

# An amphiploid hybrid of *Geum urbanum* L. and *G. molle* Vis. et Panc.

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(entered: 20.X.53)

## I. Introduction

The previously described amphiploid between two *Geum* species (W. Gajewski 1953) arose as progeny of a highly sterile hybrid of *Geum rivale* x *G. macrophyllum* with an asyndetic type of meiosis. The amphiploid plants, found in the second generation, probably arose from the union of unreduced gametes. The amphiploid here described arose in the  $F_1$  generation of a rather fertile hybrid with an almost normal course of meiosis.

*Geum rivale*, *G. macrophyllum*, *G. urbanum* and *G. molle* all belong to the *Eugeum* subgenus and like the majority of the species in this subgenus have the somatic chromosome number  $2n = 42$ . Usually, the hybrids from this subgenus have a normal course of meiosis with 21 bivalents in the majority of PMC's, and only few univalents are found in the rest of PMC's. Almost all hybrids of *G. macrophyllum* (and of two very closely related species) with other *Eugeum* species are an exception as their meiosis is asyndetic.

In my previous paper I was inclined to believe that among hexaploid *Eugeum* species the amphiploids should be obtained primarily between those species which gave asyndetic hybrids and form unreduced gametes. When in hybrids the course of meiosis is normal the progeny is composed of hexaploid or rarely of aneuploid plants. However, the second amphiploid hybrid found in my *Geum* cultures arose from two species, the hybrid of which had a normal type of meiosis. The fertility of this amphiploid, contrary to expectations, was fairly high.

The hybrid *G. urbanum* x *G. molle* has a normal course of meiosis but is only partially fertile. The  $F_2$  generation of this hybrid is also he-

xaploid like the parental species and  $F_1$  hybrids. The amphiploid described here was found in  $F_1$  generation among many hexaploid sister plants, and not till the third vegetative period of this  $F_1$  culture. In autumn when collecting seeds I noticed that one plant was more fertile and had bigger achenes than the rest of ab. forty  $F_1$  hybrids. The observation in the following season indicated that this plant differed from the rest of the sister plants in nearly all respects, e. g. the shape and size of leaves, the dimensions of sepals, petals and achenes, and the degree of pollen and seed fertility. The cytological examination showed that the chromosome number of this plant was  $2n = 84$ , which was double the number in the parental species and  $F_1$  hybrids.

It is unknown how this amphiploid originated and any conjectures are difficult to make. When the plant was identified as an amphiploid it was already three years old with a big, branched, creeping caudex already rotten in its basal parts. The shoot with the doubled chromosome number could develop as the result of bud mutation on a hexaploid plant which at the time of inspection was already dead. Also the doubling of the chromosome number could take place in a very early stage of the zygote development, then, the whole plant was dodecaploid from the very first year of growth and only escaped my attention. It is also just possible that this exceptional plant arose from the union of two unreduced gametes produced by the parental species. This last supposition seems to be the least plausible, as I have never observed the formation of unreduced gametes in any pure *Geum* species.

In the literature many examples are known of the apparition of amphiploids in  $F_1$  interspecific generation, both as bud mutation and as the result of an early doubling in the zygote. As an example of the former mode of apparition of an amphiploid can be given *Primula kewensis* (Newton a. Pellew 1929) and of the latter — *Nicotiana digluta* (Clausen a. Goodspeed 1925, Clausen 1928).

The amphiploid described here proves that polyploidy in the genus *Geum* can arise not only through gametic doubling but also as the result of somatic doubling. As in the evolution of the whole *Geum* genus amphiploidity plays decisive rôle (in the whole genus not one diploid species is so far known) the description of this new amphiploid plant and its progeny will be a contribution to the knowledge of the ways new polyploid forms in this genus appear.

## II. Parental species and $F_1$ generation

*Geum urbanum* L. is the commonest *Geum* species in Europe, often found as an anthropochoric plant in the neighbourhood of human settlements, roadsides and pastures. In more natural habitats it is found in

forests and other shadowed places. Its present large distributional area is undoubtedly partly due to human activity, especially in its northern parts. The species represents a south-european genetic element.

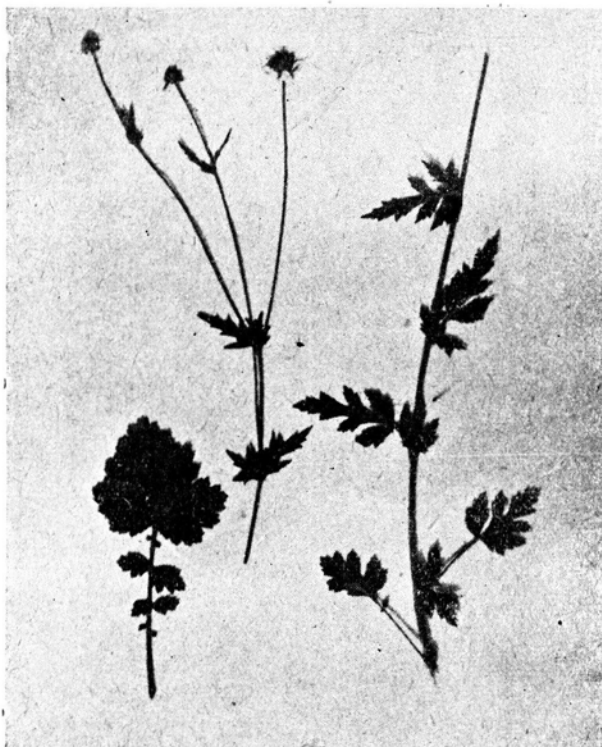


Fig. 1. *G. molle* Vis. et Panc.

*Geum molle* Vis. et Panc. is much more restricted in its distribution, it appears on the Balcan Peninsula ranging from Serbia and Montenegro to Bulgaria, Macedonia and Albania. This species also grows in the Abruzzo province in Italy. It is a plant from thinly growing forests and shrubs, where there is much light, of the lower mountain zones.

On the Balcan Peninsula both species grow together on large territories and have many opportunities to cross. Beck v. Managetta (1899) indicates natural hybrids between these two species from the Balcan Peninsula, but there are no precise data on their frequency. The parental species are represented in figs. 1 a. 2 and a map of their distribution in fig. 3.

In my cultures *G. urbanum* was obtained from natural station from the neighbourhood of Warsaw, *G. molle* was raised from seeds gathered from the natural station in Rhodope Mountains in Bulgaria obtained from

the Botanical Garden in Sofia. Both species were cultivated in Warsaw during many years and were several times propagated by seeds. During their culture both species proved to be constant and uniform in regard to major specific traits.

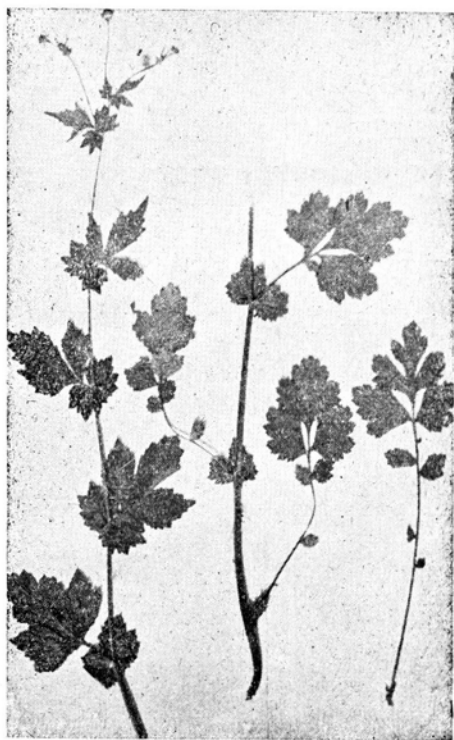


Fig. 2. *G. urbanum* L.

The crossing of the two species was done in 1949 in both reciprocal directions. Seed setting after cross-pollination was high, and in both reciprocal crosses good achenes were obtained in approx. 80%. The numerous  $F_1$  plants raised were vigorous and surpassed the parental species in height of floral stems. The reciprocal hybrids were identical. Some idea of the specific traits in the parental species and  $F_1$  hybrids may be obtained by comparing figs. 1, 2, 4 a. 5 and from the short description given below:

a) Shape of caudical and stem leaves (fig. 5): The shape of leaves of *G. molle* is very characteristic. The caudical leaves are lyrate as in all *Eugeum* species but the terminal leaflet is entire, ovoid, shallowly incised with cordate base and with sharply serrate margin. On the long petiole there are only a few pairs of small lateral leaflets. In the caudical

leaves of *G. urbanum* the terminal leaflet is large, pinnately divided into three cuneate lobes, and the lateral leaflets are more conspicuous. Also the stem leaves of these two species differ greatly. The stipules in *G. urbanum* are much greater than in *G. molle*. As can be judged from figs 4 and 5 the shape of leaves in  $F_1$  hybrids is nearly intermediate between the parental species.

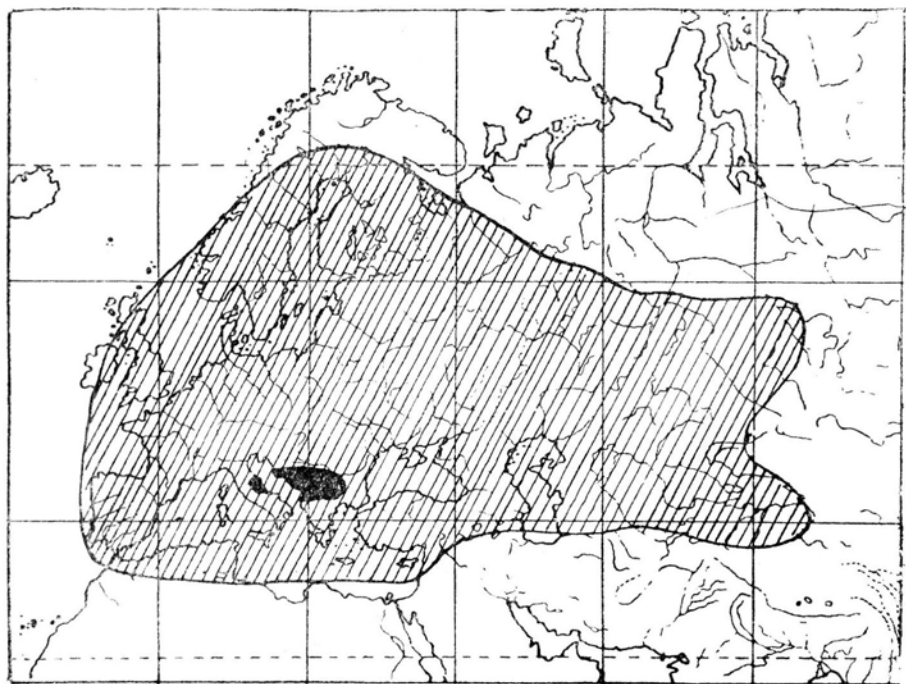


Fig. 3. The geographical distribution of *G. molle* (black) and of *G. urbanum* (hatches)

b) Floral stems: *G. molle* has floral stems from 40 to 60 cm high, usually with 1 to 3 flowers per stem. The floral peduncles after anthesis are rigid and elongated. *G. urbanum* has higher floral stems ranging from 60 to 80 cm, it is much more branched with 5 to 9 and even 12 and more flowers per stem. In  $F_1$  hybrids the floral stems are up to 90 cm high with from 5 to 9 flowers per stem like in *G. urbanum*.

c) Pubescence: *G. molle* has stems and leaves densely a. softly pubescent (the specific name reflects this character). The hairs are long, straight, and soft, usually directed downwards. The upper part of the stem together with the floral peduncles and the calyx is densely covered with glandular hairs. *G. urbanum* is sparsely haired with short, soft hairs intermingled with few longer and stiffer bristles, the glandular

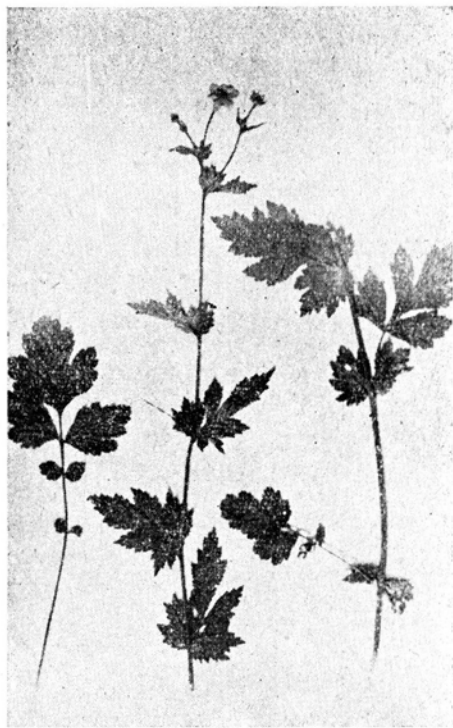


Fig. 4.  $F_1$  hybrid *G. molle* x *G. urbanum*

hairs are absent. The pubescence of  $F_1$  hybrids is dense though perhaps somewhat shorter than in *G. molle* but there are no glandular hairs in it.

d) Structure of flowers: The flowers of the two parental species are rather similar. They differ in the following traits: in *G. molle* the sepals at anthesis are horizontally spread and only during ripening of achenes they bend downward and are reflexed to the peduncle, in *G. urbanum* the sepals are reflexed already during flowering. The petals of *G. molle* are less intensively yellow than those of *G. urbanum* and are broad-elliptic in *G. molle*, and obovate in *G. urbanum*. The average length and width of petals of *G. molle* are 11,5 and 9,2 mm and in *G. urbanum* — 5,8 a. 4,6 mm respectively. *G. molle* has a hairy gynophore which is 1 mm long, in *G. urbanum* there is no gynophore. The receptacle in *G. urbanum* is densely covered with long, yellow hairs while in *G. molle* it is only sparsely haired with much shorter hairs. The achenes are numerous in both species (ab. 160 on one receptacle), they are in *G. urbanum* longer and less pubescent than in *G. molle*. The rostrum in *G. molle* is shorter and covered with many glandular hairs. In  $F_1$  hybrids the sepals are reflexed downward already during anthesis, the petals are intensively yellow like those of *G. urbanum*. The shape and size of petals are inter-

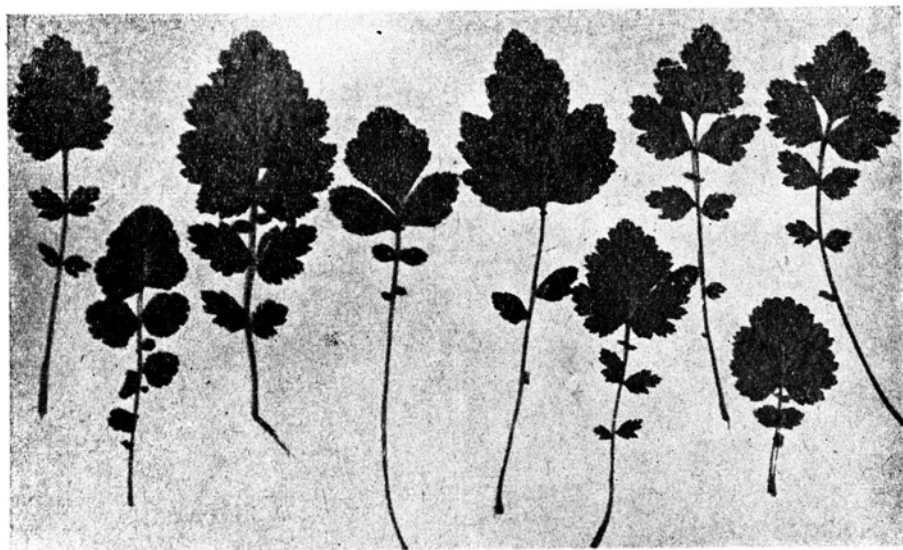


Fig. 5. Basal leaves of *G. molle* (left), *G. urbanum* (right) and of  $F_1$  hybrid *G. molle*  $\times$  *G. urbanum* (centre).

mediate, their average length and width are 9,2 a. 7,2 mm respectively. There is no gynophore and the receptacle is covered with short hairs like in *G. molle*. The dimensions of achenes are rather similar to those of *G. urbanum* but the achenes are more haired and the rostrum is glabrous.

Besides the traits mentioned above, both species differ in many other respects such as for instance: the time of flowering and fruiting, the resistance to low temperatures and to the attack of parasitic fungi. The  $F_1$  hybrids are healthy, resistant, vigorous plants showing distinct hybrid vigour. The fertility of these hybrids is distinctly lowered and varies in different years, which is apparent from the following table:

Year	Pollen fertility in %%			Seed fertility in %%		
	from	to	average	from	to	average
1950	27.9	45.7	32.6	20.0	23.6	22.5
1951	25.5	31.4	26.6	14.0	27.3	23.1
1952	19.4	26.0	21.4	13.0	28.5	18.8
1953	20.6	12.1	15.3	1.8	8.5	6.9
average:			23.9			16.3

In 1953 the fertility was distinctly lower which was most probably caused by a severe attack on all my *Geum* cultures by a parasitic fungus which was not identified.

Drawings of meiosis in PMCs of  $F_1$  hybrids are given in fig. 6. It is apparent that meiosis develops rather regularly with only few minor disturbances. In diakinesis in the 12 analysed PMC's I have found only

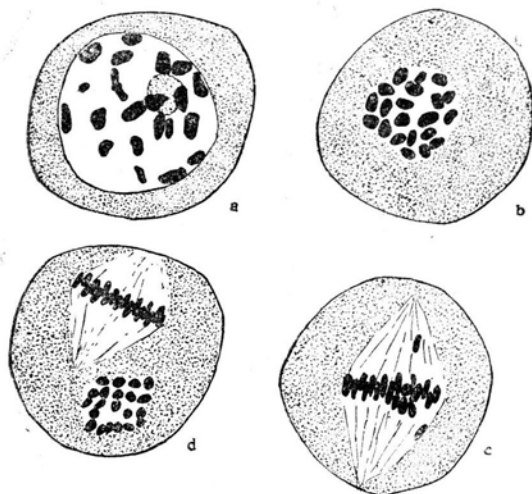


Fig. 6. The course of meiosis in PMC's of *G. urbanum*  $\times$  *G. molle*  $F_1$  hybrid: a — diakinesis with 21 bivalents, b — metaphase I with 21 bivalents, c — metaphase I with 2 univalents, d — metaphase II with 21 chromosomes on the plate.

21 bivalents in each cell. In 44 PMC's at metaphase of the first division following configurations have been observed:

21 <sub>II</sub>	. . . . .	in 34 PMC's (fig. 6b)
20 <sub>II</sub> + 2 <sub>I</sub>	. . . . .	in 8 PMC's (fig. 6c)
18 <sub>II</sub> + 6 <sub>I</sub>	. . . . .	in 1 PMC
17 <sub>II</sub> + 8 <sub>I</sub>	. . . . .	in 1 PMC

During metaphase the univalents lie on the spindle off the metaphasal plate. At anaphase, in the majority of the analysed PMC's, all chromosomes are separated to the two anaphasal groups, and only in 2—3% of PMC's some univalents lag on the spindle. In 12 PMC's the number of chromosomes in metaphase II plates has been counted, and in all instances it is 21 (fig. 6d). Similarly to the first meiotic division also the second one is almost normal. The tetrads are always composed of four normally looking spores. Nevertheless the majority of the young pollen grains degenerate.



### III. The description of the amphiploid plant.

In autumn 1951 when collecting seeds from the  $F_1$  generation of *G. urbanum* x *G. molle* I found one plant with a fertility much higher than in sister plants. The good achenes of this plant were also distinctly bigger. In 1951 this culture was already three years old. In the preceding year I did not notice this plant, which, however, did not mean that this plant appeared in 1951 as I could easily have missed it before. The high fertility and the enlarged dimensions of the achenes seemed to indicate that it could have been an amphiploid with a doubled chromosome number. The seeds gathered from this plant were sown separately. The plants obtained from them flowered abundantly in 1953.

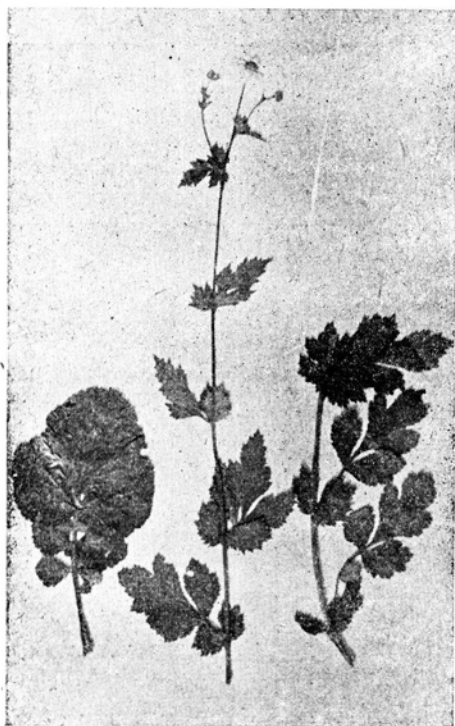


Fig. 7. Amphiploid plant from  $F_1$  *G. molle* x *G. urbanum*.

The supposed amphiploid plant flowered also in 1952 and from careful observation and measurement it appeared that it had thicker, less dissected and broader leaves, thicker and shorter floral stems, bigger floral organs, bigger achenes, and higher pollen and seed fertility. The study of meiotic divisions in PMC's confirmed the supposition that the plant was amphiploid. In metaphase I 42 bivalents instead of the 21 in

other  $F_1$  plants were found in many PMC's. The morphological differences between this dodecaploid plant and the hexaploid hybrids can be compared from figs. 4 a. 7.

A detailed description of all the specific traits of the amphiploid plant will not be given here but in order to illustrate the enlarged dimensions of organs in the amphiploid the measurements of sepals and petals are given.

Length of petals in mm	7,5	8	8,5	9	9,5	10	10,5	11	11,5	n	M	m
$F_1$ plant with $2n = 42$	3	8	10	14	15	6	1	1		58	9,0	0,19
Amphiploid with $2n = 84$			1	5	6	16	7	6	1	42	10,1	0,21

Width of petals in mm	6	6,5	7	7,5	8	8,5	9	9,5	n	M	m
$F_1$ plant with $2n = 42$	6	7	20	18	4	2	1		58	7,3	0,16
Amphiploid with $2n = 84$					3	9	19	11	42	9,2	0,19

Length of the sepals in mm	5	6	7	8	9	10	11	n	M	m
$F_1$ plant with $2n = 42$	4	8	12	7	2			33	6,9	0,18
Amphiploid with $2n = 84$			2	10	10	4	4	30	8,4	0,19

As it appears from the tables the dimensions of petals and sepals in the amphiploid are distinctly greater than in hexaploid plants. As it has often been pointed out in other polyploids, here also the width of petals is more enlarged than their length. Still more conspicuous are the differences in the shape of the leaves. The leaves of the amphiploid when compared with those of hexaploid hybrids have much shorter petioles with fewer lateral leaflets and with big, broad, intensely green, and less incised terminal leaflet. Some organs of the amphiploid and the corresponding ones of a hexaploid hybrid are illustrated to scale in fig. 8, in which the differences are plainly visible. The fertility of this amphiploid during three years was as follows:

Year	Av. pollen fert.	Av. seed fert.
1951	—	66,1%
1952	69,4%	53,5%
1953	71,2%	49,0%
Average	70,3%	56,1%



Fig. 8. Basal leaves, floral stems, flowers, fruit-heads and achenes of *G. molle* × *G. urbanum* F<sub>1</sub> hybrid (left) and of the amphiploid plant (right) drawn to scale.

When pollen and seed fertility of the amphiploid (70,3% a. 56,1% respectively) are compared to the fertility of hexaploid hybrids (23,9% and 16,3% respectively) it become apparent that the fertility of the amphiploid has increased ab. three times.

A sideview analysis of meiosis in 73 PMC's of the amphiploid showed during the first metaphase: 1) all chromosomes were tightly packed in the metaphasal plate and no univalents were visible in the spindle in 65 cells, 2) 2 univalents were visible in spindle in 3 cells, 3) from 4 to 10 univalents were off the plate in the remaining 5 cells. In the polar view analysis it was rather difficult to count exactly all chromosomes as they were crowded in large numbers in the plate. In 3 PMC's the number

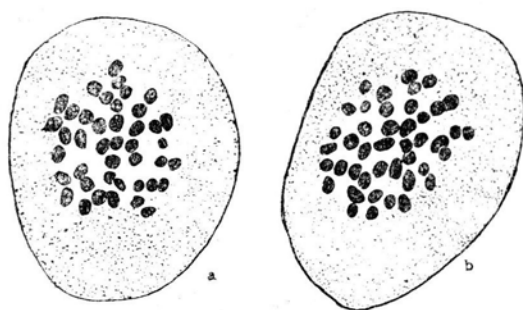


Fig. 9. Metaphase I in the PMC's of the amphiploid plant:  
a — with 42 chromosomes, b — with 43 chromosomes.

was found to be 42 and in 1 PMC —43 (fig. 9a, b). The course of anaphase I and the whole second division is nearly normal. The rare univalents are usually segregated to the polar groups together with the bivalent halves and only seldom the univalents are left on the spindle. The tetrads look quite normal but ab. one third of young pollen grains degenerates.

#### IV. The progenies of hexaploid $F_1$ hybrids and of the amphiploid plant

In 1953 I had 62 plants from the  $F_2$  generation and 45 plants obtained from the amphiploid plant. All these plants have flowered and set seeds abundantly. These rather small numbers are due to the shortness of place. Nevertheless the comparison of these two populations is very interesting. Whereas the progeny of the hexaploid hybrids is extremely variable and no two identical plants are to be found, the progeny of the amphiploid is morphologically very uniform and the differences among the individuals are small. Photographs of dried leaves from 9 plants from each of the two progenies in figs. 10 a. 11 illustrate well the great

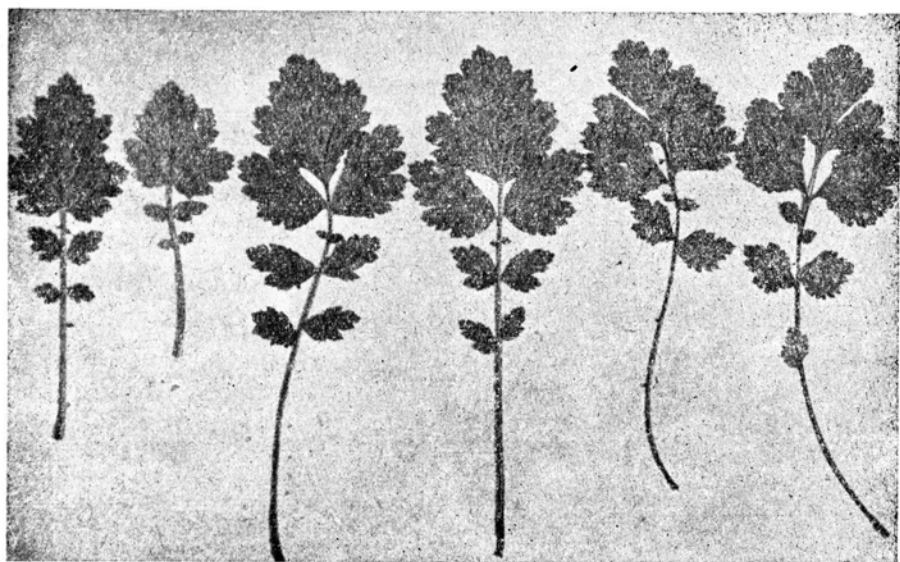


Fig. 10. Basal leaves of 9 plants from the  $F_2$  generation *G. molle*  $\times$  *G. urbanum*.

differences between the two groups. In the  $F_2$  generation raised from hexaploid hybrids the segregation is conspicuous in all studied traits: ramification of floral stems, degree and character of pubescence on leaves, stems, sepals, petals and achenes, dimensions of petals and sepals,

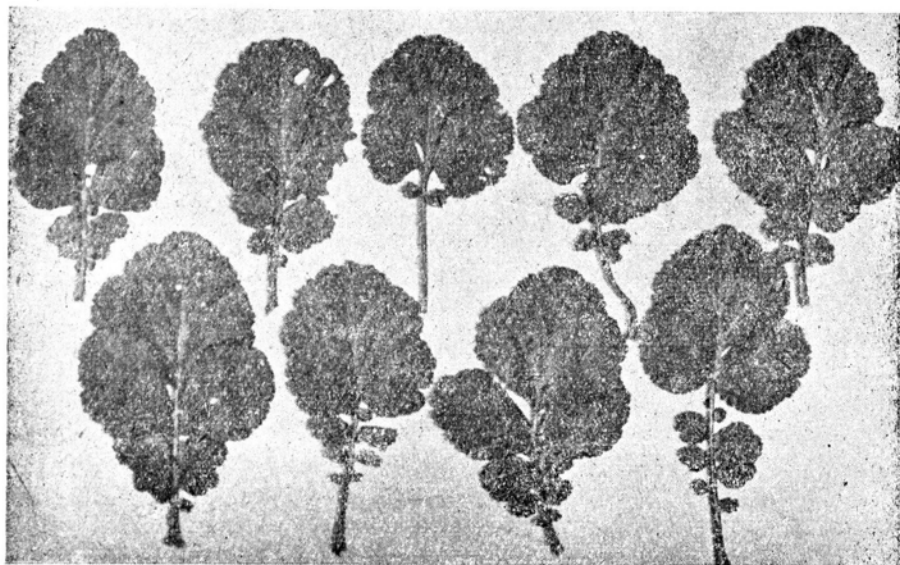


Fig. 11. Basal leaves of 9 plants from the second generation of the amphiploid plant.

length and degree of pubescence on the receptacle, length of the gynophore, dimensions of achenes, time of flowering and others. To illustrate the character of the segregation in  $F_2$  measurements of petal lengths are tabulated below:

Length in mm:	4,5	5	5,5	6	6,5	7	7,5	8	8,5	9
G. molle										
G. urbanum	2	1	18	7	3	5				
$F_1$							3	8	10	14
$F_2$			1	2	2	3	5	7	18	9

Length in mm:	9,5	10	10,5	11	11,5	12	12,5	n	M	m
G. molle		2	3	5	12	8	5	35	11,5	0,22
G. urbanum								36	5,8	0,20
$F_1$	15	6	1	1				58	9,0	0,19
$F_2$	5	3	3	2	1	1		62	8,7	0,32

Together with the morphological traits also the degree of fertility showed a marked segregation. The seed fertility of all 62  $F_2$  plants is as follows:

% of good achenes	0	10	20	30	40	50	60
number of plants	12	22	20	2	4	2	

As it appears in the majority of  $F_2$  plants fertility is lower than in  $F_1$  hybrids, though some plants are markedly more fertile.

The most striking feature in the second generation from the amphiploid  $F_1$  plant is its uniformity. Most of the traits show no or very small segregation. For comparison I give here measurements of petal lengths in the 45 plants of this generation:

Length of the petals in mm:	9	9,5	10	10,5	11	11,5	12	n	M	m
Number of plants	9	5	10	15	4	2	2	45	10,6	0,20

When the petal length of this  $F_2$  generation is compared with the variation of the same character in the original  $F_1$  amphiploid it will be seen that the average length is somewhat greater but the coefficient of variability is nearly the same. All these  $F_2$  plants similarly as the amphiploid are eglandular, have stems ranging from 53 to 71 cm with from

2 to 4 or 5 flowers per stem. In all plants the gynophore is 2—3 mm long a. hairy, and the receptacle 5—6 mm long with short pubescence. The receptacle is often flattened and sometimes bifid on the top. I have never observed this trait in parental species and their  $F_1$  hybrids. The number of the achenes on the receptacle ranges from 160 to 220. The achenes are 7—8 mm long, strongly pubescent with a glabrous rostrum 6—8 mm long. The sepals are 9,5—11 mm long and recurved at anthesis. The petals are intensively yellow, 10,5—11 mm long and 9,5—10,5 mm broad. The plants are robust and flower and set fruit abundantly. The fertility of these plants is high although not quite uniform:

Pollen fertility in %	40	60	80	100
Number of plants	21	19	5	
Seed fertility in %	40	60	80	100
Number of plants	23	22		

As we see the fertility of this  $F_2$  generation is nearly the same as of the  $F_1$  amphiploid.

In 4 plants of this  $F_2$  generation the somatic chromosome number from root tips was ascertained to be  $2n = 84$  (fig. 12a). The course of me-

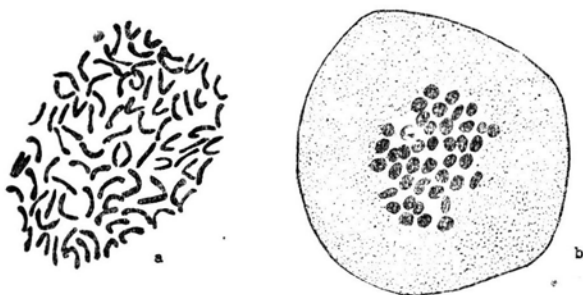


Fig 12. a — somatic plate with 84 chromosomes from a plant of the second amphiploid generation, b — metaphase I with 42 bivalents in PMC from a plant of the second amphiploid generation.

iosis was checked in several plants on aceto-carmine smear preparations of PMC's. In all plants the course of meiosis is quite normal and the percentage of cells in which 2 or more univalents are seen at meta- or anaphase is small. Cells with visible univalents are only 3—4% of the total of examined cells. On fig. 12b a regular metaphase I plate from one of the  $F_2$  plants is shown.

The  $F_3$  generations from several  $F_2$  plants were sown this year and will flower in two years.

## V. Discussion

The amphiploid described in this paper arised from an interspecific hybrid with a nearly normal chromosome coniugation. Notwithstanding the high degree of chromosome homology of both parental species the coniugation of chromosomes in meiosis of the amphiploid is highly normal with bivalents only in the majority of PMC's. In my previous papers (W. G a j e w s k i 1952, 53). I have tried to prove that the hexaploid *Eugeum* species are allohexaploids with two genomes homologous to the two genomes of the tetraploid *G. montanum* of the *Oreogeum* subgenus. The evolution in the *Eugeum* subgenus (disregarding few dodecaploid species) has consisted chiefly of genic differentiation and perhaps also of small chromosomic rearrangements that have not destroyed the gross chromosome homology of different species. The now existing hexaploid *Eugeum* species are rather old judging from their very disjunctive distribution on four continents and represent a completly „diploidized“ type of polyploids. The basic chromosome number for the *Euguem* subgenus is 21 which is triploid in relation to the basic number 7 characteristic for the whole genus *Geum* and many other rosaceous genera.

According to S t e b b i n s ' s (1947, 1950) classification of polyploid types this amphiploid should be regarded as „segmental allopolyploid“. In S t e b b i n s ' s opinion sterile interspecific hybrids with normal coniugation at meiosis indicate that the parental species have chromosomes differing in many small chromosomal segments. The coniugating chromosomes are thus only partially homologous. Due to crossing over between semihomologous chromosomes gametes with duplicated or deficient chromosomal segments arise. Such gametes degenerate. After the doubling of the chromosome number coniugation between truly homologous chromosomes takes place and fertility is restored.

I have studied many interspecific hybrids among different hexaploid *Eugeum* species and in most cases the chromosomes of the different species do coniugate. In few cases of nearly complete asynapsis, e. g. in the hybrid *G. rivale* x *G. macrophyllum* (W. G a j e w s k i 1950, 53), asynapsis is most probably due not to the lack of homology between chromosomes of the two parental species but to desynapsis caused by genic, or more generally by some pysiological factors. In many interspecific hybrids within the *Eugeum* subgenus with nearly the same high degree of chromosome coniugation I have observed differences in degree of fertility ranging from fertile hybrids to completely sterile ones. The differences in fertility of these hybrids cannot be explained solely by differences in the structural composition of chromosomes from the parental species. Both the degree of chromosome coniugation and the degree of fertility depend, above all, on the genic composition of the hybrid,



on the sensitivity of hybrids to many external factors and also on the general vigour of hybrids. The coniugation of chromosomes and the whole course of meiosis are highly sensitive to many internal and external conditions, and many facts indicate that this sensitivity may be different in different hybrids. In his recent paper G r a n t (1952) convincingly demonstrates the great sensitivity of the meiotic processes in the hybrid *Gilia millefoliata* x *achilleaefolia* to the nutritional state of the plant. In Grant's hybrid the number of bivalents formed at meiosis is greater in well nurished plants than in the starved ones. In starved plants with low bivalent number the percentage of unreduced gametes increases. The same sensitivity appears in amphiploids of the second generation, but the parental species do not react to the nutritional factors. G r a n t writes that the parental species „are presumably well buffered against a fairly wide range of environmental conditions“.

Still more complicated are the relations of the gametic fertility to the internal and external conditions. Especially complicated are the relations of amphiploid fertility to the coniugation of chromosomes before and after the doubling of the chromosome number in the hybrid. In my work on *Anemone* (W. G a j e w s k i 1946) I tried to establish a rather simple relation between amphiploid fertility and the degree of chromosome coniugation in the  $F_1$  hybrid before the chromosome doubling. These attempts, I must now admit, were based on superficial analysis of insufficient data, and led to unwarranted conclusions. The relation, however, is much more complicated than I then believed, and the fertility of the amphiploid depends on many various factors such as for instance: 1) the degree of structural homology between parental chromosomes, 2) the number of chiasmata formed at prophase and metaphase which is a function of genic action and chromosome dimensions, 3) the genes influencing different meiotic processes and the development of gametophytes and zygotes, and 4) the sensitivity of all these processes to environmental conditions which can be different in pure species,  $F_1$  hybrids and amphiploid plants.

As the  $F_1$  hybrid is rather fertile and has normal coniugation it is to be expect that the amphiploid will be rather unfertile, with polyvalents at meiosis and will not breed true. This, however, is not the case. The chief source of this discrepancy between expectations and the behaviour of the amphiploid is the fact that in the *Geum* genus the bivalents at metaphase are held usually by only one chisama and there is no opportunity to form polyvalents. The formation of bivalents only between truly homologous chromosomes assures the fertility and constancy of this amphiploid.

There must be many factors responsible for the great differences in the degree of ploidity found in different plant groups. It is a well known fact that in some groups, like for instance the genus *Geum*, the majority of the species are polyploids, whereas in other groups natural polyploids do not exist. In the genus *Geum* all cytologically examined species are polyploids, and diploid species with  $2n = 14$  are known only from related genera *Waldsteinia* and *Coluria*. The *Geum* species cross very easily, the interspecific hybrids are usually vigorous and the fertile hybrids give also healthy and vigorous progenies. This high compatibility and the ability of the different genomes to work harmoniously together is, in my opinion, one of the reasons of the fertility of polyploids and of their great rôle in the evolution of this genus.

In the evolution of the genus *Crepis* (B a b c o c k 1947), which is one of the best cytogenetically studied of all genera, polyploidity has played only a minor rôle. From Babcock's and his collaborators work we see that compatibility in *Crepis* is lower than in the *Geum* genus, and, what is more important, the hybrids are usually sterile and often weak and sublethal. Also amphiploids raised in this genus (P o o l e 1931, 32, H o l l i n g s h e a d 1930a, b) are more or less sterile and of reduced vigour. It is not an accident that the only larger group of north-american polyploids found in this genus forms an „agamic complex“ which indicates that, in this case, polyploids can be maintained when they lose the ability of sexual reproduction. These facts suggest that the relatively high viability and fertility of the amphiploid described in this paper can be explained by the genic constitution of the parental genomes which, being structurally sufficiently homologous, have at the same time the ability to work harmoniously together in the vegetative and generative development of the hybrid plants. The second cause of the high fertility and constance of this amphiploid is a strong „differential affinity“ of the coniugating chromosomes and the low chiasmata frequency.

In my previous paper (W. G a j e w s k i 1953) I expressed the opinion that the chances to obtain dodecaploid amphiploids from highly fertile with normal chromosome coniugation hybrids of hexaploid *Eugeum* species are small because the progenies of these hybrids also are always hexaploid. It appeared, however, that this was not the case and the amphiploid obtained from a fertile hybrid proved to be even more fertile than the previously described amphiploid obtained from a sterile asynthetic hybrid. Thus the possibility to obtain fertile amphiploids from fertile, with normal chromosome coniugation hexaploid *Eugeum* hybrids does exist.

## SUMMARY

1. An interspecific  $F_1$  hybrid between two hexaploid ( $2n = 42$ ) species *Geum urbanum* x *G. molle* is described. This hybrid has a nearly normal course of meiosis with 21 bivalents in the majority of PMC's and forms, on the average, 23,9% of good pollen grains and 16,3% of good achenes.

2. In the  $F_1$  generation, besides hexaploid plants, one dodecaploid plant with  $2n = 84$  was found. The amphiploid differed in many traits from the hexaploid sister plants and formed, on the average, 70,3% of good pollen grains and 56,1% of good achenes. Its course of meiosis was very normal with 42 bivalents in the majority of the PMC's studied, and with only few cells with two or more univalents.

3. The progeny from hexaploid hybrids showed conspicuous segregation of all characters studied, whereas, the progeny of the amphiploid plant was very uniform.

4. The reasons for the high fertility and constancy of this amphiploid are discussed.

## LITERATURE CITED

- Babcock E. B., 1947, The Genus *Crepis* I. The Taxonomy, Phylogeny, Distribution and Evolution of *Crepis*. Univ. Calif. Publ. Bot., 21, 1—197.
- Beck v. Mannagetta G., 1895. Die *Geum*-Arten der Balkanländer. Verh. d. Zoolog. Bot. Gez. Wien, 45.
- Clausen R. E., 1928, Interspecific hybridization in *Nicotiana*. VII. The cytology of hybrids of the synthetic species *digluta* with its parents *glutinosa* and *Tabacum*. Univ. Calif. Publ. Bot., 11, 177—211.
- Clausen R. E. a Goodspeed T. H., 1925. Interspecific hybridization in *Nicotiana*. II. A tetraploid *glutinosa*-*Tabacum* hybrid, an experimental verification of Winge's hypothesis, Genetics, 10, 278—284.
- Gajewski W., 1946, Cytogenetic Investigations on *Anemone* L. I. *Anemone Janczewskii* a New Amphidiploid Species of Hybrid Origin. Acta Soc. Bot. Pol., 17, 129—194.
- Gajewski W. 1952, The hybrids between two subgenera of *Geum* L. Acta Soc. Bot. Pol., 21, 489—516.
- Gajewski W., 1953, A Fertile Amphipolyploid Hybrid of *Geum rivale* with *G. macrophyllum*. Acta Soc. Bot. Pol., 22, 411—439.
- Grant V., 1952, Cytogenetics of the hybrid *Gilia millefoliata* x *achilleaefolia*. I. Variations in meiosis and polyploidy rate as affected by nutritional and genetic conditions. Chromosoma, 5, 372—390.
- Hollingshead L., 1930a. Cytological investigation of hybrids and hybrid derivatives of *Crepis capillaris* and *Crepis tectorum*. Univ. Calif. Publ. Agric. Sci., 6, 55—94.
- Hollingshead L., 1930b. A lethal factor in *Crepis* effective only in an interspecific hybrid. Genetics, 15, 114—140.

- Newton W. C. F. a. Pellew C., 1929, *Primula kewensis* and its derivatives. Jour. Genetics, 20, 405—467.
- Poole C. F., 1931, The interspecific hybrid *Crepis rubra* x *C. foetida*, and some of its derivatives. I. Univ. Calif. Publ. Agric. Sci., 6, 169—200.
- Poole C. F., 1932, The interspecific hybrid *Crepis rubra* x *C. foetida*, and some of its derivatives. II. Two selfed generations from an amphidiploid hybrid. Univ. Calif. Publ. Agric. Sci., 6, 231—255.
- Stebbins G. L. Jr., 1947, Types of polyploids: their classification and significance. Advances in Genetics I, 403—429.
- Stebbins G. L. Jr., 1950. Variation and Evolution in Plants, Columbia Univ. Press, New York.