An autoallohexaploid in *Cardamine* L., new to the Swiss flora

by

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Natural hybridization between *Cardamine rivularis* Schur and. *C. amara* L. is very rare. In 1971, two hybrid stations were found in Switzerland: the locality from Engadine contained a very localized hybrid representing a direct product of the cross between the diploid *Cardamine rivularis* (2n=16) and the tetraploid *C. amara* (2n=32). On the contrary, the station from Urnerboden (Central Switzerland) proved to be very unusual: a large population consisted of triploid hybrids born from the diploid parents numerically inferior to their 24chromosomic offspring in spite of the fact that the hybrids most frequently were male-sterile (URBANSKA-WORYTKIEWICZ and LANDOLT 1972, 1977).

Further investigations on the triploid hybrids from Urnerboden revealed their apparently stabilized genomic constitution RRA, 16 chromosomes of *C. rivularis* and only eight of *C. amara* invariably occurring in all studied plants.A strong vegetative multiplication and a sexual reproduction characterized by an exceedingly reduced recombination potential added up to an efficient system in which plants were able to profit from maximum hybrid vigour (URBANSKA-WORYTKIEWICZ 1976, 1977).

As it turned out, the evolution of hybrids in Urnerboden was still progressing: in 1974, fertile autoallohexaploids (2n=48, RRRRAA) were found within a sector of the population (URBANSKA-WORYTKIEWICZ and LANDOLT 1974). A survey of their expansion is continued. The present paper deals with fertility relationships between the autoallohexaploids and their original parent species i. e. *C. rivularis* and *C. amara* as well as genetical affinities between hexaploids and triploids, preceded by a taxonomical treatment of

both hybridogenous types.

Acknowledgements

CARDAMINE X INSUETA* hybr. novum

Planta perennis, stolonifera. Caules 1-4(5), 28(29) cm attingentes, erecti, 3-5 folia ferentes, pilis rarioribus, in parte inferiori saepe suffuse violacei, multiflori. Folia rosulantia ascendentiora, 3-9-foliata, 4-5cm longa, in inferiore pagina saepe suffuse violacea, petiolo interdum rare hirto pilis 0.3-0.5 mm longis, in pagina superiore per maturitatem numerosas propagulas saepe ferentia; foliolum terminale rotundato-reniforme, inconspicue 3(vel 5)-angulatum angulis mucronulatis, plerumque saltem duplo majus quam foliolum laterale proximum; foliola lateralia ovata, interdum inconspicue triangulata. Folia caulina 3-5, pinnata, 2.2-3.5(4) cm longa, interdum 6.5 (7) cm attingentia, pilos rarissimos brevesque exhibentia plerumque in axillis propagulas ferentia; folia caulina inferiora foliolo terminali munita cuneiformi apicem trilobatum exhibenti, 9-11mm longo, foliolis lateralibus lanceolatis vel obovatis; folium vel folia ambo altissima foliolis linearibus vel anguste lanceolatis praedita, 20 mm in longitudine et 7-14 mm in latitudine attingentia. Inflorescentia racemosa, (8)9-22 flora cum interdum 1-2 inflorescentiis lateralibus 4-5-floribus. Sepala elliptica vel obovata, circa 3 mm longa et 1.5-1.7 mm lata, marginibus scariosis, raro apicem versus violacei-tincti. Petala plerumque 6-8(9) mm longa, 3-4(5.5) mm lata, pallide lilacea. Antherae plerumque indehiscentes, 1-1.2 mm longae, in ambabus paginis ± uniformiter vel striatim profunde

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* from: *insuetus* = unusual

purpurea.Pistillum 0.5 mm crassum, stigmatibus plerumque distinctissimis. Siliqua 1.2-3.5 cm longa, 0.8-1.3 mm lata, 9-32 ovula continens. Semina infrequentia, 0.0-1.6 mm longa.

2n=24, planta triploidea.

Perennial, stoloniferous. Stem 1-4(5), up to 28(29) cm tall, erect, 3-5-leaved, sparsely hairy, at the base often tinged with anthocyan, multi-flowered. Rosette leaves slightly ascending, 3-9-foliolate, 4-5 cm long, often violet-green at the lower surface, petiole sometimes hairy (hairs 0.3-0.5 mm long); at post-flowering stages numerous daughter plants often develop at the upper surface; terminal leaflet reniform at the base, slightly angled, 3(5)-mucronulate, usually at least twice as large as the nearest lateral leaflet; lateral leaflets ovate or slightly angled with 3 tiny mucrons. Cauline leaves 3-5, pinnate, 2.2-3.5(4)cm long, sometimes attaining 6.5(7) cm, very sparsely hairy; axils of cauline leaves frequently with small complete daughter plants; lower cauline leaves most frequently with trilobate terminal leaflet 9-11 mm long, their lateral leaflets lanceolate or obovate; one or two uppermost cauline leaves with all leaflets linear or narrowly lanceolate, up to 20 mm long and 7-14 mm broad. Inflorescence racemose, 8(9)-22-flowered, 1-2 lateral inflorescences 4-5-flowered sometimes present. Sepals elliptic or obovate, about 3 mm long and 1.5-1.7 mm broad, with scarious margins, rarely with traces of anthocyan at the uppermost part. Petals most frequently 6-8(9)mm long, 3-4.5(5.5) mm broad, pale-lilac. Anthers usually non-dehiscent, 1-1.2 mm long, more or less uniformly dark purple or with purple streaks on both sides. Pistil 0.5 mm thick, stigma usually distinct. Siliques 1.2-3.5 cm long, 0.8-1.3 mm broad, with 9-32 ovules. Seeds rare, 0.9-1.6 mm long.

2n=24, plant triploid.

Holotype: Switzerland, canton Uri, Urnerboden, 1400 m. a.s.l., very abundant in manured hay meadows, less frequent in open pastures. 6th July 1974, K. URBANSKA-WORYTKIEWICZ (ZT).

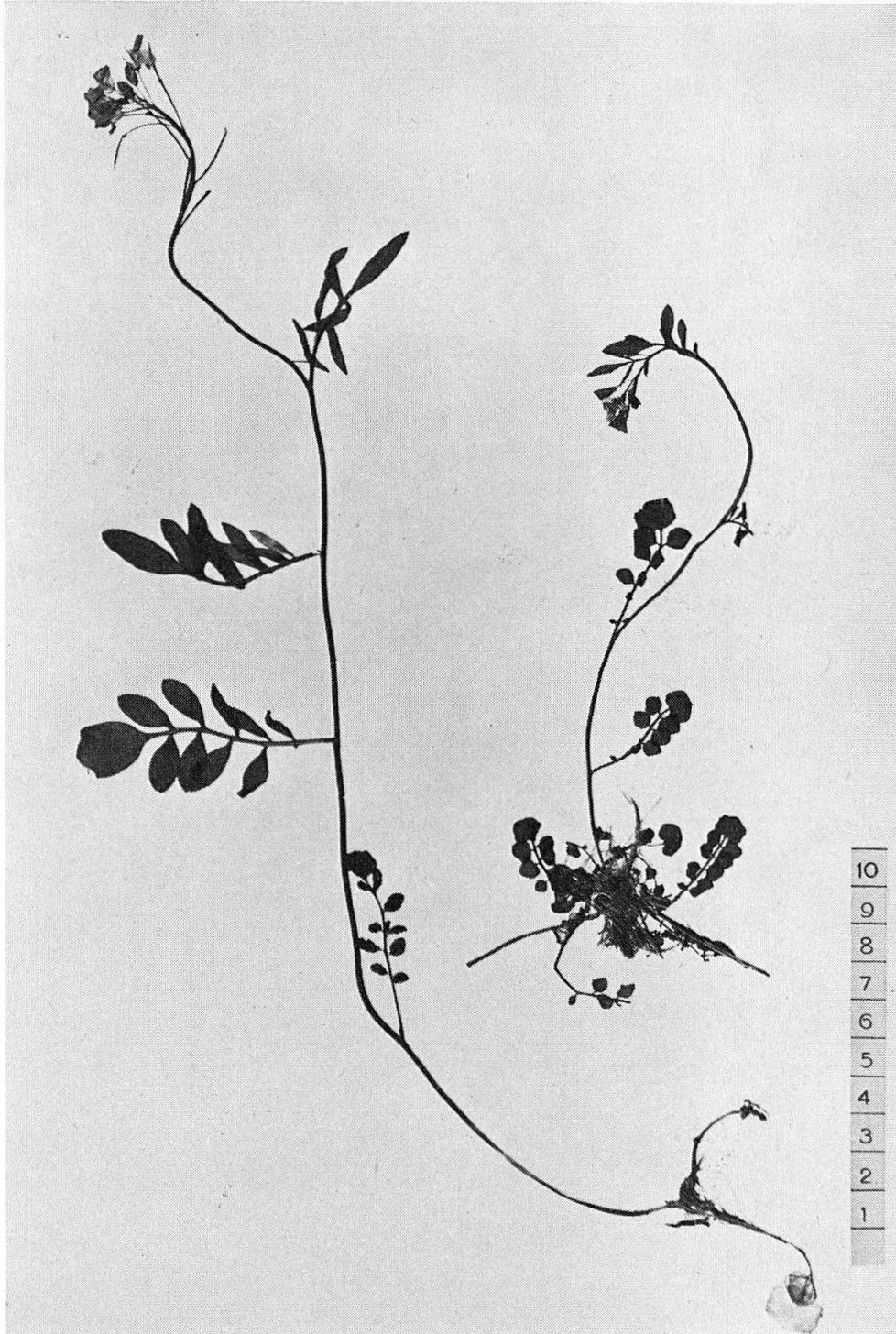Fig. 1. *Cardamine insueta*: Plants from open pastures.

Fig. 2. *Cardamine insueta:* plants from manured hay meadows.

Remarks on variation. Variation mostly quantitative: size of plants, size of cauline leaves, sometimes size of flowers. A slight variation in colour intensity of petals and anthers was observed. Plants producing viable pollen in a proportion higher than 3-4% were rare, predominating type being sterile with non-dehiscent anthers.

CARDAMINE SCHULZII * spec. nova

Planta perennis, rhizomate stolonifero. Caules 1-3, 35(38) cm attingentes, erecti, fere glabri, 3-5 folia ferentes, multiflori. Folia rosulantia prostrata vel ascendentiora, 5-11(13)-foliolata, 4-8 cm longa, petioli basin versus et in marginibus pilos raros exhibentia; foliolum terminale rotundato-reniforme, inconspicue 5-8-angulatum angulis mucronulatis, foliolum laterale proximum magnitudine circa aequans, interdum plus quam duplo majus; foliola lateralia plerumque 3-5-dentata, basin folii versus gradatim minora. Folia caulina 3-6, pinnata, (2)3.5-5(6) cm longa, pilos rarissimos circa 0.2-0.3 mm longos exhibentia, raro in axillis propagulas ferentia; folium vel folia infima ambo foliolis terminalibus trilobatis, circa 12 mm longis, foliolis lateralibus lanceolatis vel linearibus, interdum obovatis; folia superiora plerumque foliolis omnibus linearibus anguste lanceolatis munita 10-15(20) mm longa, 6 mm in latitudine attingentia. Inflorescentia racemosa simplex vel composita, inflorescentia principalis 8-15(18)-flora; laterales plerumque 1-4 , cum 2-4(5) floribus. Sepala elliptica vel obovata, cum marginibus scariosis, 4.5 mm longa, in latitudine 2(3) mm attingentia, interdum apicem versus violaceitincti. Petala 10(12)-17(19) mm longa, (5.5)6-7 mm lata, violacea, in herbario colorem amethystinam accipienta. Antherae plerumque dehiscentes, 1.6-3 mm longae, flavae cum conspicua macula violacea in pagina exteriore. Pistillum 0.6 mm crassum, interdum violaceitinctum, stigmate distincto interdum violacei suffuso. Silique 2.5-3.5 cm longa, 1.3 -1.8 mm lata, 16-34 ovula continens. Semina 0.9-1.6 mm longa.

2n=48, planta hexaploidea.

* O.E. SCHULZ, the monographer of the genus *Cardamine* (1903)

Perennial, with stoloniferous rhizome. Stem 1-3, up to 35(38) cm tall, erect, nearly glabrous, 3-5-leaved, multiflowered. Rosette leaves prostrate or slightly ascending, 5-11(13)-foliolate, 4-8 cm long, sparsely hairy at the base of the petiole and at the margins of leaflets;terminal leaflet reniform at the base, slightly angled, 5-8-mucronulate, usually subequal or equal in size to the uppermost lateral leaflet, but sometimes more than twice as large; lateral leaflets usually 3-5-dentate, diminishing slightly in size towards the base of the petiole. Cauline leaves 3-6, pinnate, (2)3.5-5(6) cm long, very sparsely hairy (hairs about 0.2-0.3 mm long), axils of cauline leaves rarely with small complete daughter plants; most frequently only one or two lowest cauline leaves with tri-lobed terminal leaflets about 12 mm long, lateral leaflets lanceolate or linear, frequently also obovate; other cauline leaves usually with all leaflets linear or narrowly lanceolate 10-15(20) mm long, up to 6 mm broad. Inflorescence racemose simple or compound, main inflorescence 8-15(18)-flowered, the lateral ones most frequently 1-4 with 2-4(5) flowers. Sepals elliptic or obovate with scarious margins, 4.5 mm long, up to 2(3) mm broad, sometimes with traces of anthocyan at the uppermost part. Petals (10)12-17(19) mm long, (5.5)6-7 mm broad, violet, turning amethyst in herbarium specimens. Anthers usually well-developed, dehiscent, 1.6-3 mm long, yellow with a distinct violet spot at the outer side. Pistil 0.6 mm thick, sometimes tinged with anthocyan, stigma distinct. Siliques 2.5-3.5 cm long, 1.3-1.8 mm broad, with 16-34 ovules. Seeds 0.9-1.6 mm long.

$2n=48$, plant hexaploid.

Holotype: Switzerland, canton Uri, Urnerboden, 1400 m m. a.s.1, in moist pastures and drainage canals. 6th July 1974. K. URBANSKA-WORYTKIEWICZ (ZT).

Remarks on variation: In general, rather a moderate variation was found, above all in some quantitative characters (size of plants, number of flowers). A slight variation was noted in the intensity of the violet colour in the anthers' spots. C. SCHULZII manifests a variable pollen fertility (Fig. 9).
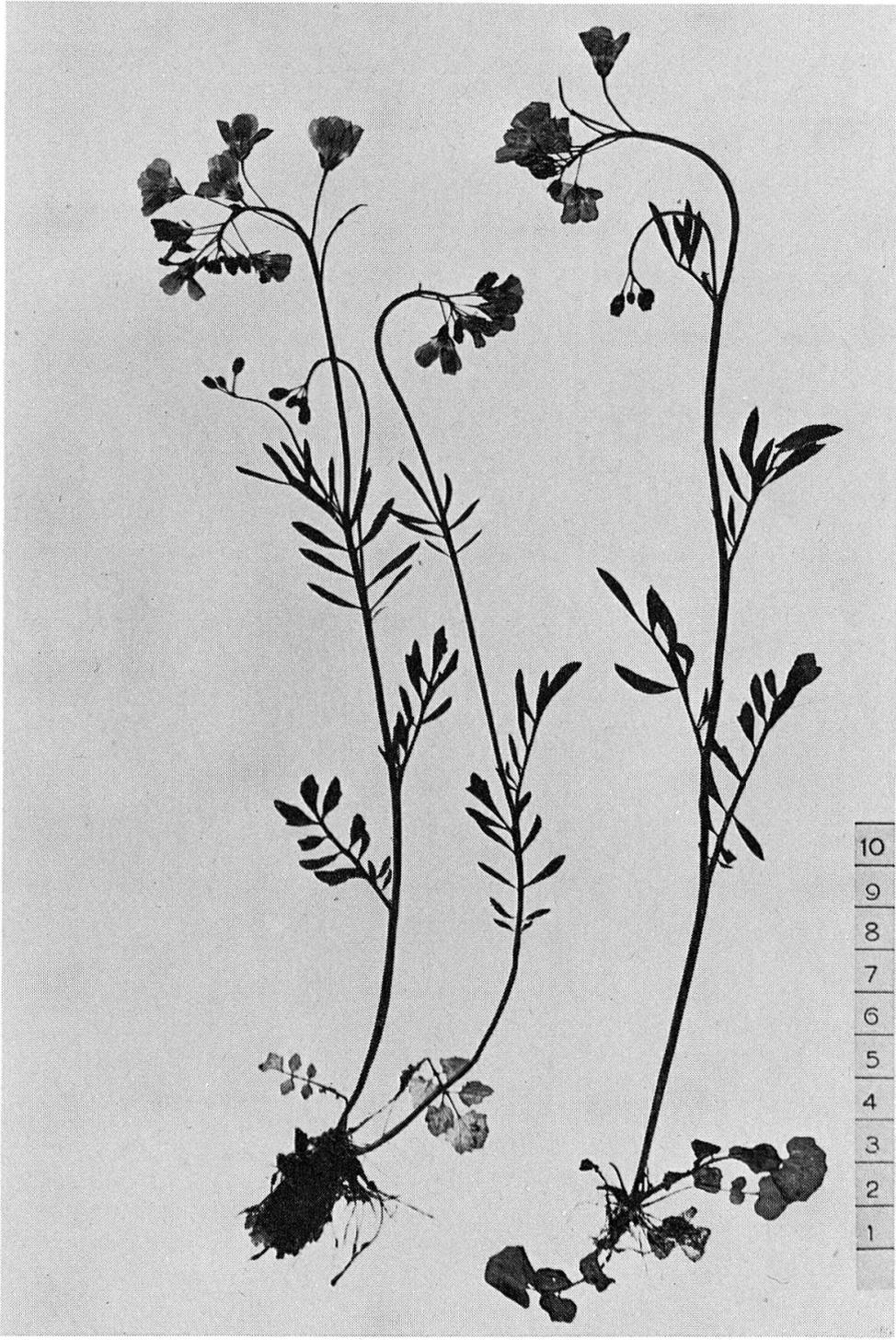
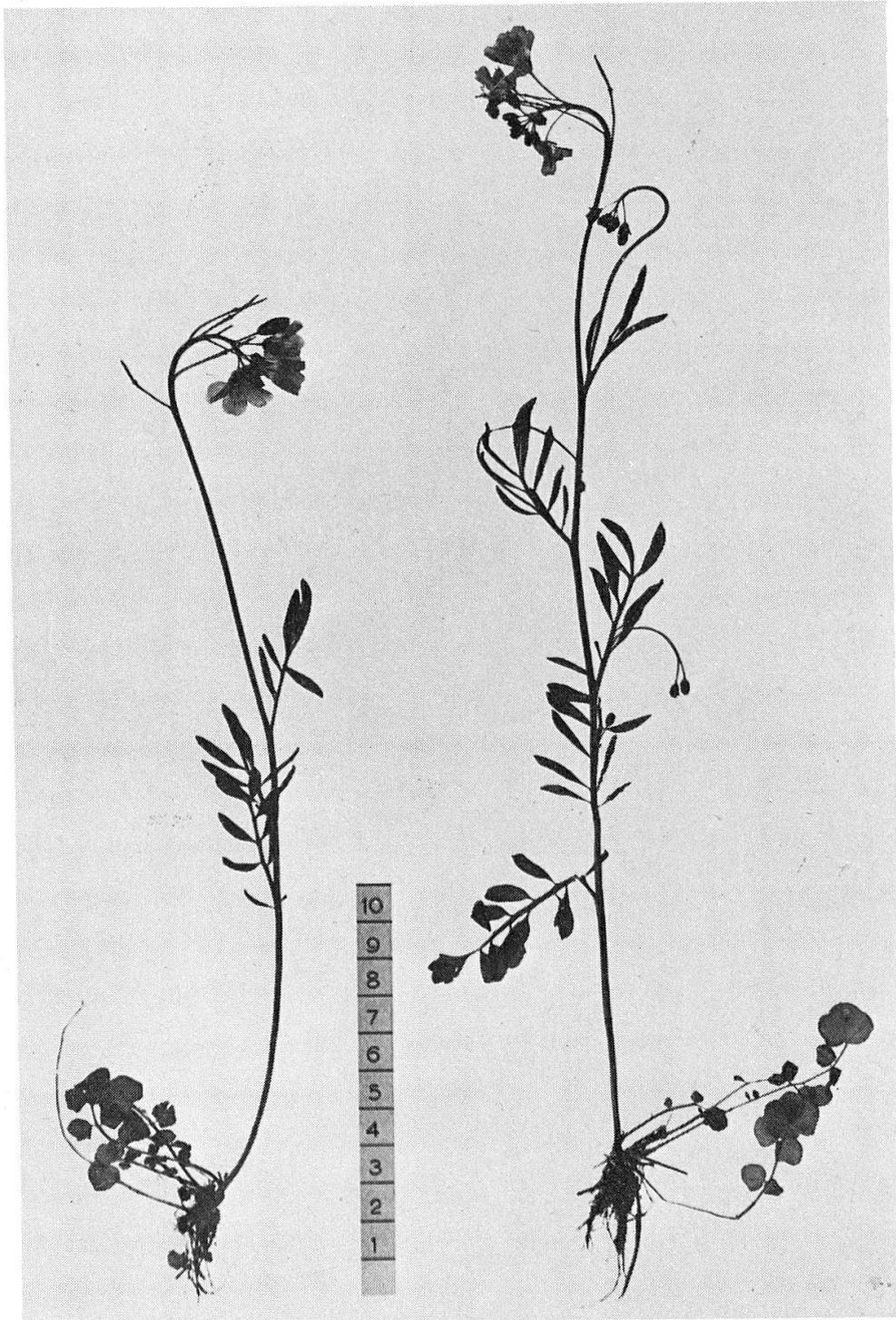Fig. 3. *Cardamine Schulzii:* plants from an open pasture.

Fig. 4. *Cardamine Schulzii:* plants from a drainage canal.

Preliminary observations on microsporogenesis revealed a rather complete chromosome pairing (Figs 5-6). Normally reduced PMCs often occurred at interkinensis (Fig. 7) and apparently normal tetrads prevailed in the material studied so far (Fig. 8). On the other hand, an individual variation in the pollen fertility (Fig. 9) suggests some meiotic disturbances. A detailed study on the development of anthers and ovules is continued, but all the obtained data indicate an open recombination system occurring in *C. Schulzii*.
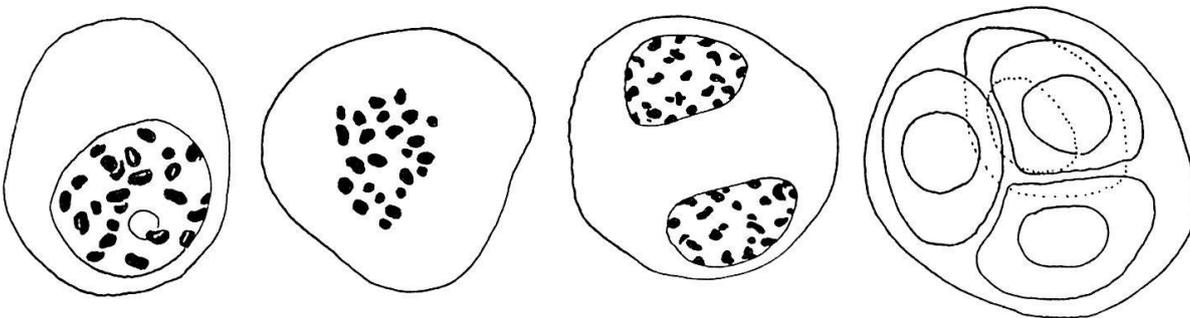
Figs 5-8. *C. Schulzii*: microsporogenesis. 5. Diakinesis: 24_{II}. 6. I metaphase with 24 bivalents. 7. Interkinensis with normally reduced nuclei. 8. An apparently normal tetrad of microspores. (c.) 2000 x.

Rather large, distinctly coloured flowers of *C. Schulzii* were frequently visited by various insects; experimental crosses confirmed the field observations, for *C. Schulzii* proved to be an allogamous species (Table 1). The seed output after cross-pollinations was rather reduced; a comparable behaviour, however, was previously noted in some other taxa of the genus *Cardamine* (URBANSKA-WORYTKIEWICZ and LANDOLT 1974) and might be related to the vegetative reproduction that occurs also in this species. It cannot be excluded, on the other hand, that the observed phenomenon might be due to an individual variation, only a few plants having been used in the present experiments.
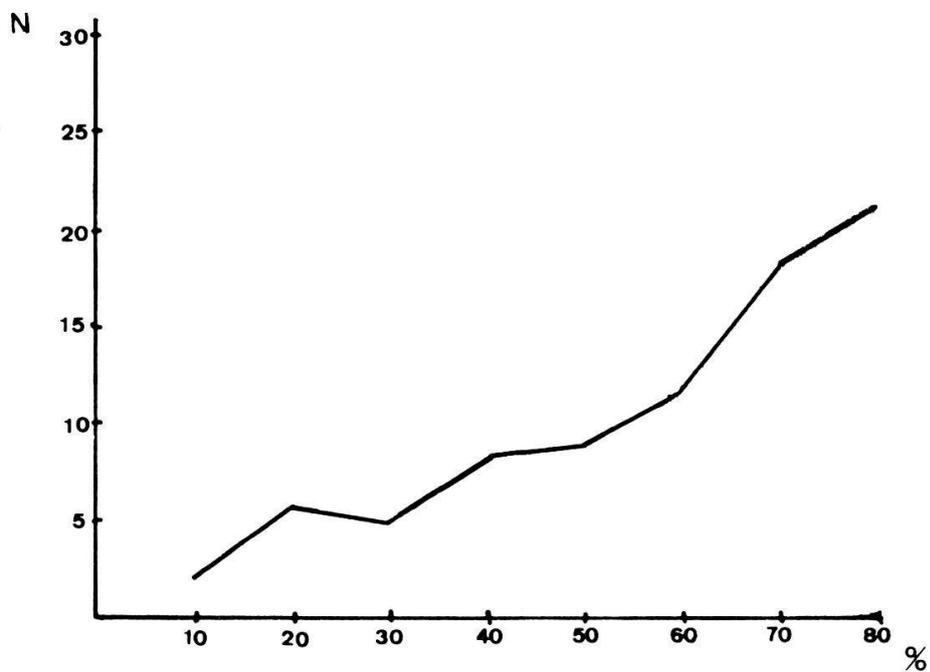
Fig. 9. Variation in pollen fertility observed in *C. Schulzii*.

Table 1. Selfings and cross-pollinations in *Cardamine Schulzii*.

Series	Number of pol-linated flowers	Number of seeds	Number of seedlings
Selfing	50	–	–
Cross-pollination	52	36	34

Fertility relationships between C. *Schulzii* and its parent species

Reciprocal crosses between *C. Schulzii* and *C. rivularis* resulted in an extremely limited seed output (Table 2). No germination occurred in normal conditions; only after removal of the seed coat, a single seedling was obtained. It was, however, very weak and perished after eleven days. No seeds at all were obtained from crosses with *C. amara* (Table 2).

Table 2. Crosses between *Cardamine Schulzii* and its parent species.

Cross type	Number of pollinated flowers	Approximate number of ovules	Number of seeds	Number of seedlings
C. *Schulzii* x C. *rivularis*	87	2440	$3_{0.12\%}$	1*
C. *rivularis* x C. *Schulzii*	90	1800	$2_{0.11\%}$	−
C. *Schulzii* x C. *amara*	84	2350	−	−
C. *amara* x C. *Schulzii*	81	2800	−	−

* a very weak seedling obtained only after removal of the seed coat.

It seems therefore that *C. Schulzii* is isolated from both its original parent species by strong incompatibility barriers. As far as *C. rivularis* is concerned, the seed incompatibility is at least partly responsible, whereas the pollen incompatibility might be a principal isolation factor acting against *C. amara*. Reproductive isolation speaks thus for the taxonomic rank of *Cardamine Schulzii* which should accordingly be considered as a polyploid species of a rather recent origin.

Fertility relationships between C. *Schulzii* and C. *insueta*

C. *Schulzii* used as the mother plant in crosses with C. *insueta* failed
to produce any offspring: only a single abortive seed was obtained (Table 3).
Crosses with C. *insueta* pollinated by C. *Schulzii* resulted in five sterile
plants, all corresponding morphologically to the latter taxon but represent-
ing two cytotypes (2n=40, 2n=48, Figs 10 - 11).

Table 3. Crosses between *Cardamine Schulzii* and *C. insueta*.

Cross type	Number of pollinated flowers	Number of seeds	Number of seedlings
C. *Schulzii* x C. *insueta*	57	1	-
C. *insueta* x C. *Schulzii*	69	6	5
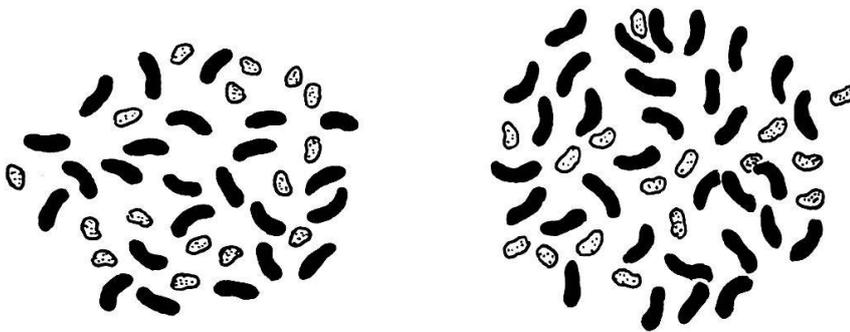
Figs 10 - 11. Plants obtained from crosses between C. *Schulzii* and C. *insue-
ta*; root-tip metaphases. 10. Pentaploid (2n=40, RRRAA). 11. Hexaploid
(2n=48, RRRRAA). (c.) 2000x.

The results of crosses suggest, on the one hand, that the autoallohexa-
ploid species is isolated from its immediate triploid ancestor by incompati-

bilitv barriers that manifest themselves at various developmental stages, the sterility of offspring included. On the other hand, they bring about a further evidence of some particular gametic types functioning in *C. insueta* (URBANSKA-WORYTKIEWICZ 1976, URBANSKA-WORYTKIEWICZ, in press): the pentaploids obtained in the course of the present study had 16 chromosomes of *C. amara* and 24 of *C. rivularis* (Fig. 10); their genomic constitution RRRAA represents thus a combination of a normal male gamete (RRA) of *C. Schulzii* and a polarized one (RA) of *C. insueta*. Three hexaploid RRRRAA plants (Fig. 11) resulting from the same cross correspond in turn to a combination of an unreduced female gamete of *C. insueta* (i.e. RRA) fertilized by a normal sperm of *C. Schulzii* (see Fig. 12). It should be added that the third possible variant viz. a tetraploid with a genomic constitution RRRA that might develop from crosses between *C. Schulzii* and *C. insueta* was not obtained in the present experiments, but such a plant has previously been found in the wild (URBANSKA-WORYTKIEWICZ 1977).

C. insueta

	R	RA	RRA
C. Schulzii RRA	RRRA	RRRAA	RRRRAA
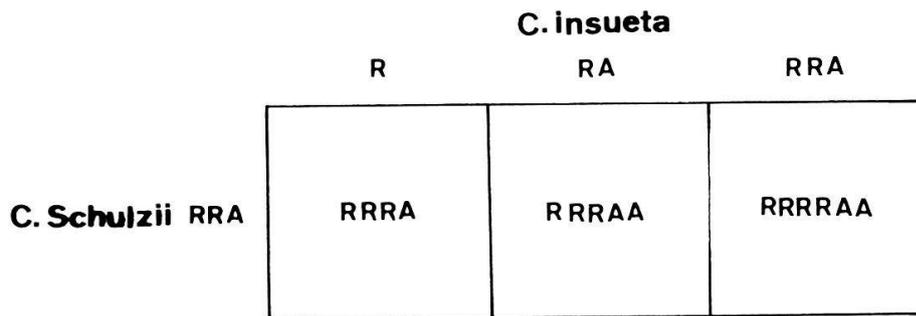
Fig. 12. Behaviour of *C. Schulzii* in crosses with *C. insueta*. RRRA = a tetraploid (2n=32) found at Urnerboden (URBANSKA-WORYTKIEWICZ 1977) that might have arisen in this way. RRRAA (2n=40) and RRRRAA (2n=48) = plants obtained experimentally.

Discussion

Two principal criteria accepted for classification of polyploids are 1/ their origin and 2/ relative age. The terms: autopolyploidy and allopolyploidy, introduced by KIHARA and ONO (1926), give a general qualitative distinction between polyploids born through a doubling of one and the same chromosome set and those of a hybrid origin. Numerous authors have further

elaborated on this general scheme and proposed various subdivisions of both opposite groups (DARLINGTON 1932, MüNTZING 1936, KOSTOFF 1939, CLAUSEN,KECK and HIESEY 1945, STEBBINS 1947, 1950). As far as the allopolyploids are concerned, three main categories have been accepted viz. segmental allopolyploids, genomic allopolyploids and autoallopolyploids, the nomenclature being based upon the degree of homology between the parent genomes.

The autoallopolyploids combine the caracteristics of auto- and allopolyploids; they can exist only at the level of hexaploidy or higher. Well-documented examples, in particular those of autoallohexaploids are rather rare in the literature. KOSTOFF (1939) reported that the behaviour of *Helianthus tuberosus* (2n=6x=102) in crosses with the diploid *H. annuus* (2n=24) suggested the genomic constitution of the former species resulting from a least one interspecific hybridization accompanied by autopolyploidy (see also STEBBINS 1950, pp. 332-333). A comparable case represents *Phleum pratense* (2n=6x=42, NORDENSKIöLD 1941, 1945, LEVAN 1941, MYERS 1944); the evidence of NORDENSKIöLD indicates that the genomic constitution of this species is AAAABB, the A genome being likely that of *P. nodosum* and the B genome that of the diploid *P. alpinum*. One might also mention *Solanum nigrum* (2n=6x=72); this taxon comprises most probably four genomes of *C. nodiflorum* or some related species, and two genomes of a diploid taxon not yet identified (JORGENSON 1928, NAKAMURA 1937).

Cardamine Schulzii represents a model example of an autoallohexaploid. The size differences occurring between chromosomes of *C. rivularis* and those of *C. amara* permit to identify the genomes derived from either parent taxon in somatic metaphases of the 48chromosomic plants, the same proportion i.e. 2 : 1 being also observable in its immediate triploid ancestor (URBANSKA-WORYTKIEWICZ and LANDOLT 1972, 1974, URBANSKA-WORYTKIEWICZ 1976, URBANSKA-WORYTKIEWICZ, in press). In this respect, the hybridogenous taxa from Urnerboden differ from *Helianthus*, *Phleum* or *Solanum*, where a direct karyological evidence was not available and identification of parent genomes based upon experimental crosses as well as morphological characters. It should be added that the genomic sonstitution of *Cardamine Schulzii* and *C. insueta* is reflected in the morphology of these taxa, the characters of *Cardamine rivularis* predominating over those of *C. amara*.

Evaluation of a relative age of a polyploid is based upon cyto-geographical data, the presence of putative parent species as well as the areas of geographical distribution being considered. FAVARGER (1961) proposed an useful classification comprising three main categories viz. paleopolyploids, mesopolyploids and neopolyploids, the latter type obviously being the youngest from a phylogenetical point of view. An instructive example offer *Tragopogon mirus* and *T. miscellus* discovered in the United States by OWNBEY (1950). Both these actually spreading hybridogenous species are tetraploid (2n=24) and manifest distinct affinities to the corresponding diploids (*Tragopogon pratensis*, *T. dubius* and *T. porrifolius*) introduced to North America only about 30 years before the finding of the allopolyploids. Another interesting case is that of *Senecio cambrensis* (2n=60) reported from England (ROSSER 1955); this allotetraploid issued from spontaneous crosses between *S. squalidus* (2n=30) and *S. vulgaris* (2n=30) is also beginning to spread.

Cardamine Schulzii exactly corresponds to the concept of a neopolyploid. The population at Urnerboden comprises both diploid parent species i.e. *C. rivularis* and *C. amara*, the triploid *C. insueta* and the autoallohexaploid *C. Schulzii*, all phylogenetical links being thus present. A further indication is the progressing spread of the 48chromosomic plants.

In conclusion, an interesting aspect should be commented. Evolutionary changes within the population from Urnerboden manifested themselves not only in two principal steps of polyploidization, but also involved alterations of the breeding system. The diploid parent species *Cardamine rivularis* and *C. amara* are both predominantly outcrossing, a certain amount of stability being assured by the vegetative reproduction; their recombination system may accordingly by considered as an open one. On the contrary, the formation of the triploid *C. insueta* brought about a changeover from allogamy to a "subsexual" reproduction accompanied by a very strong vegetative multiplication; both these mechanisms resulted thus in a nearly closed recombination system. The doubling of the triploid genome was in turn accompanied by a reverse trend, for *Cardamine Schulzii* is allogamous and frequently reproducing by seeds. This particular flexibility in reproductive features is apparently influenced by environmental factors and calls for a special attention, for it might become decisive for the future development of the hybridogenous taxa.

Summary

Cardamine Schulzii, a new autoallohexaploid species as well as its immediate triploid ancestor *C. insueta* are diagnosed. *C. Schulzii* is isolated from its original parent species *C. rivularis* and *C. amara* and also from *C. insueta* by incompatibility barriers manifesting themselves at various pre- and/or post-mating stages. Experimental crosses bring about a further evidence of particular gametic types functioning in *C. insueta.*

Résumé

Sont décrites *Cardamine Schulzii,* une espèce nouvelle autoallohexaploïde ainsi que *C. insueta*, son ancêtre direct triploïde. *C. Schulzii* se montre isolée de ses deux espèces parentales *C. rivularis* et *C. amara* et également de *C. insueta* par les barrières pré- et/ou post-zygotiques d'incompatibilité. Les croisements expérimentaux fournissent une fois de plus la preuve du fonctionnement de types gamétiques particuliers chez *C. insueta.*

Zusammenfassung

Es werden zwei neue Bastarde beschrieben: *Cardamine Schulzii,* eine neue autoallohexaploide Art, und *C. insueta,* ihr direkter triploider Vorfahre. *C. Schulzii* ist durch pre- und/oder postzygotische Unverträglichkeitsbarrieren von den ursprünglichen Elternarten *C. rivularis* und *C. amara* sowie von *C. insueta* isoliert. Die experimentellen Kreuzungen bestätigen die Wirkungen von besonderen Gametentypen bei *C. insueta.*

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