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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 scars 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 therefore 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 pinna-sect 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 occurred 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.

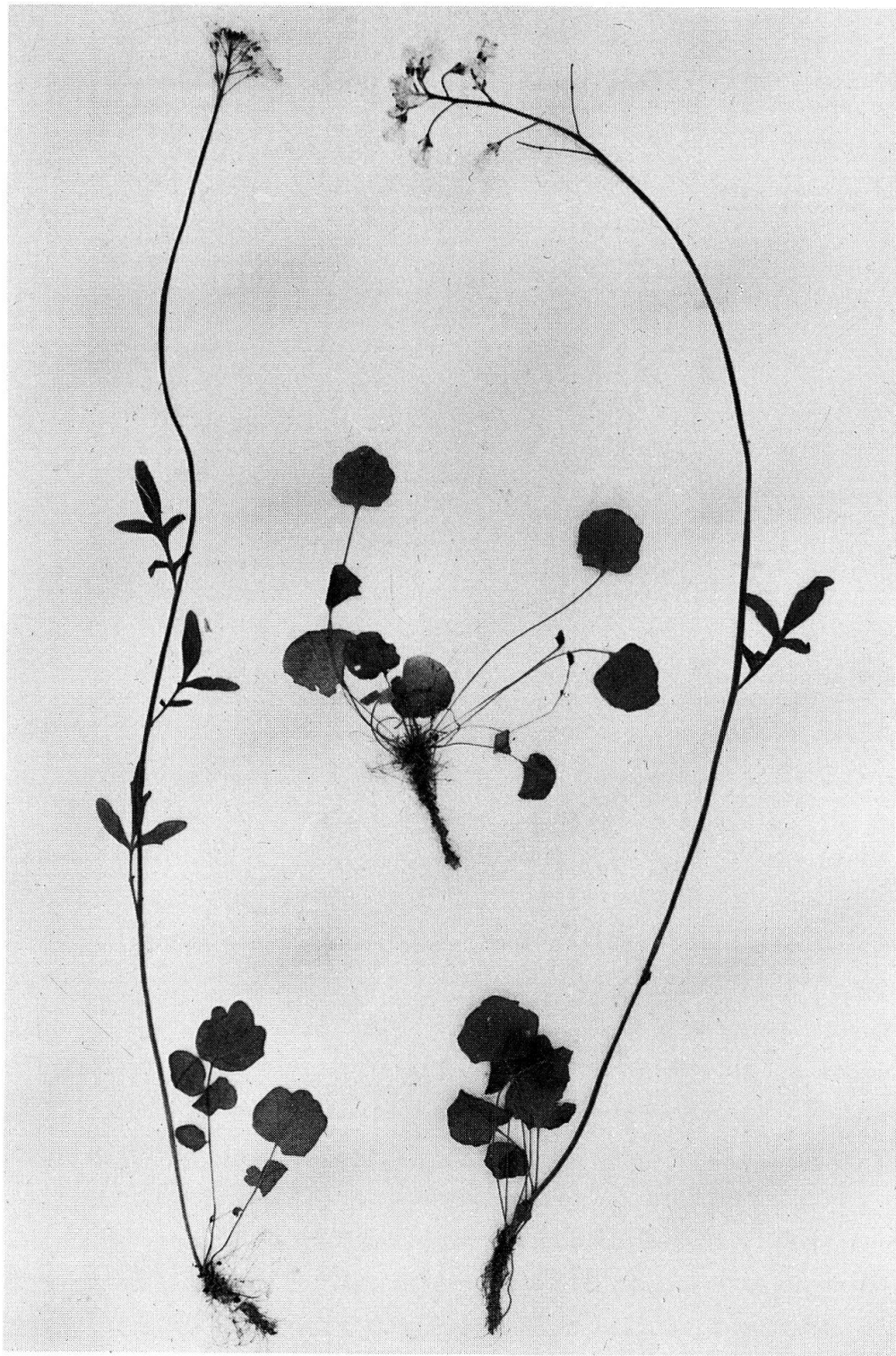


Fig. 1. *Cardamine granulosa* (560) from Avigliana, Piedmont. 1/3 natural size.



*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  $3/4 - 1\frac{1}{2}$  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  $2/3 - 1\frac{1}{4}$  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. Inflorescence 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.*

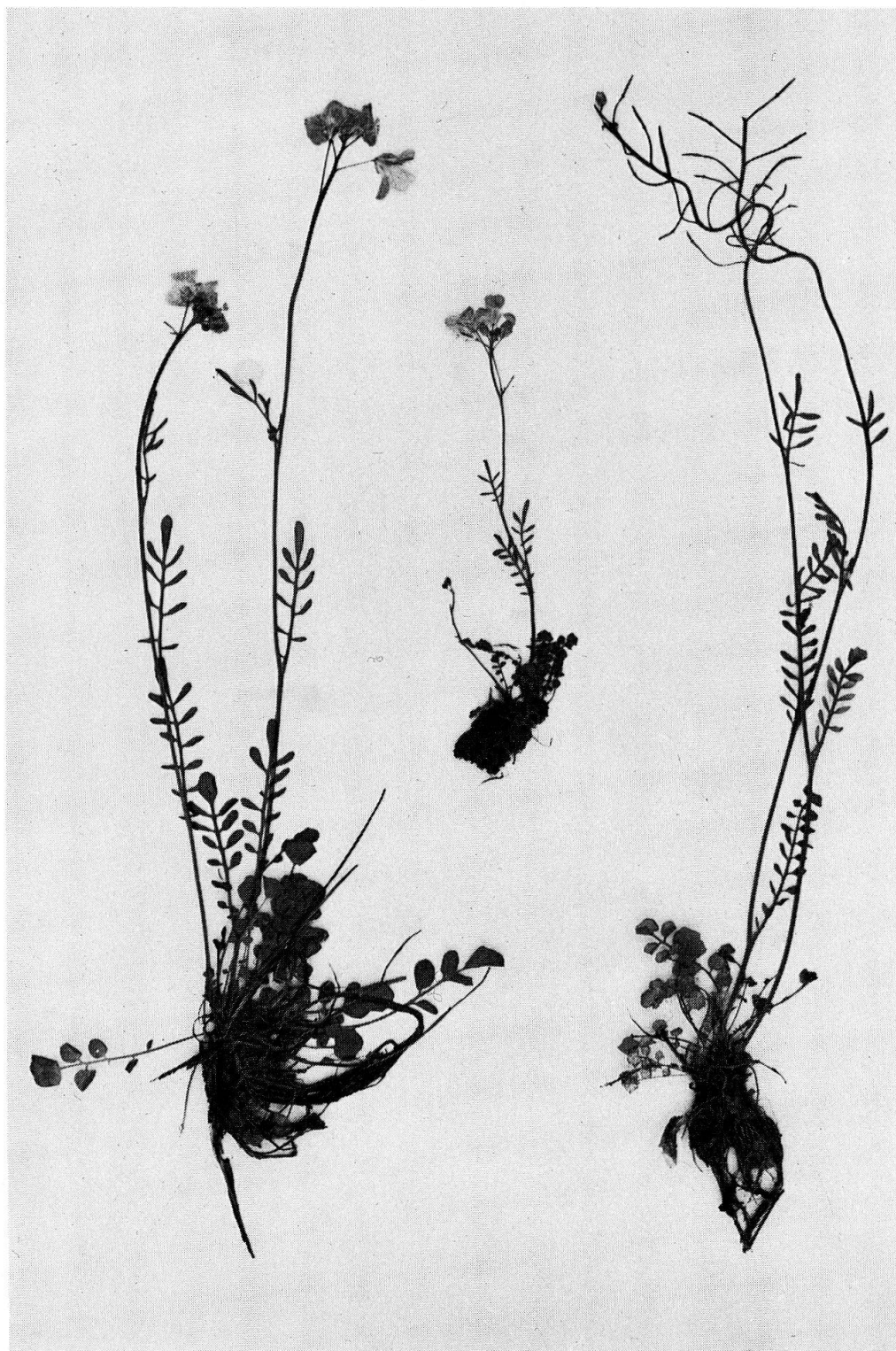


Fig. 3. *Cardamine rivularis* (33) from Valbella (Graubünden). 1/3 natural size.



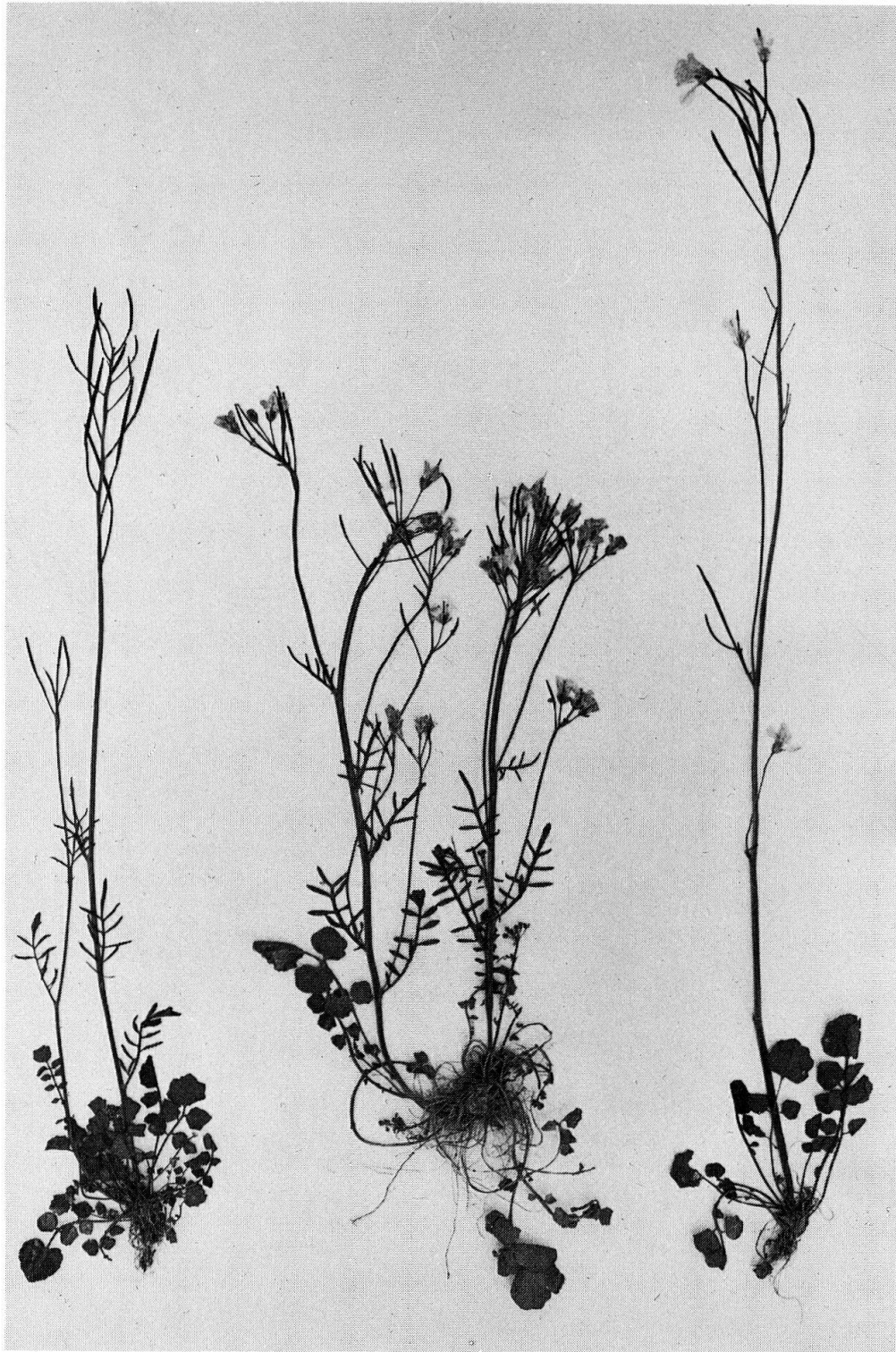


Fig. 4. *Cardamine pratensis* (38) from Gams (St. Gallen). 1/3 natural size.



Fig. 5. *Cardamine nemorosa* (65) from Les Près-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 tinged

##### *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  $\frac{3}{4}$  -  $1\frac{1}{4}$  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  $\frac{1}{4}$  -  $\frac{3}{4}$  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*