longer time at the post-glacial period in some suitable stations north of the Alps. e.g. in the region between the Lake of Constance and the valley of the Danube. Such distribution might have given an opportunity for some crosses between *C. nemorosa* and *C. rivularis*.

The results of experimental crosses as well as the observations on meiosis in F_1 hybrids represent the arguments in favour of the opinion that

C. rivularis was the second parent of *C. pratensis*. On the other hand, morphological, ecological and geographical data do not exclude a possibility that *C. udicola* might have been an alternative ancestor for this taxon. The herbarium data point to a rather wide original distribution of *C. udicola;* northern part of its former range (Bavaria) overlaps partly the actual area of *C. pratensis*. Furthermore, *C. udicola* is a lowland taxon; its incidental contact with *C. nemorosa* might have resulted in a hybridization between these two taxa. We must emphasize, however, that exact relationships between *C. udicola* and other diploid taxa of the *C. pratensis* group have not yet been sufficiently verified and further experiments are being continued.

C. pratensis has not only a distinct and continuous area of distribution but also occurs very frequently within its stations and apparently is well-adapted to the environmental conditions occurring there. This particular vigour stays rather in a sharp contrast with *C. nemorosa* and *C. rivularis* which appear to be in defensive. The differences in vigour occuring between *C. pratensis* and *C. udicola* are still more conspicuous.

Environmental isolation operates to suppress hybridization between intercompatible species in a stable, closed community; hybrid zygotes formed from time to time are eliminated by stabilizing selection almost as soon as they arise. By contrast, if natural community has been broken and new open habitats are accessible, the hybrids can and do become established because interspecific competition and stabilizing selection are more or less inefficient at that moment. This explanation of a correlation occurring between hybridization and habitat disturbance is an extension of the hypothesis of KERNER (1891) stressed by numerous authors (e.g. STEBBINS 1950, 1959, 1969, 1971, GRANT 1963, 1971, GILLETT 1966, 1972, KRUCKEBERG 1969, LEWIN 1970).

It seems probable that the creation and stabilization of the diploid *C. pratensis* might be primarily due to a human influence; new habitats could serve as breeding grounds for a new-born hybrid. The pattern of geographical and ecological distribution of *C. pratensis* studied in the course of the present work, supports this opinion. As pointed out by ANDERSON (1948, 1949), the environmental control carries beyond the F_1

to the second and later hybrid generations. ANDERSON emphasized that the first hybrid generation is more or less intermediate and rather uniform in its ecological preferences; however, in later generations a great diversity of recombination types appear and they might manifest various physiological traits. Accordingly, they would require numerous ecological niches. Introgression would further complicate the differentiation pattern of the hybrids. ANDERSON concluded that an intermediate habitat would enable the F_1 generation to survive but a varied number of ecological niches i.e. "hybridization of the habitat" must exist if any significant amount of F_2 generation is to get established (ANDERSON 1948). Such hybridized habitats are actually produced mainly under human influence. As shown above, *C. pratensis* occurs in preference within fertilized meadows that are cut or grazed; sometimes, it can also be found in forest roads or at the borders of forests. It seems possible that establishment of this hybridogene taxon might coincide with intensive development of live stock-farming.

Characteristic types of geographical distribution of *C. pratensis* might be partly due to some edaphic factors: moraine soils of the glacier of the Rhine are less differentiated and accordingly base-richer than those of non-glaciated areas NW of the Schwäbische Jura. On the other hand, limestone soils in the Jura itself seem to be rather too dry for *C. pratensis*. It should be added that a competition from polyploid taxa of the *C. pratensis* group might confine the diploid to its actual area.

One of the factors limiting the present discussion is the not yet sufficiently known relationship occuring between the diploid taxa of the *C. pratensis* group and higher polyploids of this complex. Another important problem constitutes a balance between sexual reproduction and vegetative propagation in *C. pratensis* s.l. The outbreeding, strongly marked within the group, provides undoubtedly some flexibility,i.e. high rate of variation output to be tested by selection;on the other hand, vegetative propagation may assure certain stability,i.e. gives possibilities for fixation and multiplication of successful biotypes. As far as the diploid *C. pratensis* is concerned, the potential propagation may be of adaptive value in prevailing biotope for this species: the production of small daughter plants that easily root, is apparently an effective mode of reproduction, especially in cut or grazed meadows where the plants may have considerably less chance to set seeds. A special attention is to be given to these problems in the further course of our investigations.

Summary

Six diploid taxa of the *Cardamine pratensis group* from Central Europe *(C. granulosa, C. Matthioli, C. udicola, C. rivularis, C. pratensis s. str., C. nemorosa)* are rather closely related. They are partly sympatric and to some extent differentiated in their ecological requirements. A great deal of morphological variation was found; interpopulational variation seems to be camouflaged by intrapopulational one. Allogamy that proved to be a predominating type of breeding system, plays apparently an important rôle in creation of new genotypes; however, its influence is partly counterbalanced by an intensive vegetative propagation: numerous small daughter plants that easily root are produced on leaves and stems.

Cytological variation found within the diploid taxa of the *C. pratensis* group represents diverse aspects. At least three phenomena viz. local migrations, gene flow, and aneusomy contributed to the formation of mixed populations. It seems probable that the populations inhabiting the center of the distribution area of given taxon are subject to the selection pressures which are different from those occurring within the marginal populations.

Isolation barriers that separate the studied diploid taxa are strongly diversified in their nature and strength. The external barriers are more or less reinforced by internal mechanisms of isolation; in particular, seed incompatibility appearing at various post-mating stages prevents partly or totally the gene exchange between some diploid taxa.

Evolution on diploid level within *C. pratensis* s.l. has apparently been influenced by various phenomena of primary speciation that have occurred relatively early in the phylogeny of the group. On the other hand, re-fusion was likely to contribute as well to the formation of some diploid taxa.

Human activities have notably influenced the pattern of geographical distribution of numerous diploids; in former times, creation of new biotopes such as reed-meadows and fertilized meadows apparently has promoted a wider spreading of some taxa *(C. Matthioli, C. udicola, C. pratensis* s. str.*)*. It seems probable that diploid *C. pratensis* s. str. the taxon of a putative hybrid origin, might have got established only after development of more intensive stock-farming. Recent human influence, however, being most frequently of a destructive effect, results in a rather advanced extinction of some diploid taxa within the studied area. *(C. granulosa, C. Matthioli, C. udicola)*.

Résumé

Six taxons diploïdes du group de *Cardamine pratensis* que l'on rencontre en Europe centrale (*C. granulosa, C. Matthioli, C. udicola, C. rivularis, C. pratensis* s. str. *C. nemorosa)* sont liés par une parenté plutôt étroite. Ils se montrent en partie sympatriques et assez différenciés par rapport à leurs préférences écologiques. La variation morphologique des taxons étudiés est bien prononcée; la variation à l'intérieur des populations paraît camouflager, dans une certaine mesure, celle qui sépare les populations d'un taxon donné. L'allogamie qui est le système reproducteur prédominant chez *C. pratensis* s.l. joue vraisemblablement un rôle important dans la création des génotypes nouveaux; toutefois, son influence est partiellement compensée par la propagation végétative très forte.

La variation cytologique trouvée chez les taxons diploïdes présente des aspects divers. Au moins trois phénomènes : des migrations locales, l'échange des gènes entre les populations voisines ("gene flow") et l'aneusomie, ont contribué à la formation des populations mixtes. Il est probable que les populations vivant au centre de l'aire géographique d'un taxon donné soient soumises à des forces sélectives différentes par rapport à celles qui agissent à l'intérieur des populations marginales.

Les mécanismes d'isolement qui séparent les taxa diploïdes sont fort diversifiés en leur nature et force. L'isolement externe est renforcé par des barrières internes dont la plus significante est l'inviabilité des hybrides ("seed incompatibility"). En se manifestant à divers stades de dévelopement après la fécondation, elle empêche totalement ou presque l'échange des gènes entre certains taxons diploïdes.

L'évolution au niveau diploïde du groupe de *C. pratensis* avait été apparément marquée par des phénomènes variés de apéciation primaire qui ont dû se présenter assez tôt dans la phylogénie de ce groupe. Il est fort probable que la ré-fusion ait également contribué à la formation de certains taxons diploides.

L'intervention humaine a fortement influencé la distribution géographique de nombreux taxons diploïdes; autrefois, la création des biotopes nouveaux (prairies marécageuses, prairies fertilisées) avait apparément promû la répartition assez vaste de plusieurs taxons (*C.Matthioli, C. udicola, C. pratensis* s.str.). Il semble bien que *C. pratensis* s.str. diploïde, plante des prairies de fauche et des pâturages fertilisés dont le origine est fort probablement hybridogène, n'ait pu s'établir qu'à la suite du dévelopement d'un élevage intensif. Toutefois, l'influence humaine récente, étant le plus fréquemment à effet destructif, aboutit à l'extinction bien avancée de certains taxons diploïdes sur le territoire étudié.*(C. granulosa, C. Matthioli, C. udicola).*

Zusammenfassung

Sechs diploide Sippen der Artengruppe der *Cardamine pratensis* aus Zentraleuropa (*C. granulosa, C. Matthioli, C. udicola, C. rivularis, C. pratensis* s.str., *C. nemorosa)* wurden zytotaxonomisch untersucht und Kreuzungexperimente durchgeführt. Die Sippen sind nahe miteinander verwandt, überdecken sich teilweise in ihrer geographischen Verbreitung und zeigen bis zu einem gewissen Grad unterschiedliche ökologische Ansprüche. Die morphologische Variationsbreite der einzelnen Sippen erwies sich recht gross.

Die Variation zwischen den Populationen wird weitgehend überdeckt von der Variation innerhalb der Populationen. Im Fortpflanzungssystem herrscht Fremdbestäubung (Allogamie) vor und scheint eine wichtige Rolle bei der Entstehung neuer Genotypen zu spielen; auf der anderen Seite ist die vegetative Vermehrung durch Sprossung aus Blättern und Stengeln sehr intensiv.

Zytologisch variieren die diploide Sippen von *C. pratensis* s.l. in verschiedener Hinsicht. Zumindest drei Vorgänge tragen zur Bildung von gemischten Populationen bei: lokale Wanderung, Gen-Fluss und Aneusomie. Es ist wahrscheinlich, dass Populationen im Zentrum ihres Sippenareals einem anderen Selektionsdruck ausgesetzt sind als randständige Populationen.

Die Isolationsmechanismen zwischen den einzelnen Sippen sind sehr unterschiedlicher Natur und Wirksamkeit. Externe Isolationsmechanismen werden durch interne verstärkt:, besonders Sameninkompatibilität in verschiedenen Stadien nach der Befruchtung verhindert teilweise oder völlig den Gen-Austausch zwischen einzelnen diploiden Sippen.

Die Evolution auf der diploiden Stufe von *C. pratensis* s.l. wurde offenbar von verschiedenen Vorgängen der primären Artdifferenzierung beeinflusst, welche in der Phylogenie der Artengruppe relativ früh auftraten. Auf der anderen Seite trug wahrscheinlich auch die Bastardierung zur Neubildung von diploiden Sippen bei.

Die Tätigkeit des Menschen hat die geographische Verbreitung der meisten diploiden Sippen deutlich beeinflusst. Früher hat der Mensch durch Neuschaffung von Biotopen (Sumpfwiesen, Fettwiesen) verschiedenen Sippen eine Ausbreitung ermöglicht (besonders *C. Matthioli, C. udicola, C. pratensis s.str.*). Die diploide *C. pratensis s.str.* konnte sich wahrscheinlich überhaupt erst nach Einführung der intensiven Viehwirtschaft entwickeln; ihre Entstehung dürfte hybridogen sein. In letzter Zeit hat jedoch der Mensch viele notwendige Biotope zerstört; deswegen sind im Untersuchungsgebiet einige diploide Sippen vom Aussterben bedroht (*C. granulosa, C. Matthioli, C. udicola*).

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