

# The inheritance of specific traits in the hybrid *Geum coccineum* x *rivale*

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The genetical analysis of specific differences is one of the most important tools in the study of speciation processes. Such analysis is in most cases impossible as the interspecific hybrids are usually sterile. In case of partial sterility the segregation is often disturbed by selective elimination of unbalanced gametes and zygotes.

In the genus *Geum* many species give quite fertile hybrids with normal segregation in  $F_2$ . The best known is the hybrid between *G. urbanum* and *G. rivale* studied genetically by W i n g e (1938), M a r s d e n - J o n e s (1930), P r y w e r (1932) and others. In the present paper I describe another quite fertile species hybrid and compare its behaviour with the hybrid mentioned above.

## I. THE DESCRIPTION OF PARENTAL SPECIES

### 1. *Geum rivale* L.

A) S o u r c e o f m a t e r i a l: Plants from two sources were used for the crosses described below. Plants from culture nmb. 37—2 were from living specimens transplanted from Piastów near Warsaw. Plants from culture nmb. 37—12 were raised from seeds obtained from the Botanical Garden in Copenhagen. These plants were cultured since the year 1937 for 12 years and twice propagated from seeds. A small variation in nearly all quantitative traits was observed showing that the plants were probably heterozygous for many genes with small effects.

B) Description of plants: More important characters of this species are (cult. nmb. 37—2): Stem 45—60 cm, usually with 3 flowers. Basal leaves longstalked, oddpinnate, sparingly hairy on both sides, Lateral leaflets few, small, obovate, spaced. Terminal leaflet much larger, with cuneate base rounded above. All leaflets irregularly lobed, dentate and serrate. Cauline leaves few, small, lower stalked, upper sessile with small ovate, serrate stipules. The upper part of the plant purplish-brown coloured with anthocyanin and with numerous longstalked glandular hairs. The flowers on nodding peduncles, campanulate. Sepals purplish brown from anthocyanin, erect, 10—15 mm. long, pilose and glandular, bractlets 5—6 mm long. Petals erect, obovate, emarginate, abruptly narrowed into a claw, cream coloured with plastid pigment and with purple anthocyanin in cell sap, shorter or as long as sepals. Achenes small, long haired and glandular, numerous on a short, hairy receptacle. Receptacle on a 6—10 mm long gynophore. Styles long up to 12 mm, tipped with a circular hook, long haired and glandular. Stigmatal part 5—6 mm long with plumose hairs.

This biotype represents typical *G. rivale* L. and will be referred later as *G. rivale typicum*. The plants from culture nmb. 37—12 were totally devoid of anthocyanin, both vegetative parts and calyx being green and the petals pure pale cream. Other traits are similar to the typical form, the plants being only smaller, less hairy, with more deeply lobed and serrate leaves. This form represents *G. rivale* L. var. *pallidum* Blytt. and will be referred to later as *G. rivale pallidum*.

## 2. *Geum coccineum* Sibth. et Sm.

A) Source of material: Culture nmb. 35—45 was raised from seeds obtained from the Botanical Garden in Sofia with adnotation that the seeds were collected in the Rhodope mountains. In 12 years the plants were twice propagated from selfed seeds and proved to be highly homozygous, as the segregation was negligible.

B) Description of plants: Stem 30—45 cm with 3—7 flowers. Stems and leaves densely, silky hairy with long simple hairs, the upper part of the plant glandular. Anthocyanin absent. Basal leaves short stalked, lateral leaflets small ovate. Terminal leaflet large sub-orbicular to reniform, with cordate base shallowly lobate and dentate. Flowers on erect peduncles. Flowers quite open with sepals recurved. Sepals 5 mm long, bractlets small. Petals ho-

horizontally spread, nearly twice as large as sepals, sub-orbicular, without claw and emargination, poppy red (No 16 acc. to Hort. Colour Cart). Receptaculum 4—5 mm long, shortly haired. Achenes numerous, 4—5 mm long, haired with simple and glandular hairs. The part of the style persisting on the achenes tipped with a hook-like structure (called acc. to B o l l e (1933) hereafter as rostrum) is short (3—5 mm) nearly glabrous. Stigmatal part 6 mm long, nearly glabrous. Gynophore lacking or  $1/2$ — $3/4$  mm long.

## II. THE DESCRIPTION OF $F_1$ , $F_2$ , $F_3$ HYBRIDS AND THE BACKCROSSES

In the year 1937 I have made four reciprocal crosses among *G. coccineum* and the two forms of *G. rivale*. The percentage of seed-setting in all cases was rather high, ranging from 63,5 to 85 per cent. The four  $F_1$  populations consisted of 209 plants. Owing to small heterozygosity of the parental species the hybrids showed little variation in quantitative traits such as position of petals and sepals, form of leaves, length of gynophore and other characters. Between the reciprocal hybrids any conspicuous difference was found. The vitality and vigour of the hybrids was quite normal and in the dimensions of stems and leaves hybrid heterotical effect was observed. By open pollination the seed setting was quite normal. By selfing these hybrids, like all *Geums*, showed much reduced fertility, probably as the result of partial selfsterility.

Two  $F_2$  families were raised from selfed  $F_1$  plants: one consisting of 107 plants (culture nomb. 39—55) from the hybrid *G. coccineum* x *rivale typicum* and the second — of 192 plants from the hybrid *G. coccineum* x *G. rivale pallidum* (cult. nomb. 39—56). The numbers unfortunately are small but many plants were lost during the war period (1939—46) when the work must have been postponed and now the experimental garden for these experiments is small and I was always short of place.

The  $F_3$  generations were raised from 25 selfed  $F_2$  plants, they were sown in the year 1946 and flowered in 1948 (culture nomb. 46—241 to 46—255). The numbers of plants cultivated in each  $F_3$  families were rather small; together 506  $F_3$  plants were grown to maturity in the years 1947—49.

In the year 1946 the  $F_1$  hybrid *G. coccineum* x *rivale pallidum* was backcrossed to its two parental species. The two respective backcross families cult. nomb. 46—110 with *G. rivale pallidum* and 46—111 with *G. coccineum* consisted of 102 and 42 plants. They flowered first time in 1948.

Only some of the specific traits were more precisely analysed and namely these that were easier to count or measure. Such traits as shape and size of leaves, stipules, degree and character of hairiness are rather difficult to be quantitatively described.

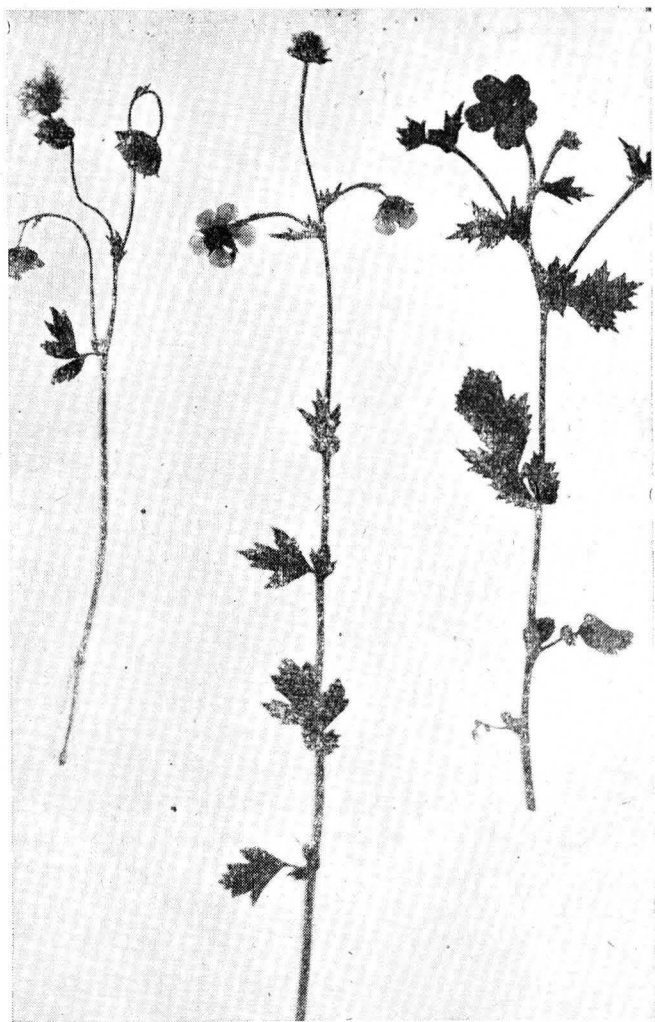


Fig. 1. *G. rivale* on the left,  $F_1$  hybrid in the centre and *G. coccineum* on the right.

1) Presence of the anthocyanin. In the cross of *G. rivale typicum* x *rivale pallidum* the presence of anthocyanin is dominant in  $F_1$  and in  $F_2$  a monogenic segregation was observed.

Actual numbers were 60 plants with anthocyanin and 19 without. The same result was obtained also by Dahlgren (1924).

The  $F_1$  hybrid *G. coccineum* x *rivale typicum* was with anthocyanin but less intensively coloured. In  $F_2$  generation a segregation into 78 plants with anthocyanin to 29 without it was found. This segregation fits with the theoretical ratio 3 : 1 (80,25 : 26,75). The plants with anthocyanin differed among them as to the amount of the pigment and in its distribution. Some plants were found with anthocyanin present only in the vegetative parts without any traces of it in the floral parts. In 25  $F_3$  families, 5 from plants without anthocyanin all bred true and in the remaining 20 families derived from plants with anthocyanin only 4 bred true and the other segregated.

2. Colour of the petals. The  $F_1$  hybrid has bright yellow petals (Buttercup-yellow no 5, acc. to Hort. Colour Cart), a colour that does not occur in any of the parental species which have cream and orange-red coloured petals. In  $F_2$  the segregation is very complicated; nearly every plant has a somewhat different shade of colour. Exact classification is impossible, but disregarding the differences in shades and intensity of the colours three main colour categories, namely yellow, red to orange and cream to nearly white could be distinguished in the following proportions:

|                                                 | yellow | red-orange | cream-white |
|-------------------------------------------------|--------|------------|-------------|
| $F_2$ <i>coccineum</i> x <i>rivale typicum</i>  | 63     | 20         | 24          |
| $F_2$ <i>coccineum</i> x <i>rivale pallidum</i> | 106    | 42         | 44          |
| total                                           | 169    | 62         | 68          |

These proportion are related to the 9 : 3 : 4 ratio and show that the synthesis of yellow pigment is due to interaction of at least two main different factor pairs.

Two  $F_3$  families nmbs. 46—243 and 46—250 from yellow flowering  $F_2$  plants bred true for this colour, but they consisted only of 15 and 17 plants. All other  $F_3$  families were segregating for the flower colour. A family nmb. 46—241 from brick-red  $F_2$  plant consisted of 29 plants with red to orange flowers and 11 yellow with reddish tint. A family nmb. 46—247 from pale cream  $F_2$  plant has segregated in 12 yellow, 11 cream, 3 red, 6 pale cream nearly white. A family nmb. 46—251 from yellow  $F_2$  plant gave 24 yellow, 6 cream,

3 salmon-cream, 5 red and 2 brick-yellow. Other families gave also complicated segregations, but as the numbers of plants are small they are not worth to be mentioned.

The backcross to *G. rivale pallidum* gave 60 plants with cream coloured petals and 52 with yellow, which fits rather well to 1 : 1 ratio expected for such cross. The second backcross with *G. coccineum* segregated in 17 yellow and 25 red flowering plants. With such complicated segregations much larger families should be grown to settle the question of flower colour inheritance. Besides the main plastid pigments, the petals in the crosses with *G. rivale typicum* have also in different quantities the red anthocyanin, which sometimes masks totally the background colour.

3. The length of gynophore. The length of the gynophore in different *Geum rivale* biotypes differ greatly. It is (1913), from herbarium material, gives its length from 0,5 to nearly 20 mm. Great care must be taken to measure gynophore length in flowers with fully ripe seeds as it elongates greatly during the ripening period of the seeds. Our two *Geum rivale* cultures differed only slightly in this character as is to be seen from the Table no 1.

Table no. 1. Length of the gynophore.

| Cul-<br>ture<br>nmb. | Name of plants                                    | Length of gynophore in mm: |    |    |   |   |   |    |    |    |   |    |    | M    |
|----------------------|---------------------------------------------------|----------------------------|----|----|---|---|---|----|----|----|---|----|----|------|
|                      |                                                   | 0                          | 1  | 2  | 3 | 4 | 5 | 6  | 7  | 8  | 9 | 10 | 11 |      |
| 37—2                 | <i>G. rivale typicum</i>                          |                            |    |    |   |   | 1 | 10 | 25 | 8  | 2 | 3  | 1  | 6,80 |
| 37—12                | <i>G. rivale pallidum</i>                         |                            |    |    |   |   | 2 | 9  | 13 | 15 | 9 | 2  |    | 7,02 |
| 37—45                | <i>G. coccineum</i>                               | 50                         |    |    |   |   |   |    |    |    |   |    |    | 0,50 |
| 37—55                | F <sub>1</sub> <i>cocc.</i> x <i>riv. typ.</i>    | 81                         | 2  |    |   |   |   |    |    |    |   |    |    | 0,52 |
| 37—55                | F <sub>2</sub> <i>cocc.</i> x <i>riv. typ.</i>    | 79                         | 12 | 9  | 6 | 1 |   |    |    |    |   |    |    | 0,98 |
| 39—56                | F <sub>2</sub> <i>cocc.</i> x <i>riv. pallid.</i> | 147                        | 20 | 12 | 5 | 8 |   |    |    |    |   |    |    | 0,98 |
| 46—110               | B <sub>1</sub> with <i>rivale pallid.</i>         | 39                         | 18 | 28 | 9 | 2 | 4 | 2  |    |    |   |    |    | 1,88 |
| 46—111               | B <sub>1</sub> with <i>coccineum</i>              | 42                         |    |    |   |   |   |    |    |    |   |    |    | 0,50 |

As we see the lack of gynophore of *G. coccineum* is completely dominant in F<sub>1</sub>. In F<sub>2</sub> the segregation is rather small, most of the plants lacking gynophore and the other have a very short one. Even in the backcross with *G. rivale* only few plants have as long a gynophore as *G. rivale*. This mode of inheritance strongly suggests that *G. coccineum* possesses many suppressors for gynophore growth.

4. The position of the sepals and petals. The  $F_1$  hybrids possess more or less horizontal or slightly recurved sepals and the petals are horizontal or somewhat erected. Different flowers on the same plant may differ in position of floral parts. Usually the sepals are more recurved after the anthesis. In  $F_2$  a great variation in the position of sepals and petals was found. It is most interesting that the position of the calyx and corolla was inherited independently. The classification is rendered rather difficult and uncertain as the position of sepals and petals varies in one and the same flower during and after anthesis. For the classification given below (Table no 2) only the flowers just after the beginning of the anthesis were used.

Table no. 2. Position of sepals and petals in the  $F_2$  family nmb. 39-56

|                    |            | Position of petals |         |            |       |
|--------------------|------------|--------------------|---------|------------|-------|
|                    |            | upright            | erected | horizontal | Total |
| Position of sepals | upright    | 4                  | —       | —          | 4     |
|                    | erected    | 10                 | 34      | 4          | 48    |
|                    | horizontal | 18                 | 34      | 54         | 106   |
|                    | recurved   | 2                  | 6       | 26         | 34    |
| Total              |            | 34                 | 74      | 84         | 192   |

As we see the upright position of calyx and corolla like that in *G. rivale* was found only in 4 plants, whereas the plants with recurved calyx and horizontal petals like that in *G. coccineum* were much more numerous (26 plants). In the backcross with *G. rivale pallidum* in 102 plants only one had the calyx somewhat recurved, 53 had the calyx horizontal or slightly erected and 48 plants had an upright calyx like *G. rivale*. In all plants the petals were more or less erected to quite upright. In  $F_3$  families the great majority show segregation like in  $F_2$  families, but in 6 families all plants have a recurved calyx and horizontal petals like *G. coccineum*, none of the  $F_3$  families was of the *rivale* type.

5. The shape and size of the petals. The  $F_1$  plants show no emargination on the top of the petals and only a very short rudimentary claw. In  $F_2$  and the backcrosses the length of the claw was as follows (Table no. 3).

Table no. 3. Length of the claw.

| Culture nmb. | Name of plants:                                     | Length of the claw in mm: |       |     |     |
|--------------|-----------------------------------------------------|---------------------------|-------|-----|-----|
|              |                                                     | absent                    | 0,5—2 | 2—4 | 4—6 |
| 38—56        | F <sub>2</sub> <i>coccin.</i> x <i>riv. pallid.</i> | 40                        | 110   | 38  | 4   |
| 46—110       | B <sub>1</sub> with <i>rivale pallid.</i>           |                           | 20    | 32  | 50  |
| 46—111       | B <sub>1</sub> with <i>coccineum</i>                | 38                        | 14    | 2   |     |

As we see from the table no. 3 and fig. 2, in F<sub>2</sub> most of the plants have a rudimentary claw as in F<sub>1</sub>, the plants without claw like *G. coccineum* are numerous whereas plants with a long claw like *G. rivale* are only 4.

The emargination is quite recessive in F<sub>1</sub> and has reappeared in F<sub>2</sub> in 56 out of 192 plants. This ratio only poorly fits to the monogenic 3 : 1 ratio (expected 48 : 144). In the backcross with *G. rivale pallidum* 54 plants were with emarginate petals and 48 with rounded tops which is near to the expected 1 : 1 segregation. In F<sub>3</sub> most of the families were still segregating but 6 were uniform without emargination.

The dimensions of petals are represented in tables nos. 4 a. 5.

Table no. 4. Length of the petals.

| Culture nmb. | Name of plants                                  | Length of petals in mm: |   |    |    |    |    |    |    |    |    |    |    |    |  |  |  | M     | δ    |
|--------------|-------------------------------------------------|-------------------------|---|----|----|----|----|----|----|----|----|----|----|----|--|--|--|-------|------|
|              |                                                 | 6                       | 7 | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 |  |  |  |       |      |
| 37—12        | <i>G. rivale pallidum</i>                       |                         |   | 2  | 8  | 20 | 12 | 7  | 1  |    |    |    |    |    |  |  |  | 9,84  | 1,05 |
| 37—45        | <i>G. coccineum</i>                             |                         |   |    |    |    | 2  | 23 | 38 | 35 | 12 | 8  | 1  |    |  |  |  | 13,01 | 1,17 |
| 37—56        | F <sub>1</sub> <i>coccin</i> x <i>riv. pal.</i> |                         |   |    |    | 4  | 21 | 32 | 12 | 8  | 1  |    |    |    |  |  |  | 11,52 | 1,03 |
| 38—56        | F <sub>2</sub> <i>coccin</i> x <i>riv. pal.</i> | 1                       | 5 | 20 | 32 | 35 | 41 | 27 | 21 | 6  | 3  |    |    | 1  |  |  |  | 11,09 | 1,78 |
| 46—110       | B <sub>1</sub> with <i>G. riv. pal.</i>         |                         |   | 2  | 2  | 18 | 50 | 26 | 4  |    |    |    |    |    |  |  |  | 11,55 | 0,27 |
| 46—111       | B <sub>1</sub> with <i>G. coccineum</i>         |                         |   |    |    | 2  | 6  | 11 | 16 | 4  | 3  |    |    |    |  |  |  | 13,05 | 1,16 |

Table no. 5. Breadth of the petals.

| Culture<br>nmb. | Name of plants                                  | Breadth of petals in mm: |    |    |    |    |    |    |    |    |    |    |    |    |    |    |  |       | M    | δ |
|-----------------|-------------------------------------------------|--------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|--|-------|------|---|
|                 |                                                 | 6                        | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |  |       |      |   |
| 37—12           | <i>G. rivale pallidum</i>                       | 6                        | 22 | 18 | 4  |    |    |    |    |    |    |    |    |    |    |    |  | 7,9   | 0,23 |   |
| 37—45           | <i>G. coccineum</i>                             |                          |    |    |    |    |    | 5  | 12 | 30 | 16 | 4  | 2  |    |    |    |  | 14,39 | 1,04 |   |
| 37—56           | F <sub>1</sub> <i>coccin</i> x <i>riv. pal.</i> |                          |    |    | 4  | 11 | 43 | 18 | 2  |    |    |    |    |    |    |    |  | 11,53 | 0,24 |   |
| 39—56           | F <sub>2</sub> <i>coccin</i> x <i>riv. pal.</i> | 5                        | 8  | 13 | 20 | 35 | 40 | 27 | 12 | 14 | 5  | 1  |    | 1  | 1  |    |  | 11,30 | 2,20 |   |
| 46—110          | B <sub>1</sub> with <i>G. riv. pal.</i>         | 5                        | 21 | 54 | 16 | 4  | 2  |    |    |    |    |    |    |    |    |    |  | 8,5   | 0,28 |   |
| 46—111          | B <sub>1</sub> with <i>G. coccineum</i>         |                          |    |    |    | 1  | 2  | 12 | 12 | 12 | 2  | 1  |    |    |    |    |  | 13,5  | 1,14 |   |



plants the number of petals was from 10 do 18, whereas parental species and  $F_1$  plants have 5 or rarely 6 petals. Both these phenomena were correlated, as in 11 out of 18 plants with supernumerary petals the margin of the petals was in the same time fringed or undulated. Perhaps they are both the expression of some morphogenetic disturbances during the floral development. In  $F_3$  families raised from  $F_2$  plants with supernumerary and fringed petals these characters did appear only in a few plants most being normal with 5 petals.

6. The size of the sepals. I have measured only the length of the sepals which in different families was as follows (Table no. 6):

Table no. 6. Length of the sepals.

| Culture<br>nmb.: | Name of plants:                                 | Length of sepals in mm: |    |    |    |    |    |    |    |    |    |    |    |    |   |       | M    | δ |
|------------------|-------------------------------------------------|-------------------------|----|----|----|----|----|----|----|----|----|----|----|----|---|-------|------|---|
|                  |                                                 | 4                       | 5  | 6  | 7  | 8  | 9  | 10 | 11 | 12 | 13 | 14 | 15 | 16 |   |       |      |   |
| 37 — 12          | <i>G. rivale pallidum</i>                       |                         |    |    |    |    |    |    |    |    | 3  | 34 | 9  | 3  | 1 | 12,86 | 0,20 |   |
| 37 — 45          | <i>G. coccineum</i>                             | 2                       | 10 | 49 | 8  |    |    |    |    |    |    |    |    |    |   | 6,42  | 0,16 |   |
| 37 — 56          | F <sub>1</sub> <i>coccin</i> x <i>riv. pal.</i> |                         |    |    |    |    | 8  | 33 | 26 | 8  | 3  |    |    |    |   | 10,05 | 0,28 |   |
| 39 — 56          | F <sub>2</sub> <i>coccin</i> x <i>riv. pal.</i> | 4                       | 13 | 25 | 29 | 51 | 38 | 8  | 13 | 5  | 1  | 3  | 2  |    |   | 8,59  | 2,03 |   |
| 46 — 110         | B <sub>1</sub> with <i>G. riv. pal.</i>         |                         |    |    |    |    | 2  | 8  | 18 | 29 | 21 | 19 | 2  | 3  |   | 11,86 | 1,43 |   |
| 46 — 111         | B <sub>1</sub> with <i>G. coccin.</i>           |                         | 1  | 18 | 20 | 3  |    |    |    |    |    |    |    |    |   | 7,10  | 0,18 |   |

The inheritance of the length of the sepals is, like the dimensions of petals, of a polygenic nature. The length of the bractlets below the calyx was inherited in a similar way but it was not measured.

7. The nodding of the floral peduncles. The nodding peduncles of *G. rivale* are nearly recessive as the  $F_1$  plants have only slightly nodding peduncles. In  $F_2$  it was observed a continuous variation between the quite erect position of flowers, like in *G. coccineum*, to nearly as nodding as in *G. rivale*. The exact classification was impossible, it can only be stated that plants with quite erect peduncles were numerous, plants of the *rivale* type only very few, most being intermediate. In the backcross with *G. coccineum* 16 plants had erect peduncles and 26 slightly nodding-ones. In the backcross with *G. rivale* all plants had nodding peduncles but in different degrees. In 25  $F_3$  families, 8 were uniform with erect peduncles and all other were segregating.

8. The length of the shoots and shape and size of the leaves.

Although the parental species differ clearly in these characters the exact analysis of different hybrid generations is extremely difficult as these characters are even in the pure species very variable. In  $F_1$  plants the height of the shoots and the number of flowers on the shoot are somewhat greater as in parental plants due probably to hybrid vigour. In  $F_2$  the segregation of the height of the shoots and number of the flowers is apparent, but strongly depending on general individual vigour of different plants, the density of planting and other external factors.

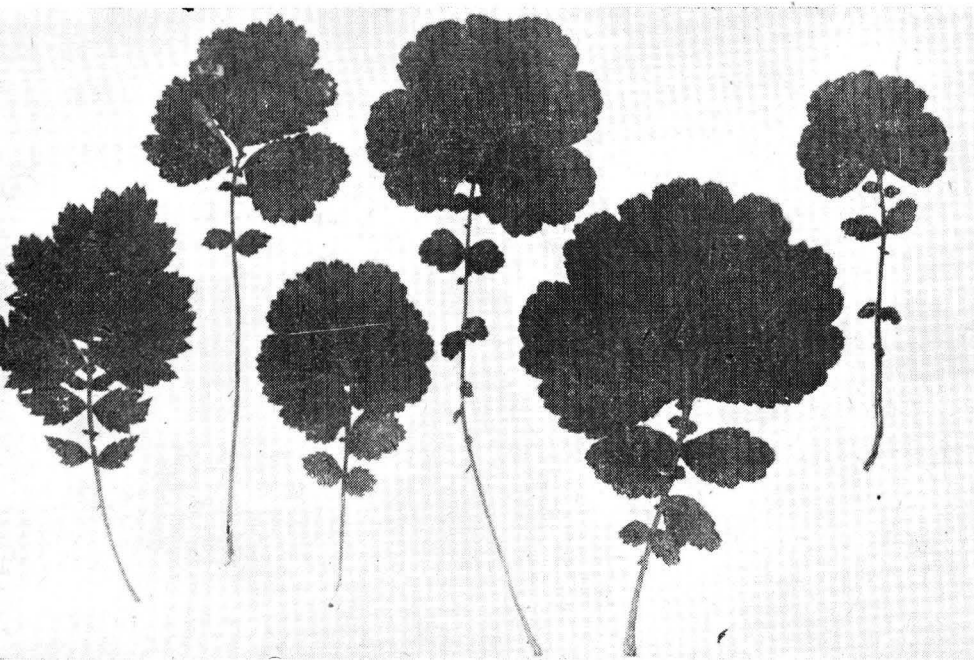


Fig. 3. Basal leaves of *G. rivale* (two on the left),  $F_1$  hybrid (two in the centre) and of *G. coccineum* (two on the right).

The variation in the shape and size of the leaves is very striking in all *Geum* species. The polymorphism of the leaves has a seasonal character as the leaves developing in early spring have more lateral leaflets and the terminal leaflet is smaller and more dissected, the later leaves have fewer lateral leaflets and the terminal leaflet is bigger and less dissected. Both parental species differ distinctly in their shape and size of the leaves but a biometrical

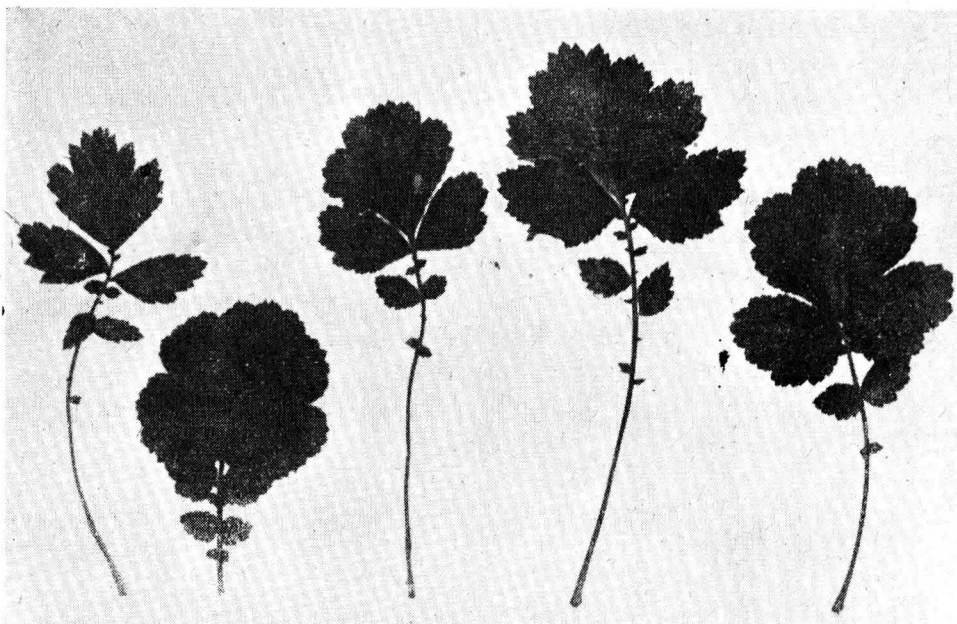


Fig. 4. Basal leaves of different  $F_2$  plants.

analysis was not attempted. The  $F_1$  leaves are in general intermediate in shape but greater, but even in one and the same plant some leaves are more alike to *G. coccineum* and others to *G. rivale*. In  $F_2$  and  $F_3$  families a great variation occurs. Many plants have leaves of a shape quite unlike to any parental species. The backcrossed plants have in general leaves very near in shape to the backcrossed parental species. Some idea about the shape of the leaves give the figs. 3 a 4.

9. The mode of hairiness. Both species have two types of hairs: simple and glandular, they differ only in the degree of hairness — *G. coccineum* has much denser simple hairs but is less glandular than *G. rivale*.  $F_1$  is intermediate and in  $F_2$  a segregation occurs, but as the differences between parental species are small, both parental types are already reconstructed in  $F_2$ .

10. The structure of achenes and styles. The structure of achenes together with the styles is a very important taxonomic character in the whole genus. Both parental species belong to the subgenus *Eugeum* with geniculate styles and to the section *Gmeliniana* with a long and slender stigmatal part. They differ

greatly in the length of their styles and mode of hairiness. *G. rivale* has a long rostrum pennately haired and with numerous glandular hairs, the stigmatal part is also long and densely haired. *G. coccineum* has a short rostrum and together with stigmatal part nearly



Fig. 5. Achenes together with styler structures: First row *G. rivale* (left) and *G. coccineum* (right), second row  $F_1$  hybrid, third row  $F_2$  plants, fourth row backcross with *G. coccineum*, fifth row backcross with *G. rivale*.

glabrous. The  $F_1$  plants have short rostra like the *coccineum* parent but the mode of hairiness is intermediate. In  $F_2$  a great segregation was found both as to the length of rostrum as to its mode of hairing too. Some idea about the different types of achenes gives the fig. 5. The segregation of the length of rostrum is given in the following Table no. 7.

Table no. 7. Length of rostrum.

| Culture nmb. | Name of plants                        | Length of rostrum in mm: |    |    |    |    |    |    |   |    |    |    | M    | $\sigma$ |
|--------------|---------------------------------------|--------------------------|----|----|----|----|----|----|---|----|----|----|------|----------|
|              |                                       | 1                        | 2  | 3  | 4  | 5  | 6  | 7  | 8 | 9  | 10 | 11 |      |          |
| 37—12        | <i>G. rivale pallidum</i>             |                          |    |    |    |    |    | 1  | 2 | 21 | 35 | 4  | 9,11 | 0,20     |
| 37—45        | <i>G. coccineum</i>                   | 3                        | 12 | 41 |    | 3  |    |    |   |    |    |    | 3,25 | 0,17     |
| 37—56        | $F_1$ <i>cocc.</i> x <i>riv. pal.</i> | 1                        | 18 | 38 | 16 | 4  |    |    |   |    |    |    | 3,52 | 0,37     |
| 69—56        | $F_2$ <i>cocc.</i> x <i>riv. pal.</i> | 1                        | 20 | 46 | 50 | 41 | 15 | 8  | 1 |    |    |    | 4,55 | 1,29     |
| 46—110       | $B_1$ with <i>G. riv. pal.</i>        |                          |    | 1  | 12 | 32 | 23 | 19 | 8 | 3  | 3  | 1  | 5,52 | 1,42     |
| 46—111       | $B_1$ with <i>G. coccin.</i>          | 1                        | 9  | 29 | 6  | 2  | 1  |    |   |    |    |    | 3,54 | 0,25     |
| 46—244       | $F_3$ <i>cocc.</i> x <i>riv. pal.</i> | 2                        | 5  | 9  |    |    |    |    |   |    |    |    | 2,93 | 0,24     |
| 46—251       | $F_3$ <i>cocc.</i> x <i>riv. pal.</i> |                          |    |    | 1  | 2  | 13 | 21 | 4 | 2  |    |    | 7,23 | 0,28     |

As we see from this table the short rostrum of *G. coccineum* is dominant. In  $F_3$  families 18 out of 25 show short styles like these in *G. coccineum* (as the family 46—244) in the table above. None of the families was of the *rivale* type: the family 46—251 had the longest styles.

11. The fertility. Both parental species have seeds and pollen fertility quite normal. The  $F_1$  plants have seeds fertility very high ranging from 74 to 93 per cent, only 4% of plants showed fertility below 80%. The pollen fertility however was distinctly lowered and it ranged in different preparations from 61,0%, to 68,6% the average being 66,6%. In  $F_2$  the majority of plants had normal pollen fertility:

| Fertility in %                 | 40—60 | 60—80 | 80—100 |
|--------------------------------|-------|-------|--------|
| Nmbs. of exam. plants — pollen | 3     | 12    | 48     |
| " " " " — seeds                |       | 10    | 53     |

The backcross with *G. rivale* has seeds and pollen fertility between 80 and 100%, whereas the backcross with *G. coccineum* has normal seeds fertility but the pollen fertility is between 60 and 80%. All the  $F_3$  families were also highly fertile.

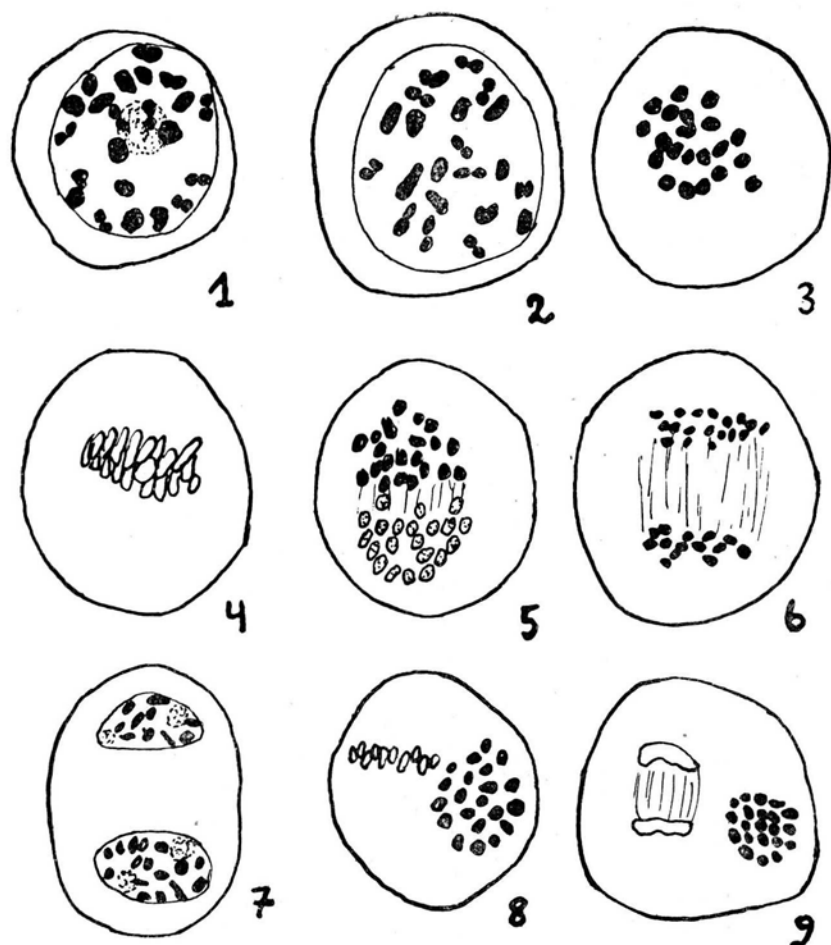


Fig. 6. The course of meiosis in P. M. C. of the  $F_1$  hybrid. 1 — diakinesis, 2 — late diakinesis, 3 — metaphase — I from polar view, 4 — metaphase — I from side-view, 5 — anaphase — I, 6 — late anaphase — I, 7 — interkinesis, 8 — metaphase — II, 9 anaphase — II.

12. The cytological analysis. I have studied only meiotic divisions in P. M. C. The permanent preparations were stained with cristall-violet acc. to Newton's method. Both parental species have 21 chromosomes as haploid number. The course of meiosis is quite normal. In  $F_1$  hybrids the great majority of P. M. C. at M—I show only 21 bivalents (fig. 6) and I have found only twice in many hundreds of examined P. M. C. one pair of univalents and

20 bivalents. In general the course of meiosis is like in the parental species. In some of the cytologically examined  $F_2$  and  $F_3$  plants any irregularities in the course of meiosis were observed.

### III. THE COMPARISON OF THE HYBRIDS OF *G. RIVALE* WITH *G. COCCINEUM* AND *G. URBANUM*

The inheritance in  $F_2$  and backcrosses of the hybrid *G. rivale*  $\times$  *C. urbanum* was studied by Winge (1938), Marsden-Jones (1930), Prywer (1932), Weiss (1912) and Rosen (1916). The comparison of the data gathered by the above authors with the inheritance of specific traits in the hybrid *G. rivale*  $\times$  *cocci-*

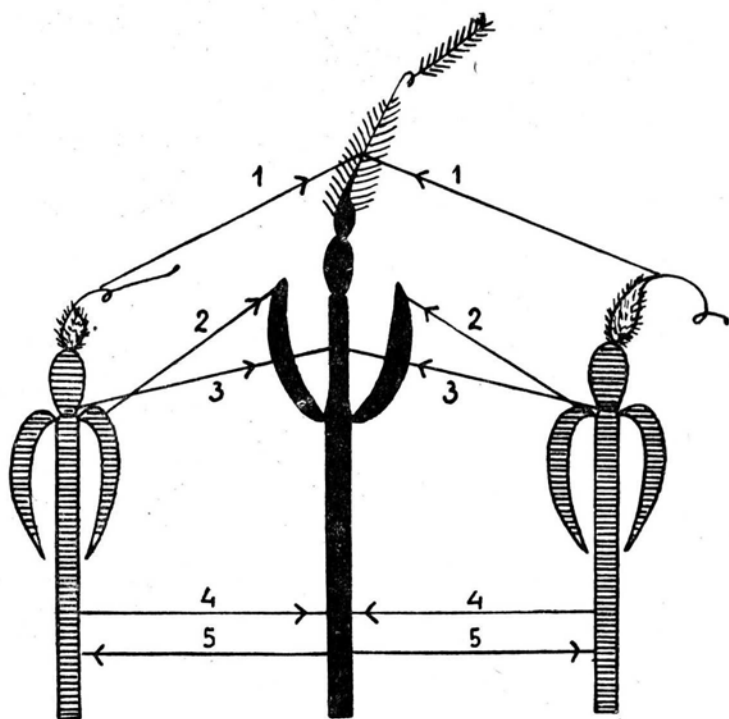


Fig. 7. A schematic representation of the genetical relationships of some specific traits among *G. rivale* and *G. urbanum* and *coccineum*. *G. rivale* centre, *G. coccineum* to the left and *G. urbanum* to the right. The arrows show the dominance of respective traits: 1 — of short and glabrous rostra of *G. coccineum* and *urbanum* over the long and hairy rostrum of *G. rivale*. 2 — of the recurved sepals of both species over erect-ones of *rivale*. 3 — of the lack of the gynophore over its presence in *rivale*. 4 — of the erect peduncles over nodding-ones in *rivale* and 5 — of the presence of anthocyanin in *rivale* over its lack in both other species.

*neum* reveals striking similarities between these two hybrids. The lack of gynophore, short and nearly glabrous rostrum, recurved sepals and horizontal petals, erect peduncles which are characteristic in common for *G. coccineum* and *urbanum*, behave in the same way in  $F_1$  and  $F_2$  hybrids with *G. rivale*. They show nearly complete dominance in  $F_1$  and polygenic segregation in  $F_2$  of nearly the same type in both hybrids. The presence of anthocyanin in *G. rivale* is dominant over its lack in *G. coccineum* and *urbanum* and in  $F_2$  a monogenic segregation occurs. The cream colour of the petals of *G. rivale*, red of *G. coccineum* and yellow of *G. urbanum* are allelomorphic and the yellow colour is synthesized in  $F_1$  plants between cream *G. rivale* and red *G. coccineum*. Probably at least three pairs of chief colour factors are present in these *Geum* species. Also the shape and size of the petals in both discussed hybrids are inherited in a very similar way. Other characters of *G. urbanum* and *G. coccineum* were not quite comparable as for instance the much branched shoots, short stigmatal part of the styles of *G. urbanum* are not present in *G. coccineum*. But the characters listed above show a curious parallelism in the mode of genic structure of both these species (see fig. 7).

All these species possess the same chromosome number  $2n=42$  and the hybrid among them (except the hybrid *G. coccineum*  $\times$  *urbanum* which was not yet studied) show a very high fertility, and nearly normal chromosome conjugation\*.

Doubtless the main differences among these species are of genic nature, the structural differences among the chromosomes, if present, play a secondary role. The presence of allelomorphic genes in all these three species and of very similar polygenic complexes strongly suggest that these species have evolved from a common ancestral population through gradual genic differentiation. The curious parallelism in genic structure of *G. coccineum* and *G. urbanum* can be explained, I think, by the action of natural selection

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\* After this manuscript was already completed, in autumn of the 1950 flowering season, some few  $F_1$  plants of the hybrid *G. coccineum*  $\times$  *urbanum* have flowered and fruited. The hybrids have dark yellow petals (Apricot 609 acc. to Hort. Colour Cart) and they show distinctly lower fertility as the hybrids discussed above. The pollen fertility was between 65% and 78% (in average 72%) and the seeds fertility was from 37,2% to 58,8% (in average 51,3%). The course of meiosis in PMC, like in hybrids of parental species with *G. rivale*, is highly normal. The majority of PMC show normal pairing with only 21 bivalents and only about 12% of PMC possess 2 to 6 univalents.

acting in the direction of better adaptation to the epizoochoric mode of seeds dissimination. It seems that the type of *Geums* with hooked rostrum adapted to epizoochorism is an advanced in this genus. The more primitive forms have long, slender, straight styles usually pinnately haired adapted to anemochorism like the species of the section *Oreogeum* yet living in the European mountains (*G. montanum*, *reptans* and *bulgaricum*) or of the section (or genus acc. to B o l l e 1933) *Erythrocoma* (*G. triflorum*, *canescens*, *ciliatum*) yet living in North America, also chiefly in mountains. The last species *G. ciliatum* possess already a primitive hooked curvature below the stigmatal part of the style. These species possess always paucifloral shoots and the calyx is upright or somewhat erected but never recurved. The section *Eugeum* comprises chiefly lowland species with wide areas, many species are pluri floral, the calyx is usually deflexed, and the rostrum short, hard, shortly haired and with a typical hook on the top. Alleraly I l t i s (1913) has noticed that in this section nearly all species with upright or erected calyx have also a long gynophore, whereas the species with recurved calyx possess no gynophore. As we have seen the position of the calyx and the length of gynophore are inherited quite independently and this coincidence found in nature can be explained by natural selection as for epizoochorism the elevation of the hooked styles above the level of the sepals acts favourably for the easiness of seeds transport by animals. In plants with recurved calyx the long gynophore is useless.

It seems to me that *G. rivale* with long, slender pinnately haired styles represents a more primitive species staying in the midway between anemochorism and epizoochorism, whereas especially *G. urbanum*, but also *G. coccineum* with short, strong, nearly glabrous rostrum represent more advanced types better adapted to epizoochorism. I do not mean that *G. rivale* represents a putative ancestor of these species, it can only have some more primitive traits. The more advanced traits as recurved calyx, short, strong and glabrous rostrum are all nearly dominant with *G. rivale*, showing polygenic inheritance, and I think they have evolved gradually through genic mutations and were favoured by selection. In both *G. coccineum* and *G. urbanum* these systems were built paralelly and independently by natural selection acting towards the best adapted epizoochoric type.

Now arises the question, how it was possible that such similar genic systems were built without any physiological barriers like species incompatibility or hybrid sterility. Even the geographical

factor (allopatric speciation acc. to M a y r) could not play the major role as the areas of these species are partially overlapping (see fig. 8). The most decisive factors separating these species are the differences in their ecological requirements, different time of flowering and differences in pollination biology. In the Balcan Peninsula and in Asia Minor, where both *G. rivale* and *G. coccineum* grow together, they are separated by differences in altitudinal distribution. *G. rivale* grows there on lower altitudes, chiefly in the forest zone, whereas *G. coccineum* is there a typical element of alpine mea-

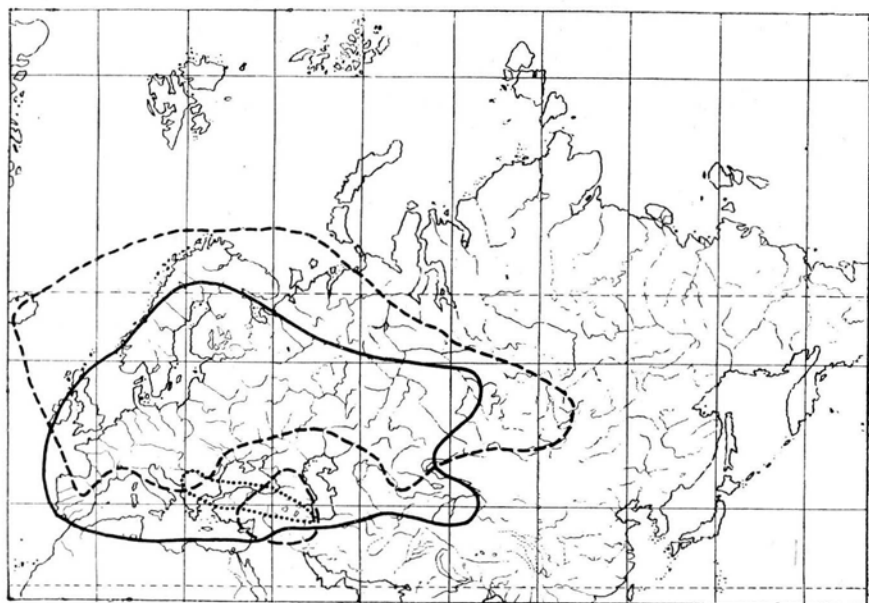


Fig. 8. Map showing the distribution in Eurasia of *G. rivale*, *G. urbanum* and *G. coccineum*.

---- *G. rivale*, ——— *G. urbanum*, ..... *G. coccineum*.

dows. They meet together only rarely and on the line of contact they form sporadically natural hybrid populations, known from taxonomic literature as *G. Jankae* G. B e c k.

The areas of *G. rivale* and *G. urbanum* overlap on a huge area of Europe and Asia although they differ in their areas- *G. rivale* having wide distribution in North America and in Europe, it is distinctly a more northern species then *G. urbanum*, which is known from America only as an adventitious species, and in Europe it has a more southern distribution covering the whole Mediterranean

territory. These species differ in their ecological requirements. *G. rivale* grows only in distinctly wet places with high water content and in the south part of its area it is a typical mountain species in the Balcan Peninsula, Asia Minor and the Caucasus. *Geum urbanum* on the other hand, tolerates much more drier conditions, it is a typical lowland plant, only rarely found in mountains. It seems to tolerate much more shaded places as does *G. rivale*.

The present area of *G. urbanum* in Europe is probably much enlarged by the human factor as most of its stations are clearly of anthropochoric character. Its relatively recent introduction to the American continent and its large area there indicates that this species is well adapted to easy dissemination and has a distinct expansive power. In Europe, *G. urbanum* and *rivale* cross often and the natural hybrids were described from a great number of localities. My own observations made in Poland in natural places have showed that in nature large hybrid populations of *G. intermedium* are very rare and usually only sporadic hybrid exemplars are to be found.

This can be partly explained by the difference in the time of flowering of these species. *G. rivale* flowers 10 to 14 days earlier than *G. urbanum* and the time when both species flower is relatively short. In culture these species cross easily and spontaneous hybrids were often observed.

Another factor is also playing the decisive rôle in nature in eliminating the hybrids, namely the elimination of hybrids in natural conditions in concurrence with parental and other plant species. I have studied in the National Park of Białowieża the distribution of *G. rivale*, *urbanum* and their hybrids and have found that in quite natural conditions these two *Geum* species practically never meet. Both species grow byside only along forest roads and in other places with the vegetation changed by human activity. But even in such places the hybrids are very rare and can be found only in single or few specimens. Mostly they represent typical  $F_1$  hybrids. After careful study of many kilometers of forest roads in the National Park, where both species were growing abundantly, I have found only one place (about two hundred square meters) where the hybrids grow copiously in more than one hundred specimens. All specimens were of  $F_1$  type, no introgression was observed, the parental species looked quite pure. This observation seems to indicate that  $F_1$  hybrids can compete with parental species only in exceptional places which are suitable for them. The ecological conditions in such places must be somewhat intermediate between the ecolo-

gical conditions required by parental species. This fact explains why both these *Geum* species remain distinct in Europe notwithstanding the fact, that hybrids between them are known from thousands of places in Europe. In most of these places hybrids are known from few individuals, whereas parental species grow there in great abundance.

This rarity of hybrid specimens can have also other causes and first of all the difference of the time of flowering of parental species. This fact causes that the cross pollination in mixed populations of both species is only rare. Secondly, the quite different structure of the flowers, which are campanulate and nodding in *G. rivale* and open and on erect peduncles in *G. urbanum* causes that these two species are pollinated by different insects. Besides, I have observed in my garden that a species of bumble-bee visiting *G. rivale* in one flight only exceptionally visits flowers of other *Geum* species. These facts cause that the interspecific pollination in nature may be quite rare. The seeds taken in Białowieża from *G. rivale* and *G. urbanum* from a station where both species were growing together and sown in Warsaw, produced only pure species. Unfortunately this experiment was on a very small scale and only 96 and 127 plants were cultivated.

Besides, W i n g e has shown for the hybrid *G. rivale* × *urbanum* and the same was observed for the hybrid *G. rivale* × *coccineum*, that the backcross hybrids are very similar to parental species. As in nature the single specimens of hybrids are most often backcrossed to parental species, the hybrids will after a few generations disappear.

It is probable, nevertheless, that further changes in natural conditions due to human culture will abolish the geological barriers separating these *Geum* species and in future in some places may arise a common population, where all plants will freely exchange genes among them. Then these species will disappear. The chances for a new reconstruction of pure species from such mixed hybrid population are extremely small as the observation of the immense segregation in  $F_2$  and  $F_3$  generations has showed. With such relatively high chromosome numbers and normal pairing of chromosomes in the hybrids the chances of reconstruction of a highly balanced genic system are practically none.

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