MONOGRAPHIAE BOTANICAE
Vol. IV — 1957

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A CYTOGENETIC STUDY ON THE GENUS *GEUM* L.

WARSZAWA

PAŃSTWOWE WYDAWNICTWO NAUKOWE — WARSZAWA 1957

Nakład 1000 + 117 egz. Ark. wyd. 27,5. Ark. druk. 26. Papier druk. sat. III kl. 80 g, 70 × 100/16. Oddano do składania 21.VII.56. Podpisano do druku i druk ukończono w maju 1957.

Zam. 1084. *B-73.* *Cena zł 83.—*

Druk. im. Rewolucji Październikowej, Warszawa

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I. INTRODUCTION

This work has been undertaken with the aim of inquiring into the mutual relations between the species of one genus and also the relations of the genus with other closely related genera. My intention has been to investigate these relations not only in their taxonomic aspect but also to inquire into their genetical and cytological nature. When beginning this work it has been my hope that a comprehensive and detailed knowledge of the conditions prevailing within a group of living organisms will help to disclose the mechanism involved in the differentiation and formation of species and other, both lower and higher, taxonomic units. The approach followed in the course of the work has primely consisted in morphological, geographical, cytological and genetical analyses of both pure species and their hybrids. Variations occurring within a species have also been analysed, though to a lesser degree.

The choice of the genus *Geum* for the experimental material in this research has been prompted by the well known facility to cross the various species composing the genus. Numerous interspecific hybrids of the genus *Geum* were already obtained in the XIX-th century by Gärtner (1849) and some years later this genus was investigated by Focke (1881) and others. The highly fertile hybrid of *Geum rivale* and *G. urbanum* has long been known in Europe and later investigations have shown that in the progeny of this hybrid the characters of the parent species are segregated (Marsden-Jones 1930, Weiss 1912, Prywer 1932). This has made possible a genetical analysis of interspecific differences. My assumption has thus been that other hybrids in the genus *Geum* will probably behave in the same manner, which would make possible an exact analysis of genetical interconnections between *Geum* species. Indeed, this has proved true in many cases so that genetical and cytological analyses of numerous hybrids have been possible.

Though the lack of clearly defined intersterility barriers makes the genus *Geum* a very convenient object for this type of research, its cytological nature makes it unfortunately much less suitable in this respect. The material is difficult to fix. The small and often very numerous chromosomes frequently stick one to the other making a detailed analysis very difficult. Moreover, the small size of the chromosomes and their slight morphological differentiation prevents the study of karyotypes which — as has been shown by the very elegant work of Babcock (1947) on *Crepis* and of Fernandes (1951) on *Narcissus* — may often throw a new and relevant light on the problems involved in the relationship and differentiation of species.

This work on the genus *Geum* was started in 1938 when I began to collect the first living plants and seeds of the genus and to grow them in the Botanical Garden in Warsaw. Even the first experimental results with crosses between these species encouraged me to extend my research as far as possible over the whole genus *Geum*. The work was hardly under way when it was interrupted by the outbreak of the war and the nazi occupation. The experiments were not resumed till 1946. In the postwar years I was at first faced by numerous difficulties mainly in connection with cytological examinations. In 1948 I spent several months in Lund working at the Genetical Institute and there, with the ardent help of Professor A. Müntzing, the head of the Institute, I was able to carry out numerous cytological examinations of many species and hybrids. Later, plants, reagents and equipment were obtained from Sweden and this made possible more intense work after my return to Warsaw.

In a research of the kind here considered it is indispensable to have in cultures as large a collection as possible of species representative for the most important forms from the group of plants under investigation. This condition I was able to fulfil only to a certain extent. My cultures included plants transplanted from natural habitats of all the *Geum* species growing in Poland. However, it was more difficult to assemble specimens from the whole distributional area of the genus. With the exception of the tropics the genus *Geum* is distributed on all the continents of the world. Owing to the very kind assistance of my fellow botanists I was able to assemble seeds of *Geum* species collected from natural habitats in many localities throughout its distributional area. Some North American species were sent me by Professor R. T. Clausen of Ithaca, others I obtained from the Botanical Gardens of Ottawa and Montreal. From Argentina I received seeds of two *Geum* species from Professor H. Bruecher of Tucuman. Professor H. Kihara supplied specimens from Japan and Professor Frankell of Christchurch from New Zealand. Moreover, a number of rare European species were received from Professor Stefanoff of Sofia and Professor O. Bolos of Barcelona. My grateful thanks go to all mentioned here and to many others not mentioned for lack of space. Their kindness and collaboration have enabled me to assemble a collection of living *Geum* plants thus making possible this research.

The interchange of seeds collected on natural habitats which has been initiated by many botanical gardens has been another source of some *Geum* species. However, it is unfortunate that some species in my collection have been derived only from plants grown in botanical gardens. There are of course many species which I have not succeeded in obtaining for my collection and these I know from herbarium specimens and in a few cases from description only.

II. SYSTEMATIC RELATIONS WITHIN THE GROUP

The genus *Geum* as classified by Linnaeus included 5 species: *G. montanum, reptans, rivale, virginianum and urbanum.* In later years, especially in the first half of the XIX-th century a great many species from both the Northern and Southern hemispheres were described. The detailed history of the genus and its often very complex synonymy will not be discussed here. In 1870 N. J. Scheutz published his "Prodromus Monographiae Georum" which was a monograph of the genus and in which as many as 43 species were listed, though some of them were only interspecific hybrids. In the years following the publication of Scheutz's work a number of new species was described, but it is not till 1933 that the genus was monographed again by Bolle. This last worker divided the genus into several separate, though related, genera: *Erythrocoma, Acomastylis, Sieversia, Neosieversia* and *Oncostylus.* In the genus *Geum* itself Bolle included only some of the species which the earlier writers classified as *Geum* in the broad sense of this denomination. In the case of the genus *Geum* and of other related genera a very unusual situation arose. Taxonomists never had much difficulty in defining the particular species, except some forming closely related groups, while the classification of species into genera, subgenera and sections varied greatly and often was most arbitrary. The resulting confusion is evident even today. The classification attempted by Bolle is neither satisfactory nor natural and cannot be regarded as the final solution to this problem.

Already in the classifications made by Linnaeus and later by

Scheutz the genus *Geum* is divided into two groups of species. In one group are plants with styles divided into the rostrum and deciduous stigmatic part. Plants from the other group have styles entirely persisting on achenes and usually covered by long pennate hairs. To the former group belongs *Geum urbanum* on the basis of which Linnaeus described the whole genus. Even today the species of this group are classified by all writers to the genus *Geum*. In the latter group are such species as for instance *G. montanum* or *reptans*. The structure of achenes and styles in these plants closely approaches that of the genus. *Dryas* and Linnaeus classified as *Dryas pentapetala* L. a species later considered by Scheutz as belonging to the genus *Geum*. Some authors, as for instance R. Braun or Wildenow, distinguished a separate genus *Sieversia* (though this denomination is used in a sense quite different to that given it later by Bolle) in which they included species with long straight and pubescent styles. This division is even today accepted in some floras, though from the scientific point of view it cannot be justified. The utter confusion prevailing in all generic considerations referring to the group here discussed is well illustrated by the following example: the same species, *Geum montanum* L., Bolle classifies with the genus *Geum*, Hegi in his flora classifies it with the genus *Sieversia*, and in the flora of the USSR it is classified as the genus *Parageum* Nakai.

Before describing the division of the genus *Geum* which is accepted here and which is based partly on experimental results, let us consider first the position occupied by *Geum* in the family of *Rosaceae*. The first generally accepted division of the rose family into subfamilies and tribes is the one introduced for the first time by Focke in Engler's and Prantl's manual "Die Pflanzenfamilien". Focke distinguishes the following subfamilies and tribes:

1. Subfamily *Spireoideae* with tribes *Spireae, Quillajeae* and *Holodisceae,*
2. Subfamily *Pomoideae,*
3. Subfamily *Rosideae* with tribes *Kerrieae, Potentilleae, Cercocarpeae, Ulmarieae, Sanguisorbeae* and *Roseae,*
4. Subfamily *Neuradoideae*
5. Subfamily *Prunoideae,*
6. Subfamily *Chrysobalanoideae* with tribes *Chrysobalaneae* and *Hirtellineae.*

The tribe of *Potentilleae* is further subdivided by Focke into three subtribes: 1) *Rubineae* with genus *Rubus,* 2) *Potentillineae* with genera *Fragaria, Duchesnea, Potentilla, Horkelia, Ivesia, Sibbaldia, Potaninia* and *Chamaerhodos,* and 3) *Dryadineae* with genera *Waldsteinia, Coluria, Geum, Fallugia, Cowania* and *Dryas.*

Focke's division was subsequently modified by Juel (1918) in the course of an extensive comparative survey of floral structures in the rose family. All the genera from the subfamily *Rosoideae* with straight ovules are classified by Juel into a separate subfamily of *Dryadoideae.* In the subfamily of *Rosoideae* Juel leaves only the genera with anatropous ovules. In the new subfamily of *Dryadoideae* he includes the genera *Cercocarpus, Chamaebatia, Cowania, Purshia, Fallugia* and *Dryas* together forming the tribe of *Cercocarpeae,* and the genera *Geum, Walsteinia* and *Coluria* forming the tribe of *Geeae.*

The tribes *Geeae* and *Cercocarpeae* in the subfamily of *Dryadoideae* are distinguished by Juel according to the structure of the carpels. In the *Cercocarpeae* the stigma is shaped into a crest descending along the style. This character in various degrees of expression can be found in all the species of the tribe except the genus *Dryas.* The other character which according to Juel distinguishes the two tribes is the position of the conducting vascular bundles which in the *Cercocarpeae* run along the inner walls of the ovary and in the *Geeae* inside the ovary walls. In the tribe of the *Geeae* the stigma is restricted to the tip of the style and only exceptionally in some species it descends in a reduced form along the style. Juel points out that typical long crested stigmata appear in such genera as *Neviusia, Coleogyne* and partly *Rhodotypus,* i. e. in genera having no perianth or with perianth greatly reduced. It may be that this trait is associated with the phylogenetic origin from anemophilous plants. Within the subfamily of *Dryadoideae* this character is most distinctly marked in the genera *Cercocarpus, Cowania* and *Chameabatia,* it is much less distinct in the genus *Fallugia,* and only traces of it remain in the genera *Dryas* and *Waldsteinia,* and in some *Geum* species. As it will be seen from further argumentation this sequence corresponds approximately to the phylogenetic sequence within the subfamily of *Dryadoideae.*

Juel's classification is based on anatomical and embryological characters and is a genuine step forward in the natural history of the rose family by that it separates from the subfamily of *Rosoideae* the group of genera forming a distinct developmental line undoubtedly related with this subfamily. Juel quite rightly removed from the tribe of *Cercocarpeae* the genera *Coleogyne* and *Adenostoma* wrongly classified by Focke. These two genera have little in common with the other members of the tribe and as early as 1898 Rydberg classified them as two separate monotypic tribes in the subfamily of *Rosoideae: Adenostomateae* and *Coleogyneae.*

Without entering into further details of the changes introduced into Focke's classification in respect to other subfamilies let us now review the alterations made by Bolle (1933) in the subfamily of *Dryadoideae*. Bolle divided it into four instead of two tribes as did Juel:

The tribe *Cercocarpeae* Rydb. with genus *Cercocarpus*,

The tribe *Purschieae* F. Bolle including genera *Chamaebatia, Purschia* and *Cowania*,

The tribe *Dryadeae* F. Bolle including genera *Fallugia, Dryas*, and *Sieversia*,

The tribe *Geeae* Juel including genera *Neosieversia, Erythrocoma, Oncostylus, Geum, Acomastylis, Coluria*, and *Waldsteinia*.

Mention will be made later of Bolle's division of the genus *Geum* into several separate genera. This division seems to be unjustified, similarly as is unwarrantable the splitting of the subfamily *Dryadoideae* Juel into four tribes. While the tribe *Geeae* Juel with the genera *Geum, Waldsteinia* and *Coluria* should be retained, the tribe *Cercocarpeae* Juel may at the most be divided into two tribes, i.e. of *Cercocarpeae* including genera *Cercocarpus, Chamaebatia and Purschia*, and of *Dryadeae* including the genera *Cowania, Fallugia* and *Dryas*.

According to this classification the tribe *Cercocarpeae* would include woody plants and shrubs growing mainly in Mexico and California with solitary pistils and long straight styles.

The genera in the tribe of *Dryadeae* are mainly shrubs from California with numerous pistils and long styles covered with feathery hairs (*Cowania* and *Fallugia*) and shrubby plants from the genus *Dryas* with a circumpolar and montane distribution.

Finally, in the tribe of *Geeae* there are mainly perennial herbs with deciduous styles (*Waldsteinia* and *Coluria*), with only the stigmatic part deciduous (*Geum* pro parte), or with styles, often long and pinnately haired as in *Dryas*, persisting on achenes. The tribe is distributed throughout the temperate zones of the Northern and partly the Southern hemispheres.

The classification outlined above is of course not free from arbitrariness and, for instance, genus *Cowania* is in some respect intermediate between *Cercocarpeae* and *Dryadeae*, while subgenus *Sieversia* — as conceived by Bolle — is intermediate between *Dryadeae* and *Geeae*. However, the genus *Sieversia* in Bolle's description differs so markedly from the genus *Dryas* and resembles *Geum* so closely in respect to the number of petals, the form of the calyx, and the shape of leaves that its classification in the latter genus seems more justifiable.

Let us now turn our attention to the genera in the tribe of *Geeae*. To begin with it must be pointed out that all the writers are in agreement as to the separate classification of *Coluria* and *Waldsteinia.* The two genera, though closely related, are quite distinct from *Geum.* They consist of forest plants partly adapted to myrmecochoric propagation which is visible from the thickened papillae covering the achenes of some species. There is no doubt that the two genera form an ancient developmentally separate line within the tribe of *Geeae* and their disjunctive distribution indicates that they are relics of an old forest flora of the arctic Tertiary type.

The genus *Geum* is far more differentiated and has many more species than *Waldsteinia* and *Coluria* which has made its definition difficult for taxonomists and has given rise to many contradictory opinions. For instance, according to Hultén (1929, 1937) the genus *Geum* includes species which Bolle classifies into five separate genera, i.e. *Sieversia, Neosieversia, Acomastylis, Erythrocoma* and *Geum.* Other workers go even further in breaking up the genus *Geum* into separate genera. Thus, for instance, Juzepchuk (1941) in the flora of the USSR distinguishes from *Geum*, as defined by Bolle, the genus *Woronowia* with one species *Woronowia speciosa* Juzep. (*Geum speciosum* Alb.), and the genus *Orthurus* Juzep. with two species *O. heterocarpus* Juzep. and *O. kokanicus* Juzep. (*Geum heterocarpus* Boiss. and *Geum kokanicum* Reg. et Schm.). Furthermore, following the opinion of Japanese writers Nakai and Hara, Juzepchuk classifies separately as genus *Parageum* Nakai et Hara the subgenus *Megacomastylis* from Bolle's genus *Acomastylis.* In this new genus Juzepchuk and the Japanese writers include, for inexplicable reasons, the montane European *Geum* species from subgenus *Oreogeum.*

The confusion in taxonomic literature is even greater when it comes to separating from genus *Geum* the so called genus *Sieversia.* In the latter Bolle includes two species: *S. pentapetala* and *S. pusilla.* Some North American workers, as for instance Rydberg or Graham, include in this genus species which Bolle considers as belonging to the "genus" *Erythrocoma* and "genus" *Acomastylis,* while several authors of European floras extend the genus to cover species from subgenus *Oreogeum* (*G. montanum, reptans* and *bulgaricum*).

Bolle's efforts to introduce some order into the confused taxonomic classification of the genus *Geum* do not seem very successful. The inclusion of some species in the genus *Geum* and of others in separate genera is not sufficiently accounted for and is based on inadequate data. Only a cytogenetic approach may in future provide a solution to this problem. For instance, *G. heterocarpum* Boiss. which Bolle classifies in the genus *Geum*, has only one genome partly homologous with species of subgenus *Eugeum*. On the other hand, species included by Bolle in the separate genus *Erythrocoma* have two homologous genomes with species of subgenus *Eugeum*, they are much easier to cross with *Eugeum* species and morphologically they are more closely related.

On the basis of my experiments, which unfortunately did not cover all the species forming the group of plants discussed here, I think that the most reasonable approach is that of Hultén who classifies all these species in the genus *Geum*. It is important to stress that by continuously forming new generic names not only is confusion produced in the synonymy, but also the more general aspects of the relationships prevailing in the group are obliterated. There is no doubt that the genus *Geum* is an ancient one and that early in its history numerous developmental lines were differentiated in it and have since reached quite considerable separation. Amphiploidy has played a most important part in the evolution of the genus *Geum* and quite certainly the various developmental lines within the genus show different degrees of relationship expressed, among other things, by the existence of various numbers of common homologous genomes. It seems therefore that as long as the mutual relations between the distinct specific groups are not clarified by extensive cytogenetic investigations it is more appropriate to include the whole group in one genus divided only into numerous subgenera more or less isolated morphologically and geographically.

In this aspect the tribe of *Geeae* would consist of only three genera: *Coluria, Waldsteinia* and *Geum*. The following principles may serve as a clue for defining them:

A. Style entirely deciduous from the fruit:
   1. Basal leaves pinnate . . . . genus *Coluria*
   2. Basal leaves tripartite . . . . genus *Waldsteinia.*

B. Style entirely persistent on fruit or only upper part deciduous . . . . genus *Geum.*

When accepting this broad approach to the genus *Geum* it is rather difficult to divide it into subgenera. I have based my arrangement on Bolle's classification by treating the genera distinguished by that writer as subgenera and by introducing modifications in several other points. As it is impossible in the present state of knowledge to base any classification of the group on satisfactory cytogenetic data this one may only be accepted provisionally.

The division of the genus *Geum* into subgenera agreed upon in the present work is as follows:

A. Plants with entire style persisting on achene:

I. Small shrubs with styles long, pennately haired, from North-Eastern Siberia and Japan . . . subg. *Sieversia*

II. Perennial herbs

a) Styles elongated, pennately haired; epicalyx doubly whorled; distribution in arctic Siberia . . . . subg. *Neosieversia*

b) Epicalyx singly whorled

1) Styles elongated, pennately haired; distribution in European mountains . . . subg. *Oreogeum*

2) Styles greatly elongated, pennately haired; stigmatic part oblique; disc forms a distinct ring; distribution in North America . . . . subg. *Erythrocoma*

3) Styles straight, short, covered wholly or partly with short pubescence:

— Styles with short hairs at base, glabrous beyond the middle, slightly elongated; plants from N. America, Himalayas, China, Japan, arctic Siberia and America . . . . subg. *Acomastylis*

— Style with long pubescence at base, glabrous beyond the middle; distribution in Chili . . . . subg. *Andicola*

4) Style with recurved stigma; distribution in the Southern hemisphere (Tasmania, New Zealand, South America) . . . . subg. *Oncostylus*.

B. Style jointed with only the basal part persisting on achene:

I. Style jointed $^1/_2$ or $^3/_4$ way up forming rostrum and deciduous stigmatic part.

a) Rostrum tipped with a hook

1) Epicalyx present; numerous species distributed in Northern temperate zone, S. America and S. Africa . . . . subg. *Eugeum*

2) Epicalyx absent . . . . subg. *Stylipus*

b) No hook between rostrum and stigmatic part, rostrum with down-pointing bristles at the tip . . . . subg. *Orthurus*

II. Style contracted just above base, upper part deciduous; plants growing in Caucasus . . . subg. *Woronowia.*

This division of the genus *Geum* differs from that of Bolle in the following respects:

1) The genera *Sieversia, Neosieversia, Oncostylus, Acomastylus* and *Erythrocoma* are defined as subgenera of *Geum.*

2) Bolle's subgenus *Orthostylus* is split into two subgenera: *Orthurus* and *Woronowia.* The two subgenera correspond to two similarly named genera formed by Juzepchuk. There can be no doubt that *G. speciosum* from subgenus *Woronowia* has little in common with *G. heterocarpum* form subgenus *Orthurus.*

3) The species *G. andicola* Reiche growing in the Chilean Andes does not seem to be sufficiently closely related to the European species from subgenus *Oreogeum* to include them in one subgenus as does Bolle. As long as more detailed knowledge is not available I suggest that it be classified in the separate subgenus *Andicola.*

It may be that further investigations will modify this system, especially if based on experimental data. For instance subgenus *Oncostylus* which includes the group of subantarctic species may finally prove to be a separate genus. However, this can be decided only in the course of further experimental investigations.

III. SPECIES IN THE TRIBE OF *GEEAE* AND THEIR GEOGRAPHICAL DISTRIBUTION

It is not my intention to make here a detailed description of all the known species in the tribe of *Geeae*, as such a description would occupy much space introducing little of what is not already known. In most cases the species of the group are well defined and in taxonomic literature there is much conformity in the manner they are classified. The few exceptions are in the group of critical species and these will be discussed more fully.

Genus *Waldsteinia* Willd. (Fig. 1, Map 1)

The shape of the plants and the structure of their more important organs may be seen on Fig. 1. This and all the following illustrations were drawn from specimens growing in the Botanical Garden in Warsaw. The genus covers the following species:

1. *W. fragarioides* (Michx.) Trattinn.
2. *W. ternata* Fritsch.
3. *W. geoides* Willd.
4. *W. lobata* Torr. et Gray.

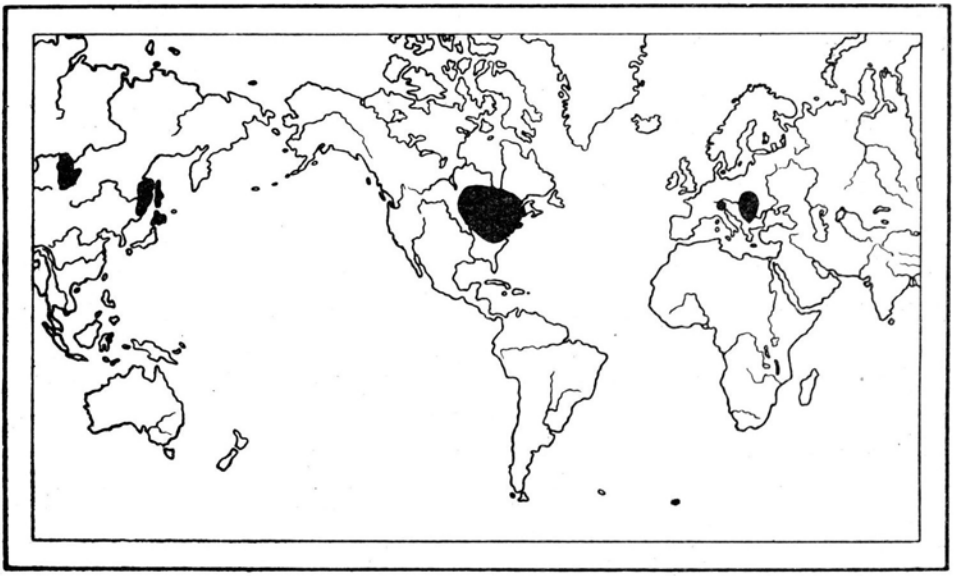
The distribution of the genus and the mutual relationship between species from the Old and the New World are very interesting. On the Atlantic Coast of North America there are two distinct species. *W. fragarioides* with tripartite leaves and *W. lobata* with trilobate leaves. On the Eurasian continent there are two closely corresponding species: *W. ternata* with tripartite leaves and *W. geoides* with trilobate leaves. The differences between *W. fragarioides* and *W. ternata* as well as between *W. lobata* and *W. geoides* are very slight and refer primely to pubescence intensity, and the shape of epicalyx and bracts. All these characters are rather variable in each species and have no great taxonomic value. It is thus apparent that North American species and the Eurasian ones form pairs of closely related vicarious species. The species *W. idahoensis* Piper which is reported from the United States differs from *W. lobata* only by glandular hairs within the inflorescence and its specific distinctness is doubtful. The distribution of the species of genus *Waldsteinia* is shown on Maps 2 and 3. Very remarkable is the disjunctive distribution of *W. ternata* in the Far East, Transylvania and the Alps. According to Juzepchuk (Flora of the USSR vol. X) Asiatic and European specimens are not exactly similar and it is possible that they may form two subspecies or geographic varieties.

From among the *Waldsteinia* species I have in my cultures the following: *W. geoides* Willd. a) plants collected from a natural habitat in the canyon of the river Dniestr in Podole, and b) obtained from the Botanical Garden in Lund, and *W. ternata* Fritsch obtained from the Botanical Garden in Lund.

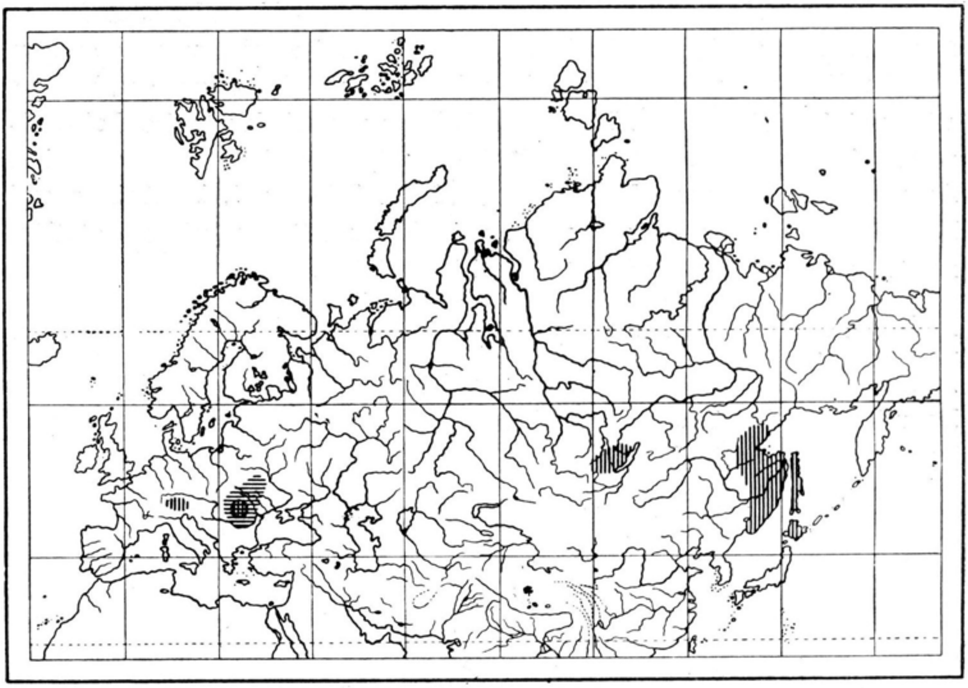
Genus *Coluria* R. Brown. (Fig. 2, Map 4)

In the genus *Coluria* five species are included by Bolle:

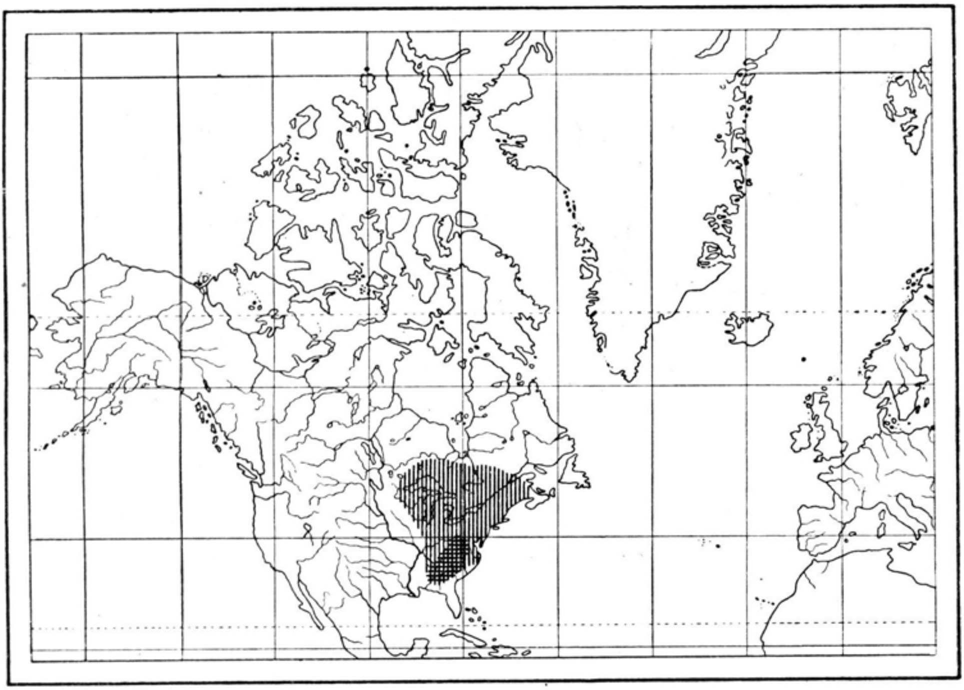
1. *C. elegans* Cardot.
2. *C. purdomii* W. E. Evans.
3. *C. geoides* (Pall.) Ledeb.
4. *C. Henryi* Batalin.
5. *C. oligocarpa* (J. Krause) F. Bolle.



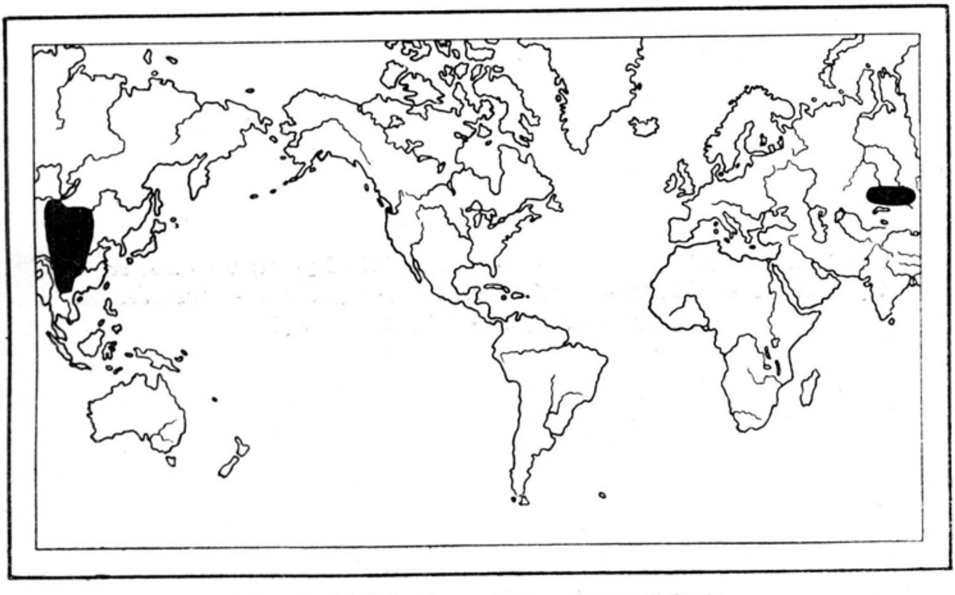
Map 1. Distribution of the genus *Waldsteinia*



Map 2. Distribution of *Waldsteinia ternata* (vertical lines) and of *Wald. geoides* (horizontal lines)



Map 3. Distribution of *Waldsteinia lobata* (horizontal lines) and of *Wald. fragarioides* (vertical lines)



Map 4. Distribution of the genus *Coluria*

Fig. 1. *Waldsteinia geoides;* a — growth habit of plant; b — flower — top view; c — flower — bottom view; d — petal; e —cross section through flower; f — achene with style

With the exception of *C. geoides* which has its habitats on the northern slopes of the Altai Mountains all other species grow in China. By the shape of its flowers and especially by the shape of pistils the genus is very closely related to *Waldsteinia* from which it differs mainly by its pinnatisect leaves and achenes covered with rounded papillae. The distribution of the species in China is as yet little known and it is hard to demarcate it even approximately.

In my cultures I have only *Coluria geoides* obtained from the Botanical Garden in Uppsala (Fig. 2).

Genus *Geum* L.

The genus *Geum* has been the principal object of this work, and before more is said, it must be stressed that unfortunately I have not been able to investigate the whole genus in the same degree. Although, the number of species examined in subgenera *Eugeum, Stylipus, Oreogeum, Orthurus, Woronowia* and *Erythrocoma* has been fairly high, in such subgenera as *Sieversia, Neosieversia, Acomastylis* and *Oncostylus* I either have not succeded in obtaining live material or the attempts at cultivation have failed.

However, to enable the reader to form a general idea of all the species included in this genus and to give some notion as to their geographical distribution a short description of all *Geum* subgenera will here be made. For full details the reader is referred to Bolle's monograph.

Subgenus *Sieversia* (Fig. 150, Map 5) includes only two species:

G. pentapetalum (L.) Makino, and
G. selinifolium Hultén.

The two species differ only slightly in the degree of leaf incisions. The plants have the form of small herbaceous shrubs, arctic and montane in character. They grow in East Siberia, Kamschatka, Aleutian Islands, Sakhalin and Japan (Map 6). There are single flowers on the scapes, calyx and epicalyx with 5 segments, 5 petals, and numerous long pistils with long styles pennately haired.

Subgenus *Neosieversia* (Fig. 151, Map 7), consists of one species only:

G. glaciale Adams.

The species grows in the arctic zone of Siberia, its distribution stretching east from the mouth of the Yenesei to Kamschatka and across the Behring Straits to Alaska (Maps 7 and 8). The species is related to those of subgenus *Sieversia* from which it differs primely by its herbaceous character and the double whorl of the epicalyx.

Subgenus *Oreogeum* (Figs. 3—5, Map 9) is composed of three species. Characteristic for these species are long styles covered with pen-

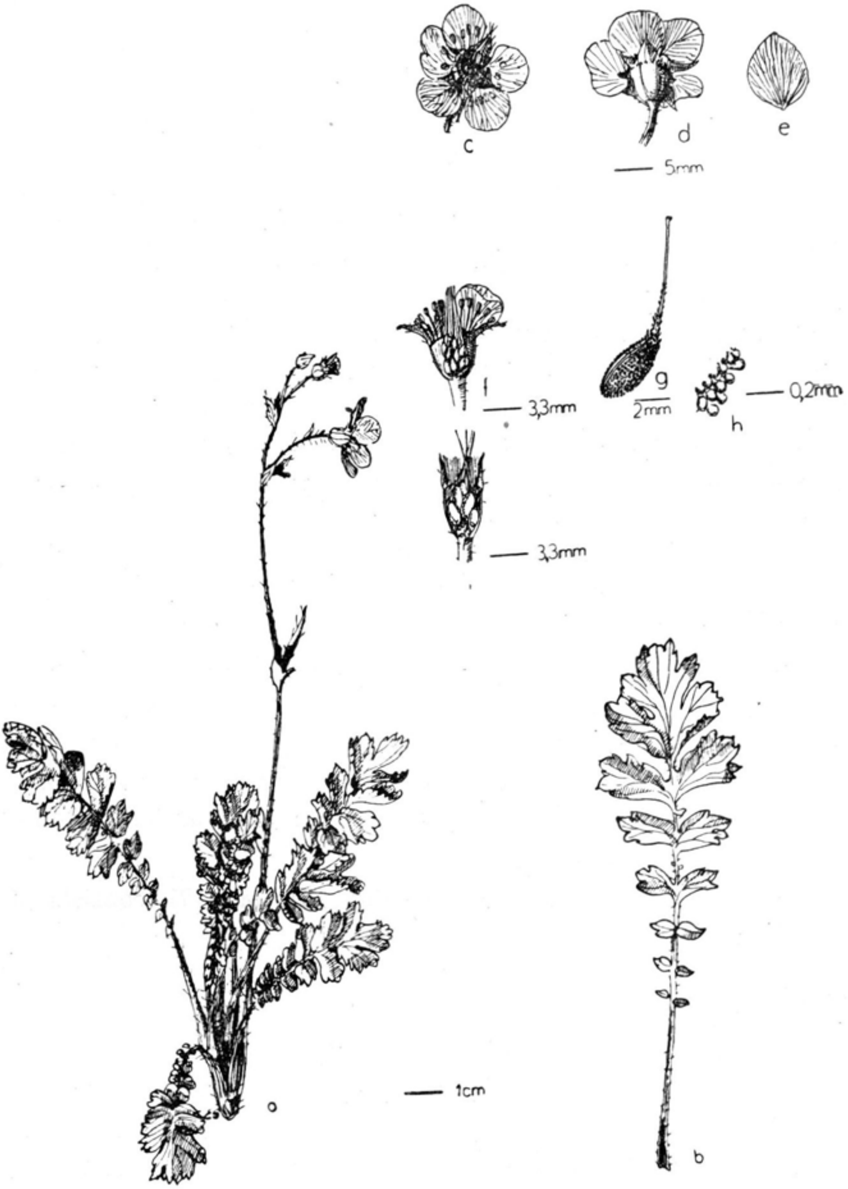
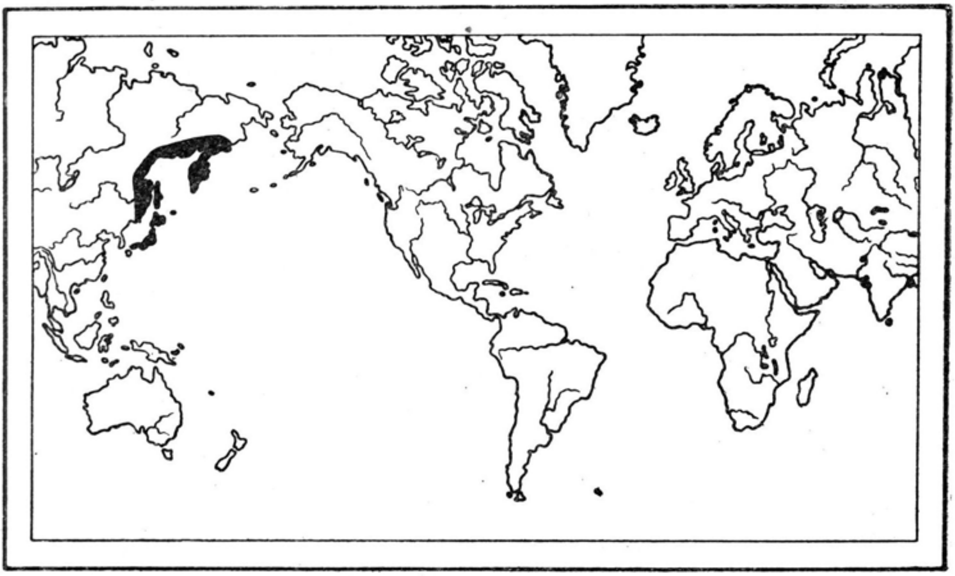
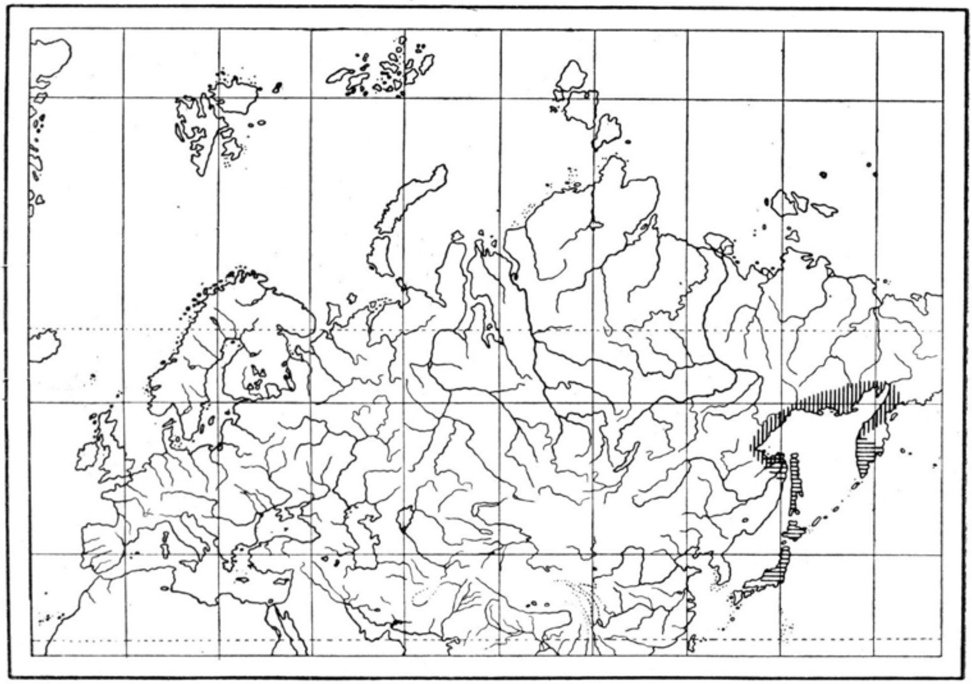


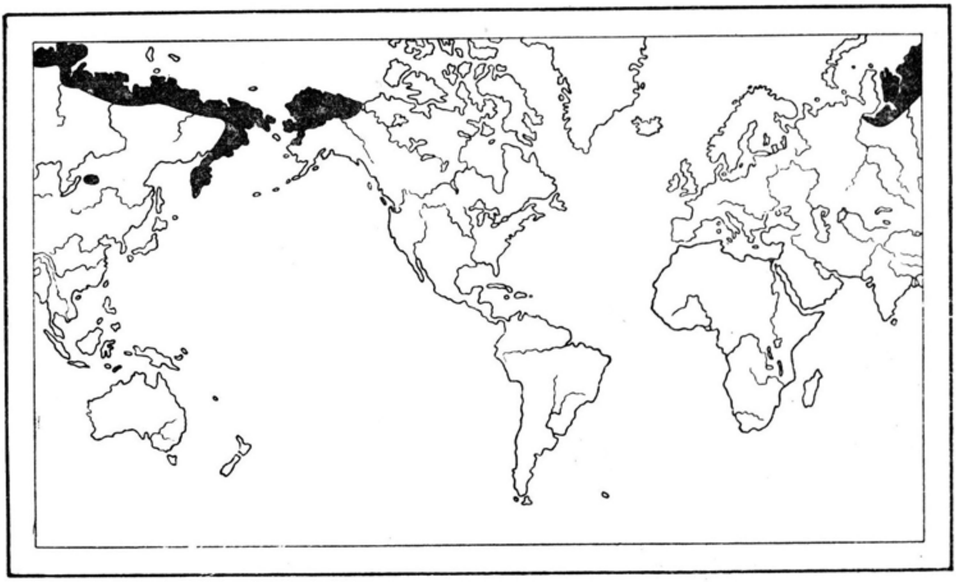
Fig. 2. *Coluria geoides;* a — growth habit of plant; b — basal leaf; c — flower — top view; d — flower — side view; e — petal; f — cross-section through flower; g — achene with style; h — papillae on achene; i — ripe achenes on receptacle



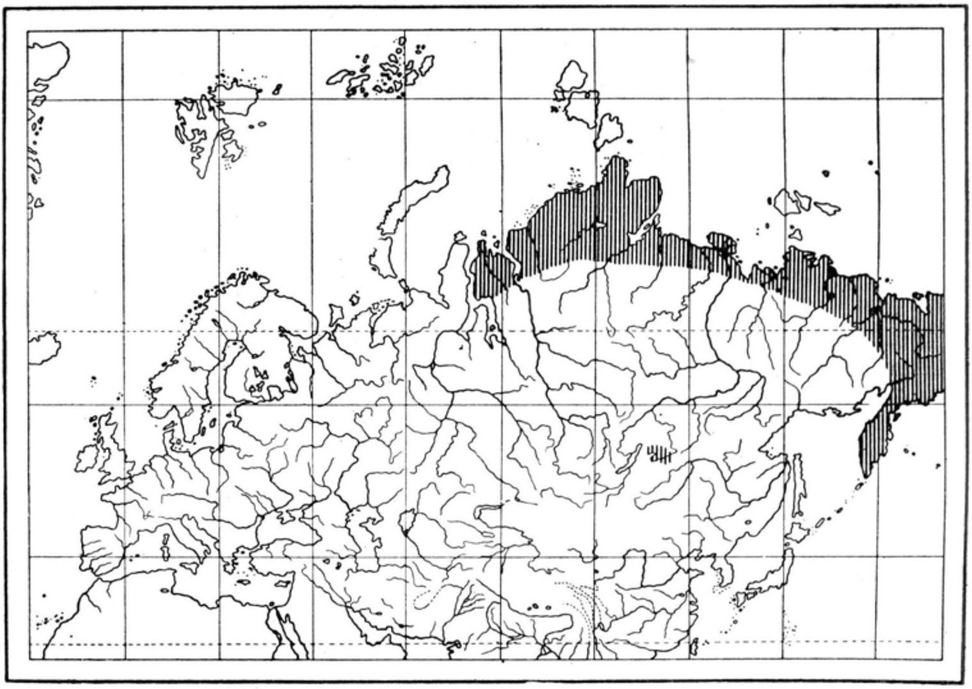
Map 5. Distribution of the subgenus *Sieversia* of the genus *Geum*



Map 6. Distribution of *Geum selinifolium* (vertical lines) and of *Geum pentapetalum* (horizontal lines)



Map 7. Distribution of the subgenus *Neosieversia* of the genus *Geum*



Map 8. Distribution in Asia of *Geum glaciale*

nate hairs and entirely persistent on the achenes, in which they resemble the subgenera mentioned above. The three species of the subgenus are:

- *G. montanum* L.
- *G. reptans* L.
- *G. bulgaricum* Panc.

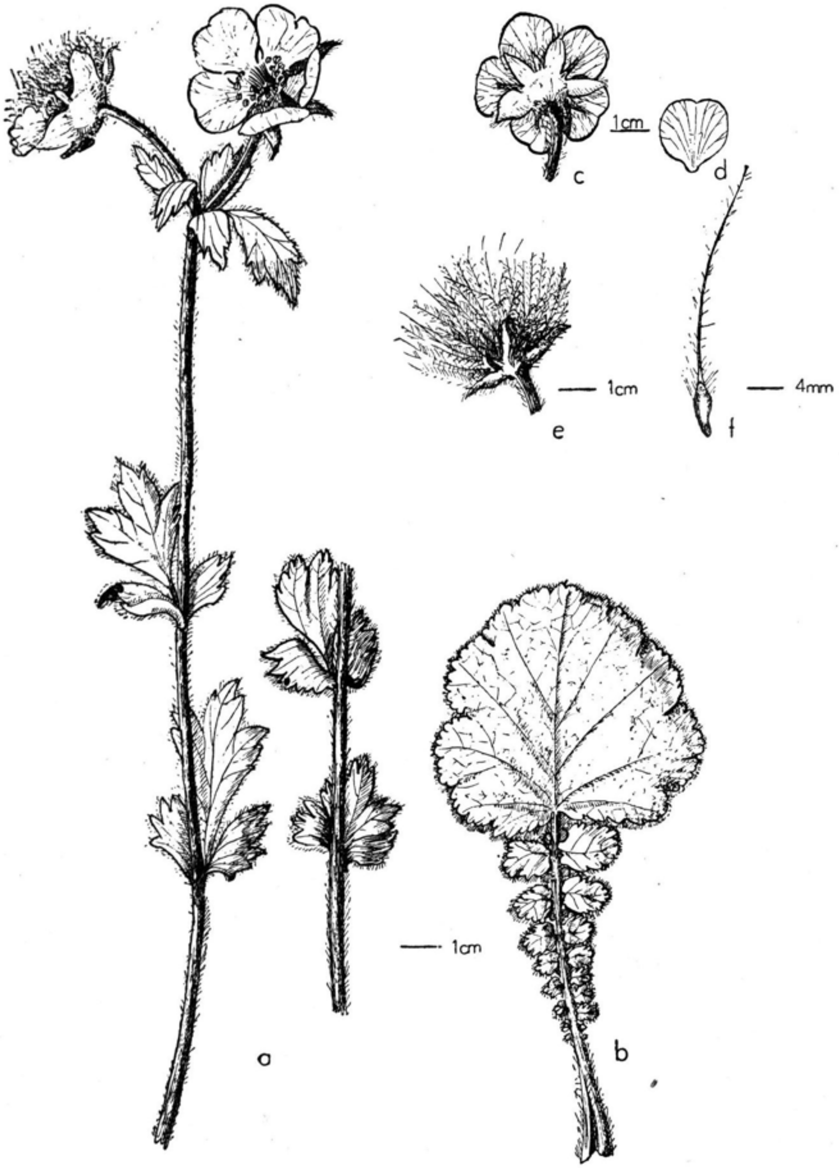
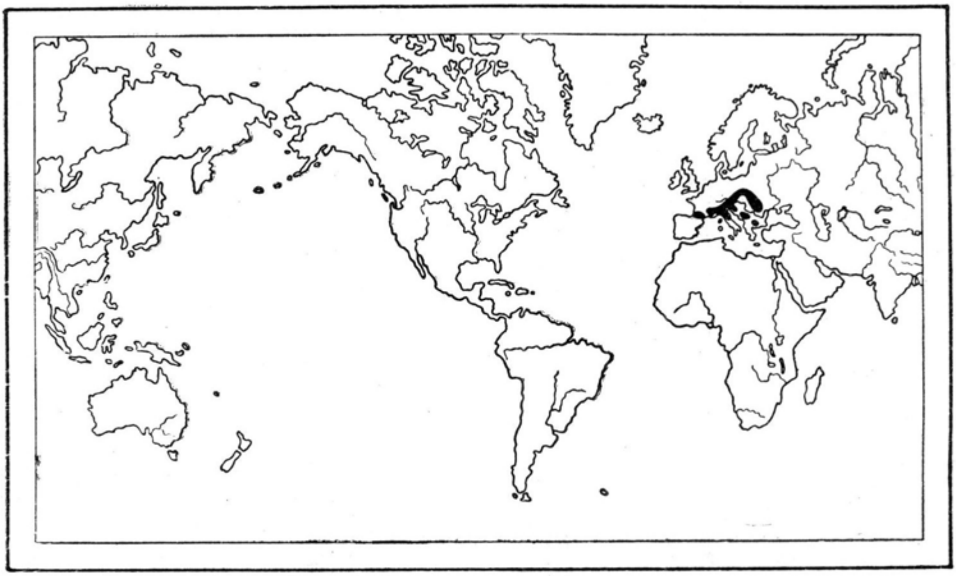


Fig. 3. *Geum montanum;* a — floral stem; b — basal leaf; c — flower — side view; d — petal; e — achenes in flower; f — achene

Of these *G. montanum* (Fig. 3) has the largest distribution. It grows in montane habitats from the Iberian peninsula and the Pyrenées in the west, through the Plateau Central, the Alps, Corsica and the Carpathians to the mountains of the Balkan peninsula (Map 10). *G. reptans* (Fig. 4) has a more restricted distribution and its alpine habitats are found in the Alps, the Carpathians and some mountain massifs of the Balkan peninsula (Map 11). The third species, *G. bulgaricum* (Fig. 5) grows only in the mountains of the Balkan peninsula.



Map 9. Distribution of the subgenus *Oreogeum* of the genus *Geum*

My cultures include all three species. The *G. montanum* plants I have obtained from natural habitats in the Tatra Mountains and East Carpathians (Czarnohora), and from Botanical Gardens in Sofia and Edinburgh. *G. reptans* has been obtained from the Tatra Mountains and grown from transplanted young plants and runners. This species is difficult to cultivate in the lowlands and seldom flowers in the Warsaw climate. In some crosses pollen brought straight from the Tatra Mountains has been used. *G. bulgaricum* has been grown out of seeds collected from natural habitats by Professor Stefanoff in the Musalah Mountains in Bulgaria. The species is also very exacting and difficult to grow and in the many years of cultivation it has never been possible to make it flower. Because of this it has been necessary in this one case to make the drawing of the plant from herbarium specimens collected on the same natural habitats as the plants in the cultures.

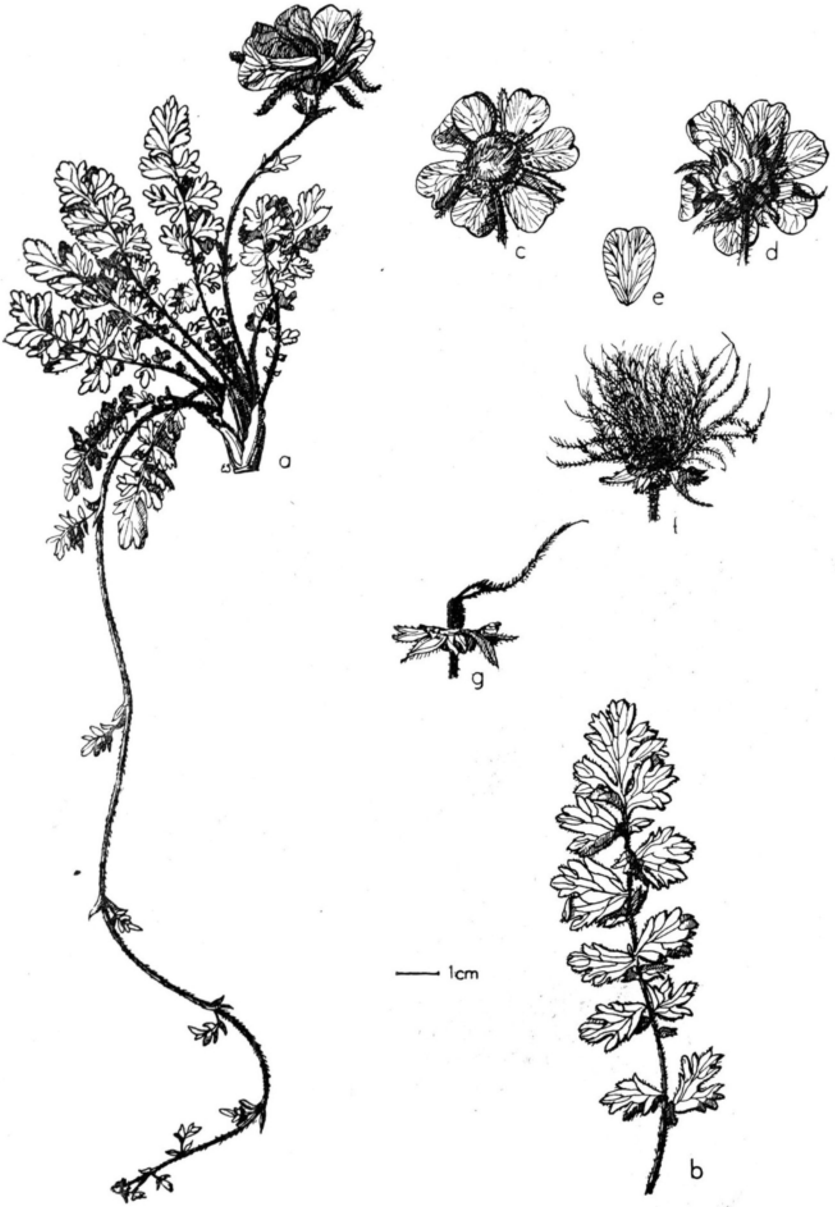
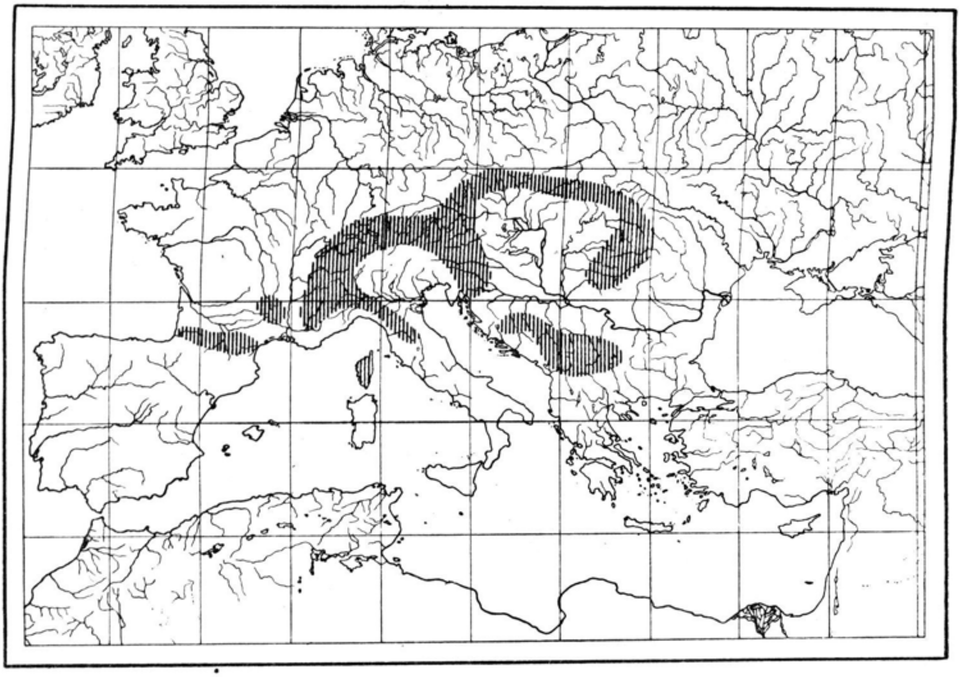


Fig. 4. *Geum reptans*; a — grawth habit of plant; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

Fig. 5. *Geum bulgaricum*; a — growth habit of plant; b — flower — bottom view; c — petal; d — receptacle with one achene; e — achene

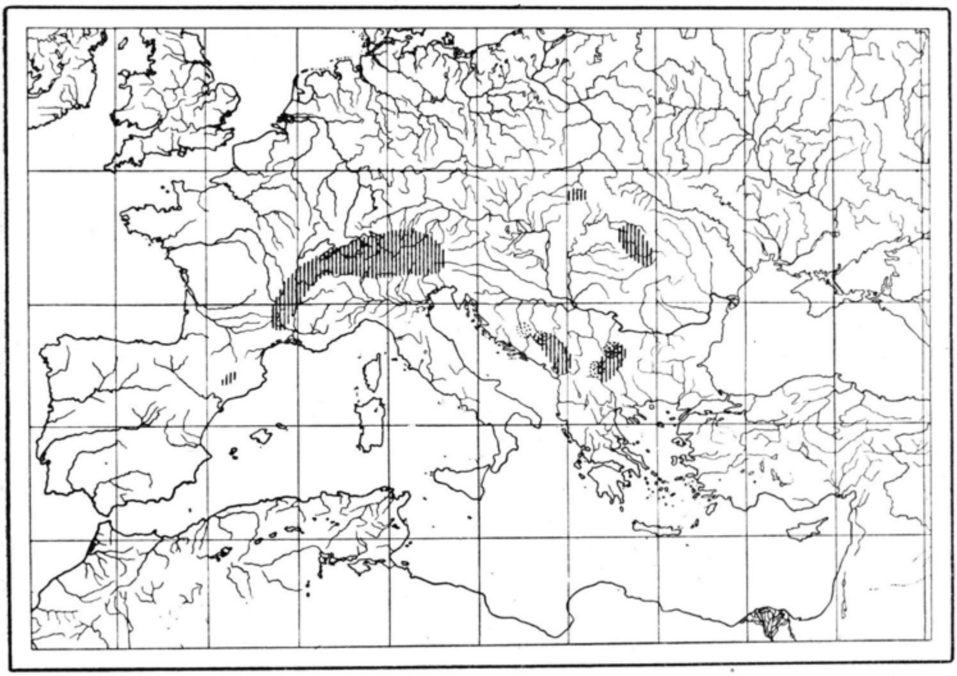


Map 10. Distribution of *Geum montanum*

Subgenus *Acomastylis* (Fig. 6, Map 12) of which I succeeded in obtaining for my cultures only one species *Geum Rossii* Seringe (Fig. 6). In Fig. 6 the principal characteristic features of the subgenus are visible: the long tubular hypanthium of the calyx and the straight styles covered either with short hairs or almost glabrous and much shorter than in the previously described subgenera. Bolle splits his genus *Acomastylis* into two subgenera differing from each other by the length of style: *Megacomastylis* and *Micracomastylis*. Classifying the genus *Acomastylis* as a subgenus of the genus *Geum* I shall consider Bolle's two subgenera as sections. In the section *Megacomastylis* are the following species:

Geum Peckii Pursh
Geum radiatum Mich.
Geum calthifolium Smith
Geum sikkimense Prain
Geum elatum Wallich.

In this section Bolle classifies also *G. macranthum*, but this is only a natural hybrid *G. calthifolium* × *G. Rossii.* I have been able to recognize the hybrid nature of these plants by examining numerous herbarium specimens from the Riksmuseet in Stockholm and also in



Map 11. Distribution of *Geum reptans* (vertical lines) and of *Geum bulgaricum* (dots)

Professor Hultén's herbarium. The plant is almost completely sterile and this opinion has been confirmed orally by Professor Hultén who had the occasion to observe and collect this hybrid on the Aleutian Islands and in Alaska. Moreover, the new species *Ac. nipponica* E. Bolle described by Bolle is nothing more than a variety of *Geum calthifolium.* This has been earlier pointed out by Franchet and Savatier and has been confirmed lately in a detailed investigation by Hara (1952).

The distributional area of *Geum calthifolium* covers the coasts of the North Pacific Ocean: the Commander Isls., Kamschatka, Kuriles, Japan, Aleutians, Alaska, and Yukon to British Columbia.*Geum Peckii* and *G. radiatum* are very closely related to *G. calthifolium* and are distributed in small disjunctive areas on high mountain tops in the White Mts. and Roan Mts. in the states of New Hampshire, Maine, North Carolina and Tennessee. Quite different is the distribution of *G. elatum* and *G. sikkimense.* The former occupies a large area in the Himalayas and China, while the latter occurs in the province of Sikkim in the Himalayas.

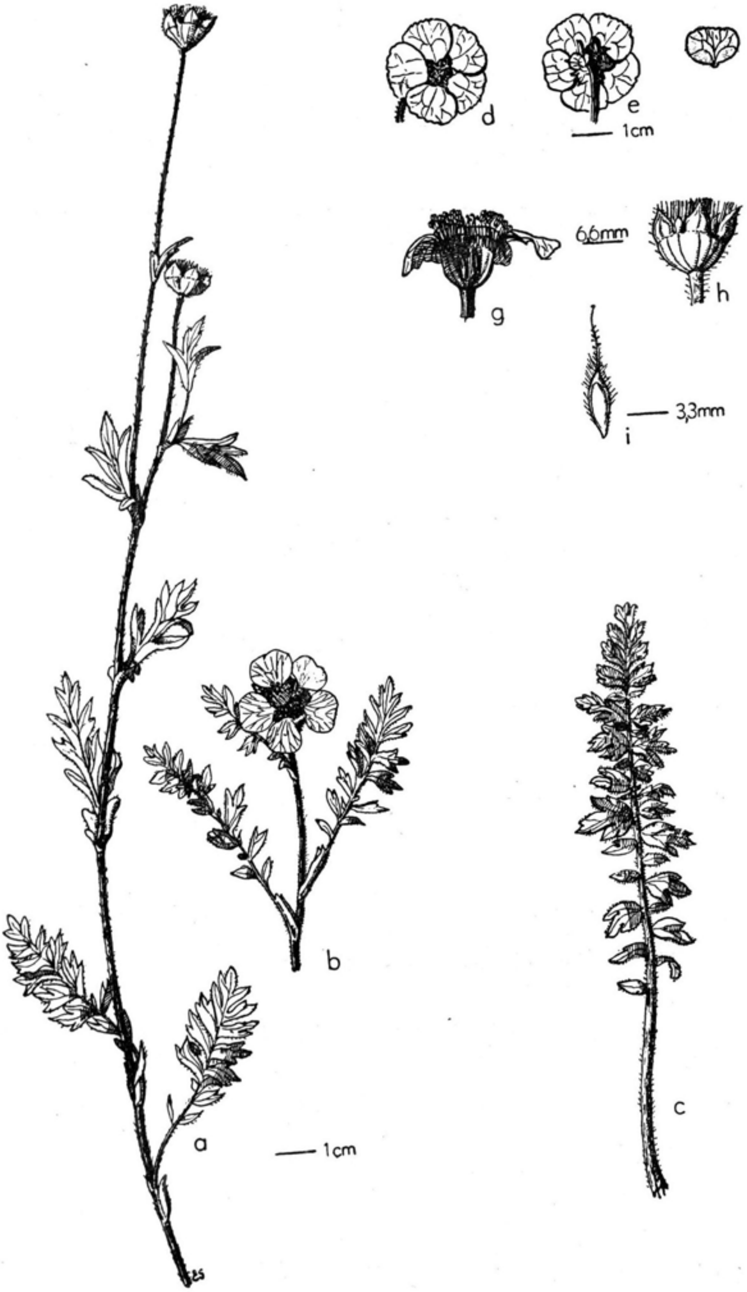
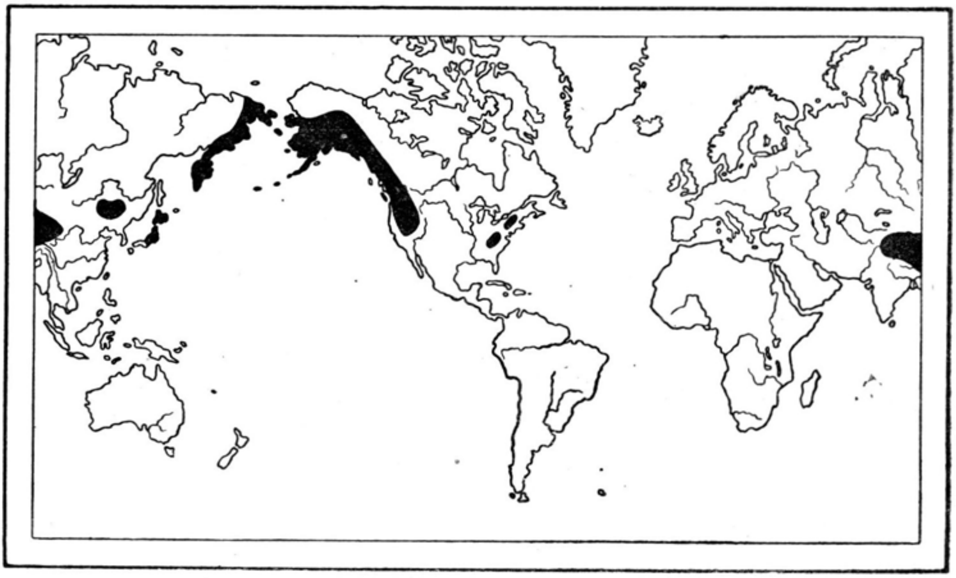


Fig. 6. *Geum Rossii*; a — floral stem; b — stem with flower; c — basal leaf; d — flower — top view; e — flower — bottom view; f — petal; g — cross-section through flower; h — withered flower; i — achene

In the section *Micracomastylis*, which is characterized by a comparatively short and sparsely pubescent style, the following species are included:

Geum Rossii Ser.	*Geum turbinatum* Rydb.
Geum depressum Greene	*Geum sericeum* Greene
Geum gracilipes Piper	

Geum Rossii has its distribution on both sides of the Behring Straits: Kamschatka, Tchouktches peninsula and Anadyr in Asia, Behring Isl., Melville Isl., Alaska and Yukon. *Acomastylis humilis* Rydb. is classified by Bolle as a distinct species, in Hultén's opinion it is not even a variety, being nothing more than a form of *G. Rossii*. In the western states of N. America grow the closely related *G. turbinatum* Rydb., *Sieversia gracillipes* Greene and *Acomastylis depressa* Greene, however, the last two are of doubtful systematic value, having been collected once only from Blue Mts (Oregon) and Mount-Stuart (Washington). *Geum sericeum* Greene is also a form very closely related to *Geum turbinatum*, but to establish its specific status a special investigation is needed.

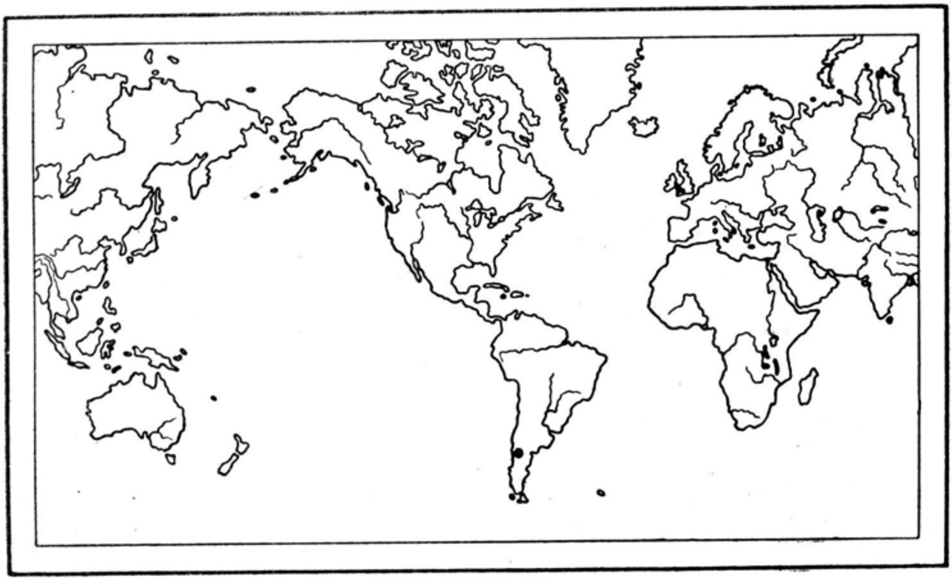


Map 12. Distribution of the subgenus *Acomastylis* of the genus *Geum*

From among the species of this subgenus I have in my cultures only *Geum Rossii* Ser., (Fig. 6), obtained from the Botanical Gardens in

Göteborg and Uppsala, *Geum calthifolium* obtained from the Botanical Garden in Edinburgh, and *Geum turbinatum* supplied by Professor C. W. T. Penland who has collected it from Hoosier Pass in central Colorado. However the two species last mentioned have not yet flowered in my cultures.

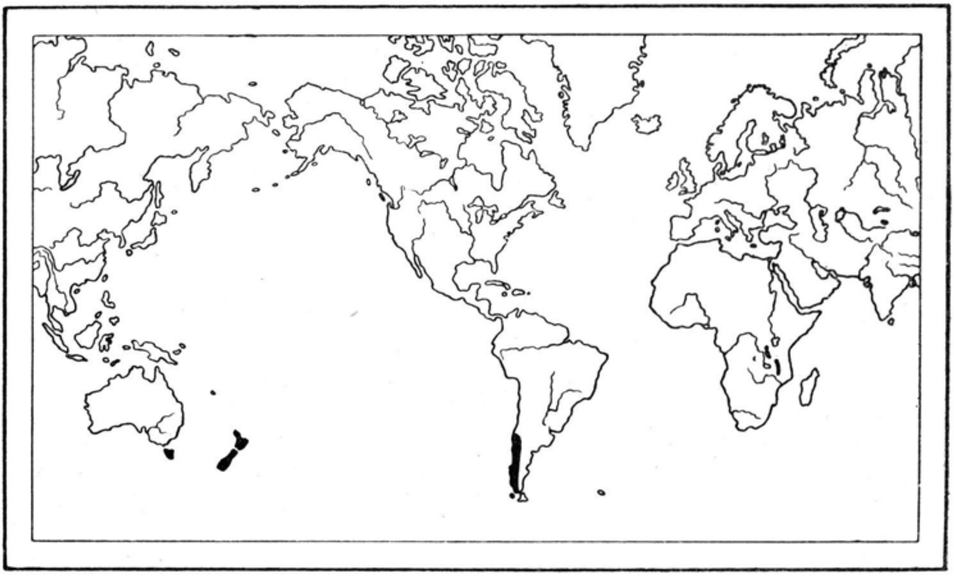
Subgenus *Andicola* is created provisionally for the little known species *Geum andicola* Reiche from the Chilean Andes (Map 8).



Map 13. Distribution of the subgenus *Andicola* (*Geum andicola*)

Bolle classified this species with the subgenus *Oreogeum*. However, because of the entirely different distribution of *Geum andicola* and the difference in the shape of styles the classification of this species with the European subgenus *Oreogeum* seems unfounded. Perhaps it would be more correct to include the species in the subgenus *Acomastylis*, but this can be confirmed only by experimental work.

Subgenus *Oncostylus* should include the group of species with quite differently shaped styles and distributions restricted solely to the Southern Hemisphere (Map 14). The form of the style in the subgenus differs in the various species. It is either elongated and pubescent or glabrous and short or finally almost non existent. In this last case the upper stigmatic part is stiff, hooked and persistent on the ripe achenes. In those species of the subgenus *Oncostylus* which have strongly reduced styles the achenes resemble in shape the achenes of some species with hooked styles from the genus *Ranunculus* or *Anemone*. In Bolle's classification the genus *Oncostylus* is divided into two subgenera, which in the system accepted in the present work form two sections: *Paleooncostylus* and *Neoncostylus*. In the former there are two species only:



Map 14. Distribution of the subgenus *Oncostylus* of the genus *Geum*

Geum renifolium F. Muell.
Geum uniflorum Buchanan.

Characteristic for the species are uniflorous scapes, large flowers, large terminal leaflets of basal leaves, and elongated styles covered with long hairs. Both are montane species with habitats situated at considerable altitudes in Tasmania and New Zealand respectively.

The section *Neoncostylus* Bolle comprises the following species:

Geum divergens Cheesem.
Geum parviflorum Kirk.
Geum albiflorum Scheutz
Geum leiospermum Petrie
Geum pusillum Petrie
Geum involucratum Persoon
Geum Lechlerianum Schlechtdl.

The species from the section *Neoncostylus* have smaller leaves, multiflorous stems, often small flowers, and strongly reduced styles. *Geum albiflorum* grows on the Auckland Islands, *G. involucratum* and *Lechlerianum* in South America (the Land of Magellan and Chile), and the other species in New Zealand.

Fig. 7. *Geum triflorum*; a — floral stem; b — basal leaf; c — flower — side view; d — flower — bottom view; e — petal; f — achenes in flower; g — achene

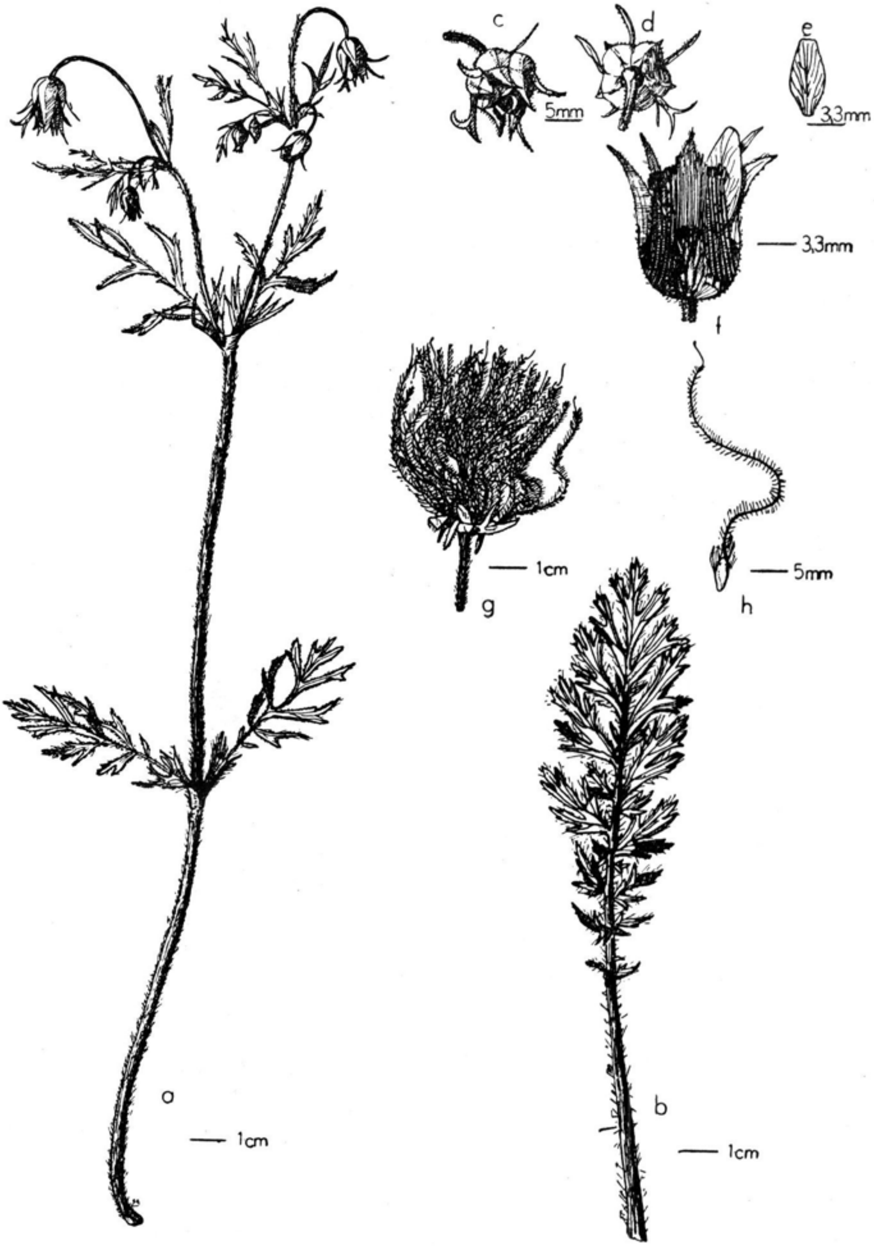
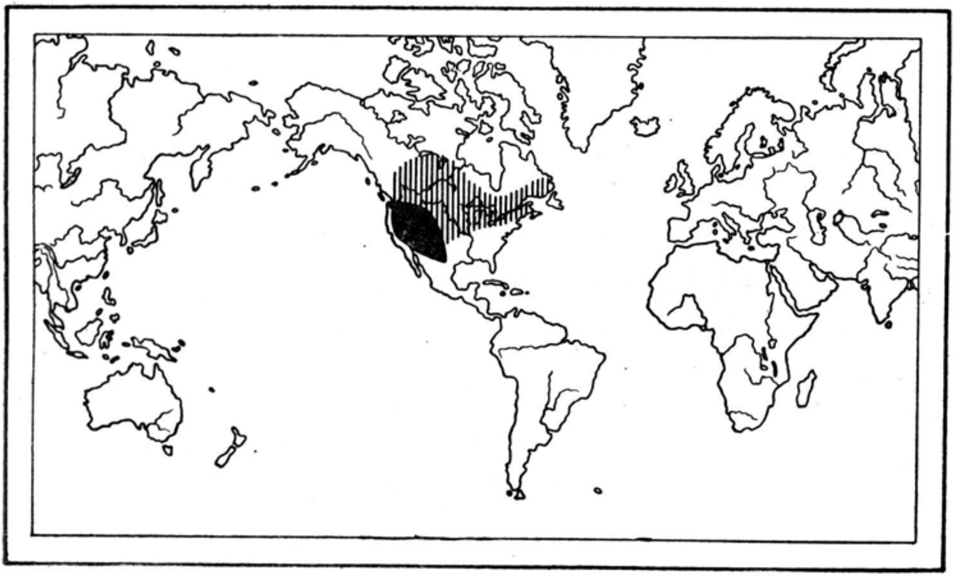
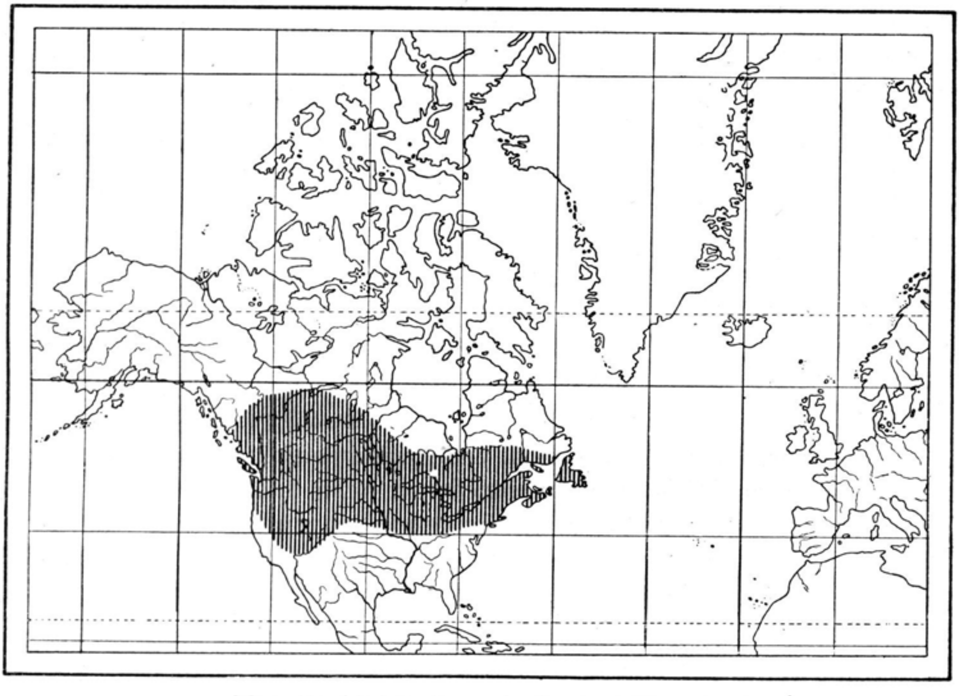


Fig. 8. *Geum ciliatum;* a — floral stem; b — basal leaf; c — flower — side view; d — flower — bottom view; e — petal; f — cross-section through flower; g — achenes in flower; h — achene



Map 15. Distribution of the subgenus *Erythrocoma* of the genus *Geum*



Map 16. Distribution of *Geum triflorum*

I have not been successful in obtaining any of the species from this subgenus for my cultures. The seeds of *G. leiospermum* and *G. parviflorum* obtained from Professor D. H. Frankel from Christchurch, N. Z. unfortunately did not germinate.

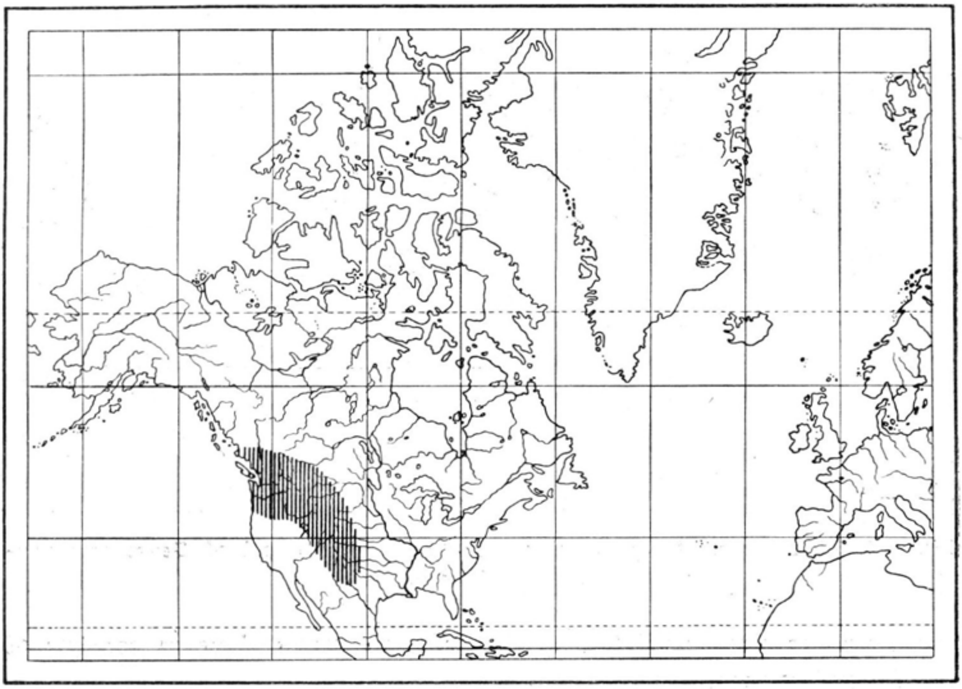
Subgenus *Erythrocoma* (Figs. 7 and 8, Map 15) has species with very long styles covered with long pennate hairs. The styles here differ from those in the subgenus *Oreogeum* od *Sieversia* by that their small stigmatic part is oblique at the tip and sometimes tends to be deciduous, though it is not separated from the rest of the style by any special cell layer, as is the case in the other *Geum* subgenera described below. The plants have leaves dissected into many laciniated leaflets, the usually drooping flowers have elliptically elongated petals, the tube of the calyx is short, with an elevated pronounced disc on the inside (Fig. 8). The subgenus consists of four species closely related morphologically and with habitats in the Pacific zone of the United States:

Geum triflorum Pursch
Geum canescens Greene
Geum ciliatum Pursch
Geum campanulatum Greene

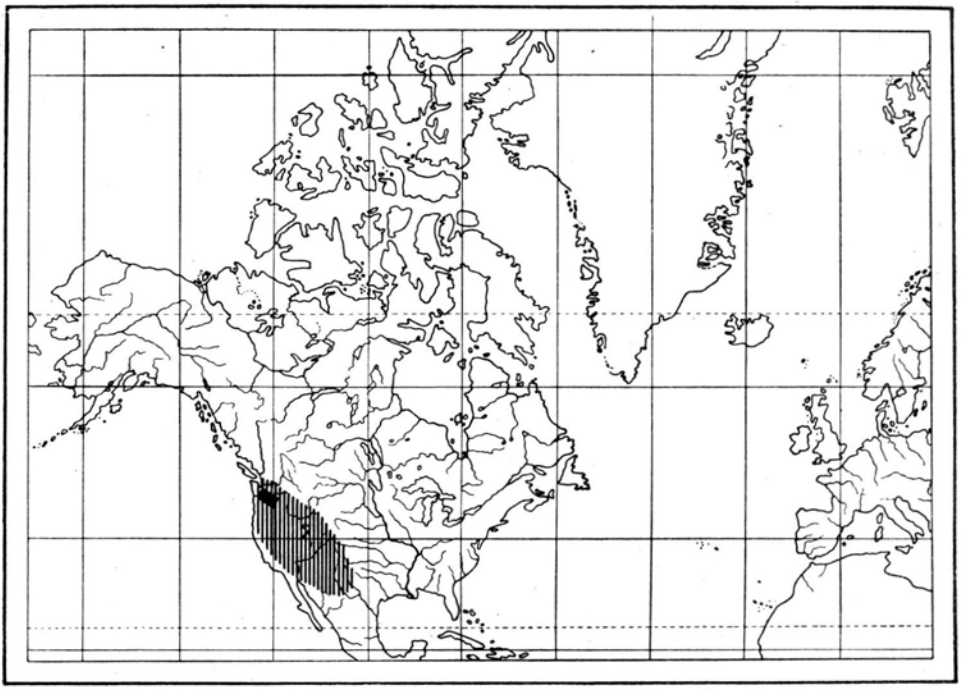
The distribution of these species is shown on Maps 16, 17 and 18. As it can be seen from the maps, the largest area is occupied by *G. triflorum* which spreads east to the Great Lakes. The distribution of *G. canescens* and G. *ciliatum* is restricted to mountainous regions and regions at the foot of mountains. *G. campanulatum* is known only from the Olympic Mts., in the state of Washington.

In my cultures I have *G. triflorum* obtained from Botanical Gardens in Lund, Göteborg and Uppsala as well as plants grown from seeds obtained from Ottawa and collected on natural habitats defined: "Native grassland western edge of Milk River Ridge, 12 miles east of Cardslin, Southern Alberta" and "Natural prairie along railroad 30 miles S. W. Winnipeg, Man". *G. ciliatum* in my cultures has been obtained from the Botanical Gardens of Uppsala and Göteborg, while *G. campanulatum* has been grown from seeds provided by the Botanical Garden in Montreal.

Subgenus *Eugeum* (Figs. 9—28, Map 19) comprises the greatest number of species and is most widely distributed all over the world. My research has been mainly concerned with the species from this subgenus as they are the most numerous in my cultures. For these reasons I shall deal with them more fully discussing morphological differences and geographical distribution of each species separately. The species of this subgenus are characterized by the form and shape of the jointed style divided into two parts. The part at base is called the rostrum, remains on the achene and is hooked at the tip. The upper stigmatic part is shed after blossoming. Bolle includes 28 species in the subgenus *Eugeum* and divides them into two sections (similarly as did Trattinnick, 1823—1824): *Gmeliniana* and *Murrayana*. According to this division plants with stems bearing few usually large flowers and long styles with stigmatic part often longer than half the rostrum are in section *Gmeliniana*. Section *Murrayana* includes species with usually multiflorous stems and a short stigmatic part shorter than half the rostrum. However, in the light of my own obserwations this division does not seem natural and, for instance, the section *Gmeliniana* with both European and South American species is rather artificial. Indeed, much greater fertility is obtained in hybrids from crosses between European species from both the *Gmeliniana* (*G. rivale*, *coccineum* and *silvaticum*) and the *Murrayana* (e. g. *G. hispidum* or *G. molle*) sections than in hybrids from crosses between European and S. American species classified by Bolle together in the section *Gmeliniana* (*G. Quellyon*, *magellanicum* and *peruvianum*). In these conditions the division into sections does not seem to be the best way out of the situation, as probably all the species in this subgenus form one morphological group of



Map 17. Distribution of *Geum ciliatum*



Map. 18. Distribution of *Geum canescens* (vertical lines) and of *Geum campanulatum* (black spot)

more or less closely related species. The subgenus *Eugeum* consists of the following species:

Geum rivale L.
Geum capense Thunb.
Geum silvaticum Pourr.
Geum pyrenaicum Willd.
Geum coccineum Sibth. et Sm.
Geum Quellyon Sweet
Geum magellanicum Pers.
Geum peruvianum Focke
Geum brevicarpellatum F. Bolle
Geum riojense F. Bolle
Geum laciniatum Murr.
Geum latilobum Somm. et Lev.
Geum molle Vis. et Panč.
Geum canadense Jacq.
Geum aleppicum Jacq.
Geum virginianum L.
Geum boliviense Focke
Geum macrophyllum Willd.
Geum perincisum Rydb.
Geum oregonense Rydb.
Geum japonicum Thunb.
Geum Fauriei Leveillé
Geum urbanum L.
Geum Roylei Wallich
Geum hispidum E. Fries.

I shall now describe in detail each of the species of this subgenus.

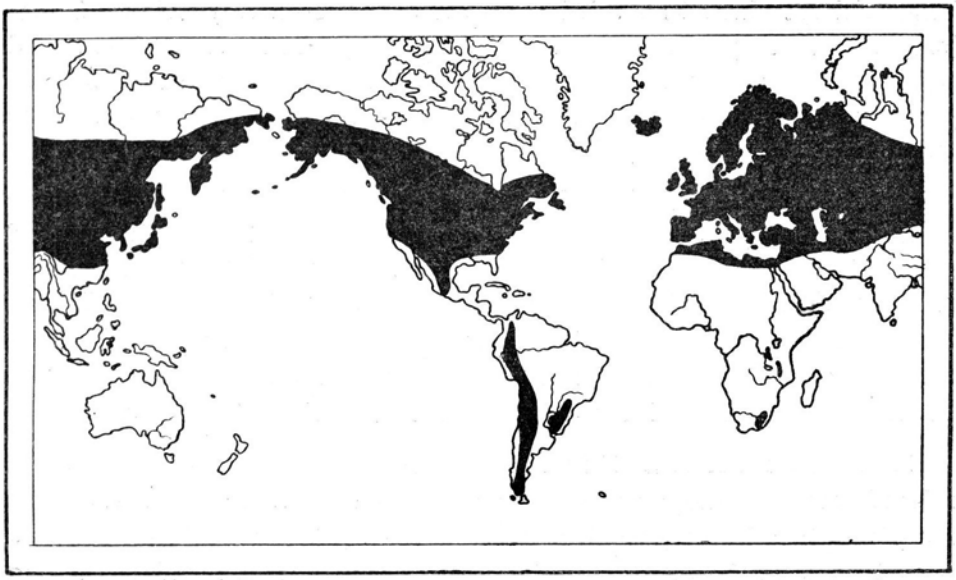
1. *Geum rivale* L. (Fig. 9) has drooping campanulate flowers with a claw on the petals and a long gynophore. The species differs greatly from others in the subgenus. Its large distributional area is shown on

Fig. 9. *Geum rivale*; a — floral stem; b — basal leaf; c — single flower; d — flower — bottom view; e — petal; f — achenes on receptacle; g — achene; h — one achene on receptacle

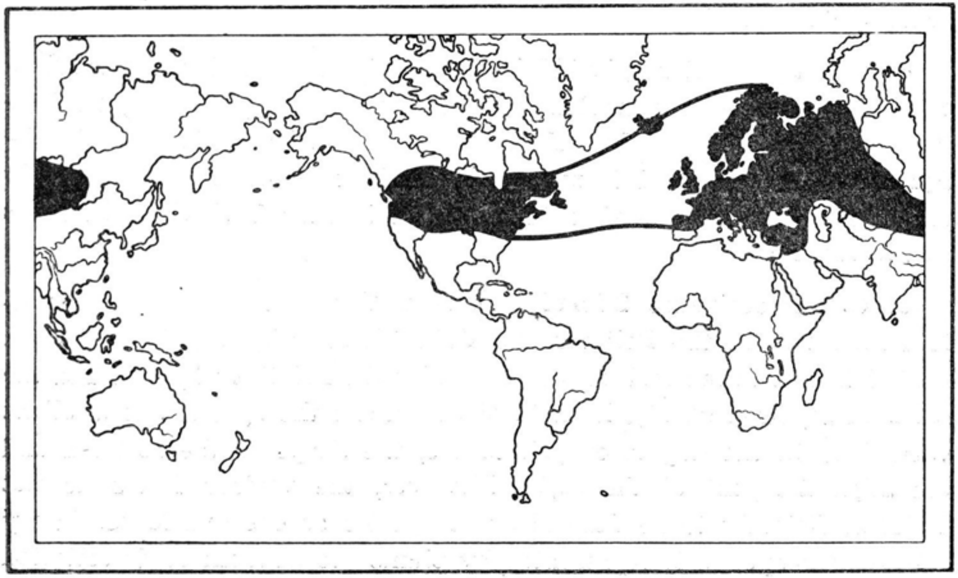
Map. 20. There are considerable variations within the species in respect to leaf size, height, flower shape, length of gynophore etc. Already Turesson (1925) reports that these variations are hereditary and that within the species numerous hereditarily stabilized ecotypes have formed. In my experiments I also have been able to show that plants of different origin when cultivated in the same conditions retain the differences in the shape and size of their organs. However, no correlation is as yet evident between morphological variation and geographical distribution and there is no sufficient data for distinguishing subspecies or varieties. The division of this species into two subspecies, sbsp. *eurivale* and sbsp. *subalpinum*, which has been introduced by Selander (1947) and accepted by Löve and Löve (1948) cannot be applied consistently. The numerous specimens of *G. rivale* collected on the Faröe Islands and in Iceland which I have been able to inspect in herbariums at Copenhagen show that the plants from these countries differ considerably from plants on the European and American continents. *G. rivale* plants from Iceland which I have grown out of seeds obtained from Professor A. Löve have retained for many years thier characteristic small height and the widespread flowers. This indicates that on those islands a markedly distinct ecotype of the species has developed. The form of *G. rivale* with stems and flowers deprived of anthocyanin which has been described as *G. pallidum* Fisch et Mey. differs from the typical form with anthocyanin by one gene only (Dahlgren 1924). Within the *pallidum* form there also are ecotypes differing in the shape and size of leaves and in other characters.

In my cultures I have numerous plants collected in Poland both from the lowlands and the Tatra Mountains, from Iceland (Pinvellier, S. W. Iceland) and grown out of seeds collected in the state of New York and obtained from Professor R. T. Clausen. The *pallidum* form I have only from seeds collected in various Botanical Gardens (Copenhagen, Stockholm and others).

Bolle (1933) mentions as closely related to *G. rivale* the North American species „*G. geniculatum* Michaux" but this probably is only a hybrid, one of the parent forms of which is *G. rivale*. Bolle who knew this species only from floras of Rydberg and of Torrey and Gray notes that the descriptions do not agree. I myself have inspected specimens classified as *G. geniculatum* Michx. from the Roan Mountains, North Carolina (three specimens on two sheets) in a herbarium in Uppsala. They all show considerable variability. One has creamy petals ± 6 mm long with claw. Another has pale yellow petals ± 5 mm



Map 19. Distribution of the subgenus *Eugeum* of the genus *Geum*



Map 20. Distribution of *Geum rivale*

long, without claw. The third has oval purple-creamy petals 2—3 mm long. The three plants differ also by the shape of leaves, achenes and styles. Their appearance seems to suggest that they are of hybrid progeny showing segregation in respect to the majority of diagnostic characters.

2. *Geum capense* Thunb. This species is the only representative of the subfamily of *Dryadoideae* growing in South Africa. It is found mainly in the provinces of Natal and Cafferland where it occupies mountain meadows (Map 21). From the numerous specimens which I have inspected in herbariums of Wrocław, Uppsala, Stockholm and Lund it appears that the species shows comparatively little variation. In spite of the many attempts I have not succeeded in obtaining seeds.

3. *Geum silvaticum* Pourr. The species differs from the other related species primely by the size of achenes (Fig. 10) inserted on a short receptacle in relatively small numbers (25—30). The receptacle is placed on a long gynophore. The species grows on mountain meadows and in lower mountain regions of the western Mediterranean area (Map 22). All herbarium specimens which I have inspected show little tendency to variation. The very strong and large plants from the Atlas Mountains have been described by H. Lindberg as var. *atlanticum* (Desf.) Lindb. In my cultures the species has been grown out of seeds obtained from the Botanical Garden at Coimbra and collected from a natural habitat in Portugal.

4. *Geum pyrenaicum* Willd. The species is related to the previous one but its achenes are smaller, more numerous and have no gynophore (Fig. 11). It has an exclusively montane character, grows only in the Pyrenees (Map 23) and is monomorphic. In my cultures I have only plants grown out of seed obtained from Botanical Gardens in Paris and Lausanne.

5. *Geum coccineum* Sibth. et Sm. The species grows on mountain meadows in the Balkans and Asia Minor (Map 24). It differs at first sight from the species listed above by the red tint of petals and the reflexed sepals (Fig. 12). In natural conditions the species shows slight variability in the degree of pubescence, the shape of the rostrum and the stigmatic part of the style. However, the various forms do not differ sufficiently to be defined as subspecies or even varieties. In my cultures the species is represented by plants grown from seeds collected in the Rhodope Mountains in Bulgaria.

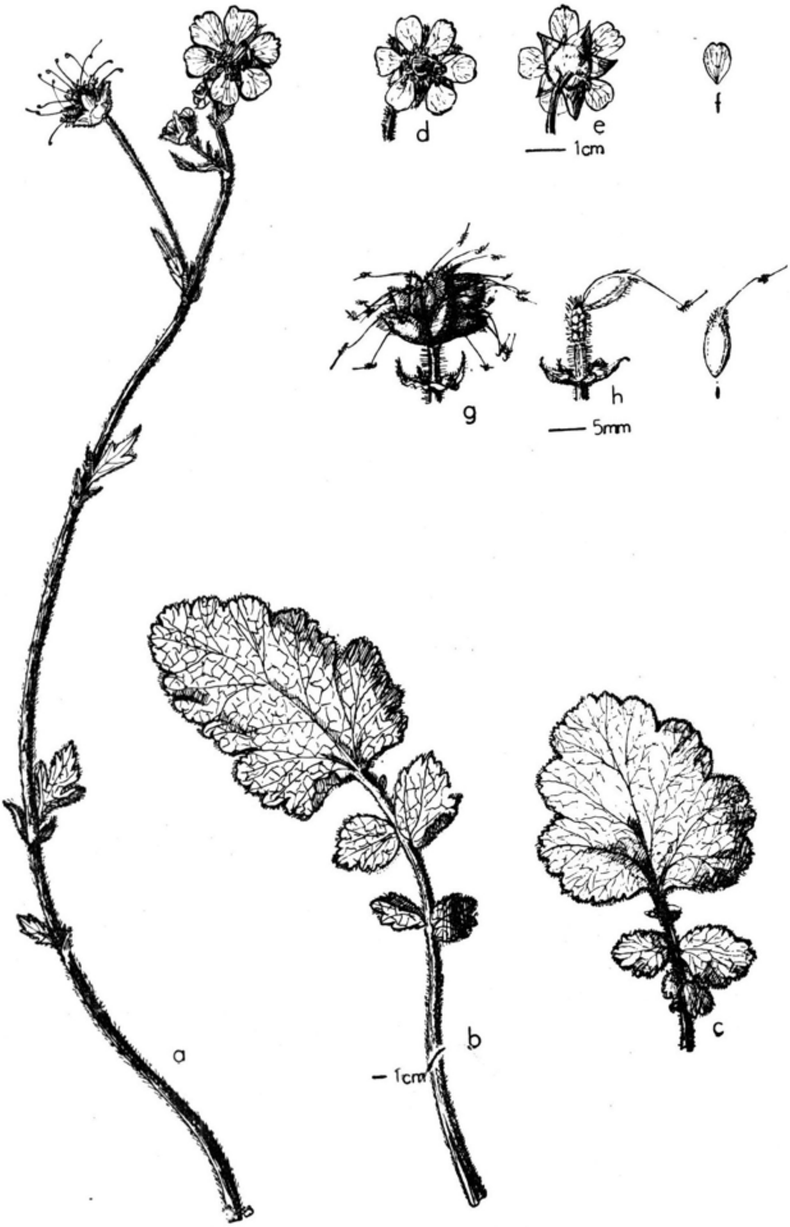
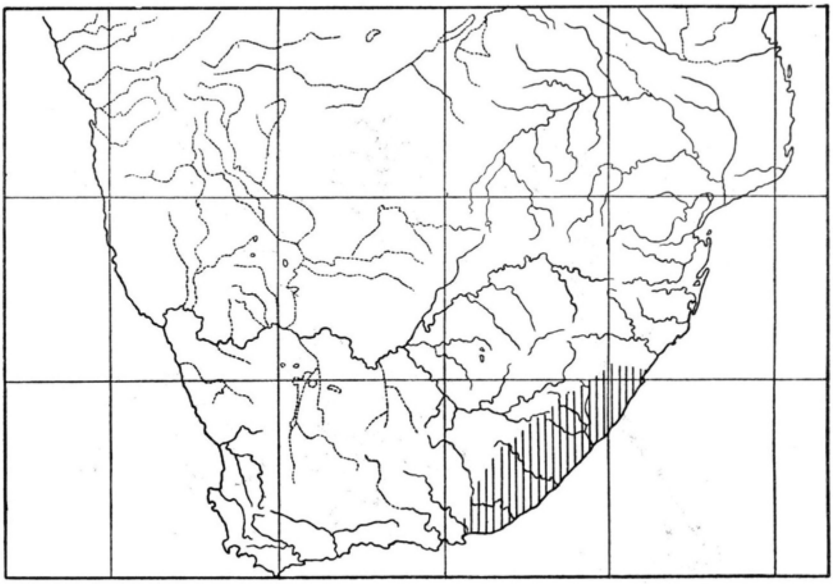
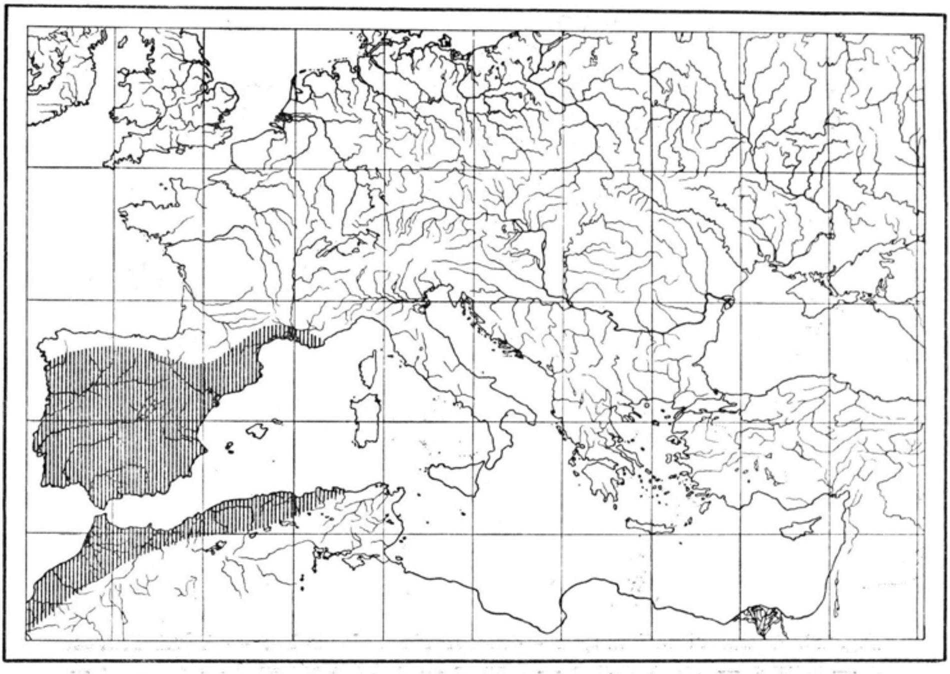


Fig. 10. *Geum silvaticum*; a — floral stem; b and c — basal leaves; d — flower — top view; e — flower — bottom view; f — petal; g — achenes on receptacle; h — receptacle with one achene; i — achene



Map 21. Distribution of *Geum capense*



Map 22. Distribution of *Geum silvaticum*

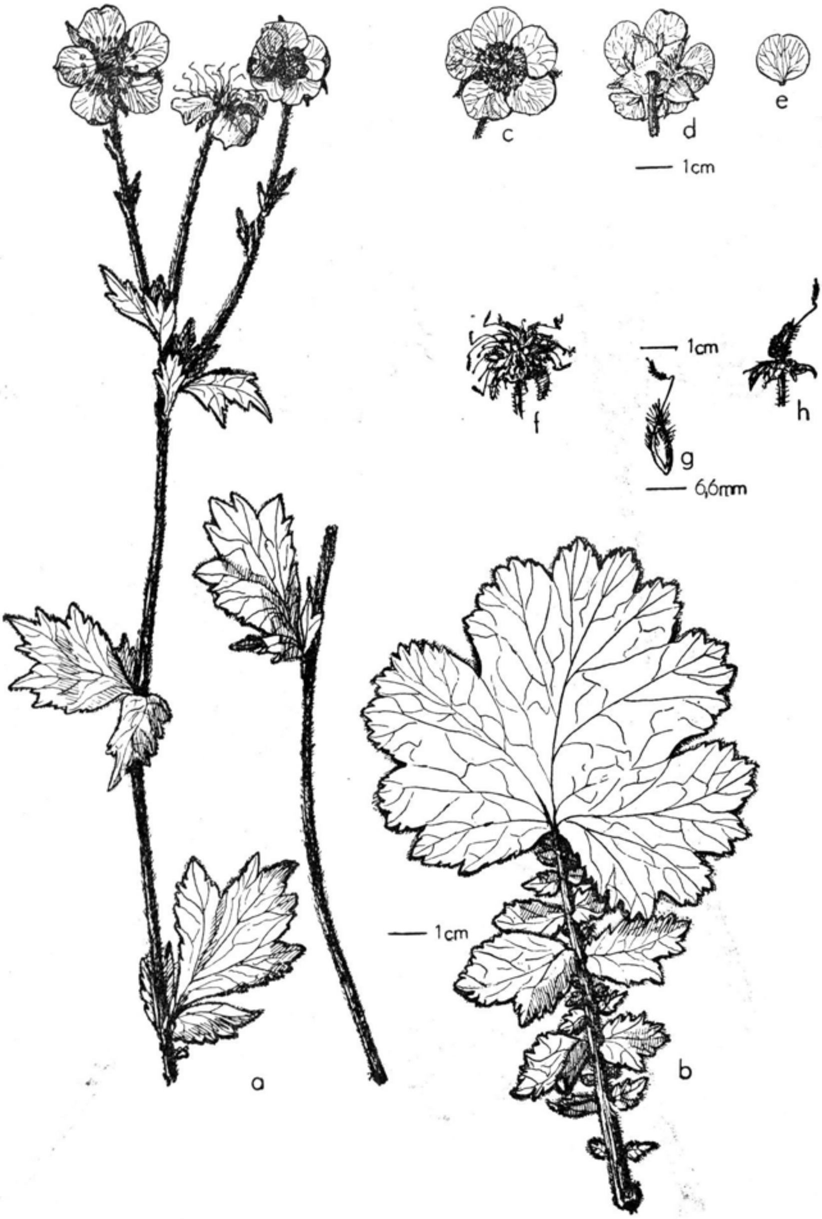


Fig. 11. *Geum pyrenaicum*; a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — achene; h — receptacle with one achene.

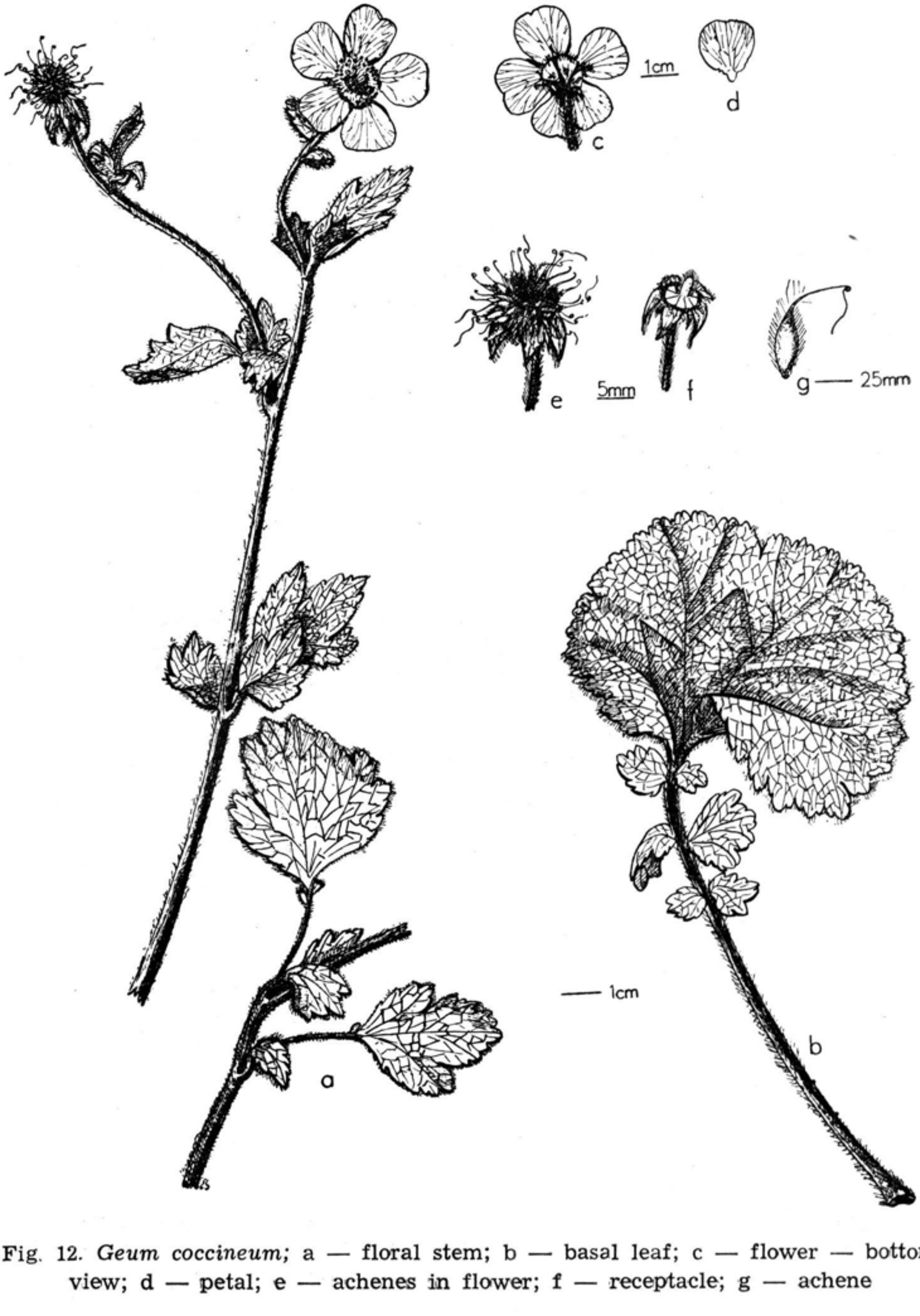
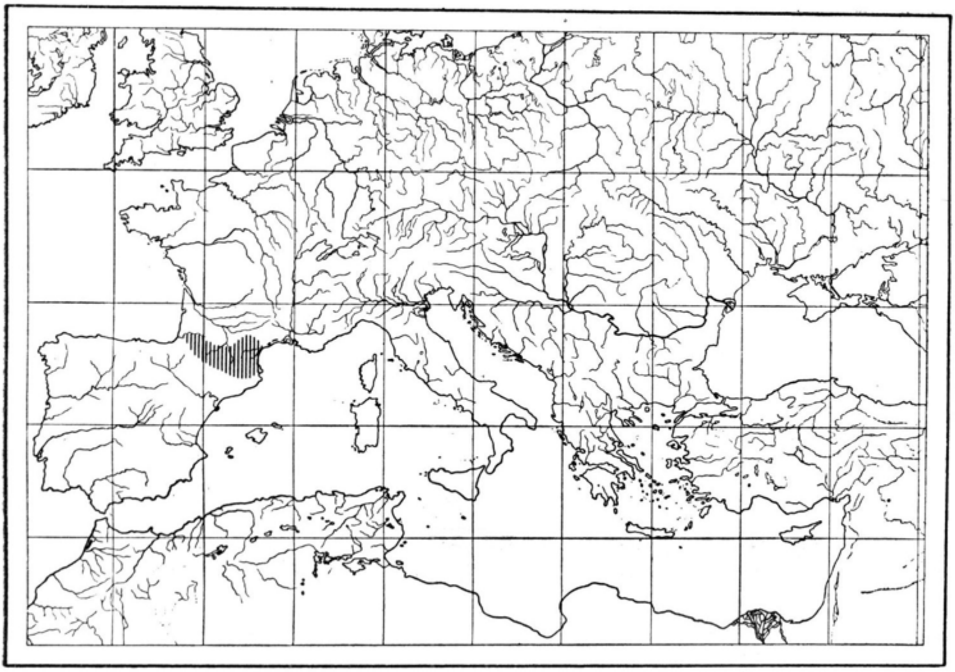
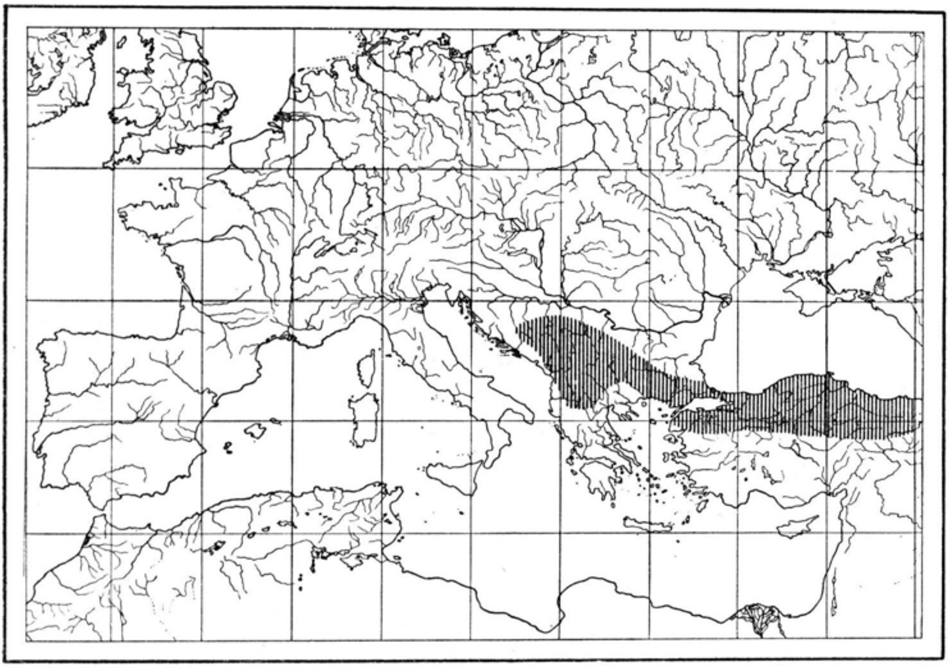


Fig. 12. *Geum coccineum;* a — floral stem; b — basal leaf; c — flower — bottom view; d — petal; e — achenes in flower; f — receptacle; g — achene



Map 23. Distribution of *Geum pyrenaicum*



Map 24. Distribution of *Geum coccineum*

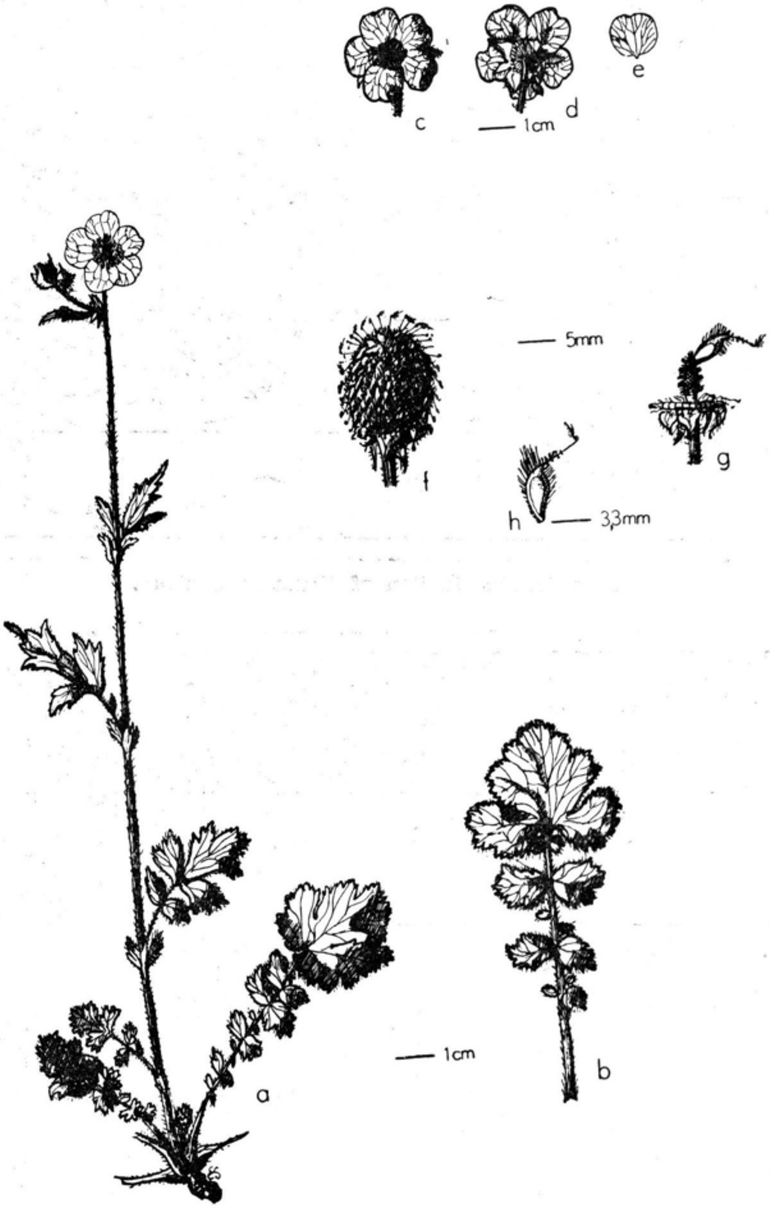


Fig. 13. *Geum Quellyon*; a — growth habit of plant; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

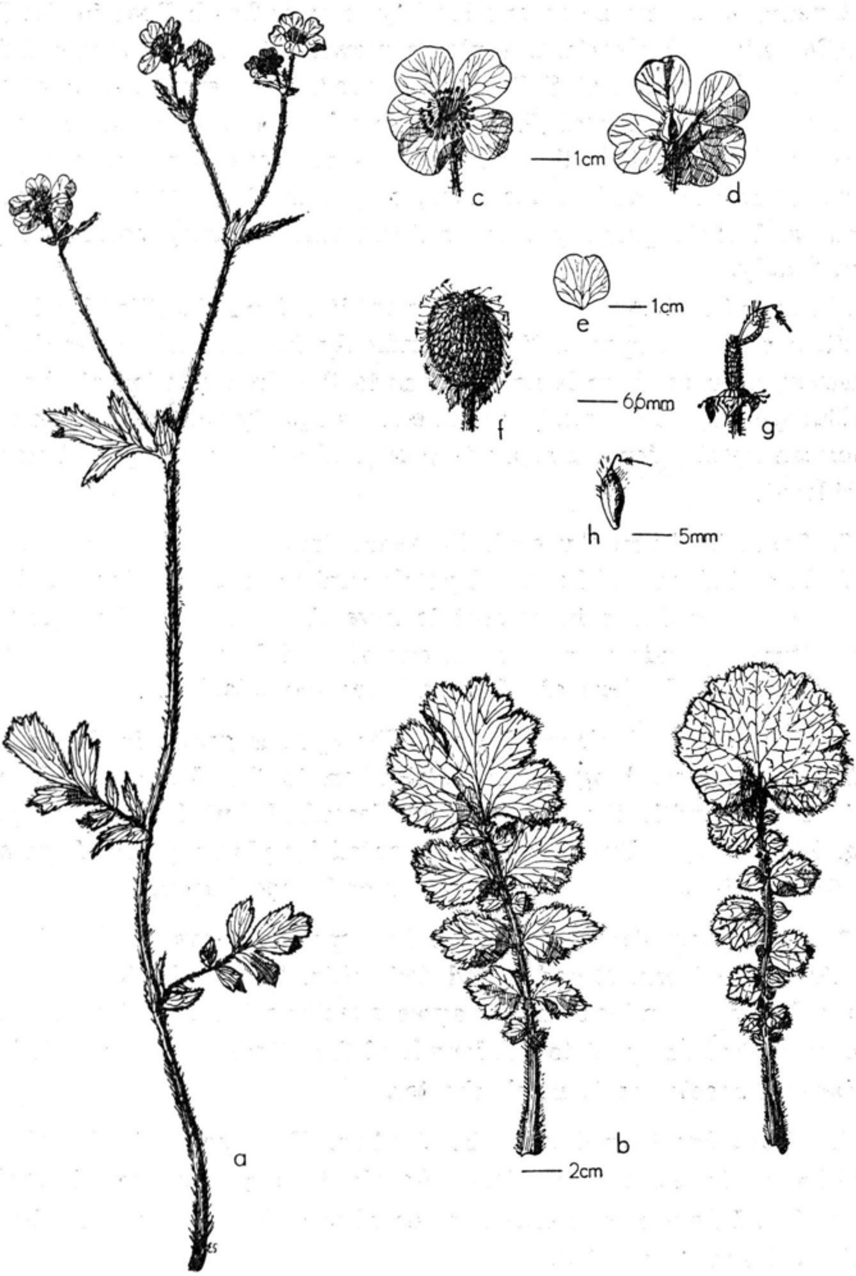


Fig. 14. *Geum magellanicum*; a — floral stem; b — basal leaves; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

Stojanoff and Stefanoff describe the endemic species *Geum rhodopeum* as appearing in one locality only at Tasch Boas in the Rhodope Mountains, Bulgaria. The plants grown out of seeds obtained from the Botanical Garden at Sofia have proved, after examination of their progeny, to be hybrids of *G. coccineum* with some other *Geum* species. It seems therefore that the classification of these plants as a separate species is rather doubtful. However, only a further examination of the plants and their progeny from natural habitats may solve the problem finally.

The four South American species next listed are classified by Bolle together with the species listed previously in the section *Gmeliniana*. However, even as there is no doubt as to the close relationship between the European species already described it is equally certain that the South American species form a separate group. The latter group will now be considered.

6. *Geum Quellyon* Sweet. These montane plants grow in the Andes in Chile and Peru and have red petals similar to *G. coccineum*, though the two species differ in respect to several other characters (Fig. 13). My cultures include plants grown out of seed from specimens obtained from Botanical Gardens of Warsaw, Kew and Istanbul.

7. *Geum magellanicum* Pers. The species grows in South Chile and Argentina reaching in its distribution to the Straits of Magellan. It is related with the species just described but has yellow petals (Fig. 14). In my cultures it is represented by plants grown from seeds obtained at Botanical Gardens in Kew and Copenhagen.

8. *Geum peruvianum Focke.* The species grows on the slopes of the Andes in Peru, Ecuador and Columbia. The herbarium specimens which I have examined do not agree exactly with Focke's description, primely in respect to the length of the stigmatic part which in the herbarium specimens is much shorter.

9. *Geum brevicarpellatum* F. Bolle. The species is described by Bolle as indigenous to Sierra Achala in the province of Cordoba, Argentina. I have not seen specimens of the species in any of the herbariums I have inspected.

A close relation to the above South American group is the species next on the list which also originates from South America but is classified by Bolle in the section *Murrayana*.

Fig. 15. *Geum riojense;* a — floral stem; b — basal leaf; c — flower — top view; d —flower — bottom view; e — petal: f — achenes in flower; g — receptacle with one achene; h — achene

10. *Geum riojense* F. Bolle. For the first time the species was described by Bolle on the basis of a herbarium specimen collected in the province de la Rioja, Argentina. Through the kindness of Professor H. Brücher of Tucuman I have obtained seeds of the species from two natural habitats near Tucuman. The habitats are described as follows: a) "feuchte Wälder an der Strasse von Salta nach Fajni" and b) "Valle Cito (ca 2000 m hoch) 130 km. süd-westl. von Tucuman in Aconguija-Gebirge". The plants (Fig. 15) differ slightly from Bolle's description which, however, is not quite sufficient for identification. I have not seen any herbarium specimens of *G. riojense* and so have no comparison with the plants in my cultures. If it proves that the plants I am growing do not belong to the species *G. riojense*, then they must belong to a new and as yet undescribed species related to *G. riojense*.

The species which will now be described are grouped according to Bolle's classification in the section *Murrayana*. They occur mainly in Europe, Asia and North America forming several closely related groups separated from each other by sharply marked hybrid sterility. The list of species belonging in this section runs as follows.

11. *Geum urbanum* L. Of all the *Geum* species this is the most common one in Europe (Fig. 16). The species covers in its distribution large areas in Europe and Western Siberia (Map 25) but this is largely due to human activity, as it is man who has carried the species so far to the north of Europe and even to North America and Australia. The species shows quite considerable variability, mainly in its southern regions where it is aboriginal and not an antropochoric element. In South Europe the var. *australe* Guss. occurs, it has larger flowers and greater fruit heads than the northern forms. My cultures include plants originating from natural habitats in the vicinity of Warsaw and from Botanical Gardens in Geneva and Tiflis.

12. *Geum latilobum* Somm. et Lev. The species is very closely related to *G. urbanum* from which it differs only by that its cauline leaves are less incised and by leaflets rounded at the tip. The species grows only in the Transcaucasian Colchide region (Map 25). It may be that it is merely a variety or subspecies of *G. urbanum* and does not merit its classification as a separate species. Unfortunately I have not obtained it for my cultures. On the other hand *Geum hyrcanum* C. A. Meyer which has been described on he basis of only one specimen

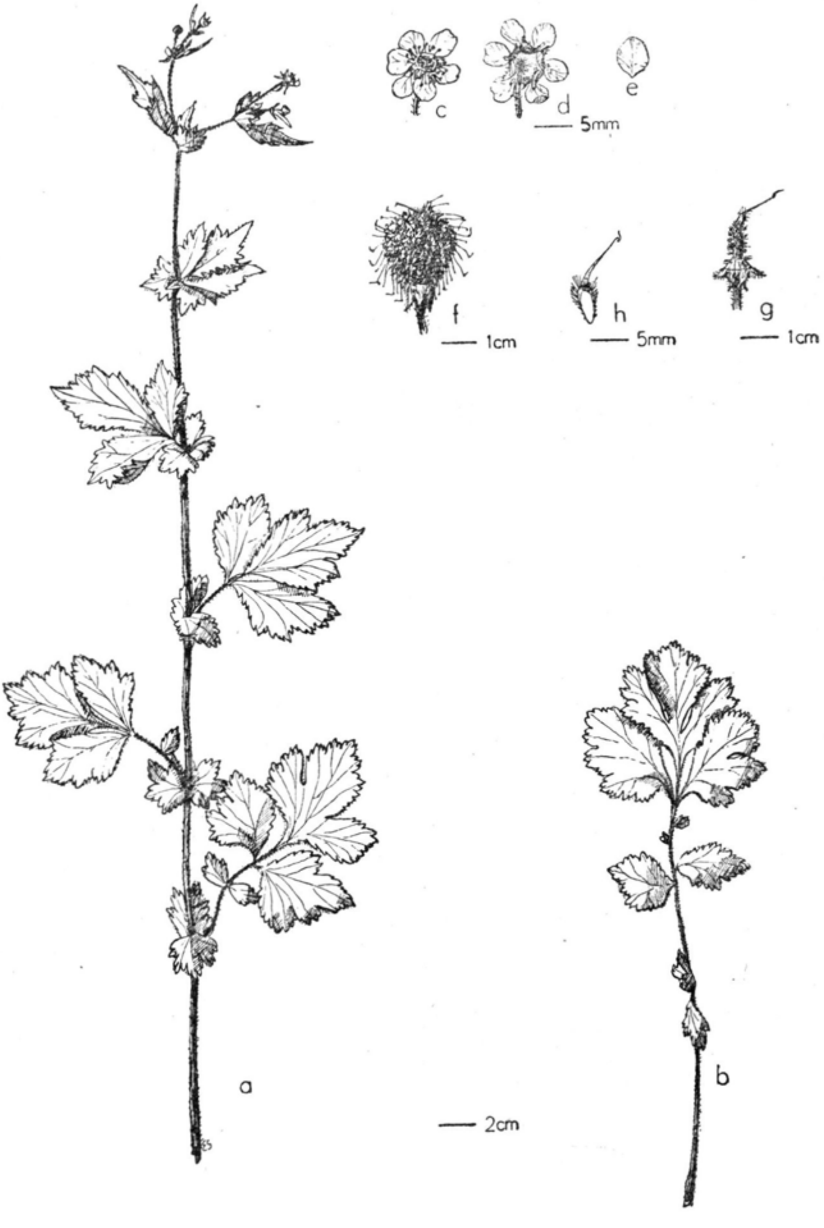
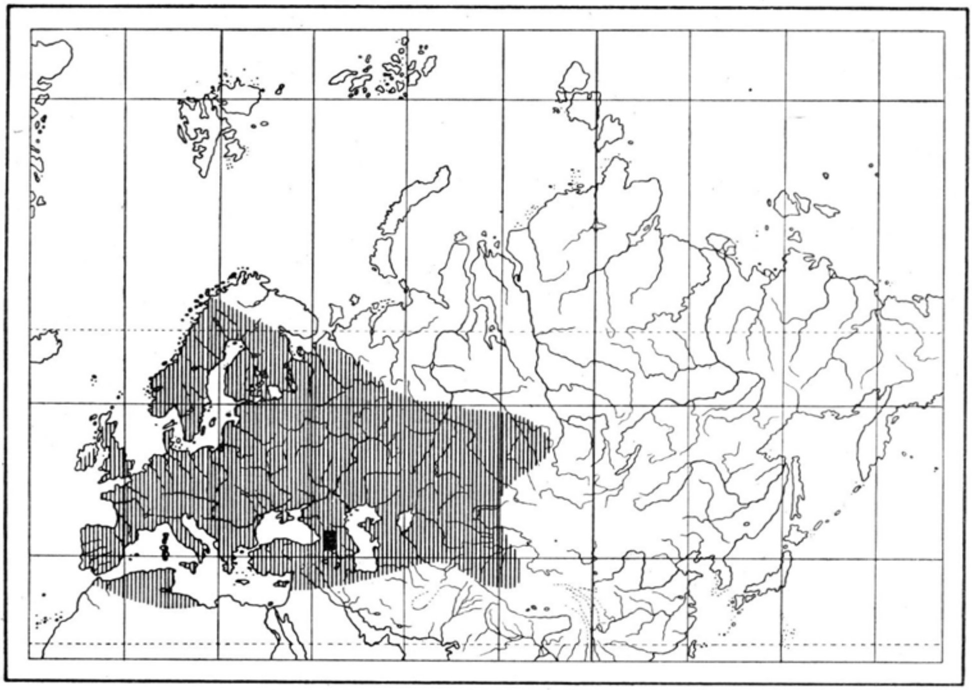


Fig. 16. *Geum urbanum;* a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene



Map 25. Distribution of *Geum urbanum* (vertical lines) and of *Geum latilobum* (black rectangle)

collected in the Talysz Mountains in the vicinity of a place called Swant is undoubtedly a form of *G. urbanum* (cf. Flora of the USRR vol. X, p. 261).

13. *Geum Roylei* Wallich. This species is also closely related to *G. urbanum*. It grows in the North-East Himalayas and differs from *G. urbanum* by smaller stipules, denser pubescence on the achenes and by glandular hairs on the rostrum. I have not succeeded in obtaining this species for my cultures.

14. *Geum molle* Vis. et Panc. The species differs greatly from the others classified by Bolle in the section *Murrayana* by the shape of the leaf blade of the terminal leaflet. The plants are wholly covered by dense soft pubescence and numerous glandular hairs and have stems bearing two or three flowers. The slight ramification of the stems and the long persisting upright calyx associate the species with the section *Gmeliniana*, while on the other hand the coma-like stigmatic part of the styles is indicative of the connection with the section *Murrayana* (Fig. 17). The species has a restricted distribution in the Balkans and

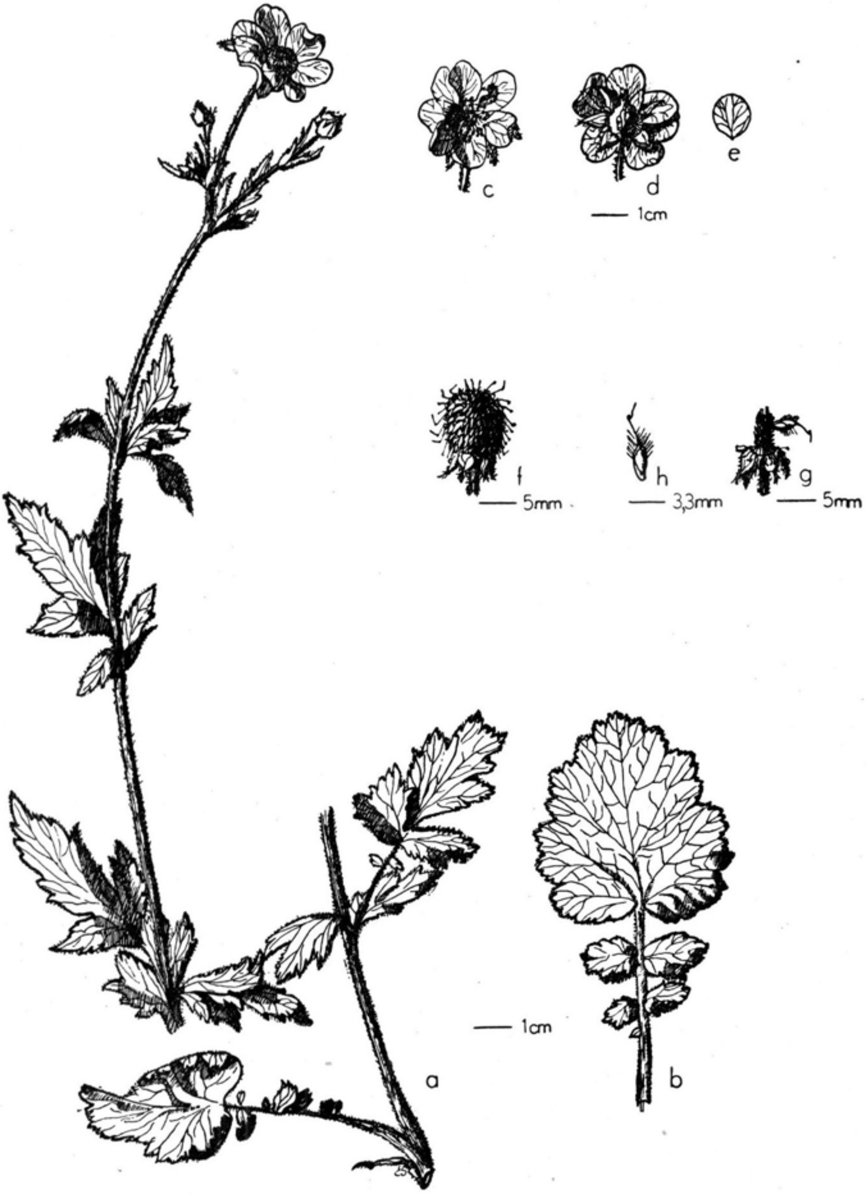
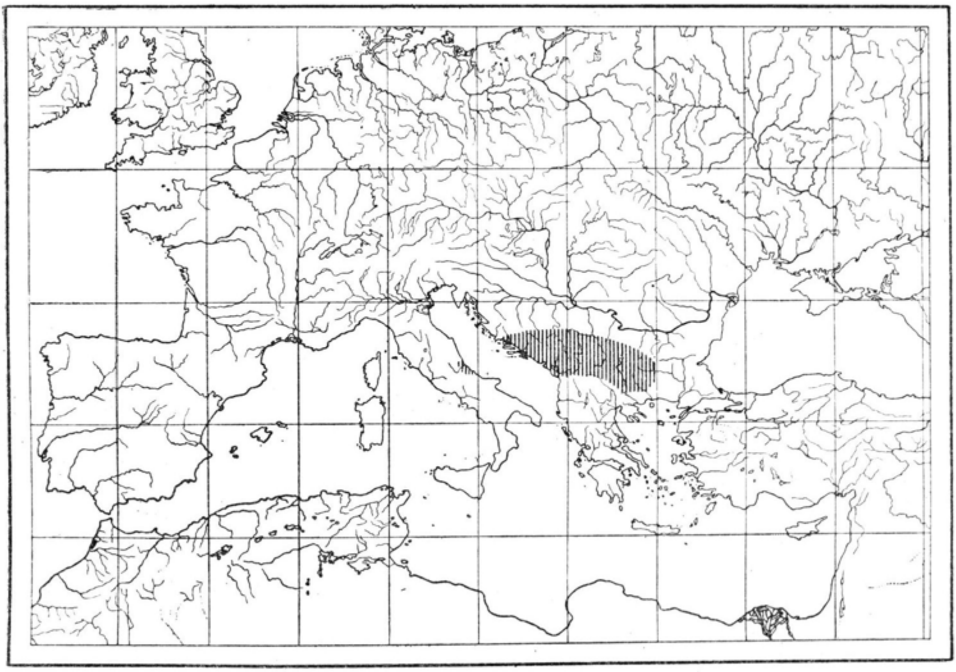


Fig. 17. *Geum molle;* a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

the Abruzzian Mountains on the Apennine peninsula (Map 26). The plants in my cultures have been grown out of seeds collected on natural habitats in Bulgaria and sent from Sofia.



Map 26. Distribution of *Geum molle*

15. *Geum hispidum* E. Fries. The species grows in the south of Sweden while its variety *albarraciense* grows in Spain. Its disjunctive distribution is of great interest and the species is undoubtedly closely related to *G. molle* from which it differs by the shape of leaves, ramification of stems and the size of flowers (Fig. 18). *G. hispidum* plants in my cultures have been grown out of seeds originating from a natural habitat in Ryssby, Kalmar district, Sweden (the seeds have been collected off a herbarium specimen at the Botanical Garden in Göteborg — legit Doctor R. Sterner, Aug. 6, 1948) and out of seeds obtained from the Botanical Garden in Stockholm. The seeds of the variety *albarraciense* have been provided by Professor A. Bolos of Barcelona and originated from a natural habitat in Hilari, Sacalm-Catalounia. The distribution of *G. hispidum* can be seen on Map 27.

16. *Geum macrophyllum* Willd. This species together with the two described next form a closely related group separated by strict

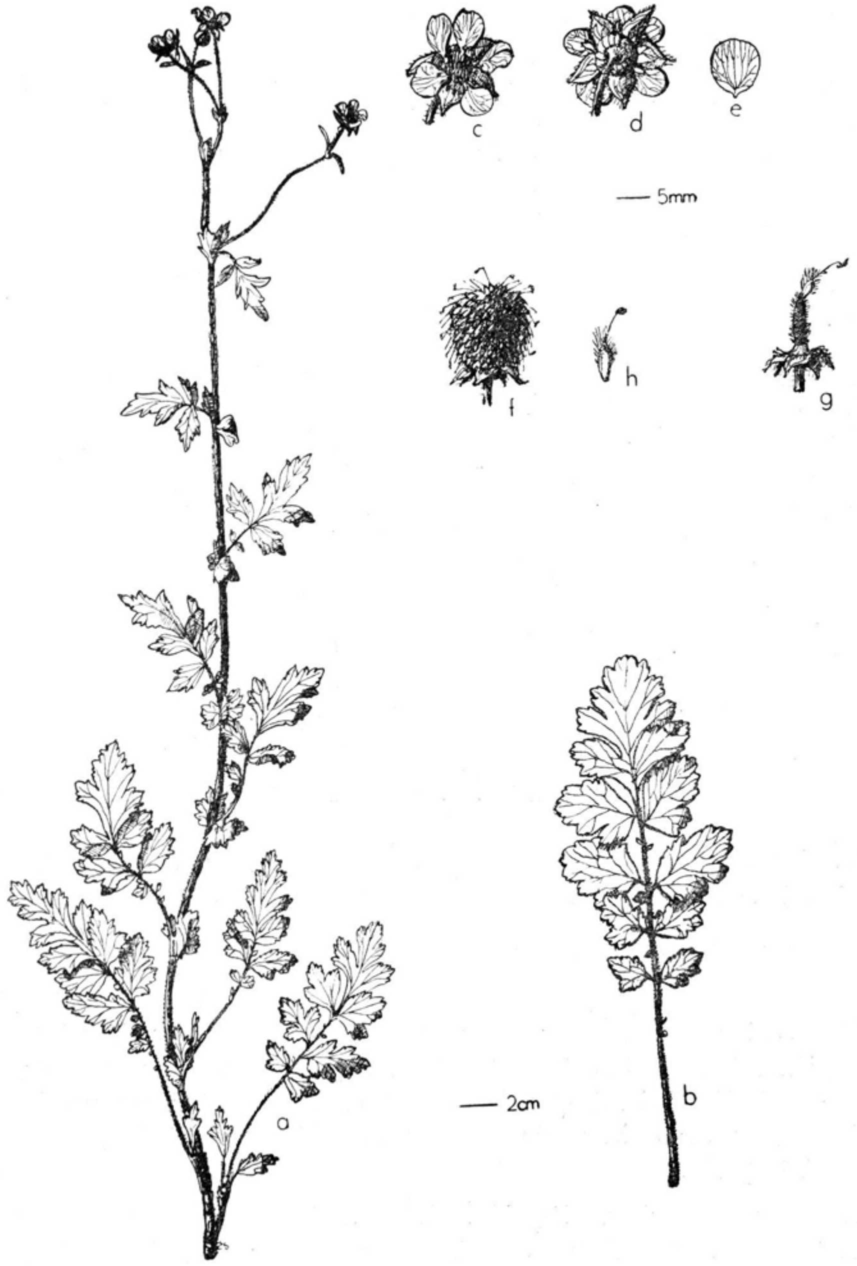
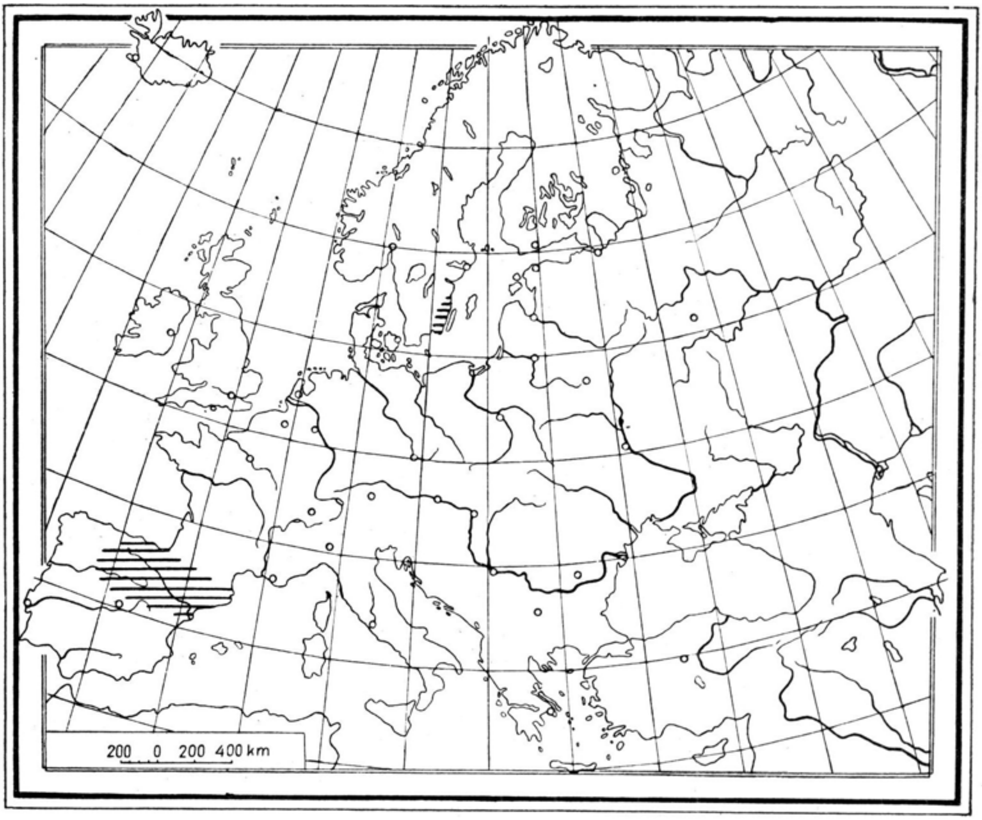


Fig. 18. *Geum hispidum*; a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene.



Map 27. Distribution of *Geum hispidum*

sterility barriers from other species in subgenus *Eugeum* (W. Gajewski 1955). It is characteristic for its basal leaves with large rounded reniform terminal leaflet. The plants are covered entirely with stiff protruding bristles, the numerous flowers have long cylindrical receptacles, and the pubescent achenes are very numerous (Fig. 19). The species is a North American one and its distribution stretches through Alaska, the Aleutian Islands to Kamschatka, Sachalin and the Commander Islands in North-East Asia. The species is represented in my cultures by plants grown out of seeds obtained from the Botanical Gardens at Kew and Uppsala.

17. *Geum perincisum* Rydb. The species is very closely related to the previous one, though, its leaves are sharply incised (Fig. 20). Moreover, it has a more continental distribution in the north of the North American continent. My cultures include specimens of the species grown out of seeds provided by the Botanical Garden in Montreal and

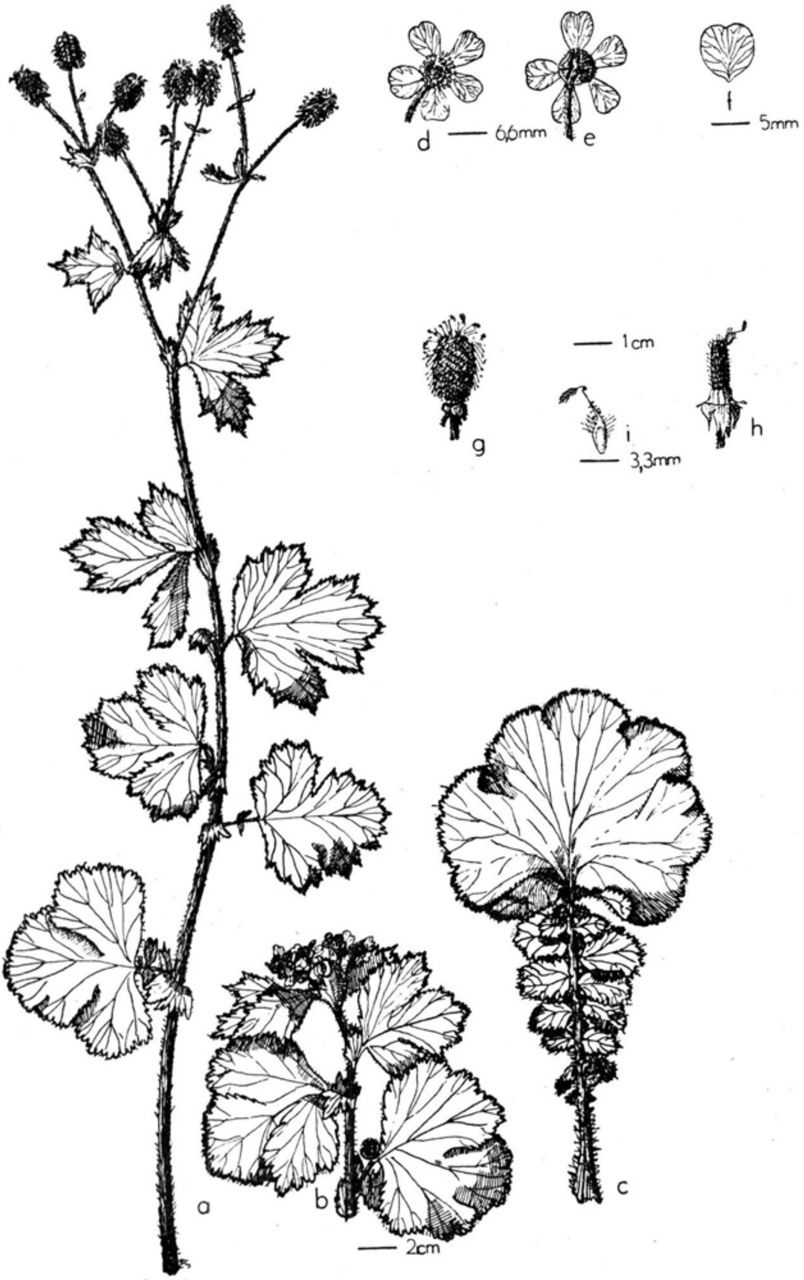


Fig. 19. *Geum macrophyllum;* a — floral stem at fruiting; b — top of floral stem at anthesis; c — basal leaf; d — flower — top view; e — flower — bottom view; f — petal; g — achenes in flower; — h — receptacle with one achene; i — achene

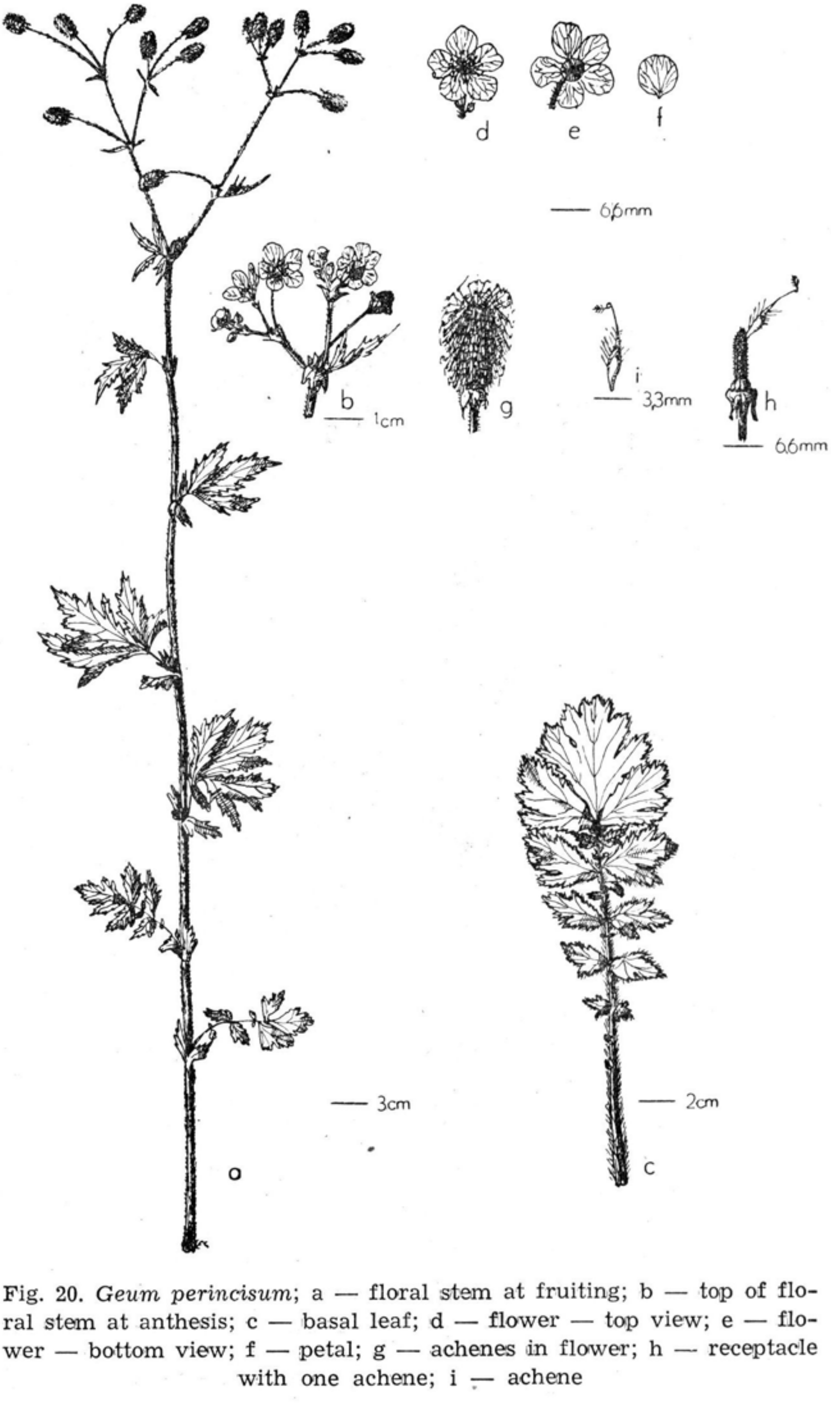


Fig. 20. *Geum perincisum*; a — floral stem at fruiting; b — top of floral stem at anthesis; c — basal leaf; d — flower — top view; e — flower — bottom view; f — petal; g — achenes in flower; h — receptacle with one achene; i — achene

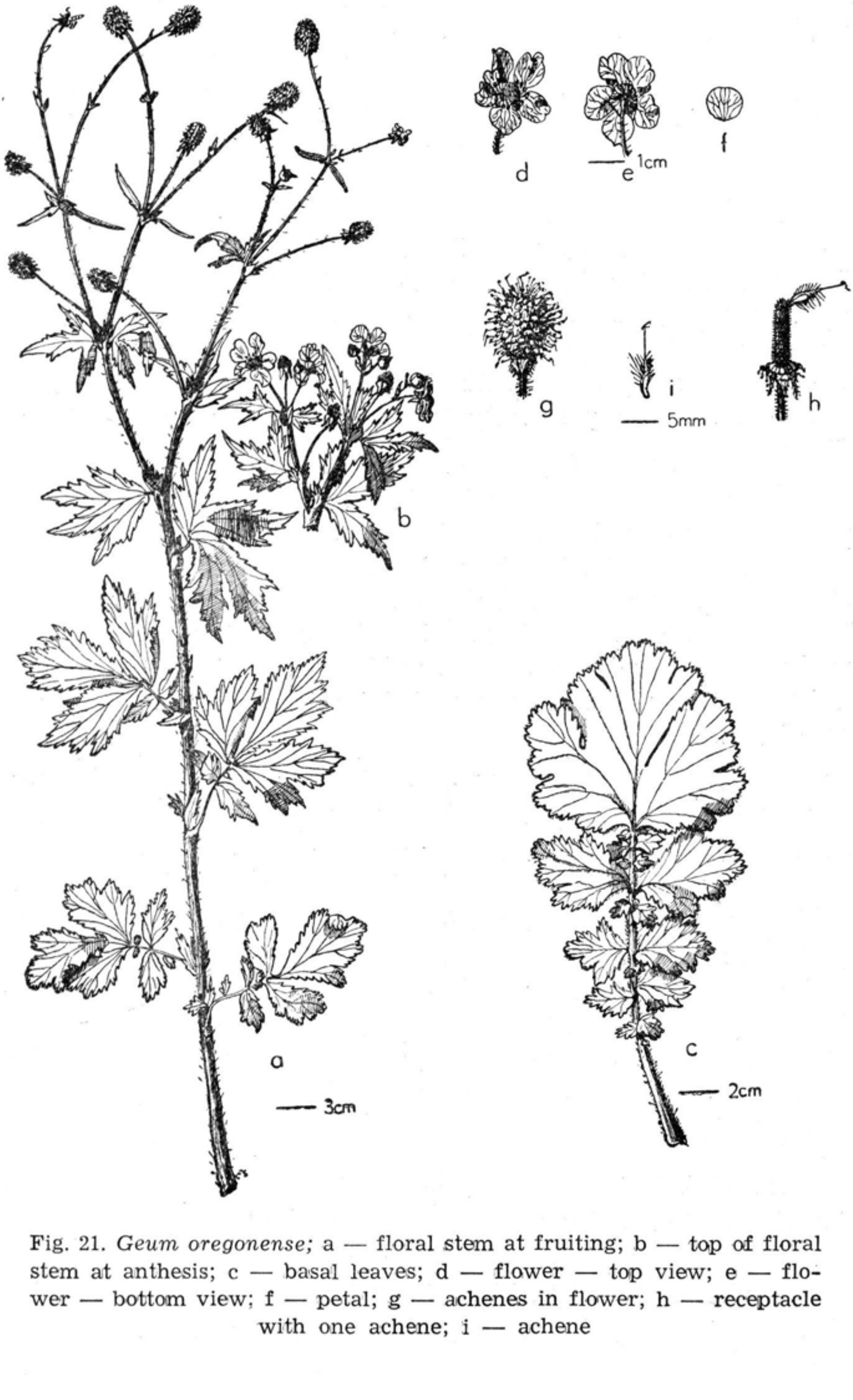


Fig. 21. *Geum oregonense;* a — floral stem at fruiting; b — top of floral stem at anthesis; c — basal leaves; d — flower — top view; e — flower — bottom view; f — petal; g — achenes in flower; h — receptacle with one achene; i — achene

collected from natural habitats described as follows: 1) Yellow Knife, Great Slave Lake, 2) Lac Makawa Distr. de North Battlefield, Sask., and 3) Grand Lac de l'Ours N. W.

18. *Geum oregonense* Rydb. This species is also very closely related to the two previous ones from which it differs slightly in the shape of leaves, the size of petals and achenes (Fig. 21), and by its distribution. The plants in my cultures have been grown out of seeds collected off a herbarium specimen defined as follows: "The Rocky Mountain Herbarium, University of Wyoming, Laramie, No. 4085. Along stream banks at Lost Creek Bridge, Hayden Division, Medicine Bow Forest, Carbon County, Wyoming, Elev. 8000 ft. Aug. 5, 1946. Collect. et Det. C. L. Porter". The plant was defined as *G. macrophyllum*. The seeds were planted in 1949 and germinated well. The geographical distribution of the last three species has been previously described elsewhere (W. Gajewski 1955).

19. *Geum japonicum* Thunb. The general appearance of the plants from this species can be seen on Fig. 22 and its distribution is shown on Map 28. The species has its wide distribution in Japan and China. It shows a tendency to variability. According to Bolle a variety defined by him as var. *chinense* Bolle occurring in China differs from the plants growing in Japan and Korea. The plants in my cultures have been grown from seeds provided by Professor T. Kihara of Kyoto, Japan.

20. *Geum Fauriei* Leveillé. This species both by its morphology and distribution in Asia (Japan and Sakhalin) occupies an intermediate position between *Geum japonicum* and *G. macrophyllum* (Fig. 23 and Map 28). Because of its dodecaploid chromosome number the species is probably an amphiploid formed by two hexaploid parent species the characters of which it combines. The species is represented in my cultures by plants grown out of seeds provided by the Botanical Garden in Lausanne as *G. calthaefolium* var. *dilatatum* and from seeds provided by the Botanical Garden in Leningrad.

21. *Geum aleppicum* Jacq. This species (Fig. 24) has the largest distribution of all the *Geum* species. Its western boundary in Europe passes through Poland and to the east of this country the species covers in its distribution entire northern Eurasia right up to China, Japan and Kamschatka, and also North America from Canada to Mexico. The species is also known from New Zealand where it has probably been carried by man (Map 29). The species is variable and in the various

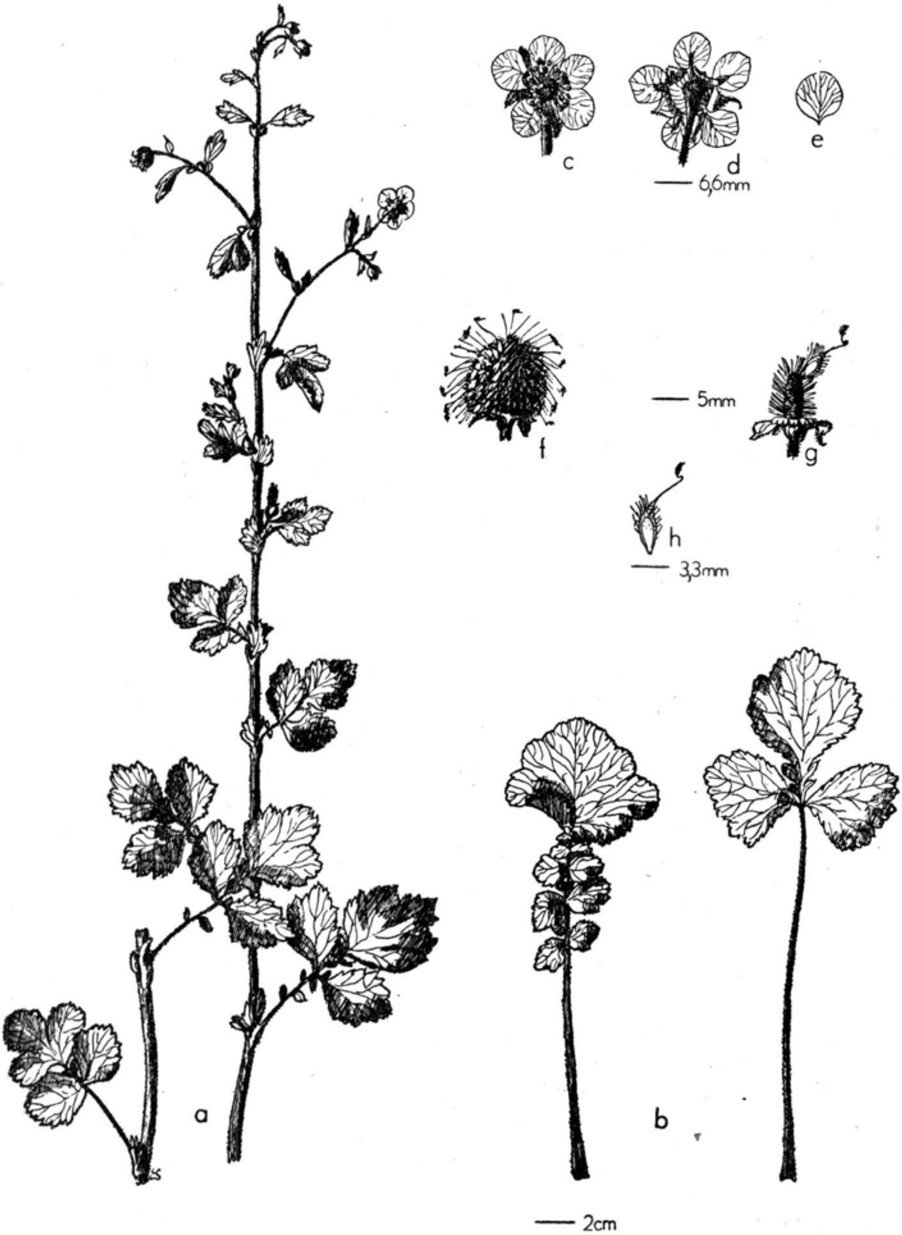


Fig. 22. *Geum japonicum*; a — floral stem; b — basal leaves; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

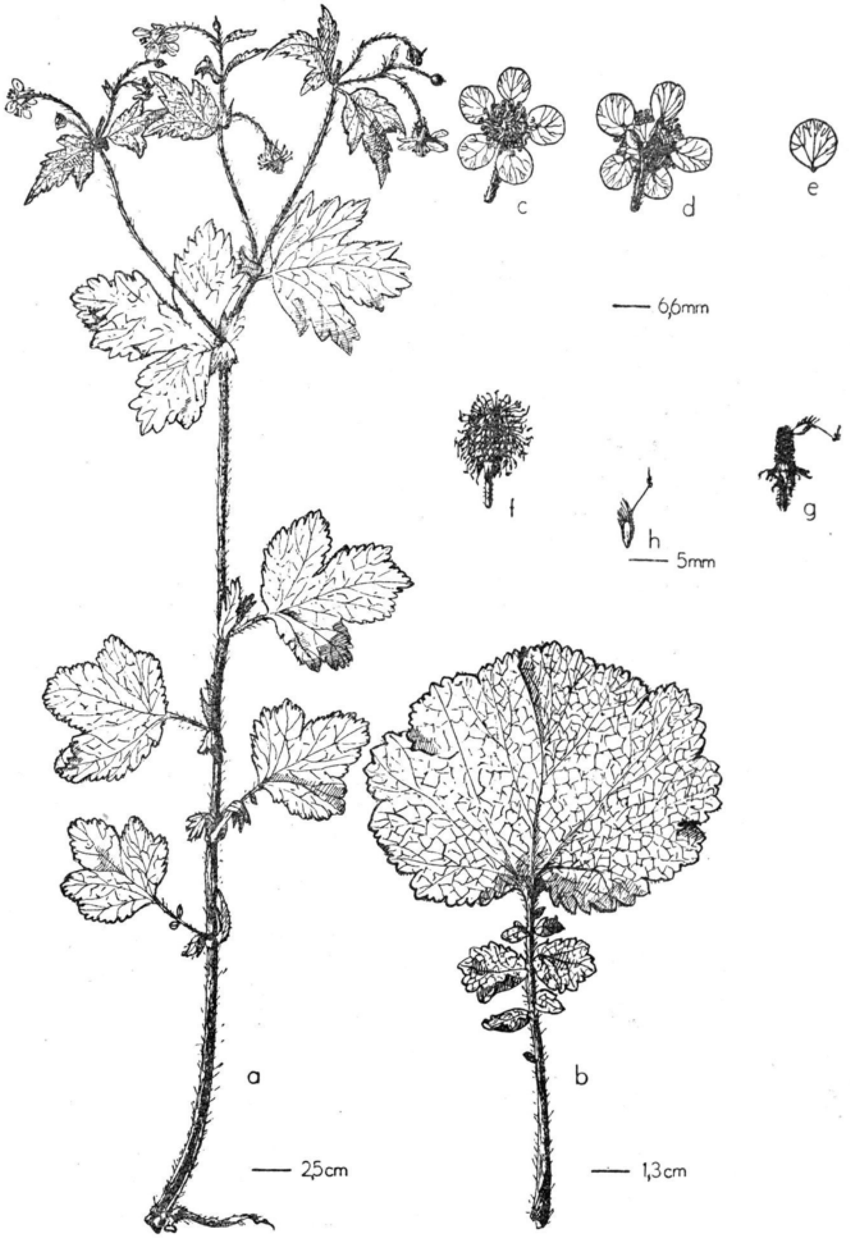


Fig. 23. *Geum Fauriei*; a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

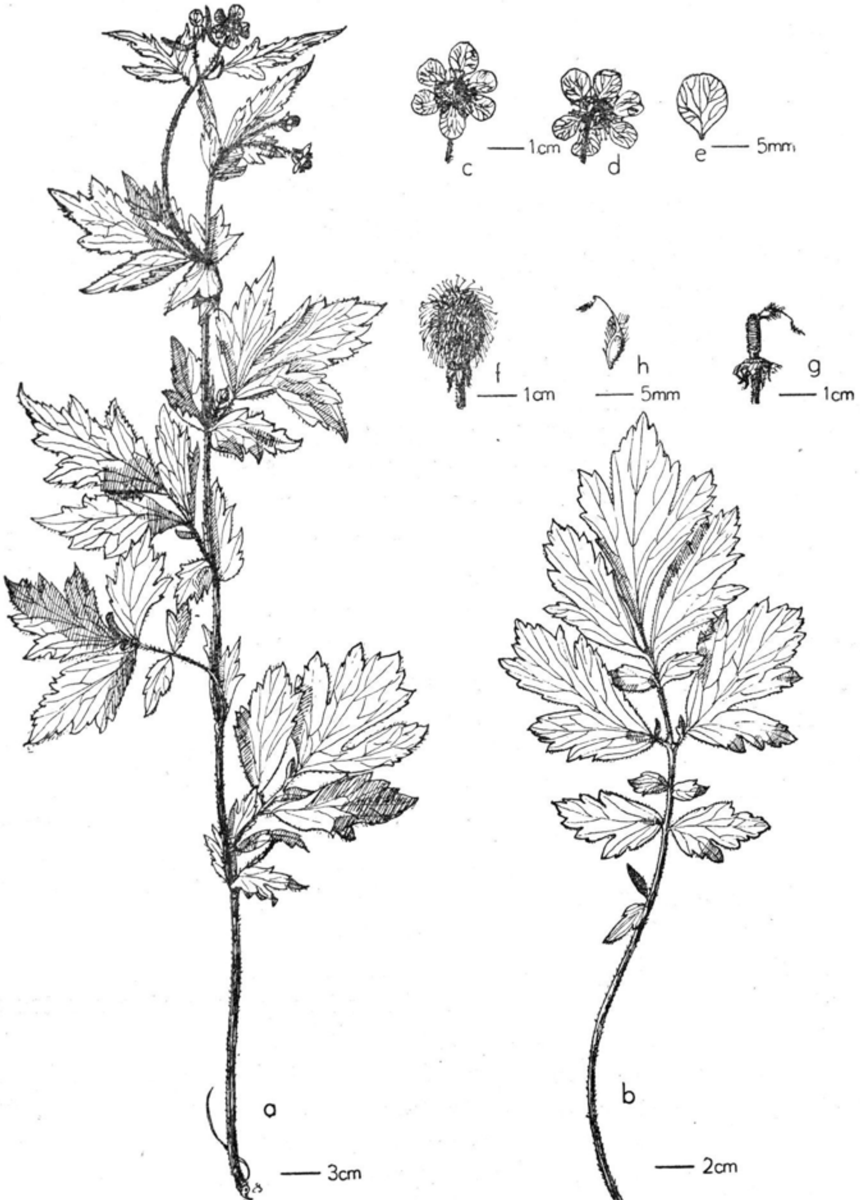
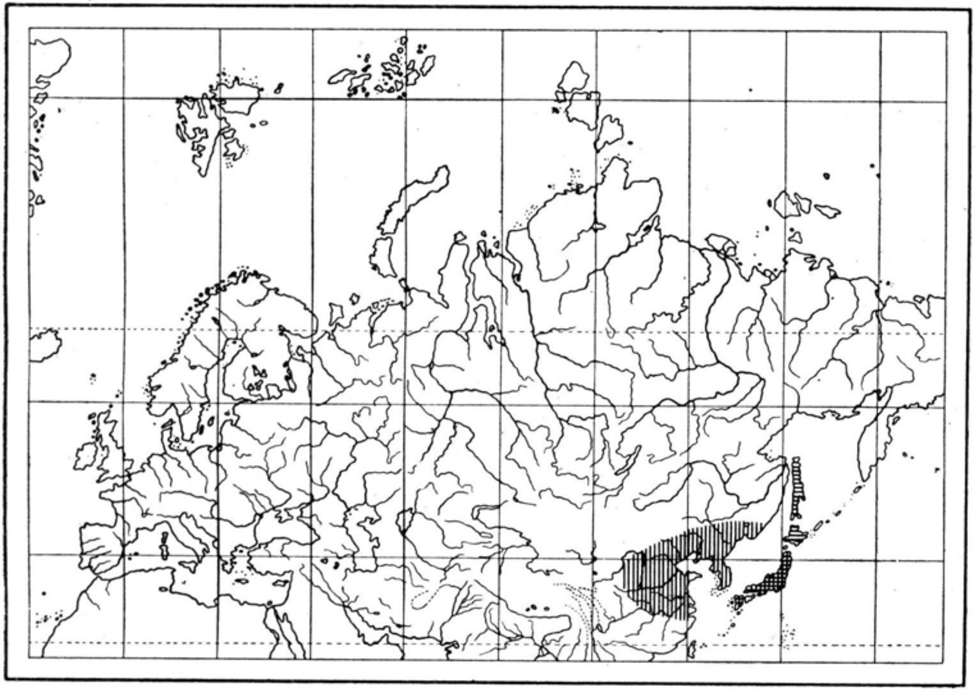
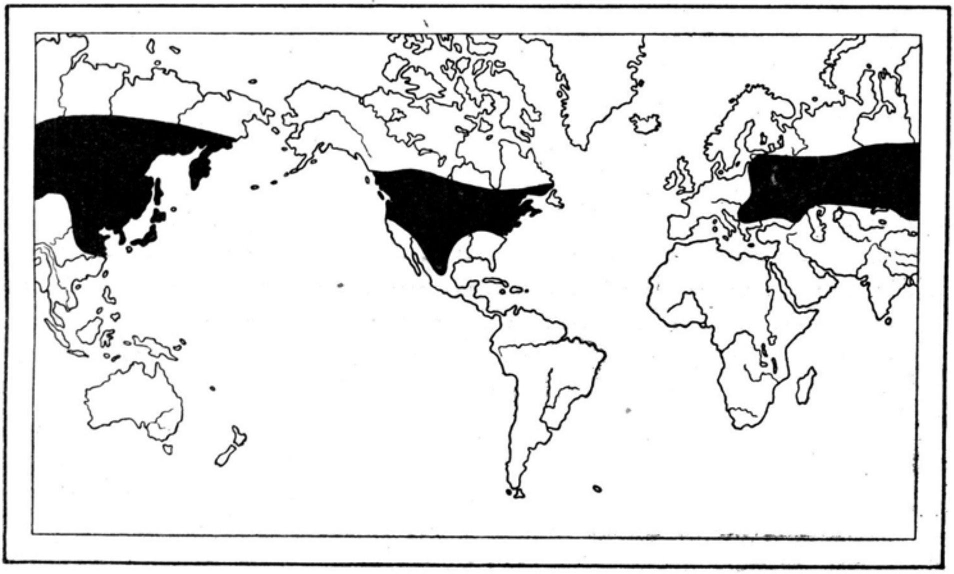


Fig. 24. *Geum aleppicum*; a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

parts of its enormous distributional area it has various forms differing among themselves in the shape of leaves, petals, fruit heads and the degree of pubescence mainly on achenes. It is mainly on the basis of the pubescence degree on the achenes that Fernald (1935) distinguishes the North American and Far Eastern specimens from the European ones, as var. *strictum* (Ait) Fer. However, this difference is very slight and concerns merely the degree of pubescence on the achenes which according to Fernald is stronger and denser in European than North American specimens. On the other hand, my observations indicate that the highly changeable degree of pubescence depends on the environmental conditions in which the plants grow. In my opinion there is so far no one character which would permit to distinguish consistently var. *strictum* from the typical *aleppicum* form. The specimen of *Geum aleppicum* (Fig. 24) collected in the Puszcza Białowieska in Poland (an area of dense forests) is of the typical form and the pubescence on its achenes is by no means denser than in the case of var. *strictum* specimens collected in the State of New York or Japan. On the other hand I have seen *G. aleppicum* specimens with denser pubescence on achenes from habitats in Slovakia and the USSR where steppe conditions prevail and maybe this has some connection with the xeric nature of these habitats. There is no doubt that on the enormous territory occupied by *Geum aleppicum* a quantity of more or less local ecotypes must appear. Bolle points out that some *G. aleppicum* specimens resemble *G. urbanum* plants in Europe and *G. japonicum* plants in Japan. It is possible that this is the result of introgressive hybridization. My experiments on *G. aleppicum* × *G. urbanum* hybrids have shown that in spite of the great sterility of the F_1 generation further generations have produced almost normally fertile plants greatly approaching *G. aleppicum.* It may be that the same effect would have been obtained even more rapidly with backcrosses. This indicates that introgression from *G. urbanum* to *G. aleppicum* is possible. The living *G. aleppicum* plants in my possession are too few to make a division into lower taxonomic units possible. However, the shape of leaves cannot be regarded as the decisive character because leaf shapes are highly susceptible to changes during vegetation. Thus any division of the species, in the case of var. *strictum* and of the typical form according to the shape of basal leaves as attempted by Hultén (1946) is not reliable. In the Flora of the USSR Juzepchuk distinguishes a related Far Eastern species *Geum Potanininii* Juz. (*G. alepp.* var. *bipinnata* Batal., *G. ranunculoides* Lev.) which differs from the typical form by sharply incised basal leaves and very dense pubescence. A second species distinguished by Juzepchuk differring from



Map 28. Distribution of *Geum japonicum* (vertical lines) and of *Geum Fauriei* (horizontal lines)



Map 29. Distribution of *Geum aleppicum*

G. alleppicum only by lesser pubescence of the stems and of the underneath leaf surfaces is probably nothing more than a form of *G. aleppicum*. Franchet and Savatier describe in the Enumeratio Plantarum Japoniae, vol. II, p. 335 (1879) the species *G. Vidalii* which also seems to be only a form of *G. aleppicum* differing from typical by its larger petals and stipules. In North America various forms of *G. aleppicum* have also been described as separate species: *G. decurrens* Rydb. and *G. scopulorum* Greene. However, to establish the correct systematic rank of these taxons special genetic and taxonomic investigations are necessary.

My cultures include numerous plants of this species obtained from various places. In approximately the same environmental conditions all the plants show small persisting morphological variations and differences in the time of flowering, resistance to parasitic fungi etc. The origin of the more important plants in the collection is as follows: a) a natural habitat in the National Park of Białowieża, b) seeds provided by Professor R. T. Clausen collected in "Woods of southern end of Cayuga Lake, N. Y." and "Ithaca, Thompkins Co, N. Y.", c) seeds obtained from Ottawa collected "In woods between Deschenes and Fairy Lake (near Hull), Quebec, Canada", d) seeds obtained from Ottawa as seeds of var. *cuneatum* collected at "Loon Lake, distr. of North Battleford, Saskatchewan, Canada", and f) Kyoto in Japan provided as *G. japonicum* by Professor Kihara.

The other group of closely related American species with small white petals and floral base covered with long hairs is formed by the four species described next.

22. *Geum canadense* Jacq. The species (Fig. 25) occupies a large territory in North America and its distribution has been probably greatly enlarged by human activity (Map 30). It is easily distinguished from the other related species by the large white petals and the small densely pubescent achenes. The species is rather variable which is demonstrated even by plants obtained from a few localities only. The variations consist in slight differences in the size of petals, achenes and stipules, and have persisted throughout the several years that the plants have been cultivated. The various forms appearing in the species are described by Fernald and Weatherby (1922, Rhodora 24, pp. 48—49). However, this work most unfortunately has been inaccessible to me and I have not been able to define the varieties of the specimens growing in my collection. The origin of the plants in the cultures is as follows: a) seeds from Ellis Hollow swamp provided by Professor R. T. Clausen, b) seeds from woods at southern end of Cayuga Lake also obtained from Professor

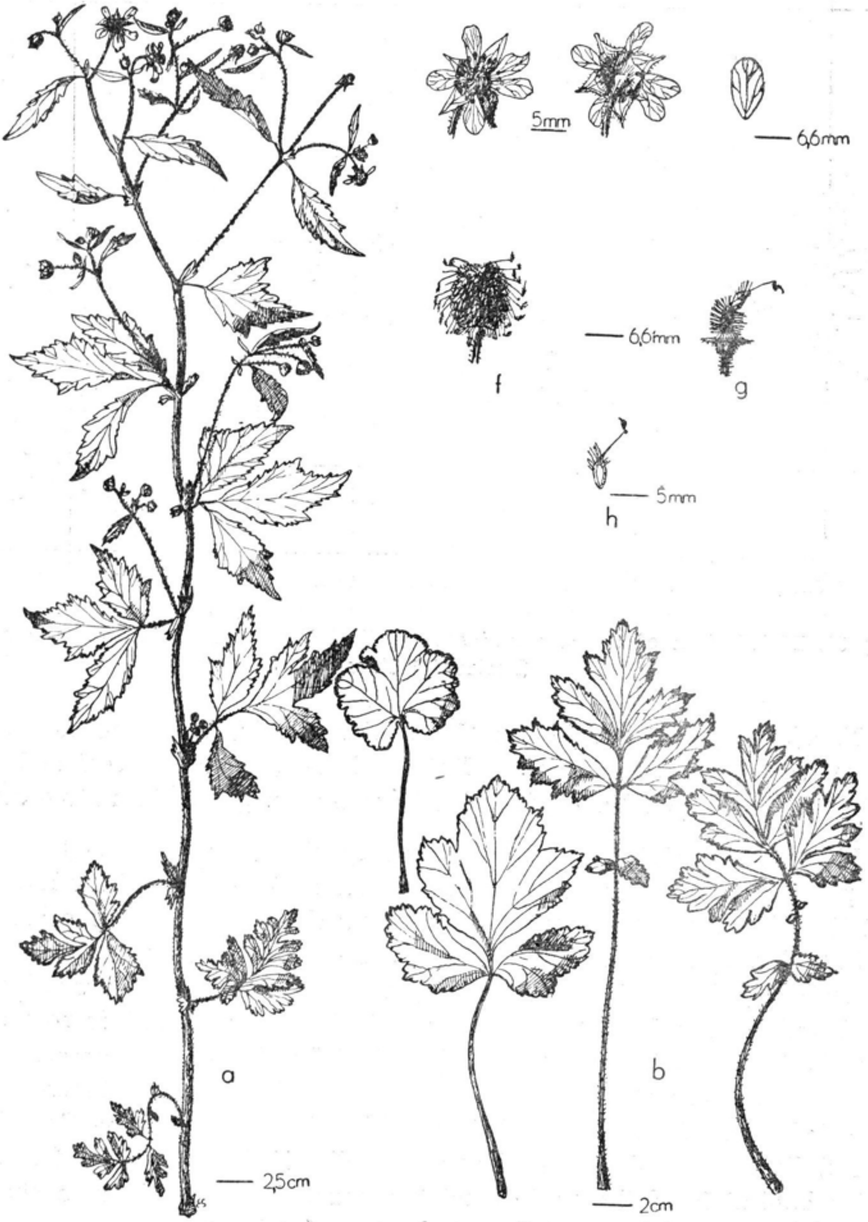
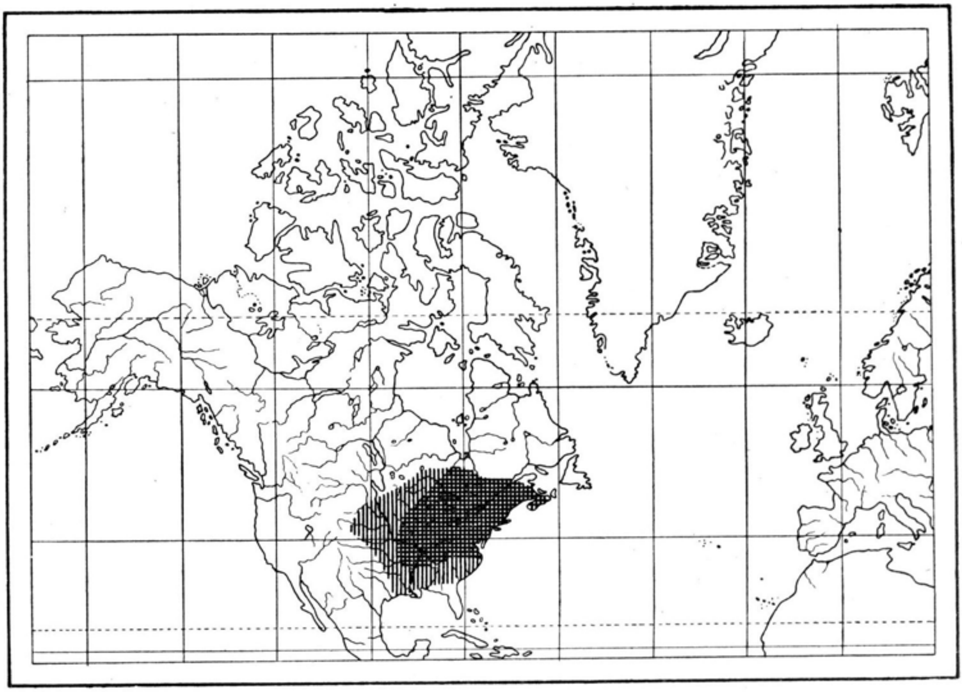


Fig. 25. *Geum canadense;* a — floral stem; b — successively developing basal leaves (right to left); c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene



Map 30. Distribution of *Geum canadense* (vertical lines) and of *Geum laciniatum* (horizontal lines)

R. T. Clausen, c) from Ithaca, Thompkins Co, N. Y., same source as above, and d) seeds sent by the Botanical Garden in Montreal and collected in the Town Park of that city where it grows in native state.

23. *Geum laciniatum* Murr. The species is closely related with the preceding one which is indicated by the high fertility of the hybrids, but it differs from *G. canadense* by leaves sharply incised especially in spring (Fig. 26), greenish white petals smaller than the sepals, dense protruding pubescence on the stems, and the almost glabrous achenes. Its distribution is less extensive than of *G. canadense* and is restricted primely to the eastern states of the U. S. (Map 30). My cultures include plants grown out of seeds obtained from Professor R. T. Clausen and collected in the following localities: a) Vestal Center, Broome Co., N. Y. and b) field south of Dryden, Thompkins Co., N. Y. The plant from the latter habitat is of the variety *trichocarpum* Fern. which is characterized by several long bristles at the top of achenes.

24. *Geum boliviense* Focke. The species is a South American one. It grows in Bolivia, South Brazil, Uruguay and Argentina and shows close relation to the North American *G. canadense* from which it differs

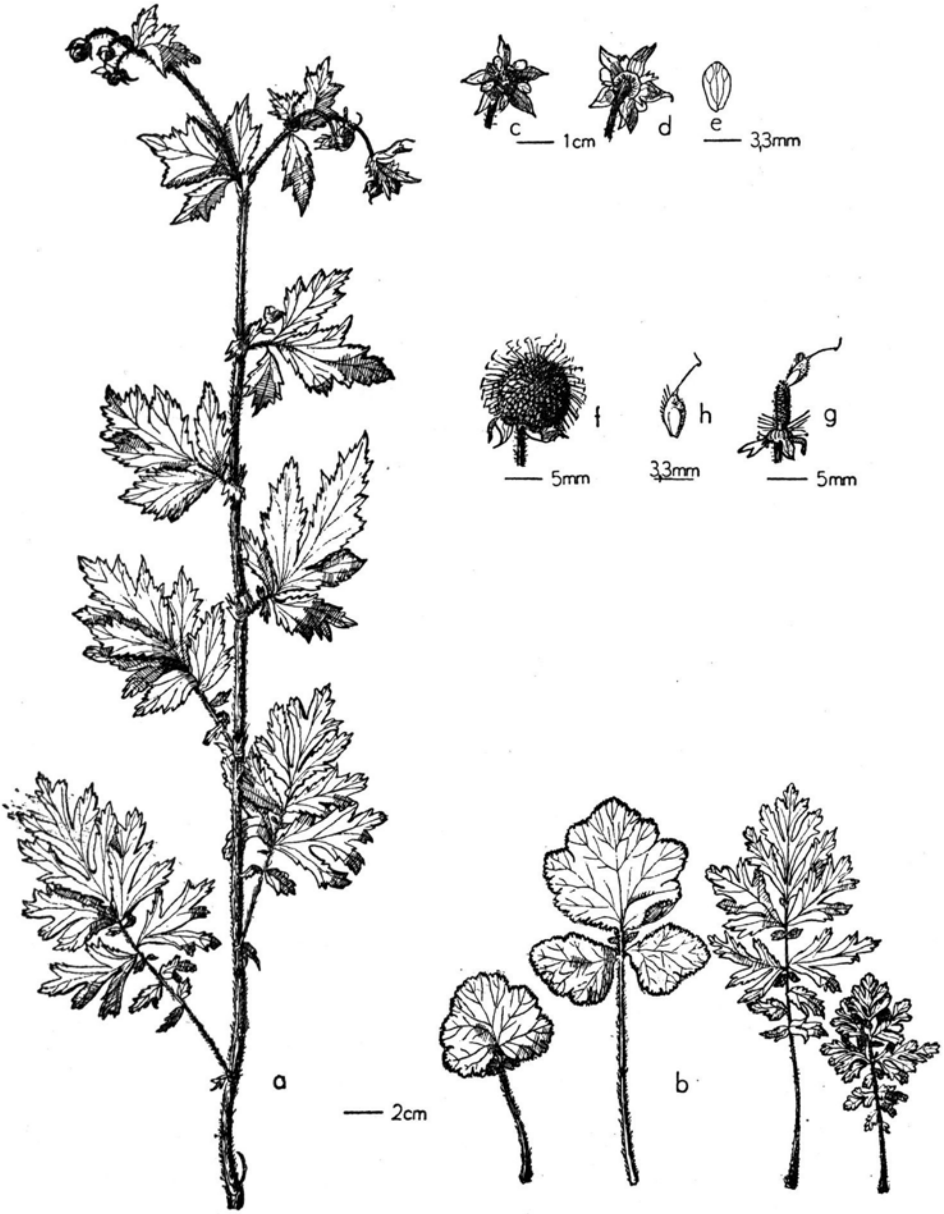


Fig. 26. *Geum laciniatum*; a — floral stem; b — successively developing basal laves (right to left); c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

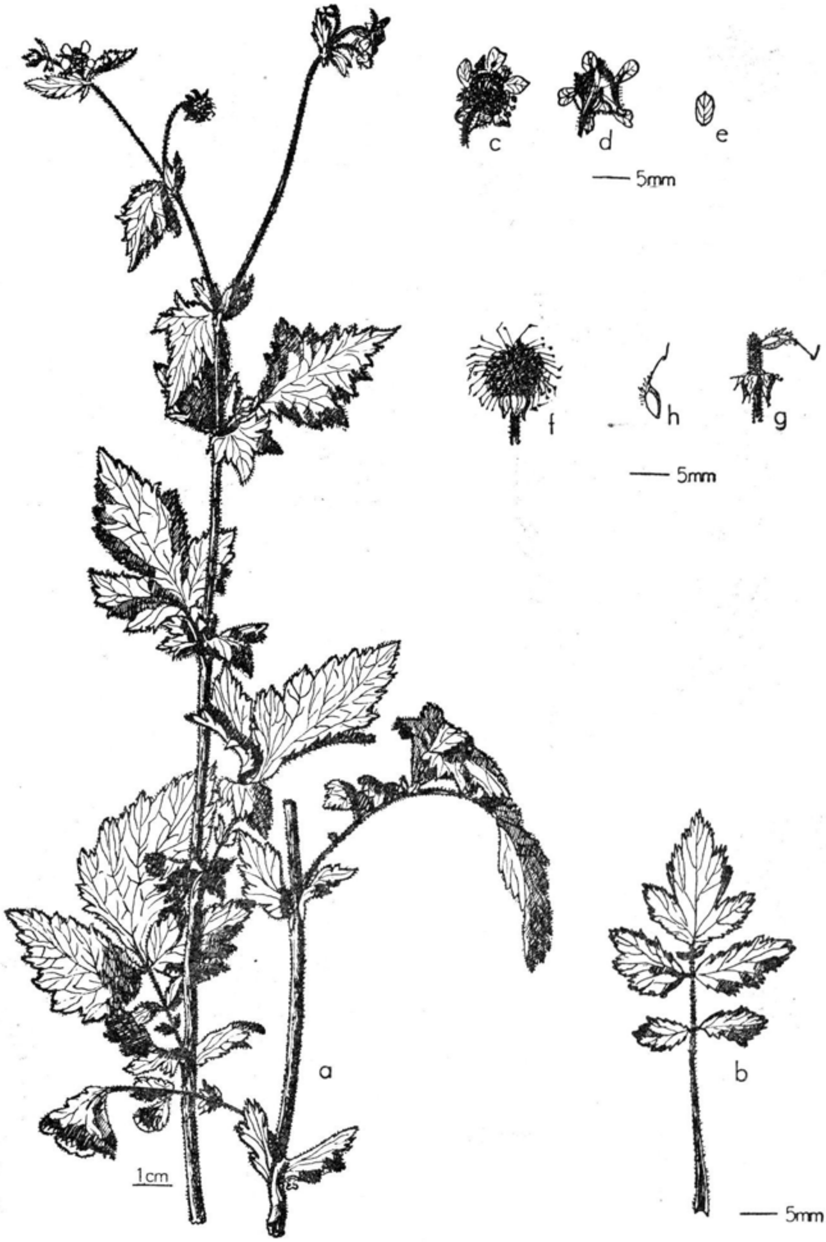
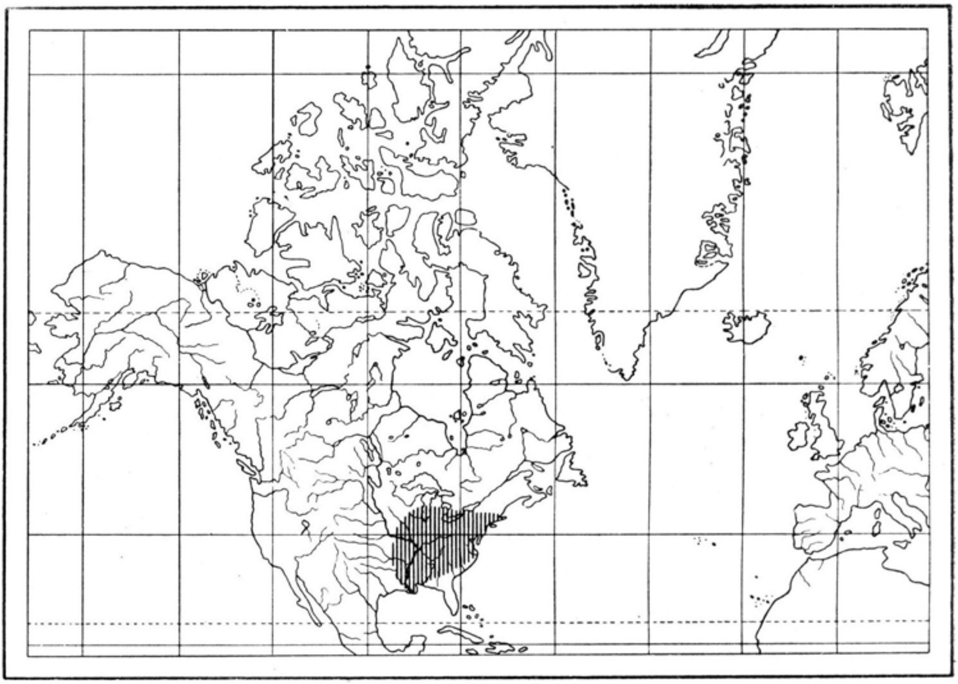


Fig. 27. *Geum boliviense*; a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

Fig. 28. *Geum virginianum*; a — floral stem; b — basal leaves; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene: h — achene

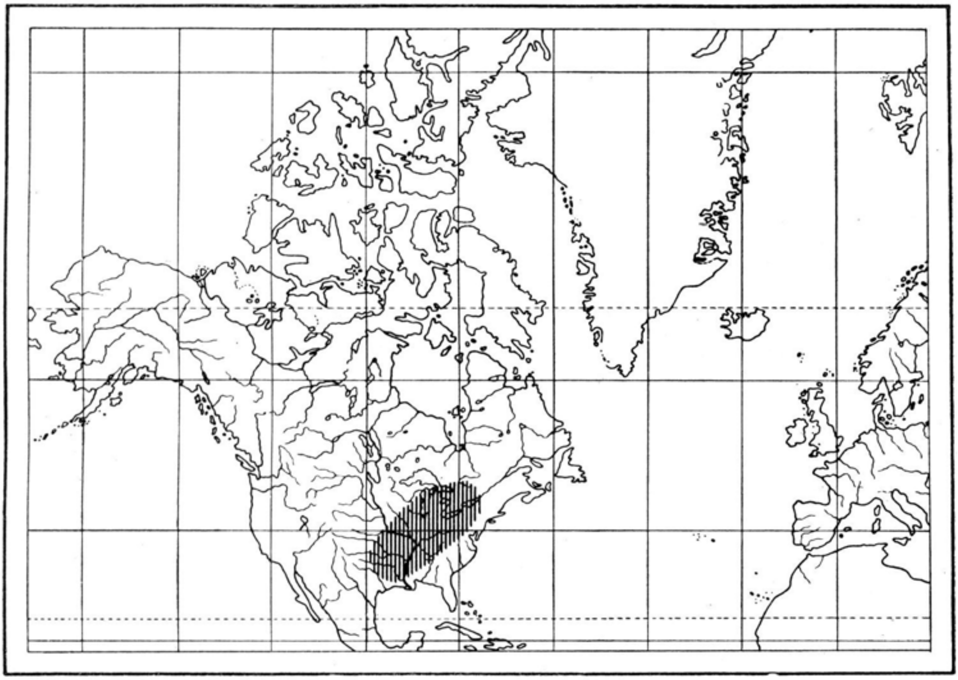
by the shape of the leaves, petals and achenes (Fig. 27). In my cultures the species is represented by plants grown out of seeds obtained from Professor H. Brücher and collected at Rio Portero, Aconguija-Gebirge, Argentina.



Map 31. Distribution of *Geum virginianum*

25. *Geum virginianum* L. The species is very much like *G. canadense* but differs primely by the pale yellow petals and the shape of the leaves with bigger stipules (Fig. 28). According to Raynor (1945, 1952) it is of hybrid origin and is derived from a cross of *G. canadense* × *G. aleppicum* var. *strictum.* The origin of this species will be discussed more fully further on together with the cross just mentioned. From the numerous herbarium specimens which I have inspected in Uppsala, Lund, Göteborg, Stockholm, Cracow and Wrocław it appears that American botanists classify as this species both the sterile hybrid forms of *G. canadense* with probably *G. aleppicum,* and the fertile forms which have petals ranging in colour from dark yellow to white and leaves of various shapes. In the latter form the plants constitute probably further hybrid generations or the progeny from back-crosses. However, in herbariums there are numerous plants corresponding approximately to the description made by Linnaeus, showing normal fertility and forming

seemingly a more or less stable species. This refers primely to territories where *G. virginianum* appears in the absence of the supposed parent species (Map 31). The plants in my collection have been grown out of seeds obtained from Professor R. T. Clausen, their origin had been in the Pigeon Mts., Iowa, but the seeds were collected from plants grown in a garden in Ithaca, N. Y. The fertility of the plants is good and no segregation is obtained in further generations.



Map 32. Distribution of *Geum vernum*

Subgenus *Stylipus* includes only one North American species: *Geum vernum* Torr. et Gray. The species and the subgenus are very closely related to the subgenus *Eugeum* and the only difference lies in the very small flowers and the lack of the epicalyx (Fig. 29). The distribution of the species is shown on Map 32. The species in my cultures is obtained from the Botanical Garden in Uppsala.

Subgenus *Orthurus* Juz. (comb. nov.) (Fig. 30, Map 33) includes the very remarkable species *Geum heterocarpum* Boiss. and the slightly different *G. kokanicum* Reg. et Schm. The former differs from the other *Geum* species primely by the structure of the style. There

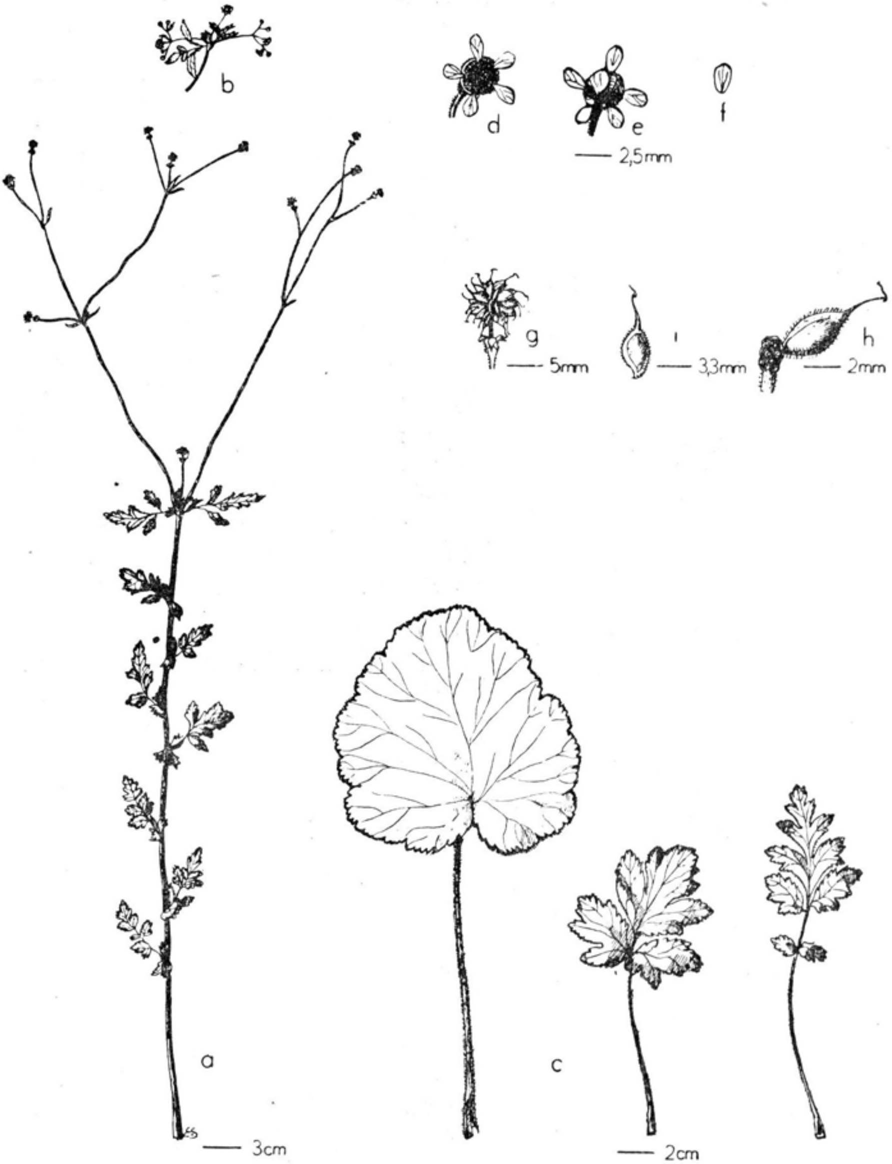


Fig. 29. *Geum vernum*; a — floral stem at anthesis; b — top of stem during flowering; c — successively developing basal leaves (right to left); d — flower — top view; e — flower — bottom view; f — petal; g — achenes in flower; h — receptacle with one achene; i — achene

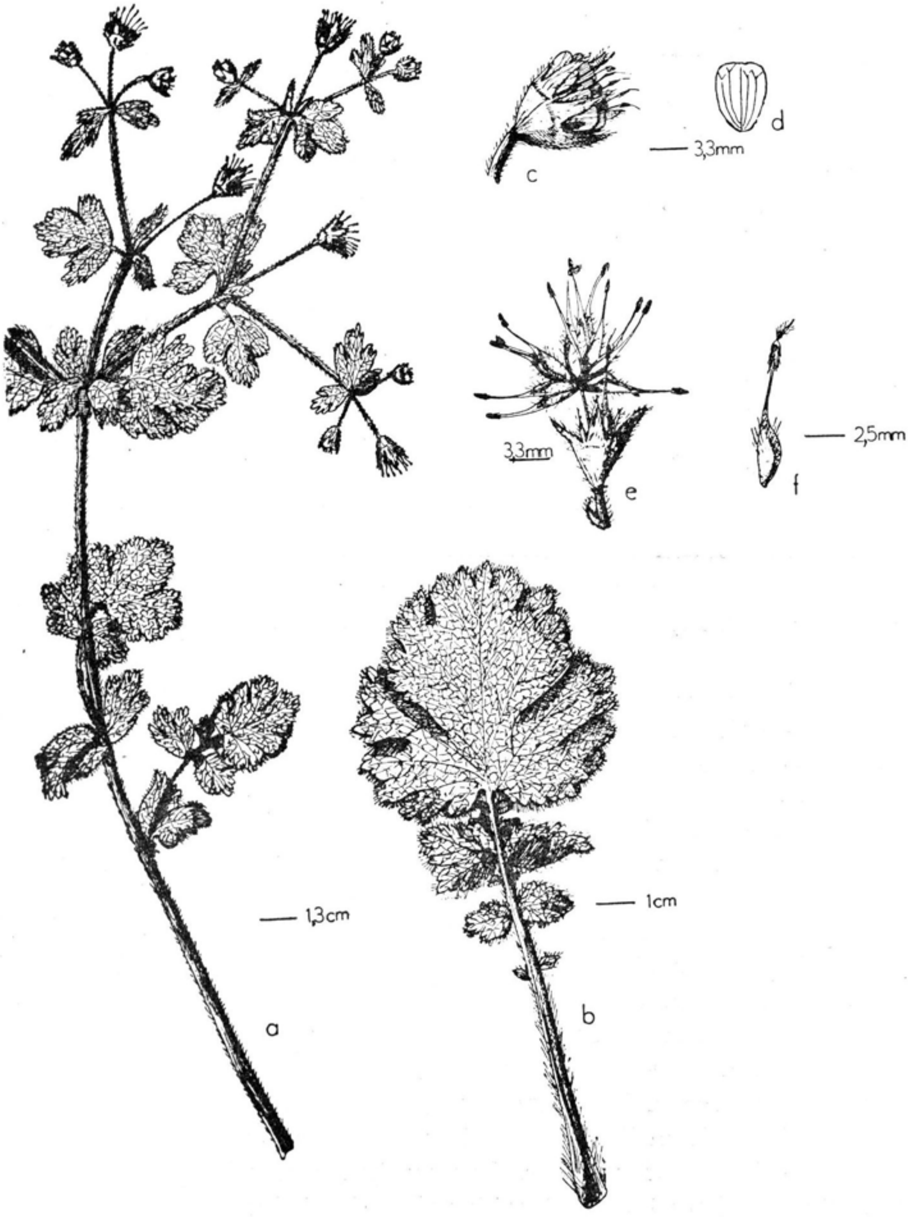
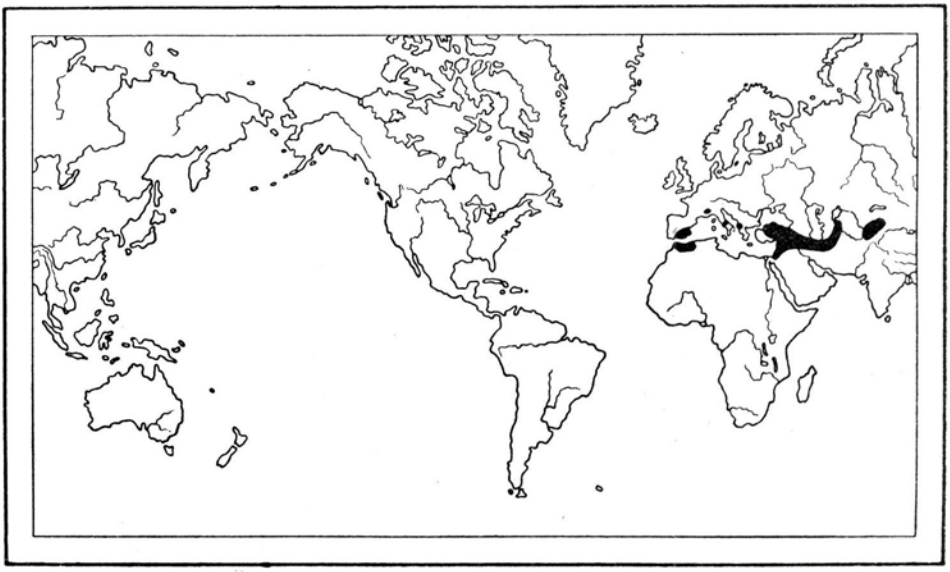


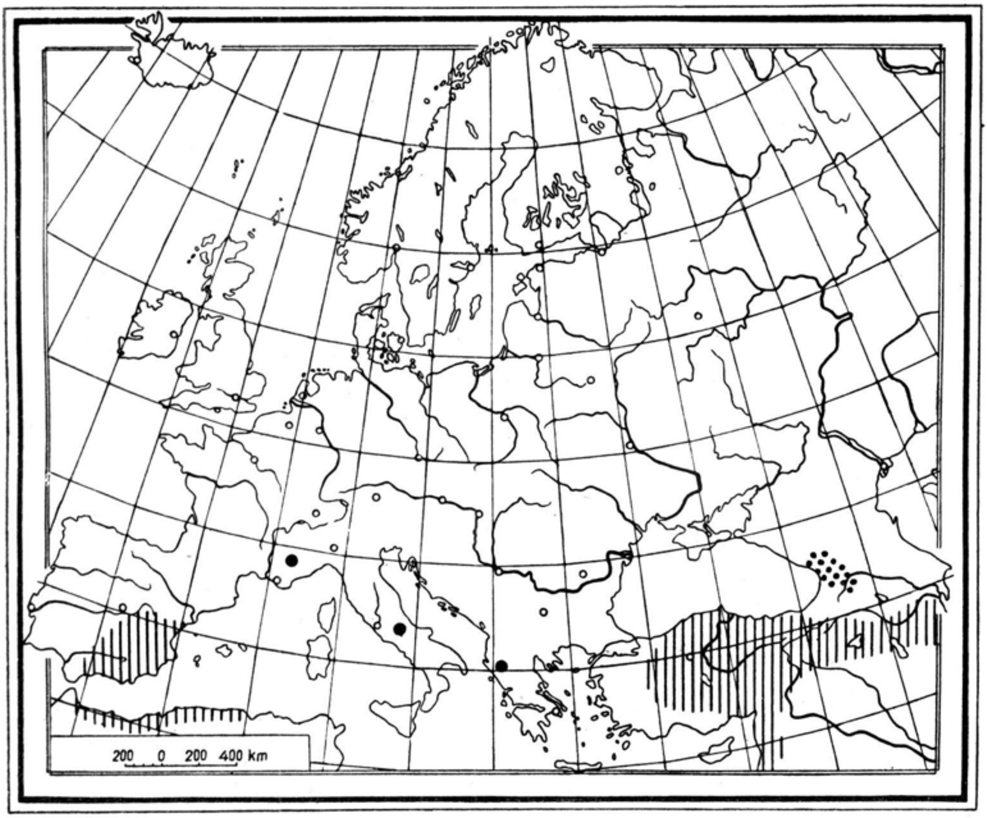
Fig. 30. *Geum heterocarpum;* a — floral stem; b — basal leaf; c — flower — side view; d — petal; e — achenes in flower; f — achene

is no hooked joint between the rostrum and the deciduous stigmatic part, at the tip of the rostrum there are downward pointing bristles acting as the adhesive organ. The number of achenes on the receptacle is a dozen or more, the receptacle is exserted beyond the hypanthium on a long gynophore and one or two achenes are inserted at the base of, or sometimes on the gynophore (Fig. 30). The species has a greatly disjunctive distribution (Map 34) occupying mainly mountainous areas in the region of the Mediterranean. The larger disjunctive areas occupied by the species are to be found in Spain and North Africa in the west of the Mediterranean region, in Asia Minor, Iran and Armenia at the eastern end of that region, and according to Juzepchuk in Tjan-Shan and Turkmenistan (Kopet-Dagh) in Central Asia. In the central part of the Mediterranean area the species is distributed only in small enclaves which are to be found in Albania in the Balkans, the Abruzzian Mountains on the Apennine peninsula and in Southern Alps (Dauphiné). In my cultures the species is represented by plants derived out of seeds obtained from the Botanical Gardens in Copenhagen and München.



Map 33. Distribution of the subgenus *Orthurus* of the genus *Geum*

Geum kokanicum Reg. et Schm. The species differs from *G. heterocarpum* by broader sepals, fewer achenes on which the rostrum is covered throughout its length with reflexed bristles and shorter and less ramified stems. However most characters distinguishing the two species are subject to considerable variation in both species and depend on the nature of the habitat from which specimens originate. *Geum kokanicum* is known mainly from the eastern parts of the Mediterranean area and Central Asia where it occupies montane habitats at greater altitudes. It is possible that the species represents merely a mountain race of *Geum* *heterocarpum*. This is all the more plausible as the latter species has its habitats in lower mountain regions in shady places as for instance in copses of various *Juniperus* species growing in the Mediterranean area. This opinion is also shared by Iltis (1913) but the problem could be answered only by fuller cultivation and genetical experiments. Unfortunately, I have no *G. kokanicum* plants in my cultures.



Map 34. Distribution of Geum *heterocarpum* (continuous distribution — vertical lines, isolated stations — black spots) and of *Geum speciosum* (dots)

Subgenus *Woronowia* Juz. (comb. nov.) consists of one species only. It is sharply isolated from the other species of the genus. The species in the monotypic subgenus is *Geum speciosum* Alboff. (Fig. 31). Bolle classifies the species together with *G. heterocarpum* into the sub-

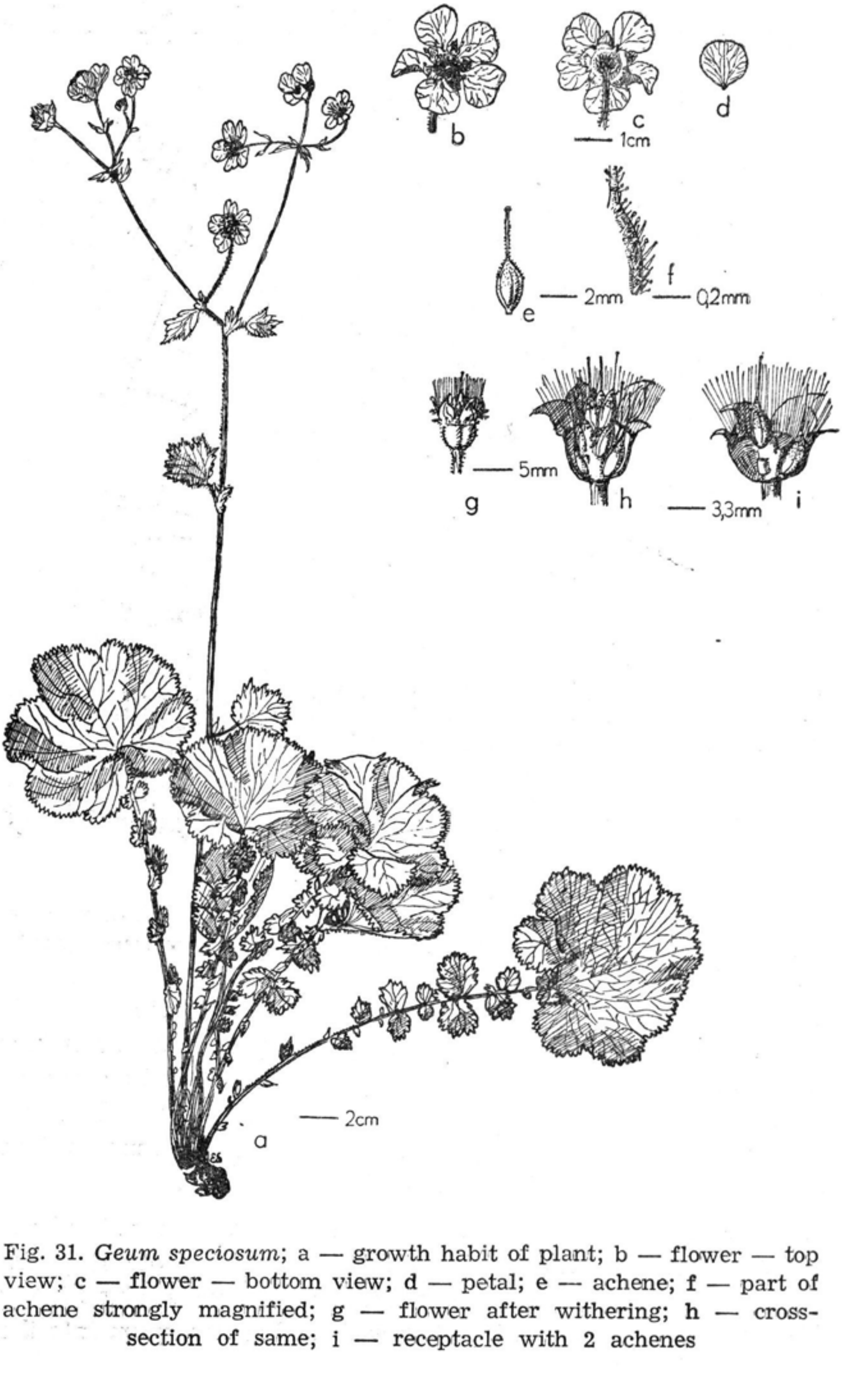


Fig. 31. *Geum speciosum*; a — growth habit of plant; b — flower — top view; c — flower — bottom view; d — petal; e — achene; f — part of achene strongly magnified; g — flower after withering; h — cross-section of same; i — receptacle with 2 achenes

genus *Orthostylus* Bolle. However, the differences between this species and the species in subgenus *Orthurus* are considerable and it seems entirely justifiable to classify it into a separate subgenus. *G. speciosum* plants have long calyx tubes equally long as the sepals, the achenes are few, 10—14 in number and are inserted on a characteristic as if ramified receptacle (Fig 31). Bolle's and Juzepchuk's description of the species, which state that a gynophore is present and the achenes are attached both at its apex and base similarly as is the case in *G. heterocarpum,* are in this respect inaccurate and differ from the existing state of things. Actually, there is only an elongated receptacle on which, throughout its length, achenes are attached on special ramifications in a manner resembling a similar structure in *Coluria.* The stamen filaments persistent after the wilting of the flowers also relate this species to *Coluria* and *Waldsteinia.* The most characteristic resemblance between this species and *Coluria* lies in the structure of the style, the greater deciduous part of which is shed at a contraction just above the style base (Fig. 31). On the other hand, the shape of the leaves and petals as well as the manner in which the stems are ramified distinguishes the species from *Coluria* and associates it with *Geum.* The species is endemic to the Transcaucasia where it grows on alpine and subalpine meadows in Abchasia, Mingrelia and Chercasia (Map 33). In my cultures the species has been obtained from the Botanical Gardens in Lausanne and München.

Here ends the list of species distinguished so far in the tribe of *Geeae* Juel. It seems likely that some more species will be distinguished in future, primely in South America and perhaps China. There is no doubt, however, that most of the now existent species have already been defined and described.

It is evident from all that has been said so far that the whole group is far from being homogenuous both in respect to morphology and the character of its geographical distribution. Quite certainly the group covers various evolutional lines of different age. The present research has been started with the aim to clarify if possible the nature of the genetical difference within and between the various sections composing the group. This objective has been reached only in a small degree primely because I was greatly handicapped by the lack of live material from the various *Geum* subgenera. The best represented in my collection of living specimens of *Geum* species is the subgenus *Eugeum.* Then come the subgenera *Oreogeum, Erythrocoma, Orthurus, Woronowia* and genera *Coluria* and *Waldsteinia.* I have not succeeded in obtaining living plants from subgenera *Sieversia, Neosieversia* and *Oncostylus* while the representation of the very extensive subgenus *Acomastylis* is much too small. Besides incompleteness my collection has another drawback. Many of the cultivated species were not collected from natural habitats but from botanical gardens, which makes thier origin somewhat doubtful: It must be stressed, however, that throughout the many years that this research has been under way I have obtained from botanical gardens far more *Geum* specimens than are mentioned here. Out of this very rich material I have chosen only those plants which seemed to represent best the pure species. Very often *Geum* plants grown out of seeds provided by botanical gardens do not correspond to what they are stated to be, and even more frequently hybrids and not pure species are supplied This is caused by the great facility with which crosses between various *Geum* species are formed. Nevertheless, for an experienced eye it is easy to distinguish any hybrid form from a pure species and this is all the more so when besides morphological characters also meiotic divisions and pollen and seed fertility are examined. I feel therefore that the material on which this work is based consists of pure species, though their origin may in some cases be unknown.

A list of species distinguished in the tribe of the *Geeae* is given on p. 81. It informs briefly on the distribution of every species, indicates whether or not a species is represented in the cultivated collection, and informs on the nature of the origin (natural habitat or botanical garden).

Out of the 65 species distinguished in the tribe of the *Geeae* my cultures include 35 which amounts to 53.8 per cent of the known species. However, only 21 species originated from natural habitats, the other 14 were obtained from Botanical Gardens.

IV. REVIEW OF THE MORE IMPORTANT MORPHOLOGICAL DIAGNOSTIC CHARACTERS FOR DISTINGUISHING GENERA, SUBGENERA AND SPECIES

PISTILS AND ACHENES

It has been pointed out earlier that the shape of pistils and achenes has a decisive significance in the systematics of this group. Besides their taxonomic significance these characters are of great biological consequence for the dissemination of plants in the various groups. All the species from the tribe of *Geeae* have an undefined number of free apocarpous pistils. The number characteristic for a particular species varies over a wide range, from 3—4 in *Waldsteinia geoides* to 300 in many *Eugeum* species (*G. aleppicum, macrophyllum,* and others). Within one species the number is also variable but to a much lesser degree. The pistil is com-

No	Specific Name	Distribution	+ included — not included in collection	
			Nat. Habitat	Bot. Garden
	Waldsteinia			
1	W. fragarioides (Michx.) Trattinn.	N. America	—	—
2	W. ternata Fritsch	Europe (Alps, Carpathians) E. Asia	—	+
3	W. geoides Willd.	Central Europe	+	+
4	W. lobata Torr. et Gray	N. America	—	—
	Coluria			
5	C. elegans Cardot	China	—	—
6	C. Purdomii W. E. Evans	China	—	—
7	C. geoides (Pall.) Ledeb.	South. Siberia	—	+
8	C. Henryi Batalin	China	—	—
9	C. oligocarpa (J. Krause) F. Bolle	China	—	—
	Geum			
10	G. pentapetalum (L.) Makino	N. Pacific area	—	—
11	G. selinifolium Hulten	East Asia	—	—
12	G. glaciale Adams	Arctic E. Asia and N. America	—	—
13	G. montanum L.	Europe	+	+
14	G. reptans L.	Europe	+	—
15	G. bulgaricum Panč.	Balkan peninsula	+	—
16	G. Peckii Pursh	N. America	—	—
17	G. radiatum Michx.	N. America	—	—
13	G. calthifolium Smith	N. Pacific area	—	+
19	G. sikkimense Prain	Himalayas	—	—
20	G. elatum Wallich	Himalayas, China	—	—
21	G. Rossii Ser	Arctic E. Asia and N. America	—	+
22	G. turbinatum Rydb.	N. America	+	—
23	G. andicola Reiche	Chile	—	—
24	G. renifolium F. Muell	Tassmania	—	—
25	G. uniflorum Buchanan	New Zealand	—	—
26	G. divergens Cheesem.	New Zealand	—	—
27	G. parviflorum Kirk	New Zealand	—	—
28	G. albiflorum Scheutz	Auckland Islands	—	—
29	G. leiospermum Petrie	New Zealand	—	—
30	G. pusillum Petrie	New Zealand	—	—
31	G. involucratum Persoon	Patagonia	—	—
32	G. Lechleriana Schlechtendal	Chile	—	—
33	G. triflorum Pursch	A. America	+	+

Contin. on p. 82.

Cont. of p. 81

No	Specific Name	Distribution	+ included — not included in collection	
			Nat. Habitat	Bot. Garden
34	G. canescens Greene	N. America	—	—
35	G. ciliatum Pursch	N. America	—	+
36	G. campanulatum Greene	N. America, Olympic Mts.	—	+
37	G. rivale L.	Europe, N. America	+	+
38	G. capense Thub.	S. Africa	—	—
39	G. silvaticum Pourr.	W. Mediterranean area	+	—
40	G. pyrenaicum Willd.	Pyrenees	—	+
41	G. coccineum Sibih. et Sm.	Balkan peninsula, Asia Minor	+	—
42	G. Quellyon Śweet.	S. America	—	+
43	G. magellanicum Pers.	S. America	—	+
44	G. peruvianum Focke	S. America	—	—
45	G. brevicarpellatum Bolle	S. America	—	—
45	G. riojense Bolle	S. America	+	—
47	G. urbanum L.	Europe	+	+
48	G. latilobum Somm. et Lev.	Caucasus	—	—
49	G. Roylei Wallich	Himalayas	—	—
50	G. molle Vis. et Panc.	Balkan peninsula, Italy	+	—
51	G. hispidum E. Fries	Sweden, Spain	+	—
52	G. macrophyllum Willu.	N. America, N.-Asia	—	+
53	G. perincisum Rydb.	N. America	+	—
54	G. oregonense Rydb.	N. America	+	—
55	G. japonicum Thunb.	Japan, China	+	—
56	G. Fauriei Leveillé	Japan, Sakhalin Isl.	—	+
57	G. aleppicum Jacq.	Eurasia, N. America	+	+
58	G. canadense Jacq.	N. America	+	+
59	G. laciniatum Murr.	N. America	+	—
60	G. boliviense Focke	S. America	+	—
61	G. virginianum L.	N. America	+	—
62	G. vernum Torr. et Gray.	N. America	—	+
63	G. heterocarpum Boiss.	Mediterranean countries Central Asia	—	+
64	G. kokanicum Regel et Schm.	S.-W. and Central Asia	—	—
65	G. sepciosum Alboff.	Caucasus	—	+

posed of an ovary terminated by a style always inserted at the tip of the ovary (in *Potentilla* the style grows out from the side of the ovary).

The style is etither wholly or partially persistent on the achene during the ripening of the fruit, as in genus *Geum*, or the whole style is shed after pollination, as in genera *Waldsteinia* and *Coluria*. *Geum speciosum* is an intermadiate form between the latter two genera and genus *Geum*. In this species only a 1—2 mm. base of the style remains on the achene and the rest is shed after pollination. The subgenera in genus *Geum* have styles shaped as follows (Fig. 32):

a. The whole style with the stigma is persistent. The stigma withers after pollination but is not shed. This type is characteristic for subgenera *Sieversia, Neosieversia, Oreogeum* and *Acomastylis* and for *G. andicola* Reiche. In the first three of the above mentioned subgenera the style is strongly elongated and long pennately haired, thus forming the organ for anemochoric dissemination. In *Acomastylis* and probably also in *G. andicola* the style is much shorter, covered with shorter hairs or almost naked. The style is not of the type distinctly adapted for anemochoric dissemination of seeds.

b. The style is strongly elongated and long pennately haired. Often the stigmatic part is deciduous, as in subgenus *Erythrocoma*.

c. The style terminates by a hooked stigma and constitutes the adhesive organ. This type is characteristic for subgenus *Oncostylus* only.

d. Between the lower part of the style (rostrum) and the upper stigmatic part a geniculate joint is formed. After pollination the stigmatic part is shed and the rostrum constitutes the adhesive organ favouring epizoochoric dissemination of fruit. This type is developed in subgenera *Eugeum* and *Stylipus*.

e. In the subgenus *Orthurus* a straight contraction appears between the rostrum and the stigmatic part. After fertilization the stigmatic part is shed and on the rostrum strong down-pointing bristles grow out, these constitute the adhesive organ defined by Iltis (1913) as the harpoon type.

The above expression types of achenes and styles distinguish genera and subgenera one from the other. Within the genera and subgenera the species differ only in the following characteristics in the expression of achenes:

a) The degree and nature of pubescence: — In genus *Coluria* some species, as for instance *G. geoides*, have achenes covered by rounded papillae (Fig. 2) and in other species, e.g. in *G. elegans*, the achenes are glabrous. Some species of subgenus *Eugeum* have almost naked achenes (e.g. *G. laciniatum*), others have achenes more or less densely haired (e.g. *G. rivale, aleppicum*) the hairs being either both simple and glandular

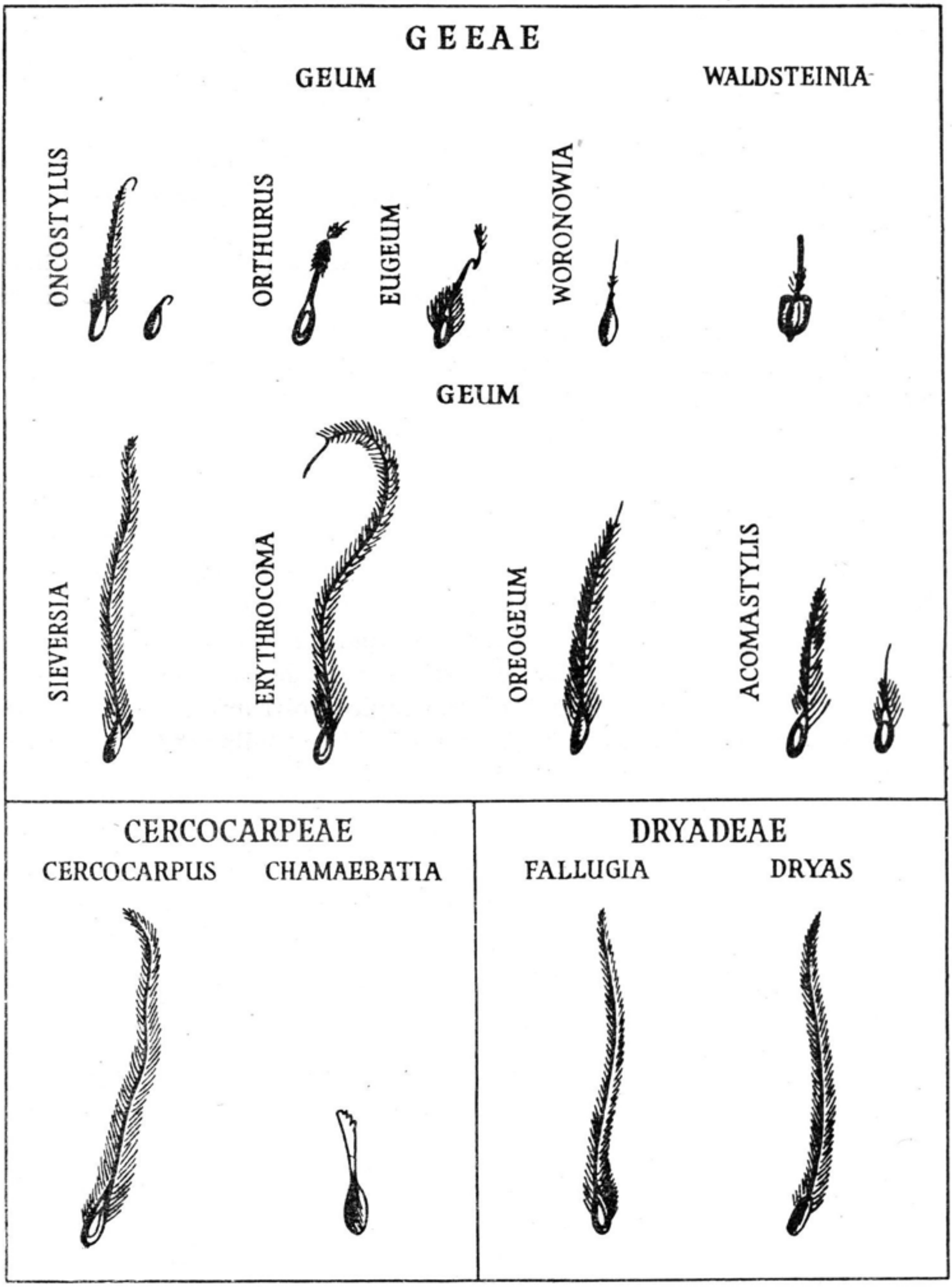


Fig. 32. Achene types of some genera in the subfamily of *Dryadoideae* and of the subgenera of genus *Geum*

(*G. rivale*) or only simple (*G. aleppicum*). In subgenus *Acomastylis* the kind of the hairs on the pistil — the hairs may be short or long and cover various parts of the style — is a diagnostic character for closely related species.

b) Size: — The lengths of the rostrum and of the stigmatic part as well as the ratio between the lengths of these two organs are important characters for distinguishing species in subgenus *Eugeum*. Considerable differences in the length of the styles appear also in subgenus *Oncostylus:* in *G. renifolium* styles are 15 mm. long while in *G. pusillum* their length is not even 1 mm (Fig. 32). The length of styles in the species from subgenus *Acomastylis* differs over a wide range. The size of achenes also differs in the various species of one subgenus and for instance the *Eugeum* species *G. silvaticum* has achenes almost ten times as big as the achenes of, for instance, *G. macrophyllum*. The size of achenes is often correlated with their number. In *G. silvaticum* the achenes are larger and their number is smaller that in any other *Eugeum* species.

THE RECEPTACLE

Most species in this group have carpels inserted on a convex receptacle and only in the genus *Waldsteinia* the receptacle is not of the typical shape. In this genus the carpels grow out on separate pedicels directly from the floral base. In the genus *Coluria* closely related to *Waldsteinia* and in *G. speciosum* the carpels grow on a convex receptacle and every carpel is inserted in a separate depression. In the other *Geum* species the carpels are compact, arranged in spirals on the receptacle and at the points of insertion there are no marked incisions of the axis. The carpels are inserted either directly on the receptacle or on slender pedicels growing out from the receptacle, as for instance in *G. montanum* and *G. reptans* from subgenus *Oreogeum* or *G. coccineum* and *G. pyrenaicum* from subgenus *Eugeum*. The pedicels in subgenus *Eugeum* are much shorter than in *Oreogeum, Waldsteinia* or *Coluria*. The receptacle may be very slightly spherically convex as is the case in subgenera *Oreogeum, Erythrocoma, Acomastylis* and *Orthurus* or it may be very elongated, cylindrical, up to 1 cm and more in length, as in some *Eugeum* species. Within subgenus *Eugeum* there is a whole range of species with receptacles of various lengths. The receptacle is shortest in *G. silvaticum* and longest in *G. aleppicum, macrophyllum* and some other species. The pubescence on the receptacle may be either short hardly noticeable or the hairs may be dense and long. E.g. the two closely related species *G. canadense* and *G. laciniatum* differ greatly by the pubescence on their receptacles. Bolle splits the section *Murrayana* into two series according to the character of pubescence on the floral base: *Pubescentia* and *Hirsuta*. However this division is altogether artificial and, for example, if it be followed the closely related *G. canadense* and *G. laciniatum* must each be placed in a different series.

The receptacle is usually inserted on the sterile part of the axis where no carpels are formed. This part which is called the gynophore may greatly differ in length. In subgenus *Neosieversia* the gynophore is very short, 1—2 mm long, it also is undeveloped in species from subgenera *Sieversia* and *Oreogeum,* and in many species from subgenus *Eugeum.* There is no trace of gynophore in subgenera *Oncostylus, Acomastylis, Erythrocoma*, and in such species of the subgenus *Eugeum,* as for instance, *G. macrophyllum, japonicum* and *urbanum.* In such numerous species as *Geum rivale, silvaticum, vernum* and *heterocarpum* the gynophore grows to the length of 1 cm or more, and probably has some biological significance for the dissemination of seeds. In these species the whole fruit head is exserted high above the calyx tube which facilitates the transportation of the seeds by animals.

THE ANDROECIUM

The character of the stamens has almost no diagnostic value for the systematic division of the plants here considered and this is in connection with the relatively small variability of the organs. The only feature with greater systematic significance lies in the pubescence of the stamen filaments. This is visible in subgenera *Erythrocoma, Neosieversia* and in some *Acomastylis* species. After pollen is spilt from the anthers the stamen filaments usually quickly wither and fall off, however in some species, as for instance in *G. speciosum, Coluria geoides* and *Acomastylis Rossii,* the stiff erect stamen filaments persist after the flowers wilt. The number of stamens is usually large and undefined, though, in some species this number is greatly reduced and may even be as small as 20. The anthers are usually elliptical, sometimes rounded, but this character does not seem to be of diagnostic significance.

THE PERIANTH

The perianth is very variable and thus it is an important systematic character. The calyx tube may be very short not exceeding $^1/_3$ — $^1/_4$ of the length of sepals, as in subgenera *Sieversia, Erythrocoma, Oreogeum* and the majority of *Eugeum* species. The hypanthium is then usually wide open and semicircular in shape. On the other hand, in numerous species the hypanthium is much longer and forms a campanulate or cylindrical calyx tube. Such for example is the case in genera *Waldsteinia* and *Coluria,* in *Geum* subgenera *Acomastylis* (some species), *Orthurus, Woronowia,* and in such *Eugeum* species as *G. rivale.* However, in the last instance the hypanthium is less elongated than in the preceding genera and subgenera. The sepals are usually triangular, rather pointed at the tip and vary greatly even in closely related species. A character of some importance is revealed by the position of sepals at blossom time and fruiting. In some species, as for instance in those from subgenus *Erythrocoma* or in *G. rivale,* the sepals remain erect during and after blossoming and are even partly closed. In species from subgenera *Sieversia, Neosieversia* and *Oreogeum,* as well as in some *Eugeum* species the sepals at blossom time are expanded horizontally or only slightly erect and remain in this position after the flowers wilt. Finally, in many *Eugem* species and in *G. vernum* the sepals are strongly reflexed and appressed to the floral peduncles either already at blossom time or after anthesis. This character is probably of consequence in the dissemination of seeds, as adhesive seeds are not covered up by the calyx primely in species not equipped with gynophore, thus facilitating dissemination.

In all species considered here the segments of the epicalyx are inserted in between the calyx sepals. The only exception to this is *G. vernum.* The segments of the epicalyx are usually much smaller (by about one half) than the sepals. In subgenus *Erythrocoma* the segments of the epicalyx are very long and usually stand out horizontally while the calyx has vertically erect sepals.

The pigment (anthocyanin) and the pubescence on the outer parts of the calyx are usually of the same kind as on the floral peduncles and other vegetative parts. The inside of the calyx and especially of the calyx tube is usually smooth, sometimes longitudinally grooved. A character of some significance from the taxonomic point of view and much stressed by Bolle is the protruding rim which is formed on the inside of the calyx tube as the termination of the so called disc and below the region from which stamens grow out. In many species there is no rim, in others there is a very slight ridge which either forms a continuous or discrete rim. In subgenus *Erythrocoma* the rim of the disc forms a high protruding ring inside the calyx tube (Fig. 8).

The petals, the number of which usually corresponds to the number of sepals, are inserted on the inside of the calyx tube and outside the region from which stamens grow out. The points of insertion are at the intervals between the sepals. The petals are an important systematic character for determining species. Their length varies greatly and ranges from 2—3 mm to 20 mm and more. Their shape may be rounded, elliptical, elliptically elongated, elliptically cuneate etc. The petal base may be obscurely rounded, cordate or auriculate. In some species the petal base is elongated forming a long narrow claw. The tips of the petals may be elongated, rounded, cordately incised, or emarginate as in *G. rivale* (Fig. 9). Their colour is white, greeny-white, creamy, yellow of various shades, or red.

In the majority of species the flowers are pentamerous in respect to both sepals and petals, though, within a species this number may be rather variable. Very often there are 6 to 8 sepals and petals and sometimes even 4 or 3. In some species, as for instance in *G. reptans,* the usual number of segments in the two whorls of the perianth is 6 to 8 and 5 is only exceptional. In *G. reptans* also the segments of the epicalyx are more numerous and there are usually 10, two in between every two sepals (Fig. 4).

LEAVES

The shape of leaves in the basal rosettes varies over a wide range even in one single plant. E.g. in *G. vernum, G. canadense* or *G. laciniatum* the first leaves which develop in the spring have numerous lateral leaflets and a terminal leaflet deeply dissected or incised. In leaves which develop later the number of lateral leaflets steadily decreases and they are less incised. Finally in the autumn the last leaves to develop often have only one large, almost entire terminal leaflet (Figs. 25, 26 and 28).

In the tribe of *Geeae* all genera and species have odd-pinnate, pinnatifid or lobed basal leaves. The only exception is the genus *Waldsteinia* which has leaves with one entire blade or with a blade dissected into 3 leaflets of equal size. In *Geum* the most common leaves are lyrate, with conspicuous terminal leaflet and several pairs of lateral leaflets often separated by additional small leaflets in between. The conspicuous terminal leaflet may be either rounded or reniform, with cuneate or cordate base, much or slightly larger than the lateral leaflets. Both the terminal and the lateral leaflets may be lobed or incised to various depths. In the extreme case of very deeply incised leaflets the whole leaf is uniformly incised and the difference between the terminal and lateral leaflets disappears (Figs. 4, 6, 7 and 8). The leaf shape is a good specific characteristic but its diagnostic value in higher taxonomic units such as genera and subgenera is small. The margin of the leaf blade may be singly, or less frequently doubly toothed, serrate or crenate in various degrees. The petiole is usually elongated, sometimes alate, and often broader at the base.

The cauline leaves usually resemble the basal ones. However, in the upper parts of the stem the petiole becomes gradually shorter and simultaneously the lateral leaflets become reduced. Within the inflorescence the leaves gradually change to bracts. In all species cauline leaves have stipules, the expression of which varies according to species, with margins more or less deeply incised and crenate.

STEMS

In subgenera *Sieversia* and *Neosieversia,* in section *Paleooncostylus,* and also in *G. montanum* and *G. reptans* from subgenus *Oreogeum* the stem is usually unifloral. In species from subgenus *Sieversia* the stem approaches a typical scapus and has usually small leaflets with reduced blades. In *G. montanum* and *G. reptans* unifloral stems are also more common, but often — especially when plants are cultivated — stems may have 2—3 flowers and more conspicuously expressed leaves. The above species constitute the intermediate link between genus *Dryas* (from the tribe of *Dryadeae*) with typical scapus and the other species from the tribe *Geeae* which have typically shaped ramified stems. Ramification may differ greatly in the various species and the stems may have from several (3—5) to some tens (50 and more) flowers. In most species the branching of the inflorescence is cymose. Monochasial cymes are the more common, though sometimes in such species as for example *G. vernum* or *G. heterocarpum* the cymes are dichasial with pseudodichotomous branching (Figs. 29 and 31). The stems, especially the floral peduncles, and to a lesser degree the bractlets and the calyx are pigmented red or in various brown shades by anthocyanin. E.g. anthocyanin pigmentation is visible in *G. rivale* or *G. triflorum.*

INDUMENTUM

Practically all the plants in the group in question are pubescent, but the expression of the pubescence often differs on the various organs. Mention has been made earlier of the differences in the pubescence on the receptacle, achenes and styles. These differences are frequently diagnostic for related species. The stems and leaves are usually haired with short straight hairs forming a more or less dense indumentum. In numerous species there are also additional, much longer, stiff, bristly hairs which produce a more or less pronounced roughness of the stems and leaves. Such is the case for instance with *G. macrophyllum* or *G. laciniatum.* In some species there are glandular hairs primarily on the upper part of stems, on floral peduncles, on the calyx and on the style. These consist of a slender pedicle composed of 2—3 cells and of a relatively large rounded secreting cell. The presence or absence of some type of hairs has often been used in the systematics of this group as a criterion for distinguishing related species and also varieties within a species.

RHIZOME AND ROOTS

All the plants in the group are perennials. However, the present research has shown that the perenniality of these plants varies greatly. This is associated with the formation of the so called rhizomes which may be developed in various degrees. Indeed, I believe that in this group of plants it is not a typical rhizome that is formed, but rather a caudex, i.e. an organ intermediate between a rhizome and an overground stem. When examining such species as for instance *G. montanum* or *G. rivale* it is apparent that the caudex is very well developed and spreads over a quite considerable distance. The caudex is flattened, creeping overground, often ramified and forms yearly new leaf rosettes at the apex. A caudex of this kind produces many vigorus adventitious roots, and as simultaneously it forms an annual growth of shoots, it can rot away at the other end and persist under favourable conditions for many years. It is even capable to propagate vegetatively by dividing. On the other hand, numerous *Geum* species primely from subgenus *Eugeum,* e.g. *G. aleppicum, canadense* and *macrophyllum,* form only one swollen root-base with a bunch of adventitious roots. During several years, sometimes 2—3, the swollen root-base produces leaf rosettes and flower stems and then dies away. The plants of such species live for a much shorter time. Bollle's supposition that *G. vernum* from subgenus *Stylipus* is an annual plant is not correct and these plants, similarly as the species mentioned earlier, can live for several years. In the group here considered there are probably neither annual nor biennial species.

To summarize, it is to be stressed once again that the expression of the style on the achenes is the basis for dividing the tribe of *Geeae* into genera. Moreover, this character is also significant when the genus *Geum* in the broader sense of this denomination is being divided into subgenera. In principle, within every subgenus the general pattern in the expression of the style is the same, though the styles in various species may differ greatly in respect to length, shape of the various parts and pubescence. For instance in subgenera *Oncostylus* and *Acomastylis* some species may be classed in sequence according to the gradual reduction in length and pubescence of the styles on the achenes. In subgenus *Eugeum* the size and shape of the rostrum and stigmatic part as well as the degree and nature of pubescence show considerable interspecific variability retaining at the same time the fundamental structural pattern of the style characteristic for he whole subgenus.

Such other traits, as for instance the leaf shape, the expression of the hypanthium and calyx, the shape and colour of petals, the presence and length of the gynophore etc., constitute only specific characters and appear in a variety of combinations in various subgenera and genera. However, in spite the general resemblance between these organs in representatives of various genera and subgenera, even in representatives of one subgenus the expression of the organs is individual and characteristic for every species. Quite certainly in the whole group there are no two species which would have, for instance, exactly the same shape of leaves or the same expression of the hypanthium. Even when in two or three species some organs are, generally speaking, very much alike they are conditioned in each case by a different set of numerous genes. This is evident from genetical analyses of crosses between closely related species. In F_2 the characters are segregating very strongly thus showing that the parent species differ in respect to the majority of characters by numerous genes and that in most cases specific characters are polygenically controlled. Only some few characters, such as the colour of petals or the presence of anthocyanin, are controlled by one or very few pairs of allelomorphic genes. In the case of these characters only, it is highly probable that when their expression is controlled by allelomorphic genes it is the same in various species.

On the whole, morphological differences in the tribe of *Geeae* are a sufficient criterion for distinguishing species. The variability in morphological characters and the various combinations of morphological elements which appear in the particular species form a noncontinuous pattern and between the majority of species existing in nature (with the exception of hybrids) there are no intermediate forms. The majority of *Geeae* species constitute monomorphic units with comparatively little variability within the particular species. Only in subgenera *Eugeum* and *Acomastylis* there are some polymorphic species having usually an extensive distribution and considerable specific variability. It is only in the case of these evolutionally most recent species that the morphological analysis is frequently insufficient for determining the systematic rank of a taxon.

V. INTRASPECIFIC VARIABILITY IN THE TRIBE OF *GEEAE*

On the basis of systematic evidence, of examined herbarium specimens and of specimens cultivated in the course of the present research it can be stated that throughout the tribe of *Geeae* monomorphic species with only slight intraspecific variability are the most common. As yet not one subspecies has been distinguished either among *Geum* species from subgenera *Sieversia, Neosieversia, Oncostylus, Woronowia,* and *Oreogeum* or in the genera *Coluria* and *Waldsteinia.* The only case of differentiation within a species is to be noted in the subgenus *Orthurus* and this alone when the opinion of some taxonomists is accepted that *G. kokanicum* Regel et Schm. is a subspecies of *G. heterocarpum* Boiss. Iltis (1913) believes that *G. kokanicum* is only an alpine form and a form of more sunny habitats of *G. heterocarpum,* and that it is a variety of this species already described by Boissier as *G. heterocarpum* Boiss. var. *oligocarpum* Boiss. in sched. *G. kokanicum* differs from *G. heterocarpum* mainly by its shorter gynophore and the smaller number of slightly larger achenes. All these characters are variable also in *G. heterocarpum* and it seems rather plausible that *G. kokanicum* is indeed merely a variety of this species. An answer to this question may alone be provided by experimental cultures.

Appreciable variability within one species is shown also by some species in subgenera *Acomastylis* and *Eugeum.* In the former of these two subgenera the species *G. rotundifolium* Fisch. (*G. calthifolium* Smith) has one variety — *dilatata* Franch. et Savat. — described by Bolle as a distinct species (*Acomastylis niponica* Bolle). According to Hara (1952) the variety which appears in Japan and on the Kurile Islands is connected by intermediate forms with the typical form and does not deserve under any respect the rank of an independent species. This opinion is shared by Hultén (1929) who is an authority on floras in those regions. The two other species in subgenus *Acomastylis* with a more extensive distribution are *G. elatum* Wall. (China and Himalayas) and *G. turbinatum* Rydb. (Rocky Mountains). The two species are rather variable and several varieties and forms have been distinguished in them. Finally, Bolle classifies the variety *G. Rossi* Ser. var. *humilis* Scheutz as an independent species, while other workers, and Hultén among them, are of the opinion that it is merely a dwarf form of this species and does not merit any higher systematic rank. Some species in the subgenus *Eugeum,* specially those with more widespread distribution, show a certain amount of inner differentiation. *G. aleppicum* may serve here as an example. According to Fernald (1935) N. American and East Asian plants differ from West Asian and European ones by longer hairs primely on the tip and the edges of achenes, while the typical form has the whole achenes uniformly long haired. The former group forms according to Fernald the var. *strictum* (Ait) Fern. In opposition to this view Hara (1925) does not see any difference between Japanese and East European plants, but finds that N. American plants from var. *strictum* are different (less pubescent peduncles and achenes). My observations indicate that differences between var. *strictum* from N. America and *G. aleppicum* from Japan and Poland are very slight and that there are intermediate forms varying by the degree of pubescence. More significant variability is shown by *G. aleppicum,* primely in the shape of leaves. A number of forms has been here described as varieties or even as independent species, as for instance *G. Vidalii* Franch. from Japan, *G. scopulorum* Rydb. and *G. decurrens* Rydb. from N. America, and *G. mexicanum* Rydb. from Mexico. In the flora of the USSR Juzepchuk also stresses the polymorphic nature of this species and describes *G. Potanini* Juz. and *G. glabricaule* Juz. However all these "species" deserve at the most the rank of a variety. Undoubtedly, on the enormous distributional area occupied by the species the effect of a gradual differentiation of geographical races can be observed and it may be that in future these races will constitute the beginning of new species. The hybrids which I have obtained between *G. aleppicum* biotypes from N. America, Japan and Europe indicate that the plants produce fully fertile hybrids and that in F_2 the differences in the degree of pubescence, leaf shape, size of petals, shape of fruit heads show a slight yet distinct segregation.

G. urbanum L. with a large distribution in Europe and Asia also shows marked variability in the degree of hairiness and leaf shape. European plants from the Mediterranean area differing by larger flowers and fruit heads and by more thickly dissected leaves have been defined as var. *australe* Guss. In the species the description of numerous forms has been based on the shape of the leaves and the absence or presence of glandular hairs, but as data on the geographical distribution of these forms are lacking it is at present difficult to form any opinion on their systematic status. *G. hyrcanum* from the Talysh Mountains in the Caspian Sea region which has been described as a separate species is classified by Juzepchuk as *G. urbanum. G. latilobum* Somm. et Lev. distinguished by Juzepchuk and by Bolle as a separate species from Transcaucasia is possibly also merely a subspecies.

Among N. American species considerable variability is seen in *G. canadense* Jacq. Many authors have described some forms of this species as independent species, but according to Bolle they are merely varieties. My observations on *G. canadense,* originating from several natural habitats in Canada and the U.S., grown in cultures have disclosed appreciable hereditary differences in leaf shape and petal size.

A separate problem is raised by the variability of *G. virginianum.*

It seems very probable that in this case various hybrids of *G. canadense* with *G. aleppicum* are frequently mistaken for that species. This I have been able to ascertain on numerous herbarium specimens which were defined as *G. virginianum.* To solve the problem of this species a detailed research based on field work and abundant herbarium materials is needed.

A very fine example of a separate geographical race is seen in the case of var. *chinense* F. Bolle from China which is a variety of the Japanese and Korean species *G. japonicum* Thunb.

Finally, the last species from the subgenus *Eugeum* showing morphological differentiation to be mentioned here is *G. rivale.* The species has an extensive distribution in Europe, Asia and N. America but has not formed any distinctly separate geographical races. Some plants originating from. N. America are almost exactly the same as the plants from Poland. On the other hand, among the plants originating from the Tatra Mountains there are ecotypes drastically differing by the expression and size of the particular organs. Perhaps the most distinct form is that of *G. rivale* obtained from Iceland. These plants are of a very small height and have widely opened flowers. My observations made in the herbarium at Copenhagen indicate that this form is found exclusively in Iceland and on the Faröer Islands. The differences between *G. rivale* biotypes are of a hereditary nature and have persisted in the plants grown in cultures for many years (Fig. 33). This is also borne out by genetical evidence from experiments on one cross between two ecotypes. One of the initial forms used for this cross was *G. rivale* from Zakopane in Poland with tall stalks and large leaves and flowers. The plant was rich in anthocyanin in stems, calyx and flowers and was of a characteristic red-brown colour. The other parent form in this cross was *G. rivale* var. *pallidum* obtained from the Botanical Garden in Copenhagen. This plant was of small height with small leaves and flowers, and was entirely deprived of anthocyanin. Besides the characters as mentioned above the plants differed in the time of flowering, degree of hairiness, toothing of leaves and many other traits difficult to perceive. The *pallidum* form is fairly common in nature and has been at first described as the independent species *G. pallidum* Fisch. et Mey. Dahlgren found (1924) that in F_1 of the cross between typical *G. rivale* and the *pallidum* form the presence of anthocyanin dominated, while in F_2 segregation took place into plants with and without anthocyanin in a ratio of 3 : 1 (391:137). A similar result was obtained in the case of the cross which I made, where out of 79 F_2 plants 60 were with and 19 without anthocyanin. The other characters were inherited so that in F_1 their expression was intermediate while in F_2 they showed a continuous segregation approximately within the limits of the parent forms.

This is illustrated on the example of petal size and gynophore length tabulated below:

Length of petals in mm.	7	8	9	10	11	12	13	14	15	16
G. rivale from Zakopane				5	8	11	10	4	3	
G. rivale v. pallidum		8	12	19	8	3				
F_1				2	18	4	1			
F_2	1	8	10	16	22	15	4	3		

Width of petals in mm.	5	6	7	8	9	10	11	12	13	14
G. rivale from Zakopane				1	6	8	15	15		
G. rivale v. pallidum	6	7	19	15	3					
F_1			2	10	12	1				
F_2		1	4	8	21	25	15	5		

Length of gynophore in mm.	4	5	6	7	8	9	10	11	12
G. rivale from Zakopane			1	3	8	15	9	1	
G. rivale v. pallidum	2	7	13	12	8	1			
F_1	1	2	10	9	4	3			
F_2	2	14	25	20	9	8	1		

From the tables it can be seen that the size of petals is in F_1 intermediate and in F_2 this character is segregated within the limits of the parent forms. The short gynophore of the *pallidum* variety is clearly dominant in F_1 while in F_2 segregation is far less marked and shifted towards the shorter gynophore. Similar intermediate size in F_1 and strong segregation in F_2 is shown also by leaves, the length of stems and rostrum, as well as by numerous other characters in which the parent forms differ. The hybrids of *G. rivale* forms are entirely fertile with absolutely normal meiotic divisions. The existence of clearly distinct ecotypes in the species *G. rivale* was already pointed out by Turesson (1925, 1931) who stressed that they differed by the height of stems, the size of leaves and the time of flowering. My observations of numerous ecotypes in this species from various parts of its distribution fully support Turesson's report on the hereditary differentiation within the species. However, I believe that in spite of the very large distributional area occupied by *G. rivale* no subspecies or varieties with separate geographical distribution have developed within this species.

Fig. 33. Drawings to scale of floral stems, basal leaves, flowers, petals receptacles and achenes of *Geum rivale* from various habitats grown in Warsaw: 1 — State of New York, U.S.A., out of seeds obtained from Professor R. T. Clausen; 2 — Zakopane, Tatra Mts., Poland; 3 — Dolina Rozpadlina, Tatra Mts., Poland; 4 — Hala Gąsienicowa, Tatra Mts., Poland; 5 — Iceland, out of seeds obtained from Professor A. Löve; 6 var. *pallidum*, out of seeds obtained from the Botanical Garden in Copenhagen

Besides hereditary variability *Geum* species display also a considerable phenotypic variability. For instance, in the Tatra Mountains I have collected very small dwarf forms of *G. montanum* with always unifloral stems, only 2 to 5 cm tall. These forms are described in floristic literature as var. *nana* or var. *minor* but are in fact merely environmental forms which when transplanted into the lowlands produce in cultures vigorous plants with stems 20 to 30 cm tall and frequently with 2—3 flowers on a shoot. Similar, though less extreme, observations refer also to other species which when transplanted for cultivation change the size of their organs, the degree of pubescence and so on.

I did not find even one case of chromosomal differentiations forming polyploidal races or aneuploidal forms in the genus *Geum*, and this in spite of the fact that in some species I examined cytologically specimens from very distant parts of their distribution and from different ecological habitats. For instance, *Geum rivale* specimens from Polish mountains and lowlands, from N. America (United States and Canada) and from Iceland were examined, and it was found that in all of them the chromosome number was the same.

VI. KARYOLOGY OF THE TRIBE OF *GEEAE* IN CONNECTION WITH THE KARYOLOGICAL CONDITIONS IN THE FAMILY OF *ROSACEAE*

There are as yet relatively few cytological researches referring to the genus *Geum* and related genera. The first report on the chromosome number in genus *Geum* was made by Winge (1925) who found the haploid number of n = 21 in *G. rivale*, *G. urbanum* and the hybrid between them. In 1932 this was confirmed by Prywer. Heitz (1926) reported the diploid number of 2n = 70 for "*G. coccineum*". In 1938 Yamazaki reported haploid numbers of n = 21 for *G. aleppicum, calthaefolium, coccineum* and *japonicum*. Of these workers only Winge and Heitz illustrated their reports with drawings of chromosomes. For the next several years there have been no cytological researches on the genus *Geum*, the only exception being a confirmation by A. and D. Löve (1942, 1944) of the diploid number 42 in *G. urbanum* and *G. rivale*.

In 1946 a short report was published on the doctor's thesis of L. A. Raynor who carried out her work at Professor L. W. Sharp's Botanical Laboratory at Cornell University. The thesis was entitled "A cytotaxonomic investigation of *Geum*" and gave chromosome numbers in numerous *Geum* species. A part of L. A. Raynor's thesis was published in 1952. This part includes numerous illustrations of both somatic chromosomes and the meiotic divisions in 20 *Geum* species and hybrids. The unpublished part of this work I know from a microfilm kindly sent me by the library of Cornell University. The authoress has assembled much data referring to the morphology, the size and the number of chromosomes in the entire family of *Rosaceae*. These informations supplemented by such more recent results as have been accessible to me form the basis for the considerations on chromosomal conditions in the family of *Rosaceae* which will now follow.

It seems that a short review of chromosomal conditions in the whole family of *Rosaceae* prior to discussing the present state of knowledge on these conditions in the tribe of *Geeae* will be very much to the point here. For this purpose the table below lists the basic chromosome numbers of the genera in question and the degrees of polyploidy observed in various species from these genera. The genera are listed according to Focke's classification as modified by Juel and others.

Name of genus	Basic chromosome number of genus x	Degree of ploidity in examined species
Subfamily of Spireoideae	8,9	
Tribe of Spiraeae	9	
Physocarpus	9	2
Spiraea	9	2,3,4,5,6
Pentactina	9	2
Sibiraea	9	2
Aruncus	9	2
Gillenia	9	2
Tribe of Quillajeae	8	
Exochorda	8	2
Quillaja	8?	4
Subfamily of Pomoideae	17	
Cotoneaster	17	2.3,4
Pyracantha	17	2
Osteomeles	17	2
Cydonia	17	2
Pyrus	17	2,3.4
Malus	17	2,3.4
Aronia	17	2.4
Sorbus	17	2,3,4
Raphiolepis	17	2
Eriobotrya	17	2
Photinia	17	2,4
Amelanchier	17	2,4
Stranvaesia	17	2

Name of genus	Basic chromosome number of genus x	Degree of ploidity in examined species
Mespilus	17	2
Crataegus	17	2,3,4
Chaenomeles	17	2
Subfamily of Rosoideae	9,8,7	
Tribe of Kerrieae	9	
Kerria	9	2
Rhodotypus	9	2
Neviusia	9	2
Tribe of Alchemilleae	8	
Alchemilla	8	4,8,ca.9,15
Aphanes	8	2,6
Tribe of Sanguisorbeae	7	
Agrimonia	7	4,8
Sanguisorba	7	2,4
Poterium	7	4
Tribe of Roseae	7	
Rosa	7	2,3,4,5,6,8, a. aneuploids
Hesperhodos	7	2
Tribe of Potentilleae	7	
Rubus	7	2,3,4,5,6,7,8,9,10,11.12
Fragaria	7	2,4,6,8
Duchesnaea	7	6
Potentilla	7	2,3,4,5,6,8,9,10,12,16
Comarum	7	2
Sibbaldia	7	2
Subfamily of Dryadoideae		
Tribe of Cercocarpeae	9	
Cercocarpus	9	2
Tribe of Dryadeae	9	
Fallugia	9	2
Cowania	9	2
Dryas	9	2
Tribe of Geeae	7	
Waldsteinia	7	2,6
Coluria	7	2
Geum	7	4,6,8,10,12
Subfamily of Neuradoideae		
Neurada	7	2
Subfamily of Prunoideae	8	
Osmaronia	8	2
Prinsepia	8	4
Maddenia	8	4
Prunus	8	2,3,4,6,8,22

It appears from the above list that in the family of *Rosaceae* the basic chromosome numbers are 7, 8 and 9. The numbers 8 and 9 appear primely in the subfamilies of *Spireoideae* and *Prunoideae* represented mainly by trees and shrubs. In the tribes of *Kerrieae, Cercocarpeae* and *Dryadeae* from subfamilies of *Rosoideae* and *Dryadoideae* also primely consisting of shrubs the basic chromosome number is 9, while in the remaining tribes with herbaceous plants the predominating basic number is 7. The basic number characteristic for the subfamily of *Pomoideae* is 17. It is most probably of amphiploid orgin and had arisen from the numbers 8 and 9. The explanation given in this connection by Darlington and Moffet (1930) and Moffet (1931), according to which this number would be a secondary one produced from the basic number 7 by unequal doubling (i.e. out of the 17 chromosomes 4 are doubled and 3 are tripled), seems rather unlikely. This hypothesis was formulated on the basis of chromosome conjugations observed by these authors, who found the effect of the so called secondary conjugation which consists in that at metaphase of the first reduction division bivalents are seen to be arranged into 4 pairs and 3 triplets besides the usual bivalents. However, similar effects may also arise in amphiploids having partially homologous chromosomes of the parent forms. The significance of basic numbers in the various groups of families for problems involved in the phylogeny of *Rosaceae* will be discussed at the end of this work.

From morphological analyses of chromosomes in the family of *Rosaceae* it is apparent that because of the small size of chromosomes and their small morphological differentiation the results obtained so far introduce nothing of significance to the investigations on the phylogeny and taxonomy of the rose family. According to the data reported by Raynor (1945) referring to 16 genera the length of chromosomes ranges from 0,5 to 3 μ, the average for the shortest chromosomes is 0,86 μ and for the longest 1,9 μ. With so small differences in the sizes of chromosomes both within a chromosome set of one species and between chromosomes from related species or even species situated far away in the system, and with the nearly nonexistent morphological differentiation in chromosomes no results are obtained from analyses of chromosome sets.

The table on p. 101 lists the chromosome numbers in the species considered here as obtained in my investigations together with results reported by other workers.

Somatic plates of some species from the tribe of *Geeae* are shown in Figs. 34 and 35.

Specific name	2 n	n	Reported by:
Waldsteinia geoides	14	7	author, (Polya 1949, Reese 1952)
Waldsteinia ternata	42	21	„
Coluria geoides	14	7	„
Geum montanum	28	14	„
Geum reptans	42	21	„
Geum bulgaricum	70		„
Geum rotundifolium	42		„ (Yamazaki 1936, Hara 1952)
Geum Peckii	42		Raynor 1945
Geum radiatum	42		Raynor 1945
Geum Rossii	56		author
Geum turbinatum	56		„
Geum triflorum	42	21	„ (Raynor 1945)
Geum ciliatum	42	21	„
Geum campanulatum	42		„
Geum rivale	42	21	„ (Winge 1925, Prywer 1932, Turesson 1938, A. and D. Löve 1942, Raynor 1945)
Geum silvaticum	42	21	author
Geum pyrenaicum	~~42~~ 84	~~21~~ 42	„
Geum coccineum	42	21	„ (Yamazaki 1936)
Geum Quellyon	70	35	„ (Heitz 1926 as G. coccineum)
	42		Raynor 1945
Geum magellanicum	84	42	author, (Raynor 1945)
Geum riojense	84	42	„
Geum laciniatum	42	21	„ (Raynor 1945)
Geum aleppicum	42	21	author, (Yamazaki 1936, Raynor 1945)
Geum canadense	42	21	„ (Raynor 1945)
Geum virginianum	42	21	„ (Raynor 1945)
Geum boliviense	42	21	„
Geum macrophyllum	42	21	„
Geum perincisum	42	21	„
Geum oregonense	42	21	„
Geum japonicum		21	„ (Yamazaki 1936)
Geum Fauriei	84	42	„
Geum urbanum	42	20	„ (Winge 1925, Prywer 1932, A. and D. Löve 1942, Raynor 1945)
Geum molle	42	21	„
Geum hispidum	42	21	„
Geum vernum	42	21	„
Geum heterocarpum	28	14	„
Geum speciosum	70	35	„

In the present cytological investigation on *Geum* species both root tips and PMCs were examined. For the examinations fixed preparations stained with crystal violet according to Newton were usually used. The roots were fixed in Navashin fluid according to Müntzing's modification and the flower buds prior to fixation with Navashin fluid were first fixed during 5—10 minutes in Carnoy's solution (3 parts of

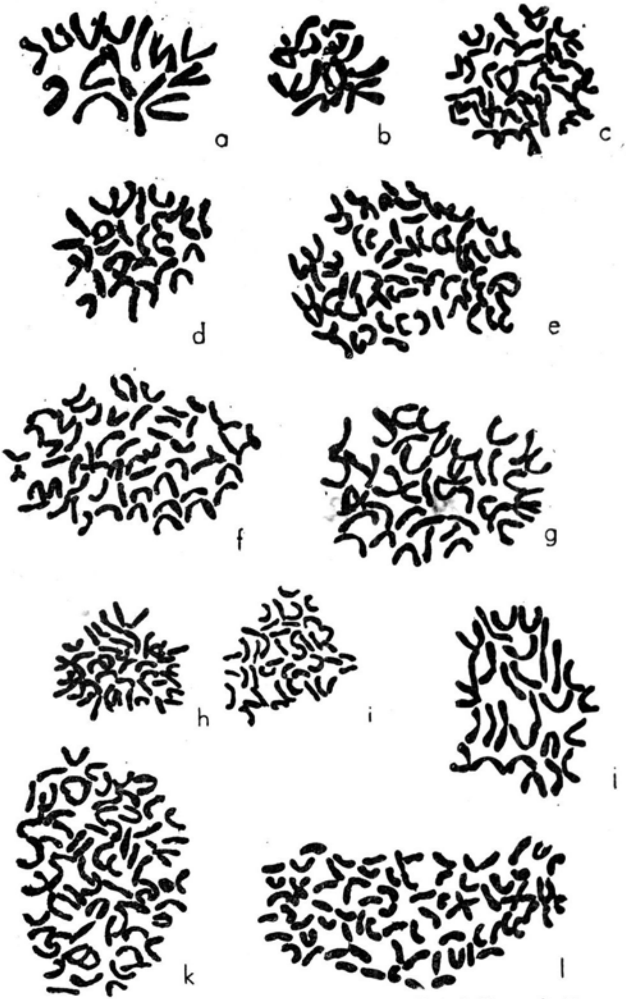


Fig. 34. Somatic chromosomes of some species in the tribe of *Geeae;* a — *Coluria geoides* (Pall.) Ledeb., 2n = 14; b — *Waldsteinia geoides* Willd., 2n = 14; c — *Waldsteinia ternata* Fritsch., 2n = 42; d — *Geum montanum* L., 2n = 28; e — *Geum bulgaricum* Panc., 2n = 70; f — *Geum Rossii* Ser., 2n = 56; g — *Geum calthifolium* Sm., 2n = 42; h — *Geum ciliatum* Pursh., 2n = 42; i — *Geum campanulatum* Greene, 2n = 42; j — *Geum heterocarpum* Boiss., 2n = 28; k — *Geum speciosum* Alboff., 2n= 70; l — F_1 *G. speciosum* × *pyrenaicum* 2n = 77.

absolute alcohol, 1 part glacial acetic acid). Smears with aceto-carmine or aceto-orceine were sometimes prepared from anthers.

All together in the whole tribe of *Geeae* 37 species have been examined cytologically which amounts to nearly 57 per cent of the species in question. In all the species with no exceptions the chromosome number is a multiple of 7 and probably this is the basic number for the entire tribe, though, unfortunately, the chromosome numbers in the subgenera *Sieversia, Neosieversia, Oncostylus* and *Andicola* are not yet known. In the other two tribes from the subfamily of *Dryadoideae,* i.e. in the tribes of *Cercocarpeae* and *Dryadeae,* all the species examined so far have the basic number x = 9.

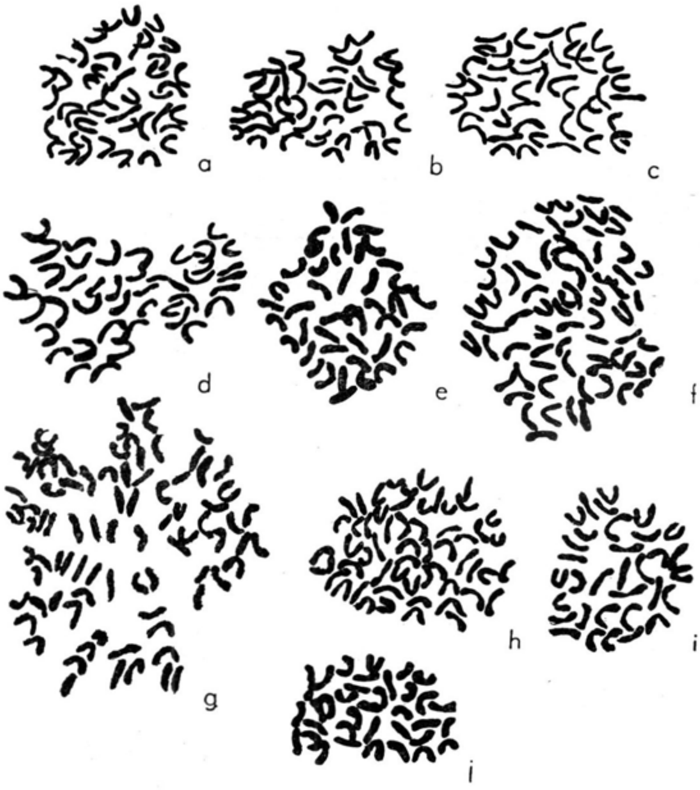


Fig. 35. Somatic chromosomes of some *Geum* species and hybrids; a — *G. canadense* Jacq., 2n = 42; b — *Geum silvaticum* Pourr., 2n = 42; c — *Geum aleppicum* Jacq., 2n = 42; d — *Geum hispidum* Fr., 2n = 42; e — *Geum perincisum* Rydb., 2n = 42; f — *Geum Quellyon* Sweet, 2n = 70; g — *Geum riojense* Bolle, 2n = 84; h — F_1 *G. speciosum* × *G. rivale* 2n = 56; i — F_1 *G. montanum* × *triflorum*, 2n = 35; j — F_1 *Geum montanum* × *rivale* 2n = 35

It is evident from the above table that the chromosome numbers established in the present investigation agree with the numbers reported by other workers, the only exception being *Geum Quellyon*. In this species according to the material in my possession the number of somatic chromosomes is 70. Heitz (1926) also reports this number to be 70 but in *G. coccineum*, though, in the drawing produced by that author there are 72 chromosomes. Raynor (1945), on the other hand, reports that for *G. Quellyon* the number is 2n = 42, while in my material it is *G. coccineum* that has this chromosome number. I believe that these differences are caused by the erroneous denomination of the species in question. I think Heitz must have examined *G. Quellyon* (and not *coccineum*) while Raynor writes of *G. coccineum* (and not *Quellyon*). I have had more than one opportunity to note that in botanical gardens these two red flowering *Geum* species are cultivated under false names.

Another fact which deserves to be stressed is the complete lack of diploids among the *Geum* species the chromosome number of which has been already established. So far the only diploids noted in the group are from the related genera of *Waldsteinia* and *Coluria*. Among the 36 cytologically examined species of this tribe there are:

2 diploid species — i.e. 5.5%
2 tetraploid species — i.e. 5.5%
24 hexaploid species — i.e. 66.6%
1 octoploid species — i.e. 2.7%
3 decaploid species — i.e. 8.0%
4 dodecaploid species — i.e. 11.1%.

This percentage of polyploid species is exceptionally high even for the rose family where polyploidy is also very common in the other genera. It may be that when all the other *Geum* species will be investigated more fully the relative numbers of the various polyploid types will change, as so far more extensive cytological examinations have been carried out only in the large subgenus *Eugeum* in which it seems that the secondary basic number is the triploid number 21. In opposition to such other rosaceous genera as *Potentilla, Rubus* or *Rosa,* in the genus *Geum* there are no species with odd numbers of genomes or with aneuploid chromosome numbers. This is in connection with the fact that all the known *Geum* species are strictly sexual and apomixis has never been observed here.

In all hexaploid *Geum* species the chromosomes are approximately of the same length and within a chromosome set their length ranges from 1.5μ to 2,5μ. Dodecaploid species, such as *G. magellanicum* and

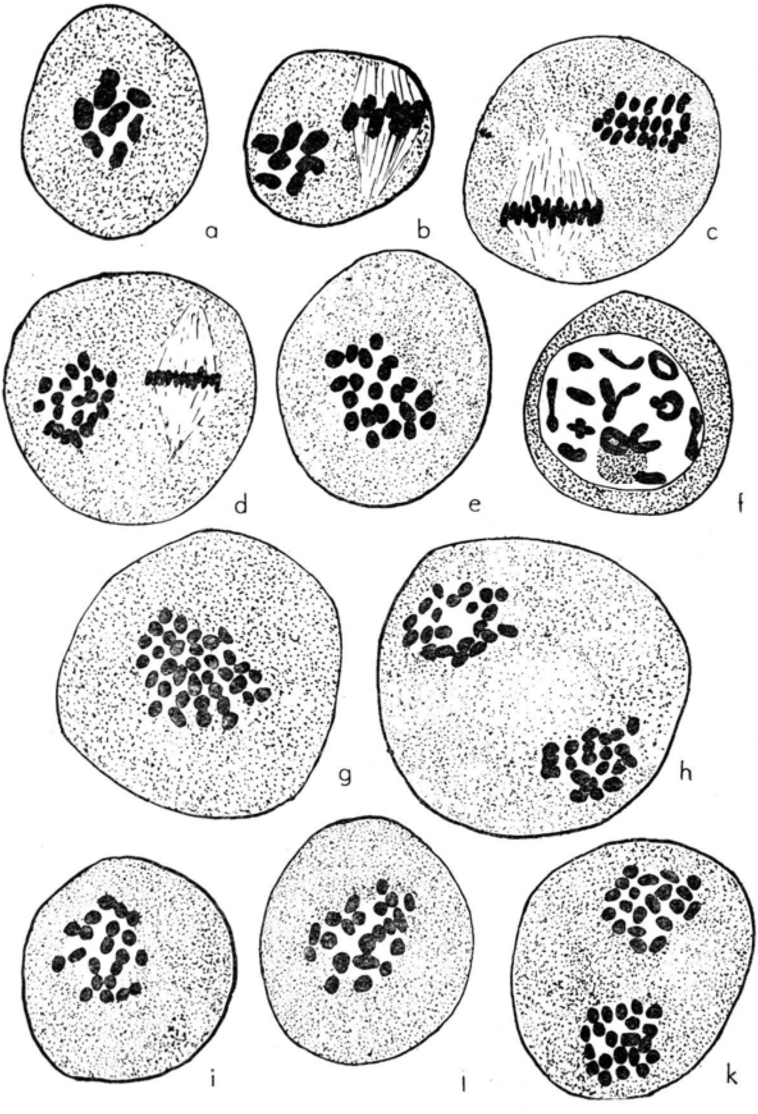


Fig. 36. Meiotic chromosomes in PMCs of some species in the tribe of *Geeae;* a — *Coluria geoides* (Pall.) Ledeb., M-I with 7 bivalents; b — *Waldsteinia geoides* Willd., M-I with 7 bivalents; c — *Waldsteinia ternata* Fritsch., M-II with 21 chromosomes; d — *Geum ciliatum* Pursh., M-II with 21 chromosomes; e — *Geum triflorum* Pursh., M-I with 21 bivalents; f — *Geum heterocarpum* Boiss., diakinesis with 14 bivalents; g — *Geum speciosum* Alboff., M-I with 35 bivalents; h — *Geum vernum* Torr., et Gray., M-II with 21 chromosomes in each plate; i — *Geum coccineum* Sibth. et Sm., M-I with 21 bivalents; j — *Geum aleppicum* Jacq., M-I with 21 bivalents; k — *Geum canadense* Jacq., M-II with 21 chromosomes in each plate

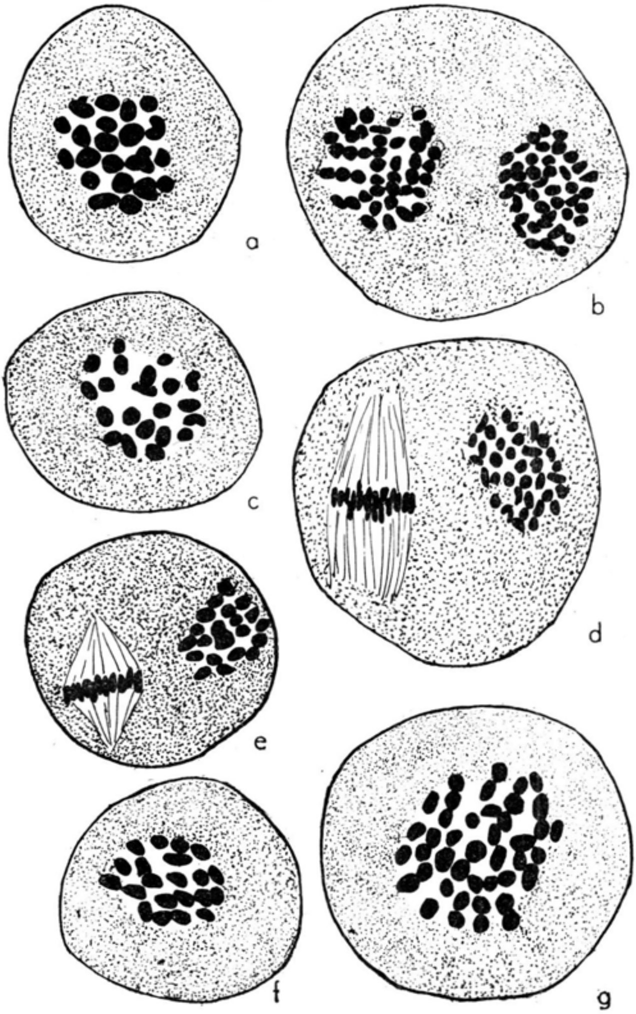


Fig. 37. Meiotic chromosomes in PMCs of some species in subgenus *Eugeum;* a — *G. virginianum* L., M-I witth 21 bivalents; b — *Geum Fauriei* Leveillé, M-II with 42 chromosomes in both plates; c — *G. macrophyllum* Willd., M-I with 21 bivalents; d — *Geum Quellyon* Sweet., M-II with 35 chromosomes; e — *Geum molle* Vis. et Panc., M-II with 21 chromosomes; f — *Geum laciniatum* Murr., M-I with 21 bivalents; g — *Geum riojense* Bolle, M-I with 42 bivalents

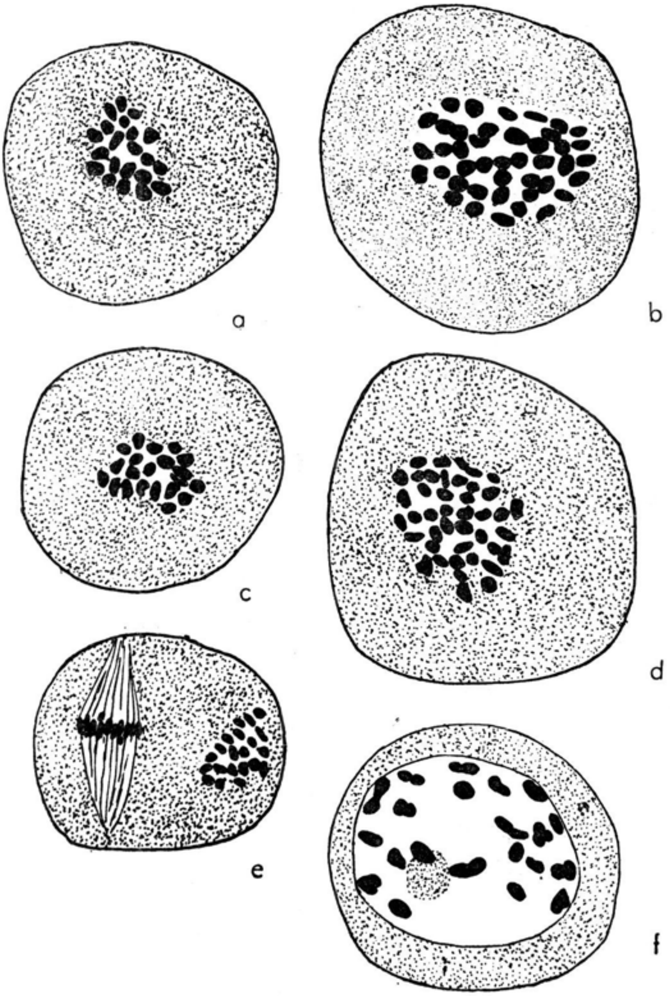


Fig. 38. Meiotic chromosomes of some species in subgenus *Eugeum;* a — *Geum hispidum* Fr., M-I with 21 bivalents; b — *Geum pyrenaicum* Willd., M-I with 42 bivalents; c — *Geum japonicum* Thunb., M-I with 21 bivalents; d — *Geum magellanicum* Pers., M-I with 42 bivalents; e — *Geum silvaticum* Pourr., M-II with 21 chromosomes; f — *Geum boliviense* Focke, diakinesis with 21 bivalents

G. riojense have distinctly shorter chromosomes than the hexaploid species, while the diploid *Waldsteinia* and *Coluria* species have longer chromosomes ranging rom 2 to 3.5 μ. This is not a generic character as the hexaploid *Waldsteinia ternata* has chromosomes of approximately the same length as hexaploid *Geum* species. Because of the very small size and the relatively small differentiation of chromosomes their morphological analysis was not attempted.

Meiotic divisions in the species from the tribe of *Geeae* usually develop quite normally (Figs. 36—38) and consequently seed and pollen fertility in pure species is relatively high. In prophase of meiotic divisions usually only late diakinesis is accessible for analysis. At diakinesis in the majority of bivalents (89 per cent of cases) there is only one chiasma, two chiasmata appear in about 10 per cent of bivalents, and three chiasmata are only exceptional having been found in less than one per cent of bivalents. Before metaphase the number of chiasmata is further reduced and at metaphase almost all bivalents have one chiasma only. On the whole, at metaphase the number of chiasmata per bivalent is about 1.2. It may be that the small number of chiasmata is the reason why polyvalents are not formed even in highly polyploid species. The only disturbances which I have observed are the occasional appearance of 2 to 4 univalents at metaphase of the I-st division and the formation of 1 or quite exceptionally 2—3 bridges — probably due to inversions — at anaphase of the I-st division. These disturbances are more frequent in *G. oregonense*, *G. Fauriei*, and *G. Quellyon*. They are very rare in *G. coccineum*, *G. canadense*, *G. laciniatum* and in other species. In the pure species also the second meiotic division develops absolutely normally and this refers likewise to the appearance of the young tetrads and pollen, thus explaining the high fertility of pure *Geum* species. Further on, fuller description will be made of the disturbances in the course of meiosis very common in hybrids and in forms of hybrid origin. However, it must be noted that fertility is high only in the case of cross pollination. Self pollination always greatly reduces fertility which may be associated with the partial self-sterility of *Geum* species.

VII. HYBRIDS IN THE TRIBE OF *GEEAE*

During the nearly twenty years that this research on the tribe of the *Geeae* has been under way I have obtained the following interspecific hybrids:

A. Intersubgeneric hybrids

- a) *Erythrocoma* × *Oreogeum*
  1. *Geum montanum* L. n = 14 × *Geum triflorum* Pursh n = 21
  2. *Geum montanum* L. n = 14 × *Geum campanulatum* Greene n = 21
- b) *Erythrocoma* × *Eugeum*
  3. *Geum urbanum* L. n = 21 × *Geum ciliatum* Pursh n = 21
  4. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum ciliatum* Pursh n = 21
  5. *Geum rivale* L. n = 21 × *Geum ciliatum* Pursh n = 21
  6. *Geum rivale* L. n = 21 × *Geum triflorum* Pursh n = 21
- c) *Orthurus* × *Eugeum*
  7. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum heterocarpum* Boiss. n = 14
- d) *Woronowia* × *Eugeum*
  8. *Geum speciosum* Alboff n = 35 × *Geum rivale* L. n = 21
  9. *Geum speciosum* Alboff n = 35 × *Geum pyrenaicum* Willd. n = 42.
- e) *Eugeum* × *Stylipus*
  10. *Geum urbanum* L. n = 21 × *Geum vernum* Torr. et Gray n = 21
  11. *Geum macrophyllum* Willd. n = 21 × *Geum vernum* Torr. et Gray n = 21
  12. *Geum perincisum* Rydb. n = 21 × *Geum vernum* Torr. et Gray n = 21
  13. *Geum oregonense* Rydb. n = 21 × *Geum vernum* Torr. et Gray n = 21
  14. *Geum aleppicum* Jacq. n = 21 × *Geum vernum* Torr. et Gray n = 21.
- f) *Eugeum* × *Oreogeum*
  15. *Geum montanum* L. n = 14 × *Geum rivale* L. n = 21
  16. *Geum montanum* L. n = 14 × *Geum silvaticum* Pourr. n = 21
  17. *Geum montanum* L. n = 21 × *Geum coccineum* Sibth. et Sm. n = 21
  18. *Geum montanum* L. n = 21 × *Geum molle* Vis. n = 21
  19. *Geum montanum* L. n = 14 × *Geum hispidum* Fr. n = 21
  20. *Geum montanum* L. = 14 × *Geum aleppicum* Jacq. n = 21
  21. *Geum montanum* L. n = 14 × *Geum urbanum* L. n = 21
  22. *Geum laciniatum* Murr. n = 21 × *Geum montanum* L. n = 14

23. *Geum montanum* L. n = 14 × *Geum canadense* Jacq. n = 21
24. *Geum montanum* L. n = 14 × *Geum macrophyllum* Willd. n = 21
25. *Geum pyrenaicum* Willd. × *Geum montanum* L. n = 14
26. *Geum montanum* L. n = 14 × *Geum magellanicum* Pers. n = 42
27. *Geum Fauriei* Lev. n = 42 × *Geum montanum* L. n = 14
28. *Geum rivale* L. n = 21 × *Geum reptans* L. n = 21
29. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum reptans* L. n = 21.

B. Intrasubgeneric hybrids

a) Subgenus *Oreogeum*

30. *Geum montanum* L. n = 14 × *Geum reptans* L. n = 21.

b) Subgenus *Eugeum*

1) Between dodecaploid species

31. *Geum magellanicum* Pers. n = 42 × *Geum riojense* Bolle n = 42
32. *Geum magellanicum* Pers. n = 42 × *Geum pyrenaicum* Willd. n = 42
33. *Geum Fauriei* Lev. n = 42 × *Geum pyrenaicum* Willd. n = 42
34. *Geum Fauriei* Lev. n = 42 × *Geum riojense* Bolle n = 42
35. *Geum magellanicum* Pers. n = 42 × *Geum Fauriei* Lev. n = 42.
36. *Geum pyrenaicum* Willd. n = 42 × *Geum riojense* Bolle n = 42.

2) Between deca- and dodecaploid species

37. *Geum riojense* Bolle n = 42 × *Geum Quellyon* Sweet n = 35
38. *Geum Quellyon* Sweet n = 35 × *Geum pyrenaicum* Willd. n = 42
39. *Geum magellanicum* Pers. n = 42 × *Geum Quellyon* Sweet n = 35.

3) Between dodeca- and hexaploid species

40. *Geum magellanicum* Pers. n = 42 × *Geum rivale* L. n = 21
41. *Geum magellanicum* Pers. n = 42 × *Geum aleppicum* Jacq. n = 21
42. *Geum magellanicum* Pers. n = 42 × *Geum hispidum* Fr. n = 21

43. *Geum magellanicum* Pers. n = 42 × *Geum canadense* Jacq. n = 21
44. *Geum magellanicum* Pers. n = 21 × *Geum macrophyllum* Willd. n = 21
45. *Geum pyrenaicum* Willd. n = 42 × *Geum rivale* L. n = 21
46. *Geum pyrenaicum* Willd. n = 42 × *Geum coccineum* Sibth. et Sm. n = 21
47. *Geum pyrenaicum* Willd. n = 42 × *Geum aleppicum* Jacq. n = 21
48. *Geum pyrenaicum* Willd. n = 42 × *Geum molle* Vis. et Panc. n = 21
49. *Geum pyrenaicum* Willd. n = 42 × *Geum macrophyllum* Willd. n = 21
50. *Geum pyrenaicum* Willd. n = 42 *Geum urbanum* L. n = 21
51. *Geum pyrenaicum* Willd. n = 42 × *Geum silvaticum* Pourr. n = 21
52. *Geum riojense* Bolle n = 42 × *Geum aleppicum* Jacq. n = 21
53. *Geum riojense* Bolle n = 42 × *Geum rivale* L. n = 21
54. *Geum riojense* Bolle n = 42 × *Geum laciniatum* Murr. n = 21
55. *Geum Fauriei* Lev. n = 42 × *Geum rivale* L. n = 21
56. *Geum Fauriei* Lev. n = 42 × *Geum silvaticum* Pourr. n = 21
57. *Geum Fauriei* Lev. n = 42 × *Geum macrophyllum* Willd. n = 21
58. *Geum Fauriei* Lev. n = 42 × *Geum urbanum* L. n = 21
59. *Geum Fauriei* Lev. n = 42 × *Geum aleppicum* Jacq. n = 21
60. *Geum Fauriei* Lev. n = 42 × *G. perincisum* Rybd. n = 21

4) Between deca- and hexaploid species

61. *Geum rivale* L. n = 21 × *Geum Quellyon* Sweet n = 35
62. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum Quellyon* Sweet n = 35
63. *Geum Quellyon* Sweet n = 35 × *Geum silvaticum* Pourr. n = 21
64. *Geum Quellyon* Sweet n = 35 × *Geum canadense* Jacq. n = 21
65. *Geum Quellyon* Sweet n = 35 × *Geum laciniatum* Murr. n = 21

66. *Geum Quellyon* Sweet n = 35 × *Geum boliviense* Focke n = 21

5) Between hexaploid species

67. *Geum rivale* L. n = 21 × *Geum urbanum* L. n = 21
68. *Geum rivale* L. n = 21 × *Geum coccineum* Sibth. et Sm. n = 21
69. *Geum rivale* L. n = 21 × *Geum silvaticum* Pourr. n = 21
70. *Geum rivale* L. n = 21 × *Geum molle* Vis. et Panc. n = 21
71. *Geum rivale* L. n = 21 × *Geum hispidum* Fr. n = 21
72. *Geum rivale* L. n = 21 × *Geum aleppicum* Jacq. n = 21
73. *Geum rivale* L. n = 21 × *Geum canadense* Jacq. n = 21
74. *Geum rivale* L. n = 21 × *Geum laciniatum* Murr. n = 21
75. *Geum rivale* L. n = 21 × *Geum macrophyllum* Willd. n = 21
76. *Geum rivale* L. n = 21 × *Geum perincisum* Rydb. n = 21
77. *Geum rivale* L. n = 21 × *Geum oregonense* Rydb. n = 21
78. *Geum rivale* L. n = 21 × *Geum boliviense* Focke n = 21
79. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum urbanum* L. n = 21
80. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum molle* Vis. et Panc. n = 21
81. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum hispidum* Fr. n = 21
82. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum silvaticum* Pourr. n = 21
83. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum aleppicum* Jacq. n = 21
84. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum canadense* Jacq. n = 21
85. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum macrophyllum* Willd. n = 21
86. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum oregonense* Rydb. n = 21
87. *Geum coccineum* Sibth. et Sm. n = 21 × *Geum laciniatum* Murr. n = 21
88. *Geum silvaticum* Pourr. n = 21 × *Geum molle* Vis. et Panc. n = 21
89. *Geum silvaticum* Pourr. n = 21 × *Geum hispidum* Fr. n = 21

90. *Geum silvaticum* Pourr. n = 21 × *Geum aleppicum* Jacq. n = 21
91. *Geum silvaticum* Pourr. n = 21 × *Geum macrophyllum* Willd. n = 21
92. *Geum urbanum* L. n = 21 × *Geum molle* Vis. et Panc. n = 21
93. *Geum urbanum* L. n = 21 × *Geum hispidum* Fr. n = 21
94. *Geum urbanum* L. n = 21 × *Geum aleppicum* Jacq. n = 21
95. *Geum urbanum* L. n = 21 × *Geum canadense* Jacq. n = 21
96. *Geum urbanum* L. n = 21 × *Geum macrophyllum* Willd. n = 21
97. *Geum urbanum* L. n = 21 × *Geum oregonense* Rydb. n = 21
98. *Geum urbanum* L. n = 21 × *Geum perincisum* Rydb. n = 21
99. *Geum urbanum* L. n = 21 × *Geum laciniatum* Murr n = 21
100. *Geum molle* Vis. et Panc. n = 21 × *Geum hispidum* Fr. n = 21
101. *Geum molle* Vis. et Panc. n = 21 × *Geum aleppicum* Jacq. n = 21
102. *Geum molle* Vis. et Panc. n = 21 × *Geum canadense* Jacq. n = 21
103. *Geum molle* Vis. et Panc. n = 21 × *Geum macrophyllum* Willd. n = 21
104. *Geum hispidum* Fr. n = 21 × *Geum aleppicum* Jacq. n = 21
105. *Geum hispidum* Fr. n = 21 × *Geum canadense* Jacq. n = 21
106. *Geum hispidum* Fr. n = 21 × *Geum macrophyllum* Willd. n = 21
107. *Geum hispidum* Fr. n = 21 × *Geum laciniatum* Murr. n = 21
108. *Geum aleppicum* Jacq. n = 21 × *Geum canadense* Jacq. n = 21
109. *Geum aleppicum* Jacq. n = 21 × *Geum macrophyllum* Willd. n = 21
110. *Geum aleppicum* Jacq. n =21 × *Geum oregonense* Rydb. n = 21
111. *Geum aleppicum* Jacq. n = 21 × *Geum laciniatum* Murr. n = 21
112. *Geum aleppicum* Jacq. n = 21 × *Geum boliviense* Focke n = 21
113. *Geum macrophyllum* Willd. n = 21 × *Geum canadense* Jacq. n = 21

114. *Geum macrophyllum* Willd. n = 21 × *Geum laciniatum* Murr. n = 21
115. *Geum macrophyllum* Willd. n = 21 × *Geum oregonense* Rydb. n = 21
116. *Geum macrophyllum* Willd. n = 21 × *Geum perincisum* Rydb. n = 21
117. *Geum perincisum* Rydb. n = 21 × *Geum oregonense* Rydb. n = 21
118. *Geum laciniatum* Murr. n = 21 × *Geum oregonense* Rydb. n = 21.
119. *Geum laciniatum* Murr. n = 21 × *Geum perincisum* Rydb. n = 21
120. *Geum canadense* Jacq. n = 21 × *Geum laciniatum* Murr. n = 21
121. *Geum canadense* Jacq. n = 21 × *Geum boliviense* Focke n = 21

The hybrids listed above do not exhaust all the possibilities of obtaining interspecific hybrids between the species considered here. Especially in the case of *Eugeum* species hybrids may quite certainly be obtained between any two parent species regardless of chromosome numbers or morphological relations. Likewise, between *Geum* subgenera a greater number of hybrids can be obtained by further pollinations. Anyway, this list of 121 hybrids shows that in the genus *Geum* the ability to produce interspecific hybrids is very high. Among the parent species of the hybrids listed above *Geum virginianum* and *Geum japonicum* are not mentioned as the two species begin to flower much later in the year than the others in my cultures and because of this it is very difficult to obtain hybrids with them. However, lately a cross between *G. japonicum* and *G. coccineum* has been succesful, but the hybrids have not flowered so far and consequently are not listed.*

In the majority of crosses both reciprocal hybrids were obtained. There were no significant differences in any of the reciprocal hybrid pairs. Because of this the order of listing the parent forms is arbitrary and the descriptions, unless otherwise stated, refer to both reciprocal hybrids. The F_1 hybrid populations were in most cases uniform and only in the few instances when the parent forms were heterozygous segregation in respect to some characters was manifested in F_1 hybrids. This will be noted in the detailed descriptions.

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* Note during correction: this hybrid flowered this year, it is partially fertile and with nearly normal meiosis.

The viability of the hybrids varied greatly ranging from sublethal to marked hybrid heterosis. Their fertility was also of various degrees from complete sterlity to almost normal fertility. The expression of morphological characters was either intermediate between the parent forms or some characters of the parent species were entirely dominant.

Because of the very large number of the crosses it seems that a description of all the hybrids is unnecessary. Thus in this chapter the descriptions will refer to all intersubgeneric hybrids and to the more characteristic hybrids chosen from among the numerous intra-subgeneric ones, with special reference to the crosses within subgenus *Eugeum*. In the list of hybrids there are as many as 22 hybrids of *G. rivale* with other *Geum* species. This species thus serves here as an analysing factor with which species from various subgenera and with various chromosome numbers are crossed. For this reason *G. rivale* hybrids will be described in more detail to make comparisons possible. In the case of many other hybrids, primarily in the case of these from subgenus *Eugeum,* only a very brief note will be made on their fertility, viability or meiosis.

Meiosis was observed more or less accurately in almost all the hybrids. In various hybrids between related species meiosis developed in almost exactly the same manner so that a detailed description will be made in some cases only.

Further hybrid generations obtained from such F_1 hybrids as proved partially fertile will be described in the next chapter.

The order of the descriptions which now follow is the same as in the list of the crosses on pages 109—114. In the largest group of 91 hybrids from subgenus *Eugeum* the division into groups according to the polyploidy of the parent species will be maintained. This method of classifying species and hybrids is of course absolutely arbitrary. However, as in many respects a division within the subgenus *Eugeum* into sections or series does not agree with cytogenetic data, the more natural division of *Eugeum* species into related groups will not be made till at the end of this work when the whole available evidence is reviewed.

Only in the case of the large group of 55 hybrids obtained between hexaploid species the descriptions are arranged according to the degree of hybrid fertility, i.e. beginning from the most sterile and ending by the most fertile. Here the order of description will not agree with the list of crosses.

INTERGENERIC HYBRIDS

I have not succeeded as yet in obtaining intergeneric hybrids between *Geum, Coluria* and *Waldsteinia,* though I do not think that this is absolutely impossible. During several years attempts were made at obtaining the following hybrids: *G. rivale* with *Waldsteinia geoides* and *ternata* in both reciprocal directions; *G. coccineum* with *Waldsteinia geoides*; *G. heterocarpum* with *Waldsteinia geoides* and *ternata* in both directions; *G. heterocarpum* and *G. rivale* with *Coluria geoides; G. montanum* with *Waldsteinia geoides* and *Coluria geoides* in both directions; and *Waldsteinia geoides* and *ternata* with *Coluria geoides* in both directions. In some crosses as for instance *Waldsteinia geoides* × *Coluria geoides* and *Geum rivale* × *Waldsteinia ternata* achenes developed at first but degenerated at a later stage. This indicates that in these cases the pollen is probably capable of fertilization, but the development of the embryo or of the endosperm is later inhibited. Consequently, it seems possible that by experimenting with a larger number of biotypes used for interspecific crosses and by creating different conditions of cultivation seeds capable of germination will be obtained. However, it may also be that in the tribe of *Geeae* there are among genera absolute intersterility barriers and, therefore, this would be a diagnostic character in the tribe for distinguishing genera from subgenera. It has already been mentioned that Bolle considers such subgenera as for instance *Erythrocoma* as separate genera and Juzepchuk assigns *G. heterocarpum* and *Geum speciosum* to two different genera: *Orthurus* and *Woronowia.* But as species from subgenera *Erythrocoma, Orthurus* and *Woronowia* can be crossed with species from subgenus *Eugeum* they are here included in the genus *Geum.* If in future the same will be demonstrated for subgenera *Sieversia, Neosieversia, Oncostylus* and *Acomastylis,* then the taxonomic division of the genus *Geum* into subgenera suggested here will also be supported by biological evidence. Unfortunately my cultures did not include the first three of the subgenera just mentioned and *G. Rossii,* the only species from subgenus *Acomastylis,* flowered so poorly that it was impossible to attempt any more extensive crosses with species from other *Geum* subgenera. The few attempts in that direction gave no results.

In the rose family there are recorded instances of intergeneric hybrids primely in the subfamily of *Pomoideae*, e. g. between *Crataegus* and *Mespilus, Sorbus* and *Aronia, Sorbus* and *Amelanchier* and *Sorbus* and *Pyrus,* thus of course the ability or disability to produce hybrids is not by itself a sufficient argument for or against generic status. However, arguments of this kind in connection with those of morphological and geographical nature may assume in such considerations a rather important significance.

Finally, in this connection I wish to mention briefly a remarkable report by A. Guillaumain and A. Eichhorn (1936) in which those authors state that they obtained from M. Gossot a supposed hybrid of *G. coccineum* Sibth. et Sm. with *Potentilla nepalensis* Hook. This "intergeneric" hybrid proved to be something different from what was supposed by Gossot who had produced the cross. Guillaumain and Eichhorn supposed that perhaps this was some unidentified *Geum* hybrid. I myself have made several attempts of pollinating *Geum* species with pollen from various *Potentilla* species and have never obtained any results whatsoever.

HYBRIDS WITHIN THE GENUS *GEUM*

This description of interspecific *Geum* hybrids begins by crosses between species from various subgenera. In his monograph of *Geum* Bolle (1933) writes that the only known hybrids of this type are between the subgenera *Oreogeum* and *Eugeum*. This fact was one of the causes which induced him to include *Oreogeum* species to the genus *Geum*, in spite of their considerable morphological differences with *Eugeum* species. Hybrids of *Oreogeum* and *Eugeum* species have long been known as the two subgenera co-exist in nature forming natural hybrids. Nevertheless, the fact that there has been till now no evidence of hybrids between other *Geum* subgenera and "genera" is no proof that such crosses are impossible, as nobody has previously undertaken systematic efforts to obtain such hybrids artificially and as the natural formation of these crosses is impossible because of the distribution of the parent species.

All earlier data on interspecific crosses within the genus *Geum* have been based on natural hybrids. These were at first classified as distinct species, as for instance in Scheutz's monograph (1870), but in most cases were later identified as mere interspecific hybrids.

Gärtner (1849) was the first to start crossing *Geum* species. He obtained a number of hybrids between the following species: *G. coccineum, G. rivale, G. urbanum, G. canadense, G. heterophyllum, G. macrophyllum,* and *G. ranunculoides*. However, it unfortunately is not quite clear what really were the species that Gärtner used and defined by these names. Focke (1881) believed that Gärtner's *G. heterophyllum* was in fact *G. virginianum* L., and that *G. macrophyllum* was *G. japonicum* Thbg., *G. ranunculoides* was *G. aleppicum* Jacq. var. *strictum* Ait., and *G. canadense* was *G. album* Gm. I myself do not think this opinion to be quite justified. From Gärtner's description of the species and of the hybrids it seems more likely that his *G. coccineum* was in fact *G. Quellyon,* his *G. rivale, urbanum, canadense,* and *macrophyllum* correspond well to the species described under these names in the present work. *G. ranunculoides* was probably — as supposed by Focke — *G. aleppicum*, while it is now difficult to decide what species was defined by Gärtner as "*G. heterophyllum*". Perhaps it was also *G. aleppicum*. In Bolle's opinion Gärtner's *G. canadense* was in fact merely a form of *G. aleppicum*. By assuming these corrected specific names the interspecific hybrids obtained by Gärtner would be thus: *G. Quellyon* × *urbanum, G. Quellyon* × *rivale, G. Quellyon* × *aleppicum, G. Quellyon* × *macrophyllum G. canadense* × *urbanum* (?), *G. canadense* × *rivale* (?), and *G. urbanum* × *rivale*. The hybrids without question mark were seen and controlled by Bolle in the herbarium at the University of Berlin. Few workers after Gärtner were concerned with *Geum* hybrids, though A. Gordon (1865) did probably obtain the hybrid *G. coccineum* × *urbanum*. The hybrid *G. rivale* × *urbanum* was afterwards frequently obtained and was investigated by Marsden-Jones (1930), Prywer (1932), Winge (1926) and others. A short note by Blaringhem (1926) on the hybrid of *G. rivale* with *G. montanum* completes the list of literature on artificially produced *Geum* hybrids which I have had access to. The fairly voluminous literature on natural hybrids will be reviewed separately.

A. Hybrids between various *Geum* subgenera

a. Subg. *Erythrocoma* × subg. *Oreogeum*

1. *Geum montanum* L. (14) × *G. triflorum* Pursh. (21), Fig. 39, culture no. 167—50. The hybrid was obtained in 1950 by pollinating a flower of *G. montanum* with pollen of *G. triflorum*. 36 seeds were obtained of which 16 germinated and only 5 plants reached the flowering stage. In the early stages of development the plants grew very slowly, but later those which survived developed rather vigorusly and flowered abundantly. The F_1 plants were undoubtedly much weaker than the pure parent species and showed no tendency for heterosis. The more important characters in the hybrids as compared with the parent spiecies were as in the table below.

The other hybrid characters not listed in the above table may be compared with the characters in the parent species on the corresponding drawings. The parent species differ considerably by the structure of the style which, although elongated and pennately haired in both, is much longer in *G. triflorum* (up to 57 mm) than in *G. montanum* (up to 29 mm). Moreover, in *G. triflorum* the stigmatic part is usually deciduous and in *G. montanum* it persists on the style. As the seeds of this hybrid are completely sterile the pistils do not develop and wither

Character	*G. montanum*	F_1	*G. triflorum*
Leaf shape	large terminal leaflet	intermediate	uniformly dissected
Stem	with 1 — 2 flowers	with 3 flowers	with 3 flowers
Floral peduncles	straight	drooping	drooping
Arrangement of calyx sepals and petals	horizontal	erect	erect
Petal size (mm)	16.8 x 15.7	13.2 x 9.4	8.8 x 4.7
Colour of petals	yellow	pale yellow	pale creamy
Disc	absent	intermediate	very pronounced
Stamen pubescence	glabrous	pubescent	pubescent
Segments of epicalyx (mm)	5.5	8	12
Anthocyanin in stems and calyx	none	intermediate	abundant
Stigmatic part of style	persistent	persistent (?)	deciduous

at a fairly early stage, it is thus impossible to examine exactly their final length and to observe the behaviour of the stigmatic part which is not shed from the degenerated pistils of the F_1 hybrid. Pollen fertility of the hybrid is also very low. This and all the other hybrids were examined for pollen fertility in smears with acetocarmine and glycerine. In this case about 0.3 per cent of pollen grains were good and stained normally.

Cytological examination: — As *G. montanum* is a tetraploid and *G. triflorum* a hexaploid the hybrid ought to be a pentaploid with $2n = 35$. This somatic chromosome number was observed directly (Fig. 35). No adequate preparations showing meiotic prophase in PMCs were obtained. In numerous preparations from metaphase of the I-st division 5 to 7 bivalents and 25 to 21 univalents were found (Fig. 40). The bivalents are arranged on the equatorial plane and the univalents are scattered irregularly throughout the spindle. Out of the 23 PMCs examined at the M. I stage it was found that 2 had 5 bivalents and 25 univalents, 10 had 6 bivalents and 23 univalents and the remaining 11 had 7 bivalents and 21 univalents. At anaphase the bivalents move to the two poles while the univalents are still on the spindle. In late anaphase the univalents often form a more or less regular ring on the equatorial plate (Fig. 40 d). Some of the univalents are divided but the majority are merely strongly stretched out and then move undivided to one of the poles. The great numerical predominance of univalents and their lagging in anaphase often cause the formation of a restitution nucleus in telophase (Fig. 40 h), but in the majority of cases two separate nuclei are formed in telophase. In the few metaphases of the II-nd division in which both plates are seen *en face* the following chromosome numbers were found: 22 and 20, 18 and 19, 19 and 20. This means that the majority of univalents are segregated undivided and only few are split into two chromatids. In the more numerous cells at the metaphase II stage where it was possible to count the chromosomes in one of the two plates the numbers found ranged from 17 to 22. In spite of the considerable disturbances in the course of meiosis there are relatively few chromosomes lagging in the cytoplasm and not included in one of the daughter nuclei. At anaphase of the II-nd division some chromosomes also lag on the spindle. Out of the 128 cells analysed at the tetrad stage

Fig. 39. F$_1$ *Geum montanum* × × *G. triflorum;* a — growth habit of plant; b — top of flowering stem after anthesis; c — basal leaf; d — flower — top view; e — flower — side view; f — petal

there were 4 dyads with only two microspores. In the remaining cells there were always 4 microspores sometimes of unequal size.

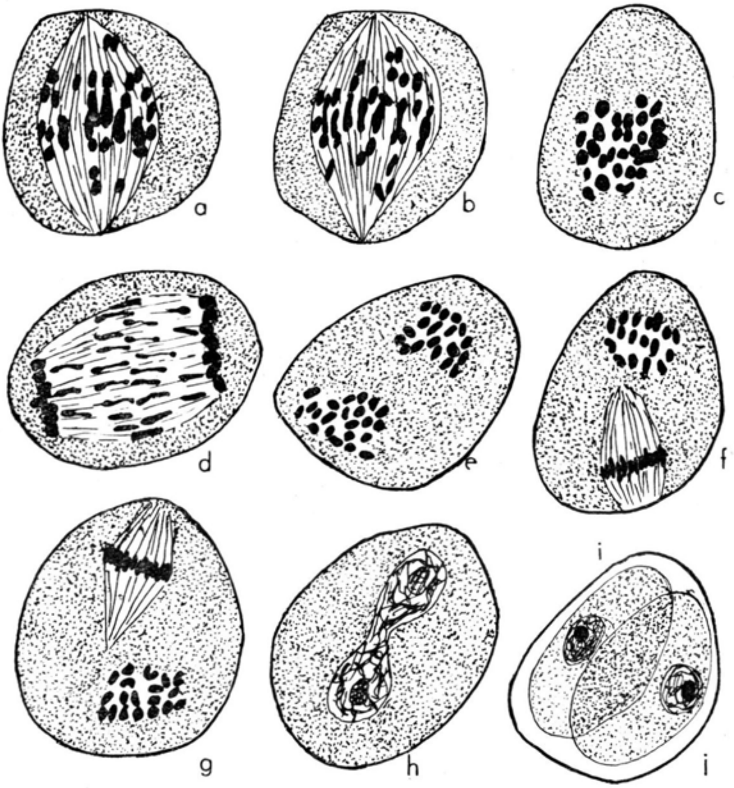

Fig. 40. F_1 *Geum montanum* × *G. triflorum,* meiosis in PMCs; a — M-I with 6 bivalents; b — M-I with 7 bivalents; c — M-I with 28 chromosomal bodies ($7_{II} + 21_{I}$), d — A-I with stretched out univalents segregating; e — M-II with 19 and 22 chromosomes in the plates; f — M-II with 17 chromosomes in a plate; g — M-II with 19 chromosomes in a plate; h — restitution nucleus; i — dyad

2. *Geum montanum* L. (14) × *G. campanulatum* Greene (21), culture no. 13—53. For the first time this hybrid flowered in 1955. Morphologically it resembles greatly the preceding one from which it differs only by more thickly dissected leaves and more vigorous growth. Floral stems are numerous, 25—30 cm tall, usually with 3 flowers and floral peduncles slightly drooping at anthesis. The plants are entirely covered by soft glandular hairs, the floral peduncles and the calyx are pigmented pink with anthocyanin. The flowers are closed, the petals erect, though less so than in *G. campanulatum,* and almost expanded after anthesis. The

petals are yellow, ovoid, 12 mm long and 11 mm wide. The stamens are numerous with pubescent filaments. The disc is residual, much weaker than in *G. campanulatum*. The other characters of the hybrid are intermediate between the parent forms. Young seedlings are strongly disturbed in their growth and difficult to cultivate, later however they grow vigorously and flower long and abundantly. The hybrid does not produce any fully developed seeds. The pollen is also degenerated and pollen grains staining normally in aceto-carmine are quite exceptional. The hybrid was not examined cytologically.

b. Subg. *Erythrocoma* × subg. *Eugeum.*

3. *Geum urbanum* L. (21) × *G. ciliatum* Pursh. (21), Fig. 41, culture no. 256—49. The hybrid was obtained in 1949 by pollinating *G. urbanum* with pollen from *G. ciliatium.* Two flowers were pollinated and 196 full seeds were obtained thus bringing the setting of seeds to 84 per cent. The seeds germinated in 91 per cent, but many seedlings were lost at an early stage through poor conditions and contamination with mildew. Only 63 plants were grown to flower. The F_1 plants form a very uniform population and are practically speaking exactly the same. They flower very abundantly producing large, strongly branched stems with more flowers than in *G. urbanum.* The more important characters of the hybrid are related with those of the parent species in the table below:

Character	*G. urbanum*	F_1	*G. ciliatum*
Leaf shape	lyrate	intermediate	uniformly dissected into narrow lobes
Stem	multifloral	multifloral	7 flowers
Floral peduncles	straight	± straight	drooping
Position of sepals	reflexed	expanded	erect
Position of petals	horizontal	expanded	erect
Size of petals (mm)	5.6 × 4.6	8.9 × 5.4	11.0 × 4.5
Disc	absent	± absent	very pronounced
Stamen pubescence	glabrous	glabrous	pubescent
Segments of epicalyx (mm)	2.5	8.2	12.5
Length of style (mm)	6	15	34
Presence of hook on rostrum	hooked	± absent	absent
Colour of petals	yellow	pale yellow	pale creamy

The hybrid is highly sterile and produces well developed pollen grains only in 0.2 per cent. During two years of flowering among several

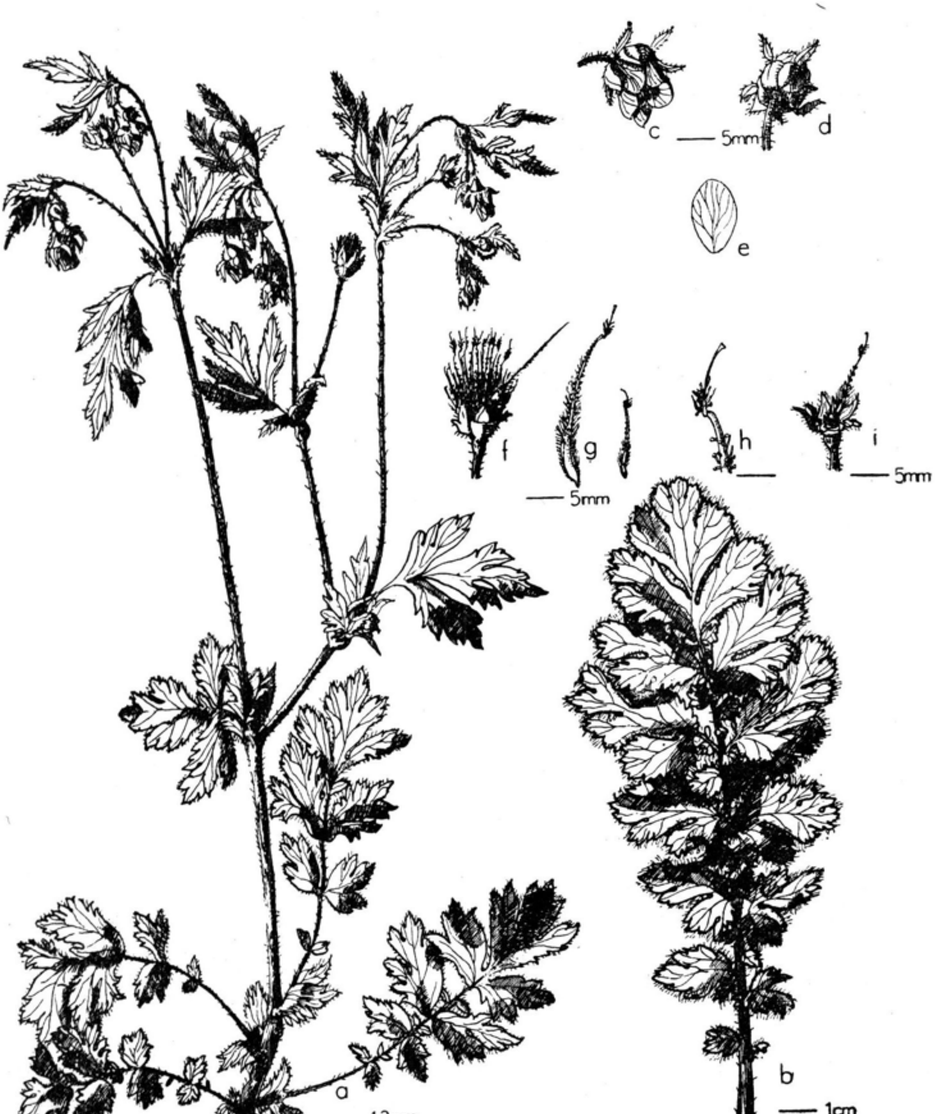

Fig. 41. F_1 *Geum urbanum* × *G. ciliatum;* a — growth habit of plant; b — basal leaf; c — flower — side view; d — flower — bottom view; e — petal; f — flower with one good achene; g — good and empty achenes; h — tip of rostrum and stigmatic part; i — receptacle with one achene

thousands flowers only serveral normally filled achenes with developed embryos were found. Unfortunately these seeds did not germinate. As unreduced gamets are formed in the hybrid it is not impossible that an amphidiploid progeny will be obtained some day.

Cytological examination: — The hybrid similarly as both the parent species is hexaploid. During reduction divisions from 7 to 14 bivalents and from 28 to 14 univalents are formed at metaphase of the I-st division (Fig. 42). In anaphase after the separation of the bivalent halfs the univalents form a fairly regular plate at the equatorial plane and begin to move to the two poles in late anaphase much later than the bivalents. Because of this in telophase restitution nuclei assembling all the chromosomes in one nucleus are frequently formed. After the second division there are nearly 10 per cent dyads among the tetrads. If from every dyad two viable pollen grains were to be formed then about 5 per cent of pollen grains would be effective. In fact it was found that there was only about 0.2 per cent of good pollen grains and this shows that even pollen grains formed from dyads are in most cases incapable of functioning.

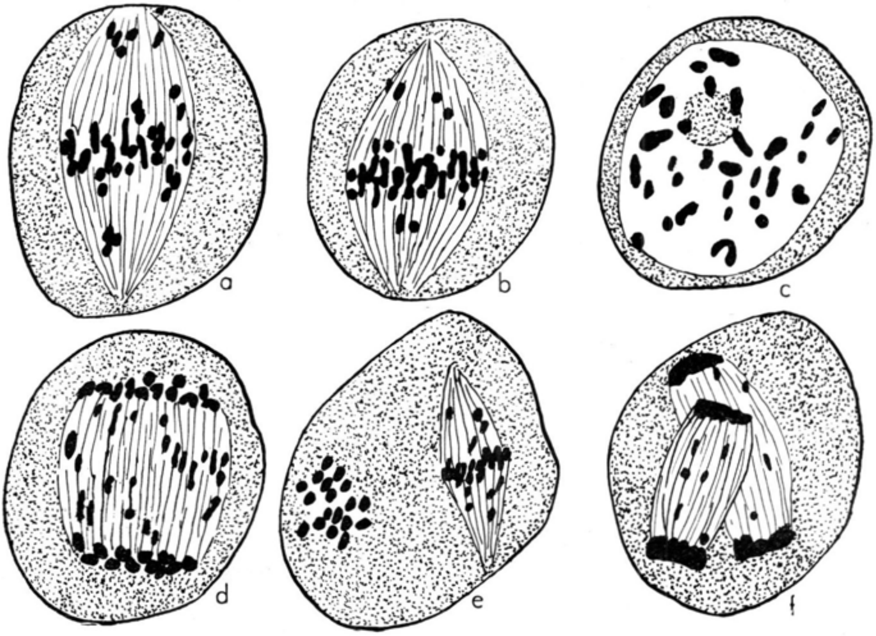

Fig. 42. F_1 *Geum urbanum* × *G. ciliatum*, meiosis in PMCs; a — M-I with 7 bivalents; b — M-I with 12 bivalents; c — diakinesis with 32 chromosomes ($10_{II} + 22_{I}$); d — A-I separating and dividing univalents; e — M-II with 18 chromosomes in a plate; f — A-II chromosomes lagging on the spindle

4. *Geum coccineum* Sibth. et Sm. (21) × *G. ciliatum* Pursh (21), Fig. 43, culture no. 257—49. This hybrid differs from the preceding one

in respect to those characters which differ *G. coccineum* from *G. urbanum*:

Character	*G. coccineum*	F_1	*G. ciliatum*
Basal leaves	large terminal leaflet	uniformly dissected	uniformly dissected in narrow lobes
Stem	3-5-floral	7-13-floral	7-floral
Floral peduncles	straight	recurved	recurved
Position of sepals	recurved	±erect later expanded	erect
Position of petals	horizontal	expanded	erect
Size of petals (mm)	13.0×14.3	11.8×7.2	11.0×4.5
Colour of petals	red	yellow	pale creamy
Segments of epicalyx (mm)	3.2	7.6	12.5

It is remarkable that the petals in the hybrid are yellow (Buttercup Yellow 5/1 according to the Horticultural Colour Chart), whereas, in *G. coccineum* the petals are red (Poppy-red according to the Horticultural Colour Chart) and in *G. ciliatum* pale creamy. The colour appearing in this hybrid is identical to the colour in the hybrid of *G. coccineum* and *G. rivale*. In the last mentioned the petals are similar in colour to those of *G. ciliatum*. This indicates that the colour of petals in *G. ciliatium* and *G. rivale* depends on the same factors, and these together with factors for petal colour introduced by *G. coccineum* produce the yellow pigment in the petals of the hybrid. The hybrid produces about 2.3 percent of good very big pollen grains, probably with an unreduced chromosome number. Though pollen fertility is here higher than in the preceding hybrid the seeds do not develop at all and during two years not even one normally developed achene was found on 15 F_1 plants.

Cytological examination: — Somatic chromosomes were not investigated. From analyses of meiosis in PMCs it appears that the hybrid, similarly as its parent species, is hexaploid, with 2n = 42. Meiosis develops here in a manner closely resembling the preceding hybrid (Fig. 44). In 14 cells analysed at metaphase of the I-st division I have found the following configurations:

$7_{II} + 28_{I}$ in 8 cells
$10_{II} + 22_{I}$ in 4 cells
$14_{II} + 14_{I}$ in 2 cells.

The later stages of meiosis are the same as in the preceding hybrid. Among 236 cells analysed at the tetrad stage there were 28 dyads and 6 tetrads with 2 additional cells. The remaining 202 cells were normal

Fig. 43. F₁ *Geum coccineum* × *G. ciliatum*; a — floral stem; b — floral stem after anthesis; c — basal leaf; d — flower — top view; e — flower — bottom view; f — petal

tetrads with four microspores. From the appearance of the tetrads it appears that the perecntage of pollen grains with the unreduced chromosome number should be about 6.2.

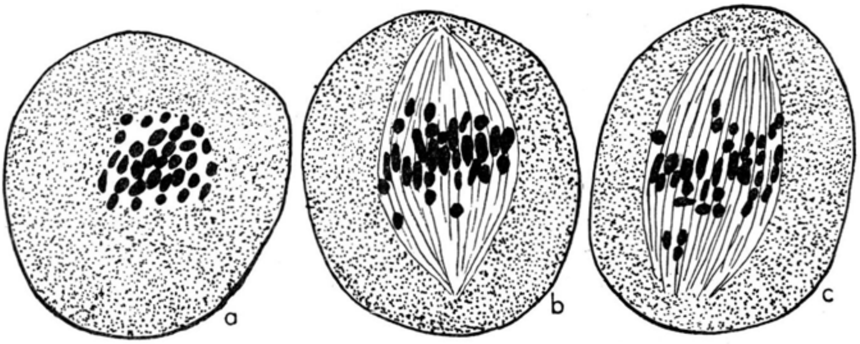

Fig. 44. F_1 *Geum coccineum* × *G. ciliatum*, meiosis in PMCs; a — M-I with 32 chromosomes ($10_{II} + 22_{I}$); b — M-I with 13 bivalents; c — M-I with 7 bivalents

5. *Geum rivale* L. (21) × *G. ciliatum* Pursh. (21), Fig. 45, culture no. 271—50. The more important characters of this hybrid and the corresponding ones of the parent species are as follows:

Character	*G. rivale*	F_1	*G. ciliatum*
Leaf shape	lyrate	intermediate	uniformly dissected into narrow lobes
Stem	3-5-floral	7-floral	7-floral
Size of petals (mm)	10.1 × 8.0	11.0 × 6.5	11.0 × 4.5
Petal shape	with claw and incision	no claw, gradually narrowed at base	no claw, gradually narrowed at base
Length of epicalyx segments (mm)	6.5	8	12.5
Length of gynophore (mm)	8-10	absent	absent
Disc	± absent	± absent	pronounced
Stamen filaments	glabrous	glabrous	pubescent

The hybrid, similarly as the parent species, has abundant anthocyanin in the stems and the calyx, floral peduncles strongly drooping, petals creamy, flowers closed, sepals and petals erect. Pollen fertility is very small ranging between 0.05 and 0.6 per cent in different smears. Normally developed seeds have not been found so far.

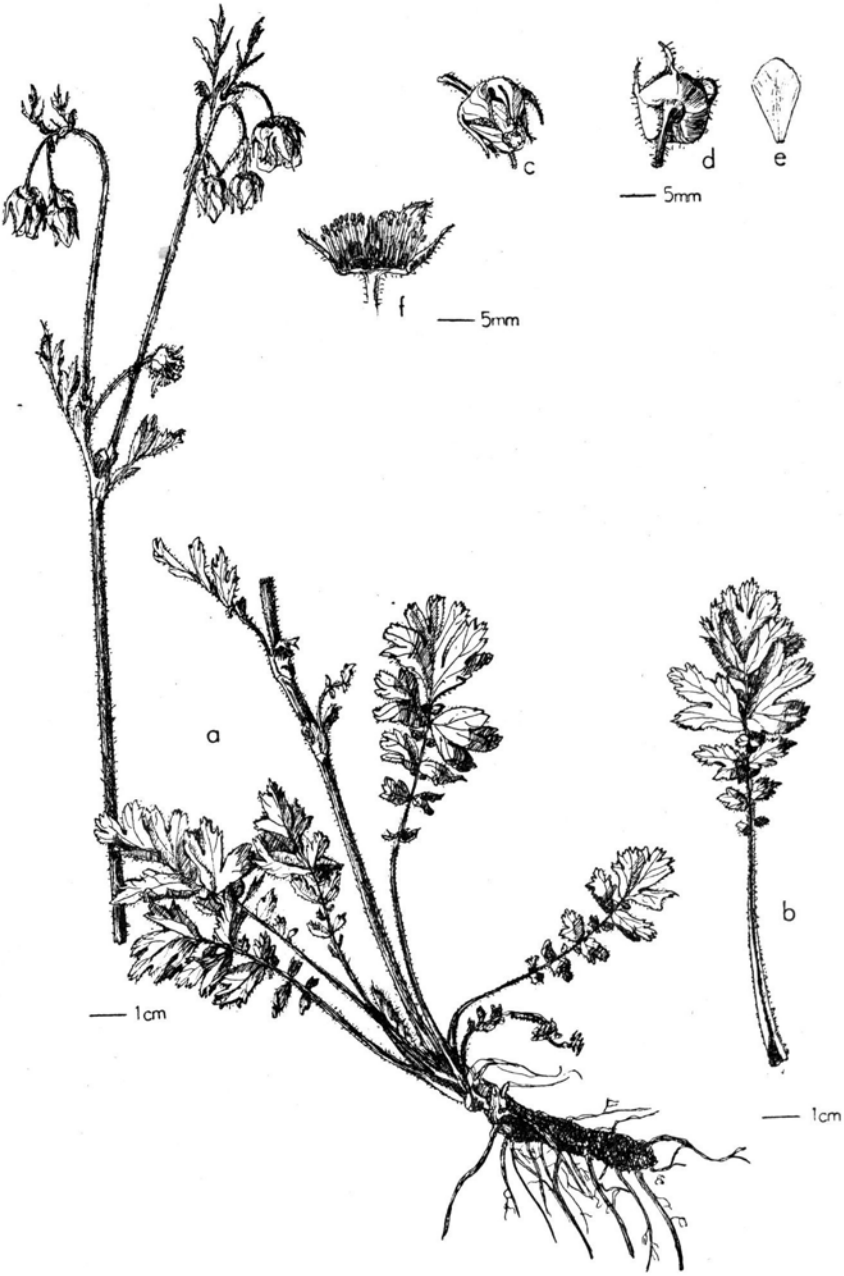

Fig 45. F_1 *Geum rivale* × *G. ciliatum;* a — growth habit of plant; b — basal leaf; c — flower — side view; d — flower — bottom view; e — petal; f — cross-section through flower

Cytological examination: — The hybrid is hexaploid with 2n = 42. In metaphase of the I-st division the number of bivalents varies between 11 and 14 (Fig. 46). In 26 analysed PMCs the following configurations were found:

$14_{II} + 14_{I}$ in 3 PMCs
$13_{II} + 16_{I}$ in 3 PMCs
$12_{II} + 18_{I}$ in 5 PMCs
$11_{II} + 20_{I}$ in 1 PMC
$10_{II} + 22_{I}$ in 2 PMCs
$9_{II} + 24_{I}$ in 5 PMCs
$8_{II} + 26_{I}$ in 4 PMCs
$7_{II} + 28_{I}$ in 3 PMCs.

In metaphase the univalents are irregularly dispersed throughout the spindle. In anaphase of the I-st division after the parting of the bivalents the univalents form a regular ring at the peripheries of the

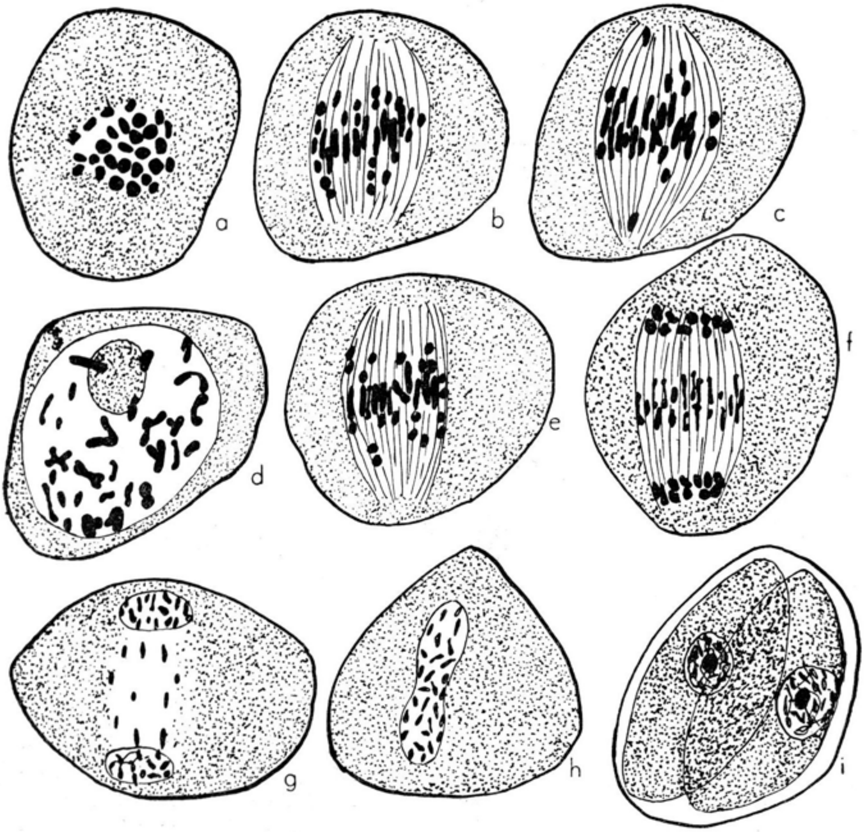

Fig. 46. F_1 *Geum ciliatum* × *G. rivale,* meiosis in PMCs; a — M-I with 28 chromosomes ($14_{II} + 14_{I}$); b — M-I with 10 bivalents; c — M-I with 14 bivalents; d — diakinesis with 14 bivalents and 14 univalents; e — M-I with 14 bivalents; f — A-I with univalents on the equatorial plane; g — T-I with lagging univalents; h — restitution nucleus; i — dyad

equatorial plane of the spindle. Usually the majority of the univalents move to the poles undivided and are often not included in the daughter nuclei. Because of the retarded segregation of the univalents restitution nuclei and then dyads are often formed (Fig. 46).

6. *Geum rivale* L. (21) × *G. triflorum* Pursh. (21), Fig. 47, culture no. 87—53. In the years 1954 and 1955 three specimens flowered. These

Fig. 47. F1 *Geum rivale* × *G. triflorum;* a — floral stem; b — basal leaf; c — flower — side view; d — flower — bottom view; e — petal

three plants are vigorous and flower abundantly. Their stems are 30—40 cm tall, with three flowers on strongly drooping peduncles. The upper part of the stem, the floral peduncles, the calyx, and partly the petals are strongly pigmented red-brown with anthocyanin. The whole stem is softly pubescent with glandular hairs beyond the middle. Cauline leaves are few, small, with terminal leaflet strongly and deeply incised. The basal leaves of the hybrid are intermediate in shape between the parent forms with lateral and terminal leaflets strongly dissected and sharply dentate. The calyx and the petals of the corolla are tightly closed as in *G. triflorum* and the long (7—8 mm) segments of the epicalyx are distinctly horizontally expanded. The petals are pale creamy, rounded at tip, elongated at base into a rudimentary claw, 9 mm long and 6 mm wide. The stamen filaments are naked and the disc is shaped into a small edge. The hybrid is completely sterile and produces no good achenes.

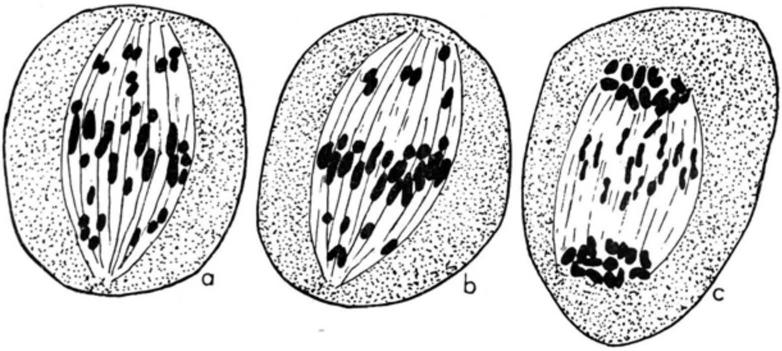

Fig. 48. F_1 *Geum rivale* × *G. triflorum*, meiosis in PMCs; a — M-I with 8 bivalents; b — M-I with 12 bivalents; c — A-I with univalents on the equatorial plane

Cytological examination: — This hybrid similarly as the preceding one produces at the M I stage in the PMCs 14 to 7 bivalents and a corresponding number of 14 to 28 univalents (Fig. 48). The most frequent are cells with between 8 and 12 bivalents. In metaphase the univalents are scattered all over the spindle and in anaphase after the separation of the bivalents the univalents form a fairly regular plate or ring on the equatorial plane. Usually the univalents are not divided in the first division but part unsplit to the poles. Sometimes not all are included in the daughter nuclei and they then remain in the cytoplasm where they are usually resorbed. In about 2 to 5 per cent of PMCs at the stage of telophase or interkinesis of the I-st division restitution nuclei are found and these give rise in the second division to dyads which constitute usually about 3—4 per cent of all PMCs at the tetrad stage.

c. subg. *Orthurus* × subg. *Eugeum*

7. *Geum coccineum* Sibth. et Sm. (21) × *G. heterocarpum* Boiss. (14), Fig. 49, culture no. 63—48. This hybrid was obtained in 1947 by pollinating *G. coccineum* with pollen from *G. heterocarpum*. From one flower 84 seeds were collected, which brought the setting of seeds to about 80 per cent. Of these seeds 56 germinated and 42 plants were brought to the flowering stage. The F_1 hybrids were very uniform, grew vigorously and flowered abundantly every year for 5 years. In the climate prevailing at Warsaw *G. heterocarpum* often freezes in winter but the hybrid similarly to *G. coccineum* is completely frost resistant. The more important characters of the hybrid in relation to the parent species are tabulated below:

Character	*G. heterocarpum*	F_1	*G. coccineum*
Leaf shape	terminal leaflet deeply incised	intermediate	terminal leaflet shallowly crenate
Stem	dichasium with 11-17 flowers	cyme with 5-7 flowers	monochasium with 3-7 flowers
Calyx	hypanthium campanulate, sepals erect	hypanthium small, sepals horizontal,	hypanthium small, sepals reflexed
Colour of petals	pale yellow	orange	red
Size of petals (mm)	4.9×4.8	11.4×11.6	13.0×14.3
Length of gynophore (mm)	11.5	absent	absent
Number of achenes	12.6	80-100	150-180
Hook on rostrum	no hook	obscure hook	hook distinctly formed
Bristles on rostrum	present	none	none

The other characters not listed in the table above may be compared on Figs. 12, 30 and 49 which show the two parent species and the F_1 hybrid. The two parental species differ so much in almost all structural details of leaves, stems, flowers and fruit that it is difficult to compare exactly all the characters. The main differences, however, refer to the structure of flowers and fruit. *G. heterocarpum* has fruit with straight rostrum terminated by a tuft of down-pointing bristly papillae. At the tip of the style there is a short stigmatic part, deciduous when the fruit begin to ripen. *G. coccineum* similarly as all species of subgenus *Eugeum* has styles with a rostrum hooked at the tip from which the deciduous stigmatic part grows out. In the completely sterile hybrid the young pistils dry up quite early and their size cannot be compared with the pistils in the parent species, but on the young styles it can be seen that

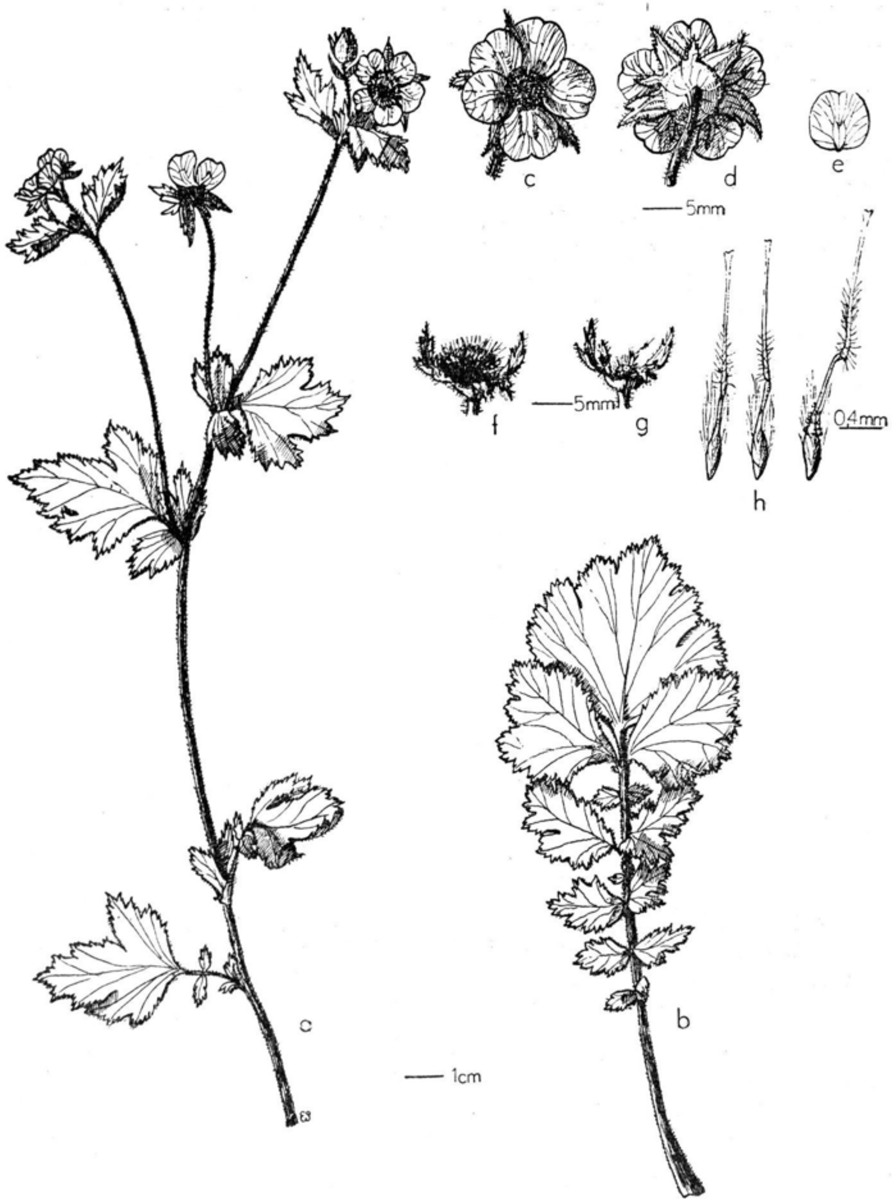

Fig. 49. F_1 *Geum coccineum* × *G. heterocarpum;* a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — cross-section of flower; g — receptacle with one achene; h — young undeveloped achenes

papillae characteristic for *G. heterocarpum* are not formed. Neither is the typical hook and only the tip of the rostrum is slightly bent so that the stigmatic part is situated almost directly in line with the rostrum.

In *G. heterocarpum* the achenes are arranged in a very characterstic manner, i.e. 10—12 achenes are inserted radially on the receptacle which exserts above the calyx tube on a 10—12 mm long gynophore. One achene is inserted on the floral base at the base of the gynophore and another achene is sometimes inserted on the gynophore itself. In *G. coccineum* there is no gynophore and the very numerous achenes — there may be as many as 160 — are inserted on a cylindrical receptacle. In the hybrid there is no trace of gynophore and the numerous achenes (about 100—130) are inserted similarly as in *G. coccineum* on an elongated receptacle growing out directly from the floral base.

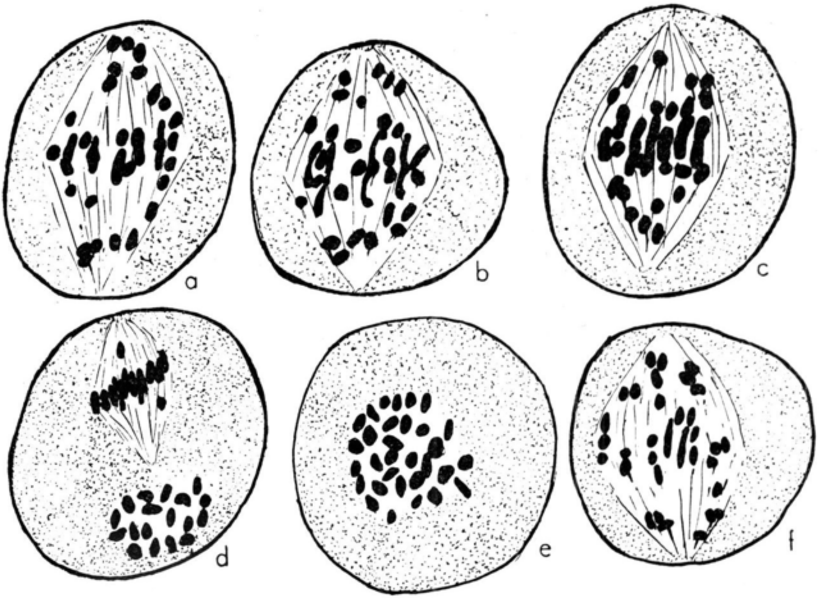

Fig 50. F_1 *Geum coccineum* × *G. heterocarpum,* meiosis in PMCs; a — M-I with 5 bivalents; b — M-I with 4 bivalents; c — M_1 with 7 bivalents; d — M-II with 18 chromosomes in plate; e — M-I with 30 chromosomes ($5_{II} + 25_{I}$)

The pollen fertility of the hybrid is very low, amounting to between 0.8 and 1.2 per cent of well developed pollen grains which stain normally in aceto-carmine. During four years from many thousands flowers of F_1 plants not one seed capable of germination was collected.

Cytological examination: — As *G. heterocarpum* is a tetraploid and *G. coccineum* a hexaploid the hybrid ought to be a pentaploid with 2n = 35. This number was not confirmed in preparations from root tips but can be deduced from the course of meiosis in PMCs (Fig. 50). In the case of this hybrid numerous preparations of PMCs at metaphase of the I-st division were obtained. In 34 of the analysed cells the following configurations were found:

$7_{II} + 21_{I}$ in 6 PMCs
$6_{II} + 23_{I}$ in 3 PMCs
$5_{II} + 25_{I}$ in 15 PMCs
$4_{II} + 27_{I}$ in 3 PMCs
$3_{II} + 29_{I}$ in 4 PMCs
$2_{II} + 31_{I}$ in 3 PMCs.

It follows that in the majority of cells 5 to 7 bivalents are formed while in some cells the number of bivalents may be smaller and even drop to two only. Unfortunately the stages from anaphase to metaphase of the second division were not found in preparations from this hybrid. In 7 cells at metaphase of the II-nd division it was possible to count the chromosomes in one of the two metaphasal plates. The following numbers were observed: 17 chromosomes in 2 plates, 20 in 1 plate, 19 in 1 plate, ± 25 in 1 plate, 23 in 1 plate, and about 12 chromosomes in 1 plate. Frequently at metaphase of the II-nd division several chromosomes remain on the spindle outside the plate and quite often also in anaphase some chromosomes lag on the spindle, while the remaining are already forming two groups at the poles of the spindle. In one case a cell was seen in which serval chromosomes formed something like a third additional plate with a small spindle of its own. In spite of these rather numerous irregularities in the course of meiosis in this hybrid an astounding majority of tetrads has a normal appearance with four microspores. Among 128 examined tetrads only 3 were dyads with 2 microspores. The presence of dyads indicates that also in this hybrid, similarly as in the case of the preceding ones, restitution nuclei are probably formed.

d. Subg. *Woronowia* × subg. *Eugeum*

8. *Geum speciosum* Alboff (35) × *G. rivale* L. (21)

9. *Geum speciosum* Alboff (35) × *Geum pyrenaicum* Willd. (42).

In 1955 both these hybrids were in their third vegetative season and in spite of this they did not yet produced floral stems. They produce, however, fairly well developed and healthy loking rosettes of basal leaves. It may be that the plants will flower in future years, as *G. speciosum* is a species which generally grows slowly and does not flower till several years after it had been sown out. On the other hand it also is possible that as a result of the union of two different genomes the plants have altogether lost the capacity to produce flowers. Cytological examination of the hybrids referred to root tips. In the hybrid first mentioned 56 chromosomes were found which equals the sum of the haploid chromosome numbers in the two parental species (Fig. 35, h).

In the other hybrid the number 2n = 77 (Fig. 34, I) was found as expected.

e. Subg. *Eugeum* × subg. *Stylipus*

10. *G. urbanum* L. (21) × *G. vernum* Torr. et Gray (21), Fig. 51, culture no. 71—49. Morphological differences between subgenera *Eugeum* and *Stylipus* are relatively small. The structure of the style is in both exactly the same. *G. vernum,* the only species of the monotypic subgenus *Stylipus,* is characterized primely by flowers exceptionally small for this tribe and the absence of the epicalyx. So far I have succeeded in obtaining without much difficulty hybrids of *G. vernum* with several species from subgenus *Eugeum.*

In 1948 three flowers of *G. vernum* were pollinated with pollen of *G. urbanum* and 200 good seeds were thus obtained. The setting of seeds in this case was about 70 per cent. Out of the great number of seedlings obtained from these seeds not all could be kept for lack of space and only 50 were transplanted. From these 43 grew up to the flowering stage. The F_1 plants show marked heterosis, the stems grow to the length of 1 m, the basal leaves reach 32 cm in length and the size of the terminal leaflet is 14 × 17 cm exceeding greatly the size of leaves in the parent species. The shape of basal leaves in *G. vernum* is very variable. The first leaves in spring have a terminal leaflet strongly dissected so that the leaf seems to be uniformly pinnatifid. In later leaves the terminal leaflet gradually increases, is less incised and simultaneously the number of lateral leaflets is reduced. The last autumn leaves have frequently only one large, round terminal leaflet. In *G. urbanum* the leaves are usually lyrate with terminal leaflets cuneate at base, dissected into three lobes. In the hybrid the leaf shape changes similarly as in *G. vernum* but the terminal leaflet is always dissected into three segments. In the table below the hybrid is compared with the parent species in respect to some important characters.

The fertility of the hybrid is very low. In pollen fertility is about 1,7 per cent and the proportion of good seeds is about 0.3 per cent. No F_2 plants have so far been obtained from these seeds.

Cytological examination: — Both parent species are hexaploids with 2n = 42. Somatic chromosomes of the hybrid were not investigated, but from the course of meiosis it is apparent that the hybrid is also a hexaploid. At metaphase of the I-st division there are 7 to 12 bivalents and respectively 28 to 18 univalents (Fig. 52). The bivalents are arranged in the equatorial plane and the univalents are scattered throughout the spindle. In early anaphase the bivalents part and the univalents move to the equatorial plane and form a ring in the

Character	*G. urbanum*	F_1	*G. vernum*
Stem	normal cyme	pseudodichotomic cyme	pseudodichotomic cyme
Glandular hairs	none	none	present
Floral peduncles	straight	drooping	drooping
Stipules	large	small	small
Anthocyanin in stems	none	present	present
Length of calyx sepals (mm)	7.2	4.4	2.8
Length of epicalyx (mm)	3.1	1.2	absent
Petal size	5.8 × 4.6	4.3 × 3.4	2.3 × 1.7
Colour of petals	yellow	yellow	pale yellow
Length of gynophore (mm)	absent	1 — 1.5	5.8
Number of achenes	150 — 200	about 100	30 — 60
Length of achenes (mm)	6	3.5 — 4	3.5
Length of rostrum (mm)	6 — 7	3.5	2
Length of receptacle (mm)	6 — 7	2 — 3	1.5
Pubescence of receptacle	long	± glabrous	± glabrous

outer layers of the spindle. In late anaphase when the bivalents are already arranged in two compact groups at the poles of the spindle the separation of the univalents begins. This separation has an abnormal course. The univalents are strongly stretched out and in the form of thick grains connected by thin threads begin to move undivided to the poles. The separation of the univalents is greatly retarded in respect to the bivalents and consequently the univalents do not often reach in time the daughter nuclei which have meanwhile formed a surrounding membrane and entered the telophase stage. If the telophase changes begin at the time when the majority of univalents are still spread along the spindle between the daughter nuclei, then a restitution nucleus is formed (Fig. 52, e).

During the second division two metaphasal plates are visible. The chromosome numbers in the plates differ and often there are also several chromosomes in the cytoplasm outside the plates. Sometimes in the M. II stage one large plate containing all the chromosomes is formed. Such a plate probably arises from the restitution nucleus formed in the first division. Among 150 PMCs analysed in the tetrad stage there were 4 dyads.

11. *G. macrophyllum* Willd. (21) × *G. vernum* Torr. et Gray. (21)
12. *G. perincisum* Rydb. 21) × *G. vernum* Torr. et Gray. (21)
13. *G. oregonense* Rydb. (21) × *G. vernum* Torr. et Gray. (21)
14. *G. aleppicum* L. (21) × *G. vernum* Torr et. Gray. (21).

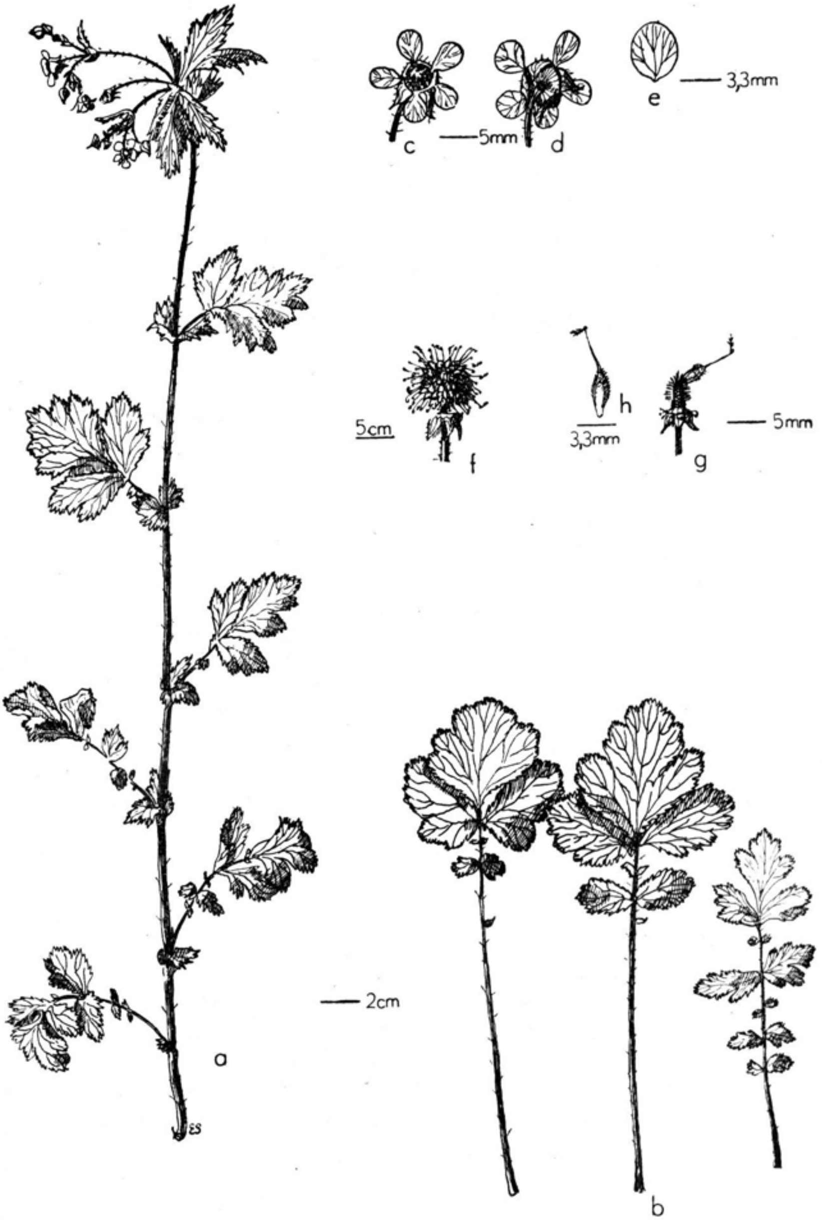

Fig. 51. F_1 *Geum urbanum* × *G. vernum*; a — floral stem; b — basal leaves; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

All these four hybrids morpholigicaly resemble greatly the hybrid *G. urbanum* × *G. vernum*, but differ slightly by the shape of leaves and the size of sepals and petals. The hybrids display heterosis in a considerable degree. For instance the hybrid *G. macrophyllum* × *G. vernum* produces in autumn enormous basal leaves with only one terminal leaflet 20 cm long and 22 cm wide. In none od the *Geum* species and hybrids which I examined did I see so large leaves.

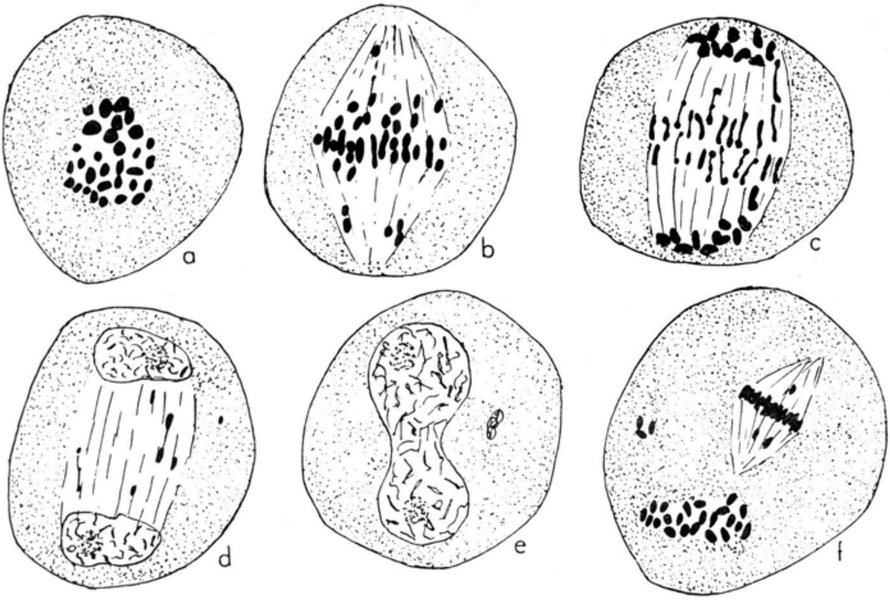

Fig. 52. F₁ *Geum urbanum* × *G. vernum*, meiosis in PMCs; a — M-I with 31 chromosomes ($11_{II} + 20_{I}$); b — M-I with 7 bivalents; c — A-I with stretched out univalents on the equator of the spindle; d — T-I with lagging univalents; e — restitution nucleus; f — M-II with 22 chromosomes in one of the plates

The hybrids with *G. macrophyllum*, *perincisum* and *oregonense* have no epicalyx similarly as the parental species *G. vernum*. The length of sepals is about 4 mm and the petals are somewhat smaller than in the hybrid with *G. urbanum* (4.1 × 3.0 mm). This is probably in connection with the smaller petals in the parent species of this hybrid as compared with the petals in *G. urbanum*. The hybrid with *G. aleppicum* has sepals about 4 mm long, epicalyx 1 to 1.5 mm long and petals 4.5 by 4.0 mm. In other characters the four hybrids rather resemble one another. The fertility of the hybrid with *G. aleppicum* is 1.2 and 0.25 per

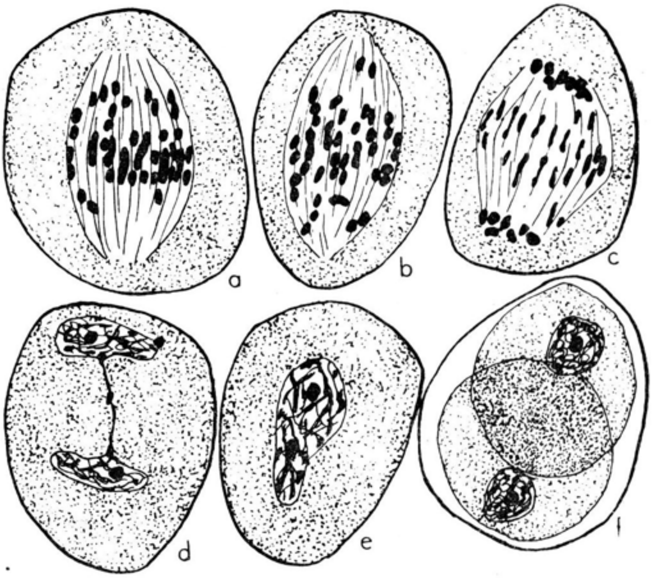

Fig. 53. F$_1$ *Geum macrophyllum* × *G. vernum,* meiosis in PMCs; a — M-I with 6 bivalents; b — M-I with 3 bivalents; c — A-I with univalents on the equator of the spindle; d — T-I with chromosomal bridge; e — restitution nucleus; f — dyad

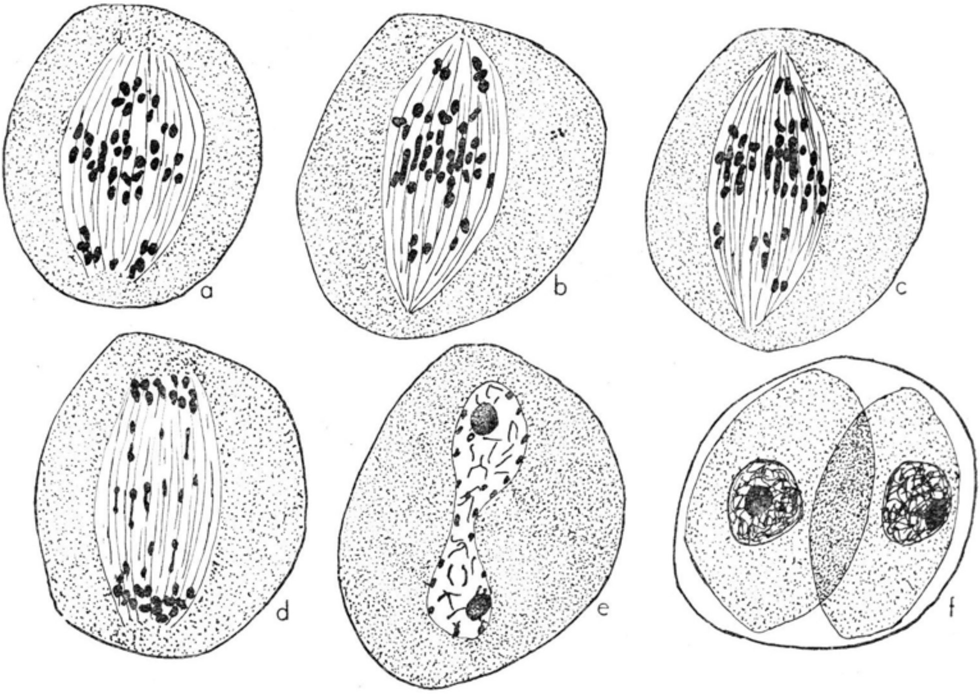

Fig. 54. F$_1$ *Geum oregonense* × *G. vernum,* meiosis in PMCs; a — M-I with one bivalent; b — M-I with 4 bivalents; d — A-I with univalents on the spindle; e — restitution nucleus; f — dyad

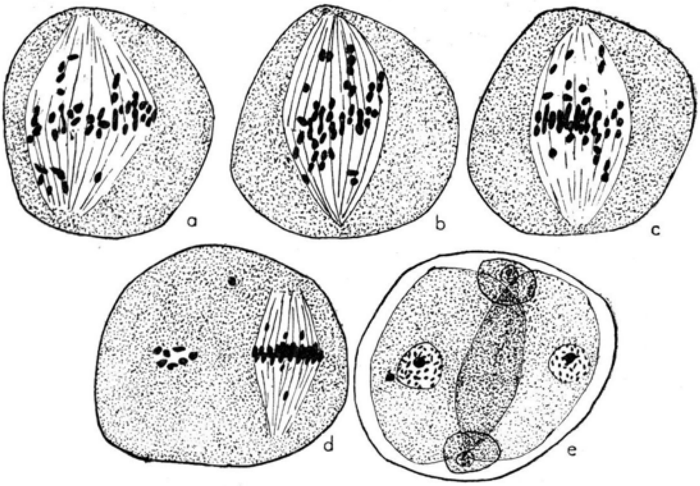

Fig. 55. F_1 *Geum perincisum* × *G. vernum,* meiosis in PMCs; a — M-I with 3 bivalents; b — M-I with 4 bivalents; c — M-I with 7 bivalents; d — M-II in restitution nucleus, one chromosome lost in cytoplasm and 6 chromosomes forming small extra plate; e — dyad with a pair of small microspores

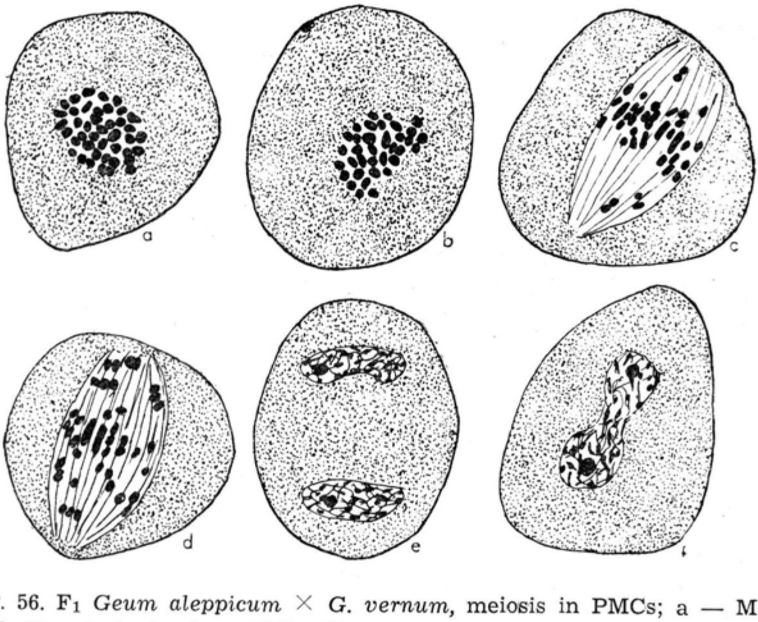

Fig. 56. F_1 *Geum aleppicum* × *G. vernum,* meiosis in PMCs; a — M-I with 42 univalents; b — M-I with 35 chromosomes ($7_{II} + 28_{I}$); c — M-I with 6 bivalents; d — M-I with 2 bivalents; e — normal A-I; f — restitution nucleus in A-I

cent for pollen and seeds respectively. The hybrids with *G. macrophyllum, G. perincisum* and *G. oregonense* are even more sterile and their fertility is about 0.6 and 0.05 per cent respectively for pollen and seeds.

The hybrids of *G. aleppicum, G. macrophyllum, G. perincisum* and *G. oregonense* usually have at metaphase of the I-st division 0 to 7 bivalents and 43 to 28 univalents, i.e. far less bivalents than the hybrid *G. urbanum* × *G. vernum* (Figs. 53—56). In other respect the course of meiosis is the same. In telophase restitution nuclei are often formed and among the tetrads there are about 2 per cent of dyads.

f. Subg. *Eugeum* × subg. *Oreogeum*

Partial results from investigations on the hybrids between these two subgenera were published in an earlier paper (W. Gajewski 1952). That report described in the first place the hybrids between *G. montanum, G. reptans* and *G. rivale*. In the course of experiments on *Geum* numerous other hybrids between the two subgenera were obtained, and therefore I shall describe them here all together, trying at the same time to bring out certain features common for all these hybrids and to characterize peculiarities of some hybrid groups or individuals.

I succeeded in obtaining the following crosses between the species from the subgenera *Eugeum* and *Oreogeum:*

15. *G. montanum* L. (14) × *G. rivale* L. (21), Fig. 57, culture no. 67—45
16. *G. montanum* L. 14 × *G. silvaticum* Pourr. (21), culture no. 180—52
17. *G. montanum* L. (14) × *G. coccineum* Sibth. et Sm. (21), Fig. 58, culture no. 29—46
18. *G. montanum* L. (14) × *G. molle* Vis. (21), culture no. 117—51
19. *G. montanum* L. (14) × *G. hispidum* Fr. (21), culture no. 150—51
20. *G. montanum* L. (14) × *G. aleppicum* Jacq. (21), Fig. 59, culture no. 12—50
21. *G. montanum* L .(14) × *G. urbanum* L. (21) Fig. 60, culture no. 34—52
22. *G. montanum* L. (14) × *G. laciniatum* Murr. (21) Fig. 61. culture no. 17—50
23. *G. montanum* L. (14) × *G. canadense* Jacq. (21) Fig. 62, culture no. 30—50
24. *G. montanum* L. (14) × *G. macrophyllum* Willd. (21) culture no. 141—51

25. *G. pyrenaicum* Willd. (42) × *G. montanum* L. (14), Fig. 63, culture no. 65—52
26. *G. montanum* L. (14) × *G. magellanicum* Pers. (42), culture no. 66—52
27. *G. Fauriei* Lev. (42) × *G. montanum* L. (14), culture no. 3—53
28. *G. rivale* L. (21) × *G. reptans* L. (21), Fig. 64, culture no. 77—52
29. *G. coccineum* Sibth. et Sm. (21) × *G. reptans* L. (21), Fig. 65, culture no. 78—52.

Hybrids nos. 15, 17, 21 and 23 were obtained in both reciprocal directions, the remaining in the one direction stated in the list (pollinated species first and pollinating second).

The thirteen hybrids with *G. montanum* as one of the parent species will be discussed first and the two with *G. reptans* later.

1. Crosses with *G. montanum* L.: — *G. montanum* is very easily crossed with most species from subgenus *Eugeum*. No significant differences in the setting of seeds between reciprocal crosses are apparent. The setting of seeds is usually at a high level: from 60 to 70 per cent to almost equal the normal settting of seeds in pollination between plants of one species. The germination rate is normal, but usually, similarly as in *G. montanum*, most seeds sown out in the autumn do not germinate till spring of the next year after they had frozen during winter.

F_1 hybrids are usually vigorous and frequently exhibit marked heterosis. They then surpass the parent species in respect to stem and leaf size, number of flowers, and resistance to frost and parasitic fungi.

For a detailed description of morphological characters and their expression in the hybrid with *G. rivale* the reader is referred to an earlier report (W. Gajewski 1952). Of the other hybrids some idea may be obtained from Figs. 57—63. It may be stated as a general principle that the leaf shape is usually intermediate between the parent species, though not in all cases to the same degree. In *G. montanum* the stem is on the whole unifloral but sometimes it has 2—3 flowers. In all hybrids of *G. montanum* with *Eugeum* species this character is recessive. The hybrids with, for instance, *G. rivale* or *G. coccineum* as one of the parent species usually have stems with 3—7 flowers and in this they resemble *Eugeum* species. Hybrids with *G. aleppicum, urbanum, macrophyllum* or other multifloral species have much branched stems. The creeping, overground caudex which is strongly developed in *G. montanum* is a dominant character and is formed in all hybrids with this species. *G. montanum* has stems long and softly haired with many glandular hairs in the upper parts. In crosses with species without glandular hairs, such as *G. aleppicum* or *G. laciniatum,* glandular hairs

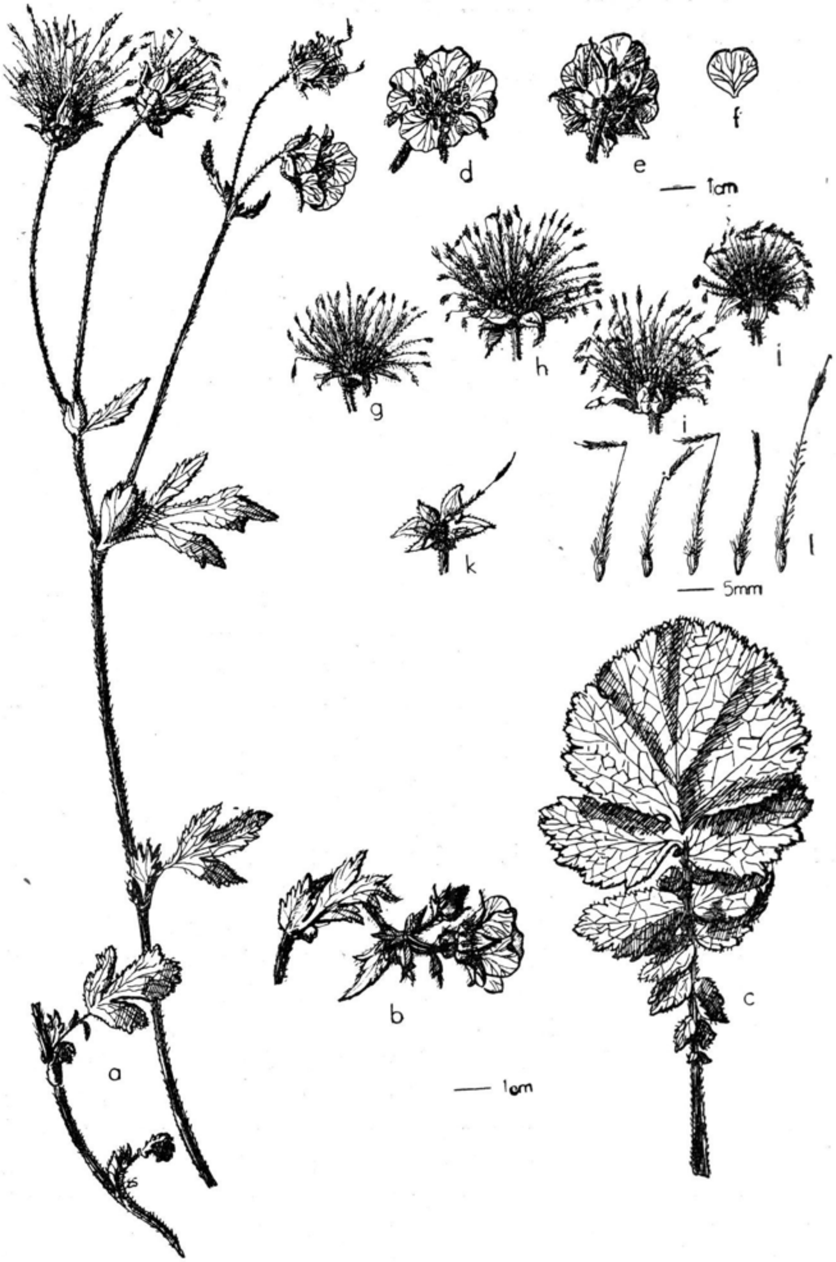

Fig. 57. F_1 *Geum montanum* × *G. rivale*; a — floral stem; b — top of young floral stem; c — basal leaf: d — flower — top view; e — flower — bottom view; f — petal; g—j — various flowers with achenes of type I, II or III; k — receptacle with one achene; l — various types of achenes from type I (right) to type III (left)

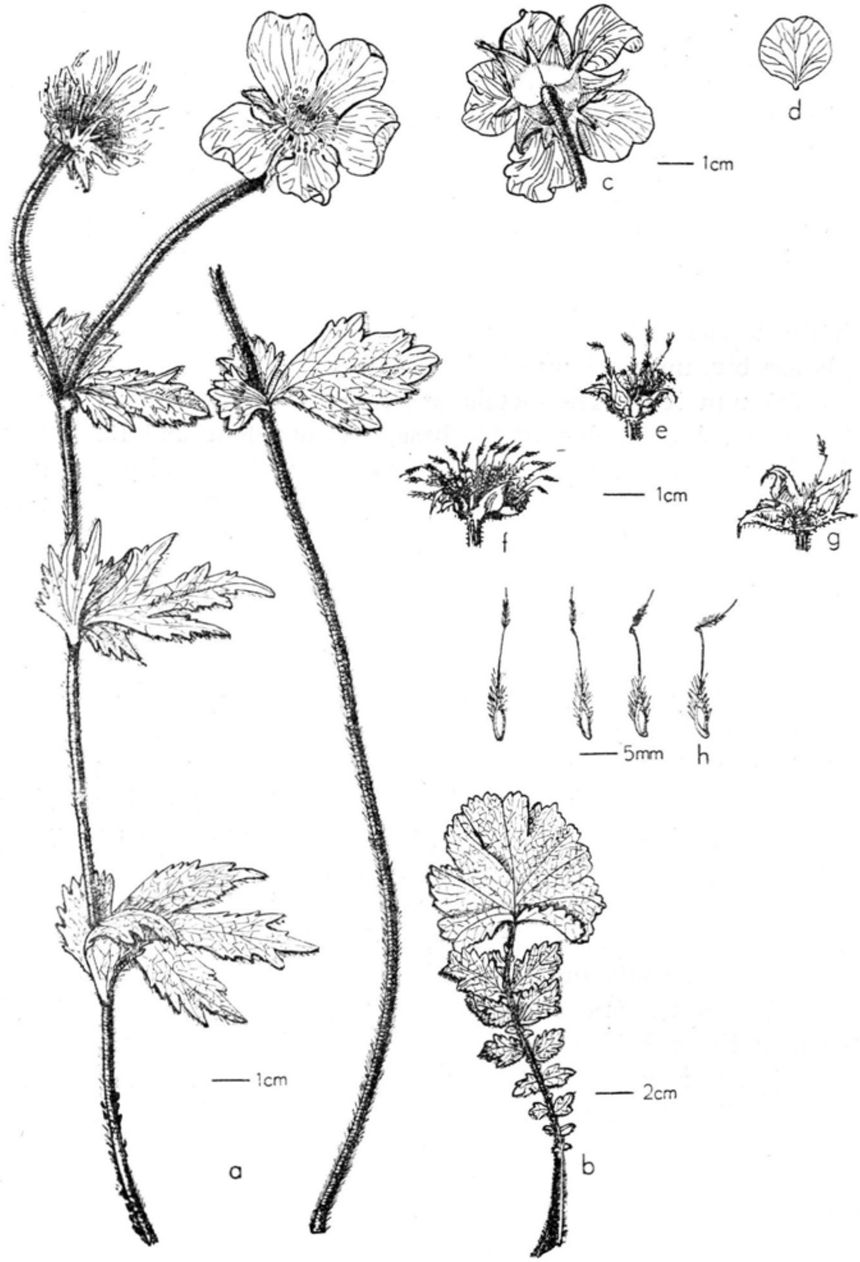

Fig. 58. F_1 *Geum coccineum* × *G. montanum;* a — floral stem; b — basal leaf; c — flower — bottom view; d — petal; e—f — achenes in flower; g — receptacle with one achene; h — achenes of different types

do not appear and therefore this character is entirely recessive. The long stiff bristles which are characteristic for some *Eugeum* species, as for instance *G. laciniatum* or *G. macrophyllum,* never reach their typical expression in crosses with *G. montanum.* In such cases the hairs are longer and stiffer than in *G. montanum* but much softer, not prickly and without thickened cell walls as in typical bristles.

G. montanum has small amounts of anthocyanin in the stems and in flowers primely in the styles. This becomes especially evident at the end of the vegetative season. In hybrids with species wholly deprived of this pigment the presence of anthocyanin is usually noticeable. The structure of calyx and corolla in *G. montanum* is usually pentamerous, both the sepals and petals spreading out horizontally at anthesis. The sepals are big, up to 11 mm in length; the segments of the epicalyx are about 5.5 mm long. The petals are more or less rounded, sometimes with a small obscure claw at the base, 16.6 mm long and 15.7 mm wide.

In hybrids the size of petals and sepals is usually intermediate between the two parent species. The following dimensions were recorded in hybrids and their parent species (length × width in mm):

1. *G. montanum* 16.8 × 15.7 ... *G. rivale* 10.1 × 8.0 ... F_1 14.2 × 12.5
2. *G. montanum* 16.8 × 15.7... *G macrophyllum* 7.6 × 7.0 . F_1 11.0 × 11.5
3. *G. montanum* 16.8 × 15.7 ... *G. laciniatum* 4.7 × 2.4 .. F_1 8.4 × 6.3.

From the above it is evident that when the petals of one parent species are smaller the petals of the F_1 hybrid become correspondingly smaller. The petals are intermediate not only in respect to size but also in their shape: the ratio length:width is in *G. montanum* approximately 1 (1.08 exactly), in *G. rivale* — 1.13, in *G. macrophyllum* — 1.08, and in *G. laciniatum* — 1.95. The corresponding ratios for the hybrids of these species are respectively 1.13, 0.95, and 1.35. This means that in hybrids with *G. rivale* and with *G. laciniatum,* which both have elongated petals, the petals are elongated intermediately between the parent species. In the hybrid with *G. macrophyllum* which has rounded petals the petals are rounded similarly as in the parental species.

Not in all cases, however, the petals in the hybrid are intermediate in shape and size between the parent species. E.g. in the cross *G. montanum* × *G. coccineum* the following measurements were recorded: *G. montanum* 16.8 × 15.7 ... *G. coccineum* 13.0 × 14.3 .. F_1 16.5 × 19.5. In this case the hybrid has much bigger petals than the parents. The emargination of the upper margin of *G. rivale* petals is wholly recessive in respect to the rounded tip of *G. montanum* and the long claw in *G. rivale* is almost entirely recessive.

The most noteworthy is the structure of the styles in these hybrids. As we know, *G. montanum* has straight styles with persistent stigmatic part which on the ripe achenes reach a length of 29—33 mm (average 29,1 mm) The styles are long pennately haired. In species from subgenus *Eugeum* the styles are shorter, usually glabrous, and geniculate. The rostrum persists on the achene and the stigmatic part is shed when the flowers are pollinated. The rostrum is hooked at the tip and constitutes the adhesive organ of the achene. The appearance and the structure of styles in the hybrid *G. montanum* × *rivale* were described earlier (W. Gajewski 1952), and I shall mention them only briefly. In the hybrid styles of various types are formed in one plant and even in one flower. The styles of F_1 plants have been divided into three groups: the styles of the first type are straight, more or less haired and with persistent stigmatic part; in the second type between the stigmatic part and the rostrum a semicircular bending is formed and the stigmatic part is usually deciduous; in the third type the rostrum is tipped with a characteristic hook and the stigmatic part is deciduous. Between the first and the third type we have a gradual change form the staight style characteristic for *G. montanum* to the hooked styles typical for *G. rivale*. The formation of the *rivale* type of styles is correlated with the reduction of pubescence and style length. Observations of style development indicate that at early stages in their growth all the styles in hybrid plants develop along the pattern characteristic for *G. rivale* with the rostrum clearly separated from the stigmatic part. However, at later stages either the typical hook is formed between the rostrum and the stigmatic part or the slight initial bending disappears completely or partially and straight styles grow out. Already Iltis (1913) demonstrated that in *Eugeum* the stigmatic part has a different anatomical structure (numerous stomata and chloroplasts) than the lower part of the rostrum which anatomically corresponds more to the carpels. Anatomically the stigmatic part in *Eugeum* corresponds to the deciduous styles in *Waldsteinia* and *Coluria*, and these organs are homologous. In *Oreogeum* species there are stomata both in the stigmatic part and in that part at the top of the style which gradually changes into the stigmatic part. In the hybrid *G. montanum* × *rivale* the geniculate joint is formed in that part which corresponds by its anatomical structure to the rostrum and consequently the anatomical differences between the structures of the rostrum and the stigmatic part are not so pronounced as in *G. rivale*.

At the same time, the shape of the styles in the hybrid *G. montanum* × *rivale* depends on the vegetative stage and usually the first flowers

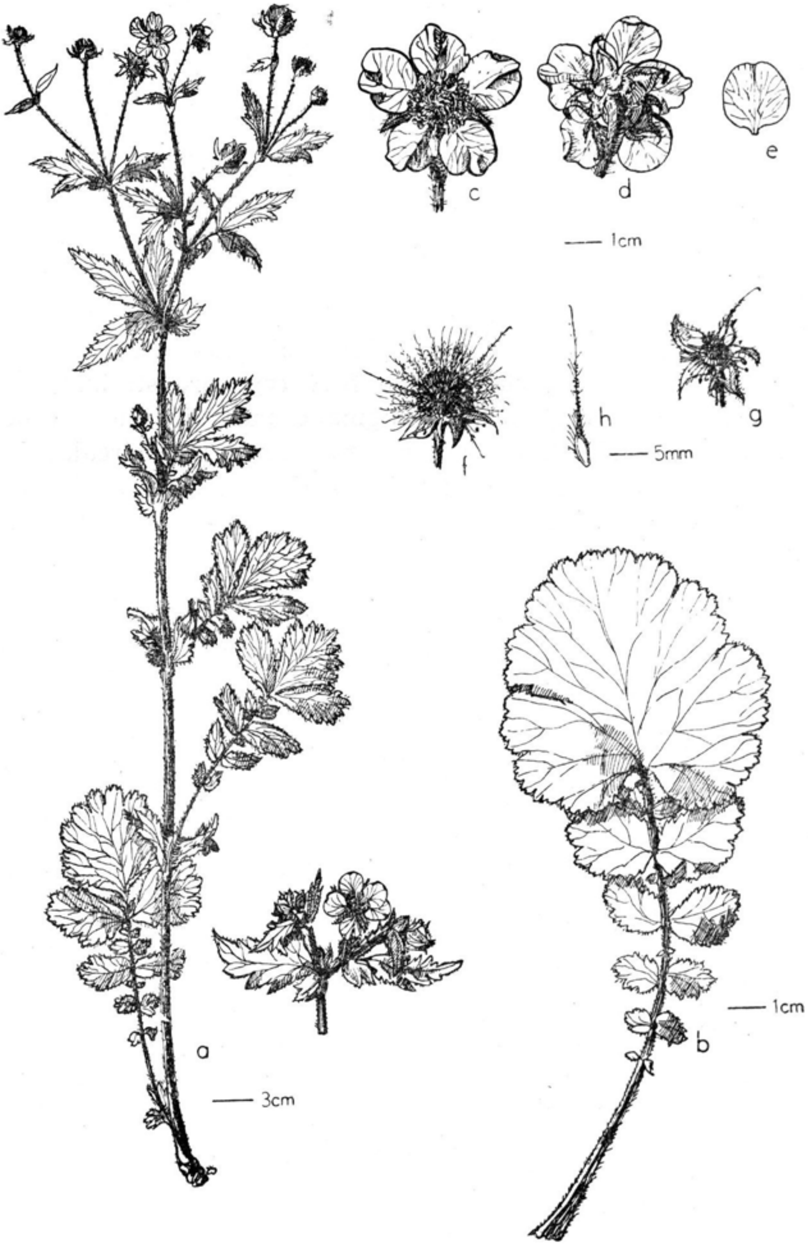

Fig. 59. F$_1$ *Geum montanum* × *G. aleppicum*; a — floral stem; b — top of young floral stem; c — basal leaf; d — flower — top view; e — flower — bottom view; f — petal; g — achenes in flower (3 are sound); h — receptacle with one achene; i — achene

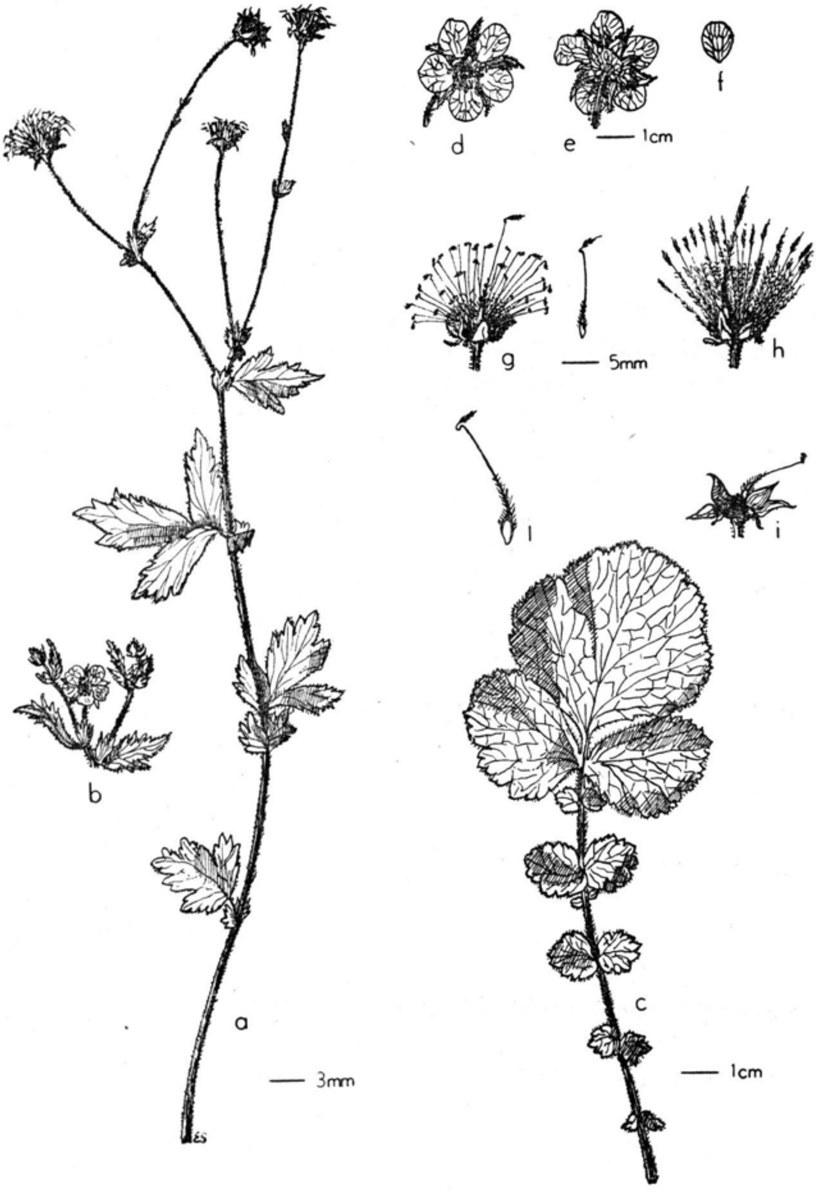

Fig. 60. F$_1$ *Geum montanum* × *G. urbanum*; a — floral stem; b — top of young floral stem; c — basal leaf; d — flower — top view; e — flower — bottom view; f — petal; g—h flowers with achenes and various types of achenes; i — receptacle with one achene; j — achene

to develop have styles resembling more the *montanum* ones, whereas, in the flowers which develop later the styles resemble more the *rivale* type. This effect is probably due to the not complete dominance and only partial penetration of the factors originating from *G. rivale* and regulating the formation of the geniculate joint on the rostrum. These factors are not completely dominant over *G. montanum* factors for the formation of the long straight pennate style.

The variability in the shape of styles was observed in many hybrids of *G. montanum* with species from subgenus *Eugeum*, though, not in every case to the same degree. The effect is very distinct in the following hybrids: *G. montanum* × *laciniatum*, *G. montanum* × *urbanum*, *G. montanum* × *aleppicum*, and *G. montanum* × *coccineum*. In *G. coccineum* and *G. rivale* the elongated stigmatic part is 4 to 5 mm long and in hybrids with these species the length of the stigmatic part differs in respect to the hybrids with species in which this organ is shorter, about 1.5 mm long. In the former case the stigmatic part in the hybrids is relatively longer than in the latter. This is shown by the data assembled below for comparison.

Crosses with species which have a long stigmatic part:

		rostrum + stigmatic part
1. *G. montanum* × *rivale*, length of style,	type I	22.5 mm
	type II	15.5 + 5.5 mm
	type III	14.0 + 5.5 mm
2. *G. montanum* × *coccineum*	type I	21.0 mm
	type II	13.0 + 7.0 mm
	type III	13.0 + 6.5 mm.

Crosses with species which have a short stigmatic part:

3. *G. montanum* × *laciniatum*	type I	16.0 mm
	type II	12.5 + 3.5 mm
	type III	12.0 + 3.5 mm
4. *G. montanum* × *urbanum*	type I	17.5 mm
	type II	12.5 + 2.5 mm
	type III	10.0 + 2.5 mm

5. *G. montanum* × *aleppicum* type I 17.0 mm
type II 12.0 + 3.5 mm
type III 10.0 + 3.5 mm.

It is apparent from the above that in crosses of *G. montanum* with species having a long stigmatic part the length of this organ ranges from 5.5 to 7 mm, while in hybrids with species having a short stigmatic part it ranges from 2.5 to 3.5 mm. However, in both cases the stigmatic part is longer than in the parent species from the subgenus *Eugeum*. Moreover, it is to be seen from the list above that the style becomes shorter as it changes from type I to type III, but it is only the rostrum which is reduced and the length of the stigmatic part remains unchanged. In type III the simultaneous shortening of hairs in respect to types II and I is often noted. The character of pubescence on the styles in various hybrids is not uniform. In crosses of *G. montanum* with *G. rivale* and *coccineum* the styles are far more pubescent and resemble more the *G. montanum* type than in crosses of *G. montanum* with *G. urbanum*, *laciniatum* and *canadense*. Similarly the overall length of the styles is shorter in the latter three hybrids than in the former two.

In crosses of *G. montanum* with *G. canadense* and *G. macrophyllum* only styles of types I and II are formed. Styles with well expressed hooked bends of type III appearing in the previously described hybrids are not developed here. Finally, in hybrids of *G. montanum* with *G. hispidum*, *G. molle* and *G. silvaticum* all styles are straight, of type I, without any bend between the rostrum and the stigmatic part. The length of styles in the hybrid with *G. silvaticum* is about 22 mm, and in the hybrids with *G. molle* and *hispidum* it is from 16 to 17 mm, about 16 mm on the average.

In hybrids of *G. montanum* with species having a long gynophore such as *G. rivale* or *G. silvaticum* this organ is very small or it is non-existent. In other hybrids the organ is not developed. In *G. montanum* the receptacle is very shortly haired, but in crosses with species having a long haired receptacle — such as *G. canadense* or *G. urbanum* — the receptacle is covered with long hairs. In *G. montanum* the number of pistils on the receptacle is between 90 and 120, averaging at 100. In hybrids of this species with *Eugeum* species the number of pistils is usually intermediate. E.g. in the hybrid with *G. aleppicum* (about 230 pistils) this number is 170 and in the hybrid with *G. silvaticum* (25—30 pistils) the number is 50 pistils per flower.

The hybrids of *G. montanum* with species from subgenus *Eugeum* described above were pentaploid which means that the parental species

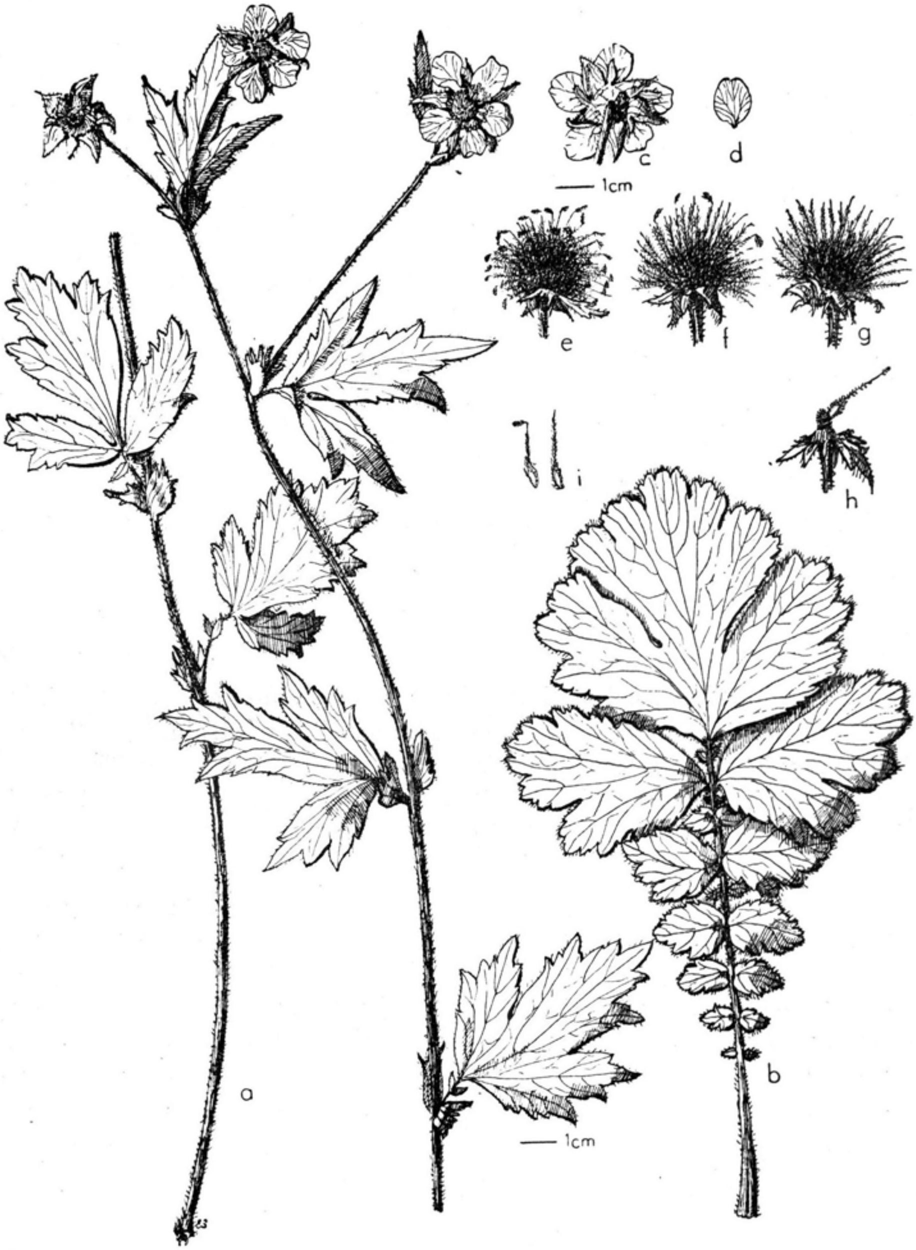

Fig. 61. F_1 *Geum montanum* × *G. laciniatum*; a — floral stem; b — basal leaf; c — flower — bottom view; d — petal; e—g — achenes of various types in flowers; h — receptacle with one achene; i — achenes of various types

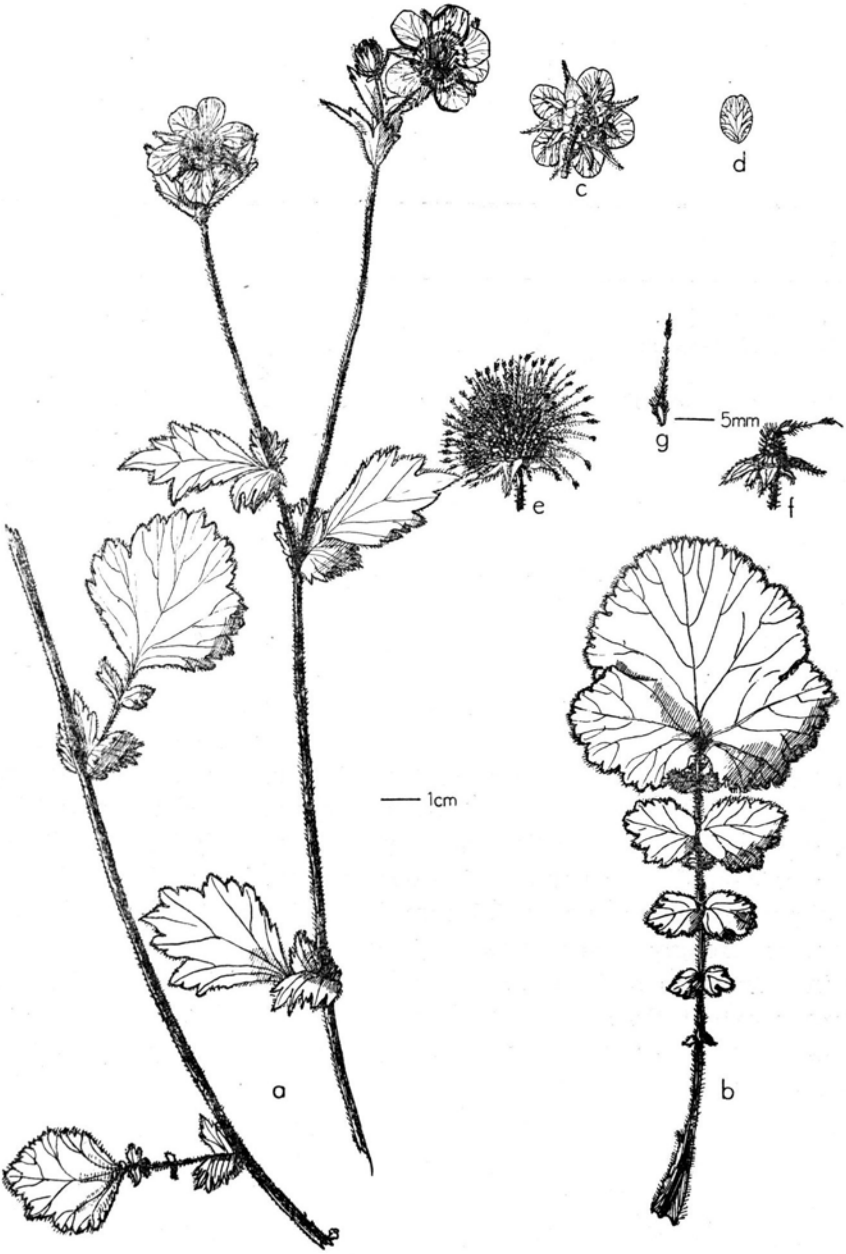

Fig. 62. F₁ *Geum montanum* × *G. canadense*; a — floral stem; b — basal leaf; c — flower — bottom view; d — petal; e — achenes in flower; f — receptacle with one achene; g — achene

from subgenus *Eugeum* were hexaploids. Besides the pentaploid ones I obtained three octoploid hybrids between *G. montanum* and the dodecaploid *G. pyrenaicum, G. magellanicum* and *G. Fauriei.* Morphologically these hybrids are far more closely related to the *Eugeum* parent species than to *G. montanum.* To illustrate this some characters of the F_1 hybrid *G. montanum* × *pyrenaicum* (Fig. 63) are here compared with the corresponding characters of the parent species.

Character	*G. montanum*	F_1	*G. pyrenaicum*
Length of stems (cm)	10–20	20–40	30–40
Number of flowers on one stem	1–2	1–4 average 3	1–4 average 3
Length of sepals (mm)	16.6 × 15.7	13.6 × 14.8	11.5 × 12.0
Number of pistils	± 100	± 65	± 55
Floral base	short haired	long haired	long haired
Style	straight	hooked	hooked

Hybrids with dodecaploid species are entirely sterile and the flowers after anthesis wither rapidly. It is thus difficult to compare the structures of the pistils in the hybrid and the parent species as the styles wither very soon. Nevertheless, from the earliest primordial stage to the moment when the styles begin drying their structure is typical for species from subgenus *Eugeum* with the characteristic hooked joint dividing the style into the rostrum and the stigmatic part. In the hybrid *G. pyrenaicum* × *montanum* full achenes were formed twice and it can be seen from Figs. 11 and 63 that they were very similar to achenes of *G. pyrenaicum.* The rostrum is glabrous or short haired, 9 mm long, and the stigmatic part is 4.5 to 5.5 mm long, haired to the middle. The rostrum is strongly recurved as in *G. pyrenaicum.* It appears, therefore, that in respect to style structure dodecaploid species are dominant to a greater extent than the hexaploid *Eugeum* species.

The fertility of hybrids of *G. montanum* and species from subgenus *Eugeum* will now be discussed. The fertility of pollen and seeds in the hybrids described above is shown below.

This list clearly shows that fertility in the various hybrids varies over a wide range. The most fertile are the hybrids between *G. montanum* and *G. rivale, coccineum* and *silvaticum.* In view of the differences in morphology and chromosome number of the parental species the fertility of their hybrids is exceptionally high. The hybrids with *G. molle, hispidum* and *canadense* are fairly fertile but much less so

		Pollen fertility in %%	Seed fertility in %%
1	G. montanum × G. rivale	27.4-46.5 mean 34.5	3.5-32.0 mean 15.5
2	G. montanum × G. coccineum	22.0-47.5 mean 35.5	9.8-3 .0 mean 18.5
3	G. montanum × G. silvaticum	22.5	34.4
4	G. montanum × G. molle	10-12	14.0-21.5 mean 16.0
5	G. montanum × G. hispidum	19.5	6.6-12.6 mean 8.5
6	G. montanum × G. canadense	21.3-46.6 mean 32.2	6.2-20.0 mean 8.5
7	G. montanum × G. aleppicum	0.5-7.3 mean 4.2	0.3-5.3 mean 2.4
8	G. montanum × G. laciniatum	0.2-1.2 mean 1.0	1.3-1.8 mean 1.6
9	G. montanum × G. urbanum	0.45	0.2-1.1 mean 0.6
10	G. montanum × G. macrophyllum	0.08 — 0.1	0.1
11	G. montanum × G. pyrenaicum	0.01	0.15
12	G. montanum × G. magellanicum	0.1	complete sterility
13	G. montanum × G. Fauriei	0.5	complete sterility

than the preceding three. High sterility is to be noted in hybrids with *G. aleppicum, laciniatum* and *urbanum*, while complete sterility is displayed by the hybrid with *G. macrophyllum* and the hybrids with the three dodecaploid species *G. pyrenaicum, magellanicum* and *Fauriei*. It is to be noted that the fertility of particular plants is also rather variable during one vegetative season and from year to year. Usually the first stems and the first flowers on the stems are far more sterile than the later ones. On the same plant of the hybrid *G. montanum* × *rivale* alongside of flowers in which not one good achene developed others were found with as much as 33 per cent of good achenes. No correlation is revealed between the percentage in the setting of achenes and the type according to which the pistils are shaped. The fertility of reciprocal hybrids is more or less the same and so are all the morphological characters.

Cytological examination: — In the first ten of the above mentioned hybrids the somatic chromosome number is $2n = 35$. In the hybrid *G. montanum* × *coccineum* the chromosome number was counted directly on metaphasal plates from root tips (Fig. 35) and was deduced from analyses of meiosis in PMCs in the other hybrids.

In all pentaploid hybrids except *G. montanum* × *macrophyllum* the course of meiosis is almost identical. In the first 9 pentaploid hybrids at metaphase of the I-st division 14 bivalents and 7 univalents are usually formed (Figs. 66—73). As this type of meiosis was described in earlier papers (W. Gajewski 1939, 1942) only the meiotic division in the hybrid *G. urbanum* × *montanum* is here described for comparison. In Fig. 69a a PMC at the stage of late diakinesis is shown and in the

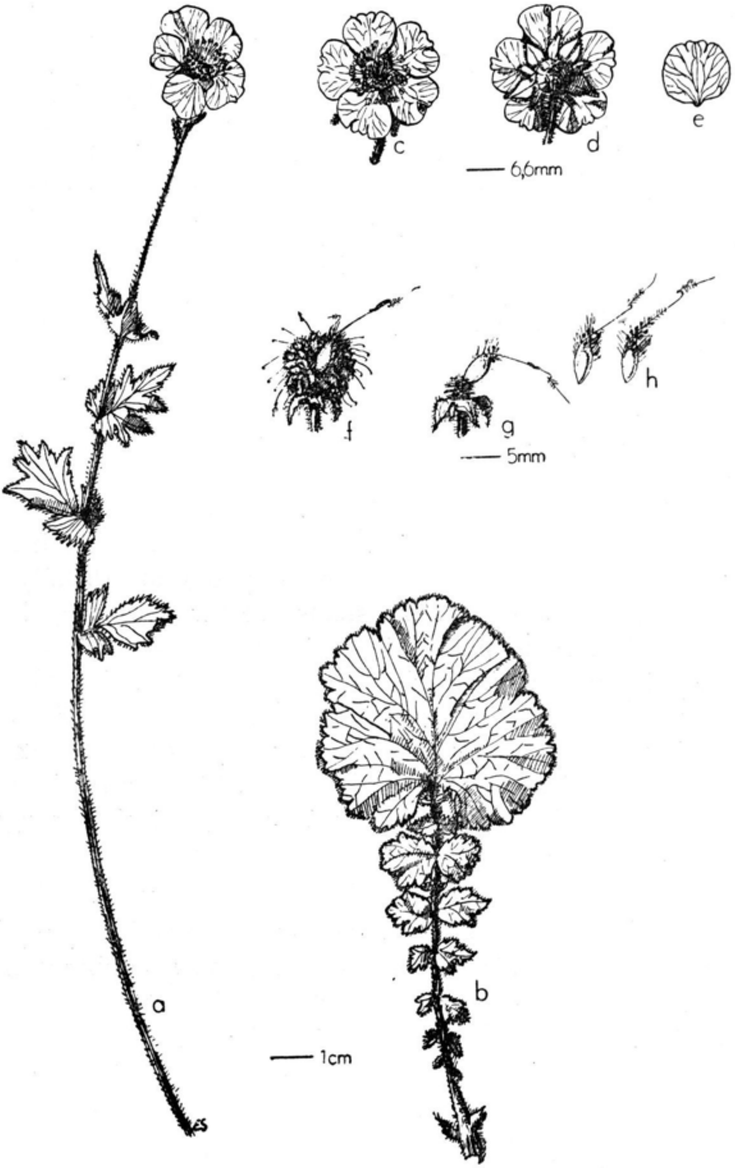

Fig. 63. F_1 *Geum pyrenaicum* × *G. montanum*; a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower (1 is sound); g — receptacle with one achene; h — achenes

nucleus 21 chromosomal bodies are visible, of these 14 are bivalents and 7 univalents. The next Fig 69b shows a metaphase of the I-st division with the same chromosome configuration. In Fig. 69c a side view of metaphase is shown with numerous bivalents arranged in a plate and univalents lying on the spindle. Figures 69d-f correspond to meta- and anaphase of the II-nd division. Metaphasal plates with 16 to 20

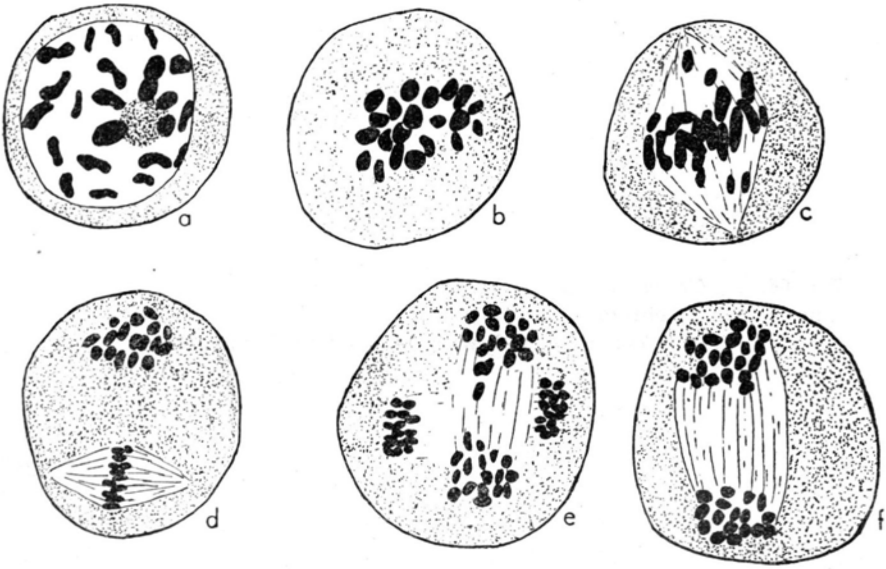

Fig. 64. F_1 *Geum montanum* × *G. silvaticum*, meiosis in PMCs; a — diakinesis with 13 bi- and 9 univalents; b — M-I with 14 bivalents and 7 univalents; c — M-I with 14 bivalents and 7 univalents; d — M-II with 17 chromosomes in one of the plates; e — A-II with 16 and 19 chromosomes in the two pairs of nuclei; f — A-I with 17 and 20 chromosomes in the two daughter groups

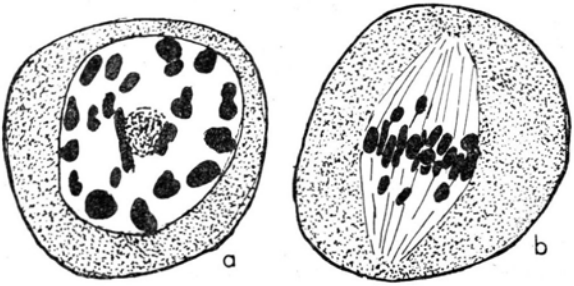

Fig. 65. F_1 *Geum montanum* × *G. coccineum*, meiosis in PMCs; a — diakinesis with 21 chromosomes ($14_{II} + 7_{I}$); b — M-I with 14 bi- and 7 univalents

chromosomes can be seen. Sometimes single chromosomes lie in the cytoplasm away from the two plates and often some chromosomes are not properly arranged and remain on the spindle off the plate itself

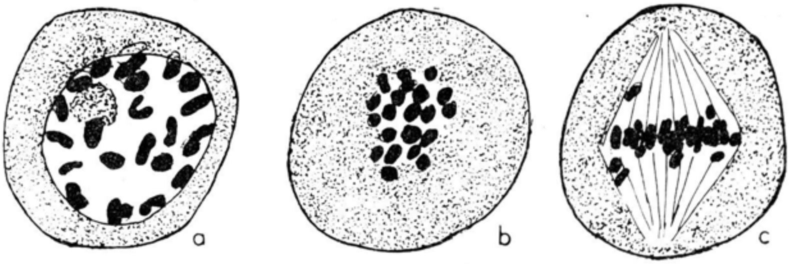

Fig. 66. F$_1$ *Geum montanum* × *G. molle*, meiosis in PMCs; a — diakinesis with 21 chromosomes ($14_{II} + 7_{I}$); b — M-I with 21 chromosomes ($14_{II} + 7_{I}$); c — M-I with 14 bi- and 7 univalents

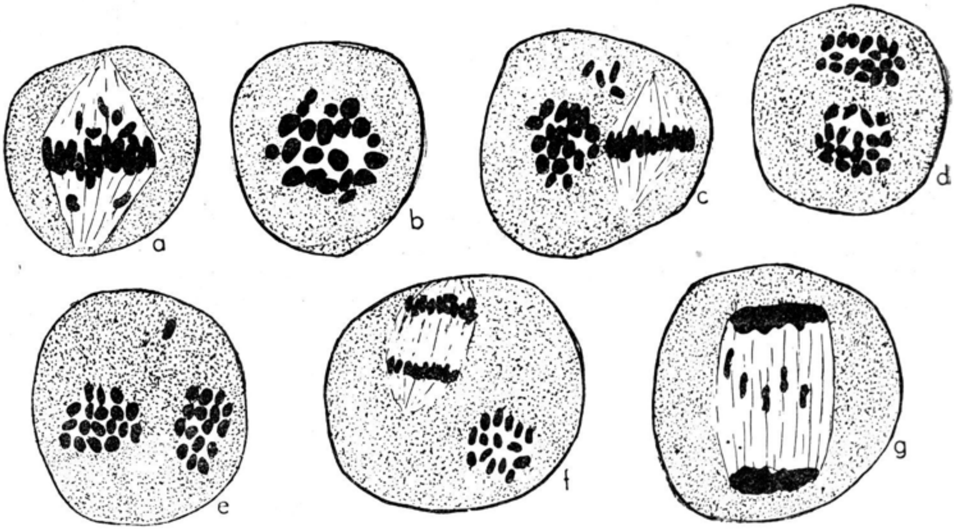

Fig. 67. F$_1$ *Geum montanum* × *G. hispidum*, meiosis in PMCs; a — M-I with 14 bi- and 7 univalents; b — M-I with 14 bi- and 7 univalents; c — M-II with 18 chromosomes in one of the plates and 4 chromosomes forming an extra third plate; d — M-II with 19 and 17 chromosomes in the two plates; e — M-II with 18 and 16 chromosomes in the two plates and one chromosome lost in the cytoplasm; f — A-II with 15 chromosomes in one of the groups; g — A-I with 5 univalents on the spindle

No PMCs. of the hybrid *G. urbanum* × *montanum* were seen at the stage of the I-st division anaphase. To enable further comparisons some stages of meiosis in the other hybrids of *G. montanum* with hexaploid

Eugeum species are shown in Figs. 64—72. It can be seen in these drawings that in anaphase univalents lag on the spindle, but with much delay in respect to the bivalents, they are segregated subsequently to the two poles (e. g. Figs. 70c, and 71c). Usually the univalents are not divided but after being strongly stretched out they move undivided to one of the poles. Very often single univalents are not included in either of the daughter nuclei. Although, at metaphase at least 7 bivalents are formed in every cell, not in all anaphases of the I-st division univalents are seen lagging in the spindle behind the separating bivalent halves. This means that univalents can be sometimes segregated to the two daughter nuclei at the same time as the bivalents. It is not quite clear why the behaviour of the univalents is not uniform, but probably it depends on the position that they occupy on the spindle at metaphase.

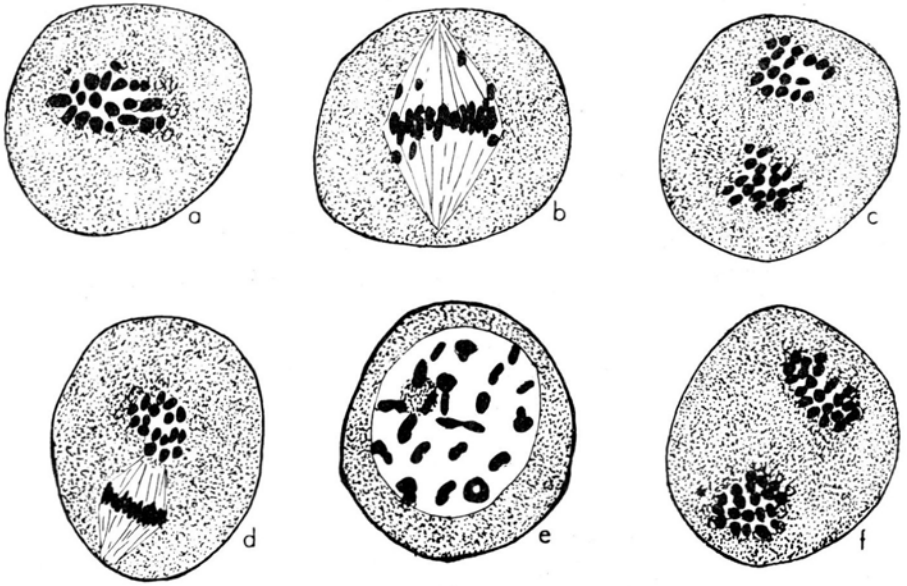

Fig. 68. F$_1$ *Geum montanum* × *G. aleppicum,* meiosis in PMCs; a — M-I with 21 chromosomes ($14_{II} + 7_{I}$); b — M-I with 14 bi- and 7 univalents; c — M-II with 17 and 18 chromosomes in the plates; d — M-II with 17 chromosomes in one plate; e — diakinesis with 21 chromosomes ($14_{II} + 7_{I}$); f — M-II with 20 and 21 chromosomes in the plates

The two meiotic divisions result in the formation of tetrads which in all the hybrids in question have a normal appearance with four microspores. Additional small microspores or dyads were never found in these hybrids.

As was reported elsewhere (W. Gajewski 1949) the number of chromosomes in the anaphasal groups ranges in the hybrid *G. rivale* × *montanum* from 14 to 21 in numerical ratios corresponding to chance

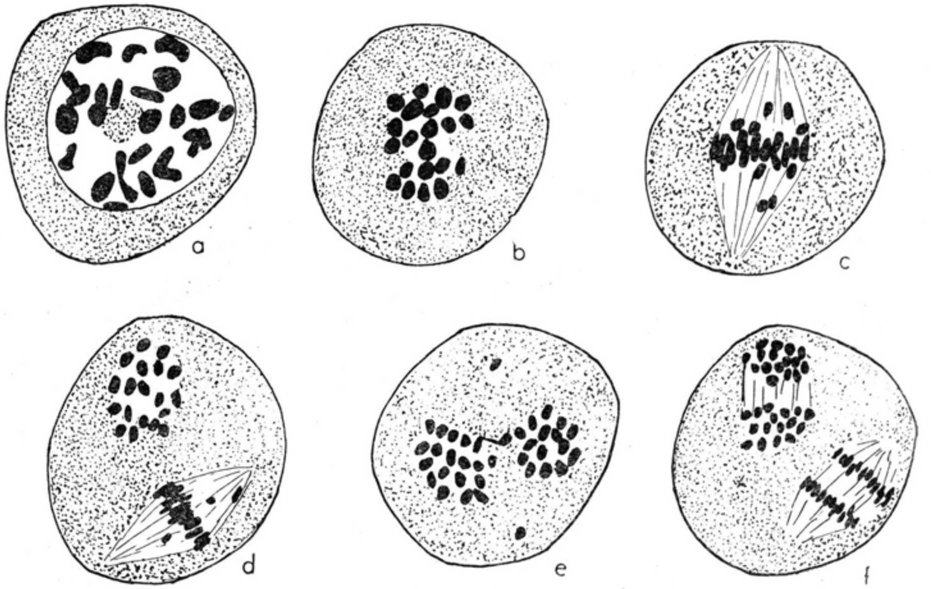

Fig. 69. F_1 *Geum montanum* × *G. urbanum,* meiosis in PMCs; a — diakinesis with 21 chromosomes ($14_{II} + 7_{I}$); b — M-I with 21 chromosomes ($14_{II} + 7_{I}$); c — M-I with 13 bi- and 9 univalents; d — M-II with 19 chromosomes in a plate; e — M-II with chromosomal bridge and 2 chromosomes lost; f — A-II with 16 chromosomes in the two sister groups

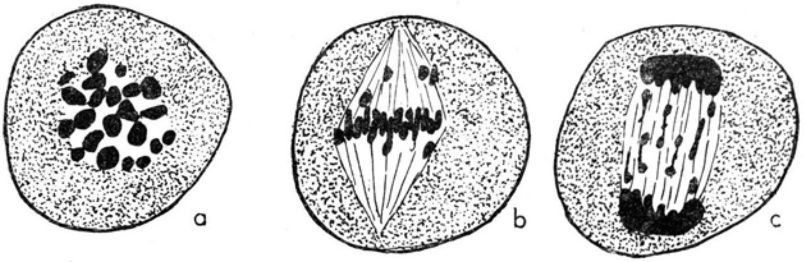

Fig. 70. F_1 *Geum montanum* × *G. laciniatum,* meiosis in PMCs; a — M-I with 22 chromosomes ($13_{II} + 9_{I}$); b — M-I with 14 bi- and 7 univalents; c — A-I with univalents on the spindle

distribution of 7 univalents to the two daughter nuclei. Similar relations occur in other hybrids of *G. montanum* with *Eugeum* species when at metaphase there are 14 bivalents and 7 univalents. In spite of the considerable likeness of the meiotic divisions in these hybrids and probably the similarity in the numerical distribution of chromosomes to the gametes, the fertility of the gametes — as already demonstrated — varies greatly. This means that in this case the fertility of the gametes is not determined by the numerical composition of chromosomes but depends primely on the composition of genes from the two chromosome sets which unite in the hybrid. The differences between chromosomal sets derived from two hexaploid *Eugeum* species, which probably consist not only in the genic differences but also in small structural mutations, cause that in some hybrids gametes with chromosomal sets composed of two kinds of chromosomes are viable while in other hybrids such gametes are not capable of carrying out their normal functions, although, in both cases the chromosomal sets are composed of the same number of chromosomes.

Separate mention must be made of the course of meiosis in the pentaploid hybrid *G. montanum* × *G. macrophyllum*. In this case 23 PMCs were analysed at metaphase of the I-st division and the following configurations were found:

$0_{II} + 35_{I}$ in 1 PMC
$2_{II} + 31_{I}$ in 4 PMCs
$3_{II} + 29_{I}$ in 2 PMCs
$4_{II} + 27_{I}$ in 11 PMCs
$5_{II} + 25_{I}$ in 4 PMCs
$6_{II} + 23_{I}$ in 1 PMC.

It is to be seen from the above that in this hybrid there is no, or almost no chromosome conjugation (Fig. 72). In metaphase the few bivalents lie on the equatorial plane of the spindle and the remaining chromosomes are scattered at random throughout the spindle. In anaphase the halfs of the bivalents together with those chromosomes which in metaphase were situated near the spindle poles form two anaphasal groups. After some time the other univalents form in the equatorial plane an arrangement somewhat resembling a plate and then very few of them are divided and the rest move without dividing to one of the two poles. The separation of the univalents is not synchronized, some of them may already be at the daughter nuclei while others are still on their way or even lag on the equatorial plane. In this manner something like a "bridge" connecting the two chromosome groups at the spindle poles may be formed. If the formation of the nuclear membrane begins at this moment, restitution nuclei will develop. From the 160 cells of this hybrid examined at the stage of interkinesis restitution nuclei were found in 6, in 22 there were single chromosomes or groups of chromosomes lying outside the nuclei and the remaining 132 cells had two nuclei only. This indicates that in spite of almost complete asyndesis in the hybrid, segregation of univalents gives rise to two daughter nuclei in most cells. At metaphase of the II-nd division in the few plates where it was possible to count the chromosomes the following counts were made: 16, 18, 23, and 15 Frequently in metaphase of the II-nd division 3—4 chromosomes form a separate group lying outside the two plates (Fig. 72, d, f). The II-nd division also progresses with many disturbances. The congression of chromosomes is not complete and at anaphase some chromosomes lag on the spindle. At the tetrad stage nearly 90 per cent of cells have 4 microspores only, in 8 per cent of

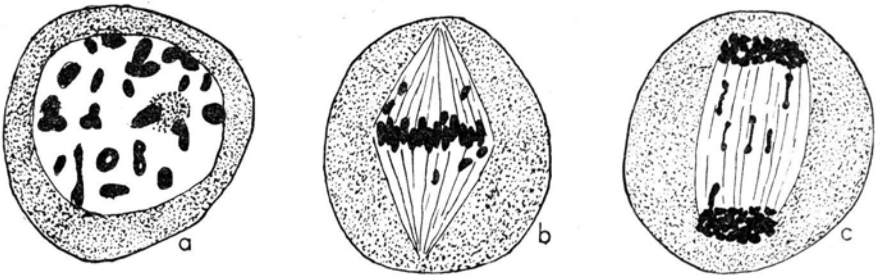

Fig. 71. F_1 *Geum montanum* × *G. canadense,* meiosis in PMCs; a — diakinesis with 21 chromosomes ($14_{II} + 7_{I}$); b — M-I with 14 bi- and 7 univalents; c — A-I with univalents on the spindle

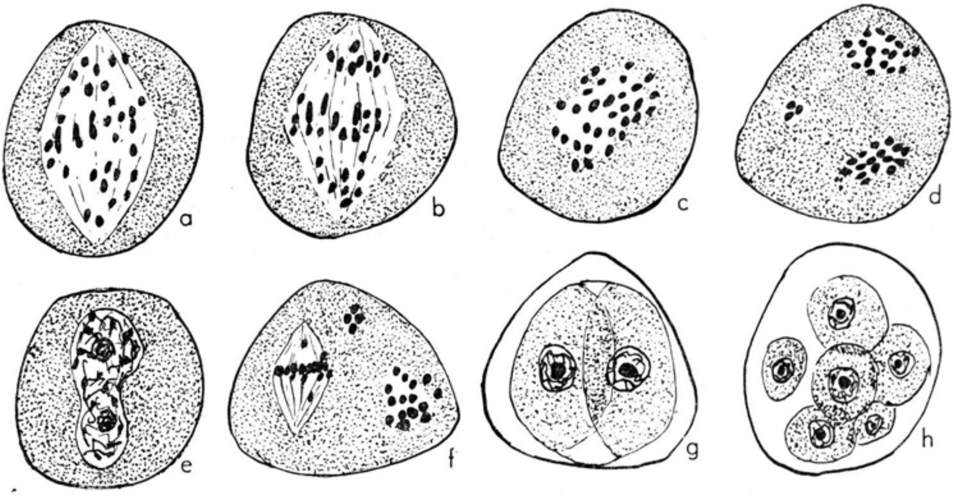

Fig. 72. F_1 *Geum montanum* × *G. macrophyllum,* meiosis in PMCs; a — M-I with 3 bivalents; b — M-I with 2 bivalents; c — M-I with 31 chromosomes ($4_{II} + 27_{I}$); d — M-II with 16 and 18 chromosomes in the plates and third extra plate with 3 chromosomes; e — restitution nucleus; f — M-II with 15 chromosomes in one of the plates and 4 chromosomes forming thrid extra group; g — dyad; h — tetrad with a pair of additional microspores

cells besides the 4 larger microspores there are two additional smaller ones (Fig. 72h), and the remaining 2 per cent consists of dyads with two big microspores. Among the proper tetrads with 4 microspores often one pair is larger than the other. As has been mentioned previously the amount of good pollen produced by the hybrid is extremely small.

Meiotic divisions in the 9-ploid hybrids of *G. montanum* with the dodecaploid *G. pyrenaicum, magellanicum* and *Fauriei* are in all three cases very similar. To illustrate them meiosis in the hybrid *G. pyrenaicum* × *montanum* will be described, as the preparations obtained from this hybrid were the most numerous and the best (Fig. 73). In metaphase of the I-st division there are 42 to 45 chromosomes which corresponds to configurations consisting of 11—14 bivalents and 34—28 univalents. Side views of the spindle show the bivalents forming a metaphasal plate and the numerous univalents some lying near the plate, others scattered throughout the spindle (Fig. 73a). The most common number of univalents is 28 or nearly 28 which indicates that in these hybrids the most frequent chromosome configuration consists of 14 bi- and 28 univalents. In anaphase some univalents are also segregated to the poles with the bivalents. However, the majority of univalents remain and in later anaphase form a conspicuous regular ring on the equatorial plane

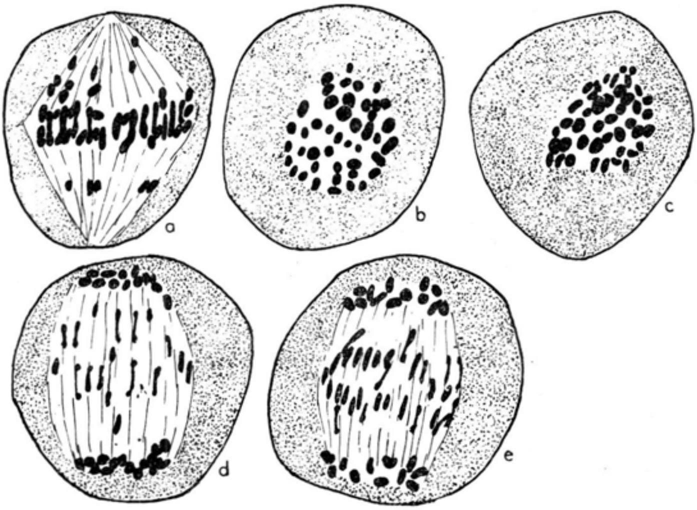

Fig. 73. F_1 *Geum pyrenaicum* × *G. montanum*, meiosis in PMCs; a — M-I with 12 bi- and 32 univalents; b — M-I with 44 chromosomes ($12_{II} + 32_{I}$); c — M-I with 43 chromosomes ($13_{II} + 30_{I}$); d, e — A-I with univalents arranged in a ring on the equatorial plane of the spindle

of the spindle with all univalents lying only in the outer peripheral part of the spindle (Fig. 73e). At an even later stage in anaphase some few univalents divide while others are only stretched out and in this condition start moving to the poles. As a result of the delay in the segregation of the univalents restitution nuclei are formed at telophase in 2—3 per cent of cells. In the remaining cells two daughter nuclei are formed, but in general some univalents are not included in the nuclei and remain in the cytoplasm. Unfortunately, none of the preparations from these hybrids show the stages of the II-nd meiotic division. Only telophase of the II-nd division and the tetrad stage are well represented in the preparations. In spite of the very numerous univalents in the I-st meiotic division the tetrads have an entirely normal appearance with four microspores. Two small additional microspores are formed very seldom and the percentage of dyads is 2,7. Some PMCs of the hybrid *G. montanum* × *G. magellanicum* are shown in Fig. 74.

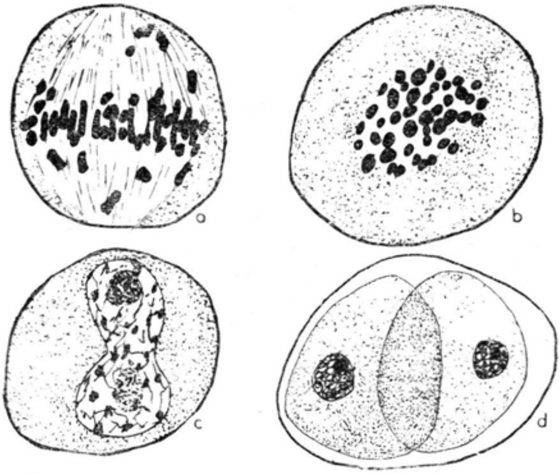

Fig. 74. F_1 *Geum magellanicum* × *G. montanum*, meiosis in PMCs; a — M-I with 12 bi- and 28 univalents; b — M-I with 44 chromosomes ($12_{II} + 32_{I}$); c — restitution nucleus; d — dyad

2. Hybrids with *G. reptans* L.: — Because of the difficulties with which *G. reptans* is grown in the lowlands I did not have a sufficient number of flowering specimens to cross it with many other *Geum* species. Besides a hybrid with *G. montanum* which will be described later the only hybrids with *G. reptans* which I produced were *G. rivale* × *reptans* and *G. coccineum* × *reptans*. These crosses were obtained by pollinating the mother plants with pollen brought directly from natural habitats in the Tatra Mountains. In both cases the setting of seeds was high and amounted to about 70 per cent. From the numerous achenes obtained from the two pollinations 28 plants of the hybrid *G. rivale* × *reptans* and 45 specimens of the hybrid *G. coccineum* × *reptans* were obtained.

The hybrids were difficult to grow, especially at the earliest stages and most of them perished when still at the early seedling stage. Later, however, when a strong root system developed they grew well and flowered very abundantly. The plants flower from early spring, beginning in April or May, till July. Most plants begin to flower again in September and continue till freezing weather sets on, sometimes even when covered with snow. The hybrid *G. rivale* × *reptans* (Fig. 75) was described in detail in an earlier paper (W. Gajewski 1942) and here only the hybrid *G. coccineum* × *reptans* (Fig. 76) will be dealt with more fully. The characters of the hybrid and of the parent species are compared in the table below:

Character	*G. coccineum*	F_1	*G. reptans*
Leaf shape	terminal leaflet big, ± rounded	intermediate	uniformly dissected
Height of stem (cm)	30 — 45	20—25	10 — 20
Number of flowers on one stem	3—7, average 3.8	1—3, average 2.7	1—2, average 1.08
Sepals	strongly reflexed	horizontal or slightly reflexed	slightly erect
Segments of epicalyx	single	single, often bifid at tip	double, or, sometimes bifid at tip
Number of petals	5—6, average 5.5	5—6, average 5.6	6—10 average 7.1
Colour of petals	red	yellow	yellow
Size of petals (length x width mm)	13.0 × 14 3	17.5 × 15.5	17.2 × 11.0
Runners	none	none	present
Styles	jointed, hooked	straight, pennate	straight, pennate

G. reptans differs greatly from *G. montanum* and other *Geum* species primely by the long overground runners which it develops. The runners produce rooting leaf rosettes similarly as in the plants from genus *Fragaria*. In the whole subfamily of *Dryadoideae* only some species from genus *Waldsteinia* have runners, but they differ slightly from those in question. In hybrids with *Eugeum* species typical runners are not produced, but in both hybrids with *G. rivale* and *G. coccineum* some stems grow to a greater length, often arch downwards to the ground, and usually after a vegetative growth lasting much longer than normally finally develop flowers and not leaf rosettes. Roots are never produced by these stems.

Both the hybrid *G. rivale* × *reptans* and *G. coccineum* × *reptans* have numerous pistils with long (22—28 mm), straight, pennately long-

Fig. 75. F_1 *Geum rivale* × *G. reptans*; a — growth habit of plant; b — basal leaf; c — cauline leaves; d — flower — top view; e — flower —bottom view; f — petals; g — achenes in flower; h — receptacle with one achene; i — achene

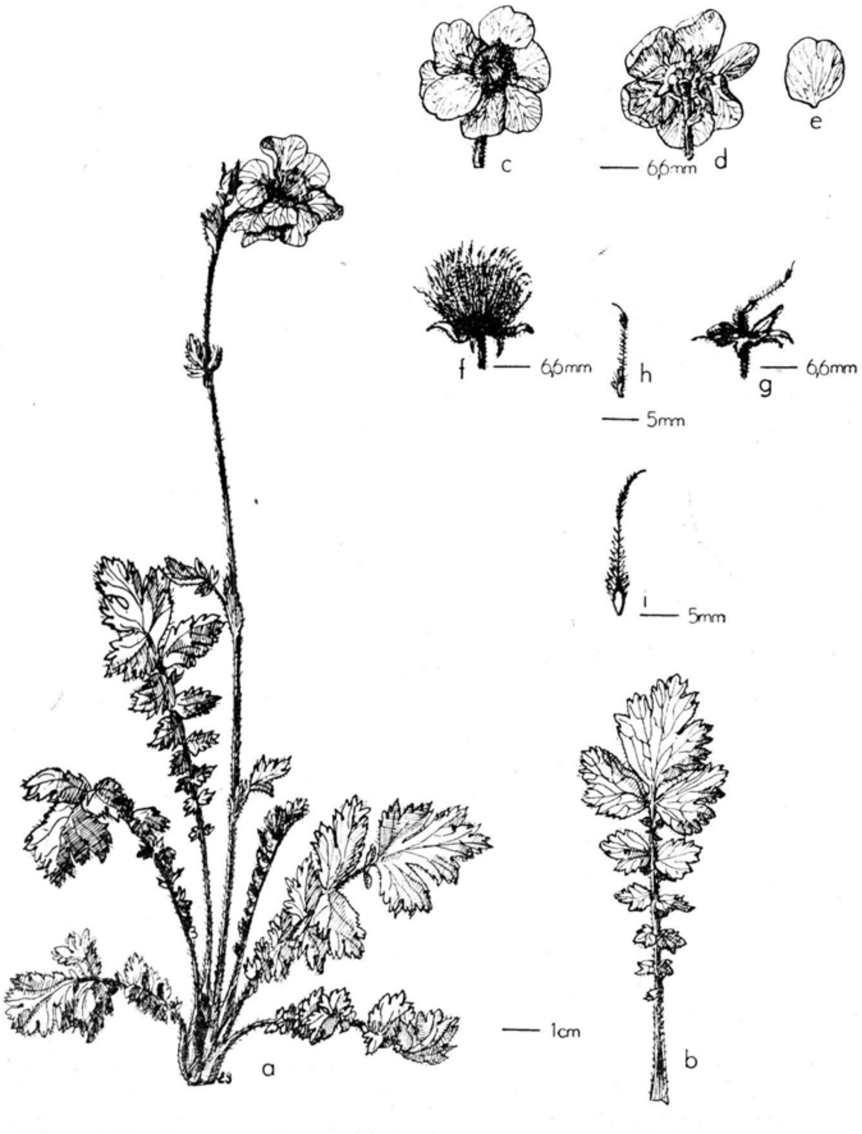

Fig. 76. F$_1$ *Geum coccineum* × *G. reptans*; a — growth habit of plant; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — undeveloped achene; i — good achene

haired styles. In the expression of the styles in the hybrids there is no trace of influence of the hooked styles characteristic for the parental species from subgenus *Eugeum*. This is all the more remarkable as of all hexaploid *Eugeum* species crossed with *G. montanum* the greatest dominance of the hooked style character over the straight style of *G. montanum* is displayed by *G. rivale* and *G. coccineum*.

The two hybrids are completely sterile and during the several years that the plants were cultivated not one good achene capable of germination was gathered from them. Pollen from the hybrid *G. rivale* × *reptans* contains from 0.5 to even over 10 per cent of grains staining in acetocarmine. Some of the grains are rather big and probably have an unreduced chromosome number. In the hybrid *G. coccineum* × *reptans* the number of good pollen grains is smaller, ranging from 0.1 to 1.2 per cent in the various preparations and it seems that here also the majority of good grains has an unreduced chromosome number. As some few achenes from the two hybrids develop occasionally and have at least partly developed embryos, it is not impossible that an amphiploid progeny will be obtained from the union of two unreduced gametes.

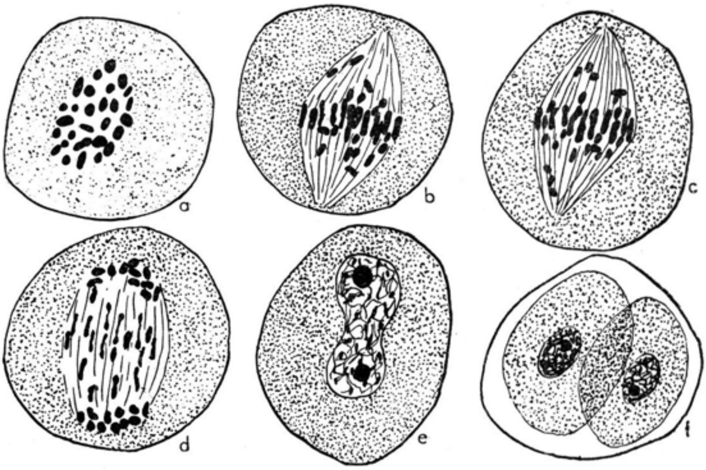

Fig. 77. F_1 *Geum coccineum* × *G. reptans*, meiosis in PMCs; a — M-I with 28 chromosomes ($14_{II} + 14_{I}$); b — M-I with 12 bi- and 16 univalents; c — M-I with 10 bi- and 22 univalents; d — A-I with univalents on the spindle; e — restitution nucleus; f — dyad

Cytological examination: — *G. reptans*, similarly as *G. rivale* and *G. coccineum*, is a hexaploid species and consequently the two hybrids are also hexaploid. The meiotic division in the hybrid *G. rivale* × *reptans* was described in an earlier report (W. Gajewski 1942). It was then stated that in the majority of PMCs at metaphase there are 14 bivalents and 14 univalents. On the whole the meiotic division in the hybrid *G. coccineum* × *reptans* is very much similar, but in the majority of PMCs the number of bivalents in metaphase of the I-st division is less than 14 (Fig 77). In 25 PMCs at the stage of the I-st division metaphase the following configurations were found:

$14_{II} + 14_{I}$ in 8 PMCs
$13_{II} + 16_{I}$ in 3 PMCs
$12_{II} + 18_{I}$ in 2 PMCs
$11_{II} + 20_{I}$ in 5 PMCs
$10_{II} + 22_{I}$ in 6 PMCs
$9_{II} + 24_{I}$ in 1 PMC

In metaphase the bivalents are arranged neatly in the equatorial plane and the univalents are scattered throughout the spindle. In anaphase after the separation of the bivalents most univalents remain on the spindle and in late anaphase they are divided between the two nuclei. In telophase restitution nuclei are occasionally found (Fig. 77e). In metaphase of the II-nd division metaphasal plates containing 18 to 23 chromosomes are to be seen. 2—3 chromosomes often lie outside the two metaphasal plates. Among the tetrads there are about 1 to 1.5 per cent of dyads and over 2 per cent of tetrads have additionally two small cells.

B. Intrasubgeneric *Geum* hybrids

Hybrids between species of subgenus *Eugeum* were the first to be identified and are the most numerous. Many of them are found in the natural state in areas where various *Eugeum* species co-exist and some were obtained artificially by Gärtner. Exact genetical investigations have referred so far only to the hybrid *G. rivale* × *urbanum* and were carried out by Winge (1926), Marsden-Jones (1930), Prywer (1932) and others. In the course of the present research I have found that any two species from subgenus *Eugeum* can be crossed without any restrictions and will give numerous, viable hybrids. So far I have obtained 91 different interspecific hybrids and this number could be further increased.

Far less complete are the data referring to interspecific hybrids within other subgenera. Some reports have been made on interspecific hybrids within the subgenera *Oreogeum, Erythrocoma* and *Acomastylis* and will be reviewed more fully in chapter IX. In my experiments, besides the hybrids from subgenus *Eugeum*, I obtained only one hybrid between two *Oreogeum* species. I shall first describe the hybrid in subgenus *Oreogeum* and then the numerous hybrids in subgenus *Eugeum*.

a. Hybrids in subgenus *Oreogeum*

30. *G. montanum* L. (14) × *G. reptans* L. (21), Fig. 78, culture no. 171/48. The hybrid was already described in detail (W. Gajewski 1952) and only its more important characters will be briefly compared with the parent species. The two species differ only slightly in respect

to the structure of flowers and pistils. *G. reptans* has 6 to 10 petals, elliptically rounded, and *G. montanum* has usually 5 or sometimes 6 round petals. The size of the petals in the parent species and the hybrid are as follows:

G. montanum (length × width in mm)	16.6 × 15.7
G. reptans	17.2 × 11.0
F_1	16.0 × 16.4

Moreover, *G. reptans* usually has 2 segments of the epicalyx between each two sepals and *G. montanum* has one segment between two sepals. In the hybrid this character is greatly variable so that on one plant there can be some flowers with a single and others with a double epicalyx, or even in one flower there can be both single and double epicalyx segments. An important character distinguishing *G. reptans* from *montanum* is the shape of the leaves which in *G. reptans* are uniformly dissected and in *G. montanum* have numerous small lateral leaflets and a big round terminal leaflet. In the hybrid the leaf shape is intermediate with a larger, deeply incised terminal leaflet. The long runners of *G. reptans* are an entirely recessive character and runners are never developed in the hybrid. *G. reptans* forms a strong central root which fixes it firmly to the ground. This is necessary as *G. reptans* grows in rock crannies and on screes where there is no surface cover of soil and where long roots are a help in fixing the plant to the ground. *G. montanum* has a long creeping caudex with many adventitious roots and grows in places where a surface layer of soil has already formed. In the hybrids the caudex is dominant and in this respect they are identical with *G. montanum*. This cross was obtained by pollinating *G. montanum* with pollen from *G. reptans* which flowered quite exceptionally in Warsaw in 1947. The setting of seeds was nearly normal and amounted to about 80 per cent. From the numerous achenes seedlings were obtained from nearly 100 per cent of the seed, but the majority of the seedlings perished in the early stages of growth. Only 10 plants out of the initial 78 seedlings survived to the flowering state. The F_1 plants flowered abundantly and some of them survieved in the cultures for 5 years, though in the Warsaw climate they are not easy to cultivate and often perish during the dry summer weather and heat waves.

The fertility of the hybrids is very low. The percentage of good pollen is about 0.7. Seemingly good achenes are extremely rare and not more than one is found on several tens or even several hundred flowers. However, none of these achenes have as yet germinated.

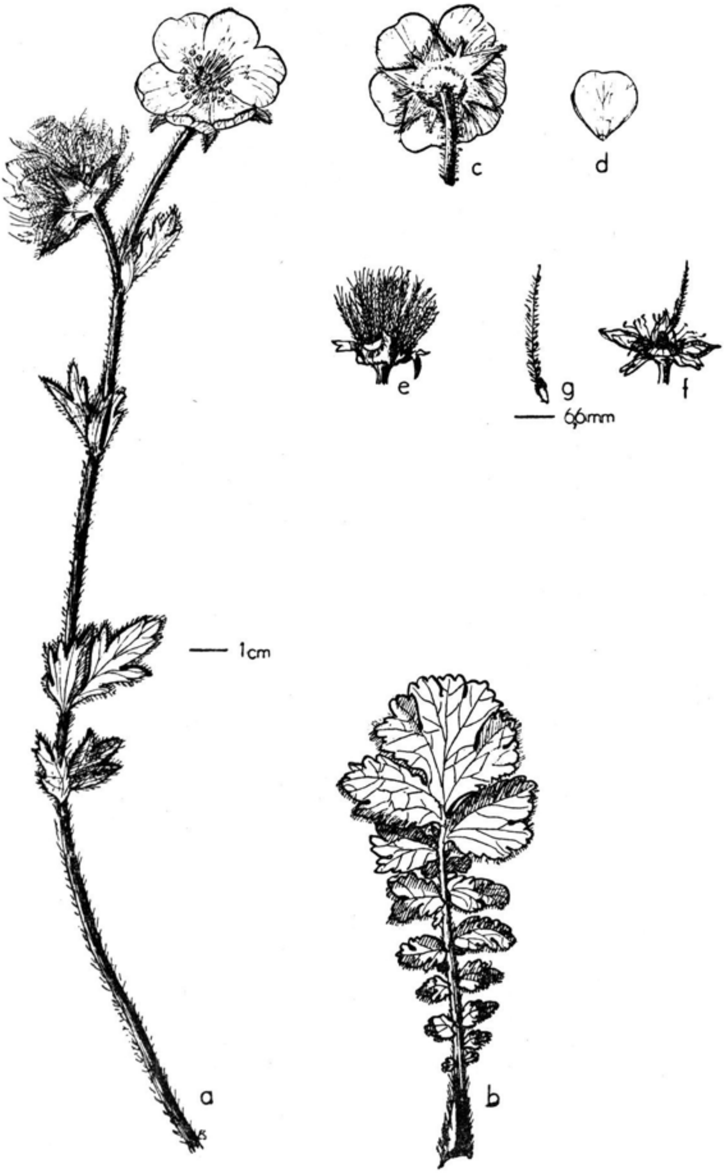

Fig. 78. F$_1$ *Geum montanum* × *G. reptans;* a — floral stem; b — basal leaf; c — flower — bottom view; d — petal; e — achenes in flower; f — receptacle with one achene; g — achene

Cytological examination: — The hybrid is pentaploid with 2n = 35. This was confirmed in metaphasal plates from root tips. Usually in the PMCs at metaphase of the I-st division 14 bivalents and 7 univalents are formed. In 28 out of the 32 analysed cells 14 bivalents were found, in 4 PMCs there were 13 or 12 bivalents and the corresponding 9 or 11 univalents. During the I-st division daughter nuclei with 18 to 20 chromosomes are formed. During the second division the disturbances are fewer and the majority of tetrads have a normal appearance. The description of the meiotic division in this hybrid and the drawings illustrating it were published earlier (W. Gajewski 1952).

b. Hybrids within subgenus *Eugeum*

This is the most numerous group of hybrids which comprises different combinations and consequently will be described only on chosen examples of the most typical hybrids. In the description which now follows the sequence will be — as stated in the introduction — according to the degree of polyploidy in the parental species.

1. Hybrids between dodecaploid species

To exemplify this group of hybrids the description will be made of hybrid no. 31 *G. magellanicum* Pers. × *G. riojense* Bolle, Fig. 79, culture no. 157—53. The characters of the hybrid in relation to those of the parent species are listed below:

Character	*G. magellanicum*	F_1	*G. riojense*
Basal leaves	long; lateral leaflets numerous, big; terminal leaflet ± round with cordate base	intermediate	terminal leaflet trilobate, cuneate; lateral leaflets elongated, rhomboid
Floral stems	straight, 70—80cm tall, 2—5-floral	creeping at base, up to 100 cm long, 9—17-floral	creeping at base, up to 50 cm long, 5—9-floral
Stipules of cauline leaves	small, entire	big, incised	big, incised
Pubescence	dense, soft, beyond the middle numerous glandular hairs	dense, soft, numerous glandular hairs	less dense, more bristly, glandular hairs less numerous
Size of petals (mm)	12.7 × 13.0	12.4 × 13.0	8.7 × 7.8
Length of floral base (mm)	6 — 10	6 — 8	5 — 8
Number of achenes	200 — 240	120 — 150	90 — 120
Length of rostrum (mm)	2 — 3	3.5 — 4	4.5 — 5
Length of stigmatic part (mm)	2.5 — 3	2	1.5 — 2

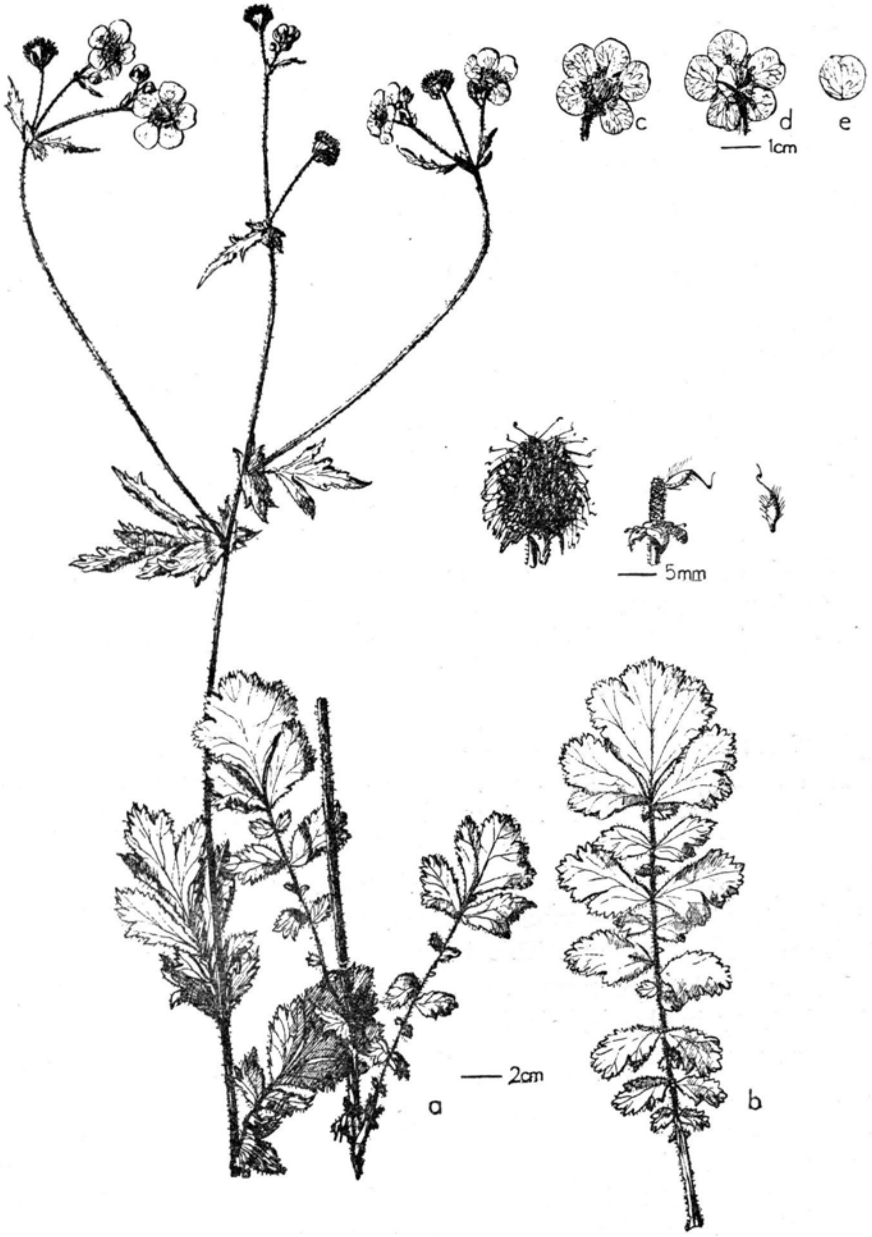

Fig. 79. F₁ *Geum magellanicum* × *G. riojense*; a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal

Besides the characters mentioned in the list above, *G. riojense* has the whole upper part of the floral stem drooping at anthesis. In the hybrid this character is recessive in respect to the erect floral peduncles of *G. magellanicum*. Moreover, in the case of this cross, as well as of all the other hybrids described next, the parental species and the hybrids differ by many minor traits such as: the character of incisions and toothings of the leaves, the distribution of various kinds of hairs on the leaves, stems, floral base, achenes, rostrum and the stigmatic part of the styles, the colour shade of petals, small amounts of anthocyanin, length of floral peduncles at anthesis and fruiting, time of flowering, and several other details not mentioned. As full descriptions of all these characters in the case of every hybrid would unnecessarily increase the volume of this work they are deliberately omitted and only the more conspicuous characters are mentioned.

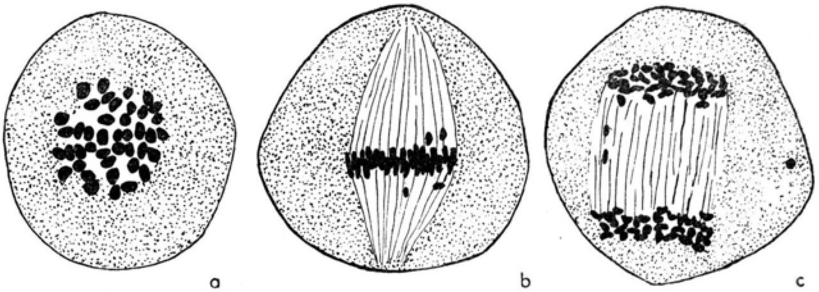

Fig. 80. F_1 *Geum magellanicum* × *G. riojense*, meiosis in PMCs; a — M-I with 42 bivalents; b — M-I with 4 univalents on the spindle; c — A-I with one dividing univalent and one univalent in the cytoplasm

The hybrid *G. magellanicum* × *riojense* displays marked heterosis and very vigorous growth. This is manifested by bigger leaves, longer floral stems and more numerous flowers than in the parental species. Pollen fertility in this hybrid is on the average 61.9 per cent. The percentage of good achenes ranges between 23.4 and 42.2 averaging at 27.3.

The meiotic divisions in the PMCs of the hybrid are almost completely normal (Fig. 80). In 47 cells at the stage of the I-st division metaphase in profile view all the chromosomes were seen to be arranged in compact metaphasal plates and rarely 2—6 univalents were lying outside the plate on the spindle (Fig. 80 b). This indicates that normally only bivalents are formed similarly as in both parental species. In two metaphasal plates viewed *en face* where it was possible to count all the chromosomes 42 bivalents were found (Fig. 80 a). The anaphase of the I-st division has also a normal course in the majority of PMCs. In the course of the II-nd division — which was not found in preparations from this hybrid — tetrads with an absolutely normal appearance are formed.

34. *G. Fauriei* Lev. (42) × *G. riojense* Bolle (42). This hybrid similarly as the preceding one is very vigorous, its numerous thick floral stems are up to 80 cm tall, strongly branched and multifloral. However, in contrast with the preceding hybrid this one has pollen fertility of only about 0.2 per cent of good pollen and forms no good seeds.

Cytological examination: — The examinations in this case were very inaccurate because of the bad preparations which were obtained, the large number of chromosomes, and great disturbances in both meiotic divisions (Fig. 81). In metaphase of the I-st division in all PMCs there are, besides the bivalents lying on the plate, 15 to 36 univalents scattered throughout the spindle. In anaphase there are very many univalents lagging on the spindle and restitution nuclei are fairly often formed. The disturbances are also numerous in the II-nd division and many chromosomes remain on the spindle both in M II and A II stages. The chromosome number varies greatly and is very difficult to assess because of the numerous chromosomes lying outside the plates. In 2 PMCs the chromosome numbers were probably about 38 and 52 and in one PMC with one plate which possibly had arisen from a restitution nucleus about 85 chromosomes were counted. The percentage of dyads at the tetrad stage was about 2.5.

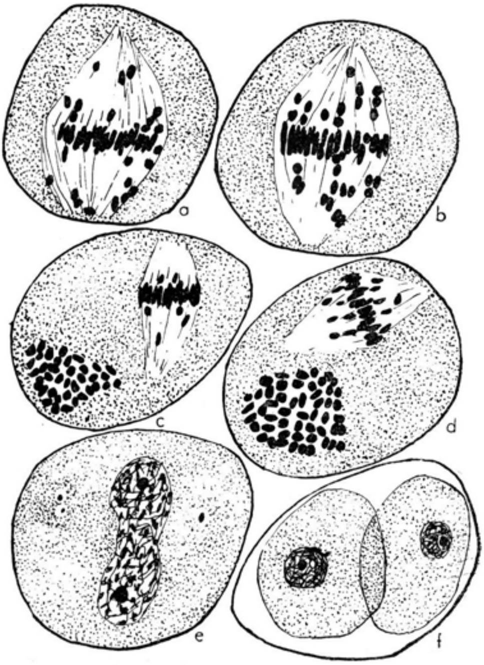

Fig. 81. F₁ *Geum Fauriei* × *G. riojense*, meiosis in PMCs; a — M-I with 23 univalents dispersed on the spindle; b — M-I with 30 univalents dispersed on the spindle; c — M-II with 38 chromosomes in one of the plates; d — M-II with about 52 chromosomes in one of the plates; e — restitution nucleus; f — dyad

The crosses *G. magellanicum* × *pyrenaicum* and *G. Fauriei* × *pyrenaicum* were obtained and sown out in 1952. Till 1955 the hybrids did not flower. Their growth was strongly inhibited and after three years most plants perished, while those which survived produced merely small rosettes of basal leaves. The hybrid *G. pyrenaicum* × *riojense* behaved similarly and after two years it did not show any tendency to flower, the plants being small and weak. It is worth noting that in all these crosses one of the parental forms was *G. pyrenaicum* and it may be that this species introduced into these combinations some factor inhibiting hybrid growth.

The last to be described among the hybrids between dodecaploid species is the hybrid *G. magellanicum* Pers. (42) × *G. Fauriei* Lev. (42). A number of plants of this hybrid flowered for the first time in 1955 displaying much hybrid vigour. The stems at fruiting are up to 120 cm tall, strongly branched at the top, with 15 to 23 flowers, and roughly bristly haired without glandular hairs. The basal leaves with a big trilobate terminal leaflet resemble in shape the leaves of *G. Fauriei*. The cauline leaves have big, elongated, deeply incised stipules, the lower cauline leaves are multifoliolate as the basal leaves and the upper ones are trifoliolate. Floral peduncles are straight, long, without anthocyanin. The calyx is recurved at anthesis, the petals are horizontal, yellow, about 11.5 mm long and 11.5 wide, cordately incised at tip. 100 per cent of pollen is sterile and so far the F_1 plants have not produced one normally developed achene. The hybrid was not examined cytologically.

2. *Hybrids between dodeca- and decaploid species*

As an example of this group of crosses the hybrid no. 37 *G. riojense* Bolle (42) × *G. Quellyon* Sweet (35) will be described. The characters of this hybrid are compared with those of the parent species:

Character	*G. riojense*	F_1	*G. Quellyon*
Basal leaves	terminal leaflets trilobate, cuneate	resembling *Quellyon*, but terminal leaflet more deeply incised	terminal leaflet round, incised, with cordate base
Floral stems	creeping at base, to 50 cm long, 5 — 9-floral	straight, to 60 cm tall, 5 — 9-floral	straight, to 70 cm tall, 7 — 12-floral
Colour of petals	yellow	pale red	red
Size of petals (mm)	8.7 × 7.8	10.4 × 8.9	10.4 × 10.8
Length of stigmatic part (mm)	1.5 — 2	2.5 — 3	3.5 — 4

Both these S. American species rather resemble each other and display few distinctly contrasting characters. Other not mentioned differences between the parental species and the hybrid consist in the shape of cauline leaves and stipules, and in the degree and nature of pubescence on cauline leaves, achenes, floral base, rostrum and stigmatic part. The fertility of the hybrid is fairly high and averages for pollen at 36.4 per cent. The percentage of well developed achenes is 15 to 32, average 24.4 per cent.

Meiotic divisions in PMCs (Fig. 82): — In view of the chromosome numbers in the parent species it seems that the hybrid should be an 11-ploid with 2n = 77. However, it was impossible to confirm this on preparations from root tips as the metaphasal plates were not clear enough to make the counting of chromosomes possible. At metaphase of the I-st division in PMCs 42 to 45 chromosomal bodies were found, but in the front view of the plates it was impossible to distinguish the uni- from the bivalents. Side views of metaphase reveal that very numerous bivalents form a compact plate and 7 to 13 univalents lie on the spindle close to the metaphasal plate (Fig. 82, b, e).

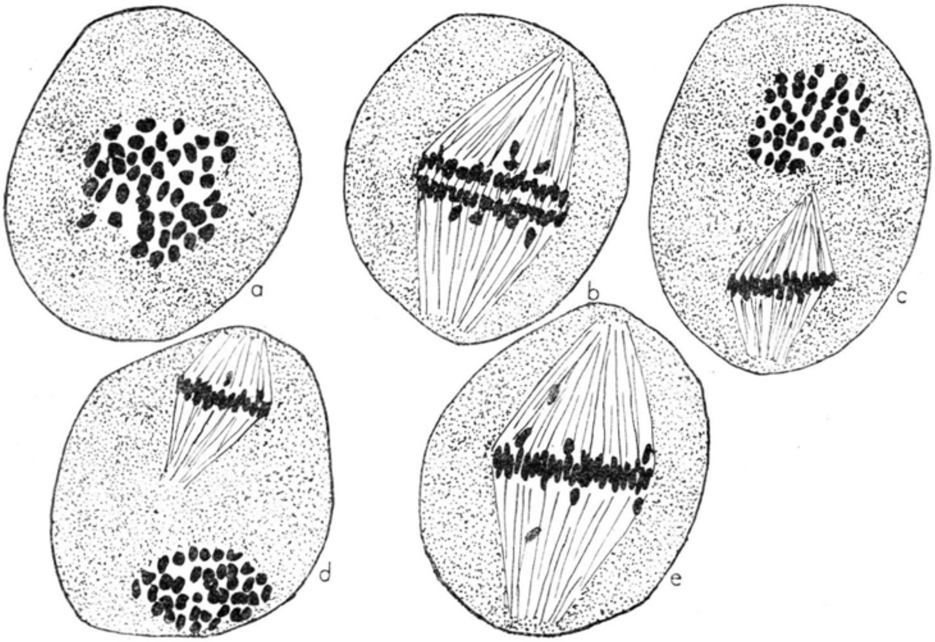

Fig. 82. F_1 *Geum riojense* × *G. Quellyon,* meiosis in PMCs; a — M-I with 44 chromosomal bodies; b — early A-I with 7 univalents; c — M-II with 40 chromosomes in one of the plates; d — M-II with 38 chromosomes in one of the plates; e — M-I with 7 univalents

At anaphase the majority of univalents are separated together with the bivalents and consequently the appearance of anaphase is very often quite normal without chromosomes lagging on the spindle. Sometimes, however, some univalents do lag on the spindle in anaphase and reach the poles much later than the bivalents. On the whole, the second division is quite normal. The number of chromosomes in two plates where it was possible to count them was 38 and 40 (Fig. 82, c, d). The tetrads look normal and there are four microspores in every one.

The cross *G. magellanicum* Pers. (42) × *G. Quellyon* Sweet (35) gives plants displaying much hybrid vigour. The stems at fruiting are up to 90 cm tall and bear 8 to 10 flowers. The stems are softly haired with glandular hairs. The glandular hairs are especially numerous on the peduncles and sepals. The basal leaves are very elongated, up to 40 cm in length, with numerous lateral leaflets, and a deeply incised cuneately based terminal leaflet. The flowers on the erect peduncles have a calyx reflexed at anthesis, the petals are orange yellow, almost round, cordate at tip, about 12 mm long and 12.5 mm wide. The percentage of good pollen in acetocarmine smears is only 0.2—0.3. So far the hybrid has not produced even one good achene. Cytological examinations were not carried out in this case.

The hybrid *G. Quellyon* Sweet (35) × *G. pyrenaicum* Willd. (42) was cultivated during three consecutive years and during this time it showed no tendency to flower forming rosettes of basal leaves only. The plants were very weak and after 3 years most of them perished.

3. Hybrids between dodeca- and hexaploid species

In this group the following hybrids were obtained: 5 hybrids, nos. 40—44, with *G. magellanicum*; 7 hybrids, nos. 45—51, with *G. pyrenaicum*; 3 hybrids, nos. 52—54, with *G. riojense*; and 6 hybrids, nos 55—60, with *G. Fauriei*. These four dodecaploid species were crossed with various hexaploid ones. It may be stated as a general rule for this group of hybrids that all of them are completely or almost completely sterile. Usually the morphological characters of the dodecaploid parent are distincly dominant. To illustrate the whole group one hybrid of the four dodecaploid species with *G. rivale* will be described here.

40. *G. magellanicum* Pers. (42) × *G. rivale* L. (21), Fig. 83, culture no. 7—49. The characters of this hybrid and the corresponding characters of the parent species are tabulated below.

The parental species are very easy to cross, the setting of seeds being in both reciprocal directions at the level of 70 to 80 per cent. The reciprocal hybrids are exactly similar, uniform, growing vigorously and

Character	*G. magellanicum*	F_1	*G. rivale*
Basal leaves	terminal leaflet ±round, with cordate base	terminal leaflet round or incised	terminal leaflet incised into 3 cuneate lobes
Floral stem	70 — 80 cm tall, 2 — 5-floral	70 — 90 cm tall, 8 — 12-floral	45 — 60 cm tall, 3 — 5-floral
Anthocyanin in stems and flowers	traces	fairly abundant	abundant
Floral peduncles	straight	straight	drooping
Calyx	sepals reflexed	± reflexed or horizontal	sepals erect
Length of sepals (mm)	± 7	± 7	± 12
Position of petals	horizontal	horizontal or ± erect	erect
Colour of petals	yellow	yellow	creamy
Size of petals (mm)	12.7 × 13.0	10.5 × 12.0	10.1 × 8.0
Claw on petals	absent	± absent	long
Gynophore	absent or 1 mm long	absent or 1 mm long	8 — 10 mm long

flowering abundantly. Pollen fertility is very low, about 0.1 per cent. The hybrid is almost entirely sterile and during three years from hundreds of flowers it developed a few achenes once only.

Meiotic divisions in PMCs (Fig. 84): — In the case of this hybrid the preparations showing the stage of late diakinesis were rather good, though, because of the large number of chromosomes it was very difficult to count them all accurately. In 4 PMCs there were probably 42 chromosomes in every nucleus, of which about half were clearly univalents and the rest bivalents. In the remaining 12 analysed cells the total chromosome number was greater than 42 and ranged between ± 43 and 47, but in no case was it possible to establish this number with any degree of accuracy. At the stage of the I-st division metaphase the analysis of the metaphasal plates is also difficult as many chromosomes lie outside the plane of the plate. The approximate chromosome numbers in the plates range from 42 to 49, which corresponds to configurations from $21_{II}+21_{I}$ to $14_{II}+35_{I}$. Relatively the easiest to count were the univalents in the side view of metaphase where on the background of the bivalents tightly packed in the plate the univalents scattered on the spindle were easy to pick out. The analysis of 43 PMCs seen in profile at the metaphase stage revealed the following numbers univalents:

21 in 8 cells
23 in 14 cells
25 in 8 cells
26 in 2 cells
27 in 10 cells.

Fig. 83. F_1 *Geum magellanicum* × *G. rivale*; a — floral stems; b — basal leaves; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

In anaphase after the separation of bivalents a ring composed of 18 to ± 23 univalents is formed on the spindle (Fig. 80 d). These univalents are stretched out in the characteristic manner which has already been described many times in the case of other *Geum* hybrids. In late

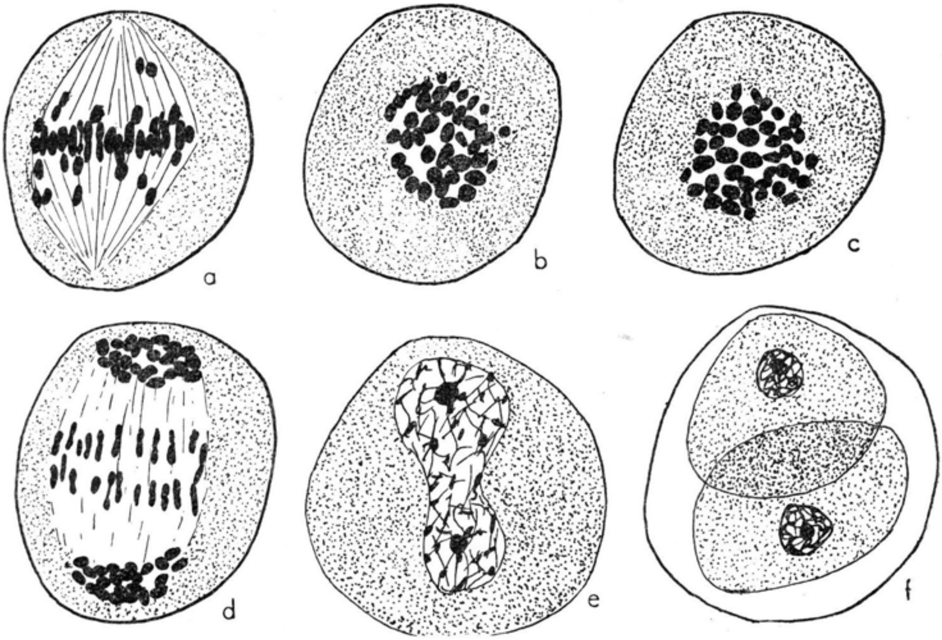

Fig. 84. F_1 *Geum magellanicum* × *G. rivale*, meiosis in PMCs; a — M-I with 21 univalents; b — M-I with 42 chromosomes ($21_{II} + 21_{I}$); c — M-I with 44 chromosomes ($19_{II} + 25_{I}$); d — A-I with 22 univalents arranged in a ring on the equatorial plane of the spindle; e — restitution nucleus; f — dyad

anaphase the univalents move away to the poles. As a result of anaphasal disturbances some univalents are frequently left out of the daughter nuclei and sometimes restitution nuclei are formed (Fig. 80 e). I did not obtain preparations showing either metaphase or anaphase of the second meiotic division. In numerous cells at the stage of II-nd division telophase 4 nuclei were the most common, two small nuclei in addition to the larger ones were rare, and in one case there were only two nuclei much larger than in the cells with four. In the last case the two nuclei had probably originated from a restitution nucleus. Similar conditions prevail among the tetrads. Among the 234 analysed cells 6 dyads were found, which amounts to 2.1 per cent.

The dodecaploid *G. magellanicum* was also crossed successfully with the following hexaploid species: *G. aleppicum, hispidum, canadense*, and *macrophyllum*. All these crosses gave hybrids intermediate between the parent species in respect to morphology, though more resembling *G. magellanicum* than the hexaploid parent. The fertility of these hybrids is similar as in the hybrid *G. magellanicum* × *rivale*, i.e. 1 to 5 pro mille.

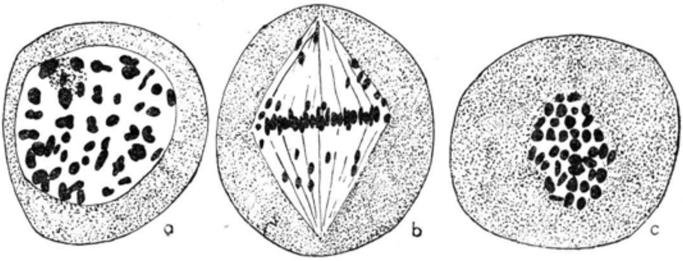

Fig. 85. F$_1$ *Geum magellanicum* × *G. aleppicum*, meiosis in PMCs; a — diakinesis with 45 chromosomes ($18_{II} + 27_{I}$); b — M-I with 25 univalents on the spindle; c — M-I with about 39 chromosomes ($24_{II} + 15_{I}$)

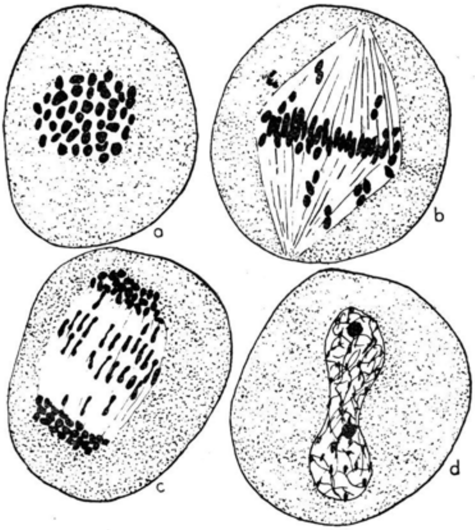

Fig. 86. F$_1$ *Geum magellanicum* × *G. hispidum*, meiosis in PMCs; a — M-I with 43 chromosomes ($20_{II} + 23_{I}$); b — M-I with 23 univalents on the spindle; c — A-I with univalents on the equatorial plane of the spindle; d — restitution nucleus

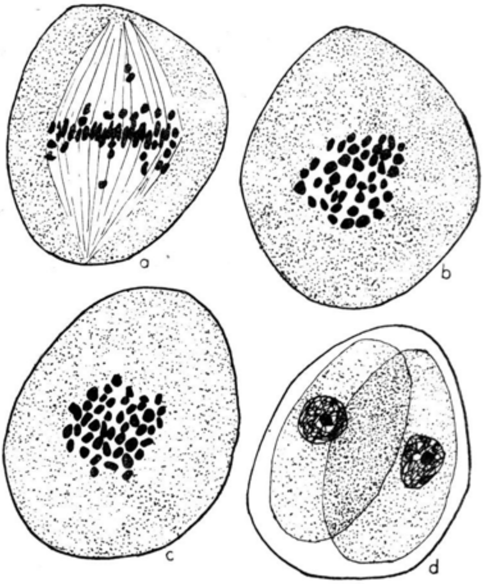

Fig. 87. F$_1$ *Geum magellanicum* × *G. macrophyllum* meiosis in PMCs; a — M-I with 25 univalents on the spindle; b — M-I with 42 chromosomes ($21_{II} + 21_{I}$); c — M-I with 44 chromosomes ($19_{II} + 25_{I}$); d — dyad

G. magellanicum × *canadense* is here an exception in that it is entirely sterile. In the majority of flowers it produces small undeveloped stamens and this is usually associated with the lack or only partial development of petals. Even in the flowers with better developed stamens the archespore in the anthers degenerates before the beginning of the reduction divisions. In the other hybrids with *G. magellanicum* meiosis in the PMCs develops on the whole according to the same pattern as in the hybrid with *G. rivale* already described, i.e. the number of bivalents is between 15 or 16 and 21 and the number of univalents is from 33 to 21 (Figs. 85—87).

45. *G. pyrenaicum* Willd. (42) × *G. rivale* L. (21), culture no. 11/39. The characters of the hybrid as compared with the parent species are the following:

Character	*G. pyrenaicum*	F_1	*G. rivale*
Basal leaves	terminal leaflet big, round, with cordate base	terminal leaflet big, round, incised, with cordate base	terminal leaflet dissected into 3 cuneate lobes
Floral stem	30 — 40 cm tall, 1 — 3-floral	30 — 60 cm tall, 3-floral	45 — 60 cm tall, 3 — 5-floral
Anthocyanin in stems and flowers	none	fairly abundant	abundant
Floral peduncles	straight	slightly drooping	drooping
Calyx	expanded	expanded	erect
Length of sepals (mm).	9	9	12
Position of petals	horizontal	horizontal or ± erect	erect
Colour of petals	yellow	yellow	creamy
Size of petals	11.5×12.0	11.5×12.0	10.1×8.0
Claw on petals	absent	absent or very small	long
Gynophore	absent	absent	8-10 mm long
Floral base	2-3 mm long, long haired	3-4 mm long, long haired	6-7 mm long short haired
Number of achenes	about 55	80-90	150-200
Length of achenes (mm)	6-7	6	3.5-4
Length of rostrum (mm)	6-8	6.5	8-10

The hybrid was obtained as early as 1939, it was propagated vegetatively by dividing the rhizomes and survived till 1953. Pollen fertility of the hybrid was about 0.8 per cent and the fertility of seeds was even less. Usually in several tens of flowers only one good achene could be found.

Meiotic divisions in PMCs (Fig. 88): Meiotic division in this hybrid was described elsewhere (W. Gajewski 1945). In that earlier paper drawings and microphotographs of various meiotic stages in this hybrid were published. In 51 cells analysed at the stage of I-st division metaphase the following chromosome configurations were found:

$21_{\mathrm{II}} + 21_{\mathrm{I}}$ in 35 cells
$20_{\mathrm{II}} + 23_{\mathrm{I}}$ in 8 cells
$19_{\mathrm{II}} + 25_{\mathrm{I}}$ in 6 cells
$22_{\mathrm{II}} + 19_{\mathrm{I}}$ in 2 cells.

The delay in the separation of numerous chromosomes results in the formation of restitution nuclei in telophase or the elimination of some chromosomes which are not included in the daughter nuclei. In the second division at metaphase some chromosomes lie frequently on the spindles outside the plates and at anaphase some of them lang on the spindles.

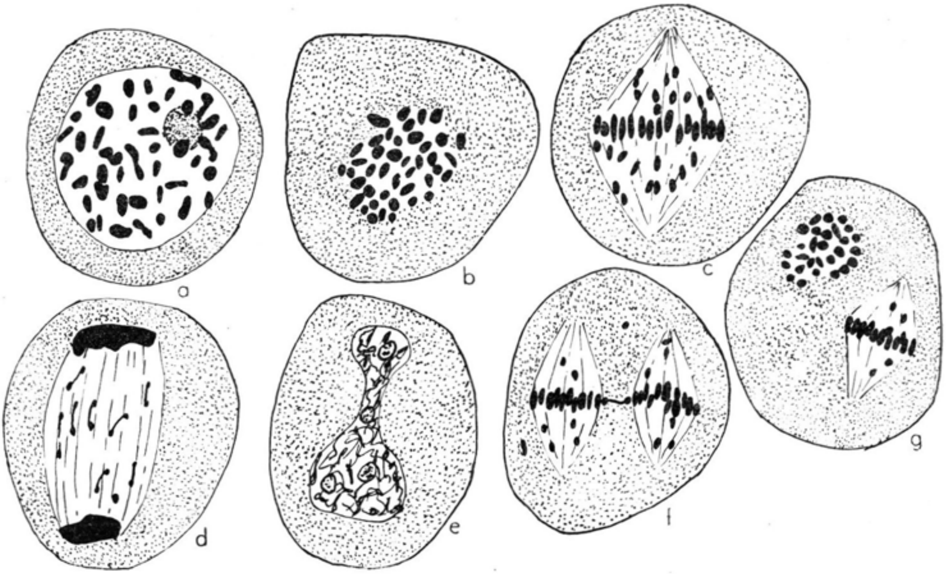

Fig. 88. F_1 *Geum pyrenaicum* × *G. rivale*, meiosis in PMCs; a — diakinesis with 42 chromosomes ($21_{\mathrm{II}} + 21_{\mathrm{I}}$); b — M-I with 42 chromosomes ($21_{\mathrm{II}} + 21_{\mathrm{I}}$); c — M-I with 23 univalents on the spindle; d — A-I with some univalents strongly stretched out on the spindle; e — restitution nucleus; f — M-II with univalents on the spindles and in the cytoplasm and a chromosomal bridge persisting from A-I; g — M-II with 28 chromosomes in one of the plates

At the tetrad stage the majority of cells contain four microspores, though hexads with 6 spores are also found, and there is nearly one per cent of dyads with two microspores.

Almost identical meiotic divisions were observed also in the hybrids of *G. pyrenaicum* with *G. urbanum, coccineum, silvaticum, macrophyllum, molle* and *aleppicum* (Figs. 89 and 90). As the meiotic division in the hybrid *G. pyrenaicum* × *rivale* was described on an earlier occasion

(W. Gajewski 1949) at present also drawings illustrating the course of meiosis in the hybrid *G. pyrenaicum* × *aleppicum* are provided. It must be stressed that when the hybrids with *G. pyrenaicum* considered here are compared with the corresponding hybrids with *G. magellanicum* the majority of cells in the former case are seen to have 21 or 20 bivalents and cells with fewer bivalents numbering 20 to 14 are either not found or are far more rare than in the hybrids of these hexaploid species with *G. magellanicum.* In the hybrids *G. pyrenaicum* × *rivale* and *G. pyrenaicum* × *aleppicum* (Fig. 89 d) inversion bridges with acentric chromosomal fragments are sometimes found at anaphase in the I-st division.

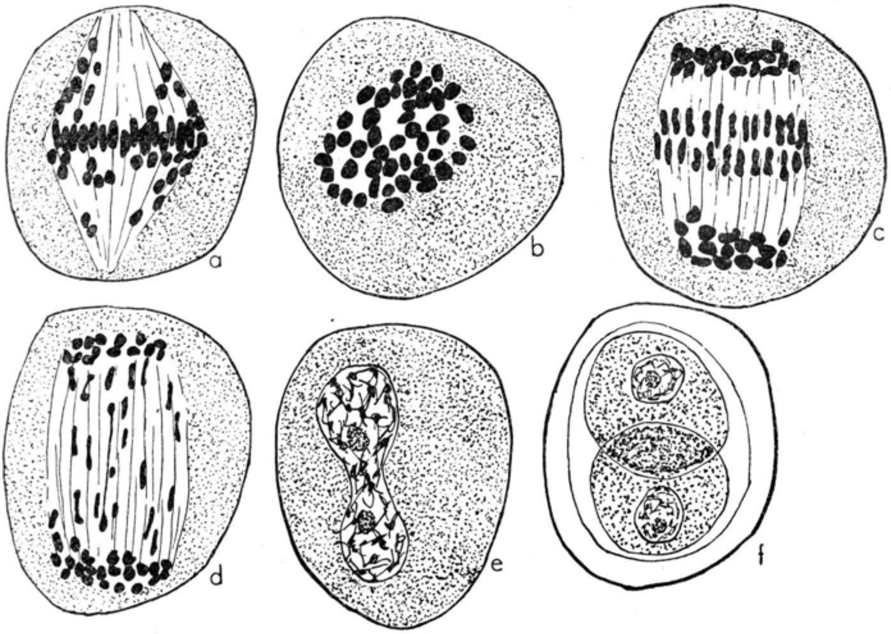

Fig. 89. F_1 *Geum pyrenaicum* × *G. aleppicum*, meiosis in PMCs; a — M-I with 33 univalents on the spindle; b — plate from M-I with 48 chromosomes ($15_{II} + 33_{I}$); c — anaphase with 24 univalents arranged in a ring on the equatorial plane of the spindle; d — later anaphase with univalents segregating to the poles and one inversion bridge; e — restitution nucleus; f — dyad

In the hybrids of *G. pyrenaicum* with *G. coccineum. silvaticum, molle, urbanum* and *macrophyllum* pollen fertility is less than 1 per cent and seed fertility is even lower. Usually, from several specimens with several tens of flowers on every one, not more than 1 or 2 normally developed achenes can be gathered.

A very remarkable phenomenon is displayed by the hybrid *G. pyrenaicum* × *G. aleppicum*. The 32 F_1 plants were of two types differing in the development of flowers. One type was represented by 11 plants with normally developed petals, androecium and gynoecium. Pollen and seed fertility were about 0.2 and 0.01 per cent respectively.

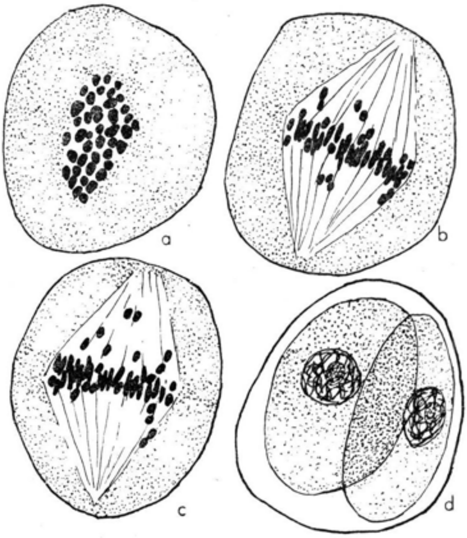

Fig. 90. F_1 *Geum pyrenaicum* × *G. molle*, meiosis in PMCs; a — M-I with 42 chromosomes ($21_{II} + 21_{I}$); b — M-I with 21 univalents lying near the plate formed by bivalents; c — same in another PMC; d — dyad

The other type was represented by 21 specimens. In flowers of these plants the androecium never developed and in some this referred also to the gynoecium. The flowers displayed also strong disturbances in the development of petals. The petals were usually rumpled, shrunken or with margins irregularly incised. Sometimes only 1 or 2 out of the 5 petals developed (Fig. 91). These plants are of course entirely sterile. It is impossible to examine the course of meiosis in this type of plants as the stamens do not develop at all. In the sister plants with normally developed flowers meiotic divisions follow the same pattern as in other hybrids of this group (c. f. Fig. 89). The plants with undeveloped flowers grow well and vigorously and in respect to all other characters do not differ in any details from the plants with normally developed flowers.

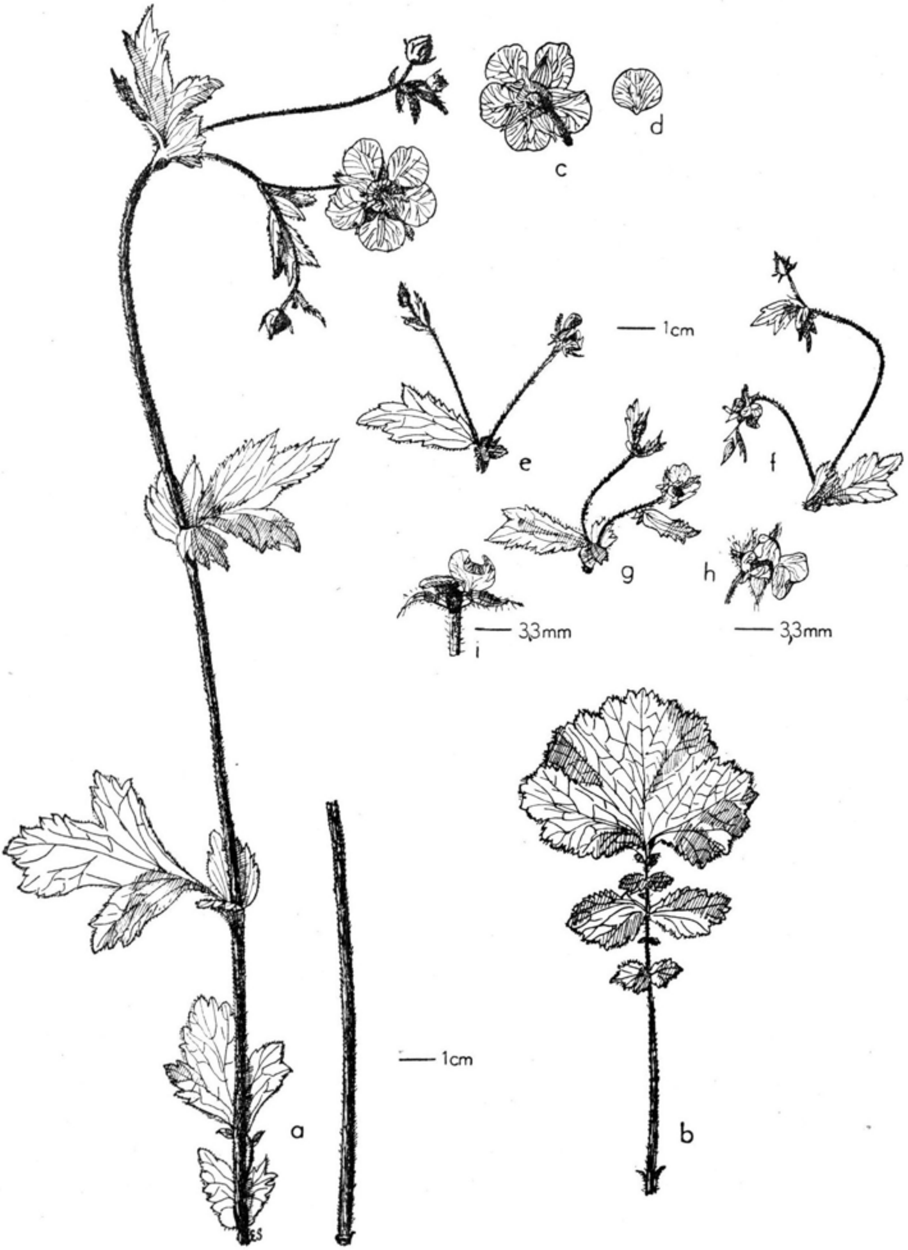

Fig. 91. F₁ *Geum pyrenaicum* × *G. aleppicum;* a — floral stem of individual with normal flowers; b — basal leaf; c — normal flower — bottom view; d — petal of normal flower; e—i — flowers from individuals with abnormal flowers, reduced petals and androecium

53. *G. riojense* Bolle (42) × *G. rivale* L. (21), culture no. 166—54. The characters of this hybrid and of the parent species are compared in the table below:

Character	*G. riojense*	F_1	*G. rivale*
Floral stems	stem arched downwards at top, growing horizontally at base	as in *riojense*	straight
Floral peduncles	straight	straight	drooping
Indumentum on stems and leaves	lower part of plant roughly haired, floral peduncles glandularly haired	as in *riojense*	whole plant softly haired, at top glandularly haired
Anthocyanin in stems and flowers	none	rather abundant	abundant
Length of stems and	40 — 50 cm	40 — 50 cm	45 — 60 cm
number of flowers	5 — 7 flowers	5 — 7 flowers	3 — 5 flowers
Calyx	reflexed	reflexed	erect
Length of sepals (mm)	7 — 8	8	12
Position of petals	horizontal	horizontal or slightly erect	erect
Size of petals (mm)	8.7 × 7.8	10.0 × 9.5	10.1 × 8.0
Colour of petals	yellow	yellow	creamy
Claw on petals	absent	absent	long
Gynophore	absent	absent	8 — 10 mm long
Stipules of cauline leaves	big, incised	big, incised	small, serrate

The percentage of pollen fertility in the hybrid is about 0.2. In 1952 the hybrid flowered very abundantly for the first time, but on the 32 plants not one well developed achene was set. In later years the hybrid was also entirely sterile.

Meiotic divisions in PMCs of the hybrid — as shown on Fig. 92 — are almost exactly the same as in the hybrid *G. pyrenaicum* × *rivale*. Among 12 PMCs analysed at the stage of the I-st division metaphase in 8 cells there were 21 bivalents and 21 univalents and in 4 cells the number of bivalents and univalents was 20 and 23 respectively. The percentage of dyads at the tetrad stage was about 2.

Geum riojense was also crossed with *G. aleppicum* as the paternal species. The setting of seeds after cross pollination was here quite normal and amounted to 96.3 per cent. From the numerous achenes 60 F_1 plants were obtained (the lack of space prevented from planting the others) all very homogeneous morphologically. The plants are enormous, very vigorous, with stems up to 120 cm tall and with 9 to 15 flowers on every stem. Basal leaves reach 33 cm in length. Pollen fertility is here about 0.4 per cent. From the several thousands flowers which opened on these plants only one normally developed achene was collected. This achene resembled closely in shape and size the achenes of *G. riojense*. The meiotic divisions in this hybrid develop along the same pattern as in the one just described (Fig. 93). The only remarkable effect in this

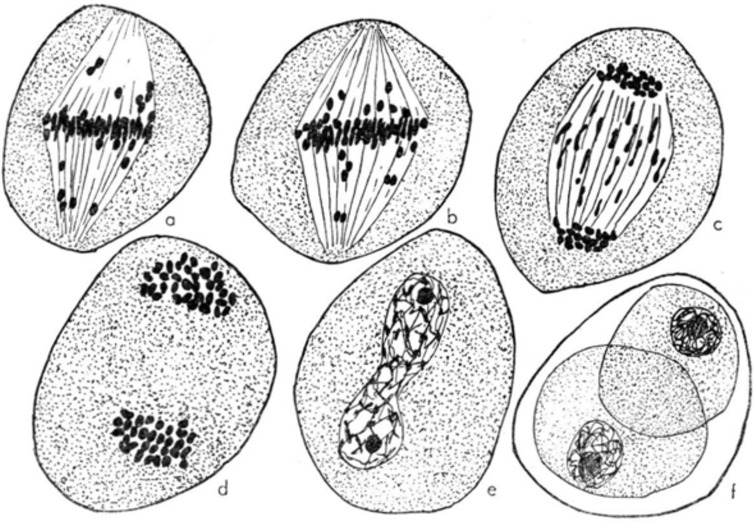

Fig. 92. F_1 *Geum riojense* × *G. rivale*, meiosis in PMCs; a — M-I with 21 univalents on the spindle and near the plate; b — M-I with 25 univalents; c — A-I with univalents segregating to the two poles; d — M-II with 30 and 33 chromosomes in the plates; e — restitution nucleus; f — dyad

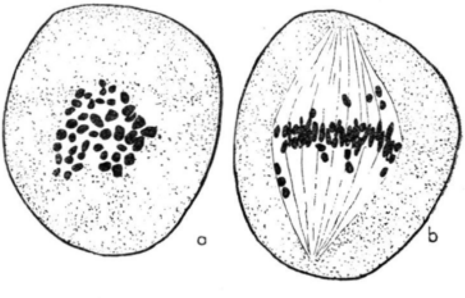

Fig. 93. F_1 *Geum riojense* × *G. aleppicum*, meiosis in PMCs; a — M-I with 43 chromosomes ($20_{II} + 23_{I}$); b — M-I with 21 univalents on the spindle and near the plate

connection is the rather high percentage of dyads which in some preparations amunted to 4 or 6 per cent.

54. The hybrid *G. riojense* Bolle (42) × *G. laciniatum* Murr. (21) resembles very closely in respect to morphology *G. riojense* and is highly sterile. It produces from 0.1 to 0.2 per cent of good pollen and only one well developed achene for every dozen or so of flowers. The hybrid was not examined cytologically.

55. *Geum Fauriei* Lev. (42) × *G. rivale* L. (21), culture no. 111—51. The characters of this hybrid as compared with those of the parental species are listed below:

Character	*G. Fauriei*	F_1	*G. rivale*
Caudex	none	none	well developed
Basal leaves	terminal leaflet big and round	terminal leaflet big, round, deeply trilobate	terminal leaflet dissected into 3 cuneate parts
Floral stems	up to 90 cm tall, 9 — 15-floral	up to 100 cm tall 9 — 17-floral	45 — 60 cm tall, 3 — 5-floral
Floral peduncles	long, somewhat drooping	long, very drooping	very drooping
Indumentum	long bristly haired	resembling *Fauriei*	abundantly glandular beyond the middle
Anhocyanin in stems and flowers	none	abundant	very abundant
Calyx	reflexed	reflexed	erect
Length of sepals (mm)	6	6 — 8	12
Length of epicalyx (mm)	2 — 2.5	3	5 — 6
Position of petals	horizontal	horizontal	erect
Colour of petals	yellow	yellow	creamy
Size of petals (mm)	8.0 × 6.2	10.0 × 7.2	10.1 × 8.0
Claw on petals	absent	absent or very small	long
Gynophore	absent	absent	8 — 10 long
Rostrum	6 — 6.5 mm long, glandulary haired	6 — 7 mm long, glandulary haired	8 — 10 mm long, with glandular and straight hairs
Stigmatic part (mm)	1.5 — 2	3 — 3.5	4.5 — 5
Achenes	several long bristles at tip	as in *Fauriei*	long softly haired and glandularly haired

The hybrid grows very vigorously and flowers abundantly starting earlier than the two parent species. In 1952 *G. rivale* started flowering on May 5, *G. Fauriei* on May 12, and the F_1 hybrid on May 1. Pollen fertility is about 0.2 per cent and fully grown achenes are not developed.

The most frequent chromosome configuration at metaphase of the I-st division in the PMCs consists of 21 bi- and 21 univalents. Cells with

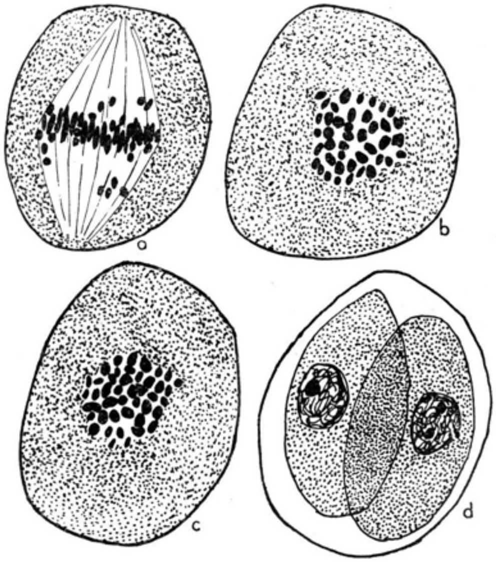

Fig. 94. F_1 *Geum Fauriei* × *G. rivale*, meiosis in PMCs; a — M-I with 21 univalents on the spindle; b — M-I with 42 chromosomes ($21_{II} + 21_{I}$); c — M-I with 43 chromosomes ($20_{II} + 23_{I}$); d — dyad

20 or 19 bivalents and a correspondingly higher number of univalents are also found occasionally. In interkinesis some restitution nuclei are observed (3 in the 197 examined cells). At metaphase of the II-nd division in one cell where it was possible to count all the chromosomes in both plates 25 and 24 were found. This indicates that in anaphase of the I-st division some univalents are divided. At the M II stage some chromosomes lie off the plates on the spindles and in the following anaphase quite numerous chromosomes lag behind. The percentage of dyads among the total number of cells at the tetrad stage is about 2.3.

Quite exceptionally vigorous is the hybrid *G. Fauriei* × *macrophyllum* (Fig. 95). The length of its stems may be even 120 cm and the basal leaves are 38 cm long and have terminal leaflets 15 cm long and 20 cm wide. This is the largest terminal leaflet that I have ever seen in the genus *Geum*. Morphologically the two parental species are fairly closely related. *G. Fauriei* differs from *G. macrophyllum* by its shorter floral base which is covered by longer hairs and has fewer pistils, by the

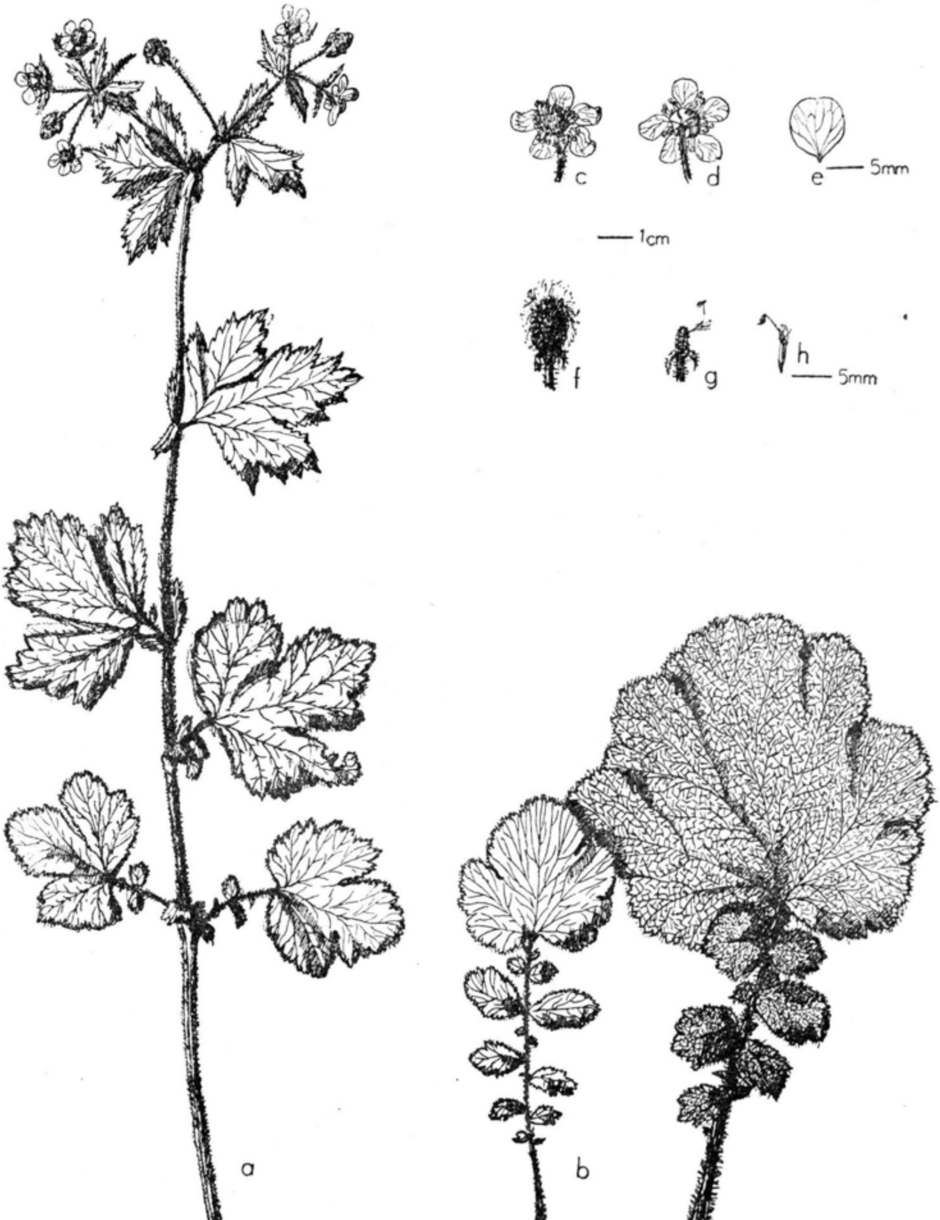

Fig. 95. F$_1$ *Geum Fauriei* × *G. macrophyllum*; a — floral stem; b — basal leaves; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

stronger branching of the stems, by slightly drooping floral peduncles, and by the earlier flowering time. All these characters of *G. Fauriei* are entirely or partly dominant over the corresponding characters of *G. macrophyllum.* The hybrid is entirely sterile and does not produce good achenes. Pollen fertility is about 0,2 per cent.

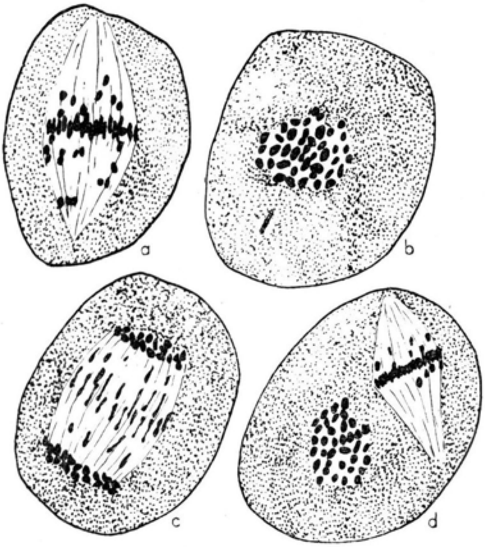

Fig. 96. F_1 *Geum Fauriei* × *G. macrophyllum,* meiosis in PMCs; a — M-I with 23 univalents on the spindle; b — M-I with 42 chromosomes ($21_{II} + 21_{I}$); c — A-I with numerous univalents on the spindle; d — M-II with 36 chromosomes in one of the plates

Similarly vigorous growth is displayed by the hybrid of *G. Fauriei* with *G. perincisum* Rydb. which is closely related to *G. macrophyllum.* This hybrid is also entirely sterile and the percentage of good pollen grains is only 0,2.

In the two hybrids 21 to 19 bivalents and 21 to 25 univalents are formed during meiosis (Fig. 96). Restitution nuclei and dyads are also formed in both cases.

Another hybrid of this group is *G. Fauriei* × *silvaticum,* which is also entirely sterile. The course of meiotic divisions is in this case of the same type as in the hybrids described previously (Fig. 97). A similar degree of sterility is observed in the hybrids of *G. Fauriei* with *G. urbanum* and *G. aleppicum.* The two last mentioned hybrids were not examined cytologically.

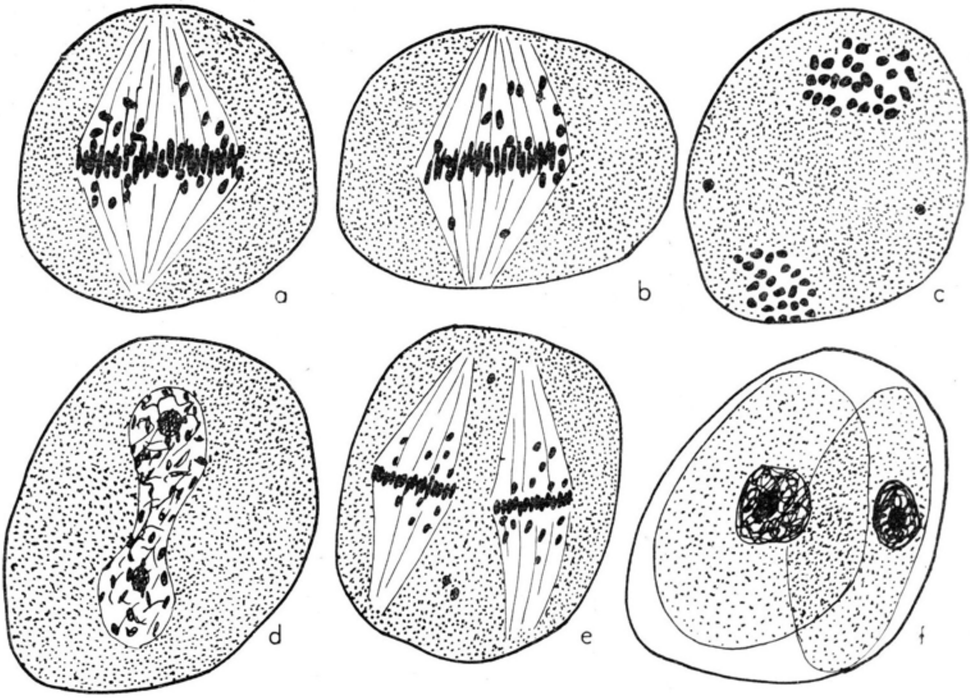

Fig. 97. F_1 *Geum Fauriei* × *G. silvaticum*, meiosis in PMCs; a — M-I with 25 univalents on the spindle; b — M-I with 21 univalents on the spindle; c — M-II with 27 and 24 chromosomes in the plates and 2 chromosomes lost in the cytoplasm; d — restitution nucleus; e — M-II with numerous chromosomes on the spindle; f — dyad

4. Hybrids between deca- and hexaploid species

The only decaploid species in my collection from the subgenus *Eugeum* is the South American species *G. Quellyon* Sweet. This species is often grown in botanical gardens under the name of *G. coccineum*. However, the two species have very little in common except that they are the only ones in the genus *Geum* with red petals. *G. coccineum* differs from the typical *G. Quellyon* by numerous such characters as leaf shape, branching of stems and size of petals. Moreover, *G. coccineum* is a hexaploid species and its distribution on the Balkan Peninsula and in Asia Minor differs from the distribution of *G. Quellyon*. The crosses of *G. Quellyon* with hexaploid species are entirely sterile, and the crosses of *G. coccineum* with such species are often highly fertile. Furthermore, the red colour of *G. coccineum* is recessive in respect to the yellow colour, whereas the red colour of *G. Quellyon* is dominant over the yellow colour of petals in the hexaploid *Eugeum* species with which it was crossed.

Hybrids of *G. Quellyon* were obtained with the following hexaploid *Eugeum* species: *G. rivale, coccineum, silvaticum, canadense, laciniatum* and *boliviense*. The corresponding hybrids nos. 61—66 are easily obtained and the setting of seeds is almost at a normal level, especially if the pistil plant is *G. Quellyon*. However, the crop of achenes was also quite high when the cross was made in the opposite direction and such hexaploid species as for instance *G. rivale* or *coccineum* were pollinated with pollen from *G. Quellyon*.

61. *G. rivale* L. (21) × *G. Quellyon* Sweet (35), Fig. 98, culture no. 20—39. To illustrate the hybrid some of its characters are compared with the characters of the parental species:

Character	*G. Quellyon*	F_1	*G. rivale*
Basal leaves	terminal leaflet round, incised, cordate base	intermediate	terminal leaflet incised into 3 cuneate lobes
Floral stems	up to 70 cm tall, 7 — 12-floral	70 — 125 cm tall, 5 — 18-floral	45 — 60 cm tall, 3 — 5-floral
Anthocyanin in stems and flowers	none	abundant	very abundant
Floral peduncles	straight	drooping	very drooping
Calyx	reflexed	reflexed	erect
Length of sepals (mm)	7 — 8	8 — 9	12
Position of petals	horizontal	slightly erect	erect
Colour of petals	red	red	creamy
Size of petals (mm)	10.4 × 10.8	10.8 × 12.2	10.1 × 8.0
Claw on petals	absent	absent or very small	long
Gynophore	absent	absent	8 — 10 mm long

The hybrid was obtained in 1939, it forms — similarly as *G. rivale* — a strongly developed rhizomatous caudex. In the Warsaw climate it is completely frost resistant and very durable, as can be seen from the fact that the specimen obtained in 1939 still persisted in 1955 and even then showed no signs of degeneration. *G. Quellyon,* on the other hand, is very difficult to preserve through winter and frequently freezes in the Warsaw climate. The growth of the hybrid is exceptionally vigorous and its stems are somentimes twice as tall as the floral stems in either of the parental species. The basal leaves may be as much as 40 cm long and have nearly twenty paris of lateral leaflets. The colour of the petals in the hybrid is not exactly the same as in *G. Quellyon*. According

Fig. 98. F$_1$ *Geum rivale* × *G. Quellyon*; a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal: f — achenes in flower; g — receptacle with one achene; h — achene

to the Horticultural Colour Chart the petals of *G. Quellyon* closely approach Brick Red no. 0.16 and of the hybrid to Saturn Red. no. 13.1. Pollen fertility of the hybrid is about 0.1 per cent. No well developed seeds are produced.

Meiotic division in PMCs (Fig. 99): — Meiosis in the hybrid was described in an earlier report (W. Gajewski 1949) and in it drawings and numerous microphotos showing various stages of meiosis were also published. At the stage of late diakinesis the following chromosome numbers were found in the 12 analysed cells: 35 in 5 cells and 36 to 38 in the remaining 7 cells. In 31 PMCs at metaphase the chromosome configurations were as follows:

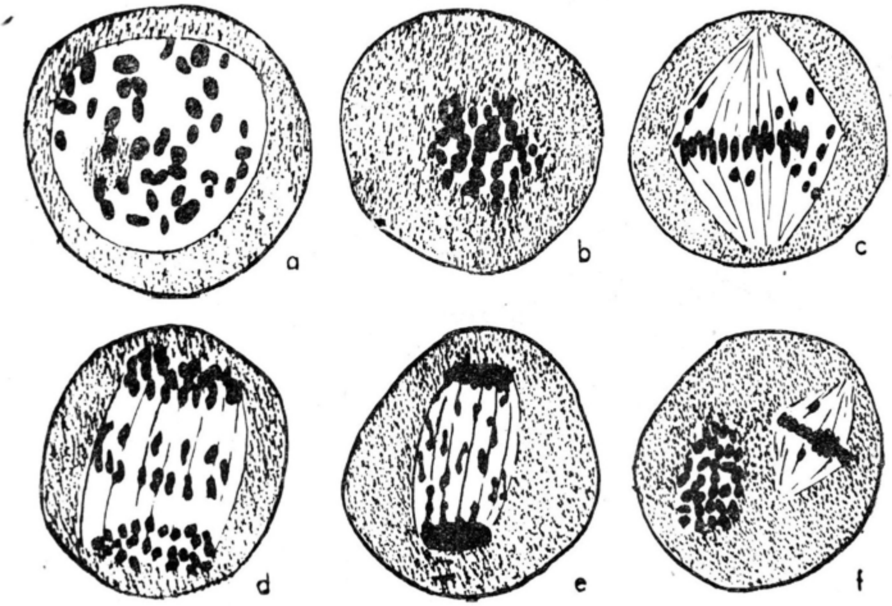

Fig. 99. F_1 *Geum rivale* × *G. Quellyon*, meiosis in PMCs; a — diakinesis with 38 chromosomes ($18_{II} + 20_{I}$); b — M-I with 35 chromosomes ($21_{II} + 14_{I}$); c — M-I with 14 univalents on the spindle; e — later anaphase with univalents segregating to the poles; f — M-II with 32 chromosomes in one of the plates

$21_{II} + 14_{I}$ in 14 cells	$18_{II} + 20_{I}$ in 2 cells
$20_{II} + 16_{I}$ in 6 cells	$17_{II} + 22_{I}$ in 2 cells.
$19_{II} + 18_{I}$ in 7 cells	

The bivalents are arranged in the usual manner in a plate on the equatorial plane and the univalents are scattered throughout the spindle. In late metaphase and in anaphase the univalents form a fairly regular ring on the equatorial plane along the peripheries of the achromatic figure. After the division of the bivalents, when they are already grouped at the spindle poles, the univalents still lie on the equatorial plane of the spindle (Fig. 99 d). The univalents are then strongly stretched out and only some are divided. Afterwards both the univalent halfs and the undivided univalents begin to move to one of the two poles and are segregated at random between the two daughter nuclei. The number of univalents in the ring at the stage of late anaphase is 14 to 18. As cells with 22 univalents at metaphase have been observed it is to be assumed that some of the univalents move to the poles in early anaphase together wiht the separating bivalent halves. As a result of the great retardation in the division and separation of the univalents many of them are seen in telophase and interkinesis lying in the cytoplasm outside the two daughter nuclei. These chromosomes very rarely form small additional nuclei composed of several chromosomes, but most often they lie separately in the cytoplasm where they are resorbed. In the 3 cells at metaphase of the II-nd division where it was possible to count all the chromosomes in both metaphasal plates the following chromosome numbers were observed: 27 and 29 (with 2 more chromosomes outside the plates), 31 and 29, 31 and 33. In the 19 cells where it was possible to count the chromosomes in one of the two plates the numbers found were: 28, 31, 33

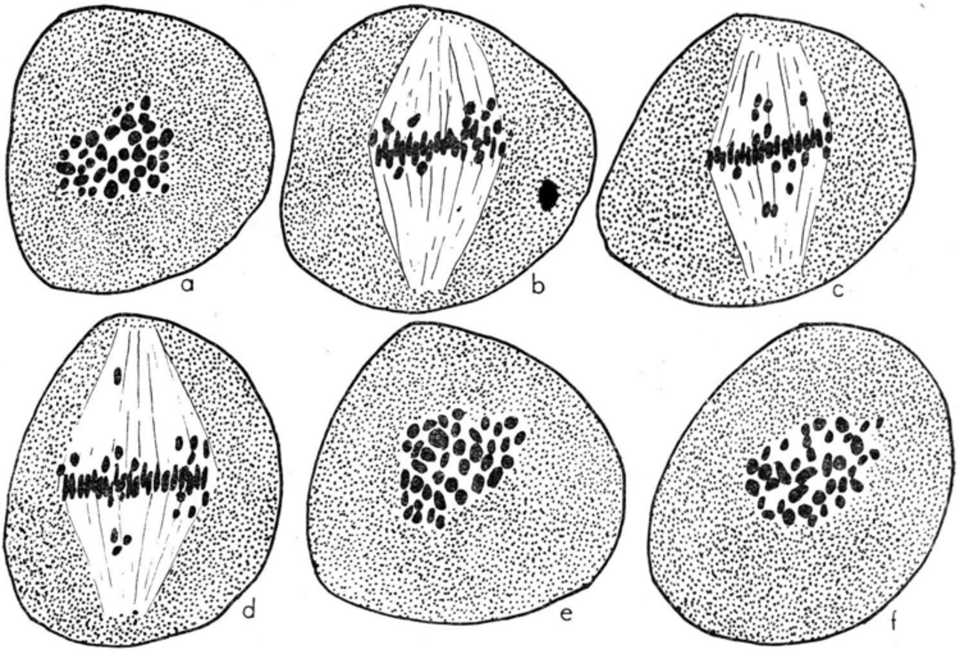

Fig. 100. F_1 *Geum Quellyon* × *G. laciniatum*, meiosis in PMCs; a — M-I with 35 chromosomes; b — M-I with 14 univalents on the spindle; c — M-I with 16 univalents; d — M-I with 18 univalents; e — M-I with 38 chromosomes ($18_{II} + 20_{I}$); f — M-I with 37 chromosomes ($19_{II} + 18_{I}$)

and 36. Usually in metaphase of the II-nd division numerous chromosomes do not lie on the plate itself but away from it on the spindle. At anaphase these chromosomes lag on the spindle and are separated with much delay. Among the 231 cells examined at the tetrad stage 2 dyads were found. This means that probably on very rare occasions during the first division restitution nuclei are formed, though this process was not directly observed in the preparations which I obtained.

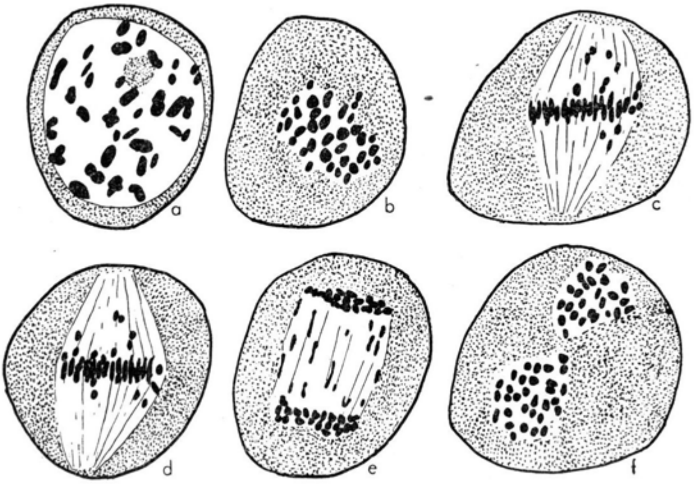

Fig. 101. F_1 *Geum Quellyon* × *G. boliviense*, meiosis in PMCs; a — diakinesis with 35 chromosomes ($21_{II} + 14_{I}$); b — M-I with 36 chromosomes ($20_{II} + 16_{I}$); c — M-I with 14 univalents on the spindle; d — A-I with 18 univalents; e — A-I with segregating univalents; f — M-II with 31 and 25 chromosomes in the plates.

Both parental species of the hybrid *G. Quellyon* × *G. coccineum* have red petals and the hybrid has red petals of a different shade than either of its parents. According to the Horticultural Colour Chart the petal colours in these plants are as follows:

G. Quellyon	Brick Red 0.16
G. coccineum	Poppy Red 16
F_1	Opriment Orange 10.

The hybrid has big petals 17.8 mm long and about 18 mm wide. It is entirely sterile and did not produce even one well developed achene. Pollen fertility of the hybrid is about 0.01 per cent. The pattern of meiotic division closely resembles that of the hybrid *G. Quellyon* × *rivale*. In metaphase the number of bivalents formed is also 21 to 18 and the corresponding number of univalents is 14 to 20.

In the hybrid of *G. Quellyon* with *G. silvaticum* which has yellow flowers the colour of petals is Indian Orange 713 according to the Horticultural Chart. The petals are 12.5 mm long and 14.3 mm wide. This hybrid, similarly as the others in this group, is completely sterile. Smears of pollen contain about 2.4 per cent of well staining big pollen grains. The chromosome configurations found in meiosis of the hybrid are the same as in the preceding one with *G. Quellyon*. The number of cells analysed at the tetrad stage was 220 and it was found that in 12 cells there were additionally from 1 to 4 small microspores. There were also 6 dyads, i.e. 2.7 per cent.

According to the Horticultural Colour Chart the colour of petals in the hybrid *G. Quellyon* × *G. canadense* is Persimon Orange 710/3. The petals are 10.2 mm long and 10.6 mm wide. The hybrid is very vigorous, the lenght of its stems averages at 110 cm, the average number of flowers on one stem is 14.5 and the basal leaves are up to 30 cm long. The hybrid is completely sterile. Meiotic divisions follow the same pattern as in the hybrids already described.

In the hybrid *G. Quellyon* × *G. laciniatum* the colour of petals is Tangerine Orange 9/2 according to the Horticultural Colour Chart. The average size of the circular petals is 9 mm. These plants are also very vigorous and entirely sterile.

In the hybrid *G. Quellyon* × *G. boliviense* the petals are of the same colour as in *G. Quellyon* and are 9 mm long and 8.7 mm wide. The meiotic divisions in the two hybrids described last are illustrated by Figs. 100 and 101.

G. canadense, laciniatum and *boliviense* all have white petals, but in spite of this the hybrids of these species with *G. Quellyon* have petals of various red and orange shades which indicates that the white colour in the three species is not governed by the same hereditary mechanism.

In the three hybrids last mentioned meiosis is of the same type as in the other hybrids of hexaploid *Eugeum* species with *G. Quellyon* and is characterized by maximum chromosome conjugation of 21 bivalents and 14 univalents. In all three hybrids the percentage of dyads is about 1 and the percentage of well staining pollen is about 0.1.

5. Hybrids between hexaploid species

(nos. 67—121 in the list of hybrids on pages 109—114).

The total number of hybrids in this group was 55. The crosses were carried out between 13 hexaploid *Eugeum* species and the number of hybrids obtained amounted to 70 per cent of all the various possible interspecific combinations between 13 species.

Fig. 102. F$_1$ *Geum macrophyllum* × *G. rivale;* a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower (one is developed normally); g — receptacle with one achene; h — achene

The hybrids differ markedly in respect to fertility which ranges from complete sterility to almost normal fertility and in this respect this group of hybrids may be divided into three categories ranging from completely or highly sterile (less than 2—3% of good achenes). through partly fertile (from 3 to 10—15% of good achenes), to fertile (more than 15% of good achenes). Obviously, it is difficult to adhere very strictly to this classification, nevertheless it will help to demonstrate how the 13 hexaploid *Eugeum* species in question are separated by hybrid sterility barriers.

Completely and highly sterile hybrids: — Almost complete hybrid sterility separates from other *Eugeum* species the three closely related N. American species: *Geum macrophyllum, G. oregonense* and *G. perincisum*. This remarkable group of species was described elsewhere (W. Gajewski 1955). The species when crossed between them produce highly fertile hybrids, but in crosses with some other *Geum* species the sterility of the ensuing hybrid is very high. At the same time many hybrids with these species display symptoms of developmental disturbances, greatly reduced viability and disturbances in the meiotic divisions leading to almost complete asyndesis. This refers to the hybrids marked in the list on pages 109—114 with nos. 75, 76, 77, 85, 86, 91, 96, 97, 98, 103, 106, 109, 110, 113, 114, 118 and 119.

To illustrate the whole group the fertility, meiosis and the morphological character of the hybrid no. 75 *G. macrophyllum* × *rivale* (Fig. 102) will now be discussed. The hybrid with its amphidiploid progeny was already described elsewhere (W. Gajewski 1953), but the description is here renewed to illustrate the present argument. Some characters of the hybrid are compared below with the characters of the parent species:

Character	*G. macrophyllum*	F_1	*G. rivale*
Caudex	± absent	present	long, well developed
Basal leaves	terminal leaflet big and round	terminal leaflet big, round, trilobed	terminal leaflet dissected into 3 cuneate lobes
Indumentum	long and bristly, no glandular hairs	similar to *macrophyllum* but bristles shorter	softly haired, numerous glandular hairs

Character	*G. macrophyllum*	F_1	*G. rivale*
Floral stems	70 — 85 cm tall, 9 —13-floral	70 — 90 cm tall, 9 — 13-floral	45 — 60 cm tall, 3 — 5-floral
Anthocyanin in stems and flowers	traces	abundant	very abundant
Floral peduncles	straight	drooping	drooping
Calyx	reflexed	horizontal or reflexed	erect
Length of sepals (mm)	4 — 5	5 — 6	12
Position of petals	horizontal	± erect	erect
Size of petals (mm)	6.6 × 5.5	8.6 × 8.8	10.1 × 8.0
Claw on petals	absent	absent or very small	long
Gynophore	absent	absent or 1 mm long	8 — 10 mm long
Length of floral base (mm)	8 — 12	5 — 6	6 — 7
Number of achenes	200 — 240	150 — 170	150 — 200
Length of rostrum (mm)	about 4	7 — 8	8 — 10
Length of stigmatic part (mm)	1.5 — 2	3 — 3.5	4.5 — 5

Pollen fertility of the hybrid is about 0.7 per cent. The fertility of seeds is even lower and usually only one good achene is developed in a score or several tens of flowers.

Meiotic divisions in PMCs (Fig. 103): — As was described in an earlier report (W. Gajewski 1949) in the PMCs of the hybrid only very few bivalents are formed during meiosis and the majority of chromosomes do not conjugate. In 31 cells analysed at metaphase of the I-st division the following chromosome configurations were observed:

$0_{II} + 42_{I}$ in 3 cells
$1_{II} + 40_{I}$ in 5 cells
$2_{II} + 38_{I}$ in 4 cells
$3_{II} + 36_{I}$ in 5 cells
$4_{II} + 34_{I}$ in 6 cells
$5_{II} + 32_{I}$ in 2 cells
$6_{II} + 30_{I}$ in 5 cells
$7_{II} + 28_{I}$ in 1 cell.

In 12 cells examined in diakinesis a somewhat greater number of bivalents was observed than at metaphase, i.e. in 5 cells there were 5 bivalents, in 3 cells there were 6, in 2 cells there were 3, and in 2 cells there were 4 and 7 bivalents. The average number of bivalents in 31 cells at metaphase was 3.8 per cell, and in 12 cells analysed at diakinesis the corresponding average was 5.0. It was unfortunately impossible to examine exactly the early stages of prophase because of the technical difficulties presented by the material from the genus *Geum*. Nevertheless, it seems that in the case of this hybrid it is rather a question of too early desynapsis than of asynapsis proper when the chromosomes do not conjugate at all. The few chromosomes from the diplotene accessible to inspection showed marked conjugation of homologous chromosomes, similarly as in other hexaploid *Geum* hybrids. However, the complete chromosomal set at diplotene could never be analysed exactly in the available preparations. Frequently at metaphase the bivalents and some univalents lie on the equatorial plane or near it while the remaining univalents lie almost at the poles. This chromosome arrangement is such that at first sigth the appearance of metaphase creates the impression of late anaphase with bivalent halves at the poles and univalents on the equatorial plane. At the beginning of anaphase the bivalents separate and some univalents move to the equatorial plane. It seems, however, that the univalents which at the beginning of metaphase were near the spindle poles remain there throughout anaphase. In late anaphase after the division of the bivalents the univalents lying on the spindle do not form a regular ring at the equatorial plane as was the case in the hybrids described previously. Most univalents move to the nearest pole without dividing. Only those univalents which lie on the equatorial plane display usually some ten-

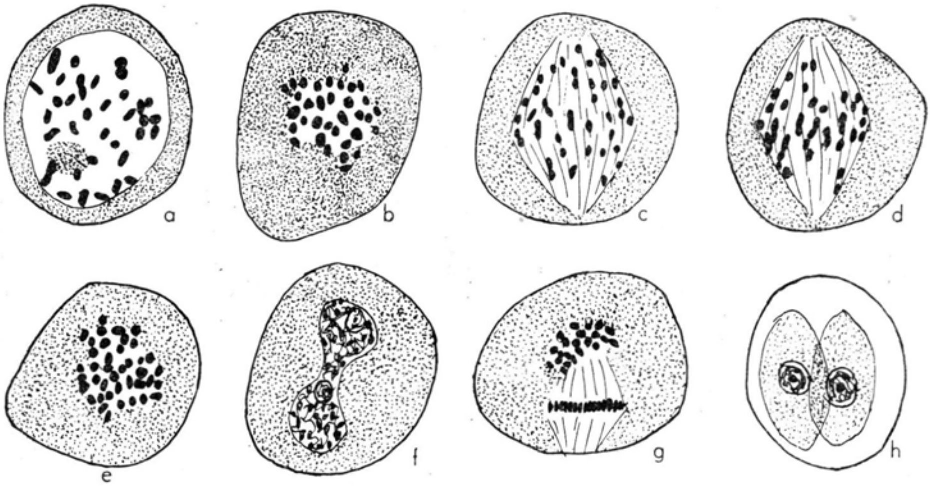

Fig. 103. F_1 *Geum macrophyllum* × *G. rivale*, meiosis in PMCs; a — diakinesis with 36 chromosomes ($6_{II}+30_{I}$); b — M-I with 34 chromosomes ($8_{II}+26_{I}$); c — M-I with 2 bi- nad 40 univalents; d — M-I with 5 bivalents and 32 univalents; e — M-I with 40 chromosomes ($2_{II}+38_{I}$); f — restitution nucleus; g — M-II with 21 chromosomes in one of the plates; h — dyad

dencies to divide but as o rule this leads only to a considerable stretching out of the univalents without bringing about their division. Generally speaking anaphase has a very irregular course. Telophasal changes often start when numerous univalents are still outside the spindle poles.

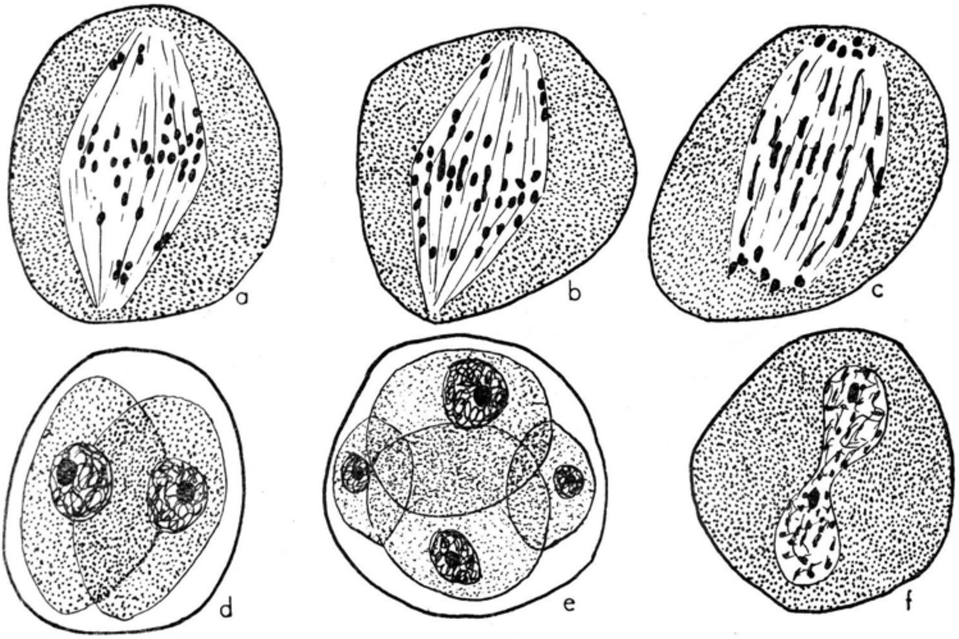

Fig. 104. F_1 *Geum silvaticum* × *G. macrophyllum*, meiosis in PMCs; a — M-I with univalents dispersed on the spindle only; b — M-I with 3 bivalents and 36 univalents; c — A-I with univalents segregating to the poles; d — dyad; e — tetrad with 2 pairs of unequal spores; f — restitution nucleus

Then quite frequently restitution nuclei are formed and /or the univalents which remain in the cytoplasm outside the daughter nuclei are eliminated. The chromosomes remaining in the cytoplasm are usually resorbed. As a result, usually in interkinesis there are only either cells with two nuclei or cells with one nucleus originating from restitution nuclei. In spite of the great disturbances in the first division, the number of chromosomes seen in the metaphasal plates of the II-nd division is frequently 21 or near to 21, as for instance 19 and 20 or 23 and 24. Nevertheless, there are sometimes 3 or 4 chromosomes in the cytoplasm outside the two plates. The course of the second division is on the whole surprisingly normal in comparison with the completely abnormal first division. Besides some chromosomes which at metaphase lie off the plates on the spindles and besides the very few chromosomes lagging at anaphase, the course of the II-nd division is normal in all other respects. The result of this state is that nothing in the appearance of the tetrads indicates the asyndesis of the hybrid. Among the 246 cells analysed at the tetrad stage there were 4 microspores in 238 cells, in 6 cells there were two small microspores in addition to the four normal ones, and the remaining 2 cells were dyads. As has already been mentioned almost all the pollen in this hybrid degenerate in spite of the normal appearance of the tetrads.

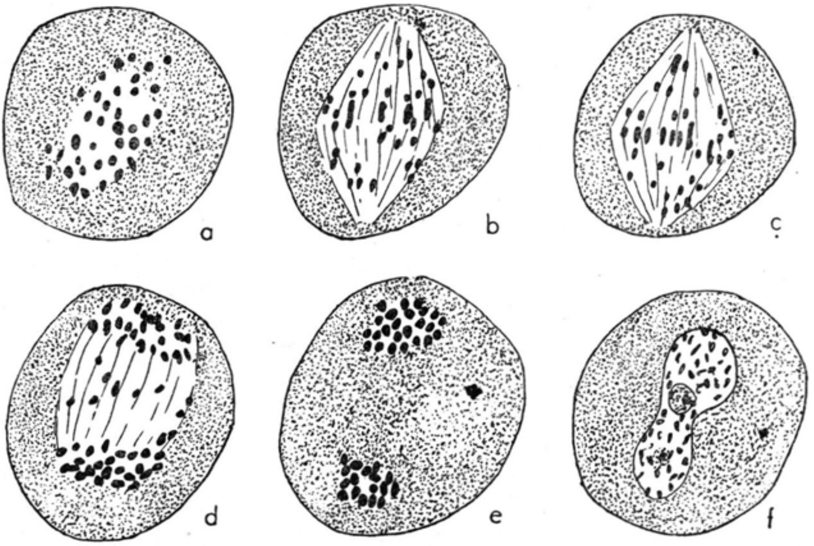

Fig. 105. F_1 *Geum urbanum* × *G. macrophyllum*, meiosis in PMCs; a — M-I with 37 chromosomes ($5_{II} + 32_{I}$); b — M-I with 4 bi- and 34 univalents; c — M-I with 5 bi- and 32 univalents; d — A-I with univalents on the spindle; e — M-II with 17 and 24 chromosomes in the two plates; f — restitution nucleus

The hybrids of *G. rivale* with *G. perincisum* and *G. oregonense*, both closely related to *G. macrophyllum*, differ only slightly in respect to morphology from the hybrid just described. Similarly as the hybrid with *G. macrophyllum* both are highly sterile. Pollen fertility in both is about 0.3 per cent and seed fertility is so low that one seed is collected from more or less a score of flowers.

On the whole meiotic divisions in the hybrids *G. rivale* × *G. perincisum* and *G. rivale* × *G. oregonense* develop along the same pattern as in the hybrid *G. rivale* × *macrophyllum*. The most common numbers of bivalents at metaphase of the I-st division are 2, 3 and 4. Among the 117 cells of the hybrid *G. rivale* × *perincisum* examined at telophase and interkinesis there were 21, i.e. nearly 18 per cent, with restitution nuclei which undoubtedly was the result of the delay in the division of univalents at anaphase. At the tetrad stage also the number of dyads is rather high. It was found that in numerous pollen cells of this hybrid pollen mother cells degenerated after the first division and the second division did not take place. What happens looks as if the cell walls dissolved and neighbouring PMCs merged forming shapeless, protoplasmic, multinucleate masses. In the cytoplasm numerous droplets of a strongly refractive substance appear and finally the whole content of the pollen sack dries up. In one flower there may be anthers in which divisions proceed till the end alongside of anthers with PMCs which degenerate in the manner just described after the first division.

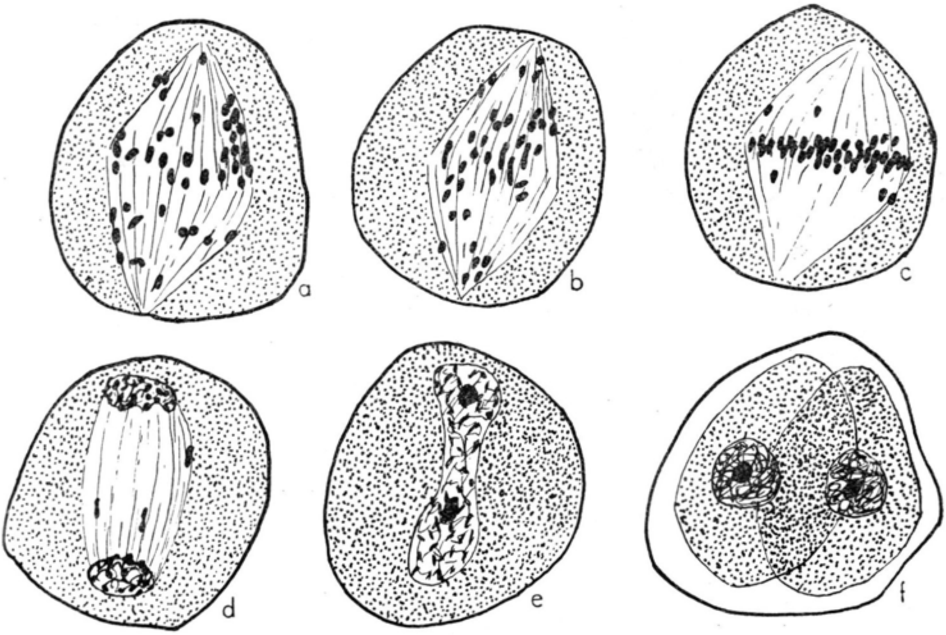

Fig. 106. F_1 *Geum urbanum* × *G. perincisum*, meiosis in PMCs; a — M-I with 42 univalents; b — M-I with 4 bi- and 34 univalents; c — M-I or A-I with univalents arranged in a more or less regular plate; d — T-I with univalents not included into the daughter nuclei; e — restitution nucleus; f — dyad

G. macrophyllum gives also completely sterile hybrids with meiosis of the asyndetic type with the following species from subgenus *Eugeum: G. urbanum, molle, hispidum* and *laciniatum*. These hybrids, in opposition to the hybrids with *G. rivale* already described, have a greatly reduced viability and represent sublethal types. The cultivation of the hybrids is very difficult and as a result of the very high mortality at the stage of cotyledons the majority of seedlings perish by the time the first leaves appear. The plants which have been brought to the flowering stage usually show many disturbances in their development, e.g. greenish-yellow leaves which often look as if curled and flowers often completely deprived of stamens or having stamens with small anthers containing no pollen. Usually also, the petals are either not developed at all or reduced and are then frequently incised and curled. None of these hybrids persisted through more than two vegetative seasons, and the majority of the flowering ones perished immediately after anthesis. Growth is not disturbed to the same degree in all specimens of one F_1 population and the intensity of the disturbance varies too in various interspecific hybrids. Among the hybrids in question sublethal symptoms are most intense in the F_1 plants of *G. urbanum* × *macrophyllum,* less so in the hybrids with *G. molle* and *hispidum* and least in the hybrid with *G. laciniatum. Geum urbanum* and *G. macropohyllum* were crossed in both directions and both populations of reciprocal F_1 hybrids displayed the same reduced viability and developmental disturbances, which indicates that cytoplasmic factors have probably no significant influence here.

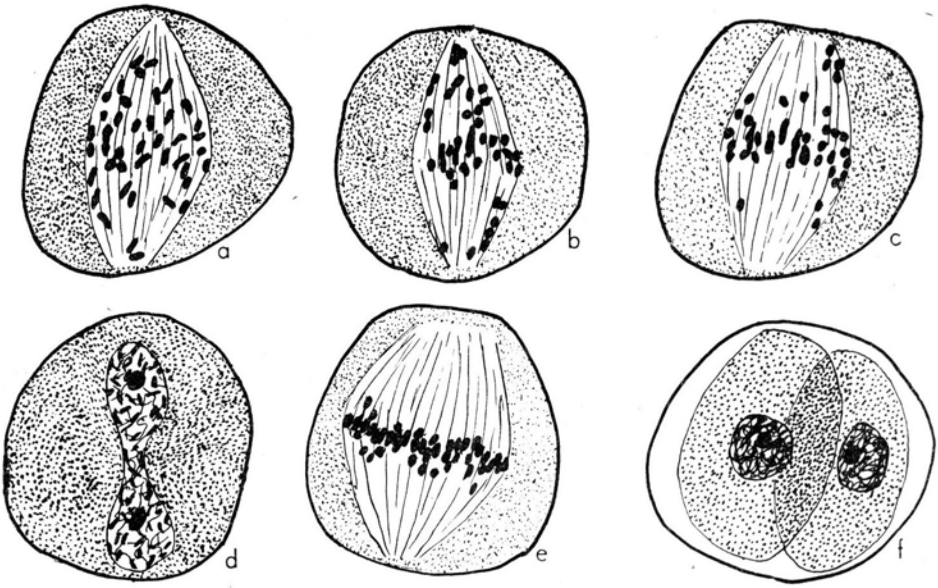

Fig. 107. F_1 *Geum urbanum* × *G. oregonense,* meiosis in PMCs; a — M-I with one bi- and 40 univalents; b — M-I with 3 bi- and 36 univalents; c — M-I with 5 bi- and 32 univalents; d — restitution nucleus; e — M-II of restitution nucleus; f — dyad

The course of meiosis is in these hybrids of the same type as in the hybrid *G. macrophyllum* × *rivale* (Figs. 104 and 105). The disturbances in the development of flowers and especially of the androecium often cause the degeneration of the archesporium even before meiotic divisions begin or the degeneration of PMCs in the course of meiotic divisions.

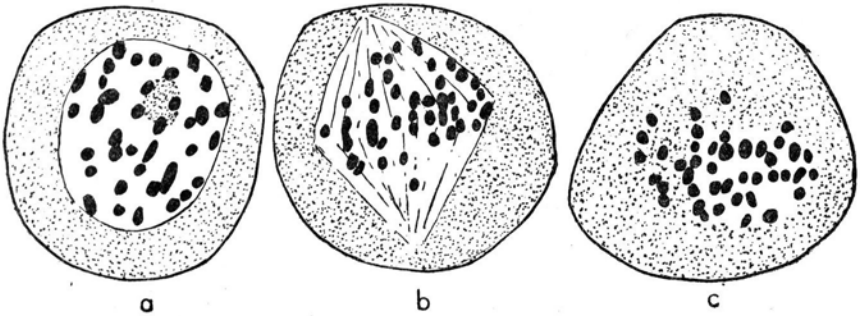

Fig. 108. F_1 *Geum laciniatum* × *G. macrophyllum,* meiosis in PMCs; a — diakinesis with 37 chromosomes ($5_{II} + 32_{I}$); b — M-I with 3 bi- and 36 univalents; c — M-I with 42 univalents

In specimens with more normal development both meiotic divisions proceed till the end and the percentage of good pollen grains formed is about 0.2. However, the sterility of these specimens in respect to seed formation is complete.

The hybrid *G. laciniatum* × *macrophyllum* grows more vigorously than the hybrids of *G. macrophyllum* with *G. urbanum, molle* and *hispidum.* The average length of floral stems is 45 cm and the flowers always have normally developed petals and androecium. The leaves, however, are pale green and often curled. After two years none of the 45 plants which flowered in the first year remained. Greater vigour is displayed by plants of the hybrid *G. laciniatum* × *G. oregonense*, the average length of their stems is 80 cm and there are 20 to 25 flowers on every stem. No developmental disturbances occur in the vegetative parts or in the flowers. The two hybrids have yellow petals, 5 mm long and 3 mm wide, whereas *G. laciniatum* has white petals 4.5 mm long and 2.5 mm wide.

The hybrid *G. silvaticum* × *macrophyllum* is of the vigorously growing type and the pattern of its meiosis is the same as in the hybrids described above (Fig. 104). It also is completely sterile.

However, not all hybrids of *G. macrophyllum* with hexaploid species from the subgenus *Eugeum* have the same course of meiosis with no or few bivalents. Meiosis in the hybrids *G. macrophyllum* × *G. aleppicum* and *G. macrophyllum* × *G. canadense* follows a quite different course (Figs. 109 and 110). The following chromosome configurations were observed at metaphase of the I-st division in these two hybrids:

Hybrid	Number of PMCs with different chromosome configurations:					
	21_{II}	$20_{II}+2_{I}$	$19_{II}+4_{I}$	$18_{II}+6_{I}$	$17_{II}+8_{I}$	$16_{II}+10_{I}$
F_1 macrophyllum × aleppicum	21	9	4	1		
F_1 macrophyllum × canadense	65	14	5	2	2	

It is evident from the above table that in both hybrids the majority of PMCs show normal conjugation of all the chromosomes from both parental species. On the whole in both hybrids meiotic divisions develop normally in most cells. In the numerous metaphases of the II-nd division 21 chromosomes were seen in both plates, but in a few cases that number differed from 21 and was for instance 20 or 23. These numbers probably arise as a result of uneven distribution of univalents, the division of univalents, or the elimination of chromosomes at metaphase of the I-st division. In the first division anaphase the univalents frequently lag on the spindle and separate to the two poles with much

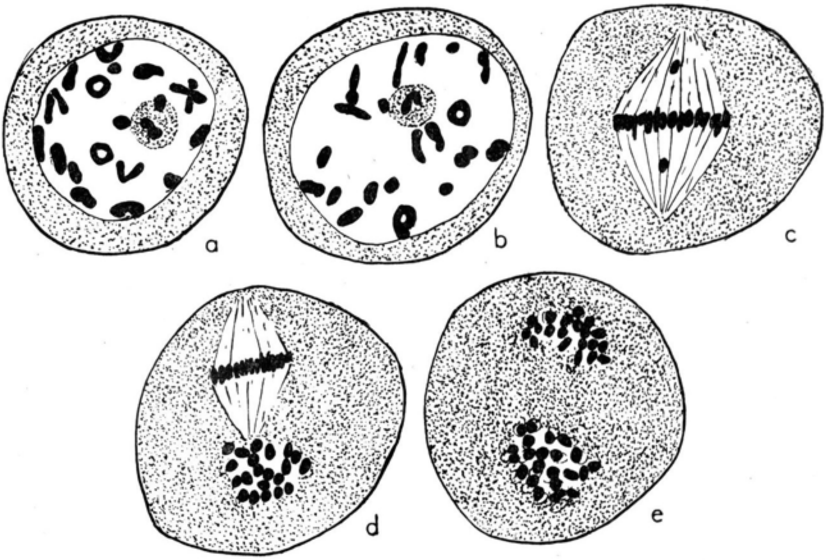

Fig. 109. F_1 *Geum macrophyllum* × *G. canadense*, meiosis in PMCs; a — diakinesis with 20 bi- and 2 univalents; b — diakinesis with 21 bivalents; c — M-I with 2 univalents; d — M-II with 21 chromosomes in one plate; e — M-II with 20 and 22 chromosomes in the plates

delay. Consequently they are often not included in the daughter nuclei. Rarely at anaphase univalents are seen to be lying in the equatorial plane of the spindle where they are strongly stretched out or divided. The appearance of the tetrads in the two hybrids is quite normal and there are no dyads. In spite of the normal meiotic divisions most of the pollen degenerate and the percentge of good pollen grains staining in acetocarmine is only 0.6. Both hybrids produce no good seeds.

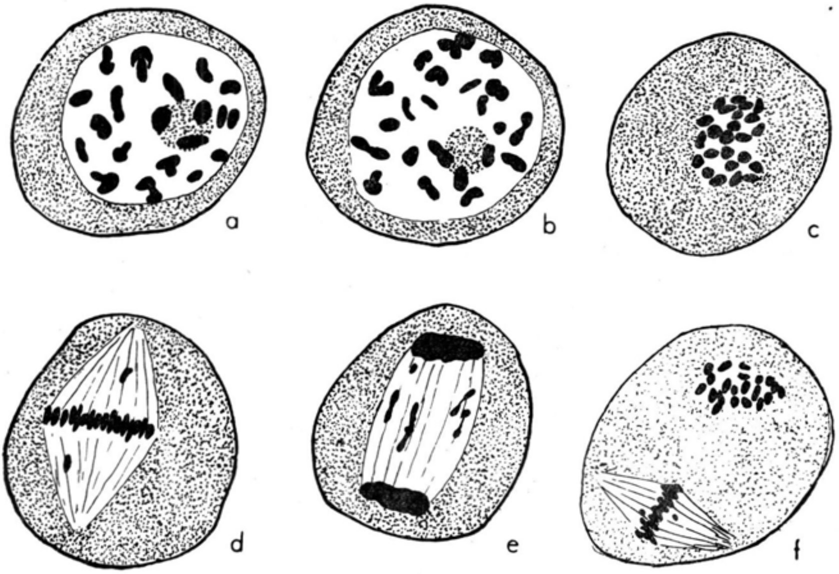

Fig. 110. F$_1$ *Geum aleppicum* × *G. macrophyllum,* meiosis in PMCs; a — diakinesis with 21 bivalents; b — diakinesis with 19 bi- and 4 univalents; c — M-I with 24 chromosomes ($18_{II} + 6_{I}$); d — side view of M-I with 2 univalents; e — A-I with univalents lagging on the spindle; f — M-II with 21 univalents on the plate

The hybrid *G. macrophyllum* × *aleppicum* was obtained in both directions. The setting of seeds was here at the almost normal level of about 80 per cent, but from the several hundred seeds obtained only several plants were brought to the flowering stage. Most plants perished at the stage of cotyledons or of the first leaves. All the plants which had passed the critical stages reached the flowering stage, but they had much curled, pale green leaves, small stems only 12 to 20 cm long and few flowers with undeveloped androecium and petals. The hybrids which had *G. macrophyllum* as the maternal plant displayed greater developmental disturbances and all perished before flowering, so that all the plants that flowered were from the reciprocal cross.

The hybrid *G. macrophyllum* × *canadense* is much easier to grow and numerous F_1 hybrids were obtained with floral stems up to 1 m tall and numerous flowers. These hybrids survived through four years without much mortality, whereas the hybrids with *G. aleppicum* all perished after the second year. The floral organs of the hybrid plants are quite normally developed and only the leaves are yellowish green and wrinkled. The stems, in spite of their considerable height, are frail and usually lie on the ground.

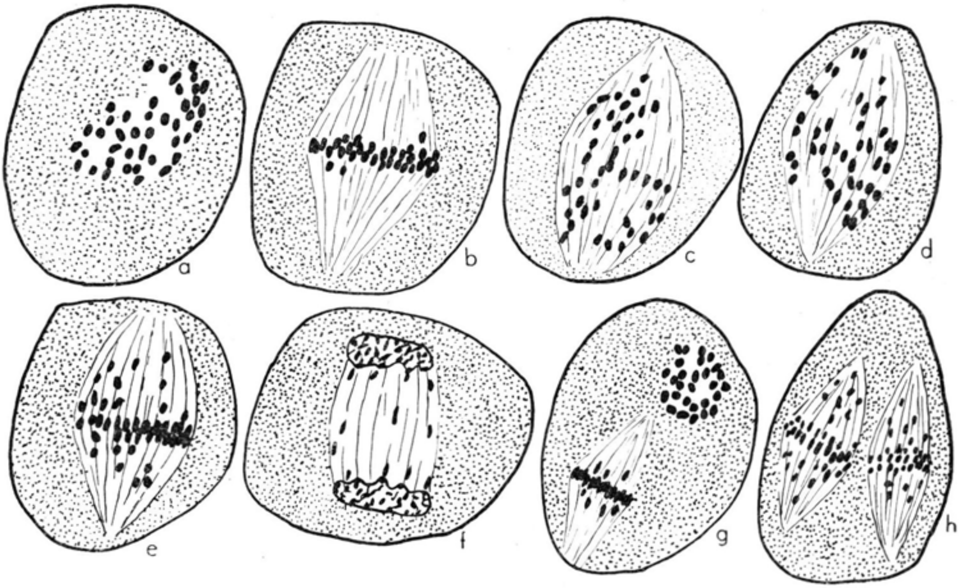

Fig. 111. F_1 *Geum aleppicum* × *G. oregonense,* meiosis in PMCs; a — M-I with 42 univalents; b — M-I with univalents forming a regular plate; c — M-I with one bivalent and 40 univalents scattered throughout the spindle; d — M-I with 42 univalents scattered throughout the spindle; e — M-I with univalents partly forming a plate; f — T-I with univalents on the spindle; g — M-II with 28 chromosomes in a plate; h — M-II with numerous chromosomes on the spindle

The hybrids just described are highly sterile similarly as the hybrids of *G. macrophyllum* with *G. urbanum* and *laciniatum*. The hybrids of *G. laciniatum, urbanum, coccineum* and *aleppicum* with *G. oregonense* and *G. perincisum* are also highly sterile and their meiosis is of the asyndetic type. This was demonstrated in the case of the following hybrids: *G. laciniatum* × *perincisum, G. coccineum* × *oregonense, G. urbanum* × *perincisum, G. urbanum* × *oregonense* and *G. aleppicum* × *oregonense* (Figs. 106 and 107). These hybrids show also symptoms of developmental disturbances of various intensity. E.g. the hybrid *G. urba-*

num × *macrophyllum* exhibits a sublethal pattern with considerable disturbances in development, in the hybrid *G. oregonense* × *urbanum* growth is inhibited, the leaves are chlorotic and the flowers often have undeveloped petals and stamens, and the cross *G. perincisum* × *urbanum* gives plants of the vigorously growing type.

Very remarkable conditions prevail in meiosis of the hybrid *G. aleppicum* × *oregonense* (Fig. 111). In numerous very fine preparations showing metaphase of the first division in 65 PMCs the following configurations were observed:

42 univalents in 22 PMCs
1 bivalent and 40 univalents in 14 PMCs
2 bivalents and 38 univalents in 15 PMCs
3 bivalents and 36 univalents in 7 PMCs
4 bivalents and 34 univalents in 3 PMCs
5 bivalents and 32 univalents in 1 PMC
6 bivalents and 30 univalents in 3 PMCs.

In some PMCs the univalents are scattered disorderly throughout the spindle (Fig. 111, c, d) and in others they form regular plates on the equatorial plane. The latter case refers primely to those PMCs in which there are no bivalents. It is of interest to note that in the same hybrid from which fixed preparations were made I found in acetocarmine preparations made before fixation in Navashin's fluid PMCs with almost normal meiosis and only few univalents. Unfortunately in the fixed preparations the cells with normal meiosis were not seen again. However, this observation indicates that the degree of conjugation or desynapsis may depend in these hybrids on internal or external factors the nature of which is not yet understood. In this aspect the presence of PMCs with a majority of bivalents in the hybrid *G. aleppicum* × *macrophyllum* does not exclude the possibility that the examination of a more extensive material fixed at various times and from many specimens would reveal also the asyndetic type of meiosis.

It may be stated as a general principle that, as *G. macrophyllum* and the closely related to it *G. perincisum* and *G. oregonense* do not produce fertile hybrids with any *Eugeum* species with which they have been crossed so far, they constitute a group of species isolated from others by complete hybrid sterility (W. Gajewski 1955). It was reported elsewhere (W. Gajewski 1953) that in the progeny of the hybrid *G. macrophyllum* × *rivale* amphidiploid plants were obtained.

The next group of highly sterile hybrids results from crosses with *G. aleppicum* as one of the parental species. Very remarkable cytogenetic conditions are exhibited by the hybrid no. 94 *G. aleppicum* × *urbanum*. Both parent species are morphologically rather closely related, but in spite of this, hybrids between them are almost completely sterile. Pollen fertility in the hybrids is only 0,6 per cent and seed fertility is even lower, so that no more than 1 or 2 well developed achenes are collected from a hundred or even several hundreds flowers.

The more important characters distinguishing the two parental species and the expression of these characters in the hybrid are as follows:

Character	*G. aleppicum*	F_1	*G. urbanum*
Basal leaves	elongated, sharply dentate lobes	intermediate, more resembling *aleppicum*	lobes more rounded, serrate
Anthocyanin	small amounts in the upper parts of plants	as in *aleppicum*	none
Indumentum	bristles fairly numerous near base of stems and on leaves	intermediate	sparse, soft, short hairs
Gynophore (length in mm)	1.5 — 2	absent	absent or to 0.5
Floral base	8 — 12 mm long, ± glabrous	5 — 7 mm long, long haired	6 — 7 mm long, long haired
Size of petals (mm)	9.0 × 9.2	7.7 × 6.8	5.8 × 4.6
Stipules of cauline leaves	elongated, not very big	resembling *urbanum*	big and round

G. aleppicum has a longer receptacle and consequently more achenes inserted on it (200 to 260). The achenes inserted on the lower part of the receptacle have the rostrum more strongly curved downwards than those inserted higher up. Associated with this is the characteristic ovoid shape of the fruiting head in *G. aleppicum*. In *G. urbanum* there are about 150 achenes on a shorter receptacle, the achenes form here a spherical fruiting head which in the hybrid is more spherical than ovoid.

In the hybrids various disturbances take place in the development of the gynoecium and androecium. The androecium is often strongly reduced and frequently the stamens do not develop at all or develop in a residual form with small degenerate anthers in which no reduction divisions take place. This refers primely to the hybrid *G. aleppicum* from Białowieża Forest with *G. urbanum* from Piastów (culture no. 177—51). In the hybrid between *G. aleppicum* var. *strictum* from the state of New York supplied by Professor R.T. Clausen and the same *G. urbanum* (culture n. 112—52) the stamens were normally developed in the majority of flowers. Moreover, in the hybrids in question the development of pistils is very characteristically disturbed primely in flowers with reduced androecium, i.e. from almost every ovary one, two or

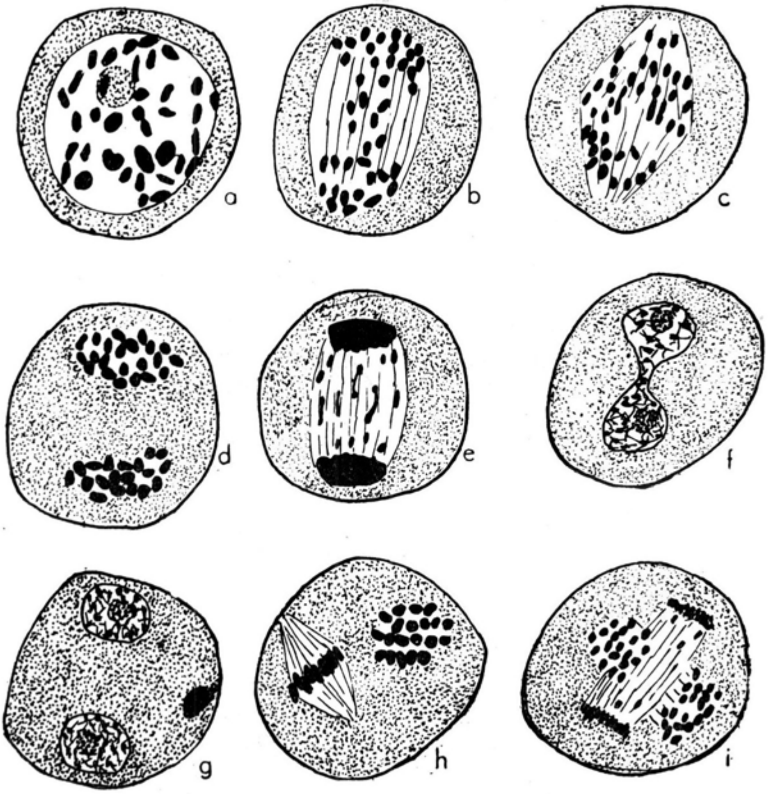

Fig. 112. F$_1$ *Geum urbanum* × *G. aleppicum*, meiosis of the asyndetic type in PMCs; a — diakinesis with 35 chromosomes ($7_{II} + 28_{I}$); b — M-I with 42 univalents; c — M-I with 3 bi- and 38 univalents; d — A-I with univalents on the spindle; e — anaphase with univalents on the spindle; f — restitution nucleus; g — T-I with two nuclei; h — M-II with 20 chromosomes in a plate; i — M-II with 19 chromosomes in two daughter groups

oven three additional styles grow out. These styles usually originate from the base of the ovary and are almost completely coalescent with the ovary walls, only the stigmatic parts of the styles and sometimes the upper part of the rostrum being free and unattached. The additional styles are visibly shorter than the main style growing out at the top of the ovary. The appearance of the fruiting head is thus very characteristic and peculiar, as besides the much protruding main style divided into rostrum and stigmatic part the very numerous small additional styles are also seen below. In such flowers well developed achenes are never formed. In the hybrid *G. urbanum* × *G. aleppicum* var *strictum* this effect is far less common and the additional styles occur only in some flowers and not in all achenes.

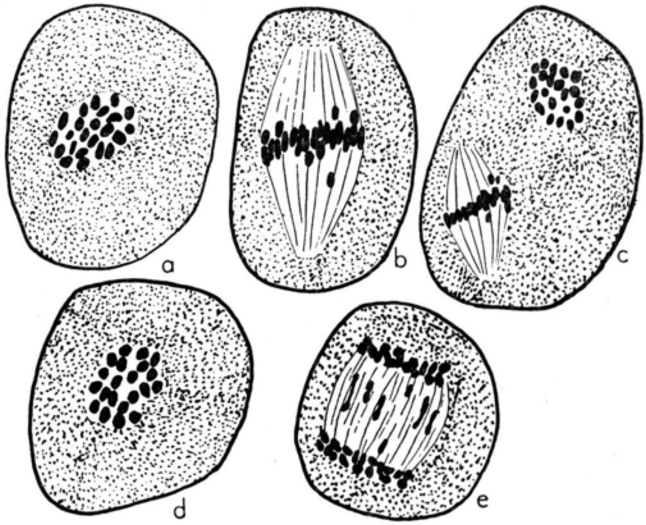

Fig. 113. F_1 *Geum urbanum* × *G. aleppicum*, meiosis in PMCs with bivalents prevailing; a — M-I with 23 chromosomes ($19_{II} + 4_{I}$); b — side view of M-I with 6 univalents; c — M-II with 21 chromosomes in one of the plates; d — M-I with 21 bivalents; e — A-I with 6 univalents on the spindle

Between the hybrid of *G. aleppicum* from Białowieża Forest with *G. urbanum* from Piastów and the corresponding reciprocal hybrid there are no significant differences.

The meiotic divisions in this hybrid either proceed almost normally or are almost completely asyndetic as in the hybrid with *G. macrophyllum*. In the first preparations obtained from smears in acetocarmine meiosis with almost normal chromosome conjugation was seen in the majority of PMCs. In the analysed 114 PMCs only 24 cells with 2 to 6 univalents were found while in all the remaining cells there were only 21 bivalents. The course of meiosis was rather normal throughout, but in spite of this all microspores degenerated and no pollen capable of functioning was produced. In 1948 during my visit at the Genetical Institute in Lund I examined the meiosis of this hybrid once again, this time on fixed preparations stained with crystal violet, and to my great astonishment I found an entirely different type of meiosis with asyndesis prevailing in all preparations. In the 30 cells examined at the stage of the first division metaphase I observed the following configurations:

$0_{II} + 42_{I}$ in 2 cells
$1_{II} + 40_{I}$ in 1 cell
$2_{II} + 38_{I}$ in 8 cells
$3_{II} + 36_{I}$ in 6 cells
$4_{II} + 34_{I}$ in 5 cells
$5_{II} + 32_{I}$ in 6 cells
$6_{II} + 30_{I}$ in 2 cells.

The further stages of meiosis are exactly similar as in the hybrid *G. macrophyllum* × *urbanum*. As a result of the disturbances in the separation of univalents restitution nuclei are also formed and after the second division dyads appear.

On finding so completely different meiotic behaviour in the same hybrid my first impression was that the first observations carried out on unfixed acetocarmine preparations were inaccurate or erroneous and in my report of 1948 I made a note to that effect (W. Gajewski 1948).

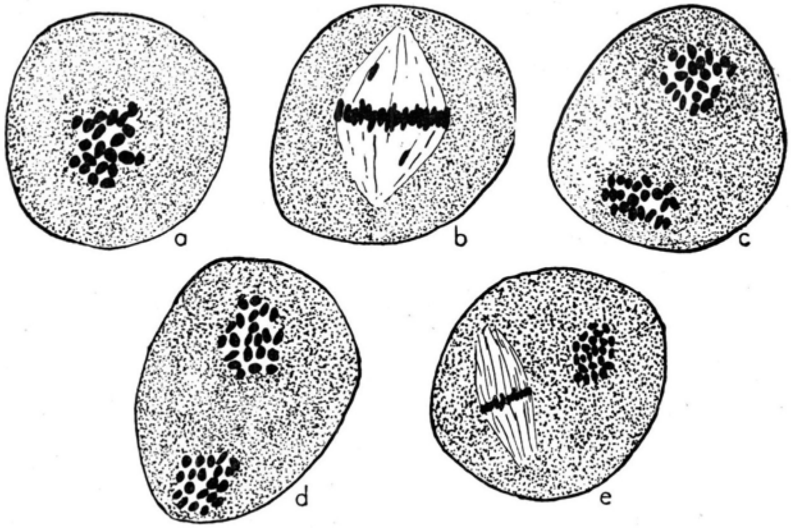

Fig. 114. F₁ *Geum molle* × *G. aleppicum*, meiosis in PMCs; a — M-I with 21 bivalents; b — M-I with 2 univalents; c — M-II with 21 chromosomes in each plate; d — M-II with 20 and 22 chromosomes in the plates; e — M-II with 23 chromosomes in one of the plates

However, later results disclosed that in various flowers of this hybrid both types of meiotic divisions may occur. Further investigations carried out in 1950 revealed that in the same hybrid plant in some flowers meiosis did not take place, as the archaesporium degenerated before meiotic divisions started, and in others meiosis proceeded to the end either along the asyndetic pattern or with almost normal chromosome conjugation (Fig. 113). Meiosis of the intermediate pattern with partial chromosome conjugation was not observed.

The hybrid *G. aleppicum* × *urbanum* grows very vigorously, its floral stems may be as much as 1 m long and the number of flowers on one stem may even be 56 while in the parents it never exceeds 11 to 15. This large number of flowers is due to that on floral stems side stems grow out from all buds in the leaf axils right to the base of floral stems. This effect is probably in connection with the complete sterility of these hybrids. Quite certainly in fertile plants the development of seeds at the apices of stems (maybe in connection with the production of auxins) inhibits the development of buds at the lower internodes of the stems.

Equally sterile are the hybrids of *G. aleppicum* with *G. molle* and *G. hispidum*. The cross *G. molle* × *aleppicum* gives vigorous plants, with much branched stems and numerous flowers. In the flowers of this hybrid, similarly as in the flowers of the one just described, the stamens are underdeveloped and additional styles grow out from the ovary. In flowers showing abnormal development of the gynoecium usually only 10 to 20 percent of the pistils have additional styles and the remaining are normal. Pollen fertility is about 0.2 per cent and seed fertility is much lower so that fully developed achenes occur at the rate of one in several tens of flowers (about 0.01 per cent). The course of meiosis in the PMCs of this hybrid is normal. At metaphase there are 21 bivalents in 85 per cent of PMCs, and in the remaining 15 per cent the number of univalents ranges from 2 to 6 (Fig. 114).

Very vigorous are also the hybrids *G. hispidum* × *aleppicum*, and their height reaches 150 cm. Pollen fertility is here about 0.6 per cent and seed fertility is about 0.2 per cent which is somewhat higher than in the preceding hybrid. Usually 1 to 3 achenes are found in 10 flowers. Meiosis in the PMCs is identical as in the preceding hybrid. No disturbances in the development of the androecium and gynoecium are observed.

The hybrid no. 108 *G. aleppicum* × *canadense* also belongs to this highly sterile group (Fig. 115). Very special attention was given to this hybrid as it was also investigated by L. Raynor, who in her doctor thesis (1945) made the supposition that the hybrid is identical with *G. virginianum* described by Linnaeus. The hybrid was obtained both with the typical form of *G. aleppicum* from Białowieża and with the form var. *strictum* (Ait.) Fern. obtained from the State of New York. The differences between these hybrid forms were small. The description which now follows refers to the hybrid with the form var.

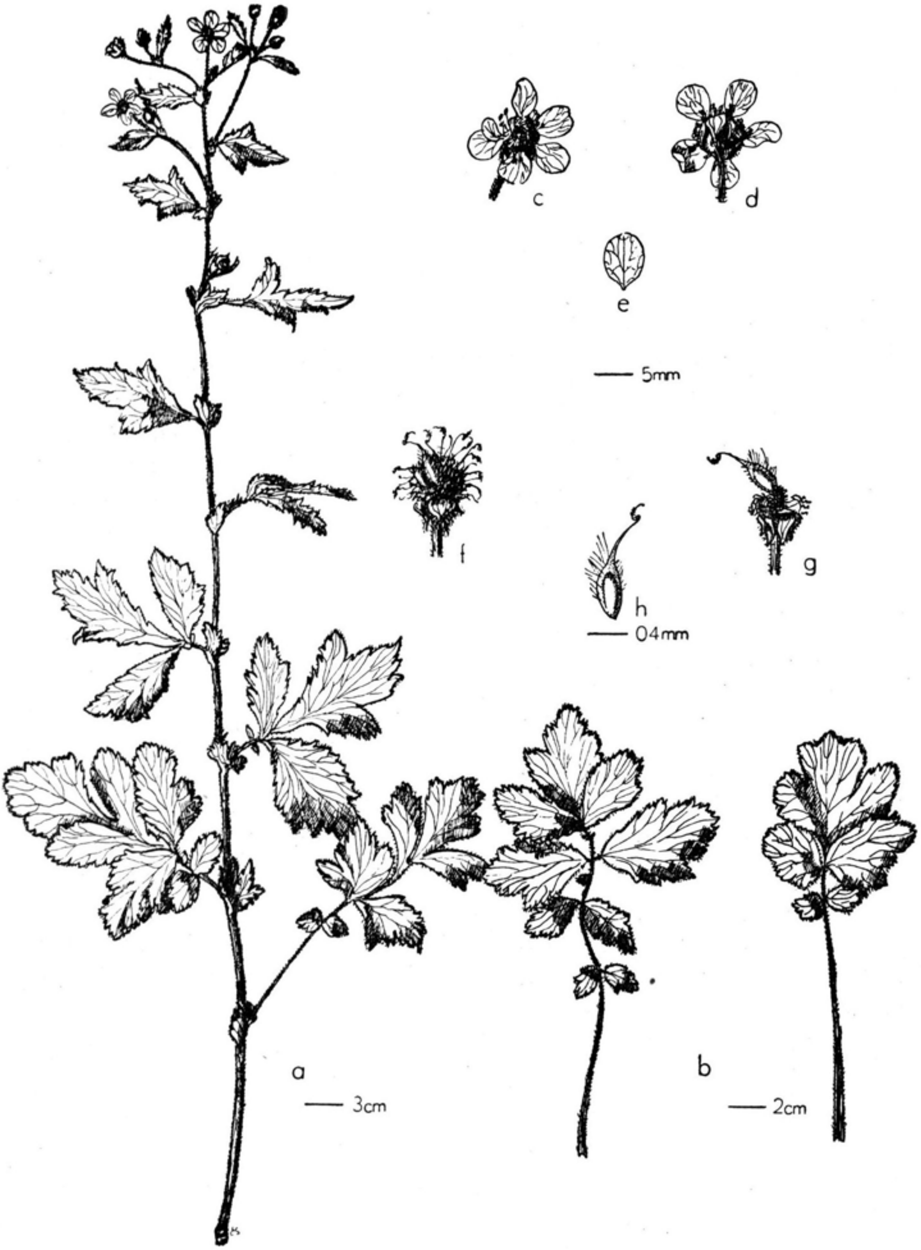

Fig. 115. F$_1$ *Geum aleppicum* × *G. canadense*; a — floral stem; b — basal leaves; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower (one is developed normally); g — receptacle with one achene; h — achene

strictum. The crosses were carried out in both directions and the total amount of F_1 specimens was 76. Both populations of reciprocal hybrids were fairly uniform and very similar. The more significant characters of the hybrid as compared with the parent species are the following:

Character	*G. aleppicum* v. *strictum*	F_1	*G. canadense*
Basal leaves	long, with rather numerous lateral leaflets, deeply serrate	intermediate, more like *canadense*	spring leaves deeply dissected, later terminal leaflet round shallowly dentate, few lateral leaflets
Cauline leaves	even the topmost leaves tripartite	as in *canadense*	upper leaves unifoliolate
Indumentum	lower part of stem stiffly fairly long haired	intermediate	lower part of stem softly sparsely haired
Stipules	big, shallowly incised	intermediate	small, elongated, deeply incised
Colour of petals	yellow	pale yellow	white
Size of petals (mm)	9.0 × 9.2	9.0 × 5.8	8.8 × 4.6
Floral base	8 — 13 mm long, ± glabrous	3 — 4 mm long, ± long haired	4 — 5 mm long, long haired
Number of carpels	200 — 250	100 — 120	80 — 100
Gynophore	1.5 — 3 mm long	absent	absent

Usually in the Warsaw climate *G. canadense* begins to flower ten days or a fortnight earlier than *G. aleppicum* and the hybrid begins to flower almost simultaneously with *G. canadense*. The hybrid is very vigorous, with stems up to 120 cm tall. The stems are strongly ramified and have 30 to 40 flowers which is nearly twice as much as in the parent species. The hybrid is highly sterile, its pollen fertility is about 0.1 per cent and the number of good seeds is even less. There are usually 5 to 6 well developed achens in every 100 flowers, i.e. in every 10 000 to 12 000 achenes.

From the course of meiosis in this hybrid (Fig. 116) it is apparent that in the majority of PMCs there are at metaphase of the I-st division 20 to 17 bivalents and the corresponding 2 to 8 univalents. Cells with 21 bivalents are rare. In anaphase univalents are fairly often seen lagging on the spindle, and sometimes inversion bridges are formed. In spite of the rather numerous univalents in the first division the majority of cells at the tetrad stage are made up of 4 microspores and only in 16 out of 234 analysed cells small additional microspores were found.

In her investigation Raynor (1945, 1952) had no hybrids obtained experimentally and, presumably, she examined only plants of hybrid origin gathered from natural habitats where they grew together with the two parental species mentioned above. These plants rather closely corresponding in their morphological character to *G. virginianum* were collected by Professor R. T. Clausen from one habitat in the State of New York and from another in the State of Virginia. Raynor assumes that the plants from the natural habitats are the F_1 generation and that the plants grown out of seeds collected from these presumed natural hybrids constitute the F_2 generation. The F_1 plants described by Raynor correspond in respect to morphology to the hybrids that I obtained experimentally and they also show more vigorous growth than the parental species. Raynor reports that the hybrids in question show partial sterility which does not agree exactly with the present observations, as the hybrids are almost completely sterile. On the other hand it is not quite clear what the authoress means by "partial sterility". The hybrids that she describes have also numerous univalents, in meiosis they display disturbances very characteristic for

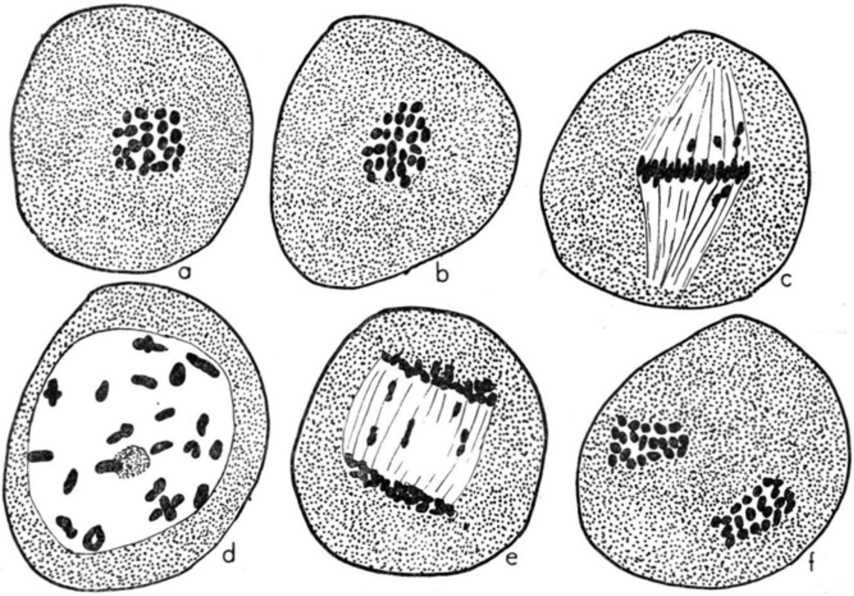

Fig. 116. F_1 *Geum aleppicum* × *G. canadense*, meiosis in PMCs; a — M-I with 22 chromosomes ($20_{II} + 2_I$); b — M-I with 25 chromosomes ($17_{II} + 8_I$); c — M-I with 6 univalents; d — diakinesis with 21 bivalents; e — A-I with univalents on the spindle; f — M-II with 21 chromosomes in each plate

hybrids and similar to those which I observed in hybrids obtained experimentally. Unfortunately, Raynor does not describe her results from cytological examinations of the plants in question, but judging by her drawings illustrating the course of meiosis meiotic disturbances in her material are even more conspicuous than in the hybrids that I examined. The description which Raynor makes of the F_2 hybrids is not quite clear to me, as it implies either that only individual specimens from the two habitats are described or that all F_2 plants are uniformly similar, which does not seem very probable and does not agree with the present observations.

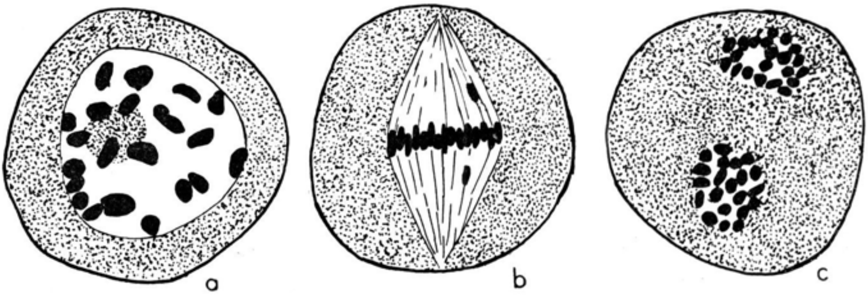

Fig. 117. F_1 *Geum urbanum* × *G. canadense*, meiosis in PMCs; a — diakinesis with 21 bivalents; b — M-I with 2 univalents; c — M-II with 21 chromosomes in each plate

G. virginianum in my collections was grown out of seeds obtained from Professor R. T. Clausen and collected from a plant grown in a garden in Ithaca where it was transplanted from a natural habitat in the Pigeon Mts., Iowa. The hybrid *G. aleppicum* var. *strictum* × *G. canadense* which I obtained is, indeed, morphologically similar to *G. virginianum*. However, *G. virginianum* has normal seed fertility ranging from 90 to 94 per cent and only its pollen fertility is reduced to an average of 73.3 per cent. Moreover it shows no signs of hybrid heterosis. These observations seem to indicate that, although the origin of *G. virginianum* from the cross *G. canadense* × *aleppicum* is not impossible, quite certainly this species does not correspond to the F_1 hybrids but rather to a product of further segregation of these hybrids. My investigations on the species *G. virginianum* carried out on herbarium specimens indicate on the basis of nearly 40 herbarium sheets originating mainly from the states of Pennsylvania, Indiana, Minnesota, Ohio, New York and others — that various specimens of this species vary greatly in respect to leaf shape, pubescence, colour and shape of petals, and fertility. Some herbarium specimens are highly sterile, as for instance the one collected by Asa Gray in the vicinity of Ohio city known to me from the herbarium of the Botanical Garden at Uppsala. This specimen has only one well developed achene in six fruiting heads with an average number of about 150 achenes in every one, all the other achenes are quite empty. It is therefore possible that at present the name "*G. virginianum* L." covers just as well the highly sterile plants of F_1 and further generations as the segregants with high fertility and morphologically stabilized progeny. The latter case corresponds to the plants obtained from Professor R. T. Clausen. As in N. America the distribution of *G. virginianum* covers areas where its supposed parental species do not appear it must be represented there by its fertile forms. It may be that further extensive researches based both on genetical experiments and herbarium investigations will permit to distinguish between *G. virginianum* proper and the sterile hybrids of *G. aleppicum* and *G. canadense* with which it is no longer identical and from which perhaps this species arose in a very distant past. Such a research is possible only for American botanists who have the possibility to undertake large scale field work.

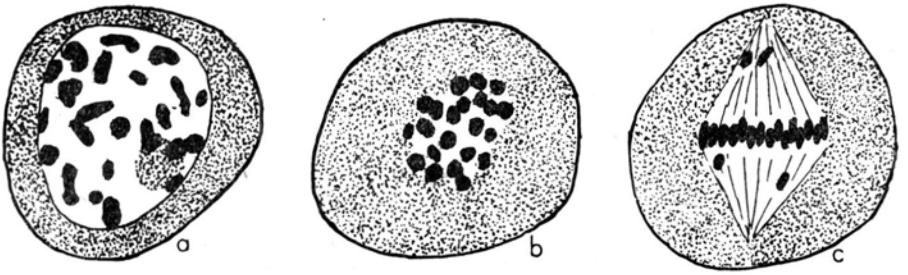

Fig. 118. F_1 *Geum urbanum* × *G. laciniatum*, meiosis in PMCs; a — diakinesis with 19 bi- and 4 univalents; b — M-I with 20 bi- and 2 univalents; c — M-I with 4 univalents on the spindle

Almost completely sterile are also the hybrids of *G. aleppicum* with *G. silvaticum* and *G. boliviense*.

Equally sterile too is the hybrid *G. canadense* × *urbanum*. The hybrid plants are very vigorous, reaching 150 cm in height and flowering abundantly from summer till late autumn. The petals are pale yellowish 7.2 mm long and 4.7 mm wide. Pollen fertility is here about 0,2 per cent and seed fertility ranges from 0,05 to 0,1 per cent. Usually there are 3 or 4 well developed achenes in 10 to 15 flowers. Meiosis of this hybrid is shown in Fig. 117. In 65 cells examined at the stage of the I-st division metaphase there were 12 cells with 21 bivalents, and in the remaining 53 cells, alongside of bivalents, there were 2 to 10 univalents. At anaphase the univalents frequently lag on the spindle and are segregated with much delay in respect to the bivalents. Often some univalents are not included in the daughter nuclei and in interkinesis single chromosomes lie sometimes in the cytoplasm outside the nuclei. The second division proceeds more or less normally so that in the tetrad stage there are four microspores in every cell. In spite of this, good pollen grains are very seldom formed. Very similar in respect to fertility and meiotic behaviour is the hybrid of *G. canadense* with *G. molle*. Pollen fertility ranges in this hybrid from 0.2 to 0.4 per cent and seed fertility is somewhat higher, ranging from 0.5 to 1 per cent.

Geum laciniatum Murr. is closely related to *G. canadense* Jacq. Hybrids between the two species are highly fertile and will thus be described later.

G. laciniatum, similarly as its close relation *G. canadense*, gives hybrids of very low fertility in crosses with *G. aleppicum, urbanum, molle* and *hispidum*. As an example illustrating the hybrids with *G. laciniatum* the hybrid no. 99 *G. laciniatum* × *urbanum* will now be described in detail.

Character	*G. laciniatum*	F_1	*G. urbanum*
Basal leaves	first leaves deeply dissected, last with terminal leaflet ± round	first leaves deeply dissected, last intermediate	leaves shallowly incised, with terminal leaflet rounded
Indumentum	stem and leaves roughly long haired	hairs rather like in *laciniatum*	stem and leaves sparsely, softly haired
Cauline leaves	lower with 5—7 leaflets, upper tripartite	intermediate	leaves tripartite almost to base
Stipules	small, elongated, deeply incised	intermediate in respect to size and shape	big, rounded, inciso-serrate
Gynophore	1—1.5 mm long, haired	absent	absent
Floral base	7—8 mm long, short haired	5—6 mm long, long haired	6—7 mm long, long haired
Number of achenes	150 — 200	200 — 240	230 — 250
Colour of petals	white with greenish tint	yellow	yellow
Size of petals (mm)	4.2 × 2.4	5.5 × 4.0	5.8 × 4.6
Pubescence of achenes	±naked	haired	densely short haired
Length of achenes (mm)	4.5 — 5	4.5 — 5	5 — 6
Length of rostrum (mm)	3 — 3.5	4 — 5	5 — 7

G. laciniatum has a character not appearing in other *Eugeum* species. Its achenes after ripening remain firmly inserted on the receptacle the base of which is very fragile. The whole fruiting head is thus easily broken away from the peduncle and may be carried and disseminated by animals. This character is recessive and does not appear in the hybrid. The hybrid is vigorous, with stems reaching 100 cm in height, and with very many flowers opening constantly from summer to late autumn. The total number of F_1 plants amounted to 24 and during two years all flowered abundantly, nevertheless, only 85 well developed achenes were gathered from the many thousand flowers which developed on the plants during that time. Pollen fertility in acetocarmine smears ranges from 0.05 to 0.15 per cent. Meiotic divisions in the PMCs of this hybrid proceed more or less along the same pattern as in the hybrid *G. canadense* × *urbanum* (Fig. 118). In 39 cells analysed at the M. I stage the following configurations were observed:

21_{II} in 2 cells
$20_{II} + 2_{I}$ in 12 cells
$19_{II} + 4_{I}$ in 18 cells
$18_{II} + 6_{I}$ in 4 cells
$17_{II} + 8_{I}$ in 2 cells
$16_{II} + 10_{I}$ in 1 cell.

The number of chromosomes found in numerous diakineses also ranged from 21 to 25. The courses of anaphase and of the second division are the same as in the hybrids with between 2 and 10 univalents described previously.

The hybrid no. 111 *G. laciniatum* × *aleppicum* is morphologically very closely related to the preceding one, but its petals are bigger and its fertility is even lower: pollen fertility was about 0.05 per cent and among several hundred flowers only one seemingly good achene was gathered. Meiotic division is in this hybrid almost exactly the same as in the preceding one.

The hybrid *G. laciniatum* × *hispidum* is likewise very vigorous in growth and flowers abundantly. The stems are up to 120 cm tall and basal leaves may be 40 cm long. The petals are yellow, about 6 mm long and 5 mm wide. The floral base is long (8—9 mm), short haired, the gynophore is absent. In contrast with *G. laciniatum, G. hispidum* is softly short haired and with numerous glandular hairs in the upper part of the plants. In the hybrid there are no glandular hairs, except some few on the rostrum, and the straight hairs are long bristly, but not as stiff as in *G. laciniatum.* The *G. hispidum* leaves have terminal leaflets elongated, deeply dissected into many lobes and diminishing towards the top. This character is seen also in the leaves of the hybrid, but under the influence of *G. laciniatum* the leaves, especially the first ones, are deeply dissected into narrow lobes. The hybrid is distinctly more fertile than those with *G. laciniatum* already described. Pollen fertility is here 4.5 per cent and the percentage of good achenes ranges from 4.4 to 8.4, average 5.6. The achenes of the hybrid are much bigger than those of *G. laciniatum* (about 6 mm long), densely haired and with glandular hairs on the rostrum.

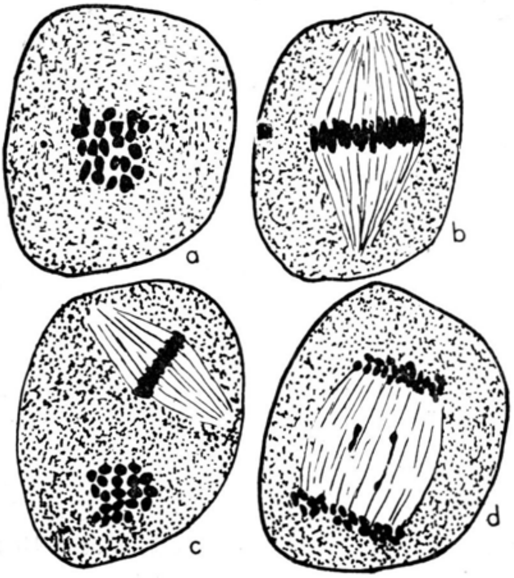

Fig. 119. F_1 *Geum hispidum* × *G. laciniatum*, meiosis in PMCs; a — M-I with 21 bivalents; b — M-I normal plate — side view; c — M-II with 21 chromosomes in one of the plates; d — A-I with 2 univalents on the spindle

Morphologically closely related to the one just described is the hybrid no. 105 *G. hispidum* × *canadense*. The fertility of this hybrid is still higher, pollen and seed fertility being 13.4 and 8.5 per cent respectively. The two hybrids have the same kind of meiotic divisions in PMCs, with 21 bivalents in the majority of cells and 2 to 8 univalents in the remaining more or less 20 per cent of cells (Figs. 119 and 120). The two hybrids are close to the fertility limit of the partially fertile hybrids which will be described now.

Partially fertile hybrids: — Remarkable conditions prevail in the group of 13 hexaploid *Eugeum* species in respect to the fertility of hybrids obtained from crosses between these species. *G. rivale, coccineum* and *silvaticum* constitute a group of species giving in crosses between them highly fertile hybrids. They also give highly fertile hybrids with a group of European species composed of *G. urbanum, molle* and *hispidum* which in turn produce between them high hybrid fertility. The species from the former group produce partially fertile hybrids with the American species *G. canadense, laciniatum* and *boliviense* which also constitute a group of species related by high hybrid fertility. The partially fertile hybrids between species of the first and the last of these three groups will now be described. *G. aleppicum* represents a quite distinctly separate type of species which gives highly sterile hybrids with all but the *G. rivale* group. Finally, come *G. macrophyllum* with the closely related *G. perincisum* and *oregonense* which between them give fertile hybrids and complete hybrid sterility with species from all the other groups just mentioned.

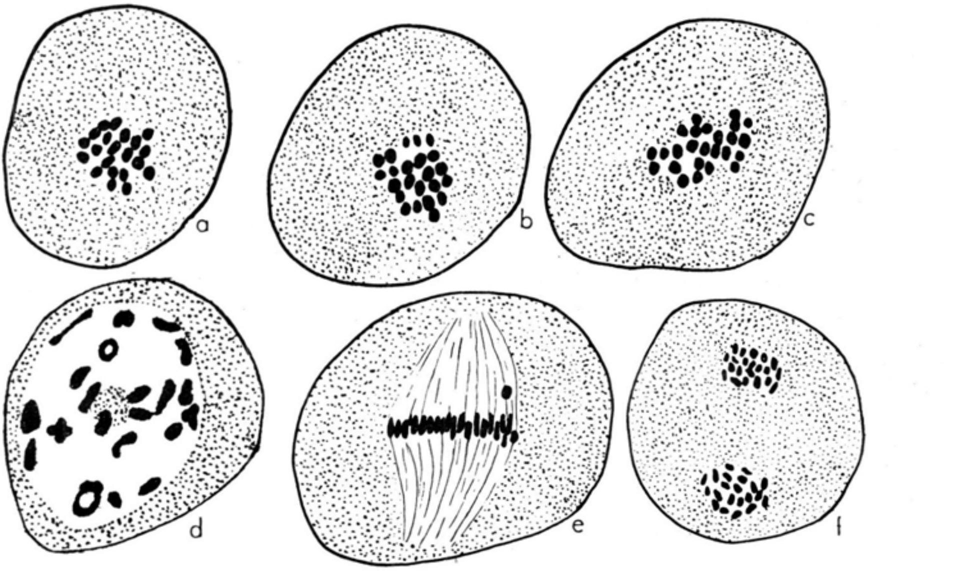

Fig. 120. F_1 *Geum hispidum* × *G. canadense,* meiosis in PMCs; a — M-I with 21 bivalents; b — M-I with 19 bi- and 4 univalents; c — M-I with 17 bi- and 8 univalents; d — diakinesis with 21 bivalents; e — M-I with 2 univalents; f — M-II with 21 chromosomes in each plate

The group of partially fertile hybrids thus includes those hybrids which have *G. rivale* or *G. coccineum* as one parent and *G. canadense, laciniatum, boliviense* or *aleppicum* as the other.

The review of the partially fertile hybrids will begin with a description of the hybrids between *G. rivale* and *G. aleppicum, canadense, laciniatum* and *boliviense.*

72. *G. rivale* L. (21) × *G. aleppicum* Jacq. (21), culture no. 213—52. The characters of this hybrid in connection with the characters of the parental species are as follows:

Character	*G. aleppicum*	F_1	*G. rivale*
Caudex	± absent	present	long, well developed
Date of flowering	May, 1 — 5	May, 10 — 15	June, 10 — 15
Length of stems (cm)	70 — 90	80 — 110	45 — 60
Number of flowers on stem	5 — 11	5 — 15	3 — 5
Indumentum	long, stiff, rough, no glandular hairs	hairs soft, longer than in *rivale*, no glandular hairs	softly short haired, glandular hairs plentiful
Floral peduncles	straight	drooping	very drooping
Anthocyanin in stems	traces	fairly abundant	very abundant
Anthocyanin in calyx and corolla	none	fairly abundant	very abundant
Calyx	reflexed	± horizontal or slightly reflexed	erect
Position of petals	horizontal	slightly erect	erect
Shape of petals	± round, no incision nor claw	with small claw, rounded at tip	with long claw, emarginated at tip
Size of petals (mm)	9.0 × 9.2	9.8 × 9.5	10.1 × 8.0
Colour of petals	yellow	yellow	creamy
Length of gynophore (mm)	1.5 — 3	4 — 7	8 — 10
Floral base	8—12 mm long, ± naked	4—5 mm long, short haired	6—7 mm long, fairly long haired
Number of achenes	200 — 250	150 — 170	150 — 200
Length of rostrum (mm)	4.5 — 6	6 — 8	8 — 10
Length of stigmatic part (mm)	1.5 — 2	2.5 — 3.5	4.5 — 5

The hybrid was obtained many times from crosses in both directions. For the crosses both the typical *G. rivale* form and the *pallidum* form without anthocyanin were used. Also in the case of *G. aleppicum* both plants from Białowieża and the *strictum* variety from N. America were used. The total noumber of F_1 specimens obtained was more than a hundred. The plants differed in some characters according to the form of the parental species. The description in the above table refers to the hybrid of *G. aleppicum* var. *strictum* from the State of New York with *G. rivale* from Piastów near Warsaw. Pollen fertility of the hybrid ranges in various smears from 10.5 to 22.4 per cent averaging at 16.6 per cent. Seed fertility in various flowers ranges from 4.1 to 18.8 per cent averaging over three years at 10.1 per cent. Detailed observation of these plants reveal that as the number of good achenes on the receptacle increases the length of the gynophore increases also. This seems to indicate that seed development stimulates the elongation of the gynophore. Both reciprocal hybrids are identical.

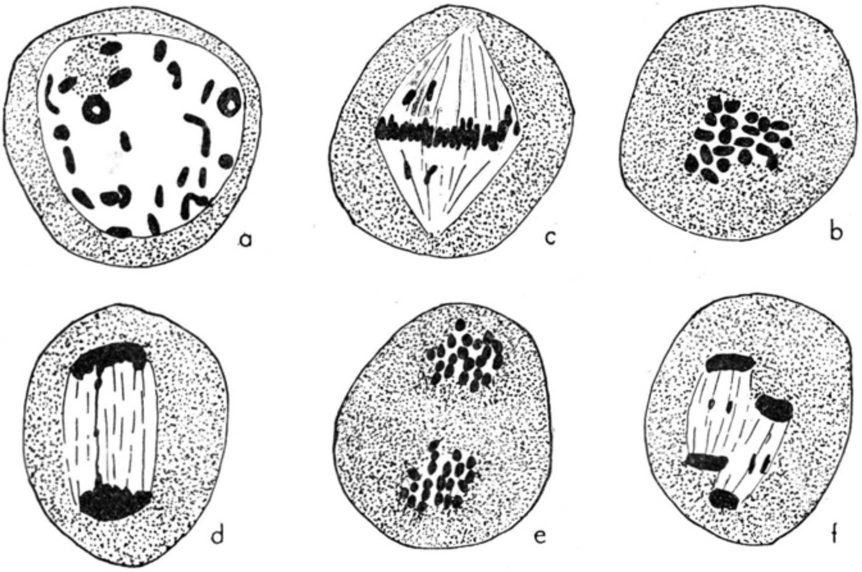

Fig. 121. F_1 *Geum rivale* × *G. aleppicum*, meiosis in PMCs; a — diakinesis with 19 bi- and 4 univalents; b — M-I with 21 bivalents; c — M-I with 4 univalents; d — A-I with chromosomal bridge; e — M-II with 21 chromosomes in each plate; f — A-II with chromosomes lagging on the spindle

Meiotic divisions are normal in the majority of PMCs (Fig. 121). Among the 96 PMCs examined at metaphase of the first division there were 58 with only the 21 bivalents, 29 cells had 2 univalents, 6 cells had 4 univalents and 3 cells had 6 univalents. At anaphase in about 15 per cent of PMCs there are 2 to 5 univalents lying on the spindle in between the two groups formed after the division of bivalents. The univalents are often unusually streched out and sometimes are not included in the daughter nuclei at telophase. In some anaphases inversion bridges with a small acentric fragment occur. In the majority of metaphases of the II-nd division there are 21 chromosomes, but in several 20 and 22 chromosomes were found. The appearance of tetrads is quite normal.

No. 73. *G. rivale* L. (21) × *G. canadense* Jacq. (21), culture no. 90—48. Some characters of the hybrid as compared with the parent species are listed in the table on p. 230.

Character	*G. canadense*	F_1	*G. rivale*
Caudex	± absent	present	long, well developed
Basal leave	spring leaves dissected, later with round, terminal leaflet	intermediate, very heterophyllous as in *canadense*	terminal leaflet dissected into 3 rhomboid lobes
Cauline leaves	lower tripartite, upper unifoliolate	resembling *canadense*	trifoliolate almost to the top of stem
Pubescence on stems and leaves	sparsely haired, no glandular hairs	densely haired, no glandular hairs	densely haired, glandular hairs plentiful
Floral peduncles	straight	drooping	very drooping
Anthocyanin in stems and flowers	only in stems, visible in autumn	abundant in stems and flowers	very abundant in stems and flowers
Calyx	reflexed	horizontal or reflexed	erect
Position of petals	horizontal	slightly erect	erect
Shape of petals	elliptical	with small claw, rounded at tip	with long claw, emarginated at tip
Size of petals (mm)	8.8 × 4.6	9.8 × 9.2	10.1 × 8.0
Colour of petals	white	yellow	creamy
Gynophore (length in mm)	absent	0 — 4	8 — 10
Floral base	4 — 5 mm long, long haired	4 — 5 mm long, long haired	6 — 7 mm long, not so long haired
Rostrum	4 — 5 mm long, naked	4.5 — 6 mm long, pubescent at base	8 — 10 mm long, haired
Length of stigmatic part (mm)	1.5 — 2	3 — 3.5	4.5 — 5
Length of floral stems (mm)	80 — 100	80 — 100	45 — 60
Number of flowers on one stem	12 — 20	15 — 20	3 — 5
Number of achenes	80 — 100	90 — 140	150 — 200

The average fertility of the hybrid is 31.3 per cent for pollen and 8.8 per cent for seed. Seed fertility varies greatly from year to year ranging between 7.6 and 12.5 per cent. Every year there are many flowers which do not produce good achenes at all and wilt early. Usually, in such flowers the gynophore is not developed.

The course of meiotic divisions in this hybryd (Fig. 122) is similar to meiosis in the preceding hybrid. Among 94 PMCs at the stage of meiosis of the I-st division in 71 cells there were bivalents only and their number was 21, in the remaining 23 cells there were besides the bivalents also from 2 to 6 univalents. At anaphase some univalents lag on the spindle, some of them are divided, but the majority move to the poles undivided. Very often the univalents are not included in the daughter nuclei and remain in the cytoplasm. In anaphase chromosomal bridges are occasionally formed; such bridges joining the two daughter nuclei were found in 3 out of 132 cells at the stage of I-st division anaphase. Among the numerous metaphases of the II-nd division which were examined 39 cells with 21 chromosomes were found, in 4 cells there were 20 chromosomes, in 5 cells 19 chromosomes and in 1 cell 23 chromosomes. In the case of this hybrid exceptionally well fixed and well stained preparations from the stage of diakinesis were obtained. It was thus possible to see that the number of bivalents at this stage was 21, but 1 to 3 bivalents were usually very loosely connected and it was impossible to decide whether they were really bivalents or univalents lying close together (Fig. 122 a). Consequently, it is not impossible that some of the univalents at metaphase are formed by the premature disjunction of the loosely conjugated partners seen in diakinesis.

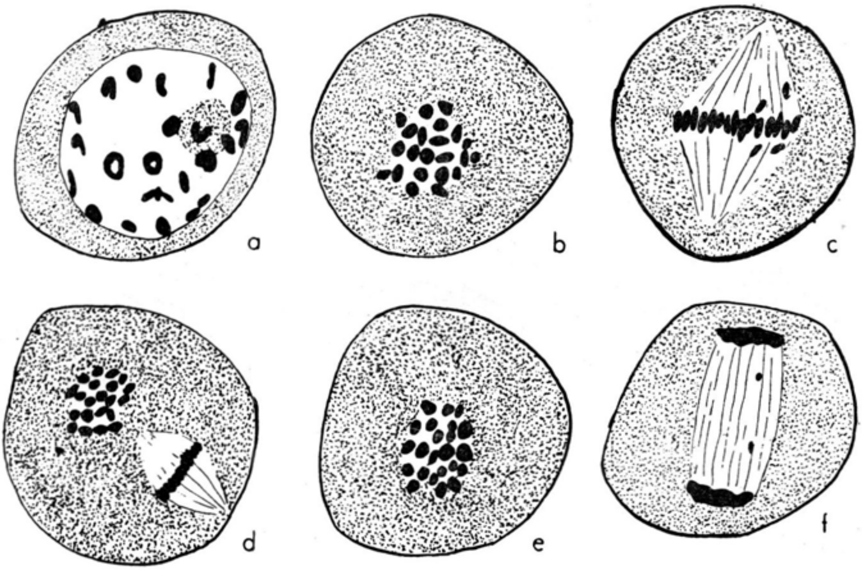

Fig. 122. F_1 *Geum rivale* × *G. canadense*, meiosis in PMCs; a — diakinesis with 21 bivalents, b — M-I with 20 bi- and 2 univalents; c — M-I with 4 univalents, d — M-II with 21 chromosomes in one of the plates; e — M-I with 23 chromosomes ($19_{II} + 4_{I}$); f — A-I with divided univalent on the spindle

No. 74. *G. rivale* L. (21) × *G. laciniatum* Murr. (21), culture no. 11—49. This hybrid closely resembles the one just described. In *G. laci-*

niatum the first spring leaves are deeply dissected into narrow lobes, but this character is not manifested in the hybrid. The partially dominant characters of *Geum rivale* are as follows: the presence of anthocyanin, the drooping of floral peduncles and the partly erect position of sepals and petals. In *G. laciniatum* the petals are white with a greenish tint, 4.2 mm long and 2.4 mm wide; in the hybrid petals are pale yellow, 8.6 mm long and 7.0 mm wide. In this hybrid, similarly as in the preceding one, it is seen that the creamy petal colour of *G. rivale* together with the white petal colour of *G. canadense* or *G. laciniatum* produces in the F_1 hybrids yellow petals. *G. laciniatum* characters dominant in the hybrid are: the rather stiff and protruding bristles on the stems, absence of glandular hairs, the lack of emargination on the tip of petals and the almost complete absence of claw on petals. The receptacle in the hybrid is about 5 mm long, fairly long haired, and is inserted on a 2 to 4 mm long gynophore. *G. laciniatum* has small glabrous achenes with short, 3 to 3.5 mm rostrum and a stigmatic part about 1.5 mm long. In the hybrid the achenes are bigger, about 5 mm long, with rostrum

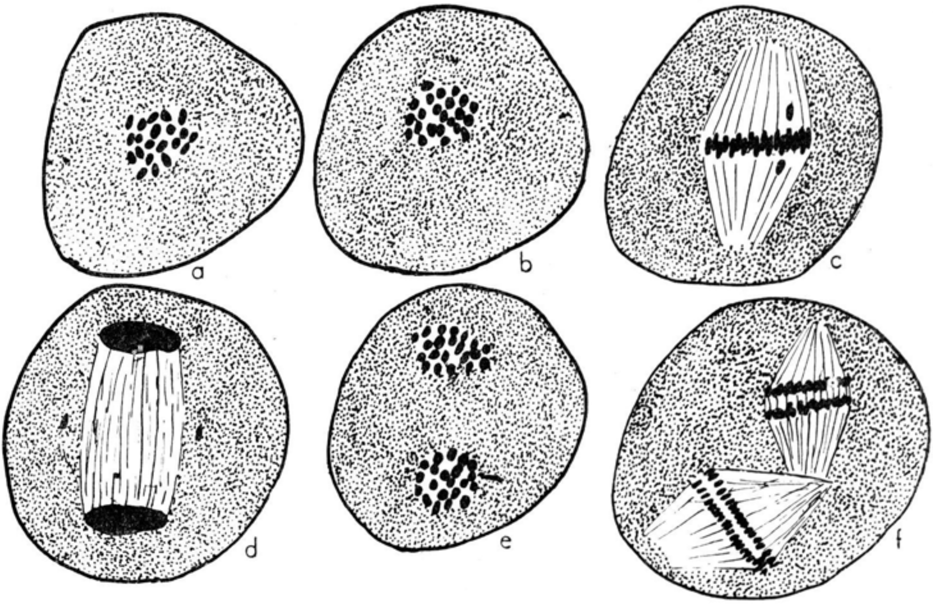

Fig. 123. F_1 *Geum rivale* × *G. laciniatum*, meiosis in PMCs; a — M-I with 21 bivalents; b — M-I with 23 chromosomes ($19_{II} + 4_I$); c — M-I with 2 univalents; d — A-I with 2 chromosomes out of the spindle in the cytoplasm; e — M-II with 21 chromosomes in each plate; f — beginning of A-II of normal appearance

up to 7 mm and stigmatic part about 4 mm in length. In the hybrid both the achenes and the lower part of the rostrum are haired as in *G. rivale* but without glandular hairs characteristic of *G. rivale*. Pollen fertility of the hybrid is about 26.0 per cent and seed fertility ranges from 12.1 to 19.4 per cent, averaging at about 15 per cent.

The course of meiosis in this hybrid is almost exactly the same as in the preceding one (Fig. 123), i.e. in about 80 per cent of PMCs there are 21 bivalents and in the remaining 20 per cent there are between 2 and 8 univalents.

The hybrid *G. rivale* × *boliviense* is closely related to the hybrids of *G. rivale* with *G. canadense* and *laciniatum*, its pollen and seed fertility is 21.0 and 17.5 per cent respectively.

The hybrids obtained by crossing *G. coccineum* with *G. aleppicum, canadense* and *laciniatum* have approximately the same fertility level. In this and other cases *G. coccineum* gives hybrids of similar fertility as *G. rivale*, although the two species differ greatly in respect to morphology.

No. 83. *G. coccineum* Sibth. et Sm. (21) × *G. aleppicum* Jacq. (21), culture no. 15—47. The more important characters of the hybrid and parental species are compared below:

Character	*G. aleppicum*	F_1	*G. coccineum*
Caudex	± absent	present	long, well developed
Basal leaves	terminal leaflet with 3 sharply dentate elongated lobes	with enormous, round, often deeply incised terminal leaflets	terminal leaflet big, round, shallowly crenate
Length of floral stem (cm)	70 — 90	40 — 70	30 — 45
Number of flowers on one stem	5 — 11	5 — 7	3 — 7
Pubescence of stems	long, stiff, rough, no glandular hairs	densely long haired, no glandular hairs	dense and soft, glandular hairs plentiful
Size of petals (mm)	9.0 × 9.2	11.2 × 11.2	13.0 × 14.3
Colour of petals	yellow	dark yellow	red
Length of gynophore (mm)	1.5 — 3	absent	absent
Length of floral base (mm)	8 — 12, naked	3 — 4, short haired	3 — 4, long haired
Length of stigmatic part (mm)	1.5 — 2	3 — 3.5	4.5 — 6

In autumn the hybrid produces enormous basal leaves, the largest that I have seen in *Geum*, their length reaches 54 cm and the dimensions of the terminal leaflet are 18×20 cm. Pollen and seed fertility in the hybrid are about 5.9 and 4.2 per cent respectively. The course of meiosis in the PMCs is characterized by the presence in the I-st division metaphase of 2 to 8 univalents in about 30 per cent of cells. In the remaining cells there are bivalents only and their number is 21 (Fig. 124). In metaphase of the II-nd division the presence of 21 chromosomes was observed in numerous plates, though plates with 19, 20, 22 and 23 chromosomes were also encountered. The appearance of tetrads is absolutely normal.

No. 84. *G. coccineum* Sibth. et Sm. (21) × *G. canadense* Jacq. (21), culture no. 111—52. The characters of the hybrid are as follows:

Character	*G. canadense*	F_1	*G. coccineum*
Caudex	± absent	present	long, well developed
Basal leaves	spring leaves dissected, later with round terminal leaflet	terminal leaflet tripartite	terminal leaflet big, round, shallowly crenate
Cauline leaves	lower tripartite, upper unifoliolate	lower tripartite, upper trilobate	tripartite almost to the top of the stems
Pubescence of stems	sparsely haired, no glandular hairs	densely, softly haired, no glandular hairs	densely, softly haired, glandular hairs plentiful
Anthocyanin in stems	visible in autumn only	as in *canadense*	none
Size of petals (mm)	8.8 × 4.6	11.3 × 8.2	13.0 × 14.3
Colour of petals	white	orange	red
Length of stigmatic part (mm)	1.5 — 2	3 — 3.5	5 — 6
Length of floral stems (cm)	80 — 100	80 — 100	30 — 45
Number of flowers on one shoot	12 — 20	7 — 11	3 — 7

Pollen and seed fertility in this hybrid average at 22.8 and 24.8 per cent respectively. *G. coccineum* begins to flower early, between May 1 and 10, and *G. canadense* much later around June 15. The hybrid begins flowering more or less at the same time as *G. canadense*. Meiotic divisions in PMCs proceed along the same pattern as in the hybrid just described

(Fig. 125), i.e. in the majority of cells there are at metaphase of the I-st division 21 bivalents only and in the minority of cells the number of univalents ranges from 2 to 8.

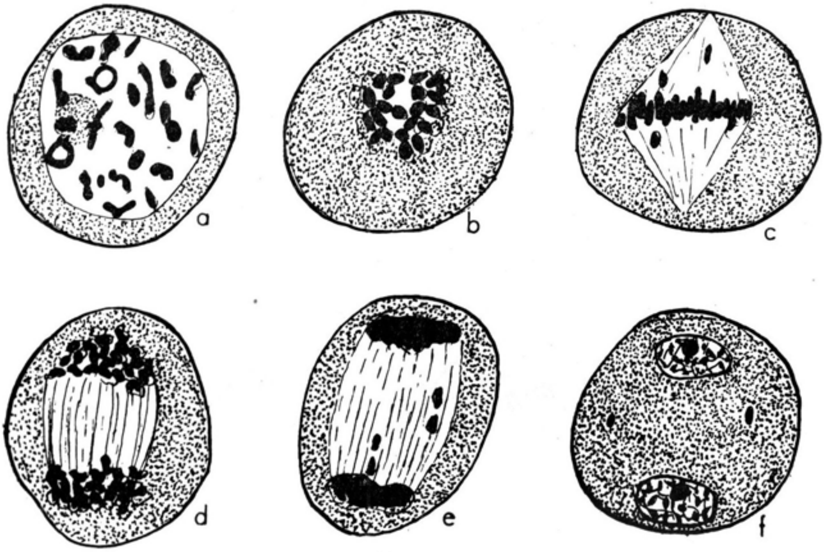

Fig. 124. F_1 *Geum coccineum* × *G. aleppicum,* meiosis in PMCs, a — diakinesis with 23 chromosomes ($19_{II} + 4_{I}$); b — M-I with 22 chromosomes ($20_{II} + 2_{I}$); c — M-I with 4 univalents, d — A-I with 21 chromosomes in each group; e — A-I with univalents on the spindle; f — T-I with 2 chromosomes in the cytoplasm

No. 87. *G. coccineum* Sibth. et Sm. (21) × *G. laciniatum* Murr. (21), culture no. 112—52. This hybrid resembles the preceding one in many respects. The stems, up to 70—80 cm tall with 5 to 9 flowers, are covered with long stiff hairs and have no glandular hairs. Basal leaves are highly heterophyllous similarly as in *G. laciniatum*. The petals are orange (Tangerine Orange no. 9 according to the Horticultural Colour Chart), their size is 8.0 × 5.9 mm and they often have recurved margins. The achenes are numerous, short haired, 4.5—5 mm long; the rostrum is glabrous, 3.5—4 mm long; the stigmatic part is ± glabrous, 3—3.5 mm long. Pollen and seed fertility of this hybrid are about 40 and 14.5 per cent respectively.

Meiosis in PMCs is of the same type as in the hybrids already described (Fig. 126). 41 cells were analysed in metaphase of the I-st division. In 30 there were only the 21 bivalents, in 6 cells 2 univalents, in 2 cells 4 univalents and in 3 cells 6 univalents. At anaphase of the I-st division the univalents often lag on the spindle and sometimes are not included in the daughter nuclei. A detail worth noting is the formation of chromosomal bridges at anaphase, they are observed in about 1 per cent of all cells analysed at anaphase. In the second division the most frequent chromosome number in metaphasal plates is 21, but plates with a different number, e.g. 19, 22 and 23 also occur. The tetrads have an entirely normal appearance.

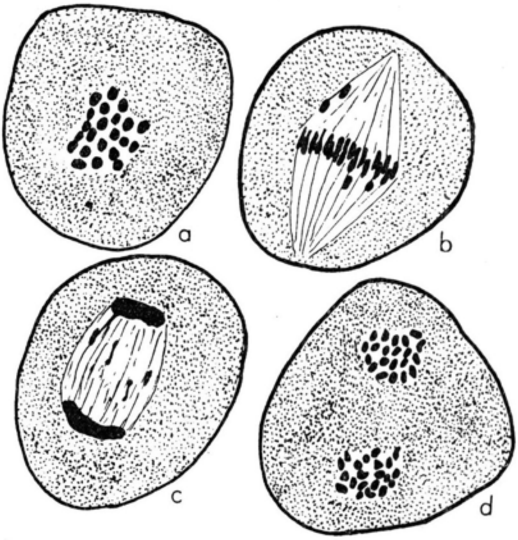

Fig. 125. F_1 *Geum coccineum* × *G. canadense*, meiosis in PMCs; a — M-I with 22 chromosomes ($20_{II} + 2_I$); b — M-I with 4 univalents; c — A-I with univalents on the spindle; d — M-II with 21 chromosomes in each plate

Fertile hybrids. The fertile hybrids are primely those obtained from crosses between species forming related groups mentioned before, i.e. hybrids between *G. rivale, coccineum* and *silvaticum*, hybrids between *G. molle, hispidum* and *urbanum*, hybrids between *G. canadense, laciniatum* and *boliviense*, and finally hybrids between *G. macrophyllum, oregonense* and *perincisum*.

Moreover, the hybrids from crosses between the group *G. rivale, coccineum* and *silvaticum* and the group consisting of *G. urbanum, molle* and *hispidum* may also be considered as fertile. The first fertile hybrids to be described will be the ones originating from crosses within the group *G. molle, hispidum* and *urbanum* which produce between them hybrids with relatively the most reduced fertility.

No. 92. *G. urbanum* L. (21) × *G. molle* Vis. et Panc. (21), culture no. 44—50. The hybrid was obtained in both directions and the two reciprocal hybrids did not differ from each other. The cross gives equally good results in both directions and the setting of seeds is between 82 and 91 per cent. The more significant characters of the hybrid and the parent species are compared in the table below:

Character	*G. urbanum*	F_1	*G. molle*
Basal leaves	terminal leaflet with 3 rhomboid elongated lobes	resembling *molle* but much more incised, often tripartite	terminal leaflet ovoid with cordate base, incised
Pubescence on stems	sparsely haired, no glandular hairs	densely long haired, no glandular hairs	densely long haired, glandular hairs plentiful
Length of stem (cm)	60 — 80	70 — 90	40 — 60
Number of flowers on stem	5 — 9	5 — 7	2 — 3
Gynophore	absent	absent	up to 1 mm long, haired
Colour of petals	yellow	yellow	pale yellow
Size of petals (mm)	5.8 × 4.6	9.2 × 7.5	11.5 × 9.2

The hybrid grows vigorously exceeding the parental species by the size of its stems and leaves. Pollen fertility of the hybrid is in various smears between 27.9 and 45.7 per cent, average 32.6 per cent of good pollen. The percentage of good achenes is also rather variable in various flowers and from year to year. E.g. seed fertility in 1950 averaged at about 22.5 per cent, in 1951 at about 23.1 per cent and in 1952 seed fertility was somewhat less being only 18.8 per cent. In 1952 it was noticed that one plant from the 26 in the F_1 generation *G. molle* × *urbanum* had darker and larger leaves, its achenes were bigger and the number of good achenes was larger than in the other plants of this F_1 generation. The average seed fertility of this plant was 66.1 per cent. Further investigations on the progeny of this plant (W. Gajewski 1954) revealed that it was an amphidiploid with $2n = 84$, which possibly was caused by the doubling of the somatic chromosome number in an early embryonic stage.

Meiosis in the hybrid plants has a fairly normal course (Fig. 127). In 34 of the 44 cells analysed at metaphase of the I-st division the conjugation of chromosomes was complete and 21 bivalents appeared, in 8 cells there were 20 bivalents and 2 univalents lying outside the plate in the remaining 2 cells there were respectively 6 and 8 univalents and the corresponding number of bivalents. In 12 PMCs examined at the stage of diakinesis only bivalents were found. Anaphase of the II-nd division has a normal course. In numerous metaphasal plates of the II-nd division 21 chromosomes were always found. The appearance of the tetrads is quite normal and the degeneration of $^2/_3$ of the pollen grains probably occurs before the first somatic division in the microspore.

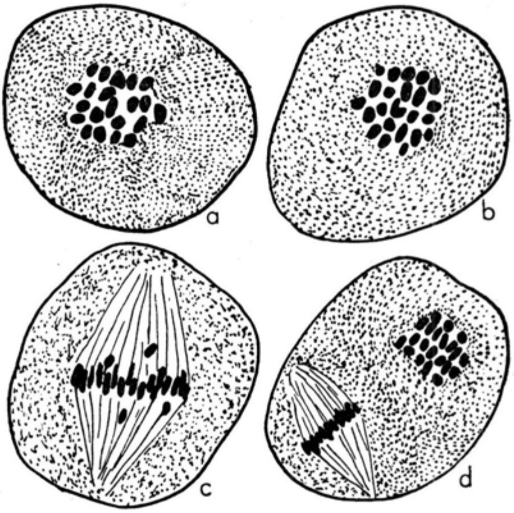

Fig. 126. F_1 *Geum coccineum* × *G. laciniatum*, meiosis in PMCs; a — M-I with 21 bivalents; b — M-I with 23 chromosomes ($19_{II} + 4_{I}$); c — M-I with 4 univalents; d — M-II with 21 chromosomes in one of the plates

The hybrid no. 93 *G. urbanum* × *hispidum* is also very vigorous with stems up to 1 m tall and basal leaves reaching 32 cm in length. From the hybrid just described it differs by the shape of leaves which is associated with the different leaf shape in *G. hispidum*. The size of petals in the hybrid is also smaller relatively to the smaller petals of *G. hispidum*. The size of petals in *G. hispidum* is 7.2×6.0 mm and in the hybrid 7.6×6.2 mm. In other respects the hybrid resembles the preceding one. Average pollen and seed fertility are 24.7 and about 34.2 per cent respectively. The course of meiosis in this and the preceding hybrid is exactly the same (Fig. 128).

G. molle, *G. hispidum* and "*G. albarraciense* Pau" form a group of closely related species in spite of their quite different geographical distributions. *G molle* is a Balkan species which occupies outside the Balkan Peninsula only a small area in the Abruzzian Mountains on the Apennine Peninsula. *G. hispidum* grows solely in the southern coastal districts of Sweden in the provinces of Halland, Blekinge, Smoland and Ostergötland.

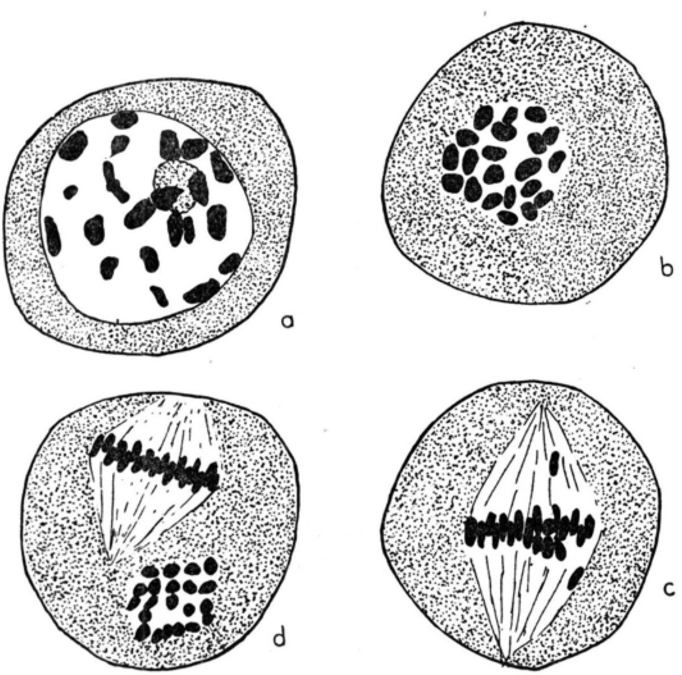

Fig. 127. F$_1$ *Geum urbanum* × *G. molle,* meiosis in PMCs; a — diakinesis with 21 bivalents; b — M-I with 21 bivalents; c — M-I with 2 univalents; d — M-II with 21 chromosomes in one plate

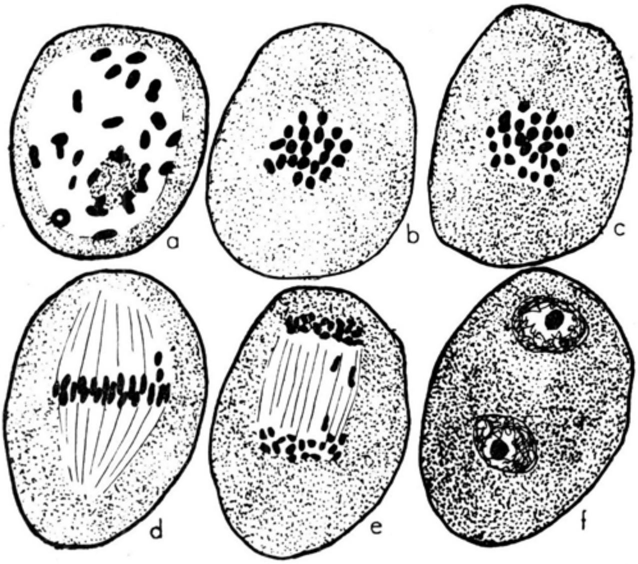

Fig. 128. F$_1$ *Geum urbanum* × *G. hispidum,* meiosis in PMCs; a — diakinesis with 20 bi- and 2 univalents; b — M-I with 21 bivalents; c — M-I with 25 chromosomes ($17_{II} + 8_{I}$); d — side view of M-I with 2 univalents; e — A-I with univalents on the spindle; f — normal T-I

Finally, the third "species" *G. albarraciense* Pau grows only on the Iberian Peninsula. The specific distinction of *G. albarraciense* from *G. hispidum* seems to me rather doubtful. As I have at present in my collection *G. albarraciense* I shall be able to look for an experimental solution to this problem. Bolle (1933) makes the following remark on these three species: " '*G. albarraciense*' bildet mit *G. molle* und *G. hispidum* zusammen eine Gruppe ausserordentliche nahe verwandter Arten. Die Unterschiede sind sämtlich gering, wenn auch *G. molle* wegen des grossen Endblättchens seiner Wurzelblätter auf den ersten Blick von den beiden anderen Arten zu unterschieden ist". *G. albarraciense* differs from *G. hispidum* only slightly by the shape of the basal leaves, which are, however, rather variable in both species.

No. 100. *G. molle* Vis. et Panc. (21) × *G. hispidum* Fr. (21), culture no. 77—51. In the table that follows the characters of the hybrid *G. molle* × *hispidum* are related with the characters of the parental species.

Character	*G. molle*	F_1	*G. hispidum*
Basal leaves	terminal leaflet ovoid, with cordate base, shallowly incised	intermediate, terminal leaflet elongated, deeply incised	terminal leaflet narrow, elongated, deeply incised or dissected into 8 — 5 leaflets
Cauline leaves	trifoliolate, very elongated, deeply dentate, stipules big	intermediate, stipules big	lower 5 — 7-foliolate, upper 3-foliolate, stipules small
Pubescence on stems	dense and soft throughout	as in *hispidum*	at base stiff and bristly, at top softly haired
Length of stem (mm)	45 — 60	70 — 100	50 — 70
Number of flowers on one stem	1 — 3	3 — 9	3 — 7
Colour of petals	pale yellow	bright yellow	bright yellow
Size of petals (mm)	11.5 × 9.2	10.0 × 8.2	7.4 × 6.0
Flowering time	May, 7 — 10	June, 1 — 5	June, 1 — 7

Pollen fertility of this hybrid ranges in various smears from about 42 to 62 per cent and averages at 55.9 per cent. Seed fertility in various flowers ranges from 43 to 74.5 per cent averaging at 54.2 per cent. The disturbances of meiosis in PMCs are few and consist in the presence of 2 to 4 univalents in some of the examined cells (Fig. 129). 63 cells were examined at the stage of the first division metaphase and in 56 only

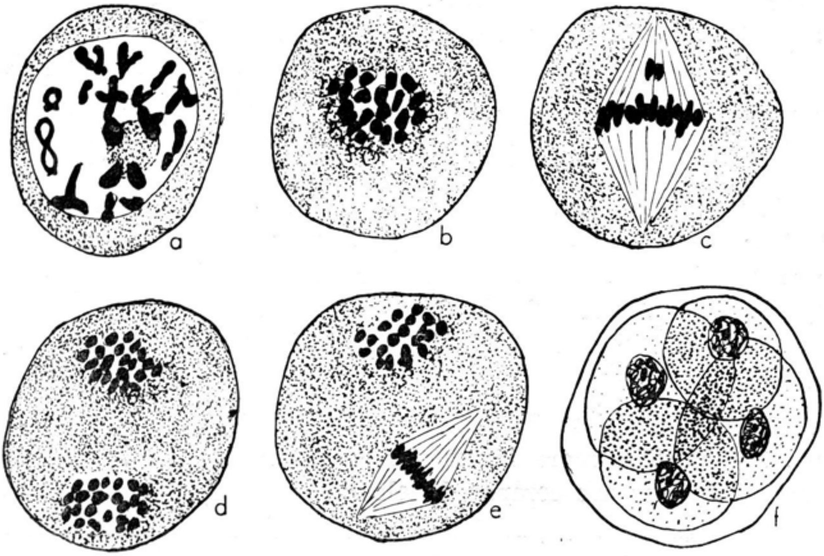

Fig. 129. F_1 *Geum molle* × *G. hispidum,* meiosis in PMCs; a — diakinesis with 21 bivalents; b — M-I with 21 bivalents; c — side view of M-I with 2 univalents; d — M-II with 21 chromosomes in each plate; e — M-II with 20 chromosomes in one of the plates; f — tetrad

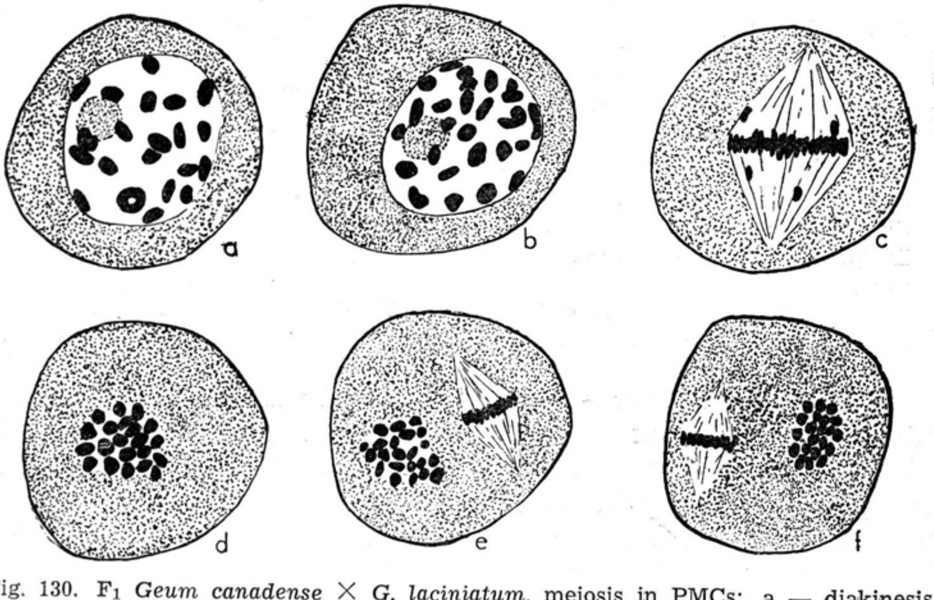

Fig. 130. F_1 *Geum canadense* × *G. laciniatum,* meiosis in PMCs; a — diakinesis with 21 bivalents; b — diakinesis with 24 chromosomes ($18_{II} + 6_{I}$); c — M-I with 4 univalents; d — M-I with 21 bivalents; e — M-II with 22 chromosomes in one plate; f — M-II with 21 chromosomes in one plate

the 21 bivalents were found, there were 20 bivalents and 2 univalents in 6 cells, and 19 bivalents and 4 univalents in 1 cell. In all examined metaphasal plates of the second division 21 chromosomes were found. The course of meiosis in this hybrid is very regular in all respects.

The second group of fertile hybrids is obtained from crosses between three species: the North American *G. canadense* and *G. laciniatum* and the closely related South American *G. boliviense*. Besides other features the most conspicuous character uniting these three species at first sight is the small size and the white colour of petals in the corolla. The two hybrids which were obtained in this group are *G. laciniatum* × *canadense* and *G. canadense* × *boliviense*, and their description will now follow.

No. 120. *G. canadense* Jacq. (21) × *G. laciniatum* Murr. (21) culture no. 13—52. The more important characters of the hybrid and of the parental species are compared below:

Character	*G. canadense*	F_1	*G. laciniatum*
Basal leaves	leaflets rounded with shallowly serrate margins, laterals few	resembling *laciniatum*	leaves deeply incised, sharply serrate, laterals more numerous
Cauline leaves	lower leaves 3-foliolate, then trilobate and entire, stipules big	lower 3-foliolate, upper trilobate, stipules small	lower leaves multifoliolate, upper 3-foliolate, stipules small
Pubescence on stems	fairly soft and sparse	resembling *laciniatum*	long, densely, stiffly haired
Peduncles at anthesis	horizontal	erect	erect
Size of petals (mm)	8.8 × 4.6	6.2 × 4.0	4.2 × 2.4
Length of floral base (mm)	4 — 5	6 — 7	8 — 9
Number of achenes	80 — 100	110 — 160	200 — 250
Achenes	haired	haired	naked

G. laciniatum has numerous achenes strongly fixed to the floral base when ripe while the receptacle is easily broken off at the base and the whole fruiting head may be thus transported. In *G. canadense* the achenes are easily detached from the receptacle which remains on the flower. In the hybrid this character is expressed intermediately and the fruiting heads are detached equally easily as the achenes from the receptacle. Pollen fertility in this hybrid averages at 42.8 per cent and the fertility of the achenes is somewhat higher ranging from 43.1 to 69.8 per cent averaging at 52.3 per cent.

This hybrid is also described by Raynor (1945). In her cultures it was marked with the numbers L8 and L9 and the presumable F_1 plants originated spontaneously in the glass-house. Her description of those plants agrees fairly well with the F_1 hybrids which I obtained in my cultures. I also had this hybrid from seeds sent me by Professor R. T. Clausen. The specification on the packet was as follows: „Oct. 23, 1948, seeds gathered form open pollinated plant in garden, Ithaca, New York". From these seeds I had 17 plants which probably constituted the second generation as they displayed marked segregation in respect to numerous characters. Their seed fertility ranged from 42.3 to 75.3 per cent.

Raynor (1945) reports that meiosis in the PMCs of hybrid *G. laciniatum* × *canadense* which she investigated is normal and she produces a drawing of a metaphasal plate with 21 bivalents. My investigations of meiosis in the PMCs of this hybrid indicate that in fact in the majority of cells at the stage of diakinesis and metaphase of the I-st division there are bivalents only and that their number is 21, but there are also some cells in which 2 to 6 univalents are found (Fig. 130). In 36 PMCs examined at the stage of diakinesis I found 28 cells with 21 chromosomes, 5 cells with 22 chromosomes which corresponds to the $20_{II} + 2_{I}$ configuration, and 3 cells with 23 chromosomes which corresponds to the $19_{II} + 4_{I}$ configuration. At diakinesis it is not always possible to distinguish accurately the uni- from the bivalents. At metaphase of the I-st division the univalents are conspicuous and can be distinguished at first sight, as they are smaller and lie on the spindle alongside the plate formed by the bivalents. I examined 123 cells at metaphase and found no univalents in 118. In the remaining 5 cells there were 2 to 6 univalents. In the second metaphase there are 21 chromosomes in an overwhelming majority of plates, though one plate with 22 chromosomes was recorded. Generally speaking, the number of univalents in this hybrid is smaller and they appear in fewer cases than in the fertile hybrids already described.

No. 121. *G. canadense* **Jacq.** (21) × *G. boliviense* **Focke** (21). Both parental species rather resemble each other in spite of their different geographical distribution in North and South America. *G. boliviense* differs from *G. canadense* by differently shaped leaves which have margins more finely serrate and by smaller petals which in both species are white. The hybrid plants are vigorous, with strong multifloral stems and leaves shaped intermediately between the parental species. The size of petals in the hybrid is also intermediate between the parental species, as can be seen from the following average sizes of petals (length × width in mm.):

G. canadense	8.8 × 4.6
F_1	7.6 × 3.0
G. boliviense	4.5 × 2.2.

Fertility in this hybrid is somewhat lower than in those described beforehand and associates it with the next group of fertile hybrids.

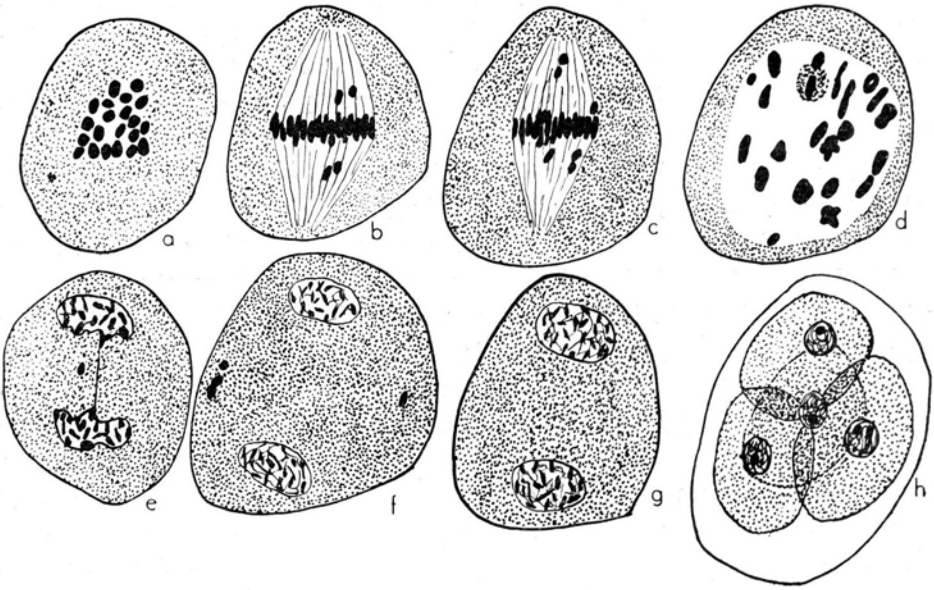

Fig. 131. F_1 *Geum canadense* × *G. boliviense*, meiosis in PMCs; a — M-I with 21 bivalents; b — M-I with 4 univalents; c — M-I with 6 univalents; d — diakinesis with 20 bi- and 2 univalents; e — A-I with chromosomal bridge; f — T-I with 2 chromosomes not included; g — normal T-I; h — tetrad

Pollen fertility is here 17.3 to 26.6 per cent and seed fertility ranges between 20.8 and 45.5 per cent averaging at 38.5 per cent. Numerous specimens of the hybrid obtained in both reciprocal directions display great uniformity and similarity between the reciprocal hybrids.

Cytological examination: — 36 PMCs were examined at metaphase of the I-st division and of these in 27 conjugation was normal and the number of bivalents was 21, in the remaining cells there were 2 or 4 univalents at metaphase (Fig. 131). The appearance of the later stages of meiosis and of the tetrads is quite normal and such disturbances as lagging and lost chromosomes appear in very few PMCs only.

Another group of closely related species giving between them highly fertile hybrids constitues of *G. macrophyllum* Willd. together with *G.*

perincisum Rydb. and *G. oregonense* Rydb. The three species and the hybrids between them were the subject of a separate report (W. Gajewski 1955) and, therefore, they will be only briefly discussed here. The following hybrids were obtained between these species:

No. 115. *Geum macrophyllum* Willd. (21)×*G. oregonense* Rydb. (21)

Nd. 116. *Geum macrophyllum* Willd. (21)×*G. perincisum* Rydb. (21)

No. 117. *Geum perincisum* Rydb. (21)×*G. oregonense* Rydb. (21).

In all three cases numerous specimens in both directions were obtained. Reciprocal hybrids were identical. All the hybrids manifest great vigour and surpass the parent species by the length of stems and the number of flowers. While referring the reader to my report of 1955 I here include drawings illustrating two of these hybrids (Figs. 132 and 133). The rather high fertility of the three hybrids is as follows:

	Pollen fertility in %%	Fertility of achenes in %%
F_1 *macrophyllum* × *oregonense*	54,6	40,3
F_1 *macrophyllum* × *perincisum*	53,1	32,1
F_1 *perincisum* × *oregonense*	47,3	46,2

In the majority of PMCs of these hybrids the course of meiosis is characterized by normal conjugation with 21 bivalents, but in some PMCs there are 2 to 8 univalents. The drawings and the detailed descriptions of meiotic divisions are published in the paper just mentioned (W. Gajewski 1955).

The last to be described is the group of the most fertile hybrids which includes crosses between *G. rivale, coccineum* and *silvaticum* or crosses between these three species and the species from the group consisting of *G. urbanum, molle* and *hispidum*. First to be discussed are the hybrids of *G. rivale, coccineum* and *silvaticum* with *G. urbanum, molle* and *hispidum*. The following highly fertile hybrids have been obtained:

No. 67. *G. rivale* L. (21) × *G. urbanum* L. (21)

No. 70. *G. rivale* L. (21) × *G. molle* Vis. et Panc. (21)

No. 71. *G. rivale* L. (21) × *G. hispidum* Fr. (21)

No. 79. *G. coccineum* Sibth. et Sm. (21) × *G. urbanum* L. (21)

No. 80. *G. coccineum* Sibth. et Sm. (21) × *G. molle* Vis. et Panc. (21)

No. 81. *G. coccineum* Sibth. et Sm. (21) × *G. hispidum* Fr. (21)

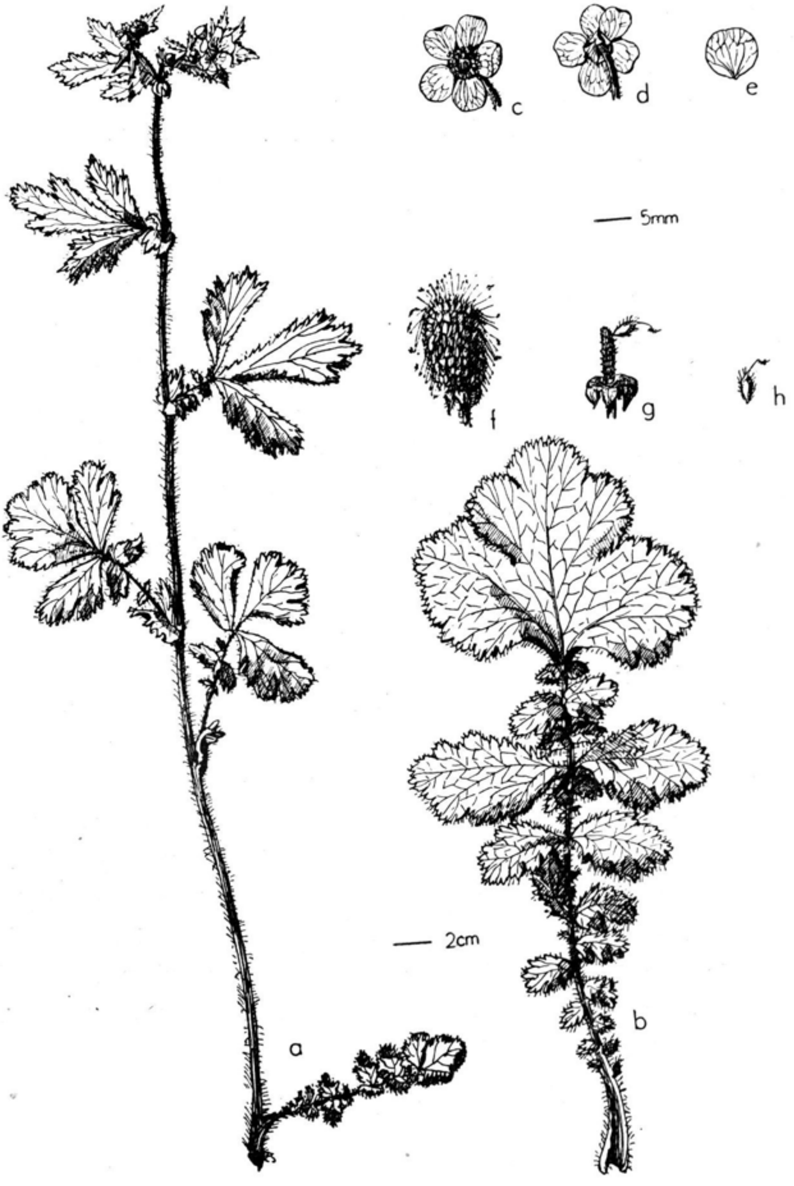

Fig. 132. F_1 *Geum macrophyllum* × *G. perincisum;* a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

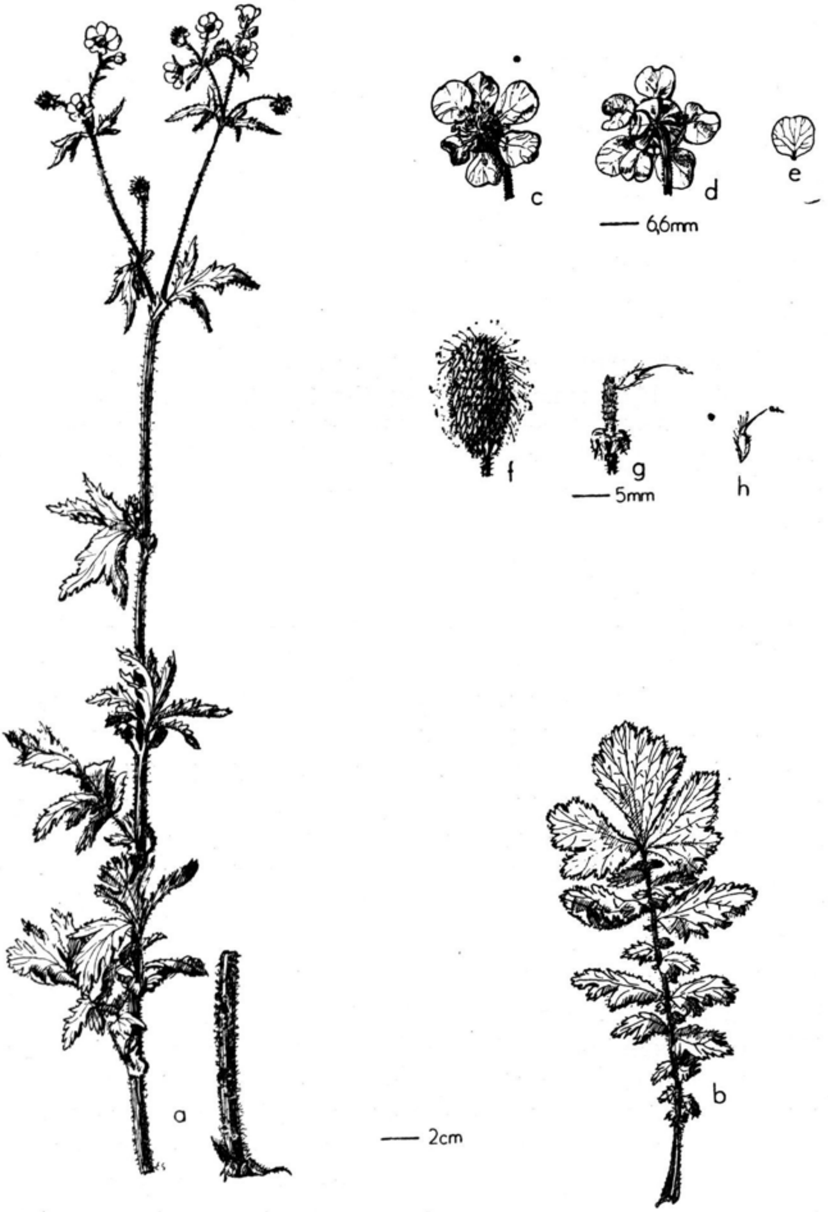

Fig. 133. F_1 *Geum perincisum* × *G. oregonense;* a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

No. 88. *G. silvaticum* Pourr. (21) × *G. molle* Vis. et Panc. (21)

It has already been pointed out that the hybrid between *G. rivale* and *G. urbanum* is very often found in nature (*G. intermedium* Ehrh.) and has been the object of many genetic investigations (Marsden-Jones 1930, Prywer 1932, Winge 1926, and others) and it seems pointless to describe it here once more. The hybrid in my culture was derived from natural habitats and was also obtained twice by experimental crossing in both directions of the two parental species. The best description of the hybrid is made by Prywer. I shall point out here only those results which are in disaccord with those of Prywer and other writers. The cross is equally succesful in both directions and the setting of seeds is at the high level of 65 to 79 per cent. The F_1 populations derived from reciprocal crosses are identical and fairly uniform. The dominant characters of *G. urbanum* are the yellow colour of petals, the lack of emargination at the tip of petals, the long haired floral base, the lack of gynophore (though in some specimens there is a gynophore 1 to 1.5 mm long) and the strongly branched stems. From *G. rivale* partially dominant are the following characters: drooping of floral peduncles, the anthocyanin in the stems, the erect position of calyx and petals, and the claw at the base of the petals. In *G. rivale* the rostrum is 8 to 10 mm long, covered to the middle with straight and glandular hairs, and the stigmatic part is 4.5 to 5 mm long and also haired. In *G. urbanum* the rostrum is shorter, only 5 to 6 mm long and glabrous, the stigmaitc part is 1.5 to 2 mm long. The achenes of *G. urbanum* are longer and much less haired than in *G. rivale* (the length of achenes in *G. rivale* and *G. urbanum* is respectively 3.5—4.5 mm and 5.5—6.5 mm). In the hybrid the achenes are 5 to 6 mm long and fairly long haired, the rostrum is 7 to 8 mm long and glabrous, and the stigmatic part is 3.0 to 3.5 mm long. The hybrid is not completely fertile as is frequently stated in reports. Pollen fertility varies within rather broad limits in various years, the average from three years being about 78 per cent. Seed fertility is about 72.1 per cent.

The course of meiosis in the hybrid is also not entirely normal. 72 PMCs were examined at the stage of I-st division metaphase and the 21 bivalents without any univalents were found only in 61 cells, in the remaining 11 cells the number of univalents ranged from 2 to 6 (Fig. 134).

At anaphase the univalents frequently lag on the spindle where they are either divided or more often segregate undivided to the two poles. Usually the univalents are not taken up in the daughter nuclei. In 6 out of the 69 examined anaphases chromosomal bridges were found. In numerous second division metaphases 21 chromosomes were seen. The appearance of the tetrads is absolutely normal.

No. 70. *G. rivale* L. (21) × *G. molle* Vis. et Panc. (21), culture no. 31—50 is the next in this group. The more important characters of the hybrid and its parent species are compared in the following table:

Character	*G. molle*	F_1	*G. rivale*
Basal leaves	terminal leaflet ovoid with cordate base, shallowly incised	terminal leaflet 3-lobate or 3-partite	terminal leaflet dissected into 3 cuneate lobes
Cauline leaves	3-partite, very elongated, sharply serrate; stipules big, elongated	intermediate, more elongated than in *molle*; stipules rather long	3-foliolate, widely triangular; stipules small
Length of floral stems (cm)	40 — 60	60 — 80	45 — 60
Number of flowers on one stem	1 — 3	3 — 9	3 — 5
Floral peduncles	straight	drooping	very drooping
Anthocyanin in stems and flowers	none	abundant	very abundant
Calyx	horizontal or reflexed	horizontal	erect
Position of petals	horizontal	± erect	erect
Colour of petals	yellow	yellow + anthocyanin	creamy + anthocyanin
Shape of petals	± round	tip round, small claw at base	tip emarginated, long claw
Size of petals (mm)	11.5 × 9.2	10.5 × 9.6	10.1 × 8.0
Length of gynophore (mm)	1	2 — 4	8 — 10
Length of rostrum (mm)	4 — 6	6 — 8	8 — 10
Length of stigmatic part (mm)	1.5 — 2	2.5 — 3.5	4.5 — 5
Length of sepals (mm)	5 — 6	9 — 10	10 — 12

The hybrid was obtained in both reciprocal directions. It grows very abundantly and surpasses the parent species by the size of stems and leaves, and the number of flowers. The average pollen and seed fertility are 62.1 and 61.8 per cent respectively. In the majority of PMCs the course of meiosis is normal. In 27 PMCs examined at metaphase of the I-st division bivalents alone were seen in 20 cells, in 4 PMCs there were 20 bi — and 2 univalents, in 3 PMCs the corresponding numbers were 19 and 4, and in 2 cells 18 and 6. In about 13 per cent of anaphases univalents lie on the spindle between the two groups of segregated bivalents. In very few cells in telophase chromosomes not taken up in

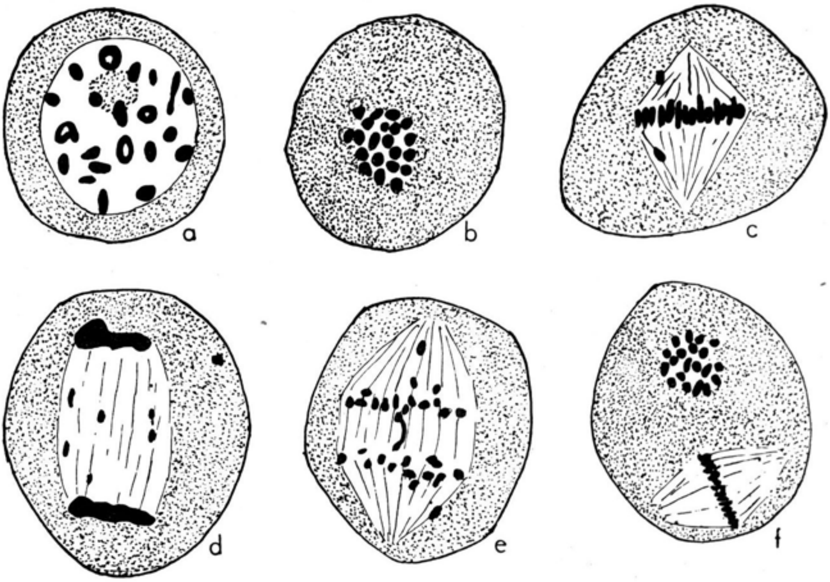

Fig. 134. F_1 *Geum rivale* × *G. urbanum,* meiosis in PMCs; a — diakinesis with 21 bivalents; b — M-I with 21 bivalents; c — M-I with 2 univalents; d — A-I with 6 univalents on the spindle; e — A-I with chromosomal bridge; f — M-II with 20 chromosomes in one plate

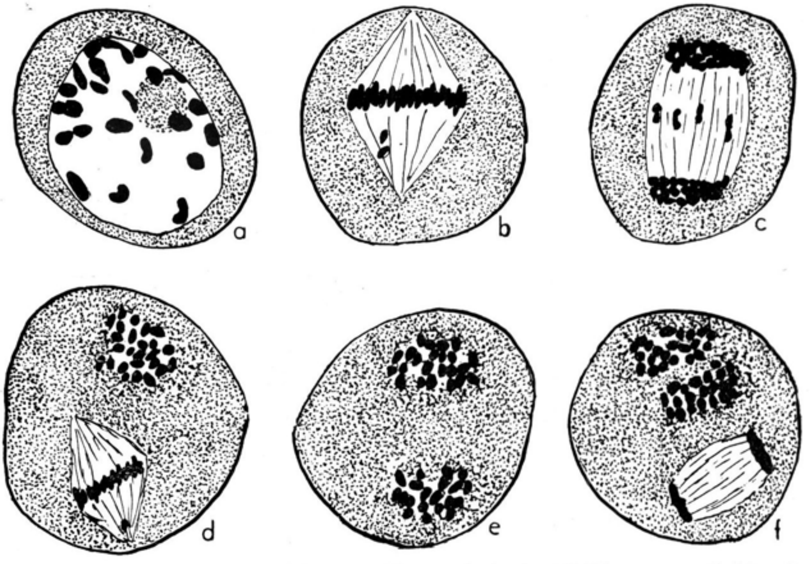

Fig. 135. F_1 *Geum rivale* × *G. molle,* meiosis in PMCs; a — diakinesis with 23 chromosomes ($19_{II} + 4_{I}$); b — M-I with 2 univalents; c — A-I with 4 univalents on the spindle; d — M-II with 25 chromosomes in one plate; e — M-II with 20 and 23 chromosomes in the two plates; f — A-II with 21 chromosomes in both daughter groups

the daughter nuclei are seen. At metaphase of the II-nd division the regular number of 21 chromosomes is found in the majority of plates and plates with one or two chromosomes above or below normal are rare. The tetrads have a normal appearance.

No. 70. *G. rivale* L. (21) × *G. hispidum* Fr. (21), culture no. 117—50. This hybrid is very much like the one just described but the two differ by the shape of leaves which in the former have an elongated terminal leaflet deeply dissected into 3 — 5 lobes. The hybrid *G. rivale* × *hispidum* has petals similar to those of the preceding one but smaller (9.8 × 9.0 mm) and in these plants the upper part of stems, the peduncles and the calyx are densely covered with glandular hairs. The stems are up to 1 m tall with 5 to 9 flowers. The other characters are the same as in the hybrid just described. Pollen and seed fertility average at 83.1 and 60.4 per cent respectively. Meiosis in this and the preceding hybrid is very much alike. Of 38 PMCs at the stage of the I-st division metaphase 21 had only the 21 bivalents, 8 had 2 univalents, 5 had 4 univalents and in 4 cells there were 6 univalents. In anaphase the univalents frequently lag on the spindle where after being strongly stretched out they are segregated to the poles. Often the univalents are not taken up in the nuclei and in telophase they are seen lying in the cytoplasm where they are usually resorbed. In the 14 metaphasal plates of the second division which were examined the chromosome number always found was 21. The appearance of tetrads is normal.

The hybrids with *G. coccineum*, similarly as those with *G. rivale* also have a high level of fertility.

No. 78. *G. coccineum* Sibth. et Sm. (21) × *G. urbanum* L. (21), culture no. 15—53. The more important characters of this hybrid and of the parental species are compared in the following table (p. 252).

The hybrid is vigorous, grows very well and flowers abundantly. Its mean pollen fertility is 72 per cent and its average seed fertility for three years is 62.7 per cent. In metaphase of the first meiotic division among the 62 PMCs examined 21 bivalents were found in 54 cells, 20 bivalents and 2 univalents in 5 cells, 4 univalents in 1 cell and 6 univalents in 2 cells (Fig. 136). In the majority of cells the course of anaphase is quite normal. In 13 out of 14 metaphasal plates of the II-nd division there were 21 chromosomes and in one cell the number of chromosomes in the two plates was 22 and 23, which seems to indicate that three univalents were divided in the first division. The appearance of the tetrads is normal.

Character	*G. urbanum*	F_1	*G. coccineum*
Basal leaves	terminal leaflet with 3 rhomboid elongated lobes	terminal leaflet deeply 3-lobate, sharply serrate	terminal leaflet big, round. shallowly crenate
Cauline leaves	3-partite almost to apex, stipules very big	intermediate, stipules big	usually unifoliolate, 3-lobate; stipules fairly big, serrate
Pubescence of stems	sparsely haired, no glandular hairs	densely, softly haired, no glandular hairs	softly, very densely haired, with glandular hairs beyond middle
Length of stem (cm)	60 — 80	65 — 85	30 — 45
Number of flowers on one stem	5 — 9	5 — 9	3 — 7
Colour of petals	yellow	yellow (apricot)	red
Size of petals (mm)	5.8 × 4.6	12.7 × 11.8	13.0 × 14.3
Length of floral base (mm)	6 — 7	6 — 7	3 — 4
Pubescence of floral base	long haired	long haired	hairs shorter
Length of rostrum (mm)	5 — 7	4 — 5	2 — 5
Length of stigmatic part (mm)	1.5 — 2	2.5 — 3	4.5 — 5

No. 79. *G. coccineum* Sibth. et Sm. (21) × *G. molle* Vis. et Panc. (21), culture no. 158—51. The more significant characters of this hybrid and of the parent species are compared in the table below

Character	*G. molle*	F_1	*G. coccineum*
Basal leaves	terminal leaflet ovoid, shallowly incised, with cordate base	terminal leaflet big, round, shallowly incised	terminal leaflet big, round, shallowly incised
Cauline leaves	3-partite, elongated, sharply serrate; stipules big, rounded	3-partite deeply serrately incised; stipules big	usually unifoliolate, 3-lobate; stipules rather big, serrate
Length of stem (cm)	40 — 60	30 — 50	30 — 45
Number of flowers on one stem	1 — 3	3 — 5	3 — 7
Colour of petals	yellow	orange yellow or yellow	red
Size of petals (mm)	11.5 × 9.2	11.8 × 12.0	13.0 × 14.3
Length of gynophore (mm)	1	absent	absent

Character	*G. molle*	F_1	*G. coccineum*
Length of floral base (mm)	5 — 6	4 — 5	3 — 4
Number of achenes	170 — 200	150 — 180	150 — 180
Length of rostrum (mm)	4 — 6	3.5 — 5	2 — 5
Pubescence of rostrum	pubescent	pubescent	± glabrous
Length of stigmatic part (mm)	1.5 — 2	3.5 — 4	4.5 — 5

The hybrid was obtained in both reciprocal direction and in both F_1 populations marked segregation occurred in respect to the colour of petals, i.e. of the 90 plants of both reciprocal hybrids 39 had dark yellow petals and in 51 the petals were yellow with a marked orange tint. In respect to other morphological characters the plants were uniform. Pollen fertility is here 51 per cent and seed fertility averages at 49.8 per cent ranging from 41.3 to 61.0 per cent. The meiotic divisions in this hybrid have a normal course (Fig. 137). Among 48 PMCs examined at the stage of the I-st division metaphase 2 and 4 univalents were found in 4 cells, in all the other cells there were bivalents alone.

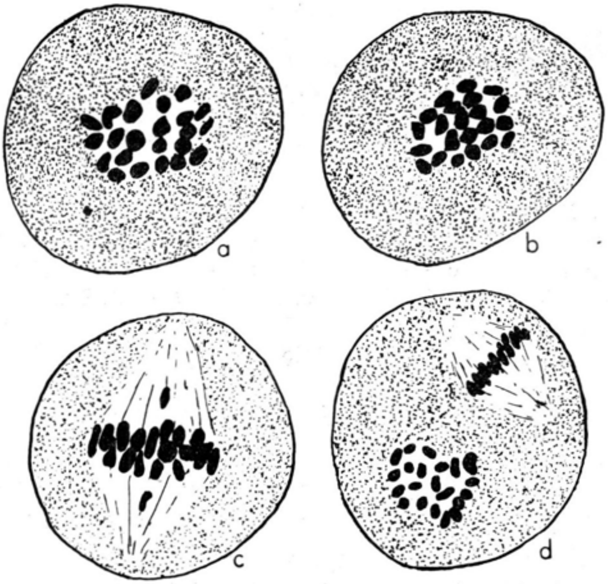

Fig. 136. F_1 *Geum coccineum* × *G. urbanum*, meiosis in PMCs; a — M-I with 23 chromosomes ($19_{II} + 4_I$); b — M-I with 22 chromosomes ($20_{II} + 2_I$); c — side view of M-I with 2 univalents; d — M-II with 21 chromosomes

In the other stages of meiosis the appearance of the divisions is also very much normal.

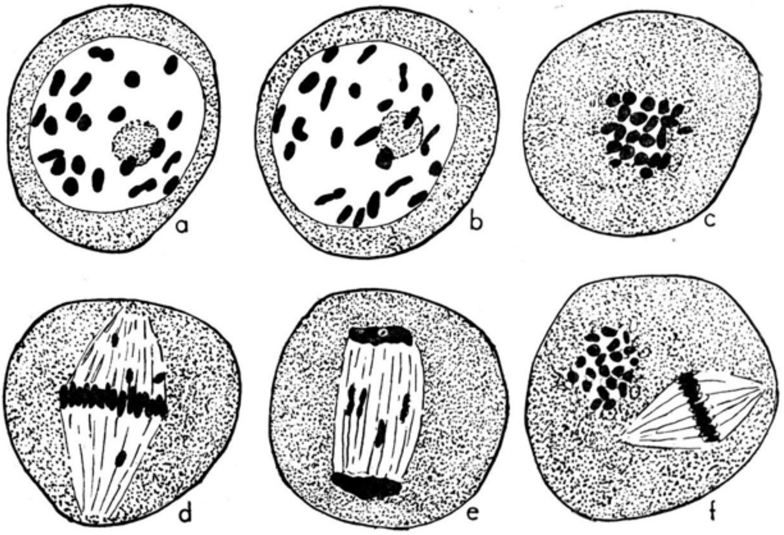

Fig. 137. F_1 *Geum coccineum* × *G. molle*, meiosis in PMCs; a — diakinesis with 21 bivalents; b — diakinesis with 23 chromosomes ($19_{II} + 4_{I}$); c — M-I with 22 chromosomes ($20_{II} + 2_{I}$); d — side view of M-I with 4 univalents; e — A-I with 4 univalents on the spindle; f — M-II with 21 chromosomes in one plate

No. 80. *G. coccineum* Sibth. et Sm. (21) × *G. hispidum* Fr. (21), culture no. 197—52. This hybrid resembles greatly the preceding one and differs from it only by the more elongated and somewhat more incised terminal leaflet of the basal leaves. The terminal leaflet here is sometimes tripartite. The petals are orange yellow (Tangerine orange 9), somewhat smaller and slightly more elongated (11.2 × 10.0 mm.) than in the hybrid just described. The floral stems are 50 — 65 cm. tall and usually there are 3 — 5 flowers on one stem. The fertility of the hybrid is somewhat lower than in the preceding one, averaging at 31 and 30 per cent for pollen and seed respectively. The course of meiosis in this hybrid is identical as in the one just described.

The two hybrids in the group of related fertile ones not yet described are those with *G. silvaticum*.

No. 88. *G. silvaticum* Pourr. (21) × *G. molle* Vis. et Panc. (21), (fig. 138) culture no. 191—52. The more important characters of the hybrid are shown on the table below.

Pollen and seed fertility in the hybrid is 50 and 33.9 per cent

Character	*G. silvaticum*	F_1	*G. molle*
Basal leaves	terminal leaflet ovoidly elongated shallowly incised	terminal leaflet resembling *silvaticum*	terminal leaflet ovoidly round, shallowly lobed
Cauline leaves	few, small, cuneate; stipules small, lanceolate	size intermediate, shape approaching *molle*; stipules small	more numerous, bigger, 3-lobate, sharply serrate; stipules big, elongated
Length of stem (cm.)	15-30	30-60	40-60
Number of flowers on one stem	1-3	1-3	1-3
Calyx	horizontal	horizontal	reflexed
Size of petals (mm)	12.0×8.2	11.2×10.3	11.5×9.2
Length of gynophore (mm)	4-6	2-4	1
Length of floral base (mm)	3-4	4-5	5-6
Number of achenes	20-30	60-70	170-200
Length of achenes (mm)	8-9	5-7	5-6
Length of rostrum (mm)	7-8	5-6	4.5-5.5
Length of stigmatic part (mm)	4.5-5	3-4	1.5-2

respectively. The meiotic division in this hybrid is somewhat more disturbed than in the hybrids described previously (Fig. 139). Among the 17 PMCs analysed at the stage of diakinesis in 8 there were 21 chromosomes, in 4 there were 22 chromosomes, in 3 there were 23 chromosomes, and in 2 cells there were 24 chromosomes. 77 cells were analysed at the stage of metaphase and the configurations were found to be as follows:

21_{II} in 15 cells
$20_{II} + 2_{I}$ in 33 cells
$19_{II} + 4_{I}$ in 20 cells
$18_{II} + 6_{I}$ in 8 cells
$17_{II} + 8_{I}$ in 1 cell.

At anaphase in numerous cells there are 2 to 8 univalents lying on the spindle when the bivalents are already separated and form two groups at the spindle poles. These univalents are seldom divided and are usually segregated to the daughter nuclei undivided. The univalents often assume the shape of two balls joined by a thread and are strongly stretched out along the spindle fibres. Chromosomal bridges are observed quite frequently. In telophase and interkinesis the univalents often remain in the cytoplasm where they are usually resorbed. Also during the second division at metaphase some chromosomes lie off the plate and in anaphase they lag on the spindle behind the other dividing chromosomes. The number of chromosomes in the metaphasal plates of

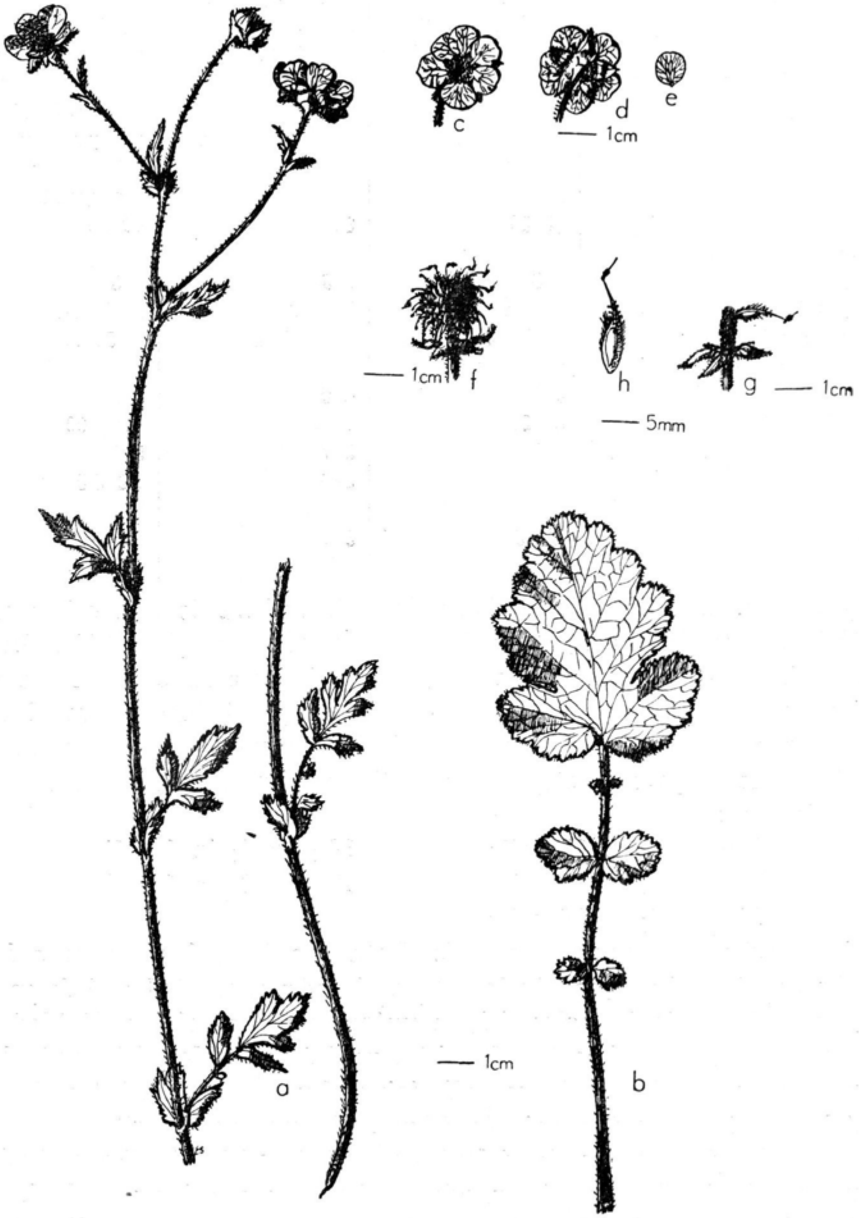

Fig. 138. F₁ *Geum silvaticum* × *G. molle;* a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

the II-nd division is sometimes other than 21 and in several plates 20, 19 or 23 chromosomes were found.

No. 89. *G. silvaticum* Pourr. (21) × *G. hispidum* Fr. (21), culture no. 138—52. The hybrid resembles the one just described, but its terminal leaflet is more elongated and more deeply incised. In the hybrid the petals are yellow and somewhat smaller (8.5 × × 7.0 mm) and the gynophore is very small, 1 to 1.5 mm long and long haired. The number of achenes ranges from 50 to 60, they are 6 — 7 mm long and densely short haired. The rostrum is usually 6 mm long and glandularly haired to the middle, the stigmatic part is about 4 mm long and haired at the base. The floral stems are up to 65 cm tall and have 3—5 flowers. Pollen and seed fertillity average at 54 and 32.8 per cent respectively. The course of meiosis in the PMCs of this hybrid is very much the same as in the hybrid described previously. In 28 PMCs analysed at metaphase of the first division the following configurations were observed:

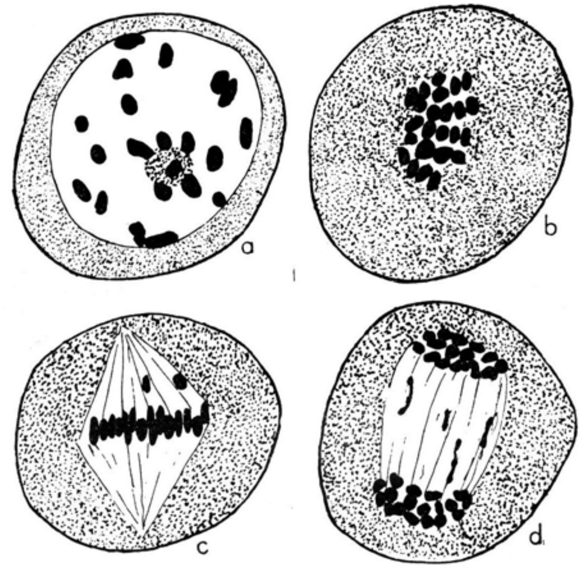

Fig. 139. F$_1$ *Geum silvaticum* × *G. molle*, meiosis in PMCs; a — diakinesis with 21 bivalents; b — M-I with 24 chromosomes ($18_{II} + 6_{I}$); c — M-I with 2 univalents; d — A-I with 4 univalents on the spindle

21_{II} in 6 cells
$20_{II} + 2_{I}$ in 10 cells
$19_{II} + 4_{I}$ in 6 cells
$18_{II} + 6_{I}$ in 3 cells
$17_{II} + 8_{I}$ in 3 cells.

As usual, the majority of univalents lag in anaphase on the spindle and some of them are not taken up in the daughter nuclei but remain in the cytoplasm where they are resorbed. During the second division too there are chromosomes lying on the spindle off the metaphasal plates and lagging chromosomes are often seen at anaphase. In spite of the rather numerous disturbances in both meiotic divisions the appearance of the tetrads is quite normal.

The final group of highly fertile hybrids to be disscussed is that formed by crosses between *G. rivale, silvaticum* and *coccineum.* Although the three species considerably differ in respect to morphology (cf. Figs. 9, 10 and 12) the hybrids between them are the most fertile. In this group the following hybrids were obtained and investigated:

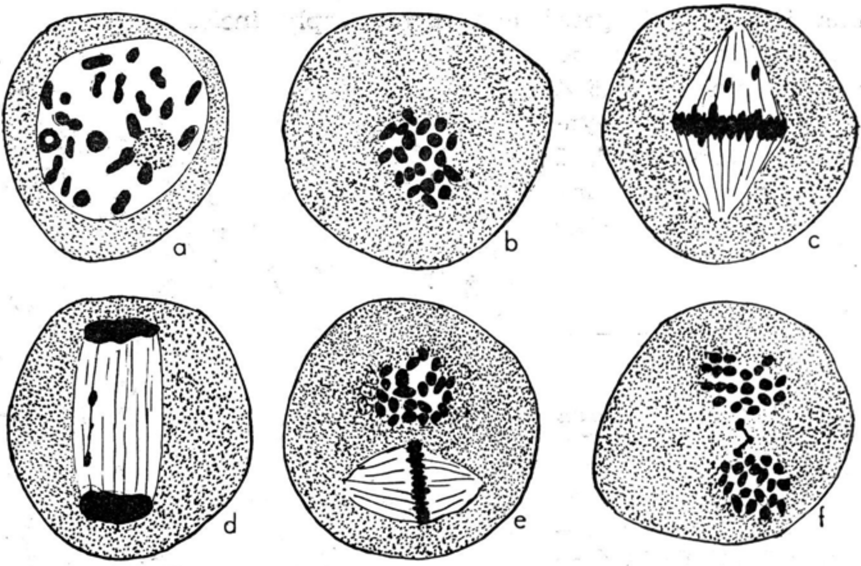

Fig. 140. F_1 *Geum rivale* × *G. coccineum,* meiosis in PMCs; a — diakinesis with 22 chromosomes ($20_{II} + 2_{I}$); b — M-I with 21 bivalents; c — M-I with 2 univalents; d — A-I with inversion bridge; e — M-II with 22 chromosomes in one plate; f — M-II with chromosomal bridge persisting from the first division

No. 68. *G. rivale* L. (21) × *G. coccineum* Sibth. et Sm. (21)

No. 69. *G. rivale* L. (21) × *G. silvaticum* Pourr. (21)

No. 82. *G. coccineum* Sibth. et Sm. (21) × *G. silvaticum* Pourr. (21).

The hybrid *G. rivale* × *coccineum* was described in an earlier report (W. Gajewski 1950) and thus its description will not be repeated here. It will only be recalled that the hybrid has yellow petals, though, the colour of petals in *G. rivale* is creamy and in *G. coccineum* red. The characters of *G. coccineum* completely dominant in the hybrid are: the lack of gynophore, the short naked rostrum and the lack of incision at the tip of petals. The intermediate characters in the hybrid are as follows: the position of sepals and petals, the expression of the claw at the base of petals, the size of petals and sepals, the drooping of floral peduncles, and the shape of leaves. The average pollen fertility in the hybrid is about 66.6 per cent of good pollen and seed fertility is 94.5 per cent. This is the highest seed fertility that has been recorded in all the *Geum* hybrids covered by my investigations. Meiosis too has the most normal course of all the investigated *Geum* hybrids and at metaphase in an overhelming majority of cases only the 21 bivalents appear (Fig. 140). 2 univalents and 20 bivalents were found in very few cells out of the several hundred examined at metaphase. The course of meiosis in the hybrid is equally normal as in the pure parental species.

No. 69. *G. rivale* L. (21) × *G. silvaticum* Pourr. (21), culture no. 149—52. Some characters of this hybrid and of the parental species are compared in the table below (Fig. 141):

Character	*G. silvaticum*	F_1	*G. rivale*
Basal leaves	terminal leaflet ovoidly elongated, shallowly incised and serrate	intermediate	terminal leaflet dissected into 3 cuneate sharply serrate lobes
Cauline leaves	few, small, cuneate; stipules small, lanceolate	small, trifoliolate; stipules small	usually big, trifoliolate, deeply incised
Pubescence of stems and leaves	dense, silky	dense, silky	longer and less dense
Length of floral stems /cm/	15 — 20	50 — 70	45 — 60
Number of flowers on one stem	1 — 3	1 — 3	3 — 5
Calyx	horizontal	erect	erect
Position of petals	horizontal	erect	erect
Colour of petals	yellow	yellow + anthocyanin	creamy + anthocyanin
Shape of petals	± round, cordate at tip	cordate incision at tip, cuneate base	with long claw at base and emarginated at tip
Size of petals /mm/	12.0 × 8.2	13.1 × 12.6	10.1 × 8.0
Anthocyanin in stems	none	present	very abundant
Floral peduncles	straight	drooping	very drooping
Length of gynophore /mm/	4 — 6	8 — 11	8 — 10
Pubescence of gynophore	long haired	long haired	short haired
Number of achenes	20 — 30	40 — 60	150 — 200
Length of achenes /mm/	8 — 9	5 — 7	3 — 4
Pubescence on achenes	short haired	intermediate	long haired
Length of rostrum /mm/	7 — 8	7 — 9	8 — 10
Pubescence on rostrum	± glabrous	haired to the middle	haired to the middle
Length of floral base /mm/	3 — 4	4 — 6	6 — 7

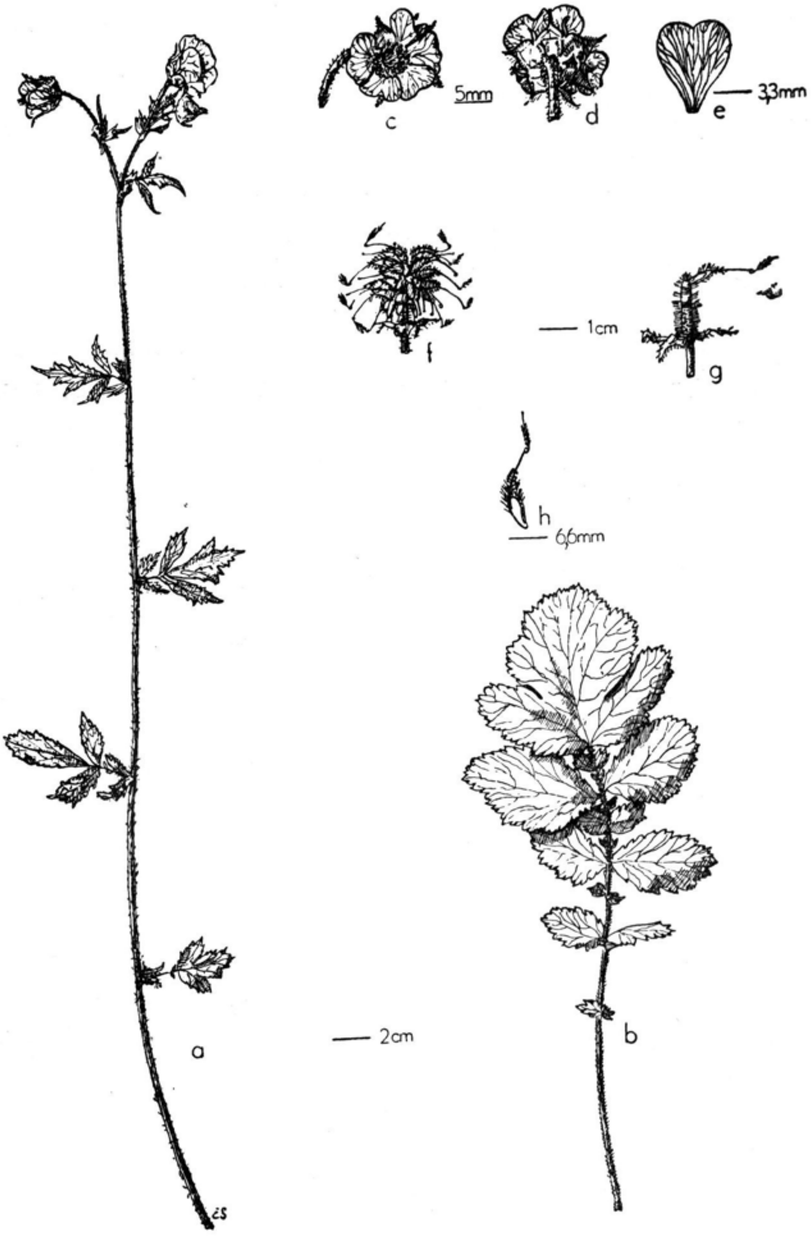

Fig. 141. F₁ *Geum rivale* × *G. silvaticum*; a — floral stem; b — basal leaf; c — flower — top view; d — flower — bottom view; e — petal; f — achenes in flower; g — receptacle with one achene; h — achene

G. silvaticum differs greatly from all the other species in the subgenus *Eugeum* by the shape of leaves and the few big achenes inserted on the short receptacle exserting on a long gynophore. In spite of the considerable differences between this species and *G. rivale* the hybrids between them are very fertile. Pollen fertility in the hybrid is on the average 74.6 per cent and seed fertility is 60.3 per cent. Meiosis in the PMCs has an almost normal course (Fig. 142). The 12 PMCs examined at the stage of diakinesis all had the 21 bivalents only. Among 70 cells examined at the stage of the I-st metaphase there were 65 with 21 bivalents only, 4 with 20 bi- and 2 univalents and one with 4 univalents. Usually, the univalents lie on the spindle symmetrically to the equatorial plane (Fig. 142), which may be caused by the premature separation at metaphase of loosely conjugated bivalents. The later stages of meiosis are in most cases normal.

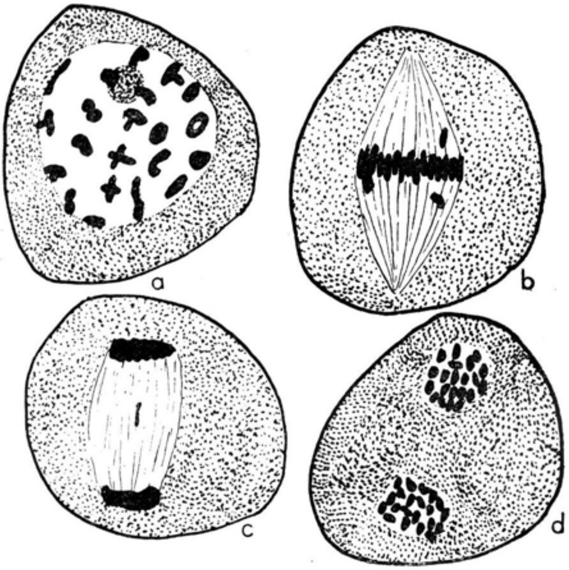

Fig. 142. F_1 *Geum rivale* × *G. silvaticum,* meiosis in PMCs; a — diakinesis with 21 bivalents; b — side view of M-I with 2 univalents; c — A-I with one univalent on the spindle; d — M-II with 21 chromosomes in each plate

No. 82. *G. coccineum* Sibth. et Sm. (21) × *G. silvaticum* Pourr. (21), culture no. 133—50. This is the last hybrid in this group and its more significant morphological characters are compared with the characters of the parental species in the table below:

Character	*G. silvaticum*	F_1	*G. coccineum*
Basal leaves	terminal leaflet elongated, ovoid, shallowly incised, and serrate	terminal leaflet intermediate	terminal leaflet big, round, shallowly incised
Cauline leaves	few, small, cuneate; stipules small, lanceolate	few, small, fairly deeply incised; stipules small	unifoliolate, 3-lobate; stipules big, dentate
Length of stems (cm)	15 — 30	30 — 40	30 — 45
Number of flowers	1 — 3	3 — 5	3 — 7
Calyx	horizontal	horizontal	reflexed
Colour of petals	yellow	orange	red
Size of petals (mm)	12.0 × 8.2	10.5 × 10.8	13.0 × 14.3
Gynophore (length in mm)	4 — 6	absent	absent
Number of achenes	20 — 30	40 — 50	150 — 180
Length of achenes (mm)	6 — 9	5 — 6	4 — 5
Length of rostrum (mm)	7 — 8	4.5 — 6	2 — 5

Average pollen fertility of this hybrid is 65.1 per cent and seed fertility is 50.3 per cent. In the majority of cells the course of meiosis is entirely normal (Fig. 143). Among 38 cells analysed at the stage of I-st division metaphase there were 32 cells with bivalents only, 5 cells with two univalents and 20 bivalents, and one cell with 6 univalents. In all 13 cells examined at the stage of diakinesis there were 21 bivalents. The later stages of meiosis in the majority of cells are entirely normal.

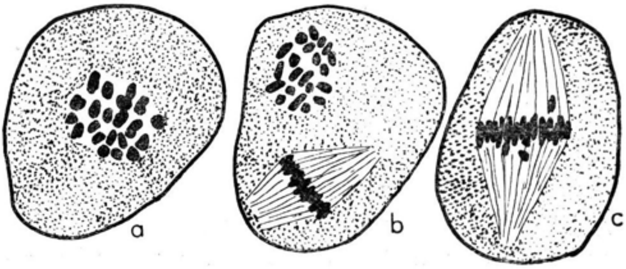

Fig. 143. F_1 *Geum coccineum* × *G. silvaticum*, meiosis in PMCs; a — M-I with 21 bivalents; b — M-II with 21 chromosomes in a plate; c — side view of M-I with 2 univalents

VIII. FURTHER HYBRID GENERATIONS AND BACKCROSSES

In the course of the present research the morphological analysis, and especially the cytological analysis, of further hybrid generations were not developed sufficiently for an accurate and detailed cytogenetic interpretation. There were two reasons for this state of things: 1) I worked alone on this investigation with no one to help me and the lack of time and other reasons prevented me from examining, especially cytologically, the large numbers of plants involved in this type of research, and 2) the space available for the *Geum* cultures was not sufficient to allow the cultivation of numerous hybrid generations. Often for lack of space it was necessary to eliminate part of the new material intended for further culture. Moreover, every year it was necessary to remove some of the plants already growing to make room for new ones. One consequence of this was the impossibility to renew those observations which proved later to need further checking. Another handicap was the very large number of new plants grown every year often making impossible an adequate care over hybrids with reduced viability. This resulted in the loss of all or almost all plants of many hybrids more difficult to cultivate, though, perhaps some of them would have survived if cultivated with greater care. In this manner some sort of selection was enforced as only those plants were transplanted to the beds which proved more viable and survived the earliest developmental stages. All my experiments were carried out on plants growing in the experimental garden and because of this some plants which might have been more amenable to cultivation in glass houses or hotbeds perished. On the other hand, this procedure had some favourable aspects, as in further hybrid generations only the highly vigorous plants were investigated in very much the same conditions for all and thus their vigour could be compared with the vigour of the parental species and the F_1 hybrids.

The restrictions of space made the cultivation of numerous progenies impossible except for some crosses investigated more fully. In all other cases the numbers of plants in the filial generations were small and merely sufficient to check whether the segregation of characters occurred according to similar patterns.

In the case of *Geum* it is not easy to obtain seeds from self-pollination for raising further hybrid generations. Usually in isolated flowers the setting of seeds is at a very low level or the seeds are not set at all, which in my opinion is caused by the partial self-sterility in all *Geum* species and hybrids. In the same F_1 plants pollinated with pollen from other sister plants the setting of seeds is always at a much higher level than from self-pollination. In *Geum* the effect of self-sterility is not absolute, though undoubtedly existing. However, the problem was not specially investigated. The best results in respect to the number of seeds were secured when several F_1 plants were isolated in a specially constructed cage made of very fine meshed wire netting. This was placed in position just before the flowers opened and when they did so they were pollinated every 2 or 3 days simply by rubbing together the stigmata and anthers of two plants.

Some further difficulties in the cultivation of F_2 plants arise from the very varied time of seed germination which may take place within very broad limits. On one occasion, of the seeds sown out in autumn some germinated after several weeks and produced quite biggish plants before winter, while others did not germinate till next spring and germination of particular seeds was stretched out over many weeks. Because of this usually the plants germinating too late were not cultivated further and the resulting selection favoured rapid germination and growth.

Even when all adverse aspects of these experiments on the progeny of *Geum* hybrids are considered the present observations on further hybrid generations indicate that in many cases characters are segregated in ratios rather closely approaching mono- or digenic segregation. It seems therefore that the selection which I carried out unintentionally did not affect in any significant manner the nature of segregations displayed by further hybrid generations. This refers particularly to crosses between species with the same chromosome numbers in which the course of meiosis is approximately normal. In hybrids with many disturbances in meiosis, and primely in those in the progeny of which plants with different chromosome numbers may occur, plants with a more unharmonized genetic chromosomal composition are undoubtedly eliminated in the early stage of growth.

No investigations were so far concerned with further generations of the *Geum* hybrids. The only exception to this is the hybrid of *G. rivale* with *G. urbanum* which was the subject of many investigations (Winge 1926, Marsden-Jones 1930, Prywer 1932, Weiss 1912 and others). In 1950 I published a report on the hybrid *G. rivale* × *coccineum* (W. Gajewski 1950) and the results then reported show that in further generations of this hybrid segregation in respect to many characters distinguishing the parent species is clearly displayed. In very few cases only, the segregation of the characters distinguishing the species follows simple Mendelian ratios. The majority of characters give continuous segregation, thus revealing the highly complex nature of genetical interspecific differences. My observation of the progeny of numerous other hybrids only confirms the earlier results.

Further generations of hybrids between species from various subgenera were obtained only from the hybrids of *Geum montanum* with hexaploid species from subgenus *Eugeum*. The hybrids between other subgenera, as for instance *G. montanum* × *G. triflorum*, *G. urbanum* × × *G. ciliatum*, *G. coccineum* × *G. heterocarpum*, and *G. vernum* × *urbanum*, *macrophyllum*, *oregonense* and *aleppicum*, either do not produce good seeds at all or the few seemingly good seeds do not germinate and consequently not one F_2 plant has been as yet derived from these hybrids. All these observations refer here only to seeds developed from open pollination. I did not attempt any artificial self-pollination or back crosses with the parent species but it seems unlikely that the results would be better. The data now at hand seem to indicate that although viable hybrids can be obtained from crosses between the subgenera *Erythrocoma*, *Oreogeum*, *Orthurus*, *Woronowia*, *Stylipus* and *Eugeum* the subgenera are strongly isolated between them by hybrid sterility. However, the appearance of new amphiploid types from crosses between these subgenera is not impossible, all the more so as the hybrids produce unreduced gametes. So far, however, I have obtained no amphiploid progeny. An exception is made here by some hybrids between subgenera *Eugeum* and *Oreogeum* which are partially fertile and which produce numerous progenies in further generations.

OREOGEUM × *EUGEUM* HYBRIDS

In this group complete sterility is displayed by the hybrids of *G. reptans* with *G. rivale* and *G. coccineum* as well as the hybrids of *G. montanum* with *G. pyrenaicum*, *magellanicum* and *Fauriei*. From the other hybrids of *G. montanum* with the hexaploid *Eugeum* species numerous F_2 plants were derived and in some cases even further generations and back-crosses were obtained. As an example illustrating the conditions prevailing in the progeny of this group the progeny of the F_1 hybrids of *G. montanum* with *G. rivale* will be described, as it is relatively the best known.

1. *G. montanum* × *rivale*. The F_1 hybrid develops on the average about 15.5 per cent of good seeds as estimated on the basis of morphology. However, the germination rate and the energy of germination of the hybrid seeds are distinctly reduced in respect to the pure species. In the course of this research the seeds of the hybrids were sown out many times and usually about 40 per cent did not germinate. Of the remaining 60 per cent some germinated 3 to 4 weeks after sowing and

some not till the next year. Lethality among the young seedlings was high, so that the number of plants transplanted to the open beds did not exceed 10—15 per cent in respect to the total number of sown out seeds.

The pentaploid nature with $2n = 35$ of this hybrid is well known and the most common chromosome configuration in meiosis is of the type $14_{II} + 7_{I}$. Because of the random segregation of the univalents the hybrid produces gametes with chromosome numbers ranging from 14 to 21. These numbers are observed in PMC preparations showing anaphase of the I-st and metaphase of the II-nd division. It might be expected that if all the gametes with chromosome numbers ranging from 14 to 21 and all the zygotes produced by the union of these gametes had the same viability, then chromosome numbers in the F_2 generation would range from 28 to 42. The chromosome numbers actually found in 21 young seedlings of the F_2 generation are as follows:

Number of chromosomes	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42
number of plants	—	3	2	3	—	1	1	3	4	--	3	—	—	1	—
% derived theoretically	0.006	0.085	0.555	2.221	6.109	12.218	18.327	20.946	18.327	12.218	6.109	2.221	0.555	0.085	0.006
% observed	0.000	14.27	9.52	14.28	0.00	4.76	4.76	14.28	19.04	0.00	14.82	0.00	0.00	4.76	0.00

From the above table it is apparent that the numbers observed differ greatly from those derived theoretically from the development of the binomial $(0.5 + 0.5)^7$. From the statistical point of view the variations appearing in the table are of no significance because of the small number of the examined plants, but the preponderance of plants with chromosome numbers less than 35 is nevertheless prominent. This effect may be associated with the elimination of some of the univalents in I-st division anaphase. It has been mentioned earlier that young seedlings perish at various stages and it seems that this refers more to the plants with smaller chromosome numbers as the distribution of chromosome numbers in flowering plants differs markedly from the above distribution referring to chromosome numbers in young seedlings. In opposition to the young seedlings plants with chromosome numbers higher than 35 predominate among the flowering plants. In 15 plants flowering abundantly in 1949 and 1950 which were carefully examined cytologically the chromosome numbers were as follows:

31 chromosomes	1 plant	38 chromosomes	2 plants
33 chromosomes	1 plant	39 chromosomes	1 plant
35 chromosomes	2 plants	40 chromosomes	4 plants
36 chromosomes	3 plants	42 chromosomes	1 plant.

In respect to morphology the F_2 generation displays a great variety of characters in various combinations. The total amount of F_2 plants obtained from seeds sown out during several years was 125. Of these 29 plants did not flower and developed small rosettes of basal leaves only, in some plants the leaves were curled and deformed. These plants represented sublethal types and usually did not survive through more than one or two years. The remaining 96 plants flowered and gave fruit but they also displayed much variability in viability and vigour of growth. The viability of more than half of these 96 plants was clearly reduced and in the second year some of them produced only 1 to 3 flowers and then perished. The lack of vigour in the plants was not always correlated with low fertility and in some of them fertility was fairly high. The clearly reduced viability of the F_2 generation does not refer to all specimens and some of them grew very vigorously, flowered profusely through 5 or 6 years and developed into big and strong plants.

It is impossible to define any simple numerical relations in the segregation of the particular characters, though all characters distinguishing the two parental species are segregated. In the shape of basal or cauline leaves continuous variability ranges from leaves characteristic for *G. montanum* with the big round terminal leaflet to leaves characteristic for *G. rivale* with the terminal leaflet composed of three rhomboid lobes. The length of stems ranges from 10 to 40 cm and some plants have unifloral stems while in others there are 2 or 3 flowers on one stem. *Geum rivale* has abundant anthocyanin in stems, calyx and petals and in *G. montanum* anthocyanin is visible in small amounts in the stems only. In F_1 anthocyanin is distributed similarly as in *G. rivale* but in smaller quantities. Of the 96 F_2 plants in 28 anthocyanin is equally abundant as in *G. rivale*, in 62 the amount of this pigment corresponds approximately to the amount in F_1 plants and only 6 plants are deprived of it. *G. rivale* has floral peduncles strongly drooping at anthesis. In F_1 this character is partly dominant over the straight peduncles of *G. montanum*. 85 of the F_2 plants had more or less drooping floral peduncles, whereas only 11 plants had straight ones.

In *G. rivale* the calyx and the petals are erect and in *G. montanum* the petals are horizontally expanded. In F_1 the flowers are intermediate and this character is much variable. In F_2 the position of the calyx and petals varies greatly:

in 7 plants the position of the calyx and petals was horizontal,

in 25 plants the calyx was horizontally expanded and the petals were more or less erect,

in 64 plants the petals and the sepals were equally erect.

The petals in *G. montanum* are yellow and in *G. rivale* creamy with traces of red due to anthocyanin. In F_1 the petals are yellow with anthocyanin and in F_2 the petals were yellow in 63 plants, creamy in 30 plants and pale creamy, almost white, in 3 plants. The yellow colour is of various shades and in plants with abundant anthocyanin the yellow or creamy colour depending on the pigments in the chromatophores is suppressed by the red of the anthocyanin present in the cell sap of the petals. Variability is considerable also in respect to the size and shape of petals in F_2 plants. *G. montanum* has big round petals and *G. rivale* has smaller ones emarginated at tip, abruptly narrowed at base into a long claw. In F_2 very few plants have petals of similar shape and size as the parental species and the majority of F_2 plants have petals with the parental characters expressed in a variety of combinations.

The gynophore in *G. rivale* is 10 mm long, in *G. montanum* this organ is not developed and in F_1 the gynophore reaches a length of 2—3 mm. In F_2 the majority of plants (58) have a gynophore ranging from 2 to 6 mm and the minority (38) have either no gynophore or its length is 1 mm or less.

The expression of styles in F_2 plants was analysed in detail. In this respect the parent species differ radically. In *G. montanum* the styles are long, straight, pennately haired, persisting with the stigmatic part on the achenes where they serve as the organ for anemochoric dissemination of seeds. In *G. rivale* the styles have a hooked joint separating them into the rostrum, which persists on the achene as an adhesive organ for epizoochoric dissemination, and the deciduous stigmatic part. In F_1 the *rivale* type of rostrum is only partially dominant and on one plant achenes may be formed with either straight styles (type I) or with styles divided into rostrum and stigmatic part but with no definite hook at the rostrum tip (type II), or finally with rostrum terminated by a hook as in *G. rivale* (type III). The variability in the expression of styles among F_2 plants is great and the following conditions were recorded:

in 52 plants all styles were of type III, more or less approaching the type characterizing *G. rivale,*

in 11 plants all styles were straight of type I, more or less approaching the type characterizing *G. montanum,* in 20 plants the styles were both of type II and III, i.e. with the hook at at the tip of the rostrum expressed in various degress,

in 7 plants the styles were both of type I and II, i.e. straight or with deciduous stigmatic part but without the characteristic hook at the tip of the rostrum,

in 2 plants all three types of styles had developed similarly as in F_1 plants,

in 4 plants all the styles were of type II.

The above list does not illustrate the full scale of variability in the expression of styles, as alongside of differences in the development of the hook greatly variable were also the size of the rostrum and stigmatic part, and the density and nature of the pubescence on the styles.

In some of the 52 plants with all the styles of type III the rostrum is 7 to 8 mm long, while in others the rostrum is 14 to 15 mm long. In some plants the rostrum is pennately long haired to the tip as in *G. montanum* and in others the pubescence on the rostrum is less dense and reaches only to the middle, more or less as in *G. rivale*. In plants with straight styles of type I the length of the styles ranges from 14 to 20 mm and the pubescence is also greatly variable. However, none of the F_2 plants have styles up to 30 mm long and as long haired as *G. montanum*. All these details refer also to all the other plants and it is not only the length of the rostrum which varies but also the length of the stigmatic part. In conclusion it must be noted that in respect to the structure of the rostrum F_2 plants approaching *G. rivale* prevail (54.1 per cent) and in some of them the rostrum and the stigmatic part are even expressed almost identically as in *G. rivale*. Plants with straight styles of the *G. montanum* type are fewer (11.4 per cent) and none have styles equally long and equally long haired as *G. montanum*.

When the great variability in F_2 in respect to such characters as leaf shape, height and branching of stems, presence of anthocyanin, drooping of floral peduncles, length of gynophore, position of calyx and corolla, the size of petals and sepals, the shape and colour of petals, and the expression of styles are considered and when, moreover, it is remembered that all these characters may appear in the particular F_2 plants in any random combination it becomes easily understood that among the 98 F_2 plants not two were alike, and that the characters of both parental species appear in a variety of combinations. However, it is not impossible that the segregation of characters is not quite random and that some combinations of 2 or 3 specific characters appear more often than might be expected from chance distribution. To illustrate that this possibility does in fact occur 7 characters from 22 F_2 plants which flowered in 1952 are correlated below. The expression of a character as in *G. rivale* is recorded by index number 2, the expression as in *G. montanum* by index number 0, and the intermediate expression of a particular character is given the index 1. In this manner the plants for which the indices of the 7 characters in question will add up to 14 will be of the *G. rivale* type, they will be of the *G. montanum* type when the indices will add up to 0, and of the F_1 type if the indices add up to 7. If the combination of characters in F_2 were random then the numbers of plants with indices from 0 to 14 would approach normal distribution. As can be seen from the table below this is not the case and the distribution of characters in F_2 plants reveals the prevailing number of plants more related to *G. rivale* and with indices ranging from 9 to 13.

The characters considered in F_2 plants are as follows:

	G. rivale	index	*G. montanum*	index
1.	Leaves with incised terminal leaflet	2	Leaves with round terminal leaflet	0
2.	Floral peduncles drooping	2	Floral peduncles erect	0
3.	Anthocyanin in leaves and flowers	2	No anthocyanin	0
4.	Sepals and petals erect	2	Sepals and petals horizontal	0
5.	Petals with claw	2	Petals without claw	0
6.	Gynophore long	2	Gynophore ± absent	0
7.	Geniculate styles	2	Straight styles	0
	Total	14	Total	0

No. of plant	Character — indices								No. of plant	Character — indices							
	1	2	3	4	5	6	7	Total		1	2	3	4	5	6	7	Total
1	0	1	2	1	1	0	1	6	12	2	2	2	1	1	2	2	12
2	0	2	2	2	1	0	2	9	13	1	1	2	0	1	0	1	6
3	0	0	1	0	0	0	1	2	14	1	0	1	0	0	0	1	3
4	2	2	2	2	2	1	2	13	15	1	2	2	2	2	1	2	12
5	1	1	0	2	0	1	2	7	16	1	1	2	2	2	2	1	11
6	0	0	2	2	1	2	2	9	17	1	1	1	2	1	2	1	9
7	2	1	1	0	1	1	1	7	18	2	2	2	2	1	2	2	13
8	2	1	1	1	0	1	1	7	19	2	1	1	2	0	1	2	9
9	0	1	1	0	1	0	1	4	20	1	1	2	1	1	1	2	9
10	2	1	2	2	2	1	1	11	21	2	1	2	2	2	1	2	12
11	0	1	1	1	1	1	1	6	22	2	1	0	0	0	0	2	5

Index 2 . . . . . number of plants 1
,, 3 . . . . . ,, ,, ,, 1
,, 4 . . . . . ,, ,, ,, 1

Index	5	number	of	plants	1
,,	6	,,	,,	,,	3
,,	7	,,	,,	,,	3
,,	9	,,	,,	,,	5
,,	11	,,	,,	,,	2
,,	12	,,	,,	,,	3
,,	13	,,	,,	,,	2

Similar conditions prevailed in other F_2 populations cultivated in different years. The above results seem to indicate that in F_2 the segregation of characters does not take place independently but that sets of characters from parental species are inherited *en bloc*. The small number of plants made a more detailed investigation of this problem impossible.

The fertility of F_2 plants is also highly variable. In 96 investigated plants seed fertility was as follows:

completely sterile			27 plants
⁰/₀⁰/₀ of good seeds from	0.01	to 3	10 ,,
,, ,, ,, ,, ,,	3.1	,, 10	8 ,,
,, ,, ,, ,, ,,	10.1	,, 20	16 ,,
,, ,, ,, ,, ,,	20.1	,, 40	16 ,,
,, ,, ,, ,, ,,	40.1	,, 60	11 ,,
,, ,, ,, ,, ,,	60.1	,, 80	8 ,,

The average seed fertility of F_1 plants is about 15 per cent and in F_2 alongside of completely sterile plants there are also plants with a much higher fertility level than in the parental plants. The highest fertility recorded in F_2 is 75.6 per cent. Similar relations refer to pollen fertility. Usually pollen fertility is slightly or considerably higher than seed fertility but for some plants the reverse is true and seed fertility greatly exceeds pollen fertility. There is no correlation between seed fertility and the type of the style or any other morphological character. Among the F_2 plants which approached *G. rivale* in their morphology there are both highly sterile and highly fertile specimens.

Unfortunately the cytological examination of F_2 plants was not sufficiently detailed to reveal any relationship between fertility and the chromosome number or the type of meiotic divisions. Only 15 F_2 plants were examined cytologically and the diploid chromosome numbers found ranged from 31 to 41. In 13 plants during meiosis univalents were seen to be always present and their number varied as shown by the following table:

No.	2n	The course of meiosis
1	31	not examined
2	33	$16_{II} + 1_{I}$ in ± 40 % of PMCs, in remaining cells 3 — 7 univalents
3	35	$17_{II} + 1_{I}$ in ± 30 % of PMCs, in remaining cells 3 — 5 univalents
4	35	not examined
5	36	18_{II} in 85 % of PMCs in the remaining $17_{II} + 2_{I}$
6	36	$17_{II} + 2_{I}$ in all PMCs
7	36	$17_{II} + 2_{I}$ in 55 % and $16_{II} + 4_{I}$ in 45 % of PMCs
8	38	19_{II} in 80 % of PMCs in remaining cells 2 — 4 univalents
9	38	$18_{II} + 2_{I}$ in all PMCs
10	39	$18_{II} + 3_{I}$ in ± 60 % and $17_{II} + 5_{I}$ in 40 % of PMCs
11	40	17 — 16_{II} and 6 — 8_{I}
12	40	20_{II} in ± 40 % of PMCs, in the remaining cells 2 — 6 univalents
13	40	20_{II} in ± 65 % of PMCs in the remaining cells 2 — 4 univalents
14	40	as in the preceding one
15	41	$20_{II} + 1_{I}$ in 80 % of PMCs, in other cells 3 — 5 univalents

From the above it is apparent that in the majority of the examined F_2 plants there is a variable number of univalents. The fertility of F_2 plants does not seem to be related with the number of bi- or univalents in meiosis and it seems more likely that some combinations are sterile and others fertile, regardless of the total chromosome number and the number of bivalents. However, for the better understanding of this problem further more detailed investigations are necessary.

As detailed cytological examinations of numerous F_2 plants and of further generations surpassed my possibilities I did not undertake any cytological investigations on the further generations of this hybrid and restricted the observations to morphological analyses and fertility records. The F_3 generations were grown from those F_2 plants which resembled most the parental species and displayed the highest fertility. This procedure was followed in order to check whether in the further generations plants more fertile and more resembling the parental species would be obtained.

a) Generation F_3 no. 178.52: — The F_2 parent plant resembled *G. rivale*. Its stems were 30 to 45 cm long, with 3 or 4 flowers, abundant anthocyanin in the stems and flowers, and very drooping floral peduncles. The characters of the flowers were as follows: calyx and corolla erect; petals with claw, emarginated at tip and yellow; the gynophore 4 to 5 mm long; all the styles of the *rivale* type with the rostrum terminated by a hook. The rostrum was 12 to 16 mm long, i.e. longer than in the pure *G. rivale*. Seed fertility of the plant was about 70 per cent. The F_3 generation consisted of 37 plants all with leaves resembling *G. rivale*, stems 30 to 50 cm long, 3 to 5 flowers on one stem, anthocyanin, and drooping floral peduncles. The calyx and corolla were erect. All these characters did not display any major segregation and their variability only slightly exceeded the variability limits in the species *G. rivale*. Distinct segregation was displayed by the colour of petals, i.e. in 27 plants the petals were yellow and in 10 creamy. This numerical ratio closely approached the ratio 3:1. Much segregation was also manifested in the size of petals which were 9.5 to 11 mm long and 9 to 12 mm wide. All the petals were with claw the length of which was 3 to 4 mm. In 12 plants the petals were round at tip as in *G. montanum* and in 25 plants they were incised at tip as in *G. rivale*. The length of the gynophore was 8 to 12 mm, i.e. within variability limits of *G. rivale*. The length of rostrum which in *G. rivale* is 8 to 10 mm in the F_3 plants was 12 to 13 mm, i.e. outside the variability limits of *G. rivale*. In general it may be said that already some of the F_3 plants differ little from *G. rivale* in respect to all characters except the length of the rostrum. The fertility of the plants in this generation ranges for pollen from 68.3 to 94.0 per cent and for seed from 67.0 to 85.4 per cent. This means that in some plants pollen fertility approaches normal and seed fertility is only slightly reduced. It seems, therefore, that in the course of 2 or 3 generations and through appropriate selection it would be possible to obtain plants with the characters of *G. rivale* and almost normal fertility.

From F_2 plants closely resembling *G. rivale* I obtained also two other very similar F_3 generations. The results obtained correspond closely to those just described and it seems pointless to repeat them again in spite of small differences in respect to some characters. One of these generations had achenes with short rostrum only 6 to 8 mm long, and shortly haired to the middle as in *G. rivale*. However, distinct segregation was here displayed in the amount of anthocyanin and the length of gynophore. The petals were yellow in all plants and pollen and seed fertility ranged from 32.3 to 88.3 and from 39.5 to 65.6 per cent respectively.

b) The F_3 generation, culture no. 175.52: — This generation was raised from a F_2 plant resembling *G. montanum*. The stems of the parental plant were 20 to 30 cm long, with 1 to 3 flowers and the basal leaves were big with round terminal leaflet. The expanded flowers had straight peduncles, yellow petals without claw or incision and with residual gynophore 1 to 2 mm long. The styles were of type I, straight, though somewhat shorter and less pubescent than in *G. montanum*. The F_3 generation consisted of 22 plants. In all the F_3 plants the floral stems were 15 to 30 cm long, with 1 to 3 flowers and with no or very little anthocyanin. The flowers were expanded, had yellow petals without claw or emargination and were of similar size as in *G. montanum* (length of petals 10 to 11.5 mm, width 9.5 to 13 mm). In all the plants there was either no gynophore or it was residual not more than 2 mm long. In 16 plants the style structure was of type I, without geniculate joint and in the other 6 plants some styles were of type I and others of type II with deciduous stigmatic part. The length of the styles ranged from 14 to 23 mm, i.e. below the limits of variation in *G. montanum*. The styles were much shorter haired than in *G. montanum*. Pollen fertility in F_3 plants ranged from 39.2 to 85.7 per cent and seed fertility ranged between 18.9 and 41.1 per cent. Two plants were completely sterile.

Besides the F_2 and F_3 generations also backcrosses were obtained by pollinating the flowers of F_1 plants with pollen of the parental species.

c) Generation B_1 (*G. montanum* × *rivale*), × *rivale*, culture no. 211.51: — This generation consisted of 46 plants. In all the plants the floral stems were 45 to 60 cm long, with 3 to 5 flowers and anthocyanin. The amount of the pigment in the stems segregated slightly. In all the plants the floral peduncles were drooping and the calyx and corolla erect. The colour of petals segregated so that 26 plants had creamy petals and 20 yellow ones. The petals displayed marked segregation in respect to the emargination at the tip, the claw at base and their size. The length of the petals ranged from 10.5 to 13 mm and the width from 9.5 to 13.0 mm. The length of the gynophore also segregated ranging between 1—2 to 10 mm. In 43 plants all the styles were of type III with the characteristic hook at the tip of the rostrum. In the remaining 3 plants there were both styles of type III and type II. The length of the rostrum in B_1 ranged from 7.5 to 15 mm and exceeded considerably the length of the rostrum in *G. rivale*. Pollen fertility was between 19.7 and 72.4 per cent and seed fertility between 28.9 and 65.4 per cent. Almost 50 per cent of the plants had seed fertility greater than 50 per cent.

From the B_1 generation one plant resembling *G. rivale* was chosen for repeated pollination with pollen from *G. rivale*. The B_2 generation which was obtained consisted of 51 plants. All these plants were highly uniform and resembled closely *G. rivale*, especially in respect to leaf shape, length of stems, number of flowers, drooping of floral peduncles, the amount of anthocyanin in stems and flowers, and the position of calyx and corolla at anthesis. Slight segregation was displayed only by the time of flowering, length of gynophore (between 2—3 and 9—10 mm), length of claw at the petal base, size of petals (length 6.5 to 11.5 mm, witdh 5.5 to 10 mm), and colour of petals (yellow in 23 plants and creamy in 28). The styles in all the plants were of the *G. rivale* type with hooked rostrum. The length of the rostrum varied greatly and ranged from 6 to 11 mm. Pollen fertility was between 38.3 and 91.5 per cent and seed fertility between 41 and 91 per cent. Many plants of this generation if found on a natural habitat would be difficult to distinguish from the pure *G. rivale,* all the more so, as fertility of some of them was almost normal.

From the B_2 generation one plant very closely resembling *G. rivale* in respect to all characters was chosen and this plant was again pollinated with pollen from *G. rivale*. The B_3 generation thus obtained was composed of 20 plants. All these plants were already virtually alike and had leaves, stems and flowers exactly the same as in *G. rivale*. The length of the gynophore was here 7 to 10 mm and the length of the rostrum 7 to 9 mm, i.e. within the range of variation of *G. rivale*. The course of meiosis was examined in three of the B_3 plants and it was found that in first division metaphase of the PMCs in 2 plants there were the 21 bivalents only and in the third plant there were 2 to 4 univalents in about 10 per cent of cells. In all other respects the course of meiosis in the 3 plants examined was exactly similar as in *G. rivale* and all had the diploid chromosome number of 42. Seed fertility in these plants was from 83.6 to 96.3 per cent.

d) Backcross generation B_1 *(G. montanum × rivale) × montanum:* — The number of plants in this generation was only 8. All these plants flowered early (May 1—5) together with *G. montanum*. The leaves were differently shaped but approached *G. montanum,* the stems were 10 to 30 cm long with 1 to 3 flowers and the floral peduncles were straight in 7 plants and drooping in one. Anthocyanin appeared in the stems and flowers of 3 plants and 5 plants were deprived of this pigment. In all the plants the calyx and petals were horizontally spread, the petals were yellow, without claw at base or emargination at tip, 9 to 12 mm long and 10 to 13 mm wide. The gynophore was lacking in all the plants. All had straight styles as in *G. montanum*, though in 2 plants 5 to 10 per cent of the styles were of type II with deciduous stigmatic part. The length of the styles ranged from 15 to 25 mm. The pennate pubescence of the styles displayed distinct segregation ranging from approximately the *G. montanum* type to the type characteristic for F_1 plants. Pollen fertility in this generation ranged from 33.7 to 67.2 per cent and seed fertility was between 22.6 and 49.8 per cent. Unfortunately I did not obtain further generations of the backcross with *G. montanum.*

The progeny of the hybrids of *G. montanum* with other species from the subgenus *Eugeum* was investigated even less completely than in the case of the cross with *G. rivale*. In most cases the investigations were restricted to relatively small F_2 generations. This was necessary because of space restrictions which made it impossible to cultivate simultaneously more than a few numerous F_2 generations.

2. *G. montanum* × *coccineum*. Of the 120 achenes gathered from the F_1 hybrid plants 72 germinated and only 20 plants were brought to the flowering stage. The majority of the seedlings perished in the early stages and 12 plants formed rosettes of basal leaves and survived through the winter but did not develop floral stems.

Of the 20 plants which flowered 6 were of the vigorously growing and abundantly flowering type with stems up to 60 cm long. The majority of characters distinguishing the two species were strongly segregated. This was most conspicuous in respect to the colour of petals which were of various yellow tints in 17 plants and red in 3. In the F_1 hybrid the petals were bigger than in either of the parental species, but none of the F_2 plants had so big petals. In F_1 the size of petals was 18.5 × 19.5 mm and in F_2 the length of petals ranged from 9.5 to 16 mm and the width from 12 to 18 mm. Distinct segregation appeared also in the expression of the styles: in 6 plants all the styles were of type III with distinctly hooked rostrum tip, 8 plants had straight styles of type I, 3 plants — similarly as the plants in F_1 — developed simultaneously straight styles of type I, hooked styles of type III and intermediate styles of type II, 2 plants developed straight styles of type I but in some flowers both type I and type II styles appeared in equal numbers, and finally in one plant the styles were of types II and III. The rostrum of the type III styles was 7 to 9 mm long and the stigmatic part 4.5 to 5 mm long. The type I styles were 14 to 18 mm long and much shorter than in *G. montanum*. In the type II styles the rostrum was 9 to 10 mm long and the stigmatic part 6 to 7 mm long. In all the plants the pubescence on the rostrum was shorter and less dense than in *G. montanum*. One plant had hairs on the rostrum base only and in the rest the rostrum was haired throughout. 6 of the plants were completely sterile and produced no good seed, in the remaining plants pollen fertility was between 1.2 and 48.2 per cent while seed fertility was between 4.2 and 34.1 per cent. In the majority of plants seed fertility ranged from 10 to 20 per cent.

3. *G. molle* × *montanum*. This F_2 generation was composed of 23 plants which flowered and fruited and of 11 plants which perished without flowering either during winter or prior to flowering. The majority of plants in this generation resembled *G. montanum* in the expression of their characters. The stems were 10 to 25 cm tall with 1 to 3 flo-

wers. The shape of basal and cauline leaves was in all cases similar to the shape of leaves in *G. montanum*. The flowers of all plants were expanded and had yellow, approximately round petals. The size of petals displayed marked segregation ranging from 10.5 × 9 mm to 18 × 16 mm.

In spite of the fact that in F_1 all the styles were straight of type I, in F_2 numerous plants had hooked styles of type III. Among 32 F_2 plants 6 had hooked styles as in *G. molle*, 7 had straight styles of type I, 9 had mostly straight styles of type I and also a varying number of type II styles with a conspicuously recurved stigmatic part, and in one plant all the styles were of type II. In the type III styles the rostrum was 6 to 10 mm long while the stigmatic part was 3 to 4 mm long and the length of type I styles was 15 to 25 mm. In type II the rostrum was 10 to 14 mm and the stigmatic part 3.5 to 6 mm long. In one plant with both type I and II styles the type I styles were 24 to 25 mm long, almost as long as in *G. montanum*, while the styles of type II were bent approximately in the middle so that both the "rostrum" and the "stigmatic part" were each 12 to 12.5 mm long. In the majority of plants with type III styles the pubescence in the rostrum was less dense and more restricted, whereas, in all the plants with type II styles the hairiness of the rostrum was longer and in some plants approached the pennate hairs of *G. montanum*.

Four plants in this generation were entirely sterile and not one sound achene was developed in their flowers. In the other plants pollen fertility ranged from 24.7 to 72.7 per cent and seed fertility from 6.2 to 60.9 per cent. In the majority of plants fertility ranged from 10 to 20 per cent.

4. *G. aleppicum* × *montanum*. This F_2 generation was composed of only 16 plants which were grown out of 154 seemingly good seeds. All the F_2 plants were very vigorous with floral stems 80 to 100 cm tall, abundantly branched and multifloral. In most cases the expression of characters resembled F_1 plants, some plants were more related to *G. aleppicum* and only two plants had leaves somewhat similar in shape to *G. montanum*.

In all the plants the flowers were expanded, with calyx horizontal in 7 plants and silghtly reflexed in 9. All the plants had yellow approximately round petals, the petals were cordately incised at the tip in 6 plants and rounded in 10. The size of the petals distinctly segregated: the size of the smallest petals was 10.5 × 13 mm and of the biggest 16 × 16 mm. In all the plants there was no gynophore. 9 plants had all the styles of type III with rostrum hooked at the tip. The length of the rostrum was in this case 7 to 12 mm and the length of the stigmatic part 3.5 to 4 mm. The rostrum was haired right to the tip or at the base only. Two plants had all the styles of type II distinctly divided into rostrum and stigmatic part but without the characteristic hook at the tip of the rostrum. In this case the rostrum was 9 to 10 mm and the stigmatic part 4 to 5 mm long. Finally in 5 plants the majority of styles were of type II but some were straight of type I. The styles were here 13.5 to 15 mm long and sparsely haired throughout their length. None of the plants had all the styles straight, of type I.

Pollen fertility of the plants was 16.6 to 48.1 per cent. Seed fertility in this generation was much lower: in 14 plants it ranged from 3.2 to 11.1 per cent, one plant was entirely sterile, though, the percentage of good pollen it developed was 12.2, and in one plant (no. 399/2) the percentage of sound seed was 42.3 while pollen fertility was 48.1 per cent. On the whole, seed fertility in these F_2 plants was lower than in other hybrids described previously. These results coincided more or less with the fertility of the corresponding F_1 hybrids: the F_1 hybrid *G. aleppicum* × *montanum* was more sterile than the F_1 hybrid *G. rivale* × *montanum, G. coccineum* × *montanum* and *G. molle* × *montanum.*

5. *G. montanum* × *canadense.* The F_2 generation in this case consisted of 36 plants of which 29 flowered and fruited. All the characters distinguishing the parental species showed marked segregation. Both parental species differ greatly by the shape of basal and cauline leaves. In F_2 plants prevailed with leaves resembling the type of leaves in F_1, in some plants the leaves resembled those of *G. montanum* and none of the plants had deeply dissected leaves as in *G. canadense.* The length of floral stems ranged from 10 to 60 cm. In the majority of plants the stems were poorly branched, 1—3-floral and stems with 5 to 9 flowers were rare. Marked segregation was apparent in the time of flowering of the plants, the differences amounting to nearly 4 weeks. The parental species differ considerably by the size and colour of petals which in *G. montanum* are big, round and yellow, and in *G. canadense* much smaller, elliptic and white. In F_2 the shape and size of petals differed somewhat in every plant. Some plants had strongly elongated petals, e.g. 12 mm long and 8.5 mm wide, and others had approximately round ones, e.g. 13.5 mm long and 13.0 mm wide. The length of the petals ranged from 8 to 14 mm and the width from 6 to 13.5 mm. The colour of petals in 19 plants was yellow, 4 plants had white petals, 3 plants had creamy petals, in 2 plants the petals were creamy-white, and in one plant they were salmon yellow. The presence in F_2, alongside of petals of the parental colours, also of petals differently coloured than in either of the parental species or the F_1 plants indicates that in this case the hereditary mechanism of colour formation is based on the

interaction of several factors. However, no further conclusions may be drawn in this connection as the number of F_2 individuals was too small.

The following conditions prevailed relatively to the expression of the styles. In 19 plants the styles were of type III with hooked rostrum. The rostrum length varied from 6 to 9 mm and the achenes were approximately glabrous in some plants or variously haired in others. The length of the stigmatic part was 3 to 4.5 mm. In 3 plants the styles were straight of type I with rostrum 10 to 14 mm long. In 6 plants among the straight, type I styles there were also more or less numerous styles of type II with the stigmatic part bent as a result of the partial hooking of the rostrum. Finally 2 plants had styles of type I and II in some flowers, whereas, in others there was additionally, a small proportion of type III styles. 7 plants were completely sterile and these did not produce even one good seed. Seed fertility in the remaining plants ranged between 3.9 and 39.1 per cent. Pollen fertility ranged from 23.5 to 69.3 per cent and on the average was clearly higher than seed fertility.

In the case of such hybrids as *G. montanum* × *hispidum*, *G. montanum* × *silvaticum* and *G. montanum* × *urbanum* only few F_2 plants were obtained and so they will not be described here.

INTERSPECIFIC HYBRIDS IN THE SUBGENUS *EUGEUM*

Most intrasubgeneric hybrids in the subgenus *Eugeum* between species which differ by the degree of polyploidy are highly sterile. No progeny was so far obtained from the following 9-ploid hybrids: *G. magellanicum* with *hispidum, canadense* and *macrophyllum, G. pyrenaicum* with *coccineum, aleppicum, molle, macrophyllum, urbanum* and *silvaticum, G. Fauriei* with *rivale, silvaticum, macrophyllum* and *perincisum,* and *G. riojense* with *rivale* and *aleppicum*. There seems to be no doubt, however, that small F_2 generations could be raised from these hybrids if more seeds were sown out and the young seedlings were given more care.

1. *G. pyrenaicum* × *rivale*

Some few F_2 specimens were obtained only from the hybrid *G. pyrenaicum* × *rivale*. The F_1 hybrid produced only one sound achene from several tens of flowers, which corresponded to a fertility rate of ± 0.01 per cent. During several years the sound achenes gathered from the hybrid were sown out and the total number of F_2 plants obtained in this manner amounted to 32 (the total number of sown out seeds was 182). In F_1 the hybrid produced about 0.8 per cent of good pollen and both the course of meiosis and the size of sound pollen grains pointed to the possibility of an unreduced chromosome number in some of these grains.

The F_2 generation was obtained from open pollination as seeds were never obtained from self pollination. In this generation considerable variability of characters was manifested in respect to the expression of leaves, stems, flowers and fruit. A remarkable feature was the appearance of a number of plants growing more vigorously, having bigger leaves and flowers and a much higher fertility than in F_1. Unfortunately, none of the plants were examined cytologically, though there were reasons to believe that some of them were amphidiploid forms which arose from the union of two unreduced gametes in F_1 plants.

From the 32 F_2 plants 6 did not flower at all or perished before flowering. The length of the stems ranged from 40 to 60 cm. The plants were softly glandularly haired, and the basal and cauline leaves were in most plants shaped like in *G. pyrenaicum* or in F_1 hybrids. Floral peduncles were straight in 5 plants, strongly drooping in 2 plants and slightly drooping as in the F_1 hybrids in the remaining 19 plants. Anthocyanin was abundant in the stems and flowers of 3 plants, the pigment in amounts smaller than in *G. rivale* was displayed by 16 plants, and 7 plants were completely deprived of it. The position of the calyx and corolla in the flowers was as follows:

calyx erect, petals horizontal in . . . . 10 plants
calyx horizontal, petals horizontal in . . . . 12 plants
calyx horizontal, petals erect in . . . . 4 plants.

Of the 26 plants 24 had yellow and 2 creamy petals. The size of petals varied over a wide range and in some plants exceeded greatly the size of petals in the parental species and F_1 hybrids. For instance, in the plant no. 342/4 the petals were 12.3 mm long and 16.6 mm wide, while in plant number 343/11 the size of the petals was 9.1 × 11.0 mm. The shape of petals also varied considerably: in 20 plants the petals were round or cordate at tip and in 6 the tip was emarginate similarly as in *G. rivale,* 19 plants had petals with claw of different length and in 17 the petals had no claw.

In 20 plants there was no gynophore and in the 6 others it was short, 1 to 2 mm long. In all plants the floral base was 4 to 5 mm long, long yellowishly haired. The numbers of achenes on the receptacle was as follows:

50 to 70 achenes in one flower in 20 plants
71 to 100 achenes „ „ „ „ 4 plants
101 to 120 „ „ „ „ „ 2 plants.

In F_2 there were no plants with 120 to 150 achenes as in *G. rivale.* The length of the rostrum ranged from 6 to 9 mm; in most plants the rostrum was 6 to 7 mm long and abundantly glandularly haired.

In F_2 fertility varied over a wide range: 6 of the plants were entirely sterile and produced no good achenes, in the remaining plants achene fertility was between 3.7 and 37.8 per cent. When this is compared with the fertility in F_1, where it was 0.01 per cent, the increase in F_2 is seen to be considerable. As some of the plants with increased fertility had also larger leaves and flowers in respect to F_1 it seems likely that at least a part of them were amphiploids. So far however this supposition has not been confirmed cytologically.

Few F_2 specimens were also raised from the F_1 hybrids *G. magellanicum* × *rivale* and *G. magellanicum* × *aleppicum.*

The sterility of hybrids *G. Quellyon* with hexaploid species of the subgenus *Eugeum* was complete. From the 6 hybrids of this type (nos. 61—66 in the list on pages 109—114 no progeny was as yet obtained.

The most numerous progenies were produced in the case of hybrids between some species with the same chromosome number, though among these hybrids there are also some completely or almost completely sterile.

From among the hybrids of dodecaploid species only the progeny of the hybrid no. 31 *G. magellanicum* × *riojense* was investigated.

2. *G. magellanicum* × *riojense*

The F_2 generation of this hybrid was composed of 42 plants. The 200 seeds sown in 1953 germinated well (in 85 per cent) and fairly rapidly. 50 plants were transplanted to the experimental garden and of these 42 survived till 1955 when the F_2 population was studied. In 1955 of the 42 plants 39 flowered and 3 were still in the stage of leaf rosettes. The vigour of the F_2 plants differed greatly, but vigorously growing plants were more common and some even displayed marked heterosis similarly as in F_1. The length of stems at the time of flowering was as follows:

40 to 60 cm.	6 plants
61 to 60 cm.	26 plants
81 to 100 cm.	5 plants
more than 100 cm.	2 plants.

The majority of plants (30) had stems more or less arching from the base as in *G. riojense* and only in 9 plants the stems were almost straight. The branching of the stems (the number of flowers on stem) was also clearly segregating:

1 to 3 flowers	in	4 plants
3 ,, 5 ,,	,,	8 ,,
5 ,, 7 ,,	,,	12 ,,

7 to 9 flowers in 10 plants
9 „ 11 „ „ 4 „
11 „ 15 „ „ 1 plant.

In all F$_2$ plants similarly as in the parental species the amount of anthocyanin in the stems was small, and the differences in the density of glandular hairs on the floral peduncles were not great. On the other hand, prominent segregation was displayed in the shape of both basal and cauline leaves. Some few plants had leaves shaped as in the parental species, but in the majority the leaves were shaped intermediately. Considerable variability occurred also in the size and shape of the stipules of the cauline leaves.

All the plants had the calyx reflexed and horizontal yellow petals, similarly as in the flowers of both parental species. The size of petals was distinctly segregating:

length of petals in mm	5	6	7	8	9	10	11	12	13	14
number of plants	1	—	2	4	5	6	11	7	3	

width of petals in mm	4	5	6	7	8	9	10	11	12	13	14
number of plants	1	—	2	1	3	6	9	14	2	1	

Segregation was also clearly displayed — but not investigated in detail — in respect to such other characters as for instance the length of the receptacle, the number and size of achenes, and the length and pubescence of the rostrum and of the stigmatic part of the style. The nature of the segregation was here more or less continuous and within the limits of the differences between the parent species.

The fertility of the plants, similarly as the other characters, was distinctly segregating:

per cent of pollen fertility	0—10	11—20	21—30	31—40	41—50	51—60	61—70	71—80	81—90	91—100
number of plants	1	1	4	5	9	6	4	3	4	2

per cent of achene fertility	0—10	11—20	21—30	31—40	41—50	51—60	61—70	71—80
number of plants	2	4	6	10	11	3	2	1

Average fertility in the F$_1$ hybrid was 61.9 and 27.3 per cent for pollen and achenes respectively. It is thus evident that in F$_2$, besides highly sterile, there are also plants greatly exceeding the fertility level of F$_1$ hybrids. Similarly as in the first generation the fertility of achenes is lower than pollen fertility.

A group of highly or completely sterile hybrids was obtained by crossing *G. macrophyllum, G. oregonense* and *G. perincisum* with other species from the subgenus *Eugeum.* From the 12 various hybrids in this group I obtained a small progeny in the case of the hybrid *G. rivale* × *G. macrophyllum* only. As a full description of this progeny was made elsewhere (W. Gajewski 1955) it will suffice to recall here that from open pollination of a few F_1 plants during several years a small number of achenes was obtained, out of which 10 plants grew out. Among the 10 plants 2 were amphiploids with $2n = 84$. These two plants arose probably from the union of two unreduced gametes produced by the F_1 hybrid. In respect to F_1 the two amphiploids had bigger petals and other organs and higher fertility. The fertility of achenes in the F_1 plants was about 0.06 per cent while the fertility of achenes in these two F_2 plants was 23.3 and 21 per cent. The rest of the F_2 plants probably arose by pollination with alien pollen. From the amphiploid plants an F_3 generation was obtained and it was found that some morphological characters were somewhat segregating while fertility was segregating strongly. Cytological examination revealed that in the amphiploids conjugation is complete in some PMCs whereas, the F_1 hybrids were almost entirely asyndetic. The other details referring to these hybrids are to be found in the paper mentioned above.

3. *G. urbanum* × *aleppicum*

Very remarkable results were obtained in the case of the progeny of the highly sterile hybrid *G. urbanum* × *aleppicum.* The F_1 hybrid manifested strong disturbances in microsporogenesis. The anthers were frequently not developed, the development of the gynoecium was disturbed and short extra styles grew out from the ovary. However, in some flowers the anthers developed and then reduction divisions could take place in the archeosporium but they were more or less disturbed. It was observed that in some flowers of one hybrid plant the course of meiosis was asyndetic with almost exclusively univalents present in metaphase of the I-st division, whereas, in other flowers in the majority of PMCs at the first division metaphase there are bivalents alone or only a few univalents. Sound achenes produced by the F_1 hybrids were very few. 26 F_2 plants were obtained from the 62 seeds sown out in 1946. Of these plants 12 were examined cytologically and the chromosome number in root tips was found to be 42, similarly as in the parental species and F_1 plants. This means that in opposition to the hybrid *G. macrophyllum* × *rivale*, where probably only the unreduced gametes functioned, in this hybrid it is primely, if not exclusively, the gametes with a haploid chromosome number that are functioning.

Among F_2 plants distinct segregation occurred in respect to the majority of traits distingushing the two parental species. This referred to the degree of pubescence, anthocyanin, leaf shape, size and shape of stipules, length of gynophore, length and pubescence of the floral base, size of petals, hairiness of achenes etc. The growth of many plants was disturbed and 4 of them were dwarf forms which did not flower at all. On the other hand, other plants were very vigorous, grew up to 120 cm and flowered abundantly. Quite unexpectedly already in this small F_2 population some of the plants resembled very closely in most characters the parental species. However, a high morphological conformity with the parental species was not always correlated with high fertility, and for instance the plant no. 150/3 which resembled greatly *G. aleppicum* in respect to the shape of leaves and stipules, the character of indumentum, the size of petals, and the length and nakedness of the receptacle was entirely sterile. On the other hand, another plant, no. 150/20, which morphologically resembled the F_1 hybrid had 78.3 per cent of fertile pollen grains and about 25 per cent of good achenes. Among the 22 flowering F_2 plants 9 were completely or almost completely sterile and in 6 of the sterile ones the growth of the floral organs was disturbed similarly as in F_1, i.e. the anthers were partially or completely degenerated and extra styles grew out on the ovaries. Of the other 13 plants in 3 fertility was 1 to 2 per cent, in 6 fertility was 2 to 20 per cent and in 4 it was 20 to 50 per cent. In some plants pollen fertility was much higher and was not correlated with seed fertility. As is seen, fertility of F_2 plants varied over a wide range.

From three F_2 plants, nos 150/24, 150/27 and 150/7, F_3 generations were obtained. These generations were composed of 18, 20 and 33 plants respectively and were marked with nos. 198, 211 and 307. The plant no. 150/24 had 42.3 per cent of fertile seeds and was morphologically intermediate between the F_1 type and *G. aleppicum*. In the plant no. 150/27 the leaves were of the F_1 type while the floral stems were very big, up to 120 cm. tall with many flowers which resembled *G. urbanum* by the size of petals and the expression of achenes. The fertility of achenes in this plant was 33.7 per cent. Finally, the plant no. 150/7 approached *G. urbanum* by the shape of leaves, the expression of stipules and the size of petals. This was especially noticeable in the case of stipules. The fertility in this last plant was 10.4 per cent.

In the F_3 generation no. 198 there were 18 plants and many of them resembled *G. aleppicum*. This was very specially visible in the plant no. 198/6 which was very much like *G. aleppicum* both in its vegetative and floral parts. The receptacle in this plant was 16 mm. long and in one flower 577 achenes were inserted on it. This is the highest number of achenes which I ever recorded in the genus *Geum*. The fertility of achenes in the plant was 14.2 per cent and the fruiting heads, similarly as those of the other plants from this generation, were ovoid as in *G. aleppicum*. The fertility of the 18 plants ranged from 5 to 56.9 per cent. None of the plants were completely sterile. Conspicuous segregation was displayed by the indumentum on the stems, the shape of basal and cauline leaves and the size of petals.

In the F_3 generation no. 211 consisting of 20 plants 9 were entirely sterile and in one of these the development of the androceum and gynoceum was disturbed similarly as in F_1. The other 11 plants were less fertile than the F_1 mother plant, their fertility ranging from 1.5 to 12.5 per cent. Morphologically the majority of these plants resembled F_1 hybrids.

The F_3 generation no. 307 consisted of 33 plants of which 6 morphologically resembled so closely *G. urbanum* that if their origin were not known they could easily be mistaken for this parental species. The other 27 plants also resembled *G. urbanum* but many of their characters still displayed some similarity with *G. aleppicum*. However, in all the plants of this generation the receptacle was short (7—8 mm), long haired, with 120 to 200 achenes, and the fruiting heads were round as in *G. urbanum*. Visible segregation referred to the shape of leaves, the size of stipules, the nature of indumentum and the size of petals. Of the 33 plants 4 were entirely sterile and in the rest the percentage of fertile achenes was between 0.3 and 68.4.

In further experiments two plants morphologically most resembling *G. aleppicum* and *G. urbanum* were chosen respectively from the F_3 generations nos. 198 and 307 and from them two F_4 generations were raised, nos. 133/51 and 4/51.

The generation no. 133/51 was composed of 25 plants all resembling pure *G. aleppicum* so closely as to be almost indistinguishable. In all cases the leaves were of the shape characteristic for *G. aleppicum*, the cauline leaves had small stipules, the petals were big and bright yellow as in *aleppicum*, and the receptacle was 12 to 15 mm long, short haired with 190 to 240 carpels. The hybrid origin of these plants was revealed only by the reduced fertility in some of them:

in 6 plants the percentage of fertile achenes was 12 to 30
,, 9 ,, ,, ,, ,, ,, ,, ,, 31 to 50
,, 5 ,, ,, ,, ,, ,, ,, ,, 51 to 70
,, 5 ,, ,, ,, ,, ,, ,, ,, 71 to 97.3.

As can be seen already in the F_4 generation plants with normal fertility appear.

The generation 4/51 consisted of 10 plants only, all of which resembled *G. urbanum* in respect to the shape of leaves, indumentum, size of petals and floral base, as well as the number and shape of achenes. Slight segregation was displayed by the size of stipules of the cauline leaves and the size of petals only. However, the fertility of the plants was still segregating considerably, as alongside of plants with the fertility percentage of 89.7 there were also completely sterile ones.

In 1952 the experiments were continued further and two F_5 generations were raised from the most fertile F_4 plants in the generations nos. 133/51 and 4/51. The F_5 generation no. 16/55 was composed of 15 plants obtained from plant no. 14 (fertility 97.3 per cent) of the generation no. 133/51. In spite of the great morphological uniformity in this F_5 generation the fertility of achenes was visibly reduced and ranged from 36.5 to 88.9 per cent. The other F_5 generation no. 17/55 consisted of 37 plants and was derived from the plant in the F_4 generation no. 4/51 with the fertility level of 89.7 per cent. In this F_5 generation fertility was still strongly segregating and ranged from 0.5 to 73.4 per cent. In 1952 this generation was badly infected with mildew and many plants perished before bearing fruit.

The above results indicate that by selection through 5 generations in the direction of the parental species the two species are reproduced almost exactly in respect to the more important morphological characters. However, the selection was not sufficient to obtain plants which would give persistently a highly fertile progeny characteristic for the parental species. Nevertheless, from the steady increase of fertility in the successive generations it seems likely that this aim could be attained but probably selection would have to be continued for a much longer time.

Similarly as in F_2 in all the plants examined cytologically in further generations the chromosome number was always the same as in F_1 and the parental species, i.e. 42. However, the number of the examined plants was not large. It was found that in F_2 and in further generations in some PMCs the conjugation of chromosomes was normal and the number of bivalents was 21, while in other cells there were 2 to 10 univalents. The number of univalents and the number of cells with univalents varied greatly in the different plants. In some F_3 and F_4 plants up to 90 per cent of PMCs had bivalents only and the number of univalents was 2 to 4. On the other hand, in 5 F_2 plants the percentage of PMCs with bivalents was 30 to 65 and the number of univalents in the other cells could even be 10. In an other F_2 plant the archeosporium degenerated before the meiotic divisions started.

The small F_2 generations obtained from the other highly sterile hexaploid hybrids will now be described.

4. *G. aleppicum* var. *strictum* × *canadense*

On the F_1 plants from this cross 23 achenes were gathered and from them only 6 plants in the F_2 generation grew out. The achenes were obtained from open pollination, as controlled-pollination gave no results and not one well developed achene was produced in that manner. All the 6 F_2 plants grew very vigorously, their stems were 100 to 120 cm tall, abundantly branched at the top and with numerous flowers. The petals in 4 plants were yellow, but the intensity of the colour differed, whereas, in the other two plants the petals were white. The size of the petals varied from small elongated (8.5 mm long and 4.5 mm wide) to relatively large (11.0 mm long and 8.2 mm wide). The F_2 plants also differed greatly in respect to the shape of basal and cauline leaves. In 4 plants the floral base was short (up 4.5 mm long), fairly long haired and with few carpels as in *G. canadense*. In the other plants the floral base was expressed approximately as in the F_1 plants. The fertility of the plants was low, the percentage of fertile pollen ranging from 0.5 to 11.7 and of fertile achenes from 0.4 to 3.8. None of the plants resembled *G. virginianum* obtained from Professor R. T. Clausen. Besides morphological characters the F_2 plants differed from *G. virginanium* also by their very low fertility. If Raynor's supposition that *G. virginianum* arose from this cross is correct then it must represent an exceptionally fertile segregate.

5. *G. canadense* × *urbanum*

The F_1 hybrid was highly sterile and produced only about 0.1 per cent of sound achenes. From the 123 achenes sown out in 1950 only 31 plants which flowered in 1952 were obtained. Of these 8 had white petals and 23 yellow ones, which corresponds rather accurately to the ratio 1 : 3. The two parental species differed greatly by the time of flowering and in F_2 this character strongly segregated: the first plant flowered on June 10, 1952 and the last on July 7 of that year. Strong segregation was also visible in the size and shape of petals: some plants had small approximately round petals (5.0 mm long and 4.0 mm wide), some had small elongated petals (5.2 mm long, 3.5 mm wide) or large round ones (10.0 mm in both directions) and some had petals of various intermediate shapes and sizes. In some plants the sepals were twice as long as the petals and in others the sepals and the petals were of equal length. The variability prevailing in respect to the shape of basal and cauline leaves was so great that it was difficult to describe accurately. Some of the plants flowering late had leaves and stems expressed very much like in *G. canadense* while the plants flowering earlier rather approached *G. urbanum* or the F_1 type. In F_2 there were some plants which grew extremely vigorously and developed stems up to 152 cm with 50 and more flowers on one stem. Marked segregation referred also to the size of achenes, the length of the rostrum and the nature of the pubescence on the achenes. The fertility of achenes in these plants was low: 14 were completely sterile or almost so, and the percentage of good achenes in the other 17 ranged from 0.1 to 21.1.

6. *G. urbanum* × *laciniatum*

The sterility of the F_1 hybrids was very high, seed fertility being only about 0.01 per cent. The F_2 generation consisted of 15 plants obtained from 85 achenes sown out in 1949 and 1950. These plants similarly as those of the F_2 generation just described displayed very distinctly segregation in respect to the colour of petals: in 3 plants the petals were white and in 12 yellow of various tints. In 1952 the first plants flowered on June 18 and the last on July 20. Similarly as in the case of the preceding cross the last to flower were the plants resembling by the shape of leaves *G. lacinatium*. The size of petals differed greatly ranging from quite small, 3.4 mm long and 2.8 mm wide, to quite large ones, 7.8 mm long and 5.9 mm wide. The size of petals was not correlated with the size of sepals which were twice as long as the petals in some plants and in others shorter than the petals. Much variability was displayed by the shape of basal and cauline leaves. The length of stems varied over a wide range from about 50 to 150 cm and the number of flowers on one stem ranged from about 7 to 45 and more. In 11 plants the lower part of the stems was roughly, bristly haired as in *G. laciniatum* and only in 4 plants the indumentum resembled that of *G. urbanum*. Out of the 15 plants 9 were completely sterile and these, although they flowered abundantly did not produce even one good achene. In the other 6 plants the percentage of seed fertility was between 0.01 and 1.5. The achenes of 2 plants were approximately naked as in *G. laciniatum* and haired in the other plants. In none of the F_2 plants the fruiting heads were easily detachable as in *G. laciniatum*.

In the case of such other highly sterile hybrids as for instance *G. molle* × *canadense, G. molle* × *aleppicum* and *G. hispidum* × *aleppicum* the F_2 generations in my cultures consisted of very few plants only and for this reason they will not be described here. All these plants were either entirely sterile or their fertility was very low, ranging from 0.1 to 1.3 per cent of good achenes.

Far more numerous F_2 generations were raised from the partially fertile hybrids and they will now be described.

7. *G. molle* × *urbanum*

In the case of this F_1 hybrid the percentage of good achenes was 18.8. The F_2 generation consisted of 62 plants. *G. urbanum* differs from *G. molle* primely by the shape of leaves, the pubescence and length of stems, the number of flowers on one stem and by smaller petals. In F_2 the segregation of the major characters distinguishing the parental species was as follows:

length of stems	40 to 60 cm	15 plants
,, ,, ,,	60 to 80 ,, ...	43 ,,
,, ,, ,,	80 to 100 ,, ...	4 ,,
number of flowers on one stem	1 to 3	4 plants
,, ,, ,, ,, ,, ,,	3 to 5	14 ,,
,, ,, ,, ,, ,, ,,	5 to 7	19 ,,
,, ,, ,, ,, ,, ,,	7 to 15	25 ,,

ength of petals in mm	5		6		7		8		9		10		11		12
number of plants		2		5		12		27		8		6		2	

The colour of petals was bright yellow in 48 plants and pale yellow in 14. On the whole the majority of plants had leaves resembling those of F_1 plants or more or less approaching the leaves in *G. urbanum*. Only 7 individuals had leaves similar to those of *G. molle*. The number of plants softly haired with numerous glandular hairs as in *G. molle* was 3 only, the rest of the plants had no glandular hairs and the straight hairs varied in length and density in the particular plants. Seed fertility in F_2 was as follows:

Per cent of fertile achenes	0		10		20		30		40		50		60
number of plants		12		22		20		2		4		2	

It is thus apparent that some of the F_2 plants were much more fertile than in F_1.

It was reported in an earlier paper (W. Gajewski 1954) that in F_1 of this hybrid there was one amphiploid plant with $2n = 84$. The fertility of this plant was much higher than in the F_1 hexaploid hybrids. The F_2 generation of this plant was also very fertile and contrary to the progeny of the hexaploid hybrids it was highly uniform in the expression of its various characters. A detailed description of the F_1 and F_2 hybrids, of the amphiploid and of its progeny are to be found in the earlier paper. In 1955 I had three F_3 generations of this amphiploid and they all were highly fertile and very uniform. This indicates that the amphiploid behaves as if it were a new dodecaploid species.

8. *G. urbanum* × *hispidum*

The percentage of fertile seeds in F_1 was about 34.2. Out of the 123 seeds sown a F_2 generation of 66 plants was obtained n 1951. Mention has earlier been made that *G. hispidum* differs little from *G. molle* and consequently the F_2 generation of this species differed little from the hybrid just described. The petals of *G. hispidum* are much smaller than the petals of *G. molle* and this was manifested by the smaller range of variations in the length of the petals in the hybrid *G. hispidum* × *urbanum* as compared with the hybrid *G. molle* × *urbanum:*

length of petals in mm	5		6		7		8		9
number of plants		15		33		13		5	

Considerable variability was displayed by the expression of the basal and cauline leaves and of stipules. The length of stems ranged from 50 to 100 cm and the number of flowers on one stem from 5—6 to 13—15. Segregation was also visible in the achenes in respect to their shape, size, expression of the rostrum, and the character and nature of pubescence. Not one of the F_2 plants had the abundant soft hairiness with numerous glandular hairs characteristic for *G. hispidum*. In respect to pubescence all the plants approached *G. urbanum*. The time of flowering in F_2 was greatly stretched out and in 1951 the first plant flowered on June 5, while the last on July 7. The fertility of the plants varied over a wide range:

per cent of good achenes	10		20		30		40		50		60		70
number of plants		9		21		16		13		5		2	

As is seen the fertility of the F_2 generation of *G. urbanum* × *hispidum* was greater than in F_2 of *G. molle* × *urbanum* and this increase coincided with the difference in fertility of the corresponding F_1 hybrids.

9. *G. aleppicum* × *rivale*

The hybrid was obtained as early as 1938 by crossing *G. rivale* from Piastów and *G. rivale* v. *pallidum* from Copenhagen and with *G. aleppicum* from Białowieża Forest. Later on, the cross was repeated and *G. rivale* was crossed with *G. aleppicum* v. *strictum*. The present description of the F_2 generation refers to the hybrids of *G. rivale* from Piastów with *G. aleppicum* from Białowieża Forest. The hybrids were investigated between 1939 and 1943 and results reported here refer to both reciprocal hybrid populations which displayed no significant differences. The total number of plants examined in F_2 amounted to 82. The mean fertility of F_1 plants was 14.8 per cent. The parental species differed greatly in numerous characters which were segregated along a more or less complex pattern in F_2.

Height of stems in cm	40	50	60	70	80	90	100
number of plants	11	15	30	16	6	4	

Anthocyanin was very abundant in the floral stems and flowers of 20 plants, the amount of this pigment was reduced to approximately the level of F_1 in 38 plants and there was no anthocyanin in 24 plants. This distribution approaches the ratio 1:2:1. The branching of the floral stems varied and the number of flowers ranged from 3 to 5 as in *G. rivale*, to 11 to 15 as in *G. aleppicum*. The number of flowers was distributed as follows:

number of flowers	1—3	4—5	6—7	8—9	10—11	12—13	14—15
number of plants	20	30	21	6	2	1	2

The floral peduncles were either strongly drooping as in *G. rivale* or partially drooping and rapidly straightening after anthesis or finally straight from the first as in *G. aleppicum*. The variation was here almost continuous and the F_2 plants could be divided only approximately into the following categories: strongly drooping peduncles in 48 plants, intermediately drooping peduncles in 28 plants and straight peduncles in 6 plants. In the flowers the calyx and corolla were either both erect as in *G. rivale*, or the calyx was reflexed and the corolla horizontal as in *G. aleppicum* or the calyx and corolla had some still other position:

calyx corolla	erect	upright	horizontal	reflexed
erect	1	—	6	1
upright	—	21	14	7
horizontal	—	—	15	17

As is seen only one plant had both the calyx and corolla erect as in *G. rivale* while the number of plants with calyx reflexed and corolla hirozontal as in *G. aleppicum* was 17. The most numerous were the plants with both calyx and corolla more or less upright but not quite erect. The above characters were difficult to classify as both calyx and corolla go through various complex movements during flowering and occupy various positions in accordance with the age of the flower. The sizes of the different parts of the perianth varied greatly:

length of sepals in mm	5		7		9		11		13		15		17		19		21		23
number of plants		2		14		27		20		10		5		2		1		1	

length of segments of epicalyx in mm	2		3		4		5		6		7		8		9		10		11		13
number of plants		4		9		27		16		13		4		4		2		1		1	

length of petals in mm	5		6		7		8		9		10		11		12		13		14		15
number of plants		1		—		5		14		20		13		21		6		1		1	

width of petals in mm	6		7		8		9		10		11		12		13		14		15		16
number of plants		1		3		15		20		15		8		11		5		3		1	

As can be seen all the series of variation are distinctly asymmetric and shifted towards the higher values. The colour of the petals was yellow of various tints in 62 plants and creamy to nearly white in 20. Because of the various yellow and creamy shades the classification of 15 plants was uncertain, as the colour was intermediate between yellow and creamy. Much variation was also displayed by the length of the gynophore:

ength of gynophore in mm	1		2		3		4		5		6		7		8		9		10		11		12		13		14		15		16		17
number of plants		17		10		14		13		22		11		7		3		3		4		2		2		4		—		—		1	

The gynophore in *G. aleppicum* is only 1.5 to 3 mm long, in *G. rivale* it is 8 to 10 mm long and in F_1 4 to 7 mm long. In F_2 the majority of plants had the gynophore of the same length as in the F_1 hybrids but there were also plants with a gynophore longer than in *G. rivale* and as much as 17 mm long.

A high variability referred also to the floral base which ranged in length from 4 to 10 mm and was haired. The number of carpels inserted on the receptacle varied together with its length, i.e. between ± 100 and ± 230 carpels on one receptacle.

Besides the characters already mentioned marked segregation was displayed also by the size and shape of leaves, the character of pubescence on the stems and leaves, and the formation of the caudex. As all these traits are difficult to classify no numerical values are given here. The most common in F_2 were the plants with leaf shape resembling F_1 hybrids, but instances of resemblance to the leaves in parental species were also noted. The pubescence in the majority of F_2 plants was of the same kind as in F_1 plants without glandular hairs and only 7 plants were abundantly glandularly haired similarly as in *G. rivale.* In *G. rivale* the caudex is long and well developed but is almost not formed in *G. aleppicum.* In F_1 the formation of the caudex was entirely dominant. In F_2 the segregation in this respect was conspicuous, though difficult to define, as in various plants the caudex is developed differently.

The fertility of the F_2 plants was as follows (pollen fertility was examined only in 45 plants):

per cent of good pollen	0—20	20—40	40—60	60—80	80—100
number of plants	22	17	1	4	1

per cent of sound achenes	0—20	20—40	40—60	60—80	80—100
number of plants	45	24	9	2	2

It is thus apparent that in F_2 there were, alongside of plants with low fertility corresponding approximately to F_1, individuals with distinctly increased fertility of which two had an almost normal fertility level of 84.7 and 83.4 per cent.

Considerable variation was shown by the expression of the achenes, size of rostrum and stigmatic part, and the character of pubescence on these organs. The length of the rostrum ranged from 4 to 12 mm and the length of the stigmatic part from 3.5 to 5 mm. The rostrum was naked in 12 plants, in the other 70 it was straight haired and in 2 it was, moreover, glandularly haired. The size of the achenes and the rostrum varied more or less continuously as can be seen from the table below showing the variations in the length of the rostrum:

length of rostrum in mm	3	4	5	6	7	8	9	10	11	12
number of plants	2	12	24	16	10	8	7	2	1	

Besides the F_2 generation both backcrosses were obtained by pollinating the F_1 hybrid with pollen of the parental species.

a) B_1 (*G. rivale* × *aleppicum*) × *aleppicum*: — This generation consisted of 63 plants. In all the plants the petals were yellow without emargination at tip and claw at base. Much variation was shown by the size of petals. Anthocyanin in small quantities was present in the stems of all the plants, but in the sepals and petals there usually was no anthocyanin. In all the plants the calyx was recurved and the petals were horizontal. The length of the gynophore varied between 1.5 and 4 mm and of the floral base between 4 and 8 mm. All the plants were long, stiffly, bristly haired without glandular hairs. Distinct segregation was shown by the shape of leaves, the length of floral stems (40 to 100 cm), number of flowers on stem (7 to 25), length of calyx (9 to 15 mm), length of epicalyx and length of petals (6 to 13 mm). The size of achenes and the length of rostrum and stigmatic part also segregated somewhat. 6 of the plants were entirely sterile and the fertility of the rest was as follows:

fertility of achenes between 0.1 and 10 per cent ... 40 plants
,, ,, ,, ,, 10 ,, 20 ,, ,, ... 15 ,,
,, ,, ,, ,, 20 ,, 30 ,, ,, ... 2 ,,

The majority of plants in this generation were more sterile than in F_1.

b) B_1 (*G. rivale* × *aleppicum*) × *rivale*: — The resemblance of the 58 plants in this generation to *G. rivale* was clearly apparent. In all the plants anthocyanin was abundant in the stems and flowers and all had drooping floral peduncles. Well evident segregation was displayed by the colour of the petals which were creamy in 28 and yellow in 30 plants; this relation corresponds very well to the ratio of 1:1 as was to be expected in the case of a backcross. The position of calyx and sepals varied greatly. The shape of petals differed too: 40 plants had petals rounded at tip and 18 plants had emarginate petals, in all plants the petals had a claw at the base but its length was very much different in the particular plants. The length of the gynophore ranged from 4 to 12 mm. In respect to the shape of leaves and the character of pubescence many plants resembled greatly *G. rivale*. This referred also to the shape of achenes, the length and pubescence of the rostrum and of the stigmatic part. In the backcross these traits approached *G. rivale*.

In respect to the fertility of achenes the plants of this backcross were clearly more fertile than in F_1 and in the backcross with *G. aleppicum*:

Fertility of achenes from 0.1 to 20 per cent ..... 16 plants
„ „ „ „ 20 to 40 „ „ ..... 23 „
„ „ „ „ 40 to 60 „ „ ..... 19 „

The plant most resembling *G. rivale* was chosen from this generation and again pollinated with pollen of *G. rivale*. In this manner a B$_2$ generation was obtained.

c) B$_2$ ((*G. aleppicum* × *rivale*) × *rivale*) × *rivale*: — This generation was composed of 41 plants. All these plants had anthocyanin in stems and flowers, much drooping floral peduncles, and flowers with erect calyx and corolla. In all cases the petals were creamy, incised at tip and with long claw at base. The gynophore was long in all the plants. The stems were 40 to 60 cm tall and with 3 to 5 flowers as in typical *G. rivale*. The shape of leaves and the character of pubescence also closely resembled *G. rivale*. Practically speaking, it was impossible to distinguish the majority of these plants from *G. rivale*. The high fertility of the plants ranged from 49.1 to 92.6 per cent for pollen and from 43.5 to 84.1 per cent for achenes.

In B$_2$ 6 plants were examined cytologically and in all cases in metaphase of the I-st division of PMCs numerous cells with 21 bivalents were found. This indicates that the somatic chromosome number of these plants was 42, similarly as in the parental species. In all the plants there were numerous PMCs with 2 to 8 univalents alongside of the relatively reduced number of bivalents. In one of the B$_2$ plants there were 8 to 14 univalents in the majority of the analysed cells.

In 3 plants in the B$_3$ generation of the backcross with *G. rivale* at the stage of the I-st division metaphase there were the 21 bivalents only in 80 to 100 per cent of the cells examined. 2 to 4 univalents were seen in a few PMCs only.

10. *G. rivale* × *canadense*

The F$_2$ generation consisted in this case of 64 plants the majority of which grew vigorously and flowered profusely. The length of stems in the particular plants was as follows:

20 to 40 cm	3 plants	60 to 80 cm	37 plants
40 to 60 cm	19 plants	80 to 100 cm	5 plants.

The average number of flowers on one floral shoot was as follows:

1 to 3 cm	10 plants	7 to 9 cm	10 plants
3 to 5 cm	30 plants	9 to 11 cm	1 plant.
5 to 7 cm	13 plants		

Great variability was displayed by the floral peduncles which ranged from quite straight to very drooping. In this case the variation was almost continuous and the following categories were established only approximately:

straight peduncles	11 plants
intermediately drooping peduncles	34 plants
peduncles strongly drooping as in *G. rivale* . .	16 plants.

In 14 plants anthocyanin was abundant in the stems and flowers, in 31 plants the amount of this pigment was distinctly less than in *G. rivale* (it often appeared only in the stems) and 19 plants were deprived of the pigment.

In respect to the position of the calyx and corolla the conditions were here similar as in the previously described hybrid:

calyx corolla	erect	upright	horizon-tal	reflexed
erect	3	—	—	1
upright	—	27	21	5
horizontal	—	—	5	2

Distinct segregation occurred in the colour of petals:

16 plants had white petals
14 ,, ,, creamy petals
34 ,, ,, yellow petals

The above refers to the three main colours, but the creamy and yellow colours were of many different tints and, moreover, in plants with abundant anthocyanin the basic colour was often masked by the red colour of the anthocyanin. This was especially true in plants with white petals. *G. rivale* has creamy petals and *G. canadense* white ones while in F_1 the petals were yellow. The segregation in F_2 closely approached the ratio 9:3:4 (theoretical numbers 36:12:16). This indicates that the yellow colour of petals is conditioned by at least two factors and very probably there are three factors, as in the cross with *G. coccineum* which has red petals, *G. rivale* also gives yellow flowering plants in F_1.

The shape of petals also differed greatly varying from narrow elliptical as in *G. canadense* to emarginate at tip with long claw at base as in *G. rivale*. Petals were clearly emarginate at tip as in *G. rivale* in two plants, less so in 21 plants, and rounded at tip in 41 plants. A long claw as in *G. rivale* (4 to 5 mm) was found in 2 plants only, the claw had 2 to 4 mm in 17 plants, 1 to 2 mm in 29 plants and 16 plants had petals without claw. The sizes of the calyx, epicalyx and petals were as follows:

length of sepals in mm	5	6	7	8	9	10	11	12	13	14	15	16	17
number of plants	1	3	9	16	10	8	8	3	2	3	—	1	

length of epicalyx segments in mm	1	2	3	4	5	6	7	8
number of plants	1	13	28	14	6	1	1	

length of petals in mm	4	5	6	7	8	9	10	11	12	13
number of plants	2	1	4	9	10	17	10	8	3	

width of petals in mm	2	3	4	5	6	7	8	9	10	11	12	13	14
number of plants	1	3	—	1	4	10	14	13	9	5	3	1	

From the above it is clearly seen that the petals and sepals exceed on the side of the higher values the size of the petals and sepals in both parental species.

Segregation referred also to the size of the gynophore:

length of gynophore in mm	0	1	2	3	4	5	6	7	8	9	10	11	12
number of plants	11	14	9	10	11	4	2	—	—	1	1	1	

It is evident that the gynophore was very short in the majority of plants or approached the length of the gynophore in F_1 hybrids. However, 4 plants had the gynophore of the same length as in *G. rivale*. Variation in this case is not continuous.

The fertility of plants in F_2 was as follows:

per cent of sound pollen grains	0—20	20 – 40	40—60	60—80	80—100
number of plants	7	10	9	12	2

(in two plants all the pollen grains were degenerated)

per cent of sound achenes	0—20	20—40	40—60	60—80	80—100
number of plants	15	25	12	11	1

Seed fertility in F_1 plants ranged from 7.6 to 12.5 per cent and averaged at 8.8 per cent. It is thus evident that in F_2 the majority of plants had an increased fertility in respect to the F_1 plants.

In *G. canadense* the receptacle (floral base) is 4 to 5 mm long, covered with long white hairs and there usually are 80 to 100 achenes inserted on it. In *G. rivale* the receptacle is longer (6—7 mm), shorter haired and with 150 to 200 achenes. The two parental species also differ greatly in the size of achenes, rostrum and the stigmatic part. All these traits were strongly segregating in F_2. The length of achenes varied from 3.5 to 5 mm, of the rostrum from 2 to 10 mm and of the stigmatic part from 1.5 to 5 mm. This is illustrated here on the example of the series of variations for the rostrum length which was as follows:

length of rostrum in mm	2		3		4		5		6		7		8		9		10
number of plants		1		6		12		18		14		10		2		1	

The length of the receptacle also varied continuously within limits of from 3 to 7 mm. The receptacle in 12 plants was long, white haired as in *G. canadense* and in the rest of the plants it was short haired or almost naked. The number of achenes inserted on the receptacle was as follows:

number of achenes	50		70		90		110		130		150		170		190		210
number of plants		2		4		12		21		11		6		5		3	

As can be seen the number of achenes on the receptacle segregated very regularly within the limits of the two parental species.

From 17 F_2 plants small F_3 generations consisting of 10 to 20 plants in every case were raised in 1948. Some of these F_3 plants showed no segregation in respect to certain characters such as the colour of petals, straight or drooping floral peduncles etc. The remaining majority of traits distinguishing the two parental species were segregating as before to a greater or lesser extent. As the number of individuals in the particular families was small it seemed useless to give detailed results of the measurements. However, the results from fertility estimations of the plants in the F_3 generation as compared with the fertility of the initial F_2 plants are assembled and presented in the table (p. 299):

No evident correlation between the fertility of F_2 and F_3 plants is apparent from the table on p. 299.

The course of meiosis in PMCs was examined in 7 F_2 plants only. Tentative examinations revealed that all the plants were hexaploids with

No.	F$_2$ fertility %	F$_3$ n	0 — 20	— 40	— 60	— 80	— 100 %
30	58.4	20	4	6	4	5	1
56	68.2	10	5	3	—	2	—
25	40·0	18	6	10	2	—	—
43	9·4	10	7	2	1	—	—
23	84·2	20	4	8	5	3	—
64	48·5	20	12	4	2	2	—
46	55·2	10	4	2	2	2	—
62	58·8	14	2	8	3	1	—
94	60·3	11	—	6	—	2	3
41	59·2	18	—	2	2	12	2
47	53·7	16	—	2	10	3	1
123	8·7	20	16	4	—	—	—
15	24·3	10	—	—	8	—	2
17	42·2	16	—	10	4	2	—
1	65·5	12	—	—	6	6	—
33	24·1	16	—	—	12	4	—
120	22·1	20	2	4	12	2	—

$2n = 42$. At first division metaphase in some PMCs there were 21 bivalents, while in other cells 2 to 14 univalents were observed. Particular plants differed greatly both by the number of univalents and the percentage of cells with univalents.

From the other partially fertile hybrids described in the preceding chapter I had small F$_2$ generations only and they will not be described here.

The descriptions which will now follow refer to the hybrids which were classified in chapter VII as highly fertile. The hybrids in this group were derived primely from crosses between *G. rivale, coccineum,* and *silvaticum* as well as between these three species and *G. urbanum, molle* and *hispidum.* All these species differ greatly by their morphology but are united by their common distribution in Europe. A highly fertile hybrid was also obtained from the cross *G. molle* × *hispidum,* the two species being morphologically alike. Among North American species fertile hybrids were obtained only from crosses between morphologically related species, such as between *G. canadense* and *laciniatum,* and between *G. macrophyllum, oregonense* and *perincisum.*

11. *G. canadense* × *laciniatum*

Both these parental species are related morphologically and have large common distribution areas in USA where they sometimes produce natural hybrids (Raynor 1945, 1952). The F$_1$ hybrids of these species had on the average 42.8 and 52.3 per cent of good pollen grains and sound achenes respectively. The F_2 generation consisted of 85 plants. Definite segregation occurred here in respect to all the characters distinguishing both parental species. The most important of these were:

1. The shape of basal and cauline leaves was very variable. Already in some F_2 plants the leaf shape of the parental species was reproduced rather accurately.

2. The character of indumentum on stems and leaves was as follows: 47 plants were long stiffly and bristly haired and their pubescence approached that of *G. laciniatum*, approximately intermediate pubescence was displayed by 34 plants and only 4 plants had the pubescence similar to that of *G. canadense.*

3. The horizontal position of floral peduncles at anthesis as in *G. canadense* was observed in 2 plants and the other 83 plants had erect peduncles as in *G. laciniatum.*

4. The petals were white in all plants, though sometimes with a creamy tint and usually with recurved margins. The size of the petals and sepals was as follows:

length of sepals in mm	4		5		6		7		8		9		10		11
number of plants		4		11		14		25		18		8		5	

length of petals in mm	3		4		5		6		7		8		9
number of plants		4		21		44		12		3		1	

width of petals im mm	2		3		4		5
number of plants		49		33		3	

As can be seen the size of petals was in most cases more related to the petals in *G. laciniatum* than in *G. canadense.*

The fertility of achenes in F_2 plants was as follows:

percent of sound achenes	20		40		60		80		100
number of plants		2		19		28		36	

As is seen close on 45 per cent of F_2 plants had normal or only slightly reduced fertility. The highest fertility recorded was 97.3 per cent which is within the limits of fertility in the pure parental species. The number of achenes on the receptacle was equally distinctly segregated.

The number of achenes on receptacle:

number of achenes	80		100		120		140		160		180		200		220		240		260
number of plants		19		25		13		10		9		6		2		—		1	

The asymmetric shift in the series of variation is quite definitely apparent. The majority of individuals had the number of achenes related to the values characteristic for *G. canadense* and only one F_2 plant had a similar number of achenes as in *G. laciniatum*. The length of the receptacle changed together with the number of achenes inserted on it and ranged from 4—5 mm to 7—8 mm. The pubescence on the receptacle also differed from long and white as in *G. canadense* to almost glabrous as in *G. laciniatum*. The pubescence on the achenes was also segregating. The achenes of *G. laciniatum* are approximately naked and those of *G. canadense* have at the tip a tuft of long bristly hairs. In F_2 10 plants had achenes haired more or less as in *G. canadense*, the achenes of 69 plants were haired but less so, and the achenes were naked as in *G. laciniatum* in 3 plants only. The size of achenes and rostrum was segregating to a small extent. It is characteristic for *G. laciniatum* that its achenes are not easily shed from the receptacle after ripening but the whole receptacle is broken off at the base in such a manner that it can be carried by animals and in this respect the species is alone in the whole genus. In F_1 this trait was recessive while in F_2 there were 24 plants in which the receptacle was broken off fairly easily and 61 in which the receptacle base was not fragile, this in spite that in some of these plants the achenes were not easily shed off the receptacle after ripening.

As a general conclusion in respect to these hybrids it can be said that in F_2 plants appeared with almost normal fertility and some of these were very closely related morphologically to the parental species.

12. *G. hispidum* × *molle*

The percentage of seed fertility in F_1 hybrids was 54.2. Both parental species are very closely related and as can be seen from the description of the F_1 hybrid they differ primely by the shape of leaves, character of pubescence, the length and branching of stems, the size of petals and the time of flowering. In F_2 which consisted of 60 plants all the characters distinguishing the parental species were markedly segregated and the extreme segregates resembled the parental species. Some of the F_2 plants had leaves shaped almost identically as the parental species, though, of course, the number of plants with leaves shaped intermediately was greatly predominant. Very definite segregation occurred in the time of flowering so that in 1953 the first plants started flowering on May 15 at the same time as *G. molle* and the last on June 10 approximately together with *G. hispidum*. The length of stems in F_2 plants was as follows:

40 to 50 cm	3 plants
50 to 60 cm	20 plants
60 to 70 cm	10 plants
70 to 80 cm	17 plants
80 to 90 cm	10 plants.

It is apparent from the above that in F_2, similarly as in F_1, some of the plants had stems longer than either of the parental species (c.f. the discription of F_1 on page 159). Similar conditions existed in connection with the number of flowers on a stem. In 30 plants there were usually 1 to 3 flowers on one stem (as in *G. molle*), in 25 plants this number was 4 to 7 (as in *G. hispidum)* and in 5 plants the number of flowers per stem was 8 to 11 and even 15, which was more than in *G. hispidum* and the same as in some F_1 hybrids. All the F_2 plants were densely glandularly haired in the upper parts and differed between them primely by the number and length of the straight bristly hairs in the lower parts of the stem. The size of the petals in F_2 plants was as follows:

length of petals in mm.	7		8		9		10		11
number of plants		12		25		17		6	

width of petals in mm.	6		7		8		9		10
number of plants		2		23		33		2	

As can be seen not one plant in F_2 had petals of the size characteristic for *G. molle*. In all cases the petals were yellow, but of various tints. Pollen and seed fertility in F_2 plants was as follows:

per cent of good pollen grains	40		60		80		100
number of plants		18		34		8	

per cent of good achenes	0		20		40		60		80		100
number of plants		2		20		23		13		2	

These numbers indicate that pollen fertility of F_2 plants was very clearly higher than seed fertility of the same plants and that seed fertility varied over a much wider range than pollen fertility. The highest recorded percentage of fertile achenes was 90.1.

13. *G. macrophyllum* × *oregonense*
14. *G. macrophyllum* × *perincisum*
15. *G. perincisum* × *oregonense.*

The above three species form a closely related group. Their mutual relation was investigated on the grounds of their geographical distribution and in an analysis of the F_1 and F_2 hybrids, as already reported elsewhere (W. Gajewski 1955). Here it will only be recalled that the shape of basal and cauline leaves, which distinguishes the parental species in the first place, was segregating in the corresponding F_2 generations within limits of the parental species. Pollen and seed fertility was also distinctly segregating in F_2 and in numerous plants fertility was at a high, nearly normal level. Many of the F_2 plants had an absolutely normal viability and even showed signs of increased vigour in respect to the parental species.

The further generations of the fertile hybrids described here referred so far to crosses between species closely related morphologically. However, fertile hybrids are also formed by species far apart morphologically and systematically. The best known in this group is the hybrid *G. rivale* × *urbanum*. The segregation in F_2 of this hybrid was described many times by such writers as for instance Prywer or Winge, and for this reason the description will not be repeated again, especially as my results agree in principle with those of other workers. I shall only mention that the majority of plants in the F_2 generation was not fully fertile and that fertility of these plants differed, being distinctly reduced in respect to the parental species. The fertility of achenes in 46 plants of the F_2 generation was:

40 to 60 per cent in 10 plants
60 to 80 ,, ,, in 26 plants
80 to 100 ,, ,, in 10 plants.

The highest recorded fertility was 92.3 per cent. The present results indicate that earlier statements defining the hybrid as fully fertile are not correct.

16. *G. coccineum* × *rivale*

The progeny of this hybrid was described in detail on an earlier occasion (W. Gajewski 1952). Consequently, it will only be reminded here that in F_1 the hybrid had almost normal seed fertility and only pollen fertility was reduced (66.6 per cent). The plants of the F_2 generation and of backcrosses showed fertility nearly at the normal level. The variation of most characters distinguishing the parental species was in F_2 and in the backcrosses more or less continuous. More simple relations were displayed only in the segregation of such traits as the presence of anthocyanin in stems and flowers, and the colour and emargination at the top of petals.

To supplement earlier reports on the experiments with the hybrid *G. rivale* × *coccineum* it must be noted here that in 1950 plants from the backcross generations B_1 were again pollinated with pollen of the parental species. The B_2 generations obtained in this manner were ((*G. coccineum* × *rivale*) × *coccineum*) × *coccineum* and ((*G. coccineum* × *rivale*) × *rivale*) × *rivale*. These plants flowered in 1952. All the individuals in both generations were fully fertile and almost indistinguishable from the pure species. In order to obtain the B_2 generations the plants most resembling by their appearance the pure species were chosen for pollination in the B_1 generations.

The B_2 generation with *G. rivale* was composed of 47 plants and displayed all the traits characteristic for *G. rivale*. Slight segregation occurred only in the length of the gynophore, the depth of the emargination at the tip of petals and the length of the claw. The other B_2 generation with *G. coccineum* was composed of 26 plants. Here too all the more impoartant traits were within the limits of variation characteristic for *G. coccineum* and only in spring the shape of basal leaves with the terminal leaflet deeply incised revealed the influence of *G. rivale* on some plants in this generation. In the two generations both pollen and seed fertility were at an entirely normal level.

Progenies were also obtained from the other highly fertile hybrids.

17. *G. rivale* × *silvaticum*

Both parental species differ greatly by numerous characters segregating in F_2 along more or less complex patterns. The fertility of the F_1 hybrids was 74.6 and 60.3 per cent for pollen and seed respectively. The F_2 generation consisted of 102 plants. The segregation of the shape of basal and cauline leaves was very marked. In F_2 6 plants had leaves very closely related to the leaves of *G. rivale*, none of the plants had leaves as in *G. silvaticum* while all the other plants had leaves of various intermediate shapes. The amount of anthocyanin in the stems and flowers was high in 24 plants and much lower in 57 plants, 21 plants were almost entirely deprived of this pigment. Much variation occurred in the degree of the drooping of the floral peduncles so that the transition from plants with drooping peduncles to plants with quite straight floral peduncles was almost continuous. In the F_2 population the following theree groups were distinguished only approximately: 22 plants with strongly drooping peduncles, 55 plants with less drooping peduncles and 25 plants with straight or almost straight peduncles. In *G. silvaticum* the flowers are expanded with calyx and petals opened out horizontally, whereas, in *G. rivale* the calyx and corolla are erect so that the flower is campanulate. In F_2 these flower forms were strongly segregated into numerous intermediate forms ranging from the expanded to the campanulate, closed flowers. When disregarding minor differences in the erect position of petals and sepals the F_2 plants could be grouped into the following categories:

flowers expanded with calyx and corolla horizontal . . .	28 plants
flowers with horizontal calyx and erect corolla	37 plants
flowers with calyx and corolla erect	37 plants.

In 76 plants the petals were yellow and in 26 creamy. The tint and the intensity of both the yellow and creamy colours varied. Moreover, in some plants intense red pigmentation of the petals was caused by anthocyanin which in some cases especially at the later stages of vegetation, entirely concealed the true colour of the petals. The shape and size of petals varied greatly:

length of petals in mm	7	8	9	10	11	12	13	14	15
number of plants	2	10	27	23	20	12	6	2	

width of petals in mm	7	8	9	10	11	12	13	14	15
number of plants	4	12	27	22	18	6	7	6	

As can be seen in F_2 the size of petals exceeded transgressively the size of petals in the parental species. The plants differed also by the shape of petals and in the whole F_2 population no two plants had petals of exactly the same shape. In *G. silvaticum* the petals are cordately incised at the tip and rounded at the base, whereas, in *G. rivale* the petals are emarginate at the tip and with a long claw at the base. In F_1 plants the tip of the petals was the same as in *G. silvaticum* and the base narrowed cuneately. In F_2 12 plants had petals with a claw 4 to 5 mm long approximately as in *G. rivale,* 73 plants had petals with a small claw 0.5 to 3.5 mm long and in 17 plants there was no claw and the petal base was cuneate or rounded as in *G. silvaticum*. The emargination at the tip of petals as in *G. rivale* appeared in 28 plants and in the other 74 plants the petals were rounded or cordate at the tip. Similar conditions prevailed in respect to the shape and size of sepals and epicalyx segments which varied greatly. The length of sepals similarly as the size of petals varied transgressively in respect to the parental species:

length of sepals in mm	5	6	7	8	9	10	11	12	13	14	15	16
number of plants	2	8	17	27	16	12	8	6	3	2	1	

Very remarkable was the manner in which the length of the gynophore from the two parental species was inherited in F_2. In *G. rivale* the gynophore is 8 to 10 mm long and in G. *silvaticum* it is 4 to 6 mm long. In the F_1 hybrids the gynophore length ranged from 8 to 11 mm and was approximately the same as in G. *rivale*. In F_2 the majority of plants had a gynophore 3 to 5 mm long which was less than in G. *silvaticum* and F_1 plants while only in several of the F_2 plants the length of the gynophore corresponded to G. *rivale* and F_1:

length of gynophore in mm	2	3	4	5	6	7	8	9	10	11	12
number of plants	5	30	25	19	9	6	1	5	1	1	

Both parental species differ greatly by the length of the receptacle and the number of achenes inserted on it. In G. *rivale* the receptacle is 6 to 7 mm long and there are 150 to 200 achenes on it. The receptacle in G. *silvaticum* is 3 to 4 mm long and the number of achenes is 20 to 30. In F_2 these traits were as follows:

length of receptacle in mm	1	2	3	4	5	6	7
number of plants	2	24	43	28	3	2	

number of achenes	10	20	30	40	50	60	70	80	90	100	110
number of plants	1	2	8	16	20	25	18	8	3	1	

As is apparent the majority of the F_2 plants had 40 to 70 achenes which corresponded more or less to the number of achenes on the receptacle in F_1 plants. Very few plants had the number of achenes within the limits characteristic for G. *silvaticum* and none had as numerous achenes as G. *rivale*.

The length of the floral stems and the number of flowers on a stem were also strongly segregating:

length of stems in cm.	20	30	40	50	60	70	80	90	100
number of plants	4	18	33	19	16	8	3	1	

number of flowers on one stem	1	3	5	7
number of plants	69	24	9	

Pollen and seed fertility in F_2 was as follows:

per cent of good pollen grains	20	40	60	80	100
number of plants	1	3	16	22	

per cent of sound achenes	20	40	60	80	100
number of plants	2	40	43	17	

In F_2 — similarly as in F_1 — pollen fertility of the plants was higher than the fertility of achenes. In numerous F_2 plants seed fertility was clearly greater than in the F_1 hybrids.

G. silvaticum differs from *G. rivale* not only by the smaller number of achenes on the receptacle, but also by their much greater size. In *G. silvaticum* the length of achenes is 8 to 9 mm while in *G. rivale* it is 3 to 4 mm. In F_1 the achenes were 5 to 7 mm long and in F_2 the following measurements were recorded:

length of achenes in mm	3		4		5		6		7		8
number of plants		16		57		22		6		1	

The above results indicate that in F_2 the size of achenes in most plants was as in *G. rivale* or the F_1 hybrids and none of the plants had achenes of the size as in *G. silvaticum.* The length of the rostrum was segregating in a similar manner as the length of the achenes.

18. *G. molle × rivale*

The F_1 hybrids showed high pollen and seed fertility of more than 60 per cent. The F_2 generation consisted of 82 plants in which all the characters distinguishing the parental species were strongly segregating.

The basal and cauline leaves were of greatly varied shapes and every plant had leaves which differed from those of other plants in shape, size and the nature of serration and pubescence. The length of the floral stems was as follows:

length of stems in cm	40		50		60		70		80		90
number of plants		13		35		24		9		1	

Plants with poorly branched 2—3-floral stems prevailed. The number of such plants was 44, there were 31 plants with 3 to 5 flowers and 7 with 5 to 9 flowers. The drooping of the floral peduncles varied too: in 38 plants they drooped strongly, in 29 they were less drooping and in 15 plants the floral peduncles were straight, but the differences in this respect between the particular plants were not great. Anthocyanin was abundant in stems and flowers of 20 plants and less so in 43 plants, whereas, 19 plants were deprived of the pigment. In *G. molle* the calyx is horizontally expanded during flowering and later it is slightly reflexed while in *G. rivale* the calyx is erect. In F_1 the position of the calyx was horizontal and in F_2 the position of the calyx was as follows:

9 plants had sepals and petals horizontally expanded
48 plants had sepals and petals in different erect positions
25 plants had sepals expanded horizontally and petals erect.

In 28 plants the petals were creamy, sometimes nearly white, and in 54 plants they were of various yellow tints. The shape of the petals was very variable. 21 plants had petals emarginated at tip as in G. *rivale*, and in 61 plants the tip of the petals was rounded, 12 plants had petals with a claw 4 to 6 mm long, 51 plants had petals with a claw 1 to 4 mm long and in 19 plants the petals were without claw but with a rounded or cuneate base. The size of the petals was as follows:

length of petals in mm	7	8	9	10	11	12	13
number of plants	2	20	28	18	11	3	

width of petals in mm	5	6	7	8	9	10	11	12
number of plants	1	3	10	36	20	11	1	

The variation in the size of petals in F_2 was of a transgressive nature. Considerable variability referred also to the length of sepals which ranged from 4.5 to 10 mm. As the calyx was not measured in all the plants the series of variation is not presented. The length of the gynophore of the F_2 plants was as follows:

length of gynophore in mm	0	2	4	6	8
number of plants	23	42	13	4	

As can be seen the most numerous were the plants with a gynophore 2 to 4 mm long as in F_1. Many plants had a very short gynophore (0—2 mm) as in G. *molle* and in none the gynophore was 8 to 10 mm long as in G. *rivale*. The fertility in F_2 was strongly segregating:

per cent of good pollen grains	20	40	60	80	100
number of plants	5	11	27	38	

per cent of sound achenes	20	40	60	80	100
number of plants	14	37	25	6	

Similarly as in the other hybrids pollen fertility of F_2 plants was at a higher level than the fertility of achenes. The shape, the pubescence and the size of achenes, the rostrum and the stigmatic part showed great variation in F_2. This is illustrated on the example of the length of rostrum and stigmatic part of the styles

length of rostrum in mm	3	4	5	6	7	8	9	10
number of plants	1	12	16	26	22	4	1	

length of stigmatic part in mm	1		2		3		4		5		6
number of plants		1		32		36		12		1	

These measurements show that in F_2 the plants with a rostrum of the same length as in F_1 or shorter, as in *G. molle*, were the more common. On the other hand, the length of the stigmatic part in this generation was similar to F_1 or approached *G. rivale*.

19. *G. urbanum* × *coccineum*

The F_2 generation of this hybrid consisted of 118 individuals. Similarly as in the case of the other fertile hybrids already described the majority of characters were segregating. This referred very distinctly to the shape of the basal and cauline leaves. In some F_2 plants the leaves approached very closely to the shape of leaves in the parental species. In *G. coccineum* the pubescence is dense, silky and with abundant glandular hairs whereas in *G. urbanum* the pubescence is not so dense, the hairs are straight and longer, and there are no glandular hairs. In almost every F_2 plant the kind of pubescence was somewhat different. In 104 plants there were no glandular hairs at all and in 14 plants the scarce glandular hairs were present only on the peduncles and calyx. The length of the floral stems was as follows:

20 to 40 cm	38 plants
40 to 60 cm	59 plants
60 to 80 cm	11 plant.

The number of flowers on a stem ranged from 2 to 9. The petals were yellow in 92 plants, and red in 26. The yellow colour in the particular plants was of various tints including bright yellow, orange-yellow and salmon. Similarly as in both parental species all the F_2 plants had flowers with reflexed calyx, horizontally expanded petals and with straight peduncles. The shape of the petals ranged from approximately round to ovoid. The following measurements of the petal size were made:

length of petals in mm	5		6		7		8		9		10		11		12		13		14
number of plants		3		14		21		21		24		15		15		3		2	

width of petals in mm	4		5		6		7		8		9		10		11		12		13		14		15		16
number of plants		2		15		12		17		21		17		23		8		1		—		1		1	

Both these series of variation are very irregular. The length of the sepals varied in a manner resembling the variability of petals ranging from 5 to 11 mm. The receptacle was long haired as in *G. urbanum* in

23 plants, it was less pubescent in 68 plants and very short haired as in *G. coccineum* in 30 plants. The length of the receptacle was:

3 mm in 12 plants　　5 mm in 50 plants
4 mm in 40 plants　　6 mm in 16 plants.

The fertility of these plants was as follows:

per cent of good pollen grains	0		20		40		60		80		100
number of plants		7		5		31		43		32	

per cent of sound achenes	0		20		40		60		80		100
number of plants		6		24		43		35		10	

Here too pollen fertility was at a higher level than seed fertility. The achenes, the rostrum and the stigmatic part differed greatly in respect to size and pubescence. This is illustrated by the length of the rostrum and the stigmatic part:

length of rostrum in mm	1		2		3		4		5		6		7
number of plants		1		11		16		10		3		1	

length of stigmatic part in mm	1		2		3		4		5
number of plants		3		12		22		5	

In this F_2 generation 3 plants resembled *G. urbanum* so exactly that they reproduced in almost all details the pure species, which indeed was most remarkable in view of the relatively small number of plants in this generation.

20. *G. coccineum* × *molle*

The F_2 generation of this hybrid was composed of 74 plants. The variability in the shape of the basal and cauline leaves was considerable and several plants reproduced fairly accurately the shape of leaves in the parental species. The indumentum in all the plants was silky and dense with numerous glandular hairs on the floral peduncles and calyx. The length of the floral stems was as follows:

20 to 30 cm 11 plants　　50 to 60 cm 13 plants
30 to 40 cm 28 plants　　60 to 70 cm 4 plants.
40 to 50 cm 18 plants

The number of flowers on the stems was in most plants 3 to 5 and more rarely 1 to 3 or 5 to 7. All the plants had straight peduncles. In 5 plants the calyx was horizontally expanded at anthesis and in 49 plants it was distinctly reflexed downwards. Later on when the flowers withered the calyx was completely appressed to the peduncle. The petals were approximately round usually cordately incised at the tip or distinctly elongated and elliptically ovoid in shape. 58 plants had yellow or orange-yellow petals and 16 plants had red petals. The size of the petals was as follows:

length of petals in mm	7		8		9		10		11		12		13		14
number of plants		2		10		18		20		16		5		3	

width of petals in mm	7		8		9		10		11		12		13		14
number of plants		4		8		20		23		13		4		2	

None of the plants had a gynophore, the receptacle in all plants was sparsely haired and its length was:

1 to 3 mm	26 plants
3 to 5 mm	35 plants
5 to 7 mm	13 plants.

Fertility of the plants in F_2 was as follows:

per cent of good pollen grains	20		40		60		80		100
number of plants		2		11		27		10	

per cent of sound achenes	20		40		60		80		100
number of plants		10		18		31		15	

The achenes differed considerably in the length of the rostrum and of the stigmatic part as well as in the pubescence and anthocyanin pigmentation. In F_2 plants the following recordings were made of the length of rostrum and stigmatic part:

length of rostrum in mm	1		2		3		4		5		6
number of plants		6		33		19		12		4	

length of stigmatic part in mm	1		2		3		4		5
number of plants		3		21		39		11	

21. *G. hispidum* × *rivale*

In F_1 the hybrid had 83.1 per cent of good pollen grains and 60.4 per cent of sound achenes and was regarded consequently as highly fertile.

The F_2 generation consisted of 26 plants exhibiting a segregation pattern very similar to that in F_2 of the hybrid *G. molle* × *rivale* already described. The majority of the plants in this generation perished after infection with mildew and as the number of individuals was thus very small the biometric data have no significance and will not be reported. The character of the segregation of the traits distinguishing the parental species will be merely described. Segregation was very distinct in the following points:

1. the time of flowering stretched out in this small population through nearly two weeks,

2. the height and branching of stems which were 33 to 77 cm tall and had 1—3 to 7—9 flowers,

3. the shape of basal and cauline leaves was already closely related in some F_2 plants to the leaves of the parental species,

4. the floral peduncles ranged from quite straight as in *G. hispidum* in 6 plants to variously drooping in the rest,

5. the positions of sepals in the calyx and petals in the corolla were very different. Usually the sepals were more or less horizontally expanded and the petals distinctly erect, but there were also plants with both sepals and petals erect as in *G. rivale* or with sepals recurved downwards and petals horizontal as in *G. hispidum,*

7. the colour of petals was creamy in 4 plants and yellow of different tints in the rest.

8. the shape of petals was greatly different varying from petals without claw through forms with a claw of different length to petals with a long claw at the base as in *G. rivale*. The petals were either rounded at the tip as in *G. hispidum* (22 plants) or had the tip emarginated as in *G. rivale* (4 plants),

9. the size of petals varied greatly ranging from 6.5 mm long and 4.5 m wide to 9.5 mm long and 8 mm wide,

10. the gynophore was almost entirely absent in 6 plants (only 0.5 to 1 mm long) and 2 to 7 mm long in the other plants. The length and character of the pubescence on the receptacle were also very different in the particular F_2 plants,

11. the number of achenes on the receptacle ranged from 96 to 171, the length of achenes ranged from 3.5 to 5 mm, the length of rostrum varied from 6 to 10 mm and the length of the stigmatic part differed

from 2.5 to 4 mm. The nature and the degree of pubescence on the achenes and the styles differed greatly in the particular F$_2$ plants.

In F$_2$ the plants had a high fertility both in respect to pollen and seed, as is shown by the table below:

fertility in percentages	20		40		60		80		100
for pollen — number of plants		3		4		9		10	
for seed — number of plants		7		9		7		3	

As is apparent, even in a so small F$_2$ generation some plants had pollen fertility at a nearly normal level distinctly higher than in F$_1$ hybrids.

22. *G. molle* × *silvaticum*

Pollen and seed fertility in F$_1$ of this hybrid was 50 and 33.9 per cent respectively. In F$_2$ there were 40 plants exhibiting distinct segregation primely in the shape of basal and cauline leaves which varied continuously from an ovoidly elongated terminal leaflet as in *G. silvaticum* to an ovoidly round terminal leaflet as in *G. molle*. Quite numerous plants had terminal leaflets shaped very similarly or even almost exactly as one of the parental species. The length of the floral stems varied between 15 and 75 cm and the majority of plants had stems with 1 to 3 flowers similarly as both parental species.

In *G. silvaticum* sepals and petals are horizontally expanded at anthesis while in *G. molle* the sepals are recurved. In F$_1$ the calyx was horizontal and out of the 40 F$_2$ plants only 4 had a recurved calyx. Similarly as both parental species the F$_2$ plants all had yellow petals. The yellow colour was of various tints from pale yellow as in *G. molle* to bright yellow as in *G. silvaticum*.

The dimensions of the petals were not uniform as is seen from the following data:

size of petals in F$_2$ in mm	8		9		10		11		12		13		14
length — number of plants		1		7		12		15		3		2	
width — number of plants		1		3		13		19		2		2	

The length of the gynophore, which in *G. molle* is not more than 1 mm long, in *G. silvaticum* 4 to 6 mm long and in F$_1$ 4 to 5 mm long, also varied greatly in F$_2$ as is shown by the following recordings:

length of gynophore in mm	1		2		3		4		5		6		7		8		9
number of plants		9		8		5		12		5		—		—		1	

It is apparent that the most numerous were the plants with a very short gynophore as in *G. molle* and those in which the length of the gynophore corresponded to the F_1 hybrids. The length of the receptacle varied within broad limits from 2.5 to 7 mm, i.e. within the limits of differences between the two parental species. The length of the receptacle was strictly correlated with the number of achenes inserted on it. In *G. silvaticum* the receptacle is short and the number of achenes is between 20 and 30, whereas, on the long receptacle of *G. molle* there are 170 to 200 achenes. The receptacle in the F_1 hybrid was 4 to 5 mm long and the number of achenes was here 60 to 70. The number of achenes in F_2 was as follows:

number of achenes on receptacle	20	50	70	90	110	130	150	170
number of plants	2	12	14	8	1	2	1	

As is seen in F_2 the majority of plants had a similar number of achenes inserted on the receptacle as the plants in F_1 and only very few plants approached in this respect either of the two parental species.

The achenes in *G. silvaticum* are few but much bigger (8 to 9 mm long) than in *G. molle* (5 to 6 mm long). In F_2 most plants had achenes 5 to 7 mm long similarly as in *G. molle* and F_1, and not one plant had achenes approaching in size the achenes of *G. silvaticum*. Similar variations in F_2 were also apparent in the size of the rostrum and of the stigmatic part of the pistil.

Pollen and seed fertility in the F_2 generation were as follows:

percentage	10	20	30	40	50	60	70	80	90
pollen fertility — number of plants	1	1	2	4	5	14	7	6	
seed fertility — number of plants		1	4	8	16	7	2	2	

It is evident that the fertility of the plants was strongly segregating and transgressed on both sides the fertility of F_1 plants.

23. *G. silvaticum* × *coccineum*

Pollen and seed fertility in F_1 of this hybrid was 65.1 and 50.3 per cent respectively. Because of the strong invasion by fungi in 1953 the F_2 generation of this hybrid consisted only of 25 plants which flowered and fruited normally. The small number of plants made impossible a more detailed analysis of the F_2 progeny. The few plants which survived displayed a great variety of combinations in the characters of the two parental species, similarly as was the case in the hybrids discussed previously. All the traits distinguishing the parental species segregated, i.e. the shape of basal and cauline leaves, the length and branching of stems, and the position of the sepals. Out of the 25 plants 15 had orange-yellow petals, 6 had yellow petals and 4 had red petals. The size of petals also differed greatly, varying from 10 to 20 mm in length and 8 to 19 mm in width. In 18 plants there was no gynophore or it was very short (0.5 to 1 mm long) and the remaining plants had a gynophore 2 to 4 mm long. The number of achenes on the receptacle varied from 29 as in *G. silvaticum* to 80 approximately as in the F_1 plants, and none of the plants had 150 to 180 achenes as in *G. coccineum*. The size of the achenes, of the rostrum and of the stigmatic part was also different in almost every plant.

Pollen fertility in the 15 plants examined in this respect varied from 39.1 to 87.2 per cent and seed fertility ranged from 25.6 to 63.8 per cent.

In spite of the absolute insufficiency in the number of the F_2 individuals the pattern of variations as outlined above indicates that in F_2 of this hybrid the segregation of most characters distinguishing the two parental species was continuous and the great majority of the F_2 plants represented forms of normal viability and relatively high fertility.

IX. NATURAL HYBRIDIZATION IN THE GENUS *GEUM*

The not very clearly defined intersterility barriers make possible natural crosses between *Geum* species, and indeed such crosses were observed on numerous occasions. There are extensive geographical areas where two or more *Geum* species grow together and on those territories interspecific hybrids are found. In the early days when the taxonomic relations in the genus *Geum* were only beginning to be understood the hybrids were not always correctly defined and often were mistaken for separate species. For instance Scheutz in his monograph of the genus *Geum* published in 1870 considered many hybrids as distinct species, e.g. *G. intermedium* Ehrh., *G. rubellum* C. A. Mey., *G. brachypetalum* Ser. were only hybrids of *G. urbanum* with *G. rivale* and *G. inclinatum* was a hybrid of *G. montanum* with *G. rivale*. However, owing to the work of Gärtner (1850), and later of Focke (1881), Kerner (1867) and others the hybrid nature of numerous such "species" was determined either by experimental crossing and the consequent reproduction of the natural hybrids or by detailed morphological analysis of the hybrids and their supposed parental species. In the contemporary systematic literature of this group of plants the hybrids are distinguished from the species and as will be seen in this chapter the list of all natural hybrids is rather long.

The present state of knowledge on the occurrence of natural hybrids in the genus *Geum* must be considered as entirely preliminary and in no way sufficient to define the extent of this phenomenon in nature. The available informations in this respect are few and rather fragmentary being derived from accidental discoveries of natural hybrids. No deliberate researches aimed at investigating quantitatively the occurrence of hybrids between *Geum* species in nature have been attempted hitherto. The researches initiated in recent years by Anderson on hybridization between species in natural conditions and on the so called introgressive effect indicate that in some genera these phenomena are far more common than has been assumed so far and that for their detection special methods of gathering and describing the material from the natural habitats must be applied. The new techniques if applied to investigations on populations of *Geum* species growing in some one territory would quite certainly reveal the effect of natural hybridization on a much wider scale than is apparent from the present accidental observations. Some *Geum* species, as for instance *G. urbanum, aleppicum, canadense* and *macrophyllum*, are frequently distributed over areas with an unnatural vegetation, developed as a result of human activity which probably extended greatly the distribution of these species. In the new territories they occupy the species come in contact with other *Geum* species and the possibilities for crossing are consequently greatly increased. On the territories with altered ecological conditions the hybrids may easily find a suitable environment intermediate between the requirements of the parental species and thus obtain favourable developmental conditions. When the great facility with which hybrids between *Geum* species are formed and the high hybrid fertility reported in the earlier part of this work are considered it seems that further investigations of natural hybrids in the genus *Geum* would be very instructive.

There now follows a list of natural *Geum* hybrids which has been assembled on the basis of examined herbarium specimens and reports in the taxonomic and floristic literature. The following hybrids have been so far distinguished:

1. *G. canescens* Greene × *G. ciliatum* Pursh. This is the only interspecific hybrid known in the subgenus *Erythrocoma*. Greene described it as a species, *Erythrocoma australis*, but Rydberg recognized its hybrid nature.

In view of the high morphological conformity between the species in the subgenus *Erythrocoma* it seems very likely that on the territories of North America more hybrids in this group will be revealed by further investigations. In 1955 I pollinated *G. triflorum* with pollen of *G. cilitatum* and the resultant setting of seeds was at a high level, though at the time of writing no further results have been obtained yet.*

In the subgenus *Acomastylis* only one interspecific hybrid is known:

2. *G. calthifolium* Sm. × *G. Rossii* Greene. The hybrid was described as the separate species *Sieversia macrantha* Kearney and it was by this name that it was defined in Bolle's monograph. In the herbariums at Lund, Göteborg and Stockholm there are numerous specimens of this hybrid gathered by Professor E. Hultén from the following habitats: on the Aleutian Isls. — Unalaska, Akutan, Atka, Kiska; the Nikolski Isl. — Umuale; Unimak Isl. — False Pass leg. Eyerdam. Morphologically these specimens are intermediate between the parent species, they have entirely sterile pollen and I did not find one sound achene on any of them.

G. calthifolium is a hexaploid with $2n = 42$ and *G. Rossii* is a decaploid with $2n = 70$ and the hybrids are completely sterile, as might have been expected. On the Aleutian Islands as well as in Alaska and Kamschatka both parental species grow side by side and thus the possibility of crosses between them arises. The other species of this subgenus seem to be more isolated geographically and ecologically and hybrids between them are not known hitherto.

Within the subgenera *Sieversia, Oncostylus, Orthurus, Woronowia* and *Stylipus* and between those subgenera no natural crosses have been so far recognized. Neither within the genera *Waldsteinia* and *Coluria* and between these genera and the genus *Geum* have hybrids been found.

On the other hand, natural hybrids are very common within the subgenera *Oreogeum* and *Eugeum* and between the two subgenera. In subgenus *Oreogeum* the following hybrids are known:

3. *G. montanum* L. × *G. reptans* L. The hybrid was reported from the Alps under the names of *G. rhaeticum* Bruegg and *G. Kolbianum* Obrist et Stein. I myself have seen the hybrid on the following numerous natural habitats in the Tatra Mountains: Pańszczyca valley, on screes at the foot of Mięguszowieckie Mt. near Morskie Oko, on screes over the Czarny Staw lake near Morskie Oko, on the slopes of the Miedziany Mt. above Dolina Pięciu Stawów valley, and near Krzyżne pass. In the Tatra Mts. the hybrid usually grows on screes together with both

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*** Note during correction: The F_1 hybrids between these two species are vigorous and will flower next year.**

parental species and is often quite numerous. The hybrids transported from the mountains and grown in pots in Warsaw flowered abundantly but were completely sterile. The plants were exactly like the F_1 hybrids obtained by artificial pollination of the parental species (W. Gajewski 1952). The hybrid is a pentaploid with $2n = 35$ and chromosome conjugation in meiosis of the $14_{II} + 7_{I}$ type. When examining the habitat in the Tatra Mountains on the slopes of the Miedziany Mt. where the F_1 hybrids were numerous I noticed many plants which had leaves shaped intermediately between the F_1 plants and pure *G. montanum.* The plants looked as if they were backcrosses with *G. montanum.* However, they were not investigated more fully and the problem was left open. I obtained plants similar morphologically out of *G. rhaeticum* seeds supplied by the botanical garden in Edinburgh. These plants were partially fertile (fertility of achenes was about 42 per cent) with a chromosome number of $2n = 40$ which means that they might be backcrosses between the F_1 hybrid and *G. montanum.* This fact indicates that under some conditions it is possible for backcrosses to appear in nature.

In herbariums I saw only specimens corresponding to the typical appearance of F_1 plants originating from the following natural habitats: the Alps, Wallis Riffelberg, 2570 m, leg. S. Briger (Stockholm); Engadin, one plant without any further specification (Lund); and Flora Helvetica: Berner Oberland, Rolkihorn, leg. I. Peyron (Stockholm sub *G. reptans*). In the literature the hybrid is reported from the Alps where, according to Fiori Nuova Flora Analitica Italiana, it grows in "Alto Adige, nell gruppo dell' Ortler, M. Rosa".

4. *G. bulgaricum* Panc. × *G. reptans* L. (*G. Borisii* Kellerer). I have seen no herbarium specimens of this hybrid reported from the Rila Mountains in Bulgaria in any of the herbariums which I have examined. However, in his monograph Bolle states that he has seen herbarium specimens of the hybrid.

The third possible hybrid in the subgenus *Oreogeum*, i.e. the hybrid between *G. montanum* and *G. bulgaricum*, has not been reported hitherto.

The hybrids between species of the subgenera *Oreogeum* and *Eugeum* observed in nature are as follows:

5. *G. rivale* × *G. montanum* L. The latter of these species grows in European mountains within very broad altitudinal limits. For instance in the Tatra Mountains its limits lie between about 1000 and 2500 m. On the other hand, the distribution of *G. rivale* reaches in the mountains to considerable elevations, e.g. in the Tatra Mountains to about 1900 m. There is, therefore, a wide belt where the two species can contact and, indeed, they often meet and cross together. The hybrids of these two

species are konwn from numerous habitats in the Alps, the Plateau Central, the Sudeten Mts., the Carpathian Mts. and in the mountains of the Balkan Peninsula. In the Tatra Mts. I observed several specimens of the hybrid in Rozpadlina valley (this habitat was pointed out to me by Professor B. Pawłowski) and on Hala Pyszna in the Dolina Kościeliska. I saw more numerous specimens of the hybrid on Babia Góra Mt. where the two parental species often grow together in the *Pinus mughus* region and from where 7 hybrid plants were transplanted to experimental garden in Warsaw. Cytological examinations of these plants revealed that all had the chromosome number of $2n = 35$. Very probably the plants were F_1 hybrids. In respect to the somatic chromosome number, the course of meiotic divisions in the PMCs (14 bivalents and 7 univalents), morphological characters and fertility of these hybrids corresponded very well to the F_1 hybrids obtained experimentally. Pollen fertility in various preparations from these plants ranged from 39.4 to 50 per cent and the fertility of the achenes was much lower varying in the 7 plants from 3.5 to 14.4 per cent. In some plants there were numerous flowers which did not set good seeds at all.

My observations on natural habitats and of herbarium specimens seem to indicate that in certain conditions introgression may occur between the two species in nature. In the Rozpadlina valley in the Tatra Mts. I found alongside of the F_1 hybrids individuals of *G. rivale* which had leaves with a completely round terminal leaflet, big petals, big sepals and a short gynophore. These plants were normally fertile with $2n = 42$ and normal meiosis. They undoubtedly belonged to *G. rivale* but resembled some plants of the third back-cross generation between the hybrid *G. montanum* × *rivale* and *G. rivale* obtained experimentally in my cultures. Kerner who described the hybrid in detail on the basis of specimens gathered in the Tirol and other parts of the Alps reports its two forms. One of these forms more related to *G. rivale (suprarivale* × *montanum)* corresponds to *G. tirolense* Kerner and the other more approaching *G. montanum (subrivale* × *montanum)* corresponds to *G. inclinatum* Schleicher. When herbarium specimens of these hybrids are compared with the hybrids obtained experimentally it is seen that *G. inclinatum* probably corresponds to the F_1 hybrid and *G. tirolense* may be a backcross with *G. rivale*.

The hybrids that I examined in herbariums were gathered on the following habitats (the original wording of the specifications on the herbarium sheets is observed):

1. Puy de Dôme, Mont Dore, massif de Sancy, alt. 1700—1750, leg. Ch. Oranon (Lund)
2. Mont Seüse, Hautes Alpes, leg. Girod (Göteborg)

3. Auvergne: Pentes sud-est du Plomb du Cantal, 1100 m. (Stockholm)
4. Alpes de Bix, Mont Dovonar, leg. Haussknecht (Wrocław)
5. Bouvanat sur Bix (Stockholm)
6. Tirol Centr.: Lesens in valle Selaria, 5000, leg. Kerner (Kraków)
7. Tirol Centr., In monte Patscherkofel ad Oenipontem, leg. Kerner (Uppsala)
8. Tirolia Centr. In valle Selaria in ditione Oenipontana, 5500, leg. Kerner (Lund)
9. Flora Austriae inferioris, Heukuppe der Raxalpe im Krumholz, leg. Rechinger (Lund)
10. Schneeberg am Rand d. Budenwiese, leg. Rechinger (Lund)
11. Riesengebirge, Kl. Teich, leg. Pax (Wrocław)
12. Flora sudetica, Koppenbach, leg. Ticinus (Wrocław)
13. Mühlbachgebirgen, Gebüsche und Matten an der Hohen Rinne, leg. Pax (Wrocław)
14. Flora exicc. Rep. Bohem., Slovenica n. 513, Liptovske hole, mt. Banikow, alt. 1500—1600, leg. Suza (Uppsala, Kraków)
15. Herb. Uechtritz. Am Bache um N. Fluss der Pyszna im oberen Thal von Kościelisko, ca. 1400 (Wrocław)
16. Weisser See (Tatra), leg. Zheuser (Wrocław)
17. Flora der Tatra. Hintere Kupferschichte gegen den Kopapass, leg. Ticinus (Wrocław)
18. Dittmansdorf prope Waldenburg, in Silesia media, 425 m., leg. Delsmann (Göteborg)
19. Serbien, Ulanica Gb., leg. Ilic (Göteborg).

Very numerous habitats of the hybrid are mentioned in the floristic literature but it seems pointless to enumerate them all. It is quite certain, however, that in all European mountain massifs where the two parental species grow together hybrids between them were also found.

6. *G. montanum* L. × *G. coccineum* Sibth. et Sm. The two species appear together in the mountains of the Balkan Peninsula, especially in Thracia, Macedonia, Bulgaria nad Serbia. Quite often the two species grow side by side on the mountain meadows. The hybrids between them have been reported from Bulgaria and Macedonia (Golešnica-pl.). In the Botanical Museum at Lund I saw a herbarium specimen gathered by Ilic in the neighbourhood of the town of Nisch in Serbia which probably corresponded to that hybrid. There are no available data on the frequency with which this hybrid occurs in the Balkan mountains.

The most common interspecific hybrids are those between the species from the subgenus *Eugeum*. The following are known:

7. *G. rivale* L. × *G. urbanum* L. (*G. intermedium* Willd., *G. rubrifolium* Lej., *G. rubellum* C. A. Mey and many others). The hybrid is very common in Europe and Asia from the Pyrenees to Altai in western Siberia and Tian-Shan in central Asia. The hybrid usually appears sporadically in relatively small numbers among the parental species. The observations which I made in Poland and especially those made in the National Park of the Białowieża Forest lead to the conclusion that the hybrids usually appear on territories with a disturbed vegetation, whereas, in natural associations there are pure species only. The parental species are isolated from each other by different ecological requirements and a partly different time of flowering. In some areas the hybrid is quite common and for example from Marsden-Jones's (1930) report it appears that in some localities in England the hybrid with its backcrosses and segregation products occurs more frequently than the pure species. Local introgression between the two species has been demonstrated beyond doubt. The specimens of the hybrid are very numerous in all herbariums and I have seen more than 200, so it seems pointless to enumerate them all here. A review of the herbarium specimens seems to indicate that in nature, besides the F_1 hybrids, also the products of backcrosses and segregation are to be found.

8. *G. aleppicum* Jacq. × *G. urbanum* L. The hybrid has been described under such names as *G. teszlense* Simonk., *G. spurium* Fisch., *Geum Kerneri* Błocki (in herb.). It has been reported from several localities lying along the eastern boundary of *G. aleppicum* in Europe, e.g. East Prussia, Lithuania, Białowieża Forest, Podole and Transylvania. In Poland I saw the hybrid in Białowieża Forest. During three years of observations on excursions to the National Park in Białowieża Forest I found only one individual and this one corresponded well to the F_1 hybrids obtained experimentally. The plant when cultivated in the experimental garden in Warsaw proved to be completely sterile. In herbariums there are numerous specimens of the hybrid gathered by Błocki from Podole where probably it is more common than in the Białowieża Forest. The list of herbarium specimens which I examined is as follows:

1. Dubienko bei Monasterzyska, unter den Eltern, leg. Błocki (Lund, Kraków, Göteborg)
2. Cygany leg. Błocki (Uppsala, Kraków, Lund, Göteborg)
3. Herb. Mus. Nat. Vindebon. Na Jarzynie w lesie janowskim k/Lwowa, leg. Wołoszczak (Stockholm)

4. Flora Poloniae exicc. Nr. 820, Niańków, distr. Nowogródek, leg. Dybowski (Kraków)
5. Herb. Europ. dr C. Baenitz, Königsberg in Pr. Caymen, in fruticetis rara, leg. Weiss (Stockholm).

Moreover, in Swedish herbariums and in those at Copenhagen there are specimens of the hybrid gathered in botanical gardens. All the plants of this hybrid are either completely or highly sterile with occasionally single sound achenes. Most of the plants are probably F_1 hybrids. The hybrid is also reported from Transylvania (Teszla and Büdös mountains) and from territories in European Russia (the provinces of the Volga, Don and Central Dniepr). On these last territories the hybrid is probably much more common but it is not always recognized in view of the considerable resemblance between the parent species.

The results obtained with the hybrids produced in the course of the present research indicate that in further generations fertile plants arise and frequently closely resemble one of the parental species. It thus seems that introgression in nature is not impossible. In this connection very remarkable is Bolle's statement (page 14) that in the Ukraine *G. aleppicum* closely approaches the local forms of *G. urbanum* while in China it is related with the local forms of *G. japonicum* var. *chinense* and in America with *G. macrophyllum* and *G. oregonense*. It may be that this coincidence is not only accidental but results from introgression to *G. aleppicum* of other species with which it coexists on its huge distributional area.

9. *G. aleppicum* Jacq. × *G. canadense* Jacq. The hybrid is probably rather common in the USA and Canada, though not always identified. Mention has already been made that Raynor (1952) supports R. T. Clausen's supposition that *G. virginianum* is a hybrid of *G. aleppicum* var. *strictum* with *G. canadense*. Clausen has found that in the state of New York "*G. virginianum*" always appears in company with the two presumable parental species. When transported to experimental gardens the natural hybrids correspond well with the description of *G. virginianum* and the hybrids which I obtained experimentally in my cultures.

The hybrids investigated by Raynor were partially sterile and had many disturbances in the course of meiosis. She assumes that the plants were F_1 and F_2 individuals of the cross *G. aleppicum* var. *strictum* × *canadense*. The hybrids obtained in the present experiments were almost completely sterile, but this may be caused by racial differences in the parental species used for the crosses and also by cultivation in a different climate. On the other hand, it also is possible that the plants which

Raynor investigated represented not the F_1 but F_2 and further generations with fertility already stabilized at a higher level. The plants of *G. virginianum* obtained from Professor R. T. Clausen which I grew in Warsaw were almost normally fertile and in this respect as well as in some morphological details they differed from the experimental hybrids. To elucidate the problem of the origin of *G. virginianum* more detailed investigations with special emphasis on field work are necessary. However, the fact that this species grows also in the south-eastern regions of the USA where *G. aleppicum* does not appear must be explained if Raynor's hypotheis as to its hybrid origin is to be accepted.

The numerous herbarium specimens of *G. virginianum* which I had the occasion to examine indicate that plants differing greatly in appearance and fertility level are defined by this name. Some of them are completely sterile hybrids, as for instance is the case of the specimen gathered from Ohio by A. Grey now in the herbarium at Uppsala which in 6 fruiting heads has only one sound achene. Some of the plants defined as *G. virginianum* have white petals others yellow of various shades. On the other hand, I saw herbarium specimens which seemed to be normally fertile. All this indicates that at present both sterile hybrids and fertile forms are included in *G. virginianum*, and their mutual relationship still awaits a full investigation. The fact that the two parental species and *G. virginianum* often grow on waste land, by roads and in other places with vegetation altered by human activity corroborates the supposition that in this group of species hybridization has played in the past and still does play an important part.

10. *G. rivale* L. × *G. silvaticum* Pourr. The distributions of the two species coincide only on a small area in Spain and the natural hybrid between the two species is reported by Pau under the name *G. pratense* Pau from Sierra de Javalambre, Aragon, where the hybrid appears together with both parental species at an elevation of about 2000 m.

11. *G. urbanum* L. × *G. silvaticum* Pourr. The natural hybrid between the two parental species is reported by Coste and Soulié (1911) under the name of *G. cebennense* from the eastern slopes of Montagne Noire — Cévennes Les Verrières, dép. Hérault at an elevation of 700 m. The authors describe the hybrid in detail and stress its sterility. In their opinion it should also be found in other localities of southern France. In the south of France the parental species are usually separated ecologically as *G. urbanum* usually grows there in moist, shadowed habitats whereas *G. silvaticum* favours open pastures and dry forests. However, the two species often meet together.

I did not see this hybrid in herbariums, but in the herbarium of the Botanical Garden at Lund I found one specimen defined as *G. urbanum* L. var. *mauritanicum* Pomel which was probably the hybrid *G. urbanum* × *G. silvaticum* (E. Jahandier, Plantes Marocaines 1923, no. 397, Daï el Achlef (Moyen Atlas), montagnes calcaires, boisées, 1800 m). It is possible that the hybrid also grows in other areas of the Mediterranean where the two parental species appear in common.

12. *G. pyrenaicum* Willd. × *G. rivale* L. The two species grow together in the not very elevated zones of the Pyrenées where the hybrid was found and described under the name of × *G. Thomasianum* Ser. (more like *G. rivale*). The locality was defined as "Pyrénées Orientales: environs de Mont-Louis et Finestres". It was also reported under the name × *G. Timbalianum* Rouy et Camus (more like *G. pyrenaicum*) from "Haute Garonne: prairies du sommet du Gagire (with parents)". These informations are reported by Rouy and Camus in the Flore de France, Vol. VI, pp. 156—166.

13. *G. coccineum* Sibth. et Sm. × *G. rivale* L. The two species grow in common in numerous mountain massifs of the Balkan Peninsula and Asia Minor. The natural hybrids are known to occur in Bulgaria and the Rhodope Mountains *(G. Jankae* G. Beck). It seems greatly plausible that the occurrence of the hybrid is far more frequent than is indicated by the reports now available.

14. *G. aleppicum* Jacq. × *G. rivale* L. The hybrid of these species is known so far only from eastern European territories. Graebner found it in the Białowieża Forest and according to Bolle his specimen of the hybrid was in the herbarium in Berlin. My searches for the hybrid in the Białowieża Forest were successful as in 1947 I found several individuals growing among the parental species on the side of a road in the National Park. One specimen was transplanted to Warsaw and was grown for several years. Its resemblance to the F_1 hybrids obtained experimentally was considerable but it differed from them by such traits as the greater length of the gynophore and a longer and less pubescent rostrum. The greatest difference appeared, however, in fertility. While in F_1 of the experimental hybrid pollen and seed fertility were about 15 and 10 per cent respectively, in the natural hybrid pollen and seed fertility were about 50 per cent. It is difficult to decide at present whether this difference of fertility was caused by the difference between the parental forms of the natural and experimental hybrids or by that the natural hybrid was a F_2 segregate morphologically related to F_1.

From the natural hybrid plant I obtained the next generation consisting of 40 plants which displayed segregation in respect to all characters distinguishing the parental species. In the case of most characters the nature of the segregation resembled greatly the segregation in the F_2 generation of the experimental hybrid *G. aleppicum* × *rivale* described previously. In this generation fertility was also much higher:

per cent of achene fertility	0		20		40		60		80		100
number of plants		2		6		9		16		7	

As can be seen in this case seed fertility in the majority of plants was above 60 per cent, whereas, in the F_2 generation of the experimental hybrid the fertility of most plants was below 40 per cent.

Natural hybrids between the two species were reported too from East Prussia in Kreis Labiau, Grabenwall and from several localities in the European part of the Soviet Union. It may be that the hybrid will also be found in North America where the two species have common distributions over large areas.

15. *G. macrophyllum* Willd. × *G. rivale* L. The natural hybrid of the two species was described under the name of *G. pulchrum* Fernald and reported from the state of Vermont in the USA and from the provinces of Quebec and Alberta in Canada. I did not find the hybrid in any of the herbariums to which I had access. As in the progeny of the species amphiploid plants were obtained (W. Gajewski 1952) an investigation on populations of this hybrid in nature would be of great significance.

16. *G. coccineum* Sibth. et Sm. × *G. molle* Vis. et Panc. The hybrid was found in several localities on the Balkan Peninsula, i.e. Witoša Mts. in Bulgaria and Golešnica in Macedonia, where it has been described under the name of *G. Velenovski* Borb.

17. *G. molle* Vis. et Panc. × *G. rivale* L. The hybrid under the name of *G. pseudomolle* Pant. was reported from Bulgaria from the Witoša Mts. and from Črna-Planina, Virus valley in Montenegro. In the herbarium at Lund I saw a specimen of the hybrid from the Witoša Mts. in Bulgaria, ca 2000 m, leg J. Hruby, no 1417 sub *G. molle*. I saw another specimen of the hybrid in the herbarium at Stockholm with the inscription: "Herb. Horti Bergiani. Cult. in hort. e Serbiae spont sub nom *G. molle* Panc. June 28, 1894".

18. *G. aleppicum* Jacq. × *G. oregonense* Rydb.

19. *G. aleppicum* Jacq. × *G. macrophyllum* Willd.

20. *G. macrophyllum* Willd. × *G. oregonense* Rydb.

These hybrids are described by Rydberg in North American Flora, vol. XXII, pp. 400—405. This information I repeat after Bolle, as I have no more detailed information about the hybrids.

21. *G. hispidum* Fr. × *G. urbanum* L. The hybrid is very common in the South of Sweden where the two parental species grow together. R. Sterner (1921) reports from this territory about 20 habitats and adds that at present *G. hispidum* extends its distribution in Sweden to new territories usually already occupied by *G. urbanum*. The two species frequently cross producing quite numerous partially fertile hybrids. In Sweden I saw about 30 herbarium specimens of the hybrid which usually were rather sterile.

22. *G. molle* Vis. et Panc. × *G. urbanum* L. According to Beck von Mannagetta (1895) the hybrid was found on the Balkan Peninsula, but no further details are available.

23. *G. albarraciense* Pau × *G. urbanum* L. The hybrid was described by Sennen under the names of *G. Navarroi and G. Josephii*. The herbarium specimen which I saw at Lund was defined: "Flora de Cerdagne, Omes, 1130 m, Sept. 19, 1927, leg Sennen". The specimen was sterile with 1 to 3 sound achenes per flower.

The above list of natural interspecific hybrids was assembled either from reports in floristic literature or from my own observations in nature and herbariums. Quite certainly the list does not illustrate fully either the extent or the degree of hybridization of *Geum* species in nature. Indeed, the observations reviewed here refer to facts assembled accidentally mainly by florists not specially interested in problems of interspecific hybridization in nature. My observations of *Geum* hybrids in Poland were also not very intensive but, nevertheless, they indicate that whenever two *Geum* species appear in common hybrids between them may almost always be found. Contemporary researches by Anderson and his school have shown that when special methods facilitating the detection of introgression are applied large scale interspecific crossing can be observed in very many plant genera. This is supported by such more recent investigations as of Anderson (1936, 1948) on *Tradescantia,* Camp (1942) on *Vaccinium*, Dansereau (1941) on *Cistus*, Heiser (1947, 1949) on *Helianthus*, Riley (1938) on *Iris,* Hall (1952) and Fassett (1944—45) on *Juniperus,* Muller (1952), Stebbins, Matzke and Epling (1947) and Tucker (1952) on *Quercus,* and many others. All these researches have shown that in some cases large territories may be occupied by natural hybrids morphologically related to one of the parental species and displaying sometimes only slight traces of characters from the other species. Frequently this refers to species which occupied areas with changes in vegetation caused by human activity. On such territories the barriers of the ecological nature which separated the species growing on territories with a natural vegetation have been often partially abolished and consequently the hybrid exhibiting new ecological properties frequently find there suitable conditions for mass reproduction.

Owing to the work of Anderson in this field there is a constantly increasing number of reports describing the phenomenon of introgression which consists in some sort of penetration of hereditary properties from one species to another, resulting in an increase in the range of morphological variability in the species affected and also in changes of its physiological and ecological properties. The species of the genus *Geum* here considered undoubtedly constitute a group which by the lack of intersterility barriers between numerous species and by the frequent expansions of these species to new territories would, if studied purposely in nature, disclose numerous instances of mass hybridization and introgression.

X. DISCUSSION

COMPATIBILITY OF SPECIES

The research with which this work is concerned referred, as has been shown, to a group of species belonging to one genus or several related genera. These species, in spite of their quite considerable differentiation in respect to morphological characters, degree of polyploidy and geographical distribution, have a high ability to cross-pollinate and to produce viable hybrid progenies.

The problem of the factors on which the ability or disability to produce interspecific hybrids depend constitutes at present only an accumulation of empirical and factual data for which in most instances there is no causal interpretation. For instance, why are interspecific hybrids very common in the rose family while in the *Papilionaceae* family they are relatively very rare? Sometimes even related genera from one family exhibit diametrally different abilities to form interspecific hybrids. For example in the *Ranunculaceae* family within the genera *Aquilegia*, *Delphinium or Clematis* interspecific hybrids are very common and easy to obtain even between species with different chromosome numbers, whereas, within the genus *Nigella* they are very rare. This fact I was able to observe when between 1945 and 1947 I grew 12 various species from the genus *Nigella* and attempted crosses between them in all possible interspecific combinations. The only result which I arrived at in these numerous pollinations was one completely sterile hybrid individual between *N. hispanica* and *N. sativa,* this in spite that all *Nigella* species have the same chromosome number of n = 7 and the chromosomes are morphologically very similar. These results agree with those of D. J. Reinders (1942).

In the family of *Papilionaceae* interspecific hybrids have not been obtained in the genus *Lathyrus* in spite of numerous attempts (Senn 1938), while in the genus *Phaseolus* even species belonging to very distant subgenera and sections give fertile hybrids (Grant 1952).

Within the very large family of *Compositae* numerous genera with species which are easily crossed are known, whereas, in other genera hybrids are almost not found or can be obtained only in quite exceptional cases. The best known in the former group are the genera *Hieracium* and *Cirsium* in which numerous natural hybrids have been identified, though, the genera are not very well known genetically. In the genus *Crepis* Babcock (1947) reports that on 43 interspecific crosses attempted between diploid species of one section 40 gave positive results and that on 127 crosses attempted between species of various sections viable hybrids were obtained from 77 only, but many of the hybrids had reduced vigour and/or were sterile.

The work of Clausen, Keck and Hiesey (1945) on the subtribe of *Madiinae* which includes many genera and species growing in western North America, primely in California, show that from 400 crosses involving 70 various species from 6 genera about 200 hybrids were obtained, whereas, in the other crosses either fertilization did not take place or the hybrids were inviable. Many other examples can be quoted from the *Compositae* which demonstrate the wide possibility of hybridization within various genera or even larger systematic groups. However, in that family there are genera the species of which are much less compatible and where crosses are obtained only very rarely. For instance, R. C. Thompson, T. W. Whitaker and W. F. Kosor (1941) state that they carried out 81 different interspecific crosses between 18 species of the genus *Lactuca* with n = 8, 9 and 17 and obtained seeds only in 28 cases. Most of the hybrids grown from these seeds perished at the cotyledon stage. Only 10 hybrids between very closely related species were viable and of these 6 alone were partially fertile. It is difficult to enumerate all the very numerous and extensive researches on interspecific hybrids within various groups of flowering plants. The first to attempt such investigations were Gärtner and

Focke. Their work has been continued later by many gardeners and plant breeders so that during the past 50 years numerous investigations have been carried out on a large scale throughout the world especially in respect to species with agricultural interest. For instance the researches carried out by numerous workers (Goodspeed, Clausen, Kostoff and many others) on the genus *Nicotiana* and the even more numerous researches on interspecific and intergeneric hybrids in the genera *Triticum, Aegilops, Secale, Agropyrum, Elymus* and *Haynaldia* revealed the possibility of obtaining hybrids between groups situated far apart systematically. To supplement the above considerations here are some examples from the rose family with which this work is more closely concerned. In the enormous genus *Potentilla* composed of about 200 species which is not far removed systematically from *Geum* interspecific hybrids are much more difficult to obtain than in *Geum,* though, the structure of these species is seemingly less differentiated. A. Popoff (1935) for instance carried out crosses between 15 *Potentilla* species with 2n = 14, 28, 56 and 98 and out of 200 pollinations he obtained seeds in 71 instances only. In 18 of these cases the progeny was entirely of the maternal type which points to the occurrence of apomixis and true viable hybrids were obtained in three cases only. Similar results were obtained by Araki (1932) who crossed 18 *Potentilla* species in various combinations and obtained one hybrid only. On the other hand, in the genus *Fragaria,* which in the tribe of *Potentilleae* is equally far removed systematically from *Geum* as is the genus *Potentilla,* interspecific hybrids were obtained for almost all the possible interspecific combinations regardless of differences in chromosome numbers, expression of morphological characters or geographical distribution (Schiemann, Lilienfeld and others).

Danser (1934) found on the basis of observations and experiments with the species from the genus *Rumex* that among 22 species in the section *Lapathum* crosses occurred with great facility in nature. The very vigorous hybrids were highly sterile. By sowing out seeds of "pure" species growing together in nature with other species Danser obtained numerous hybrids. He also found that only species from this section could be crossed one with the other and stated that crosses between sections were unknown. On the basis of his observations and of other reports Danser coined the new term „syngameon" for defining such groups of species between which there were no intersterility barriers (of course not in the sense of hybrid fertility). In his next report Danser (1929) referred to such a group of individuals connected by the ability of mutual crossing as "comparium".

On the basis of their own researches and the researches of many other workers Clausen, Keck and Hiesey (1939) attempted a biosystematic classification which in opposition to the approach of descriptive systematics was based not only on morphological characters and geographical distribution but also on the genetic analysis of populations appearing in nature. They assumed that the ability for hybridization together with the vigour and fertility of the hybrids could constitute a biological basis for classifying living organisms into biosystematic units of various ranks. By utilizing partially the concepts of Danser and Turesson they suggested the following biosystematic units:

1. The ecotype, that is the population or populations within a species adapted to some specific ecological niche but separated by no intersterility barriers or hybrid sterility from the other ecotypes of the same species. Because this classification is based on biological and not only morphological evidence — as in the case of descriptive systematics — the ecotype may, but not necessarily, correspond to a subspecies in the conventional approach or one species may correspond to one ecotype. Sometimes two ecotypes are described by systematists as two separate species and only by the analysis of their hybrids it can be established that in fact they should be treated as two ecotypes of one species. Ecotypes are usually separated geographically or ecologically.

2. The ecospecies differ from ecotypes by that they must not be isolated geographically but can coexist together. Every ecospecies has its own genetic system sufficiently differentiated and distinct from the genetic systems of other ecospecies to produce hybrids, if such are formed at all, with reduced fertility and/or reduced vitality, which last trait is often not manifested till the second generation. The genetic factors causing the genetic and physiological barriers preserve the distinctness of coexisting ecospecies. Most often, though not always, ecospecies correspond in rank to species in descriptive systematics.

3. The coenospecies comprises ecospecies having the ability for restricted interchange of genes in spite of partial hybrid sterility. A coenospecies frequently corresponds to a whole section, sometimes even to one genus, but may also consist of one species only.

4. The comparium comprises coenospecies capable to produce sterile interspecific hybrids. There is no possibility to obtain hybrids between two comparia. Although, among different coenospecies of one comparium the exchange of genes through crosses is no longer possible because of hybrid sterility, the formation of fertile amphiploid hybrids by the doubling of the chromosome number in the sterile interspecific hybrids is not impossible.

The principles of classification outlined above may in certain circumstances have some value for investigations concerned with the evolution of flowering plants, but they cannot always be applied in practice and are undoubtedly far less convenient than the classification adopted by the conventional systematic approach. First of all, it seems that the possibility of obtaining partially fertile hybrids between species belonging to one coenospecies proves experimentally the close phylogenetic relation between these species. Then, as a result of hybridization and amphiploidy, the formation of new species within one coenospecies and also one comparium can take place both through crosses and through changes within the population of one species. The phylogenetic connections between species of one comparium may be thought of as a net the knots of which represent the separate species. On the other hand the evolution of species belonging to various comparia can be imagined only as taking place in sudden or gradual differentiation and bifurcation which usually is represented as a "family tree". Genetic analysis of mutual connections between species belonging to two different comparia is quite impossible. Obviously, the greater the number of species within a comparium the greater are the possiblities of detecting the evolutional processes.

There remains, however, the unanswered problem of why some comparia cover a whole genus or even several genera while others may consist merely of one species. In some cases monotypic species or genera represent simply greatly reduced comparia in which in the course of a long evolutional history all related species died out and only isolated ones survived to our times. A classical instance of this course of events is presented by the genus *Ginkgo*. In the Tertiary this genus consisted of numerous species of which only one completely isolated survived to the present times. However, this is not the only cause of sexual isolation exhibited by some species of the contemporary flora. Although it is correct to assume that the ability to form interspecific hybrids undoubtedly discloses a rather close relationship, the statement cannot be reversed into one according to which the disability to form hybrids proves the lack of relationship, especially when two plant groups situated far apart in the system are being considered.

The effect of interspecific intersterility is brought about by numerous and different factors. The causes of intersterility may be diverse and may lie, for instance, in the inability of alien pollen to germinate on the stigma, the too slow or abnormal development of pollen tubes in the style tissue, the disability of the generative nuclei from the pollen tube to fertilize the egg cell or the endosperm nucleus, or finally the disability of the zygote to develop. The development of a zygote may be inhibited by its own unharmonized genetic composition, or by the unharmonized cooperation between the hybrid embryo, the endosperm tissue and the tissue of the maternal organism. By using embryological techniques it has been found that in various plant groups entirely different factors are responsible for the disability to produce interspecific hybrids. In cases when fertilization does take place the unfavourable influence of the maternal organism on the embryos can be counteracted in some cases by cultivating the embryos *in vitro*. In this manner vigorous hybrids have been obtained which would have never developed in nature. In other cases it has been found that for instance the disability of pollen to germinate or the abnormal development of pollen tubes from pollen grains of one species on the stigma and in the styles of another species may be due to an inadequate osmotic pressure in the style cells. By changing the conditions in which the plant is grown the osmotic pressure in the cells can be changed so that the pollen tubes develop normally and the hybrid is produced. However, in most cases the causes preventing the development of hybrids are far more fundamental and cannot be removed by so simple means.

Frequently very different factors may be responsible for interspecific intersterility even in closely related groups of plants, but the problem is as yet not sufficiently understood. The presence in one family or section of some genera or sections where crossing results in the formation of numerous hybrids and of other genera in which crosses give no effects may be caused by differences in the physiological mechanism of sexual isolation alone and needs not have a deeper phylogenetic significance. As is well known, various ecotypes and even biotypes of one species sometimes give different results in crosses. In one case the result may depend on the direction of the cross and in another on the environmental conditions in which the cross is carried out. The process of sexual reproduction is of the highest complexity and its selective specialization is due to the very long history of the development of a species so that it can function successfully in a wide range of internal and external factors within the population of one ecospecies only. The process has been established by selection acting towards maximum fertility, as all forms with reduced fertility are selectively negative and are rapidly eliminated. In the case of interspecific crosses the process of sexual reproduction takes place between individuals differing physiologically and not adjusted through natural selection to mutual pollination. Because of this, interspecific intersterility is very common. It would seem plausible to assume that interspecific intersterility tends rather to be intensified by the processes of selection. It is obvious that from the point of view of gamete economy the formation of natural interspecific hybrids is a "wasting" of gametes on the production of organisms vitally handicapped in respect to "pure" species. It would thus be reasonable to expect that species not isolated geographically should exhibit a higher sexual isolation than those which are geographically completely separated. However, such a supposition is not fully supported by the researches carried out hitherto and it seems that in some groups where interspecific hybrids are easily obtained the ability of producing hybrids refers both to species growing together on one territory as well as to species isolated geographically. In Grant's opinion (1949, 1952) a sufficiently efficient mechanism of physiological isolation, on which interspecific intersterility and hybrid sterility depend, was not developed in those genera in which the mechanism of interspecific isolation developed along the lines of special adaptation in the flower structure to pollination by some special kind of insects or brids. According to Grant examples of such genera are furnished by *Aquilegia, Delphinium, Antirrhinum, Pentstemon*, and the greater part of the family of *Orchidaceae.*

The researches which I carried out on the genus *Geum* indicate that the ability to cross exists between all species from the subgenus *Eugeum* and also between this subgenus and species from subgenera *Oreogeum Erythrocoma, Orthurus* and *Woronowia.* It may be that the subgenera *Acomastylis* and *Oncostylus* also belong to the same comparium but this was not established because of the lack of material. Most probably the genera *Waldsteinia* and *Coluria* which belong to the same tribe of *Geeae* constitute separate comparia. The differences in the ability to form crosses by the various species belonging to the same comparium were very small. The ability to produce hybrids between two species does not seem to be directly correlated with the systematic relationship of these species or with chromosome number. It does not depend either on the direction of the cross or the biotype used for crossing. The cross between the tetraploid *G. montanum* from subgenus *Oreogeum* and the dodecaploid *G. pyrenaicum* from subgenus *Eugeum* was equally easily obtainable as crosses between any two hexaploid species from the subgenus *Eugeum.*

However, some species in this comparium show a much greater isolation in the formation of interspecific hybrids than others. This refers first of all to *G. heterocarpum* and partly too to *G. reptans. G. heterocarpum* was crossed in both directions with many *Geum* species and so far I obtained its hybrids only with *G. coccineum,* but it must be stressed that seeds were never set if *G. heterocarpum* had been the pistilate plant. When *G. heterocarpum* pollen was used for pollinating other species the setting of seeds was at a rather high level, up to 50 per cent and more, but the seemingly well developed seeds had a low germinating energy and the lethality among the young seedlings was high, so that the overwhelming majority of these hybrids perished at an early stage without producing fully developed plants. I believe, however, that if the young plants were given more care during the critical seedling stages better results would be reached and the obtaining of hybrids between *G. heterocarpum* and other *Geum* species would be possible. Similar effects of high lethality rate among the hybrids at the early stages were observed when the paternal species was *G. reptans*. Strictly speaking these effects are not the result of interspecific sterility but rather they are connected with the reduced vigour of some interspecific hybrids.

The overwhelming majority of species from the subgenus *Eugeum* cross among themselves quite easily and almost the whole of the subgenus could be included in one coënospecies. Some species in the group, as for instance *G. rivale* and *G. urbanum* or *G. rivale* and *G. coccineum*, produce in F_1 and in the next generations hybrids of high viability and almost normal fertility. In Clausen's system of classification they could be even included into one ecospecies. However, such a procedure would be absolutely arbitrary as these species differ radically by their morphology, ecological requirements and geographical distribution. On the other hand, for example, *G. macrophyllum* with the related *G. oregonense* and *G. laciniatum* are almost completely isolated from the other species in the subgenus *Eugeum* by hybrid sterility and in Clausen's classification should be regarded as a separate coenospecies. This would lead to separation of these species from the others in the subgenus *Eugeum* with which they undoubtedly form one natural group.

The conclusion which is to be drawn from these considerations is that incompatibility barriers often depend on factors which are not distributed within a genus in a manner strictly correlated with the degree of morphological differentiation between species. The ability to cross fertilization seems to correspond to the actual relationships existing between species of a given group in a much greater degree than does hybrid fertility. It is possible that the greater compatibility between *G. montanum* and the species of the subgenus *Eugeum* than, for instance, between *G. heterocarpum* or *G. reptans* and the *Eugeum* species consists in that both genomes of *G. montanum* are homologous with the genomes of the *Eugeum* species, whereas *G. heterocarpum* and *G. reptans* probably have one genome each which is nonhomologous with the genomes of the species from the subgenus *Eugeum*. It must be stressed, however, that these conclusions refer to one group of organisms only and by no means can be generalized.

In the group of species under investigation the high ability to produce interspecific hybrids refers to species both isolated geogrophically (European, East Asiatic, North and South American) and growing together on one territory. The question thus arises of how, in view of such a high ability to form interspecific hybrids, can the species occupying the same territory maintain their specific distinction? However, it should be remembered that it is the extent to which natural crosses actually do occur that is essential for the differentiation of specific populations in nature and this does not always coincide with the potential ability to form crosses observed experimentally. The extent of interspecific crossing depends in nature on numerous factors, such as ecological conditions, the biology of fertilization, the time of reaching sexual maturity etc. These factors may prevent the frequent occurrence of natural crosses despite the high ability for crossing displayed in experimental cultures.

HYBRID VIABILITY

The viability, or vigour as it is also called, of hybrids or any other plant, is a highly composite phenomenon depending on a complex of physiological factors most of which are little understood as yet. Quite obviously, the notion of high or low vigour of a plant has a meaning only when considered in connection with all existing environmental conditions. When the vigour of hybrids is being compared with that of the parental species all efforts are made to cultivate them all in conditions as uniform as possible. However, it must not be forgotten that in experimental gardens the conditions are frequently far from being the most favourable for a given species which may be, for example, a montane species. It seems not impossible that some hybrids exhibiting reduced vigour in certain conditions would behave quite differently if grown in another environment. Despite these objections, fundamental though they are, some conclusion may be reached when the growth of the hybrids and of the parental species are related. The vigour of hybrids may be different in the first and the next generations. Clausen, Keck and Hiesey (1941) report instances from the tribe of *Madiinae* when interspecific hybrids are vigorous and fertile in F_1, whereas in F_2 most of the plants are weak and even invialable. In natural conditions these hybrids would be completely eliminated within a short time. Many examples of similar reports could be easily quoted here (cf. Stebbins, 1950, p. 227).

In F_1 the vigour of the hybrids may be greatly reduced in respect to the parental species so that the hybrid plants represent sublethal or even lethal types but, on the other hand, the vigour of the hybrids may greatly exceed the vigour of the parental species. There are very many records of strong hybrid vigour in the case of interspecific crosses. In some crosses between *Geum* subgenera I observed considerable inhibition and disturbance of growth in its early stages which may easily cause the death of the hybrid plants. However, if the hybrids survive the critical stage they later grow very vigorously and exhibit marked heterosis. This indicates that disturbances in the growth of hybrids depend, among other factors, on the stage in the life of plants.

The inhibition of hybrid growth results from unharmonious interaction between two genomes in one hybrid zygote. As a consequence of the long developmental history the two parental genomes united in the zygote of one species form a harmonious system which determines the normal development of the plant for a certain range of external conditions in which the given species is capable of developing. The mechanism of the system is usually such that it makes possible normal growth over a fairly wide range of external conditions different for every species. The normal vegetative and generative development harmonized with such environmental condition, as for instance the distribution of rainfalls, temperatures and photoperiods, is undoubtedly the result of selection acting over a very long period. As we know in the various parts of the geographical distribution of an ecospecies there may be a variety of ecotypes adapted to the different local environmental conditions. The ecotypes may represent species *in statu nascendi* which in the course of further processes involved in selective differentation may form separate species with a more extensive range of requirements than the original ecospecies from which they arose. If in the course of the differentiating processes the new species did not lose their ability for mutual cross fertilization then the formation of hybrids between them is possible. However, the hybrids arising from crosses between these species will represent forms not fitted to any actual environmental conditions and sublethal in the conditions in which the parental psecies can thrive. Instances have been reported when a hybrid does not develop normally in the usual conditions of insolation and air moisture very suitable for the parental species, whereas it develops vigorously when grown in a shadowed and moist glass-house.

Moreover, numerous cases are known when in a species there are genes which in connection with the genome or cytoplasm from another species give lethal or sublethal effects. Smith (1951) reports very remarkable results from an investigation on interspecific hybrids in the genus *Melilotus*. The seedlings obtained by this worker from crosses of *M. alba* with *M. altissima, M. dentata, M. taurica* or *M. wolgica* were entirely deprived of chlorophyll and could survive not more than several days. The same *M. alba* in crosses with *M. polonica* and *M. suaveolens* gave normal chlorophyll producing hybrids. *M. officinalis* is sexually isolated and does not produce hybrids with the species mentioned above. A genetic analysis of the hybrid *M. alba* × *dentata* revealed that the lethal effect caused by the lack of chlorophyll resulted from the action of several allelomorphs existing in the genome of *M. dentata*. Instance of inhibited hybrid growth as a result of disaccord between the hybrid genome and the cytoplasm of the maternal species are well known from the extensive researches of Michaelis, Lehmann and others on the hybrids in the genus *Epilobium*.

In the genus *Geum* which was the subject of the present research the overwhelming majority of interspecific hybrids exhibits in F_1 growth at least equal in vigour to the vigour of the parental species and numerous were the cases when the hybrids were more vigorous than the parents. Nevertheless, some of the F_1 hybrids have distinctly reduced viability and among these lethality is high in the early stages of growth. Such, in the first place, is the case of the hybrids between species belonging to various subgenera, as for instance the hybrids of *G. heterocarpum* and *G. speciosum* with the species from the subgenus *Eugeum* and *Oreogeum*, the hybrids of *G. triflorum* and *G. ciliatum* from the subgenus *Erythrocoma* with the species from the subgenera *Eugeum* and *Oreogeum*, and the hybrids of *G. reptans* from the subgenus *Oreogeum* with the species from the subgenus *Eugeum*. However, those intersubgeneric hybrids which are brought successfully to the flowering stage develop normally and survive for several years growing quite vigorously, e.g. the hybrids *G. heterocarpum* × *coccineum* and *G. ciliatum* × *urbanum*.

Within the subgenus *Eugeum* most interspecific hybrids are normally vigorous or even surpass in vigour the parental species. An exception to this are some hybrids with *G. macrophyllum* and the related *G. oregonense* and *G. perincisum*. The F_1 hybrids of *G. macrophyllum* with *G. aleppicum, G. urbanum, G. molle, G. hispidum, G. laciniatum* and *G. pyrenaicum* are strongly inhibited in growth and have leaves abnormally curled and often chlorotic. These hybrids are strongly liable to invasion by parasite fungi and usually most of them perish during winter while the survivors which flower the next year frequently have abnormally developed flowers. The same *G. macrophyllum* produces normally viable hybrids with *G. rivale, canadense, Fauriei, silvaticum* and *montanum*. However, regardless of the nature of their development all these hybrids are completely sterile or almost so. Mention has already been made that some of these hybrids have a strongly disturbed course of meiosis as manifested by the almost complete asyndesis in metaphase. The disturbances in the growth of the hybrids are not correlated with the disturbances in the course of meiosis. It does not seem either that these disturbances are conditioned by cytoplasmatic factors as no differences were observed in reciprocal crosses. It is to be assumed that the reason for the differences between hybrids of *G. macrophyllum* with the various *Eugeum* species lies in the genome of *G. macrophyllum* in which there must be some factors giving in connection with the genomes of other species either viable or sublethal zygotes.

At the same time the difference existing between the hybrids of *G. macrophyllum* with other species from the subgenus *Eugeum* point to the considerable genetic differentiation among the species of this subgenus. *G. macrophyllum* together with *G. oregonense* and *G. perincisum* are a good example of a group of species which is in the course of genetic isolation from the other species in the coenospecies *Eugeum*.

Strong disturbances occur in the growth and development of hybrids of *Geum speciosum* with *G. rivale* or *G. pyrenaicum*. The few surviving hybrids from these combinations do not form floral shoots at all having persisted through three years in the stage of leaf rosettes. Similar symptoms of reduced vitality and not passing to the flowering stage are displayed by hybrids of *G. pyrenaicum* with *G. magellanicum, Fauriei, riojense* and *Quellyon*. It seems that in this case the growth inhibiting factors originate from *G. pyrenaicum*, as the other dodecaploid *Eugeum* species (*magellanicum, Fauriei, and riojense*) as well as the decaploid *G. Quellyon* give between them vigorously growing hybrids that flower in the second year in the usual manner. However, the same *G. pyrenaicum* in crosses with numerous other *Eugeum* species produces normally viable hybrids frequently even more vigorous than the parental species.

Mention must still be made of the further hybrid generations. On the whole the progeny of vigorous and fertile hybrids is composed of normally growing plants, but ordinarily not showing symptoms of heterosis in the same extent as the F_1 hybrids. However, in many F_2 generations there are also, alongside of plants developing normally, segregates with distinctly diminished vigour. Quite often such plants are small and dwarfish and perish rapidly in the cultures. Most frequent instances of this kind occur in the progeny of strongly sterile hybrids and especially in the progeny of hybrids between species with different chromosome numbers, e.g. *G. montanum* × *G. rivale*. It seems that in most cases the appearance of the weak plants is connected with the extent to which meiotic divisions in the F_1 hybrids are disturbed. As a result of uneven chromosome distribution gametes with missing or extra chromosomes are formed and these, if able to function at all, produce zygotes with a chromosomal composition causing lethality or sublethality. Unfortunately, in the majority of cases cytological support to this supposition is lacking. In the cross *G. aleppicum* × *urbanum* and in some other hybrids it was found that the weakly growing F_2 plants had the normal somatic chromosome number with $2n = 42$. It seems that in these cases the diminished vigour of the plants was caused by the segregations of genes or of small structural mutations in the chromosomes from the parental species.

HYBRID FERTILITY

The effect of partial or complete sterility of interspecific hybrids has been observed ever since the earliest investigations on plant hybrids. It was known already to such writers as Kölreuter and Gärtner, and from these early days it has been regarded as one of the characteristic traits distinguishing the interspecific hybrids from the intraspecific ones. The researches of the past 50 years show that hybrid sterility is not a rule without exception, though it does occur in most interspecific hybrids. Indeed, instance of fertile interspecific hybrids and sterile hybrids between biotypes of one species are both known at present.

There may be many causes of hybrid sterility and they may be manifested at various stages in the development of the hybrid plants. Renner (1929) and Müntzing (1930) make a distinction between gametic or haplontic sterility in opposition to zygotic or diplontic sterility. In the former case the gametes or the gametophytes degenerate at the stage between the reduction divisions and fertilization, whereas in the latter it is the young zygotes formed by pollination that degenerate or the development of the floral organs in the hybrid is disturbed prior to the meiotic divisions. The cause of sterility in both cases is the cytogenetic composition of the hybrid causing disturbances at various stages of sexual development. Dobzhansky (1941) attempted a division of hybrid sterility effects into more fundamental categories, i.e. chromosomal and genic sterility. Chromosomal sterility covers all these cases when the chromosome conjugation in meiosis of the hybrid has been disturbed as a result of the chromosomes from the parental species not being homologous. It leades usually to the formation of gametes with a variable chromosome number which are unable to function because their chromosome composition is unsuitable. Genic sterility results from unharmonious interaction of genes from the two parental species. This type of sterility may show itself either by disturbances in the development of the reproductive organs in the hybrid, making meiotic divisions impossible, or by disturbances in meiosis itself such as, for instance, genically induced asynapsis and malformation of the spindle. However, it is not always possible to decide what kind of sterility occurs in the case at hand.

Stebbins (1947) points out that the frequent occurrence of strongly or completely sterile hybrids with seemingly normal chromosome conjugation and regular distribution of chromosomes to the macro- and microspores is probably associated with the heterozygozity of chromosomes in respect to small structural differences in the chromosomes of the two parental species. If the differences are small, the chromosomes will conjugate despite the fact that they are only partially homologous. The conjugation, and consequently the segregation, of partially homologous chromosomes differing by small translocations or inversions will lead to the formation of gametes with small chromosomal segments either lacking or doubled and this may cause the lethality of some or even all gametes. This "cryptic structural hybridity", as Stebbins calls it, may give the appearance of Dobzhansky's genic sterility, although it should in fact be classified as sterility of the chromosomal type.

In the same way as no clearly defined boundary can be drawn at present between genic and chromosomal mutations, no sharp distinction can be defined between genic and chromosomal sterility. Dobzhansky considers the behaviour of chromosomes in the hybrids after the doubling of the chromosome number to be an important criterion for distinguishing between the two types of sterility. In his opinion, if normal chromosome conjugation follows the doubling of the chromosome number in the F_1 hybrid with complete or strong asyndesis, then this proves that asyndesis is caused by the lack of homology between the chromosomes of the parental species. If, on the other hand, the chromosomes after the doubling of their number continue to appear in meiosis as univalents then sterility is of genic nature. But not even this criterion is always decisive. In an earlier paper (W. Gajewski 1935) I reported on an amphidiploid hybrid which appeared in the progeny of the asyndetic hybrid *G. macrophyllum* × *rivale* and which had in the majority of cells bivalents only, although there were very good reasons to believe that in the F_1 hybrid asyndesis was caused by genic factors and not by the lack of homology between the chromosomes.

Hybrid sterility in the group of interspecific hybrids from the genus *Geum* covered by the present investigation varies over a very wide range, from complete sterility to nearly normal fertility. This is well illustrated by the table below:

Hybrid	Pollen fertility %	Seed fertility %
Subsp. Oreogeum x Erythrocoma:		
1. G. montanum x G. triflorum	0.3	0.0
2. G. montanum x G. campanulatum	0.1	0.0
Subsp. Eugeum x Erythrocoma:		
3. G. urbanum x G. ciliatum	0.2	0.01
4. G. coccineum x G. ciliatum	2.3	0.0
5. G. rivale x G. ciliatum	0.6	0.0
6. G. rivale x G. triflorum	0.1	0.0
Subsp. Eugeum x Orthurus:		
7.' G. coccineum x G. heterocarpum	1.2	0.0
Subsp. Woronowia x Eugeum:		
8. G. speciosum x G. rivale	does not flower	
9. G. speciosum x G. pyrenaicum		
Subsp. Eugeum x Stylipus:		
10. G. urbanum x G. vernum	1.7	0.30
11. G. macrophyllum x G. vernum	0.6	0.05
12. G.oregonense x G. vernum	0.6	0.05
13. G. perincisum x G. vernum	0.1	0.05
14. G. aleppicum x G. vernum	1.2	0.25
Subsp. Oreogeum x Eugeum:		
15. G. montanum x G. rivale	34.5	15.5
16. G. montanum x G. coccineum	35.5	18.5
17. G. montanum x G. silvaticum	25.5	34.4
18. G. montanum x G. molle	11.0	16.0
19. G. montanum x G. hispidum	19.5	8.5
20. G. montanum x G. canadense	32.5	8.5
21. G. montanum x G. aleppicum	4.2	2.4
22. G. montanum x G. laciniatum	1.0	1.6
23. G. montanum x G. urbanum	0.45	0.6
24. G. montanum x G. macrophyllum	0.1	0.1
25. G. montanum x G. pyrenaicum	0.01	0.15
26. G. montanum x G. magellanicum	0.1	0.0
27. G. montanum x G. Fauriei	0.5	0.0
28. G. coccineum x G. reptans	1.2	0.05
29. G. rivale x G. reptans	1.0	0.05
Subsp. Oreogeum x Oreogeum:		
30. G. montanum x G. reptans	0.7	0.0
Subsp. Eugeum x Eugeum:		
31. G. magellanicum x G. riojense	61.9	27.3
32. G. magellanicum x G. pyrenaicum	does not flower	
33. G. Fauriei x G. pyrenaicum		
34. G. Fauriei x G. riojense	0.2	0.0
35. G. magellanicum x G. Fauriei	0.0	0.0
36. G. pyrenaicum x G. riojense	does not flower	
37. G. riojense x G. Quellyon	36.4	24.4
38. G. Quellyon x G. pyrenaicum	does not flower	

Hybrid	Pollen fertility %	Seed fertility %
39. G. magellanicum x G. Quellyon	0.3	0.0
40. G. magellanicum x G. rivale	0.1	0.01
41. G. magellanicum x G. aleppicum	0.04	0.01
42. G. magellanicum x G. hispidum	0.02	0.02
43, G. magellanicum x G. canadense	0.0	0.0
44. G. magellanicum x G. macrophyllum	0.01	0.1
45. G. pyrenaicum x G. rivale	0.8	0.2
46. G. pyrenaicum x G. coccineum	0.6	0.1
47. G. pyrenaicum x G. aleppicum	0.5	0.01
48 G. pyrenaicum x G. molle	0.4	0.05
49. G. pyrenaicum x G. macrophyllum	0.1	0.1
50. G. pyrenaicum x G. urbanum	0.2	0.2
51. G. pyrenaicum x G. silvaticum	0.6	0.3
52. G. riojense x G. aleppicum	0.2	0.0
53. G. riojense x G. rivale	0.2	0.01
54. G. riojense x G. laciniatum	0.2	0.2
55. G. Fauriei x G. rivale	0.2	0.0
56. G. Fauriei x G. silvaticum	0.1	0.0
57. G. Fauriei x G. macrophyllum	0.1	0.0
58. G. Fauriei x G. urbanum	0.0	0.0
59. G. Fauriei x G. aleppicum	0.1	0.05
60. G. Fauriei x G. perincisum	0.2	0.0
61. G. Quellyon x G. rivale	0.1	0.0
62. G. Quellyon x G. coccineum	0.01	0.0
63. G. Quellyon x G. silvaticum	0.1	0.0
64. G. Quellyon x G. canadense	0.05	0.0
65. G. Quellyon x G. laciniatum	0.01	0.0
66. G. Quellyon x G. boliviense	0.1	0.0
67. G. rivale x G. urbanum	78.0	72.1
68. G. rivale x G. coccineum	66.6	94.5
69. G. rivale x G. silvaticum	74.6	60.3
70. G. rivale x G. molle	62.1	61.8
71. G. rivale x G. hispidum	83.1	60.4
72. G. rivale x G. aleppicum	16.6	10.1
73. G. rivale x G. canadense	31.3	8.8
74. G. rivale x G. laciniatum	26.0	15.0
75. G. rivale x G. macrophyllum	0.7	0.1
76. G. rivale x G. perincisum	0.5	0,1
77. G. rivale x G. oregonense	0.1	0.0
78. G. rivale x G. boliviense	21.0	17.5
79. G. coccineum x G. urbanum	72.0	62.7
80. G. coccineum x G. molle	51.0	49.8
81. G. coccineum x G. hispidum	31.0	30.0
82. G. coccineum x G. silvaticum	65.1	50.3
83. G. coccineum x G. aleppicum	5.9	4.2

Hybrid	Pollen fertility %	Seed fertility %
84. G. coccineum x G. canadense	22,8	24.8
85. G. coccineum x G. macrophyllum	0.2	0.0
86. G. coccineum x G. oregonense	0.01	0.01
87. G. coccineum x G. laciniatum	24.3	10.5
88. G. silvaticum x G. molle	50.0	33.9
89. G. silvaticum x G. hispidum	54.0	32.8
90. G. silvaticum x G. aleppicum	0.0	0.0
91. G. silvaticum x G. macrophyllum	0,3	0.05
92. G. urbanum x G. molle	32.6	18.8
93. G. urbanum x G. hispidum	24.7	34.2
94. G. urbanum x G. aleppicum	0.6	0.01
95. G. urbanum x G. canadense	0.2	0.1
96. G. urbanum x G. macrophyllum	0.1	0.0
97. G. urbanum x G. oregonense	0.01	0.01
98. G. urbanum x G. perincisum	0.2	0.0
99. G. urbanum x G. laciniatum	0.1	0.01
100. G. molle x G. hispidum	55.9	54.2
101. G. molle x G. aleppicum	0.2	0.01
102. G. molle x G. canadense	0.3	0.7
103. G. molle x G. macrophyllum	0.2	0.0
104. G. hispidum x G. aleppicum	0.6	0.2
105. G. hispidum x G. canadense	13.4	8.5
106. G. hispidum x G. macrophyllum	0.5	0.0
107. G. hispidum x G. laciniatum	4.5	5.6
108. G. aleppicum x G. canadense	0.1	0.01
109. G. aleppicum x G. macrophyllum	0.6	0.0
110. G. aleppicum x G. oregonense	0.05	0.02
111. G. aleppicum x G. laciniatum	0.05	0.01
112. G. aleppicum x G. boliviense	0.3	0.05
113. G. macrophyllum x G. canadense	0.6	0.0
114. G. macrophyllum x G. laciniatum	0.0	0.0
115. G. macrophyllum x G. perincisum	53.1	32.1
116. G. macrophyllum x G. oregonense	54.6	40.3
117. G. perincisum x G. oregonense	47,3	46.2
118. G. laciniatum x G. oregonense	0.01	0.0
119. G. laciniatum x G. perincisum	0.01	0.01
120. G. canadense x G. laciniatum	42.8	52,3
121. G. canadense x G. boliviense	25.5	35.2

The frequent occurrence in all these hybrids of lower seed than pollen fertility, the reduced germination rate of seeds and the presence of seeds strongly inhibited in development indicate that hybrid sterility results from both gametic and zygotic sterility acting simultaneously. In the majority of hybrids from the subgenus *Eugeum*, where both the parental species have the same chromosome number, it is impossible to distinguish between sterility of the genic and the structural types. An exception are the hybrids between species belonging to various subgenera and hybrids between species with a various degree of polyploidy, as in these cases the cause of sterility seems to consist primely in the lack of homology or the lack of partners in the chromosome conjugation at meiosis. Anyway, it seems useless to make these differences at all, as both effects always appear together. In interspecific hybrids all such processes as the differentiation of sexual organs, the course of meiosis and the development of the gametophyte similarly as the processes of fertilization and the development of zygotes are distinctly disturbed at different stages and to different degrees in the various hybrids, and all these disturbances are caused by the discordant interaction of the two united genomes from the parental species. These processes are more sensitive to the complex whole of external and internal conditions of the plant. In many *Geum* hybrids the differences in fertility are connected with the period at which flowers develop and achenes ripen and this indicates that in the hybrids seed production depends also on external conditions and the physiological state of the plants.

In the hybrids where there is at least a potential possibility of full chromosome conjugation at meiosis the distinction between genic causes of sterility and those associated with chromosomal structure can not be carried through. Within the group of hybrids between hexaploid species where potentially full chromosome conjugation can take place and where the number of univalents changes from 2 to 10 in some of the PMCs fertility varies greatly, ranging from almost normal to almost complete sterility. The differences in fertility are correlated only in a small extent with the number of univalents present at meiosis and cannot be explained by this effect alone. Quite certainly the presence of univalents, probably due to the reduced number of chiasmata, as well as the chromosomal bridges often found at anaphase, point to small structural differences between the not completely homologous chromosomes of the parental species. Presumably, hybrids between various pairs of parental species are unequally heterozygous in respect to small chromosomal segments and this may partly explain the differences in their fertility. However, it is my opinion that the results of fertility analyses in various interspecific combinations within a group of several parental species cannot be explained solely by the differences in chromosome structures. In the table below the fertility of achenes in 15 hybrids between 6 hexaploid *Eugeum* species is compared. All these hybrids have the same type of meiosis with complete chromosome conjugation potentially possible. For comparison the fertility of the hybrids between these 6 species (*G. rivale, coccineum, molle, urbanum, canadense* and *aleppicum*) and *G. macrophyllum* is also tabulated. Some of the hexaploid species (*G. rivale, coccineum, molle* and *urbanum*) produce with *G. macrophyllum* asyndetic hybrids. Moreover, the table includes the results for the crosses of all the above species with the tetraploid *G. montanum* from the subgenus *Oreogeum* and the dodecaploid *G. magellanicum* from the subgenus *Eugeum.*

		1	2	3	4	5	6	7	8
1	Geum rivale								
2	G. coccineum	94.5							
3	G. urbanum	72.1	62.7						
4	G. molle	61.8	49.8	18.8					
5	G. canadense	8.8	24.8	0.1	0.1				
6	G. aleppicum	10.1	4.2	0.01	0.01	0.01			
7	G. macrophyllum	0.1	10.0	0.0	0.0	0.0	0.0		
8	G. montanum	15.5	18.5	0.6	16.0	8.5	2.4	0.1	
9	G. magellanicum	0.01	?	?	?	0.0	0.01	0.0	0.0

In addition to the above table mutual fertility relations between hybrids of hexaploid species from the subgenus *Eugeum* are shown in Fig. 144. From the diagram and the table the following conclusions are to be drawn:

1. Among the hexaploid *Eugeum* species there are groups of species which between them produce highly fertile hybrids. The following groups can be distinguished: a) *G. rivale, G. coccineum, G. silvaticum,* b) *G. canadense, G. laciniatum, G. boliviense,* c) *G. macrophyllum, G. oregonense, G. perincisum* and d) *G. urbanum, G. molle, G. hispidum.*

2. The hybrids between these groups are usually more or less sterile and this refers primely to the hybrids between species of groups b, c and d. An exception here are the species *G. rivale, coccineum* and *silvaticum* from group a, which not only give highly fertile hybrids among them but also produce relatively fertile hybrids with the species from

groups b and d and with *G. aleppicum*. The last mentioned species forms as if a group by itself and can be included in none of the four groups.

3. In direct contrast to group a the species from group c, *G. macrophyllum, oregonense* and *perincisum*, are isolated from nearly all species in the subgenus *Eugeum* by almost complete hybrid sterility.

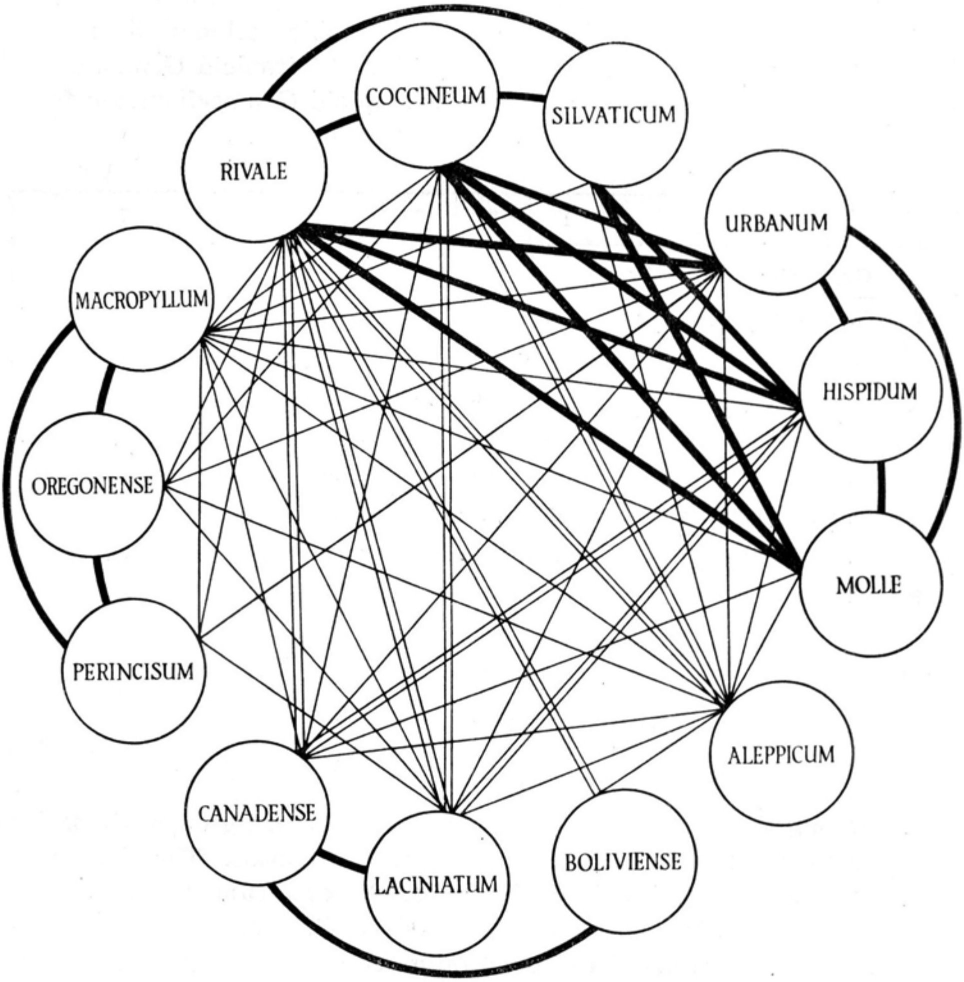

Fig. 144. Diagram illustrating hybrid fertility among 13 hexaploid *Eugeum* species. The solid black lines indicate fertile hybrids, double lines — partially fertile hybrids and single lines — sterile hybrids

4. The difference in the fertility of hybrids from groups a, b and d and of the hybrids between these groups cannot be explained by the

differences in the course of meiosis as it is in principle the same, regardless of whether the crosses are made within or between the groups.

5. The hybrids of the hexaploid *Eugeum* species with the tetraploid *G. montanum* from the subgenus *Oreogeum* may be more fertile than some hybrids between even morphologically closely related hexaploid *Eugeum* species with almost normal meiosis (i.e. with bivalents predominating at metaphase), whereas, hybrids with *G. montanum* have at meiosis at least 7 univalents in all the PMCs.

6. The hybrids of the hexaploid *Eugeum* species with the dodecaploid or decaploid species from the same subgenus are all almost completely sterile regardless of the group to which the hexaploid parental species belong. In this case the sterility of the hybrids seems to be caused by chromosomal sterility due to the lack of conjugation between some chromosomes in meiosis.

The complex relations in respect to hybrid fertility existing at present among the hexaploid *Eugeum* species are undoubtedly primely the result of genic differentiation between these species. The interspecific relationships within the particular groups seem to be closer than between the species belonging to various groups. This is brought out in the first place by similarities in the geographical distribution as well as by the frequent close morphological conformity. However, the geographical and morphological relations are not necessarily very strict as, for instance, group b comprises two North American species, *Geum canadense* and *laciniatum*, and the South American *G. boliviense*, while in group a the species differ considerably by their morphology.

It is worth stressing that, as will be demonstrated more fully later on, the species *G. rivale, coccineum* and *silvaticum* from group a may be regarded, because of their morphology and geographical distribution as the most primitive species in the whole subgenus *Eugeum*. These species too have more traits than any other in common with *G. montanum* which is one of the presumable ancestral forms for the whole subgenus *Eugeum*. The circumstance that it is these three species that produce the most fertile hybrids with *G. montanum* as well as with other hexaploid species from the subgenus *Eugeum* is most noteworthy. It may be assumed as a kind of hypothesis that these species, as the most primitive, have genomes best equipped for harmonious cooperation with the genomes of *G. montanum* and at the same time with the genomes of the other species in the subgenus *Eugeum*. Owing to this quality the three species give the most viable and usually the most fertile hybrids with the rest of *Eugeum* species. The other species, e.g. those of group e or *G. aleppicum*, represent in the subgenus *Eugeum* the species with more advanced characters and are probably the most recent in the evolutional history of the subgenus. Moreover, their geographical distribution is usually the most distant from the supposed centre in southern Europe where the subgenus originated.

The species with the more advanced characters give with the species from other groups entirely or almost completely sterile hybrids. In this manner simultaneously to the evolutional progress within the subgenus more defined sexual isolation of the most advanced species is achieved. This process manifests itself by the reduced viability or diminished fertility of the hybrids.

In the subgenus *Eugeum* the process of sexual isolation of species is the most advanced in the group comprising *Geum macrophyllum* with the two related species and in *Geum aleppicum*. These species in crosses with numerous others give hybrids with a strongly disturbed course of meiosis and a majority of univalents at metaphase.

Besides gametic sterility, as it is called, *Geum* hybrids also display the type of sterility which could be defined as zygotic. This latter kind of sterility consists in various disturbances in the development of flowers which makes reduction divisions impossible and consequently gametes are not formed.

In the hybrid *G. urbanum* × *aleppicum* the disturbances in the development of flowers are manifold and consist in the complete or partial degeneration of the androecium with simultaneous abnormal expression of petals. In addition to this, in the flowers with the reduced androecium, also the development of the gynoecium is disturbed and from most ovaries 1, 2 or 3 extra styles grow out. Similar symptoms are displayed by the hybrid *G. molle* × *aleppicum*, though to a lesser degree. When the development of the stamens is strongly inhibited the archesporium is not formed at all. In better developed stamens, relatively to the degree of development, the archesporium is formed but degenerates before the reduction divisions begin. In other cases degeneration occurs after the prophases of meiotic divisions which can still be observed. Finally, in still other flowers meiosis proceeds to the end and may be either of the asyndetic type with almost exclusively univalents in metaphase or with bivalents prevailing in the majority of PMCs similarly as in most hybrids between *Eugeum* species. However, even when meiosis has a normal course almost all the pollen degenerates prior to the first somatic division and only single good pollen grains can be found. The hybrid produces only few good achenes. In F_2 the plants segregate strongly, some showing similar disturbances in floral development as in F_1, others with flowers well developed and normal meiosis. In the latter case some of the plants are distinctly more fertile than in F_1.

Even in some F_3 generations, alongside of highly fertile plants, there are some completely sterile individuals with degenerate androecium. It seems, therefore, that in the progeny of the hybrid the factors responsible for floral degeneration segregate. The existence in the hybrids of factors causing developmental disturbances in flowers is supported by observations on the behaviour of the F_1 hybrid *G. pyrenaicum* × *aleppicum* where segregation took place giving 11 plants with normally developed flowers and 21 entirely deprived of stamens and with strongly inhibited development of petals. Unfortunately the hybrids are completely sterile and the inheritance of this trait could not be investigated further. Nevertheless it can be presumed that the segregation in F_1 is the result of heterozygozity in one parental species in respect to the factors inhibiting the formation of stamens. Frequently at the end of the vegetative season the plants without stamens developed occasionally single normal flowers and this shows that the expression of this character depends also on the physiological state of the plants or on some special combination of external conditions.

The circumstance that in all the three interspecific hybrids with disturbances in the development of the androecium one of the parental species is *G. aleppicum* lets it be assumed that the factors causing the disturbances in the hybrids are primely from this species.

Quite probably hybrid sterility depends on numerous other factors affecting the various phases of reproduction and not having such a drastic influence as those just described causing the severe disturbances in the development of the flowers. The factors are probably responsible for the sterility of other hybrids where the development of the flowers and the course of meiosis are seemingly normal. In the further generations the factors segregate causing segregation of fertility in the progeny of hybrids.

The system of hereditary factors present in populations of species and responsible for reduced fertility of interspecific hybrids is greatly varied in the various groups of species. In *G. rivale* or *coccineum* it allows for normal growth and high fertility of hybrids with numerous other species, wheras, in *G. macrophyllum*, for instance, it is responsible for strong disturbances in development, asyndesis and sterility in most interspecific combinations giving fertile hybrids with closely related species only. In *G. aleppicum* too there is a set of factors causing high sterility and developmental disturbances in hybrids with nearly all species from the subgenus *Eugeum*.

In conclusion it must be stressed that in the group of species from the genus *Geum* covered by the present investigation no simple relation is apparent between hybrid fertility and the systematic position, the degree of morphological differentiations or the degree of polyploidy of the parental species, this being especially true within the subgenus *Eugeum*. The processes of morphological and cytological differentiation only partly coincide with the physiological and genic differences on which hybrid sterility depends.

CYTOGENETIC CONDITIONS

All the species in the tribe *Geeae* Juel examined thus far have the basic chromosome number x = 7. Throughout the tribe of *Geeae* the chromosomes are small and differ little in their size and appearance making the analysis of specific and generic karyotypes impossible. Such an analysis could throw much light on the problem of interspecific relationships as was shown by the very elegant work of Babcock on *Crepis* and Fernandes on *Narcissus*.

However, because of the unfavourable conditions the cytogenetical analysis in the plant group considered here was concerned in the first place with problems of polyploidy and conditions of chromosome homology and was carried out by analysing the conjugation of chromosomes in interspecific hybrids.

In the table below the results from examinations of the course of meiosis in 108 interspecific hybrids are assembled.

From the table the following conclusions are to be drawn:

1. Ten hexaploid species with n = 21 belonging to the subgenus *Eugeum* when crossed among them produce in F_1 hybrids with the highest possible chromosome conjugation in meiosis of 21 bivalents. The ten species in question are *G. rivale, coccineum, silvaticum, urbanum, molle, hispidum, aleppicum, laciniatum, canadense* and *boliviense*. This conclusion is based on the analysis of 36 hybrids which amounts to 80 per cent of the possible interspecific combinations. It is thus apparent that the chromosomes of all these species are at least partly homologous, whereas the varying number of univalents present in meiosis of these hybrids probably indicates that this homology is not complete and that the interspecific hybrids possess chromosomes heterozygous in respect to more or less numerous chromosomal segments. Further support to this supposition is given by the frequent occurrence in first division anaphase of chromosomal bridges and acentric fragments probably resulting from the formation of chiasmata between nonhomologous segments.

2. The morphologically very closely related hexaploid species *G. macrophyllum, G. perincisum* and *G. oregonense* form a distinct group among the hexaploid species in the subgenus *Eugeum*. The isolation of this group is shown by the complete or nearly complete asyndesis obser-

No. of hybrid	Hybrid	Maximum conjugation	Minimum conjugation
1	G. montanum (14) x G. triflorum (21)	7 B,* 21 U*	5 B, 17 U
3	G. urbanum (21) x G. ciliatum (21)	14 B, 14 U	7 B, 28 U
4	G. coccineum (21) x G. ciliatum (21)	14 B, 14 U	7 B, 28 U
5	G. rivale (21) x G. ciliatum (21)	14 B, 14 U	7 B, 28 U
6	G. rivale (21) x G. triflorum (21)	14 B, 14 U	7 B, 28 U
7	G. coccineum (21) x G. heterocarpum (14)	7 B, 21 U	2 B, 31 U
10	G. urbanum (21) x G. vernum (21)	12 B, 18 U	9 B, 24 U
11	G. macrophyllum (21) x G. vernum (21)	8 B, 16 U	42 U
12	G. oregonense (21) x G. vernum (21)	7 B, 28 U	42 U
13	G. perincisum (21) x G. vernum (21)	7 B, 28 U	42 U
14	G. aleppicum (21) x G. vernum (21)	6 B, 30 U	42 U
15	G. montanum (14) x G. rivale (21)	14 B, 7 U	12 B, 11 U
16	G. montanum (14) x G. silvaticum (21)	14 B, 7 U	10 B, 15 U
17	G. montanum (14) x G. coccineum (21)	14 B, 7 U	12 B, 11 U
18	G. montanum (14) x G. molle (21)	14 B, 7 U	11 B, 13 U
19	G. montanum (14) x G. hispidum (21)	14 B, 7 U	11 B, 13 U
20	G. montanum (14) x G. aleppicum (21)	14 B, 7 U	13 B, 9 U
21	G. montanum (14) x G. urbanum (21)	14 B, 7 U	9 B, 17 U
22	G. montanum (14) x G. laciniatum (21)	14 B, 7 U	9 B, 17 U
23	G. montanum (14) x G. canadense (21)	14 B, 7 U	10 B, 15 U
24	G. montanum (14) x G. macrophyllum (21)	6 B, 23 U	35 U
25	G. pyrenaicum (42) x G. montanum (14)	14 B, 28 U	10 B, 36 U
26	G. montanum (14) x G. magellanicum (42)	14 B, 28 U	9 B, 38 U
27	G. Fauriei (42) x G. montanum (14)	14 B, 28 U	6 B, 44 U
28	G. rivale (21) x G. reptans (21)	14 B, 14 U	9 B, 24 U
29	G. coccineum (21) x G. reptans (21)	14 B, 14 U	8 B, 26 U
30	G. montanum (14) x G. reptans (21)	14 B, 7 U	12 B, 11 U
31	G. magellanicum (42) x G. riojense (42)	42 B	38 B, 8 U
34	G. Fauriei (42) x G. riojense (42)	34 B, 16 U	24 B, 36 U
37	G. riojense (42) x G. Quellyon (35)	35 B, 7 U	33 B, 11 U
40	G. magellanicum (42) x G. rivale (21)	21 B, 21 U	18 B, 27 U
41	G. magellanicum (42) x G. aleppicum (21)	21 B, 21 U	15 B, 33 U
42	G. magellanicum (42) x G. hispidum (21)	21 B, 21 U	17 B, 29 U
44	G. magellanicum (42) x G. macrophyllum (21)	21 B, 21 U	14 B, 35 U
45	G. pyrenaicum (42) x G. rivale (21)	21 B, 21 U	17 B, 29 U
46	G. pyrenaicum (42) x G. coccineum (21)	21 B, 21 U	17 B, 29 U
47	G. pyrenaicum (42) x G. aleppicum (21)	21 B, 21 U	16 B, 31 U
48	G. pyrenaicum (42) x G. molle (21)	21 B, 21 U	18 B, 27 U
49	G. pyrenaicum (42) x G. macrophyllum (21)	21 B, 21 U	15 B, 33 U
50	G. pyrenaicum (42) x G. urbanum (21)	21 B, 21 U	19 B, 25 U
51	G. pyrenaicum (42) x G. silvaticum (21)	21 B, 21 U	18 B, 27 U
52	G. riojense (42) x G. aleppicum (21)	21 B, 21 U	17 B, 29 U
53	G. riojense (42) x G. rivale (21)	21 B, 21 U	17 B, 29 U

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* B — bivalents, U — univalents

No. of hybrid	Hybrid	Maximum conjugation	Minimum conjugation
55	G. Fauriei (42) x G. rivale (21)	21 B, 21 U	16 B, 31 U
56	G. Fauriei (42) x G. silvaticum (21)	21 B, 21 U	17 B, 29 U
57	G. Fauriei (42) x G. macrophyllum (21)	21 B, 21 U	13 B, 37 U
60	G. Fauriei (42) x G. perincisum (21)	21 B, 21 U	14 B, 35 U
61	G. rivale (21) x G. Quellyon (35)	21 B, 14 U	18 B, 20 U
62	G. coccineum (21) x G. Quellyon (35)	21 B, 14 U	18 B, 20 U
63	G. Quellyon (35) x G. silvaticum (21)	21 B, 14 U	19 B, 18 U
64	G. Quellyon (35) x G. canadense (21)	21 B, 14 U	18 B, 20 U
65	G. Quellyon (35) x G. laciniatum (21)	21 B, 14 U	18 B, 20 U
66	G. Quellyon (35) x G. boliviense (21)	21 B, 14 U	18 B, 20 U
67	G. rivale (21) x G. urbanum (21)	21 B	18 B, 6 U
68	G. rivale (21) x G. coccineum (21)	21 B	19 B, 4 U
69	G. rivale (21) x G. silvaticum (21)	21 B	18 B, 6 U
70	G. rivale (21) x G. molle (21)	21 B	17 B, 8 U
71	G. rivale (21) x G. hispidum (21)	21 B	18 B, 6 U
72	G. rivale (21) x G. aleppicum (21)	21 B	17 B, 8 U
73	G. rivale (21) x G. canadense (21)	21 B	16 B, 10 U
74	G. rivale (21) x G. laciniatum (21)	21 B	16 B, 10 U
75	G. rivale (21) x G. macrophyllum (21)	7 B, 28 U	42 U
76	G. rivale (21) x G. perincisum (21)	5 B, 32 U	42 U
77	G. rivale (21) x G. oregonense (21)	9 B, 24 U	42 U
78	G. rivale (21) x G. boliviense (21)	21 B	18 B, 6 U
79	G. coccineum (21) x G. urbanum (21)	21 B	19 B, 4 U
80	G. coccineum (21) x G. molle (21)	21 B	19 B, 4 U
81	G. coccineum (21) x G. hispidum (21)	21 B	18 B, 6 U
82	G. coccineum (21) x G. silvaticum (21)	21 B	18 B, 6 U
83	G. coccineum (21) x G. aleppicum (21)	21 B	17 B, 8 U
84	G. coccineum (21) x G. canadense (21)	21 B	17 B, 8 U
85	G. coccineum (21) x G. macrophyllum (21)	5 B, 32 U	42 U
86	G. coccineum (21) x G. oregonense (21)	7 B, 28 U	2 B, 38 U
87	G. coccineum (21) x G. laciniatum (21)	21 B	16 B, 18 U
88	G. silvaticum (21) x G. molle (21)	21 B	19 B, 4 U
89	G. silvaticum (21) x G. hispidum (21)	21 B	16 B, 18 U
90	G. silvaticum (21) x G. aleppicum (21)	21 B	17 B, 8 U
91	G. silvaticum (21) x G. macrophyllum (21)	6 B, 30 U	42 U
92	G. urbanum (21) x G. molle (21)	21 B	17 B, 8 U
93	G. urbanum (21) x G. hispidum (21)	21 B	18 B, 6 U
94	G. urbanum (21) x G. aleppicum (21)	21 B	42 U
95	G. urbanum (21) x G. canadense (21)	21 B	16 B, 10 U
96	G. urbanum (21) x G. macrophyllum (21)	7 B, 28 U	42 U
97	G. urbanum (21) x G. oregonense (21)	5 B, 32 U	42 U
98	G. urbanum (21) x G. perincisum (21)	4 B, 34 U	42 U
99	G. urbanum (21) x G. laciniatum (21)	21 B	16 B, 10 U
100	G. molle (21) x G. hispidum (21)	21 B	19 B, 4 U
101	G. molle (21) x G. aleppicum (21)	21 B	18 B, 6 U

No. of hybrid	Hybrid	Maximum conjugation	Minimum conjugation
102	G. molle (21) x G. canadense (21)	21 B	16 B, 10 U
103	G. molle (21) x G. macrophyllum (21)	6 B, 30 U	42 U
104	G. hispidum (21) x G. aleppicum (21)	21 B	16 B, 10 U
105	G. hispidum (21) x G. canadense (21)	21 B	17 B, 8 U
106	G. hispidum (21) x G. macrophyllum (21)	5 B, 32 U	42 U
107	G. hispidum (21) x G. laciniatum (21)	21 B	17 B, 8 U
108	G. aleppicum (21) x G. canadense (21)	21 B	18 B, 6 U
109	G. aleppicum (21) x G. macrophyllum (21)	21 B	18 B, 6 U
110	G. aleppicum (21) x G. oregonense (21)	6 B, 30 U	42 U
111	G. aleppicum (21) x G. laciniatum (21)	21 B	16 B, 10 U
112	G. aleppicum (21) x G. boliviense (21)	21 B	13 B, 16 U
113	G. macrophyllum (21) x G. canadense (21)	21 B	17 B, 8 U
114	G. macrophyllum (21) x G. laciniatum (21)	3 B, 36 U	42 U
115	G. macrophyllum (21) x G. perincisum (21)	21 B	19 B, 4 U
116	G. macrophyllum (21) x G. oregonense (21)	21 B	20 B, 2 U
117	G. perincisum (21) x G. oregonense (21)	21 B	17 B, 8 U
118	G. laciniatum (21) x G. oregonense (21)	3 B, 36 U	42 U
119	G. laciniatum (21) x G. perincisum (21)	5 B, 32 U	42 U
120	G. canadense (21) x G. laciniatum (21)	21 B	19 B, 4 U
121	G. canadense (21) x G. boliviense (21)	21 B	19 B, 4 U

ved frequently in the hybrids between the species of this group and the majority of the previously discussed hexaploid species from the subgenus *Eugeum*. It has been shown in an earlier paper (W. Gajewski 1953) that the asyndesis observed in the I-st division metaphase results probably from premature desynapsis and is not associated with structural differences between the chromosomes of the parental species. This is indicated by the fact that the hybrids between the species in this group and *G. aleppicum* or *G. canadense* may have meiosis with normal chromosome conjugation. Besides, all the hybrids between these three species and all the other *Eugeum* species are completely or very highly sterile and often have a lowered viability, whereas, the hybrids between the three species themselves are fertile with meiosis of the same kind as in the hybrids between the group of 10 hexaploid species mentioned previously.

It follows that the group of the three species is probably characterized by a combination of factors causing asyndesis, sterility and sometimes disturbances in the vegatative development in hybrids with the other groups of species. Owing to these factors the group is strongly isolated sexually from the rest of the hexaploid *Eugeum* species.

It must be reminded, however, that also in the group of the 10 *Eugeum* species some species are similarly, though not so strictly, isolated from the rest of the species. *G. aleppicum*, for instance, gives highly sterile hybrids with most of the species in the group and its hybrids often exhibit disturbances in the development of floral organs. In the hybrid of *G. aleppicum* with *G. urbanum* the course of meiosis in at least some flowers is of the same asyndetic type as in the hybrids of *Geum macrophyllum* and the species related to it with the other *Eugeum* species.

3. In the hybrids between the decaploid *G. Quellyon* with $n = 35$ and the hexaploid species with $n = 21$ meiosis is of the type $21_{II} + 14_{I}$, whereas, in the hybrids between the dodecaploid species *G. magellanicum, G. pyrenaicum, G. riojense* and *G. Fauriei* with $n = 42$ and hexaploids species with $n = 21$ meiosis is of the type $21_{II} + 21_{I}$. These configurations appear in some PMCs only while the rest have a larger number of univalents and a correspondingly smaller number of bivalents. It is very interesting that the same type of meiosis is found in the hybrids of *G. macrophyllum* with the dodecaploid *Eugeum* species and desynapsis is never observed in these hybrids.

The type of meiosis in the hybrids now being considered may be interpreted by that the dodeca- and decaploid species originated through amphiploidy from hybrids between hexaploid *Eugeum* species. Some confirmation to this supposition is given by the fact that in my cultures the appearance of dodecaploid forms from hybrids between hexaploid *Eugeum* species has twice been observed (W. Gajewski 1953, 1954).

These examples show that the dodecaploid species in the subgenus *Eugeum* could be formed through amphiploidy from the hexaploid species in this subgenus. It is not impossible that the hexaploid parental forms of these species are in some cases still in existence and that it is possible to reproduce these species again experimentally.

4. All the hexaploid species from the subgenus *Eugeum* crossed during the present research with the tetraploid *G. montanum* ($n = 14$) from the subgenus *Oreogeum* give hybrids with the chromosome conjugation at meiosis of the type $14_{II} + 7_{I}$. The only exception here is *G. macrophyllum* which with *G. montanum* produces asyndetic hybrids. The type of meiosis observed in the hybrids of *G. montanum* with hexaploid *Eugeum* species indicates that two genomes of these *Eugeum* species are homologous with two genomes of *G. montanum*. The possibility arises, therefore, that the hexaploid species in the subgenus *Eugeum* originated by means of amphiploidy from hybrids between tetraploid species of the *G. montanum* type and a diploid species not yet identified. The more primitive type in the genus *Geum* is undoubtedly represented by *G. montanum*,

which has straight long haired styles adapted to anemochoric dissemination, whereas, the *Eugeum* species with pistils adapted to epizoochoric dissemination represent the advanced type. In this connection it seems plausible that the whole subgenus *Eugeum* owes its differently shaped styles to ancestral hybrids between tetraploid plants with straight styles and a diploid plant which caused in the styles of the hybrids a tendency for evolution in the direction of the epizoochoric type. However, this hypothesis is not supported by any experimental evidence.

5. The hexaploid *G. reptans* from the subgenus *Oreogeum* differs greatly from the other species in this subgenus. In its hybrid with *G. montanum* the conjugation at meiosis is of the type $14_{II} + 7_{I}$, whereas, the conjugations in meiosis of the hybrids between *G. reptans* and *G. rivale* or *G. coccineum* are of the type $14_{II} + 14_{I}$. Thus, it seems that *G. reptans* and *G. montanum* have two common genomes which are the same as the two genomes common for the hexaploid *Eugeum* species, while the third genome of *G. reptans* is not homologous with the third genome of the *Eugeum* species. If the two genomes in *G. montanum* are denoted AB and the three genomes in the hexaploid *Eugeum* species as ABC, then the genomes of *G. reptans* will be ABD.

6. *G. vernum,* the only species in the separate subgenus *Stylipus,* is closely related to the *Eugeum* species with which it is associated by the same type of pistils. The hybrid of this species with *G. urbanum* from the subgenus *Eugeum* produces in meiosis 9 to 12 bivalents and this seems to indicate that both species have at least two genomes partly homologous. *G. vernum* when crossed with *G. macrophyllum, oregonense* and *aleppicum* produces hybrids with much fewer bivalents in meiosis or with univalents alone. It cannot be decided on the basis of the results now available from cytological analyses of the hybrids to what extent the considerable reduction in the number of bivalents in the hybrids of *G. vernum* with *Eugeum* species is accounted by the different phylogenetic origin of these species. In view of the closely related morphology of *G. vernum* and *Eugeum* species I think it more likely that *G. vernum* has also the ABC kind of genotype as the *Eugeum* species and that complete chromosome conjugation is not observed because the chromosomes of these species are less homologous.

7. *Geum heterocarpum* (n = 14) from the morphologically very distinct subgenus *Orthurus* produces with *G. coccineum* (n = 21) hybrids which in meiosis have 2 to 7 bivalents. *G. heterocarpum* has probably only one genome homologous with the *Eugeum* species. As the suitable crosses are lacking it is impossible to decide whether it is one of the two genomes AB or the genome C.

8. The hybrids of *G. triflorum* (n = 21) and *G. ciliatum* (n = 21) from the subgenus *Erythrocoma* with *G. montanum* (n = 14) from the subgenus *Oreogeum* and with *G. rivale, urbanum* and *coccineum* (n = 21) from the subgenus *Eugeum* have at the most only one genome in common with the *Oreogeum* species *G. montanum* and two common genomes with the *Eugeum* species. In this case it seems likely that the common genomes are homologous with one of the AB genomes in *Geum*

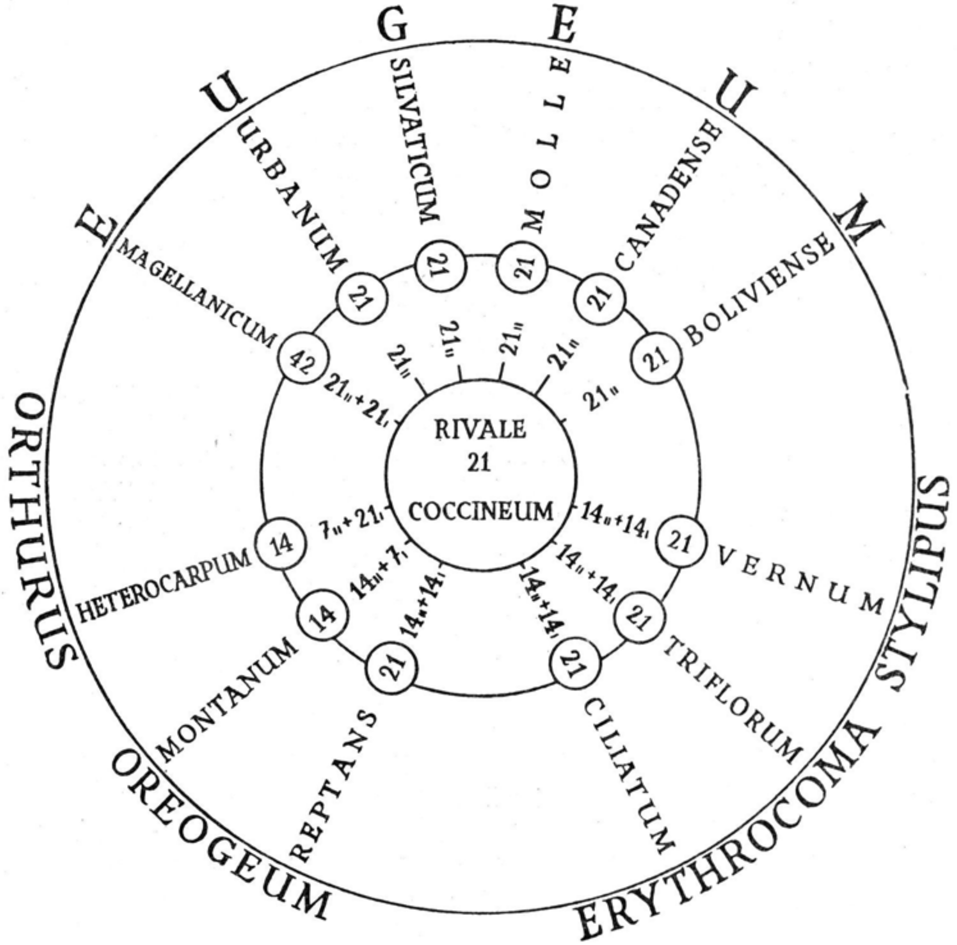


Fig. 145. Diagram illustrating chromosome conjugation in meiosis of hybrids of *G. rivale* and *G. coccineum* from subgenus *Eugeum* with various species from subgenera *Eugeum, Oreogeum, Erythrocoma, Orthurus* and *Stylipus*. All the hybrids were obtained with *G. rivale*, except *G. heterocarpum* the hybrid of which was obtained with *G. coccineum* only

montanum and with the genome C in the subgenus *Eugeum*. The homology of these genomes is, however, greatly weakened so that the number of bivalents in the hybrids is usually far from the possible maximum of 7 and 14 bivalents respectively.

The final conclusion to be drawn at this point of the considerations from the cytogenetic analysis of interspecific hybrids within and between subgenera in the genus *Geum* is that most probably amphiploidy has played an important part in the development and evolution of the genus. Furthermore, it seems that the subgenera *Erythrocoma, Orthurus, Oreogeum* and *Eugeum* have different genomic compositions, the subgenera *Oreogeum, Erythrocoma* and *Eugeum* have two common genomes, but the subgenera *Orthurus* and *Eugeum* have one common genome only.

The now existing numerous *Geum* subgenera constitute probably separate developmental lines with common ancestors in the very distant past. The species in the subgenus *Eugeum* — and probably also of *G. vernum* in the subgenus *Stylipus* — constitute a group of allohexaploids with a common homologous genome. This group has spread widely and has become strongly differentiated without losing completely the homology of its chromosomes. As a result of further crossing and doubling of the chromosome number, fairly numerous dodecaploid species were formed in this subgenus and these species represent the youngest links in the evolutional cycle of the genus.

Figure 145 is an attempt at a diagrammatic illustration of the cytogenetic conditions existing among the *Geum* subgenera investigated in the course of this work. The diagram shows the chromosomal relations between the hybrids of *G. rivale* from the subgenus *Eugeum* with various other species from the subgenera *Eugeum, Stylipus, Oreogeum, Erythrocoma* and *Orthurus*. As no hybrid was obtained between *G. rivale* and *G. heterocarpum* but one was obtained with *G. coccineum* the last species is also placed in the central circle of the diagram. From it it is clearly apparent that *Geum rivale* and *coccineum* which represent the whole subgenus *Eugeum* have 1, 2 or 3 genomes common with all the other *Geum* subgenera covered by this investigation.

RESULTS OF GENETIC ANALYSES OF INTERSPECIFIC HYBRIDS

It has already been mentioned that numerous hexaploid species from the subgenus *Eugeum* produce fertile hybrids with more or less normal chromosome conjugation and that in the next hybrid generations many characters distinguishing the parental species segregate. Out of the intersubgeneric crosses only some hybrids of *G. montanum* from the subgenus *Oreogeum* with species from the subgenus *Eugeum* are partially fertile and make possible a cytogenetic analysis of interspecific differences. The detailed results obtained from genetic analyses of the progeny of interspecific hybrids are assembled in chapter VIII so only the phenomena of a more general nature and throwing some light on the mutual relations between species will be discussed here.

Perhaps the most significant result obtained from the genetic analyses of the hybrids between hexaploid *Eugeum* species is the fact that these species have some allelomorphic genes segregating in F_2 according to Mendelian ratios. The characters displaying Mendelian segregation are as follows:

a) The presence or absence of anthocyanin: — Abundant anthocyanin as in *G. rivale* dominates in F_1 over the absence of anthocyanin in hybrids with *G. coccineum, molle, urbanum, hispidum* and *silvaticum,* whereas, in F_2 the number of plants with and without anthocyanin approaches the ratio 3 : 1.

F_2 of hybrid	No. of plants with anthocyanin	No. of plants without anthocyanin	Percentage ratio
G. aleppicum × rivale	58	24	70.7 : 29.3
G. canadense × rivale	45	19	68.2 : 31.8
G. coccineum × rivale	78	29	72.8 : 27.2
G. silvaticum × rivale	81	21	79.4 : 20.6
G. molle × rivale	63	19	76.8 : 23.2
Total	325	112	74.3 : 25.7

As is seen the observed values fit the theoretical ones almost exactly. In F_1 anthocyanin is not entirely dominant and in F_2 homozygotes can be partly distinguished from heterozygotes but because of the not always distinct differences all plants with anthocyanin are assembled together in the table.

In the backcross of the heterozygote with the recessive homozygote in the hybrid (F_1 *coccineum* × *rivale)* × *coccineum* there are 19 plants with and 23 without anthocyanin, which closely corresponds to the expected ratio 1 : 1. Similar results for the F_2 hybrid *G. rivale* × *urbanum* were obtained by Prywer (1932) and Winge (1926). The latter worker observed, moreover, segregation in the backcross giving the ratio 1 : 1. Within the species *G. rivale* there is also the form *G. rivale* var. *pallidum.* The cross between this form and the typical *G. rivale* with abundant anthocyanin gives hybrids with anthocyanin segregating in F_2 along the 3 : 1 ratio. Dahlgren (1924) who also investigated the hybrid reports segregation giving 137 plants without and 391 plants with anthocyanin and these values correspond rather exactly to the ratio 3 : 1 (74% : 26%).

It appears, therefore, that in respect to the presence of anthocyanin the differences between species in one subgenus are of the same nature as the differences within one species.

b) Colour of petals: — Within the genus *Geum* there are four main petal colours: white, creamy, red and yellow. The yellow colour in the various species is of different tints and of different intensity, ranging from pale yellow to bright gold yellow. The various colours are produced by the corresponding pigments present in the chromoplasts of the petal cells. Anthocyanin when present in the cell sap may suppress the basic petal colour characteristic for the species.

The hybrid between *G. coccineum* with red petals and *G. rivale* with creamy petals has yellow petals. In F_2 of this cross the plants segregate and may have yellow, red or creamy petals. Not considering the various tints of these colours the segregation is as follows:

yellow petals	169	plants
red petals	62	,,
white and creamy petals	68	,,
total	299	,,

The numbers as observed correspond fairly well to the theoretical value for the ratio 9 : 3 : 4 (the theoretical numbers are 168.3 : 56.1 : 74.8). This means that the yellow colour depends on two complementary factors of which *G. rivale* and *G. coccineum* have only one each.

When crossing *G. coccineum* with such yellow flowering species as for instance *G. urbanum* or *G. molle* plants with orange-yellow petals are obtained in F_1 whereas in F_2 the segregation is as follows:

	red		yellow + orange - yellow
F_2 G. urbanum × coccineum	26		92
F_2 G. molle × coccineum	16		58
	42	:	150

The ratio of 42 : 150 between plants with red petals and plants with yellow or organe-yellow petals is rather close to the ratio 1 : 3 (theoretical values are here 48 : 144), i.e. the ratio which should be obtained when the difference between yellow and red colours consists in one allelomorphic pair of genes.

The same results are obtained in crosses between *G. rivale* with creamy petals and species with yellow petals, e.g. *G. silvaticum, aleppicum* or *molle*. The F_1 hybrids in these crosses have yellow petals and the segregation in F_2 is the following:

	Yellow colour	Creamy colour	Percentage ratio
F_2 G. aleppicum × rivale	62	20	75.6 : 24.4
F_2 G. molle × rivale	54	28	65.8 : 34.2
F_2 G. silvaticum × rivale	76	26	74.5 : 25.5
Total	192	74	72.2 : 27.8

From the above results it is apparent that the creamy and yellow colours also differ by one pair of allelomorphic factors.

The ratio of 3 : 1 in the cross *G. rivale* × *urbanum* can also be deduced from the results reported by Rosen (1916) who in F_2 obtained 158 plants with yellow petals and 50 with petals of another colour (creamy?). From her extensive investigations Prywer (1932) reports that in F_2 of this cross there were 291 plants with yellow petals of various shades and 249 plants with white and creamy petals which corresponds fairly accurately to the ratio 9 : 7.

It cannot be decided at present what is the cause for this discrepancy between the results in the segregation of petal colour in the same hybrid.

There are different tints of yellow in the various *Geum* species with yellow petals and this is also the case in the F_1 and F_2 hybrids of these species with *G. rivale*. It is to be assumed, therefore, that in those crosses the colour of petals depends not only on the principal factors determining this trait but also on numerous genes of minor effect modifying the basic colour .This causes the frequent appearance of intermediate colours between yellow and creamy as well as between creamy and white which may change completely the segregation ratios in some crosses.

Very remarkable are the results of the cross between *G. canadense* with white petals and *G. rivale* with creamy petals. In F_1 of this cross the petals are yellow and in F_2 the colour segregates in the following manner:

Yellow colour	Creamy colour	White colour
34	14	16

If the ratio is to be 9 : 3 : 4 the theoretical numbers ought to be 36 : 12 : 16 and as can be seen the values obtained from observations agree closely with the expected ratio 9 : 3 : 4.

The hybrid between *G. canadense* with white petals and *G. coccineum* with red petals has orange yellow petals and such is also the colour of petals in the hybrid of *G. coccineum* with the yellow flowering *G. urbanum* or *molle*. The petals in the hybrids of *G. canadense* with such species as for instance *G. aleppicum* or *G. urbanum* which have yellow petals also have yellow petals, but the nature of the segregation in F_2 could not be established as the hybrids were highly sterile. In the F_2 generation of the hybrid *G. aleppicum* × *canadense* 4 plants had yellow petals and 2 white ones. In F_2 of *G. urbanum* × *canadense* 23 plants had yellow petals and 8 white ones. These relations closely approach the ratio 3 : 1.

From this review of the manner in which the colour of petals is inherited the following picture of the allelomorphic genes present within the group of various hexaploid species in the subgenus *Eugeum* can be constructed.

There are three main allelomorphic pairs defining the following colours of petals:

Gene C is the basic colour factor, its recessive allelomorph causes white colour of petals,

Gene A in the presence of C determines the creamy colour of petals.

Gene B in the presence of C determines the red colour of petals.

Genes A and B together determine in the presence of C the yellow colour of petals.

Such species with yellow petals as *G. aleppicum, urbanum, molle* and *silvaticum* have thus the formula CCAABB, *G. coccineum* has the formula CCaaBB, *G. rivale* the formula CCAAbb and *G. canadense* the formula ccAABB. The petals in the hybrids with the formula CCAaBb and CCAABb are yellow though of various shades. These assumptions explain all the results obtained in F_1 and F_2 hybrids. It is thus evident that numerous hexaploid species in the subgenus *Eugeum* with very different morphological characters and geographical distribution have an allelomorphic set of three pairs of factors producing the different pigments in petals. It undoubtedly is a substantial proof of the common phylogenetical origin of the whole group of species.

All the factors just discussed refer to the pigments in the chromatophores but have nothing in common with the red anthocyanin pigmentation considered earlier. This pigment may also be present in the petals and may obliterate completely the basic petal colour. Quite certainly alongside of the main genes there are also other factors defining various shades in the colour of petals.

It seems likely that the same factors which govern the colour of petals in the subgenus *Eugeum* are present too in the other subgenera. For instance, the yellow flowering *G. montanum* from the subgenus *Oreogeum* in crosses with such *Eugeum* species as *G. rivale* or *coccineum* produces in F_1 the same colour of petals as do the yellow flowering species from the subgenus *Eugeum*. In F_2 of the crosses with *G. montanum* the segregation is the same as in the corresponding crosses within the subgenus *Eugeum,* though, in view of the small number of individuals it has been impossible to observe the same numerical ratios. It is remarkable that *G. ciliatum* from the subgenus *Erythrocoma* which has creamy petals like those in *G. rivale* gives with the red flowering *G. coccineum* the same yellow colour of petals as in F_1 of the hybrid *G. rivale* × *G. coccineum*. It is unfortunate that the F_2 generation of the hybrid *G. ciliatum* × *coccineum* could not be analysed because of its complete sterility.

c) The emargination on the tip of petals as in *G. rivale* is recessive in respect to the rounded tip. The recessive character of this trait was observed by Prywer (1932) and Rosen (1916) in the hybrid *G. rivale* × *G. urbanum* and in the course of the present investigations it was observed also in many hybrids between *G. rivale* and species with nonemarginate petals. Prywer found that in F_2 of the hybrid *G. rivale* × *G. urbanum* the petals without and with emargination at tip were segregating at the ratio 3 : 1. (370 plants without and 122 with emargination, i.e. 3.03 : 0.97). The segregation of this character in the hybrids covered by the present investigation is as follows:

Hybrid	No. of F_2 plants with petals		Percentage ratio
	emarginate	nonemarginate	
G. aleppicum × rivale	56	26	68.3 : 31.7
G. canadense × rivale	41	23	64.0 : 36.0
G. coccineum × rivale	136	56	70.3 : 29.7
G. silvaticum × rivale	74	28	72.5 : 27.5
G. molle × rivale	61	21	74.4 : 25.6
Total	368	154	70.5 : 29.5

As is shown above the segregation ratio in F_2 of all the crosses approaches the ratio 3 : 1, which seems to indicate that the emarginate tip of the petals depends on one factor recessive in respect to the rounded tip petals characteristic for the majority of species in the subgenus

Eugeum. However, in F_2 generations it is frequently observed that in plants with emarginate petals the incision is of various depth and this indicates that besides the basic factor determining emarginate petals there are also other factors modifying its effect.

When examining the segregation of other traits in interspecific hybrids it is almost impossible to classify the individuals into a few classes of contrasting characters, as individuals with intermediate traits are too numerous. And so, for instance, in respect to the presence or absence of claw at the base of the petals and the straight or drooping floral peduncles it is still possible to distinguish that the segregation approaches the ratio 3 : 1, but both the length of the claw and the degree of drooping of the peduncles differ so much that the variations are more continuous-like. It seems that in the case of these characters there are probably basic factors defining the presence or absence of the claw or the drooping of the peduncles, but at the same time the number of the modifying factors is so great that the segregation of the traits is almost completely obliterated. These two characters are in a way transitional to traits inherited in F_2 in a continuous manner. Among the traits giving continuous segregation are, for instance, the size of sepals and petals, the length of the gynophore and receptacle, or the number and size of achenes. Continuous segregation is also shown by such characters difficult to estimate as the degree of pubescence and branching of stems, and the shape and size of leaves. A remarkable circumstance is that continuous segregation in F_2 is shown primely by all the characters which have a greater significance in the systematic classification of the whole group. In F_1 these characters are usually intermediate between the parental species and in F_2 as a rule they segregate within limits of both parental species but sometimes transgression is observed. Numerous examples illustrating this type of segregation are assembled in chapter VIII.

In backcrosses individuals almost identical with the pure parental species appear already in the second backcross. Some plants in F_2 and in the next generations also display a striking resemblance to the parental species and this in spite of the small number of examined individuals. In view of the great number of characters (consequently also of factors) distinguishing the parental species, the so rapid appearance of hybrids with characters approaching the parental forms is certainly very unlikely, if independent segregation of all pairs of the distinguishing factors is accepted. This phenomenon was already observed many times in the progeny of interspecific hybrids and was investigated most fully by E. Anderson (1939). Anderson suggests that this effect is primely due to the restriction of segregation by the linkage of parental genes. As a result, in F_2 or in the backcross only a small proportion of the theoretically possible combinations do in fact appear. Consequently in F_2 plants with the combinations of traits characteristic for the parental species and F_1 hybrids are far more frequent than might be expected on the basis of an entirely independent segregation of hereditary factors.

It is worth noting that in F_1 as well as in F_2 among the traits inherited in a more or less continuous manner, i.e. those determined by many hereditary factors with a relatively small individual effect, there are almost no new ones not already present in the parental species, in contrast to what is observed in the case of petal colour which depends on relatively few hereditary factors with contrasting phenotypic effects.

Although the problem has not been investigated more fully it is apparent that in interspecific crosses not only the morphological traits segregate, but segregation refers also to physiological properties, and these are perhaps the most significant for the biology of a species. This can be readily seen in F_2 plants from the differences in the flowering time, the length of the vegetative period, resistance to frost and parasite fungi (primely mildew), the general viability of the hybrids etc. These and many other traits associated with thermic and photoperiodic requirements, growth, differentiation and with other processes of vital importance for the properties of a species are probably in many instances strictly correlated, as a result of the pleiotropic effect of hereditary factors with morphological effects. The plants showing physiological properties strongly reducing viability are eliminated from the progeny of the hybrids at various stages of growth. In F_2 the elimination of zygotes at the various phases of development is often observed in interspecific hybrids. It seems that such an elimination may favour the plants more related with the F_1 hybrids and parental species. This would also cause the more rapid reproduction of parental forms in the progeny of interspecific hybrids.

The results obtained in the course of my investigations on the interspecific hybrids within the subgenus *Eugeum*, as outlined in chapter VII and VIII of this work, are very similar to the results reported by many workers from other genera of flowering plants. It will be sufficient to mention here as an example the brilliant work of Baur (1932) and his school (Kühl 1937, Hackbarth *et al.* 1942) on the section *Antirrhinastrum* in the genus *Antirrhinum*. These investigations show that *A. sempervirens, glutinosum, litigiosum, Ibanyezi, Linkieanum, tortuosum* and *latifolium* constitute a group of closely related species forming one coenospecies. Such taxonomically significant characters as for instance the size of organs, growth habit, nature and degree of pubescence, and ecological properties are usually inherited polygenically. Crosses of these wild species with the cultivated forms of *A. majus* show that all the wild species have allelomorphic genes corresponding to numerous recessive genes of *A. majus,* e.g. those determining the colour of flowers.

These results coincide very well with those obtained in the subgenus *Eugeum* where various species have allelomorphic genes affecting the presence of anthocyanin or different colours and shapes of petals. On the other hand, the majority of the other characters are inherited polygenically. Consequently, it can be assumed as highly probable that numerous species in the subgenus *Eugeum* have many common allelomorphic genes and many analogous polygenic systems. The polygenic systems in the particular species determine most of the morphological and probably too of the physiological traits of an adaptive nature. At the same time these traits make possible the isolation and maintenance of specific differences, despite the lack of intersterility between the species. It seems also that these complex polygenic systems determine ecological requirements which are different in every species, the time of sexual maturity, floral structures and expression of achenes. In respect to these characters the *Eugeum* species show no fundamntal qualitative differences in contrast to differences between the subgenera of the genus *Geum*.

The chief evolutional developmental trends within the subgenus *Eugeum* seem to have been tending away from plants with strongly developed caudex, short, scapus-type stem with one or few flowers, large conspicuous flowers, large achenes and haired rostrum. These primitive plants had a calyx with erect sepals and a conspicuous hypanthium. In connection with the change to the epizoochoric propagation some of the species developed a gynophore of various lengths. The species were long perennials and were clearly associated with the mountain ranges where they originated. Of the now living species in the subgenus *Eugeum* the best fitted to this description of the primitive type are such species as *G. silvaticum, G. coccineum, G. rivale* and *G. capense*. However, numerous traits in these plants are of an advanced type and have developed in the course of the long evolutional history. The advanced traits within the subgenus *Eugeum* are characteristic for the younger species growing in the lowlands and on territories more xeric than in the mountains. These species have a less developed caudex and associated with this a shorter lifetime, their stems are numerous, profusely branched with numerous small flowers. The calyx has reflexed petals, there is no hypanthium and usually no gynophore, the achenes are small, very numerous with distinctly reduced and glabrous rostrum. The species of this type are represented primely by *G. aleppicum, G. macrophyllum, G. canadense* and *G. laciniatum,* and of the European species by *G. urbanum.*

A circumstance of some interest is that most traits in the evolutionally younger species are determined polygenically. In crosses of theses species with the more primitive ones the expression of the traits is not always intermediate but usually the characters from the evolutionally more advanced species partly dominate. Also in F_2 the curves of variations illustrating the segregation of particular traits are usually not symmetrical and are clearly shifted towards the end of the scale representing the trait from the evolutionally younger species. This refers for instance to such characters as the size and branching of stems, and the size of petals, rostrum and achenes. It seems, therefore, that in the subgenus *Eugeum* natural selections aimed at the partial dominance of factors determining the most effective adaptation to efficient dissemination by means of epizoochory. This could be achieved by an increase in the number of achenes compensated by the decrease of their size and the more efficient structure of the flower and the adhesive apparatus (calyx reflexed, rostrum short and stiff). The system of traits favouring effective epizoochoric dissemination is based on polygenic systems partially dominant over the genes from the species showing less efficient adaptation to that type of dissemination. Numerous examples of heredity along these patterns are assembled in chapter VIII and so it would be useless to repeat them all over again.

It has been shown in chapter V that analogically to the interspecific differences there are also, though on a smaller scale, differences within some species of the subgenus *Eugeum.* For instance, my experimental cultures included plants of *G. rivale* from a variety of habitats which differed greatly by the size of leaves, the length and branching of stems, the size of sepals and petals, length of gynophore, size of rostrum etc. The differences are hereditary and persisted through the many years that the plants were cultivated under approximately the same conditions of an experimental plot. Even considerable differences are not always connected with a separate geographical origin, e.g. my cultures comprised two ecotypes of *G. rivale* from habitats in the Tatra Mts. near Hala Gąsienicowa that differed radically by the size of leaves, stems and flowers. On the other hand some North American specimens were closely related to ecotypes from the Polish lowlands. Perhaps the most distinctly separate is the *G. rivale* from Iceland, it has very short stems, half opened flowers, petals with very short claw and floral base almost without gynophore. This form may be a separate geographical race of *G. rivale* which, according to my investigations on herbarium specimens, is probably restricted to Iceland and the Faröe Isls. Already Turesson (1925, 1931) reports that within *G. rivale* there is a distinct differentiation into ecotypes varying by the height of stems and flowering time. The crosses that I made between extremely different ecotypes show that in the F_1 generation the traits are expressed intermediately and segregate distinctly within the limits of the parental forms. The segregation is of the same continuous character as in interspecific crosses. The only difference consisted in the smaller range of variations and the complete fertility of the hybrids. A similar ecotype variation is exhibited by other *Geum* species with a large geographical distribution, this being especially true in the case of such species as for instance *G. aleppicum* and *G. canadense*. These results seem to indicate that the difference between interspecific and intraspecific variations within the group of hexaploid species in the subgenus *Eugeum* is rather quantitative than qualitative in character. Thus, the species in this group arose probably by way of gradual differentiation of the primitive ancestral form of the subgenus and constitute a common monophyletic group with homologous chromosomal sets and many allelomorphic genes.

With the techniques of genetic analysis much new knowledge has been gained on those groups of the youngest species in the genus which make up the subgenus *Eugeum*, but by contrast very little has been added to our understanding of the origin of the group as a whole and its relationship with the other *Geum* subgenera. This is primely due to the high sterility of intersubgeneric hybrids. Only the pentaploid hybrids of the tetraploid *G. montanum* from subgenus *Oreogeum* with the hexaploid species from subgenus *Eugeum* are sufficiently fertile to enable their genetic analysis. The most interesting in this connection are probably the results referring to the manner in which the pistil structure is inherited, a trait that has passed through a very fundamental evolution during the developmental history of the genus.

Much attention has been given earlier in this work to the F_1 hybrids between *G. montanum* with straight, long, pennately haired styles and the species from the subgenus *Eugeum* with styles very differently expressed according to the species used in the cross. For instance the hybrids of *G. montanum* with *G. canadense, silvaticum, molle* and *hispidum* have in most cases straight styles and only a small proportion of styles with a weakly marked geniculate bend. In the hybrids of *G. montanum* with *G. rivale, aleppicum, coccineum, urbanum, laciniatum* and *macrophyllum* there is a great variety in the expression of styles even in one plant. The styles range from quite straight to typically hooked. Finally the hybrids of *G. montanum* with the dodecaploid *G. magellanicum* and *G. pyrenaicum* have all the styles hooked in the manner characteristic for the subgenus *Eugeum*. The hexaploid *G. reptans* in crosses with *G. rivale* or *G. coccineum* gives hybrids with long, straight styles as in the subgenus *Oreogeum*. These results indicate that the particular species of the subgenus *Eugeum* possess various sets of hereditary factors determining the expression of the achenes in these species. These sets when united with the set of genes from *G. montanum* may be in F_1 completely recessive, they may be partially dominant or even completely dominant as in the case of the dodecaploid species. In the F_2 generation of the cross *G. montanum* × *rivale* segregation occurs giving forms with achenes shaped as in the parental species and numerous plants of the F_1 type. In backcrosses the type of styles characteristic for the species used in the cross dominates. These results seem to indicate that the main differences in the style structure of both subgenera are determined by a relatively small number of hereditary factors giving even in a scanty F_2 the reconstruction of both parental style types. As has been mentioned earlier, the hybrids of *G. montanum* with the hexaploid species from the subgenus *Eugeum* segregate in F_2 also in respect to the other characters distinguishing the parental species, e.g. leaf shape, height and branching of stems, shape and colour of petals, the presence of anthocyanin, drooping of floral peduncles, length of gynophore and so on. However, in view of the high lethality of the aneuploid F_2 plants a detailed analysis of segregation was impossible. Nevertheless, it seems that in the two homologous genomes of the species in the subgenus *Eugeum* and *G. montanum* there are allelomorphic factors indicating the common origin of both subgenera.

XI. AN ATTEMPT AT RETRACING SOME EVOLUTIONAL STAGES OF THE GENUS *GEUM* ON THE BASIS OF MORPHOLOGY, CYTOLOGY, GENETICS AND GEOGRAPHICAL DISTRIBUTION

INTRODUCTION

If one wishes to retrace the evolutional history of any group of plants one must first get fully acquainted with its taxonomy, so as to be able to judge with great precision the true value of the various systematic units of different ranks distinguished in the group. The tendency of taxonomists to divide systematic units into ever new genera and species is often met with, but this procedure in many instances only obscures the significant relationships existing between units of various ranks. When investigating a whole genus or a group of related genera a very good understanding can be acquired of the diagnostic value of various taxonomic traits. However, in many cases this kind of morphologically comparative or morphologically developmental approach does not reveal the true nature of the relations between systematic groups. In this connection cytogenetic investigations are of great value, as some measure of the relationships between species or their groups can be obtained from an analysis of chromosome homology or hybrid fertility.

In the plant groups where polyploidy played a more important part in evolution no serious researches or considerations can be imagined without a full understanding of the mutual relations between the various polyploid types. The results obtained from cytological and genetic analyses of hybrids reveal much significant data on the nature of those processes in the formation of species which are responsible for the development of separate systematic units. The primitive and ancestral traits in a group of species under investigation can be distinguished with some success from the secondary traits acquired in the course of the evolutional history only when the data gained from morphological and cytogenetic researches are at hand.

When, furthermore, the geographical distribution of the plants studied by the morphological and cytogenetic techniques is also known it becomes possible to define the past and existing evolutional centres in which the various forms are concentrated and to retrace the probable routes of migration.

The ever more exact picture of the historical changes in plant life on earth, form the Mesozoic era when the Angiosperms originated to the present day, which is being reconstructed in our times by palaeobotany, constitutes the necessary background for any attempts to trace the evolutional history of a group of plants without recourse to direct palaeobotanical evidence.

Researches aimed at the reconstruction of the evolutional history of plant groups by means of morphological and geographical analyses, started by the excellent works of Engler, Diels and Wettstein and later continued by Gams, Scharfetter as well as many other systematists and geographers of plants, entered a new phase in the present century when the cytogenetic techniques were developed. The understanding of the significance which the processes of amphiploidy have for the evolution of flowering plants has made possible an experimental "synthetization" of species already known in nature and in many cases has permitted to reach deeper into the relations between the various plant groups. It is apparent from the modern monographs of such genera as *Nicotiana* (Goodspeed 1953, 1954), or *Gossypium*

(Hutchinson, Silow and Stephens 1947) that in these genera whole groups and sections arose through amphiploidy. In other genera such as *Crepis* (Babcock 1947) or *Narcissus* (Fernandes 1951) polyploidy as a factor in the development of species was less important, but the analysis of chromosomes has made it possible to trace more exactly the distinct developmental lines.

This work on the genus *Geum* is far less detailed than the investigations on other genera just mentioned, but nevertheless I believe that the results as outlined here are sufficient to attempt some general conclusions on the probable developmental directions in the genus.

BASIC CHROMOSOME NUMBERS IN THE VARIOUS GROUPS OF THE ROSE FAMILY AND THE MUTUAL RELATIONS BETWEEN THE SUBFAMILIES

The four basic chromosome numbers in the family of *Rosaceae* are 9, 8, 7 and 17. The distribution of the basic numbers is the following:
The whole subfamily of *Prunoideae* has x = 8.
The whole subfamily of *Pomoideae* has x = 17.

The subfamily of *Spireoideae* has x = 9 in the tribe of *Spireae,* x = 8 in the tribe of *Quillajeae,* whereas the chromosome numbers in the tribe of *Holodisceae* are unknown to me.

The subfamily of *Rosoideae* has x = 9 in the tribe of *Kerrieae,* x = 8 in the tribe of *Alchemilleae* and x = 7 in the tribes of *Potentilleae, Ulmarieae, Sanguisorbeae* and *Roseae.*

The subfamily of *Neuradoideae* has x = 7.

The subfamily of *Dryadoideae* has x = 9 in the tribes of *Dryadeae* and *Cercocarpeae,* and x = 7 in the tribe of *Geeae.*

The basic chromosome number in the subfamily of *Chrysobalanoideae* is not known to me.

The *Chrysobalanoideae* which comprise numerous tropical tree species are loosely related with the subfamily of *Prunoideae,* whereas, by the zygomorphic flower structure in many genera they are related to the family of *Leguminosae.* Quite certainly this subfamily, growing mainly in the tropical zone, represents a very ancient and distinct developmental line in respect to the other members of the rose family. In the more recent systems of the *Angiospermae,* as for instance in that of Gundersen (1950), the *Chrysobalanoideae* are classified as a separate family differing from the family of the *Rosaceae,* among other things, by wood anatomy.

The subfamily of *Prunoideae* with x = 8 comprises woody plants only and represents a distinct and primitive developmental line of the *Rosaceae.* It is related on one side with the *Chrysobalanoideae* and on the other with the subfamily of *Spiraeoideae.* The *Prunoideae* occupy mainly areas in the temperate zones, though the genus *Pygeum* and some species of the genus *Prunus* grow in the tropics. The genus *Nuttalia* from western North America which has flowers with 5 pistils connects the *Prunoideae* with the subfamily of *Spireoideae*.

The subfamily of *Spireoideae* is undoubtedly another primitive type of the *Rosaceae* relating them to the family of *Saxifragaceae*. The *Spireoideae* are mainly shrubs, sometimes trees and more rarely perennial herbs which occupy extratropical areas on both hemispheres. They are distinctly related with the subfamilies of *Pomoideae* and *Rosoideae* which may be regarded as side lines developing from the *Spireoideae* type.

The subfamily of *Pomoideae* represents a decidedly distinct evolutional line with x = 17. It comprises exclusively woody species from the northern temperate zone and is related with the subfamilies of *Prunoideae* and *Spireoideae*. Its basic chromosome number of x = 17 shows that this subfamily could arise through amphiploidy between species with x = 8 and 9, which as we know are the basic numbers in the subfamilies of *Spireoideae* and *Prunoideae*.

The four subfamilies mentioned above, i.e. *Chrysobalanoideae, Prunoideae, Pomoideae* and *Spireoideae* comprising trees and shrubs are, in my opinion, four ancient and distinct evolutional lines in the family of *Rosaceae*, with the reservation, however, that the *Pomoideae* are of amphiploid origin which developed from species with x = 8 and 9.

The subfamilies of *Rosoideae* and *Dryadoideae* are undoubtedly closely related and probably developed from the subfamily of *Spireoideae* with which the *Rosoideae* are connected primely by the tribe of *Kerrieae*. The subfamily of *Dryadoideae* with its tribes of *Dryadeae* and *Cercocarpeae* is related with the tribes of *Holodisceae* and *Spireae* in the subfamily of *Spireoideae*.

Both the *Rosoideae* and *Dryadoideae* developed whole tribes and numerous genera of herbaceous plants which are not present in any of the subfamilies mentioned earlier. It is very remarkable that almost all these herbaceous genera have the basic chromosome number x = 7, the only exception being the two related genera *Alchemilla* and *Aphanes*. The subfamily of *Rosoideae* is associated through the shrubby tribe of *Kerrieae* with x = 9 to the tribe of *Spireae* with x = 9. On the other hand in the tribe of *Spireae* there is a transition through the genera *Eriogynia* and *Gillenia* from shrubs to herbs. The remaining tribes of the subfamily of *Rosoideae* all have, with the exception of *Alchemilleae*, the basic chromosome number x = 7 and represent the youngest evolutional branch in the family of *Rosaceae*. The numerous genera in these tribes, such as for instance the genera *Rubus, Rosa,* and *Potentilla,* are at present still in the course of intense processes of species formation.

In a similar manner in the subfamily of *Dryadoideae* the woody and shrubby tribes of *Cercocarpeae* and *Dryadeae* with x = 9 constitute the primitive ancestral forms for the herbaceous genera in the tribe of *Geeae* with x = 7. However, this problem will be dealt with more fully later on.

It seems very likely, therefore, that for numerous tribes of the subfamily of *Rosoideae*, similarly as for the tribe of *Geeae* with x = 7, the original forms were trees or shrubs with x = 9. This ancient ancestral group is represented in our days by the genera in the tribes of *Spireae, Kerrieae, Cercocarpeae* and *Dryadeae.* The majority of genera in these tribes are monotypic with small relic geographical distributions lying primely on both sides of the Pacific Ocean. For instance the tribe of *Spireae* consists of:

genus *Pentactina* with one species in Korea,
genus *Stephanandra* with 4 species in China, Korea and Japan,
genus *Pterophytum* with one species in Pacific North America,
genus *Gillenia* with 2 species in Pacific North America,
genus *Neillia* with about 10 species in China and the Himalayas and
genus *Lutkea* with one species in Pacific North America.

The tribe of *Kerrieae* consists of:

genus *Rhodotypus* with one species in Japan and China,
genus *Kerria* with one species in Japan and China and
genus *Neviusia* with one species in North America (Alabama).

Most of the genera and species in the tribe of *Cercocarpeae* and *Dryadeae* also grow in Pacific North America (genera *Cercocarpus, Purshia, Chamaebatia, Fallugia* and *Cowania*).

In the tribe of *Spireae* and in the tribe of *Dryadeae* only some few genera — e.g. *Spireae* and *Dryas* — have more extensive circumboreal distributions to which they spread in the course of their later evolutional history, whereas, the majority of the genera have very few species with distributions restricted to refugia and quite certainly represent very ancient primitive forms in the rose family.

THE TRIBES OF *CERCOCARPEAE* AND *DRYADEAE* AND THEIR RELATION TO THE TRIBE OF *GEEAE*

The tribe of *Cercocarpeae* comprises in the classification here adopted 3 genera: *Cercocarpus* H.B.K., *Purshia* DC and *Chamaebatia* Benth.

The genus *Cercocarpus* comprises about 10 species of shrubs and small trees growing in the Cordilleras from Oregon to Mexico. The flowers here have a long calyx tube and one pistil with a long pennately haired style (Fig. 146).

The genus *Purshia* has two species distributed in the Cordilleras from Oregon to Mexico. The species are represented by shrubs with one straight haired pistil in the flower, with hypanthium and style much shorter than in *Cercocarpus*. In the flowers of these plants the stigma is elongated and runs down along the style.

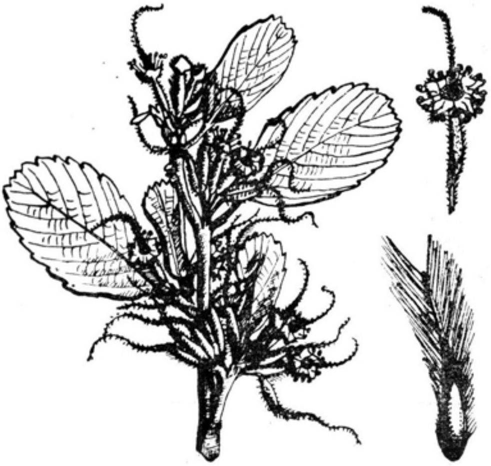


Fig. 146. *Cercocarpus fothergilloides* H.B.K. (After A. Engler and K. Prantl, Die natürlichen Pflanzenfamillen)

The genus *Chamaebatia* has two species growing only in the Cordilleras and California. The species comprise shrubs with tripinnate leaves and flowers with one pistil at the bottom of a short hypanthium.

It is shown on Map 35 that the whole tribe is distributed only in refugial regions, primely in California and Mexico. The number of pistils reduced to one only dissociates the tribe from the type of plants in the tribes of *Dryadeae* and *Geeae*.

The tribe of *Dryadeae* comprises the genera *Cowania, Fallugia* and *Dryas* which by the type of flower and pistil structure are very closely related to some *Geum* species.

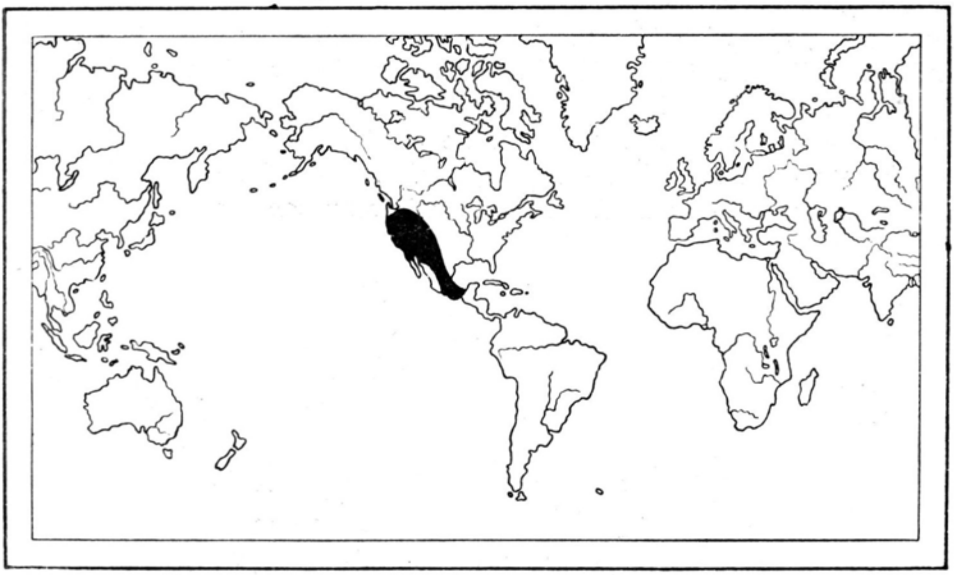
The genus *Cowania* (Fig. 147) consists of 6 species appearing in the Cordilleras, primely in California and Mexico. The plants are shrubs with a flat floral base, numerous achenes in a flower and long, pennately haired styles.

The genus *Fallugia* (Fig. 148) comprises only one species growing in the Cordilleras in California and Mexico. It is a shrub with numerous achenes and long, pennately haired styles which resemble greatly the structure of styles in the genus *Dryas*.

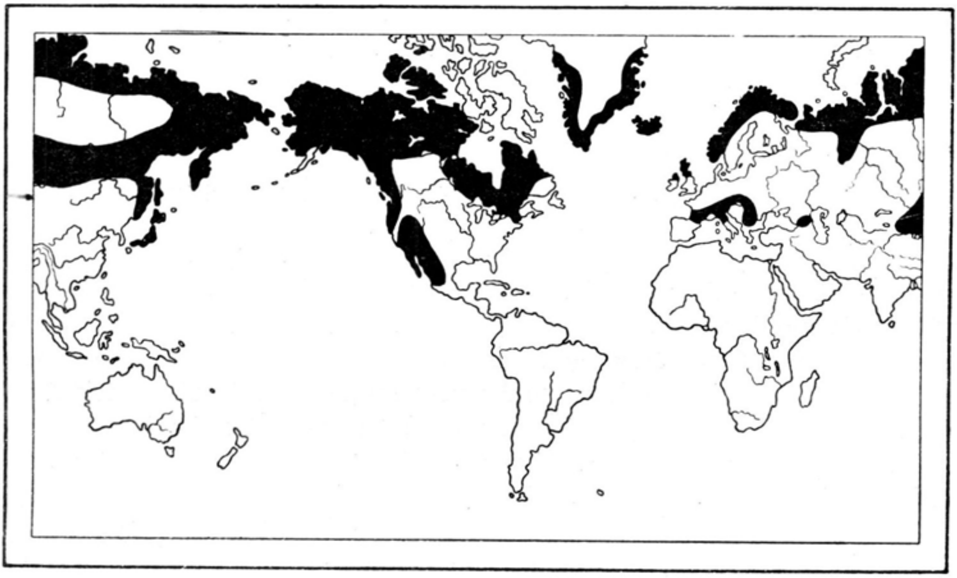
Fig. 147. *Cowania mexicana* Don. (After A. Engler and K. Prantl, Die natürlichen Pflanzenfamillien)

Fig. 148. *Fallugia paradoxa* Endl. (After A. Engler and K. Prantl, Die natürlichen Pflanzenfamillien)

The genus *Dryas* (Fig. 149) has an extensive distribution in the holarctic regions and in the mountains of Eurasia and North America (Map 36). The species of the genus *Dryas* are closely related with one another and the number of species which are distinguished depends greatly on the opinion of the particular systematists. The main species



Map 35. Distribution of the tribe of *Cercocarpeae*



Map 36. Distribution of the tribe of *Dryadeae*

in North America are *Dryas Drummondii* and *integrifolia*. Another species, *Dr. octopetala*, has a large distribution in the arctic region and many disjunctive areas in the mountains of Europe, on Iceland and in Greenland. Many small species such as *Dr. grandis, viscosa, oxyodonta, caucasicum, ajanensis, Tschonoskii* and *crenulata* grow in northern Asia and in Asiatic mountains. All these forms are closely related, and though Juzepchuk in the Flora of the USSR distinguishes them as separate species, they form one large composite species.

Characteristic for all the three genera in the tribe of *Dryadeae* are the numerous achenes in the flowers and long, pennately haired styles adapted to anemochoric dissemination which, perhaps, is associated with their montane or arctic distribution. The genera *Cowania* and *Fallugia* occupy refugia only, whereas, it is known from palaeobotanical evidence that the genus *Dryas* underwent numerous migrations together with the rest of the arctic vegetation. As a result of the Pleistocene migrations the various disjunctive areas it now occupies were isolated and constitute today small local species of a relatively recent origin.

Fig. 149. *Dryas octopetala* L. (After G. Hegi Illustrierte Flora von Mitteleuropa)

The tribe of *Geeae*, especially the species from the genus *Geum*, is closely related with the species in the tribe of *Dryadeae*, so that it is not easy to define a line separating them. Bolle (1933) includes in the genus *Sieversia*, which he distinguishes, two *Geum* species, *G. pentapetalum* (L.) Makino and *G. selinifolium* Hultén. The species are represented by small shrubs and are related to the genus *Dryas* (Linnaeus classified *G. pentapetalum* simply in the genus *Dryas*). They grow in north-eastern Asia and have pistils of the same structure as in *Dryadeae*. If it will be found that the basic chromosome number in these species is 9, then it will probably be best to transfer the two species from the genus *Geum* to the tribe of *Dryadeae* as did Bolle. In any case they are undoubtedly near the boundary between the two tribes.

TAXONOMIC DIFFERENTIATION WITHIN THE TRIBE OF *GEEAE* AND THE GENUS *GEUM*

The three genera in the tribe of *Geeae* are *Waldsteinia, Coluria* and *Geum*. The first to be discussed will be the division of the genus *Geum* into subgenera, and the other genera will be dealt with later. In the approach followed in the course of this work the genus *Geum* is divided into the following subgenera: 1. *Sieversia* 2. *Neosieversia* 3. *Oreogeum* 4. *Andicola* 5. *Erythrocoma* 6. *Acomastylis* 7. *Oncostylus* 8. *Woronowia* 9. *Orthurus* 10. *Eugeum* 11. *Stylipus*.

The morphological differences between the subgenera are described at the beginning of this work, but it is worth reminding that the first 6 subgenera listed above have styles elongated, usually long haired and more or less related to the styles in the tribe of *Dryadeae*. In the subgenus *Oncostylus* the styles have a hooked stigmatic part which is thus adapted to epizoochoric dissemination. In the subgenera *Orthurus, Eugeum* and *Stylipus* the stigmatic part of the style is deciduous while the persisting rostrum is hooked in the subgenera *Eugeum* nad *Stylipus,* and equipped with adhesive bristles in the subgenus *Orthurus*. These are also adaptations to epizoochory. Finally in the subgenus *Woronowia* the style is deciduous from the achene almost at the base. This last subgenus approaches in the structure of its pistils to the genera *Waldsteinia* nad *Coluria*, where the styles are entirely deciduous from the achenes.

GEUM SUBGENERA WITH STRAIGHT STYLES PERSISTENT ON THE ACHENES

The subgenera to be considered here are the first six listed in the preceding paragraph. The subgenus *Sieversia,* as has been mentioned, is situated on the boundary line between the *Dryadeae* and *Geum*. Its two species, *G. pentapetalum* and *G. selinifolium* represent small shrubs with slightly convex floral base, numerous pistils and long, haired styles (Fig. 150). Both species grow in the Pacific regions of north-eastern Asia on the south coastal territories of the Sea of Okhotsk, in Kamschatka, Japan and on the Kuriles (Maps 5 and 6).

The subgenus *Neosieversia* with its one species. *G. glaciale* Adams (Fig. 151) has also a long, pennately haired style. The plant is a herb and the floral base in the flower is convex in a manner decisively characteristic for the genus *Geum*, but in other respects the species is related to the *Dryadeae*. According to Hultén (1937) the distribution of *G. glaciale* indicates its migration from Behringia along the coastal regions of artic Asia to the river Yenesei and on the American continent to the Arctic Archipelago (Maps 7 and 8).

Fig. 150. *Geum pentapetalum* (L.) Makino
(After Flora of the USSR v. X)

These two *Geum* subgenera are the most related to the *Dryadeae*. They are of an arctic and montane character and their centre of distribution lies in north-eastern Asia. The subgenus *Acomastylis* is both arctic and montane in its distribution (Map 12), whereas, the other subgenera, i.e. *Erythrocoma* (Map 15), *Oreogeum* (Map 9) and *Andicola* (Map 13), comprise montane species alone. *G. calthifolium* from the subgenus *Acomastylis* grows at present round the Behring Sea reaching on one side to the Aleutians, Alaska and the Rocky Mountains, and on the other along the coastal areas of Asia south to Yezo. Two species, *G. Peckii* and *G. radiatum* closely related to *G. calthifolium* grow today only on high mountain peaks in the White Mts. and Roan Mts. in the states of New Hampshire and North Carolina. *G. Rossii* grows too in the arctic zone of the Pacific, in N. America and north-eastern Asia. This species is closely related to the montane species *G. turbinatum* and the "species" *gracilipes, depressum* and *sericeum* which all grow in the Rocky Mountains and the Cordilleras. The last two *Acomastylis* species, i.e. *G. elatum* and *G. sikkimense,* represent in the subgenus the Himalayan sieries and show no close relationship with any arctic species. This refers also to the remaining three *Geum* subgenera with straight styles entirely persisting on the achenes. The three subgenera comprise montane specsies showing today no direct relation with the arctic species. The subgenus *Oreogeum* is distributed in the mountains of Europe, the subgenus *Erythrocoma* in the monutains of North America (*G. triflorum* spreads also to the lowlands), and the subgenus *Andicola* with its one species *G. andicolum* is found on the southern hemisphere in the mountains of Chile.

Fig. 151. *Geum glaciale* Adams (After Flora of the USSR v. X)

RELATION BETWEEN *GEUM* SUBGENERA WITH STRAIGHT STYLES AND THE SPECIES IN THE TRIBES *CERCOCARPEAE* AND *DRYADEAE*

It seems that in the subfamily of *Dryadoideae* the same evolutional process occurred which was characteristic for numerous families of the Angiosperms, i.e. the primitive plants were trees and from them the herbs originated at a later stage. The arborescent genera still existing in the tribe of *Cercocarpeae* probably represent the last survivals of the primitive arborescent types in this subfamily. The specialization which the now living genera have passed through is indicated by the reduction to one in the number of pistils and the strongly elongated hypanthium in the tribe of *Cercocarpeae*. The tribe of *Dryadeae* probably arose as a separate evolutional line of this subfamily in the very remote past when it produced the type of shrubs with numerous achenes in the flower. The genera *Cowania* and *Fallugia* existing at present have flower and fruit structures very closely related to the genus *Dryas* and numerous *Geum* subgenera.

Similarly as the tribes of *Kerrieae* and *Spireae*, the primitive relic genera in the tribes of *Cercocarpeae* and *Dryadeae* grow on refugial areas, primely montane ones, far away from the territories affected by diluvial glaciations, mainly in the coastal regions of the Pacific Ocean.

Presumably all these four tribes are relics of very ancient types in the rose family which is probably one of the older families among Angiosperms. The tribes of *Cercocarpeae* and *Dryadeae* comprise montane plants of the temperate climate. It seems that in the Tertiary numerous arctic and boreal genera arose from the primitive trees and shrubs in the boreal and circumpolar zones and as the climate became more severe in the late Tertiary period these genera spread to new areas. In the new climatic conditions the primitive shrubby plants gave rise to herbaceous plants, better adapted to the new environment. When in turn during the late Tertiary oreogenic movements the mountains of Eurasia and America were formed numerous groups of boreal species passed to the mountains and in many cases migrated along them far to the south. In the course of these processes the groups were strongly differentiated and formed numerous new genera, subgenera and species. The once continuous distributions were later disrupted falling apart into numerous disjunctive ones.

In north-eastern Asia the ancient Pleistocene arctic and boreal flora has survived in a great extent to our times, because these territories were never completely glaciated. Moreover, palaeobotanical investigations — primely those of Krysztofowicz — have revealed that on the north-eastern Asiatic territories the Tertiary floras always had a more temperate character than, for instance, the corresponding floras of Europe, where according to region and period they were more or less tropical. Hultén (1937) points out that the territories surrounding the Behring Sea, which territories he calls Behringia, constitute one of the largest refugial centres of arctic and boreal flora from where the species migrated to the Eurasian and North American continents during various Pleistocene interglacial and postglacial periods. In Hultén's opinion many genera and species spread from Behringia to the arctic and boreal territories of Eurasia and North America as well as to the mountains of these continents. In north-eastern Asia not all mountain ranges were completely covered by the Pleistocene glaciations and these connect directly the arctics with the mountains of central Asia from where a more or less unbroken mountain range stretches through Persia, the Caucasus and Asia Minor to Europe. Fernald (1925) states that on the North American continent a similar refugium for Pleistocene arctic flora existed in Alaska where glaciation was not complete. From Alaska the arctic flora migrated southwards along the mountain ranges.

If the distribution of the *Dryas* "species" is scrutinized carefully it is seen that their greatest concentration occurs in north-eastern Asia where the ancient arctic flora survived. It is seen from the material assembled by Juzepchuk in the Flora of the USSR that the species appearing on those territories are *Dr. grandis* Juz., *Dr. viscosa* Juz., *Dr. punctata* Juz., *Dr. octopetala* L., *Dr. ajanensis* Juz., *Dr. Tschonoski* Juz., *Dr. crenulata* Juz. and *Dr. Chamissonis* Spreng. Further to the west along the Arctic coast and in the mountains of Eurasia only some few species of this genus occur, such as *G. punctata* which reaches to the Karelian Isthmus, *Dr. octopetala* distributed over almost the whole of the arctic region in Eurasia and in numerous mountain ranges, *Dr. oxyodonta* Juz. spreading west over the mountains of Asia to the Altai, and *Dr. caucasica* growing in the Caucasus.

Similarly, the most primitive species of the genus *Geum* in the subgenera *Sieversia* and *Neosieversia* grow in our times only in the refugia of boreal flora in north-eastern Asia and North America. This distinct evolutional line of the *Geeae* separated away from the tribe of the *Dryadeae* probably already in the Tertiary period. At first the *Geeae* were presumably small shrubs and later perennial herbs which formed part of the arctic and boreal vegetation, similarly as is at present the case with the species from the subgenera *Sieversia* and *Neosieversia*. In the course of later evolution in the genus *Geum* the various groups of arctic and boreal species spread to the mountains of Eurasia and North America.

In the mountains the evolution of the particular groups had its own independent history leading to the formation of separate subgenera in the different mountain ranges. In this way the species of the subgenus *Oreogeum* developed in Europe and of the subgenus *Erythrocoma* in North America. The subgenus *Acomastylis* developed new sections in the mountains of both these continents. Consequently, the species of these three subgenera are undoubtedly very ancient montane elements related at present only very indirectly in their phylogeny with the original arctic and boreal representatives of the tribe of *Geeae*. The cytogenetic conditions in the subgenera *Sieversia, Neosieversia, Oreogeum, Erythrocoma* and *Acomastylis* are not yet sufficiently understood to permit an interpretation of the mutual genetic relations between them. The now living representatives of these subgenera represent probably only a small proportion of much more numerous species which existed during the long history of this evolutional stage of the genus *Geum*. Most of them are polyploids of various kinds. These polyploids can have only very few homologous genomes and, for instance, it seems from the chromosome conjugation in the hybrid of the tetraploid *G. montanum* of the subgenus *Oreogeum* with the hexaploid *G. ciliatum* of the subgenus *Erythrocoma* that the two species have in common only one partly homologous genome. To establish more closely what are the relations between all these subgenera an extensive cytogenetic investigation is necessary and this has not been carried out because of the difficulties in assembling the necessary material and growing the plants in experimental cultures.

The mutual relationship of all these subgenera is revealed by one trait common to them all and relating them to the *Dryadeae,* i.e. the numerous achenes with long, straight, usually pennately haired styles persisting entirely after the achenes ripen. However, in other respects the subgenera represent various evolutional trends and rather differ morphologically. Even the three species of the subgenus *Oreogeum* — i.e. *G. montanum* ($2n = 28$), *reptans* ($2n = 42$) and *bulgaricum* ($2n = 70$) — differ by their chromosome number and the expression of many traits. It is seen from cytogenetic experiments that the hexaploid *G. reptans* has two genomes common with the genomes of the tetraploid *G. montanum,* whereas, the third genome of *G. reptans* differs from the third genome in the species of the subgenus *Eugeum*. What is the relation of the 5 genomes of the decaploid *G. bulgaricum* to the genomes of *G. montanum* and *G. reptans* is unknown.

It is remarkable that in the subgenus *Oreogeum* the tetraploid *G. montanum* has the most extensive distribution, growing as it does in the Pyrenees, the Plateau Central, the Carpathians, the mountains of the Balkan Peninsula and on Corsica, which testifies to the very ancient origin of this central European oreophyte. The hexaploid *G. reptans* has a more restricted distribution in the Pyrenees, Alps, Carpathians and the Balkan Peninsula, whereas, the dodecaploid *G. bulgaricum* occupies a small area only in the Balkan Peninsula. There seems to be no doubt that the three species of the subgenus *Oreogeum* still living represent only the last surviving members of the complex of di- and polyploid Tertiary species.

The results from crosses between the species in the subgenus *Oreogeum* and the species in the subgenus *Eugeum* indicate that the more recent evolutional line in the genus *Geum* represented by the subgenus *Eugeum* probably arose by means of amphiploidy from the montane species with long straight styles related to *G. montanum* of our days and species with entirely deciduous styles. It is, therefore, to be concluded that the montane species related by the structure of achenes to the *Dryadeae* type gave rise in the genus *Geum* to new evolutional lines characterized by an entirely different expression of styles.

Before moving on to considerations over the youngest group in the tribe of *Geeae,* which undoubtedly is represented by the species from the subgenus *Eugeum,* let us first consider the *Geum* subgenera growing on the other side of the Equator on the Southern hemisphere.

RELATIONS OF THE *GEUM* SUBGENERA FROM THE SOUTHERN HEMISPHERE AND THE SPECIES FROM THE NORTHERN HEMISPHERE

A very interesting but entirely different problem is presented by the relation of the subgenera from the Northern hemisphere already discussed to *Geum andicola* and the subgenus *Oncostylus* from the Southern hemisphere. *G. andicola* is know to me only from descriptions. It also has straight, persistent haired styles. Bolle classifies this species together with the subgenus *Oreogeum.* It seems, however, that such a procedure in the present state of knowledge is unwarranted, as *G. andicola* differs from the subgenus *Oreogeum* not only by a different geographical distribution but also by a different expression of pistils. This relic species is known only from a few stations in the Chilean Andes and its genetic relation to the other subgenera distinguished on the Northern hemisphere cannot at present be established. For this reason I include it for the time being in the separate subgenus *Andicola.*

Besides *Andicola* there is on the Southern hemisphere the whole subgenus (and according to Bolle even the genus) *Oncostylus* with species distributed disjunctively in Tasmania, New Zealand, on the Auckland Islands and in South America (Map 14). The subgenus *Oncostylus* can be divided into two sections (subgenera, according to Bolle), *Paleooncostylus* and *Neooncostylus.* The former has only two species living in very high mountains and representing ancient forms ancestral for the whole subgenus, i.e. *G. renifolium* Muel from Tasmania and *G. uniflorum* Buchanan from New Zealand. They represent high montane plants with small relic distributions. The plants have big flowers, singly on stems of the the scapus type, the achenes are numerous and with long, pennately haired styles. The section *Neooncostylus* comprises about 7 species. The plants are profusely branched, have numerous small flowers, the number of achenes is usually smaller, the styles are reduced and the stigmatic part forms a conspicuous hook inserted at the tip of the achene (the achenes resemble somewhat the achenes of some *Ranunculus* or *Anemone* species). The species in the section *Neooncostylus* can be arranged into a very distinct sequence according to their adaptation to epizoochoric dissemination, whereas, the ancient original species from the section *Paleooncostylus* have still long, pennately haired styles.

Similarly as on the Northern hemisphere, where the younger forms adapted to epizoochoric dissemination (subgenus *Eugeum*) developed from the more ancient ones with straight pennately haired styles, on the Southern hemisphere te same process occurred. Probably the evolution in the direction of epizoochory progressed among *Geum* species quite independently on both hemispheres. This is indicated by the circumstance that the same adaptation was reached by the subgenus *Eugeum* in a different manner than by the subgenus *Oncostylus.* In the subgenus *Eugeum* the stigmatic part of the style is deciduous and the rostrum persisting on the achene forms a hook, whereas, in the subgenus *Oncostylus* the hook is formed by the stigmatic part remaining on the style. This is a very fine example of convergent evolutional processes progressing independently. The subgenus *Oncostylus* represents thus a quite independent evolutional line in the genus *Geum* isolated from the species from the Northern hemisphere by the great geographical disjunction as well as probably by the long time that the isolation lasted.

There remains the question of what is the genetic relation between the species with long, straight, pennately haired styles appearing on both hemispheres? The ancient genera of the tribes of *Cercocarpeae* and *Dryadeae* in North America reach only to Mexico. Their habitats in Central America most advanced to the south are separated by an enormous disjunction from the habitats of *G. andicola* in the Chilean

Andes. An even greater disjunction separates the species of the section *Paleooncostylus* living in the mountains of Tasmania and New Zealand from the genera in the tribe of *Geeae* on the Northern hemisphere.

As is known, in the mountains of Australia, New Zealand and Tasmania there are many species which appear in the circumboreal territories of the Northern hemisphere, e.g. *Carex Lachenallii, diandra* and *stellulata*. Similarly, there are many boreal species at the extreme end of South America, e.g. *Carex magellanica* and *microglochin, Draba magellanica* and others. Some fairly numerous species have their distribution both in the Northern hemisphere and on disjunctive areas in Australia, New Zealand and/or South America, e.g. *Carex canescens*. Besides bipolar species very many instances are known of higher systematic units, such as sections or genera, with bipolar distributions and closely related vicarious species growing on both the northern and southern polar territories. Numerous similar examples may be quoted from the genera *Carex, Primula, Chrysosplenium, Empetrum* and others. Du Rietz (1940) who studied fully and in great detail the problems of bipolar distribution of plants quotes also numerous examples of mosses and lichens with bipolar distributions. This writer reviews critically the very rich literature of bipolar plants and on the basis of his studies it seems most likely that the numerous species and higher systematic units with bipolar distribution represent an extremely ancient element on the Southern hemisphere, especially if the character of the distribution on the Southern hemispere is disjunctive with habitats both in Australia, New Zealand and in South America. All attempts at explaining these enormous disjunctions by the polytopic formation of species, the transportation of seeds by birds or other means over great distances or even a relatively early Pleistocene migration through the Andes are absolutely indefensible.

The existence of numerous species and genera common for the Patagonian region of South America and the Australian and New Zealand territories as well as the existence in the Antarctic of Tertiary fossil remains of *Nothofagus* and *Araucaria* (Seymour and Kerguelen Islands) seem to indicate that at that period the territories of South America, the Antarctic and the territory of Australia and New Zealand were connected. On the whole of that region there was then a common flora of the holantarctic character the relics of which, represented by identical or closely related species, grow in our times on the continents and antarctic islands separated by enormous oceanic stretches. When the American continent and New Zealand broke away from the Antarctic the representatives of the flora on the Antarctic perished under the ice cover, but survived in Patagonia the mountains of South America, Australia, New Zealand, Tasmania and on some islands of the Pacific Ocean.

Thus the subgenus *Oncostylus* with a distribution similar to that of *Nothofagus* cannot be considered as a boreal element which reached the Southern hemisphere in the course of Pleistocene migrations through the Andes, as at that time the connection of South America with New Zealand through the Antarctic already did not exist and the Antarctic was already covered by ice. It seems far more plausible that the subgenus *Oncostylus* as well as *Nothofagus* and many other genera owe their disjunctive distribution on the Southern hemisphere to the disappearance of intermediate Tertiary habitats on the Antarctic continent.

The species from the section *Paleooncostylus* which appear in New Zealand and Tasmania are probably the relics of a very ancient aboriginal flora, as the undoubtedly younger species in the section *Neooncostylus* have a distribution that can be identified as being of Tertiary origin.

The above considerations lead to the conclusion that the members of the rose family characterized by the long, pennately haired styles related to the tribe of *Dryadeae,* similarly as the old tribes of *Spireae* or *Kerrieae,* were present on both the Southern and the Northern hemispheres since very remote geological times. These plants were adapted to a temperate climate but during Tertiary climatic changes they developed many arctic and montane genera and species. On the Northern hemisphere the species spread extensively and survived in large numbers to the present times owing to the favourable configuration of the continents and mountain ranges, whereas, on the Southern hemisphere they were exterminated almost completely. A circumstance witnessing the long and independent evolutional history of the rosaceous plants on the Southern hemisphere is the existence in the tribe of *Sanguisorbeae* of some genera — namely *Acaena, Polylepis, Tetraglochin* and *Margyricarpus* — widely spread on the Southern hemisphere only. It seems, therefore, that the present differentiation between the floras of the Southern and Northern hemispheres was not always equally definite and that in the early Tertiary period and perhaps even in the Cretaceous the flora of the Angiosperms was more uniform on both hemispheres than is now apparent.

It may be that the Angiosperms originated in the highlands of the tropical zone during the Jurassic and Cretaceous periods or even earlier and consequently extended their distribution both north and south (Axelrod 1952). If the course of events were as outlined, then it would follow that *G. andicola* and the species from the section *Paleo-oncostylus* are very ancient elements characteristic for the Southern hemisphere and that these species — similarly as the related *Geum* subgenera from the Northern hemisphere — differentiated from common ancestors.

The division of these subgenera must have occurred long ago, perhaps even in early Tertiary periods. Nevertheless, they retained the related structure of the pistils producing achenes with a long, entirely persistent, pennately haired style. As *G. andicola* and the species from the subgenus *Oncostylus* have not been studied cytogenetically further speculation on their relation to the species from the Northern hemisphere would be entirely premature.

GEUM SUBGENERA WITH DECIDUOUS STIGMATIC PART OF THE STYLES

The *Geum* subgenera discussed previously have elongated styles entirely persisting on the achenes which relates them distinctly to the primitive tribes of *Cercocarpeae* and *Dryadeae*. In respect to the style structure they differ only by the length of the styles or the degree to which it is haired.

As was mentioned earlier, in the subgenus *Oncostylus* the type of straight styles adapted to anemochoric dissemination changed directly to the epizoochoric type through the reduction in the length of the style and the development of the hooked stigmatic part which on the ripe achene acts as the adhesive organ.

The same process directed towards epizoochory occurred on the Northern hemisphere but the result was reached in a different manner than in the subgenus *Oncostylus*. In the subgenera *Eugeum, Stylipus* and *Orthurus* the stigmatic part of the style is deciduous and the persistent lower part of the style (the rostrum) forms the adhesive organ. In the very closely related subgenera *Eugeum* and *Stylipus* a hook develops at the tip of the rostrum and this serves for adhesion, whereas, in the subgenus *Orthurus* bristly papillae at the tip of the rostrum act as the adhesive organ.

The style is deciduous from the achene almost completely in the subgenus *Woronowia* and entirely in the genera *Waldsteinia* and *Coluria*.

The *Geum* subgenera with the stigmatic part shed from the style as well as the genera *Waldsteinia* and *Coluria* undoubtedly represent a secondary type of *Geeae* in respect to the more primitive *Geum* subgenera and the genera from the tribe of *Dryadeae* where the straight styles persist entirely on the achenes. All these plants without exception are herbs with a basic chromosome number x = 7. The subgenera *Woronowia* and *Orthurus* constitute developmental lines independent of *Eugeum* and their mutual phylogenetic relations cannot be established exactly.

At present the species best known cytogenetically in the genus *Geum* are the numerous and widespread species from the subgenus *Eugeum*. It has been found that their basic chromosome number is x = 21. Numerous species in this group have all the three sets of 7 chromosomes at least partly homologous. The group is thus phylogenetically uniform. It can be assumed that in none of the *Eugeum* species as yet unexamined cytologically the chromosome number will be less than 42. Nearly normal chromosome conjugation is observed in the hybrids of *Eugeum* species both geographically related and growing in Europe or North and South America.

The few hybrids between *Geum* subgenera with straight styles (e.g. *Oreogeum* × *Erythrocoma*) so far investigated seem to indicate that phylogenetically these subgenera represent greatly varied groups with only some homologous genomes. In spite of the similarity in the structure of their styles the ancestral subgenera originating from the *Dryadeae* are more ancient phylogenetically than *Eugeum* and quite certainly do not form a monophyletic group.

On the other hand, the subgenus *Eugeum* forms a decided monophyletic group of species which is much younger than the *Geum* subgenera characterized by the straight styles entirely persistent on the achenes.

The subgenus *Eugeum* exhibits close relationship with the subgenus *Oreogeum*. This is witnessed by the circumstance that all the hybrids of the various hexaploid *Eugeum* species with the tetraploid *G. montanum* from the subgenus *Oreogeum*, so far examined cytologically, have in meiosis the type of chromosome conjugation consisting of 14 bi- and 7 univalents. The hybrids of the hexaploid *Eugeum* species with the hexaploid *G. reptans* from the subgenus *Oreogeum* have in meiosis the type of chromosome conjugation characterized by 14 bi — and 14 univalents, which shows that probably the same two genomes are here homologous while the third genome of the subgenus *Eugeum* and the third genome of *G. reptans* differ and are not homologous. The hexaploid species of subgenus *Erythrocoma* and the hexaploid *Eugeum* species probably have also only two partially homologous genomes, the third genomes in both subgenera not being homologous. The close relation of *G. montanum* with the species in the subgenus *Eugeum* is shown not only by the homology of chromosomes but also by the high fertility in hybrids with some *Eugeum* species, in spite of the fundamental differences between the species in the structure of styles which is so important for the taxonomy of the whole genus.

It is readily seen that there is no fundamental difference in the structure of styles between the tribe of *Dryadeae* and the *Geum* subgenera with straight styles and even a series of forms intermediate in this respect exists. On the other hand *Geum* subgenera with partly or entirely deciduous styles introduce a new quality in the type of style structure which does not appear in the primitive plants from the tribes of *Dryadeae* or *Cercocarpeae.*

In the subfamily of *Rosoideae* in the tribe of *Potentilleae,* for instance, most genera have styles deciduous right at the base of the achenes. The same type of deciduous style is seen in the genera *Waldsteinia* and *Coluria* and this closely relates the subfamilies *Rosoideae* and *Dryadoideae.*

Undoubtedly the two genera, related though they are, differ entirely from *Geum* and in the tribe of *Geeae* constitute an ancient separate evolutional line comprising mainly species growing in shadowy forests.

The plants in the two genera are small perennials which have unconspicuous and small flowers with well expressed hypanthium and few achenes inserted on a ramified receptacle. The deciduous styles have no significance for the dissemination of achenes inserted at the bottom of a tubular calyx. In some *Coluria* species there are on the achenes numerous papillae probably representing an adaptation in the direction of myrmecochoric dissemination. The geographical distribution of the species from the genera *Waldsteinia* and *Coluria* (Maps 1 to 4) shows that they can be considered as relics of an ancient, arcto-tertiary forest flora now appearing only in or near refugial areas. The majority of the *Coluria* species grow today in China and only *Coluria geoides* has a disjunctive distribution in southern Siberia on the slopes of the Altai and Sajan Mountains. The genus *Waldsteinia* has even a more decidedly relic distribution. Two of its species, *W. fragarioides* and *W. lobata,* grow in Atlantic North America, *W. ternata* has an extensive distribution in East Asia and disjunctive stations in Transylvania and the Alps in Europe. *W. geoides* has a small relic distribution in East Carpathians and on the Balkan Peninsula. The disjunctive distribution of *W. ternata* and the characteristic distribution of the *Waldsteinia* species show that the genus was widely spread in the circumpolar arctic Tertiary forests and that to-day the few surviving species are restricted to refugia or the adjacent areas only. The only two diploid species within the whole tribe of *Geeae* have been found in these genera, they are *Waldsteinia geoides and Coluria geoides* with $2n = 14$.

Probably the two separate evolutional lines in the tribe of *Geeae* were differentiated already in the Tertiary. One consisted of species growing in the lowlands and forests with deciduous styles and the other of montane species with styles entirely persisting on the achenes. The former is represented in our times by the genera *Waldsteinia* and *Coluria* and the latter by the primitive *Geum* species.

It seems highly probable that on the territories where these two separate developmental lines met crossing could occur. From such hybrids the subgenus *Eugeum,* with the lower part of the style (rostrum) persisting on the achenes and a deciduous stigmatic part, developed through amphiploidy. The present hexaploid basic chromosome number in the subgenus *Eugeum* with two genomes homologous to *G. montanum* could be then explained as follows: the subgenus arose from a cross between a tetraploid species from the subgenus *Oreogeum* (related to *G. montanum*) and a diploid species related to the diploid *Waldsteinia* or *Coluria* species, or perhaps some other genus now extinct. In spite of many attempts my efforts at crossing *Waldsteinia* and *Coluria* species on one side with species from the genus *Geum* on the other were unsuccessful. Consequently there is no direct evidence supporting the supposition that the third genome in the species from the subgenus *Eugeum* is in fact homologous with one genome of *Waldsteinia* or *Coluria,* as is the case of the other two genomes in *Eugeum* which are evidently homologous with two genomes in *G. montanum.* However, the negative result of these crosses cannot be, of course, regarded as disproof for the above hypothesis on the origin of *Eugeum,* especially if it is remembered that, on the evidence of its present distribution, the subgenus originated not later than in the middle of the Tertiary when the then existing species could have different abilities to form hybrids than the species of today.

Indirect support for the above hypothesis on the origin of the subgenus *Eugeum* is supplied by the anatomical structure of the style in *Geum.* It was already shown by Iltis (1913) that the epidermal cells of the deciduous stigmatic part in the subgenus *Eugeum* are different than the cells in the epidermis of the rostrum, and that in the former organ there are numerous stomata, and transitorily chlorophyll, which are lacking in the latter. The structure of the long, haired style in the subgenus *Oreogeum* is more related with the rostrum in the subgenus *Eugeum,* i.e. it has no stomata and chloroplasts. In *G. montanum* the very few stomata appear only on the 2—3 mm. of the style tip which acts as the stigma. The long, straight style in the subgenus *Oreogeum* is more homologous with the rostrum than with the deciduous stigmatic part in the subgenus *Eugeum.* In the genera *Waldsteinia* and *Coluria* the style is shed at the very base and its structure corresponds closely to the structure of the deciduous stigmatic part in the subgenus *Eugeum,* where the stomata are numerous and the chlorophyll abundant. Both at the base of the stigmatic part in the subgenus *Eugeum* and at the base of the style in the genera *Waldsteinia* and *Coluria* there is a special interlying layer of small, thin-walled cells. This layer causes the shedding of the part of the style above it when the fruit get ripe. It seems, therefore, that the style in the genera *Waldsteinia* and *Coluria* is an organ homologous to the deciduous stigmatic part in the subgenus *Eugeum.*

By assuming the amphiploid origin of the subgenus *Eugeum* from species in the subgenus *Oreogeum* and species related to *Waldsteinia* and *Coluria* the composite structure of the *Eugeum* styles can be explained by that the lower part of the style (rostrum) corresponds to the long style persistent on the achene from the subgenus *Oreogeum,* whereas, the deciduous stigmatic part is a homologue of the styles in the genera *Waldsteinia* and *Coluria.*

The primitive hybrids between these two *Geeae* forms had an elongated persistent lower part of the style and inserted on it a deciduous stigmatic part. Probably at a later stage there appeared among these amphiploid hybrids, possibly by means of a mutation, the type with the hook at the tip of the rostrum, which in the course of time developed into the epizoochoric type of achenes in the subgenus *Eugeum.* Because of its more efficient dissemination the type was selectively positive, which in turn caused the extensive spreading and strong differentiation of the subgenus *Eugeum.*

In the genus *Geum* there are, besides the subgenus *Eugeum,* two other subgenera with the deciduous stigmatic part of the style, i.e. the monotypic and relic subgenera *Woronowia* and *Orthurus.* These two subgenera represent evolutional lines different from *Eugeum* and indicate that in the history of the *Geeae* there were too forms intermediate in respect to style structure. The extreme forms are represented today by the *Geum* subgenera with styles entirely persistent on the pistils and the genera *Waldsteinia* and *Coluria* with styles entirely deciduous.

SUBGENERA *WORONOWIA* AND *ORTHURUS*

Geum speciosum Alboff., *G. heterocarpum* Boiss., and *G. kokanicum* Reg. et Schm. are all classified by Bolle in the subgenus *Orthurus.* On the other hand in the flora of the U.S.S.R. Juzepchuk distinguishes *G. speciosum* as a separate genus *Woronowia* and the other two species he classifies as the genus *Orthurus*. Juzepchuk's decision to separate *G. speciosum* from the other two species in the subgenus *Orthurus* seems fully justified, as indeed the species differ to a great extent. On the other hand, Bolle's opinion that they should be included in the genus *Geum* seems more fortunate, though, with the restriction that for the species *G. speciosum* I suggest to form the separate subgenus *Woronowia*. The only species of this subgenus *G. speciosum* Alboff grows on mountain meadows of Transcaucasia (Map 34) and represents a relic form uniting the traits of both the genus *Geum* and the genera *Waldsteinia* and *Coluria*. The leaf shape, growth habit and the expression of the sepals and petals of this species are related to the genus *Geum,* whereas, the character of the style shed almost at the base and the achenes inserted on a ramified receptacle associate this species with *Waldsteinia* and *Coluria* (Fig. 31). Also the tubular hypanthium and the stamen filaments persisting long after the flower withers associate the species with the genus *Coluria*. *G. speciosum* is decaploid with 2n = 70 and represents a relic type of *Geum* dating from the times when the forms with the deciduous stigmatic part were differentiating. The rostrum in the species is almost not developed and has no significance for the dissemination of the achenes. This highly polyploid species represents to-day an evolutional line which is on the way to extinction.

Another relic group consists of *G. heterocarpum* and the closely related with it *G. kokanicum*, the latter being perhaps only a subspecies of the former. These species have a deciduous stigmatic part inserted on a straight, relatively short rostrum, few achenes inserted on a receptacle which is supported by a gynophore. Single achenes are inserted at the base of the gynophore. The calyx forms a tubular hypanthium. *G. kokanicum* grows in the mountains of Central Asia and Persia together with *G. heterocarpum,* but the latter species has also an extensive distribution in the eastern and western regions of the Mediterranean basin and disjunctive station in the central regions of that area, i.e. in Albania, on the Apennine Peninsula and the Dauphiné in the south of France (Maps 33 and 34).

The species is montane and grows in shadowed habitats, mainly in thickets of *Juniperus* sp. The disjunctive distribution of *G. heterocarpum* indicates that the species had at one time a continuous uniform distribution in the Mediterranean area.

G. heterocarpum is a tetraploid and it is seen from the conjugation of chromosomes in the hybrids of this species with the species of the subgenus *Eugeum* that it has at most one genome partly homologous with one of the three genomes in the species of the subgenus *Eugeum*. There can be no doubt that the species from the subgenus *Orthurus* represent an ancient evolutional line which differentiated independently of the species in the subgenus *Eugeum*. The subgenus *Orthurus* developed achenes adapted to epizoochoric dissemination on different lines than the hooked rostrum of the subgenus *Eugeum*, i.e. by forming stiff bristles pointing obliquely downwards at the tip of the rostrum (the harpoon type as Iltis calls it). In *G. heterocarpum* the hypanthium is tubular and the achenes are, in the course of ripening, exserted on a long gynophore which faciliates their epizoochoric dissemination. The same effect is to be seen in some species from the subgenus *Eugeum*. It is thus apparent that the subgenus *Orthurus* and the subgenus *Woronowia* are relics of evolutional lines different from the one characterized by the deciduous stigmatic part represented by *Eugeum*. It may be that in the *Woronowia* and *Orthurus* species the style is inserted on a protruding beak-like process which forms the apex of the achene itself, as suggested by Regel. The process is very small in *Woronowia* and conspicuous in *Orthurus*. If it were so, then the rostrum in these species would not be homologous with the rostrum in the subgenus *Eugeum*. However, there is no answer to this problem at present. Nevertheless, there is no doubt whatever that in a quite independent manner and through morphological changes in different organs the subgenera *Oncostylus, Eugeum* and *Orthurus* in the genus *Geum* developed the type of achenes adapted to epizoochoric dissemination.

Of these three lines the subgenus *Eugeum* proved to be the most expansive and developed numerous species which spread their distribution over large areas of both hemispheres.

EVOLUTION OF SPECIES WITHIN THE SUBGENUS *EUGEUM*

The question now arises whether from the present distribution of the species in the subgenus *Eugeum* it would be possible to establish with some degree of probability the centre of its origin, when its amphiploid and monophyletic character, indicated by the numerous experimental interspecific crosses, is assumed. It seems highly probable that the territories where the subgenus *Eugeum* originated and from where it then spread throughout the world lay in Europe, or more precisely in the mountainous territories surrounding the Mediterranean.

This is indicated by the greatest concentration in this area of *Eugeum* species characterized by traits more primitive than in the species growing mainly in other distributional centres of the subgenus. The most primitive *Eugeum* species such as *G. silvaticum, coccineum* and *rivale* have their habitats in the southern European centre. Here numerous other *Eugeum* species appear, e.g. *G. molle, hispidum* and *urbanum. G. montanum* grows in the mountains of Spain, in the Alps, on Corsica, in the Apennines and on the Balkan Peninsula, whereas, *Waldsteinia geoides* and *Waldsteinia ternata* grow in the Alps and the Carpathians. According to the hypothesis on the amphidiploid origin of the subgenus *Eugeum* these species are the ancestral forms for this evolutional line of *Geum*. Finally, the relic species from the subgenera *Orthurus* and *Woronowia* have their distribution in the Mediterranean area and in the Caucasus. In no other part of the world a similar centre with so great a concentration of various subgenera and genera from the tribe of *Geeae* can be found.

The species growing on the mountains surrounding the Mediterranean basin exhibit undoubtedly a set of the most primitive traits in the whole subgenus *Eugeum*.

The characters considered as primitive in the subgenus *Eugeum* are those which approach most closely the characters of the subgenus *Oreogeum* or *Waldsteinia* from which the subgenus *Eugeum* probably developed. These traits are as follows:

Primitive trait — stem with one or at the most 2—3 flowers, poorly expressed cauline leaves and scapose growth habit as in the subgenus *Oreogeum*.

Corresponding secondary trait — stems big, profusely branched, multifloral, with big and numerous cauline leaves.

Primitive trait — perennial plants with big, thick caudex creeping on the ground and terminating in a leaf rosette, as in the subgenus *Oreogeum*.

Corresponding secondary trait — perennial plants less long-lived which do not develop the strong creeping caudex.

Primitive trait — the lower part of style long and haired, the deciduous stigmatic part also long (6—8 mm). The long, haired rostrum corresponds to the long and haired style of *Oreogeum*, whereas, the long stigmatic part corresponds to the style of the *Waldsteinia* type.

Corresponding secondary trait — rostrum short and glabrous, the stigmatic part small, 2—3 mm long.

Primitive trait — the calyx tube forms a more or less distinct hypanthium as in *Waldsteinia*.

Secondary trait — sepals reflexed downwards, appressed to the floral peduncle. In plants with erect sepals often a long gynophore develops and this organ exserts the achenes while they ripen above the sepals, thus facilitating epizoochoric dissemination of seeds. A small, 2 mm long gynophore is seen in *G. montanum*, whereas, a gynophore 15 mm long and more is seen in *G. rivale, silvaticum* and *heterocarpum.* In species with a reflexed calyx the gynophore is not developed or it is very short. Moreover, large flowers may also be regarded as a primitive character and their number on a stem is usually small. The corresponding secondary trait is that of numerous small flowers.

The following European species can be considered as primitive: *G. silvaticum* which grows in the mountains surrounding the western Mediterranean Sea, *G. coccineum* living in the mountains of the Balkan Peninsula, and *G. rivale* which has, alongside of a large lowland distribution in Europe, also montane habitats in the Mediterranean area. There is also *G. capense* which is probably closely related to the above species and occupies a small area in the mountains of South Africa.

All these species are characterized by the traits listed above as primitive: few floral stems poorly branched and poorly leaved, well developed creeping caudex, big flowers usually with erect calyx and achenes with elongated rostrum and long stigmatic part.

It is seen from the genetic investigations that *G. rivale, silvaticum* and *coccineum* have three genomes completely homologous and the hybrids between them are almost normally fertile. These results show that the relationship between these species is very close, despite the quite serious morphological differences. Unfortunately, the genetic relation between these species and *G. capense* has not been examined as my cultures did not include this last species. In his monograph of the genus *Geum* Bolle (1933) includes in the so called section *Gmeliniana* the species which will be mentioned now. First comes *Geum geniculatum* Michaux from North America, but this species has a very doubtful status and the herbarium specimens of it which I examined were hybrids of *G. rivale* and some other *Geum* species. Another species, *Geum rhodopeum* Stoj. et Stef., is known from one habitat only in Bulgaria and is probably a hybrid of *G. coccineum* with *G. rivale.* This is revealed by the observations on a specimen brought to Warsaw from the Botanical Garden in Sofia which in the next generation gave a decided segregation. Furthermore, Bolle includes in the section *Gmeliniana G. pyrenaicum* which is probably an amphiploid between *G. silvaticum* and an unidentified hexaploid species. Finally, to this section Bolle includes the South American species *G. Quellyon, G. magellanicum, G. peruvianum* and *G. brevicarpellatum.* My experimental cultures included the first two of these species and the third I know from herbarium specimens. Except the rather long stigmatic part of the style these species have no common characters with the previously mentioned European species of the section *Gmeliniana.* Nor do the results of interspecific crosses of *G. Quellyon* and *G. magellanicum* with the other members of the section *Gmeliniana* point to any close relationship.

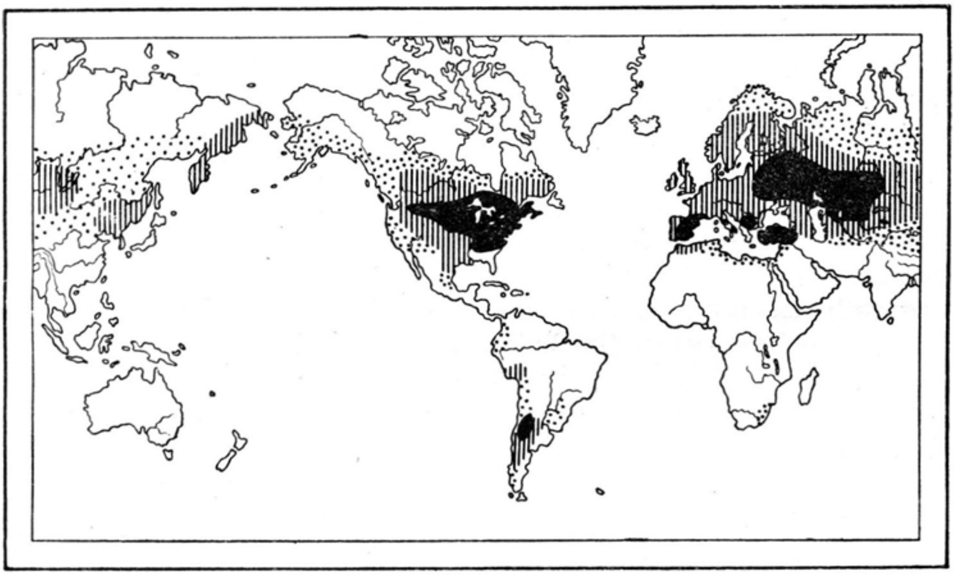
The conclusion to be drawn here is that within the subgenus *Eugeum* only *G. silvaticum, coccineum* and *rivale*, as well as probably *G. capense,* represent a group of related species with many primitive characters. The present distributional centre of these species lies in southern Europe, but *G. capense* has a disjunctive habitat in South Africa and *G. rivale* has, besides the habitats in the Mediterranean area, a widespread lowland distribution of the amphiatlantic type. The Mediterranean-South-African disjunction bears witness to the very ancient origin of this group of species and to their association with the ancient group of Mediterranean species related with the vegetation of the Cape region in South Africa. This is best seen in the case of the families of *Geraniaceae, Polygalaceae, Ericaceae, Thymelaceae* and *Globulariaceae* which all have numerous species from the same genera in both these centres.

The present distribution of *G. rivale* with its north Atlantic disjunction and the intermediate habitat in Iceland is also probably of Tertiary origin. This distribution is readily explained if it is assumed that in the Tertiary the North American continent was connected with Europe through Greenland and Iceland and that over this land bridge the migration of American plants to Europe and European plants to America took place. Both in Greenland and in Iceland there are in our times plants which probably survived *in situ* the last glaciation and maybe the whole of the Glacial Age. A. and D. Löve (1947) assume that at least 55 per cent of the present day flora in Iceland survived *in situ* the last glaciation and perhaps even throughout the Pleistocene. This group of plants probably comprises also *G. rivale*. In their next report these writers (A. and D. Löve 1951) state that in the Miocene flora of Iceland Lindquist found a form related to *Betula callosa* which still lives there.

A. and D. Löve suppose that the numerous amphiatlantic plants appearing at present in eastern North America, north-western Europe, Iceland and/or Greenland are not relics of an earlier circumboreal distribution formed by migration to the east and west from territories of Behringia, as is believed by Hultén (1937). They think it more likely that the distribution of these plants resulted from a connection between Europe and America through Greenland and Iceland which either consisted of a land-bridge or a once different relative position of the continents.

In the light of the above statement the explanation seems to be highly plausible that the present distribution of *G. rivale* is of Tertiary origin when this species spread from Europe, where it arose, to North America. During the glaciations and later the species extended further its distribution to the glaciated areas. The other *Eugeum* species of the primitive type did not have similar expansive abilities and remained on the refugia.

Considering all these circumstances I am inclined to assume that the centre where the whole subgenus *Eugeum* originated lay on southern Europe. The time when these new amphiploid *Geum* forms developed could be only the Tertiary period and at this time also the primitive species reached South Africa (*G. capense*) and North America (*G. rivale*). Probably still in the course of Tertiary migrations the species related to the primitive forms spread from North America through the Andes to South America (Map 37).



Map 37. Concentration of species of the subgenus *Eugeum:* dots — one species, vertical lines — two species, black spots — three species or more

LATER EVOLUTION OF SUBGENUS *EUGEUM*

The further evolution in the subgenus *Eugeum* tended towards plants with stronger and more branched stems and numerous small flowers. The number of achenes on the receptacle increased and their size diminished. Simultaneously, as the adaptation to epizoochory progressed the hairiness of the rostrum disappeared and the length of the stigmatic part was greatly reduced, though in the more primitive *Eugeum* species these organs were still similar to the initial forms of this amphiploid subgenus. The further phase in the adaptation to epizoochoric dissemination were marked by the disappearance of the hypanthium and the reflexion of the calyx sepals dawnwards. At the same time the overground creeping caudex was reduced which resulted in the shortening of the life of plants. Such was the development of the species which Bolle included in the section *Murrayana* and which represent phylogenetically the youngest group in the subgenus *Eugeum* and in the whole genus *Geum*. Some of the now existing species in the so called section *Murrayana* as for instance the south European *G. molle* and *G. hispidum* or the south American *G. magellanicum* and *G. Quellyon* have a morphological character intermediate between the typical representatives of the section *Gmeliniana,* e.g. *G. silvaticum*, and the most advanced forms of the section *Murrayana*, e.g. *G. macrophyllum, canadense* or *aleppicum*.

The initial forms well adapted to epizoochoric dissemination exhibited considerable expansiveness and differentiated into many species with frequently extensive distributions. While the ancient *Geum* subgenera and even Bolle's section *Gmeliniana* in the subgenus *Eugeum* comprise primely monomorphic species with relatively slight intraspecific differentiation, in the youngest section *Murrayana* some species are polymorphic with geographical races and varieties. This indicates that the differentiation processes in these species are still in progress.

The species representing the youngest forms in the subgenus *Eugeum* are concentrated in four centres:

1. In Europe where grow *G. urbanum* with its close relations *G. latilobum* and *G. Roylei* (this one spreads to the Himalayas), *G. molle* and *G. hispidum*.

2. In North America where grow *G. laciniatum*, *G. canadense, G. macrophyllum* with the related *G. oregonense* and *G. perincisum, G. virginianum* and *G. vernum*. This last species belongs to the separate subgenus *Stylipus* but is, nevertheless, closely related with *Eugeum*.

3. In South America where grow *G. Quellyon, G. magellanicum, G. peruvianum, G. brevicarpellatum, G. riojense* and *G. boliviense*.

4. In the East Asiatic centre grow *G. japonicum* and *G. Fauriei*. Moreover, *G. aleppicum* has a widespread distribution in central Europe and throughout the whole of northern and eastern Asia, as well as an extensive distribution on the North American continent.

G. aleppicum and *G. urbanum* are also reported from Australia and New Zealand, but their habitats there are probably due to human activity, similarly as the presence of *G. urbanum* in North America.

Although these species occupy separate centres isolated one from the other by enormous disjunctions many of them produces hybrids of relatively high fertility and almost normal chromosome conjugation. For instance *G. canadense* from the North American centre gives with *G. urbanum* from the European centre and *G. boliviense* from the South American centre hybrids with a high degree of chromosome conjugation and partial fertility. These species, though strongly isolated at present, are closely related cytogenetically which proves the monophyletic character of the origin of the whole group.

The existence of species closely related cytogenetically in distant and separate centres can be explained only either by long range transportation of seeds from the centre where the group developed or by assuming migrations over great distances from the original centre and the subsequent disappearance on the intermediate habitats in the course of climatic and geological changes. The polytopic formation of species so closely related cytogenetically seems to be absolutely improbable.

Of the first two hypotheses — long range transport and migration — the former seems to me improbable, as it would imply that the seeds had to be carried by birds over the Atlantic from Europe to North America and from North to South America through the tropical zone.

I think it much more plausible to assume that in the Tertiary when the subgenus *Eugeum* developed its primitive forms had a much more widespread distribution than at present and its species thus reached from the northern hemisphere to South Africa and South America. Later the contacts between the present centres of the subgenus *Eugeum* were interrupted and in the particular centres isolated by enormous disjunctions the *Eugeum* species of our days developed.

From the moment when the isolation occurred enough time has elapsed for new species to develop in the various centres occupied by the subgenus *Eugeum*, but not enough to obliterate the features of the primitive common origin of the species as expressed today by the high homology of the chromosomes, the allelism of various genes and the relatively high fertility of the interspecific hybrids.

In accordance with what has been said earlier the most primitive of the species in the subgenus *Eugeum* are those in the section *Gmeliniana* which most probably arose in the south European mountains surrounding the Mediterranean basin. It is in this centre that the whole subgenus probably arose and from there it probably spread to other continents.

The question arises of how the subgenus *Eugeum* migrated from Europe to the North American continent. There are in this respect two possibilities: one through the Eurasiatic continent and Behringia to Alaska and North America, and the other over the hypothetic land connection through the Atlantic.

In the first case no hypothetic land connections between America and Europe are necessary except one over the Behring straits and this alternative seems at first glance more promising. This is supported by sufficiently reliable geological and historical evidence that as late as the Pleistocene there was a wide connection between the two continents. Moreover, the comprehensive researches carried out by Hultén indicate that in the course of Pleistocene migrations numerous arctic and boreal species spread along this way from one continent to the other. In Hultén's (1937) opinion even the species which have at present a typically amphiatlantic distribution and are restricted solely to the Atlantic coastal regions of North America and Europe, as for instance *Spiranthes Romanzoffiana* known on the European side of the Atlantic only from Ireland, represent extreme instances of reduction in the old, once continuous circumboreal distribution of which the intermediate habitats in Eurasia disappeared.

On the other hand many European species, especially montane ones, exhibit a very decisive relationship with North American species and have no representatives on the east Asiatic territories. According to the results reported by Kulczyński (1924) among 77 species representing the ancient Tertiary elements in the European mountains only 7 reach western Siberia, whereas 29 reach Iceland, 24 Greenland and 19 North America. Kulczyński writes that "without deciding at present on the age of these migrations there seems to be no doubt that migrations of European plants to eastern America through Iceland and Greenland did indeed take place on a large scale in the Tertiary or perhaps even in the Pleistocene period".

Even more ancient connections between the Mediterranean region and North America are shown by pairs of closely related vicarious species growing both in Europe and in North America primely in the eastern Atlantic regions. Examples of such species are *Platanus orientalis* and *Pl. occidentalis, Cercis siliquastrum* and *Cercis canadensis* or *Comandra elegans* and *Com. umbellata.*

In his list of genera with disjunctive distributions R. Good (1953) mentions 18 genera appearing in our times in North America, Europe and western Asia. Quite certainly in the Tertiary the floras migrated on a much larger scale between America and Asia as well as between Europe and Asia than between Europe and America. This is especially true with regard to the floras of the arctic Tertiary forests (Szafer 1946). According to Good there are as many as 81 genera common for North America and east Asia. Nevertheless, I think that besides the plant migrations between Europe and America through Iceland and Greenland over the ice bridge in the Quaternary the possibility cannot be excluded of plant migrations between the two continents in earlier periods. The present distribution of *G. rivale* in Europe and eastern North America with an intermediate habitat in Iceland may be the result of migrations prior to the Quaternary and the species may represent a preglacial element of Iceland flora. In the past years it has been shown by Nannfeldt (1940), Samuelsson (1943), and Selander (1950) that even in Scandinavia numerous plant species survived through at least the last glaciation if not through the whole Quaternary.

The circumstance that in the floras of Iceland and Greenland there are many species in respect to which the probability of other than land migrations is very unlikely, i.e. they could not be transported by birds or sea currents, supports the supposition that these islands had a land connection with North America or Europe. In the case of many species growing today in Europe, North America, Iceland and/or Greenland Hultén's assumption that their present distribution represents only the remains of earlier circumboreal distribution seems highly improbable, as was already pointed out also by Nannfeldt, Samuelsson and Selander.

After this digression on the possibilities of an exchange between European and North American floras over a North Atlantic connection the problem of the present day distribution of species in the subgenus *Eugeum* must be once again resumed. In view of the circumstance that in East Asia the subgenus is represented in fact only by the species *G. japonicum* Thbg., which is characteristic for that centre alone, whereas, the European and North American centres have many related or even the same species such as *G. rivale*, it seems more plausible that in the Tertiary the subgenus *Eugeum* spread from its centre of origin in southern Europe to the American continent over the North Atlantic. According to this hypothesis the centre in East Asia owes its *Eugeum* species not to Europe, but rather to the American continent. Apart from the aboriginal *Geum japonicum* of the other *Eugeum* species in East Asia there is *G. macrophyllum* which from a large distributional area in North America spread through Alaska and the Aleutians to a small strip of the Asiatic continent where, according to Hultén, it grows in Kamschatka and perhaps Sakhalin. *G. macrophyllum* is a late arrival in Asia where possibly it did not reach till the Holocene. Another East Asiatic species, *G. Fauriei* Lev., is a dodecaploid growing in north Japan and on Sakhalin. This species is of amphiploid origin probably from a cross between *G. japonicum* and *G. macrophyllum*. The distribution of *G. Fauriei* covers territories adjoining those occupied by its two supposed parental species (Map. 28). The close relation of this dodecaploid species to the hexaploid *G. japonicum* and *G. macrophyllum* is shown by its numerous traits common with the two other species. Because of this relationship Koidzumi classifies this species as a variety of *G. japonicum (G. japonicum* Thbg. var. *sachalinensis* Koidzumi, in Bot. Mg Tokyo 29:157 (1915)), and Hara (1952) classifies it as a variety of *G. macrophyllum* (*G. macrophyllum* Willd. var. *sachalinensis* (Koidzumi) Hara comb. nova). The third species in this region is *G. aleppicum* which at the same time has a large distribution in North America and to the west reaches central Europe.

Possibly *G. aleppicum* spread simultaneously from the territories of the so called Behringia to the North American and the Eurasiatic continents or it originated in one of these centres and spread to the other through Behringia. At present there is no evidence whatsoever for deciding which alternative is the correct one. Whatever may be the case, the centre in East Asia with only one hexaploid species proper to this region alone is an entirely secondary one for the subgenus *Eugeum*.

From the assumption on the European origin of the subgenus *Eugeum* it follows that the widespread extension of the subgenus on the northern hemisphere both in North America and Asia went longitudinally. The migration of *Eugeum* proceeded probably from Europe westwards to the American continent and from there to East Asia. The opposite direction through Asia to America seems less likely in view of the present day distribution of the *Eugeum* species, though, of course this possibility cannot be entirely discarded. Due consideration must be given to the possibility that the present distribution of the species may be quite secondary and may result from the disappearance of numerous species from territories which they occupied at earlier stages in their evolutional history.

Besides the east-west expansion the subgenus *Eugeum* also migrated extensively to the south penetrating to the Southern hemisphere. It has been mentioned earlier that in South Africa in the province Albany there is the species *G. capense* which is closely related to such south European species as *G. silvaticum*. In South America numerous species from the subgenus *Eugeum* stretch from Columbia along the Andes to Patagonia.

In contrast to the subgenus *Oncostylus* which on the Southern hemisphere has an extensive disjunctive distribution in Tasmania, New Zealand, the Aucklands and South America, the subgenus *Eugeum* occupies in the south only the South American centre. This is in accord with the opinion outlined earlier that the subgenus *Oncostylus* is a far more ancient representative of the flora of the Southern hemisphere and that it originated through differentiation of primitive local species with long straight style. At the time when a common Antarctic flora existed the subgenus attained a widespread and now disjunctive distribution, whereas, the subgenus *Eugeum* is a much later arrival on the Southern hemisphere where it spread from its centre of origin on the Northern hemisphere.

In all probability the subgenus *Eugeum* arrived to South America from the northern part of that continent. In South America there is a number of genera with distribution centres on the Northern hemisphere some of which, as for instance *Litorella, Chrysosplenium* or *Primula,* have extensive distribution in the north and only disjunctive habitats of single species in the Antarctic zone of South America. Such others, as *Saxifraga,* have numerous habitats throughout the Andes and the genus *Alnus,* to quote another example, has an almost unbroken line of intermediate habitats joining its distribution in the Northern hemisphere and its habitats in the subantarctic zone. Alongside of the common genera there also are some common species, though these are very few. For instance *Carex magellanica* (sens. lat.) has a widespread circumpolar distribution on the Northern hemisphere and a disjunctive one at the southern extremity of South America, and *Carex macloviana* D'Urv. (sens. lat.) is distributed over a large area including North America, Greenland, North-East Asia and Scandinavia with a disjunctive distribution in Patagonia, Argentina and several intermediate habitats in Central America and the Andes. Detailed lists of genera and species with similar distributions have been assembled by Steffen (1939) and E. Du Rietz (1940).

It is not only the arctic or boreal genera and species that the flora of South America shares with the Northern hemisphere. Also some representatives of desert floras are common for these two regions. Johnston (1940) demonstrated that in the xerophytic flora of the North American deserts (Texas, California, Mexico) and in the mountain deserts in South America from Bolivia to Patagonia the same species appear separated by the Central American disjunction, e.g. *Larrea divaricata, Atamisquea emarginata, Koeblinia spinosa* and others. Even more numerous are the pairs of closely related vicarious species. Johnston supposes that this kind of xerophytic flora is very ancient and that a Tertiary connection existed between the desert floras of North and South Americas. The work carried out by Stebbins (1947 b) on the

North American complex of species *Bromus carinatus* indicates that this complex is composed of octoploid species which originated from the hexaploids in the section *Ceratochloa* and the diploids of the section *Bromopsis*. At present in North America there are only the species from the section *Bromosis,* whereas the hexaploid species from the section *Ceratochloa* are known only from South America. Stebbins concludes that in the Tertiary times the hexaploid species from the section *Ceratochloa* grew on both American continents, but later disappeared from North America for unknown reasons. On the basis of palaeobotanical data which Elias assembled Stebbins reports that in North America (Great Plains) fruit of Pleistocene grasses from the tribe of *Stipeae* have been found. The grasses are either identical or related to the genera living today exclusively in South America. All this seems to indicate that the Tertiary floras of both Americas had more extensive contacts and that then the possibility for migrations of temperate plants was greater than in our times.

On the ground of all these facts it may be assumed that the group of primitive *Eugeum* species which developed in Europe during the Tertiary spread on one side to South Africa (*G. capense*) and on the other to the North American continent and from there in the furher course of events to South America. Later the contacts between the particular centres in South Africa, North and South America and Europe disappeared and in the various isolated centres the further evolution of the species in this subgenus proceeded independently. In every centre the evolution proceeded along different lines. In South Africa no new species were developed and only one relic species survived to our times. In South America numerous new species arose and as a result of crosses and amphiploidy the decaploid *G. Quellyon* and the dodecaploid *G. magellanicum* and *G. riojense* appeared. With the exception of the hexaploid *G. boliviense* the other species from this centre have not yet been studied cytogenetically. Moreover, as is known, the species of the subgenus *Oncostylus* reached that centre quite independently and represent there an element of the palaeoantarctic flora. In the North American centre too numerous species were formed and the process of producing new species is still continuing. For instance *G. macrophyllum, G. oregonense* and *G. perincisum* represent three young species forming units not as yet perfectly isolated morphologically, genetically and geographically (W. Gajewski 1955). According to Raynor's (1945) investigations *G. virginianum* may also be a species which is still in the course of isolation from a population of hybrids between *G. aleppicum* var. *strictum* and *G. canadense.*

It seems that in the whole tribe of *Geeae,* and perhaps in the whole subfamily of *Dryadoideae,* only the relatively youngest subgenus *Eugeum* is at a stage when it expands its distribution and forms new systematic units. With the exception of the subgenus *Eugeum* the majority of the species in the subfamily of *Dryadoideae* are either arctic or montane and usually monomorphic. In many instances they have small relic distributions.

The species from the subgenus *Eugeum* with an efficient epizoochoric dissemination have distributions larger than any other member of this family and many of them are decisively polymorphic. Owing to human activity some species from this subgenus were carried to new continents where they exhibited expansive tendencies. Many of these species have proved capable of occupying territories where the natural vegetation was disturbed by men. On such territories the once isolated species meet and produce interspecific hybrids from which by means of amphiploidy new species may in future arise. The cytogenetical analyses in the subgenus *Eugeum* prove that the processes which lead to the formation of new species are based in this case primely on genic mutations or small chromosomal mutations occurring in the original forms in the geographically isolated parts of their distribution. The process of cytogenetical differentiation causes an ecological and consequently a physiological isolation which is manifested by the varying decrease in fertility of interspecific hybrids. It is shown by the present research that the degree of morphological and genetical differentiation is not decisively correlated with the degree of sexual isolation. The further stage of evolution in this subgenus is seen in the formation of the amphiploid dodecaploid species arising from hybrids between hexaploid species.

PALAEONTOLOGICAL EVIDENCE

The attempted reconstruction of the evolutional history of the genus *Geum* as outlined so far has been based solely on systematical, morphological, cytogenetical and geographical evidence. However, the history of this plant group reaches far into the past, right to the mesophytic period when the Angiosperms originated. Quite evidently the most serious arguments as can be supplied by palaeobotanical evidence are lacking in these considerations. Unfortunately there are no fossil data referring directly to the genus *Geum.* From Kirchheimer's monograph in Fossilium Catalogus (1942) on the palaeontological data referring to the rose family the following facts relevant for the history of this family are apparent. The most ancient fossil froms of the rose family are the lower Cretaceous *Amygdalus taurica* and *Cerasus meridio-*

nalis from south-eastern Europe. The upper Cretaceous forms reported from North America are species of the genera *Amelanchier, Crataegus, Prunus, Pyrus* and *Sorbus*. If these reports are to be accepted as correct, then the rose family would be one of the most ancient families of the Angiosperms. However, according to Kirchheimer these informations are unreliable. Nevertheless, as early Tertiary representatives of several subfamilies of the *Rosaceae* are known, it seems quite certain that the family is of Cretaceous origin at the latest, though, fossils which could be exactly defined were not preserved till now. Kirchheimer believes that at least the subfamilies of *Rosoideae, Prunoideae* and *Pomoideae* existed in the Cretaceous flora. The subfamily of *Pomoideae* with x = 17 and with a specialized structure of flowers and fruit represents rather a secondary evolutional line in the rose family. In my opinion its early appearance in the history of the family indicates that the primitive forms with x = 8 and 9 from which it originated had existed even ealier. It may be that they grew in the Cretaceous or even Jurassic mountains in conditions which did not favour the formation of fossils. Such an intepretation agrees with Axelrod's (1952) opinion that the primitive Angiosperms were much more ancient than of Cretaceous origin and that they probably appeared in the highlands of the tropical zone where their fossils were not preserved. Axelrod's considerations over the geographical distribution of the families of the Angiosperms and his analysis of the fossil floras lead him to the conclusion that the three main lowland Cretaceous floras of Angiosperms — arctic, tropical and antarctic — were not differentiated till in the course of Cretaceous migrations from the mountain territories where the flora of Angiosperms appeared already in the Triassic period or even earlier. The territories where the Angiosperms developed lay in the tropics, whereas, the holarctic and antarctic temperate zones are areas of their secondary evolution. In the Eocene of the Tertiary period the tropical zone still reached to the latitudes of about 55° north and south, and later in the Tertiary when the climate became colder and drier the belt of tropical floras narrowed and the Tertiary arctic and antarctic floras moved to lower latitudes. The appearance of Tertiary steppe, desert and arctic floras disrupted the more uniform primitive forest flora of the tropical and temperate zones which became differentiated both in the latitudinal and longitudinal directions.

Already early Tertiary fossil forms from the subfamilies of *Spiraeoideae, Dryadoideae, Rosoideae, Prunoideae* and *Pomoideae* are known and this refers also to the *Chrysobalanoideae*, but these are at present considered to form a separate family.

From the subfamily of *Dryadoideae,* with which the present considerations are more closely concerned, some fossil remains are known only from the genus *Cercocarpus.* On the evidence of numerous fossil floras Axelrod (1948) demonstrates that in California this genus was present already in the Miocene chaparral with a floristic composition similar to that of the present times. The genus is even reported from the Eocene of Canada. Miocene and Pliocene fossils from California, New Mexico and Idaho are very similar to the present day species *Cercocarpus betulifolius and parviflorus.* Miocene fossil leaves found in Idaho and defined as *Chamaebatia praefoliosa* Brown which resemble the leaves of the now growing *Chamaebatia foliosa* quite certainly do not belong to this genus. However, from the palaeobotanical evidence it is clearly apparent that the tribe of *Cercocarpeae* together with its three genera represents a very ancient group, which conclusion coincides with the present deliberations on the phylogenesis of the subfamily of *Dryadoideae.* Unfortunately no fossil remains from the tribes of *Dryadeae* and *Geeae* have been found so far, except of course those of the genus *Dryas* known from numerous glacial floras when the genus constituted a typical plant for subarctic tundra floras.

In the related subfamily of *Rosoideae* Eocene fossil remains of seeds and fruit of the genus *Rubus* and Miocene fossils of the genus *Potentilla* are known. This indicates that on the Northern hemisphere the formation of the present day shrubby and herbaceous genera with the basic number of 7 chromosomes started already early in the Tertiary and perhaps included not only the subfamily of *Rosoideae* but the family of *Dryadoideae* also.

As can be seen from the above considerations little support is forthcoming from palaeobotanical evidence for the attempt to retrace the evolutional history of the genus *Geum.* It may be that decisive proof wil never be supplied by palaeobotany as this group of plants does not enter today, and probably did not enter in the previous geological periods, into the composition of those plant associations which live on marshes and in the deltas of rivers where, owing to conditions very favourable for fossilization, most fossil remains are found.

Even in the absence of palaeobotanical evidence an all-sided morphological, cytogenetic and geographical analysis, although as incomplete as in the case of the genus *Geum* studied in the course of this work, may throw new light on the evolutional differentation processes of plants.

Table I

Geum montanum from Tatra Mts. (Sucha Kasprowa)

All photographs by Zofia Zwolińska, Zakopane

Table II

Geum reptans from Tatra Mts. (Sucha Kasprowa)

Geum rivale from Tatra Mts. (Dolina Kościeliska)

Geum urbanum from Tatra Mts. (Dolina Kościeliska)

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