Cytogenetical Studies with *Geum hispidum* Fr.

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INTRODUCTION

G. hispidum was described by Elias Fries in "Flora Hallandica" in 1818 from the province Halland in Sweden. The description was short and rather inaccurate. Nevertheless the newly described species was easily distinguishable from *G. rivale* and *G. urbanum* ubiquitous in Sweden. E. Fries considered it to be related to the *G. macrophyllum* of North America and Eastern Asia. The species was subsequently found occurring in other localities in neighbouring Swedish provinces. In 1921 the study of this curious "endemic" species of Sweden's flora was taken over by R. Sterner. In his considerations on the taxonomy of this species, Sterner came to the conclusion that it is very closely related to *G. aleppicum* Jacq. He considered both *G. hispidum* and another Balcan species *G. molle* Vis. et Panc. as varieties of this species. He reached no final conclusion however, due to the lack of a suitable wide range of comparative material. The results of my studies on interspecific hybrids in the genus *Geum* tend to disprove Sterner's views. *G. aleppicum* does not seem to be closely related either to *G. hispidum* or to *G. molle*. The hybrids between these species are highly sterile.

The distribution of *G. hispidum* in Sweden is of considerable interest. It was recorded as very rare by E. Fries from one sea-side locality in the province of Halland. Since no one after Fries ever reported this species from this locality, Sterner was led to suspect some mistake or interchange in Fries herbarium labels. However, at about the same time that Fries reported *G. hispidum* in the Halland province, the species was found occurring in the neighbouring province of Blekinge, also near the sea shore, on the main-land as well as on the numerous islets belonging to the archipelago of the town Karlskrona. In the following years it was found in similar localities in the neighbouring provinces of Småland, Östergötland and Södermanland. As Sterner's distribution map shows (Fig. 1), *G. hispidum* occurs in Sweden in a narrow belt which stretches

along the sea shore from about Kalmar through the port Oskarshamn as far as Västervik in the north. Discussing the local distribution of this species in Sweden Sterner emphasizes that it occurs naturally mainly

Fig. 1. Distribution of *Geum hispidum* Fr. in Sweden acc. to Sterner (1921). Circles with dots denote hybrids with *G. urbanum* L.

among shrubby vegetation of the islets archipelago, whilst its inland sites are mainly road-sides and pastures where it no doubt appears due to the dispersion of its seeds by man and animals. According to Sterner this species is now expanding its area, spreading inland. He considers the

small number of individuals occurring in local populations of this species as evidence for its rapid spread. Competition with the wide-spread *G. urbanum* often occurring together with *G. hispidum* in analogous semi-natural environments may be a factor hindering its migration. In localities of common occurrence of both species natural hybrids between them are often found. These hybrids are of clearly lowered fertility. On Sterner's map (Fig. 1), only a part of the known localities of this hybrid are marked. Since species of the subgenus *Eugeum* are mainly cross-pollinated, individual members of *G. hispidum* appearing in new localities, previously occupied by *G. urbanum*, can be in a large measure pollinated by *G. urbanum*, which of course tends to slow down the spreading of this species.

S t e r n e r in his detailed analysis of the distribution of *G. hispidum* in Sweden shows that the migration from its main centre of distribution in the neighbourhood of the ports Oskarshamn and Rysby to its more distant, marginal sites follows the system of the main roadways and other communication arteries. S t e r n e r holds the opinion that the rate of spread of *G. hispidum* will increase in the future and that this species may become very common in South-Eastern Sweden. It seems that it would be of interest to check whether S t e r n e r's predictions are being fulfilled.

S t e r n e r was furthermore concerned with the question of whether *G. hispidum* is endemic to the flora of Sweden, whether it can be considered an old "paleoendemic" type or a younger "neoendemic" type formed through mutations or hybridization? S t e r n e r, incorrectly according to the views of the present author, takes *G. aleppicum* to be the original species, the starting point. He considers it possible that in the Eastern European *G. aleppicum* localities *G. hispidum* might also be found. He contends that *G. aleppicum* had previously been growing in South-eastern Sweden, where *G. hispidum* arose in a fashion, not clearly defined. It may be of interest that the fact that *G. hispidum* has been reported from Spain by Willkcm and Lange: "Flora Hispanica" vol. III pg. 238 is almost disregarded. S t e r n e r considers the Spanish plants as probably identical to the Balcanic species *G. molle*, which was also held by the authors of the Spanish flora (Suppl. Fl. Hisp. pg. 228). Finally, drawing botanists' attention to the interesting problem presented by *G. hispidum* he appeals that in the future, the behaviour of this species should be observed. It was the aim of the present work to respond to S t e r n e r's appeal and to draw the attention of botanists to the probable origin of this "endemic" member of the Swedish flora.

G. *HISPIDUM* FR., PROBABLE RELATIONSHIP

As has been previously shown *G. hispidum* has little in common with *G. aleppicum* Jack. (W. Gajewski, 1957). *G. hispidum* appeared to be closer to a *Geum* discovered at a later period in Spain. Willkcm and Lange at first regarded the Spanish plants as identical to *G. hispidum* Fr. but later came to the conclusion that they were more likely members of the species *G. molle* Vis. et Panc., previously recorded from the Balcan peninsula. In 1887, C. Pau described the same plants as a separate species *Geum albarraciense* Pau in *Notas Botanicas a la Flora Espanola*. He emphasized that he considered this species to be more closely related to *G. hispidum* than to *G. molle*. F. Bolle (1933) in his monograph of the genus *Geum* expressed the same view. *G. albarraciense* and *G. hispidum* were treated as two very closely related species, whilst a relationship with *G. molle*, more distant from both of them, was recognized. In recent work of A. Bolos (1951) it is mentioned that authorities on the Spanish flora Cuatrecasas and Rothmaler regard the differences between the Spanish and Swedish plants but of a varietal degree, and so consider the Spanish plants to be *G. hispidum* Fr. var. *albarraciense* (Pau) Cuatr. (in hb.).

From this point of view therefore, there would be but one species with a disjunctive distribution, embracing the Iberian peninsula on the one side and the South-eastern coast of Sweden on the other. A problem now arises how to explain the present distribution of this species.

In Spain *G. hispidum* occurs mainly in mountains, from the Pyrenees through coastal chains of Catalonia to the high mountains of Cantabria and Galicia. The map on Fig. 2 (from Bolos 1951) shows the distribution of this species in Spain. Bolos regards the *G. hispidum* sites in the Spanish mountains as one of the more interesting examples of the boreal element in the flora of Spain. He considers the "Scandinavian and northern Russian" area of this species as the main one, while the Spanish localities would be relics formed during the migration from the north in the glacial ages.

The reverse would seem more probably to be the case to the present author. The Spanish *G. hispidum* sites on unglaciated areas seem to be very old, like numerous oreophytes of Spanish mountains. There, even whole genera or whole groups of species are either endemic or else their centre of distribution is on the Iberian peninsula, as was recently well demonstrated for the genus *Narcissus* (Fernandes 1951). At the same time the Swedish *G. hispidum* distribution covers only a small belt on the coast, and is situated on the youngest geological territory of Europe. It is known that the islets of the coast of Scandinavia originated during

the postglacial rise of the landmasses of Scandinavia, a result of the retreat of the landice. According to the geologists these islets have emerged from the sea only some five thousands of years ago. It would seem from

Fig. 2. Distribution of *G. hispidum* Fr. in Spain acc. to Bolos (1951)

the work of Sterner however, that the majority of the Swedish *G. hispidum* sites are still younger, originating through migrations in historic times. All taken into account therefore, it becomes difficult to imagine with Bolos, *G. hispidum* as a boreal element of the Spanish flora. It is more likely that *G. hispidum* was man-introduced into Sweden from Spain, probably carried over by ship. It is not known when this could have occurred. The event may date back to Norman times. In any case it seems that the first settlement occurred in the regions of the ports of Oskarshamn and Rysby followed by further spreading inland.

As has already been shown (W. Gajewski 1957) *G. hispidum* and *G. molle* are two very closely related vicarious species. Meiosis in the hybrids between these two species is almost normal and their average percentage fertility is 55,9 for pollen and 54,2 for seeds. The two species are likewise very close morphologically. The distribution of *G. molle* on the Balcan Peninsula and on the small area of the Apenine peninsula in Abruzzi, and of *G. hispidum* on the Iberian peninsula, shows the two taxa are two vicarious forms occupying the outskirts of the western mediterranean region, which region, according to the results previously reported,

probably formed the centre of origin of the whole subgenus *Eugeum* L. There is no doubt that the disjunction separating *G. hispidum* of Spain from the *G. molle* of the Balkan peninsula is of very long standing, dating

Fig. 3. Distribution of *G. hispidum* Fr. and *G. molle* Vis. et Panc. in Europe

back, at least to the late Tertiary ages. In this case the isolation period was sufficiently long to allow a distinct morphological differentiation of the two species particularly in the shape of leaves (Figs. 4—6) and

a partial loss of the chromosome homology as can be seen from the occurrence of univalents in the meiosis in F_1 hybrids. The two species are also partially sexually isolated as the level of fertility lowered to 50% in the interspecific hybrids demonstrates.

Fig. 4. *G. molle* Vis. et Panc.

The case of the relationship between the Spanish and Swedish *G. hispidum* populations is somewhat different. Even though previously described as distinct species, the differences between them are very small. Bolle (1933) in his *Geum* monograph treats *G. albarraciense* as a separate species differing from *G. hispidum* in having basal leaves with a more rounded outline at the top, and with a less obvious and less sharp indentation. He remarks that he has never met with flowers as small in size in

G. hispidum, as one can sometimes see in *G. albarraciense*. Judging from the comparison of Bolle's descriptions of the two species, they differ also in the degree of indentation of the terminal leaflet, in the length of the gynophore and in the proportion of the length of the rostrum to

Fig. 5. *G. hispidum* Fr. from Sweden

the stigmatic part of the style. The present work suggests that most of these differences, indicated by Bolle, are rather apparent than real and not really significant.

A thorough investigation of the differences between the Spanish *G. hispidum*, the Balkan *G. molle* and the *G. hispidum* of Sweden is not only of significance from a taxonomic point of view, but is also of some broad evolutionary importance. It seems that it is possible in this case, to compare the degrees of morphological and cytogenetic differentiation as

dependent upon the length of the period during which the original population subdivided into the three derivative and separate populations. Whilst *G. hispidum* from Spain and *G. molle* have been isolated for several hundred thousand years, in the case of Spanish and Swedish populations

Fig. 6. *G. hispidum* Fr. from Spain

of *G. hispidum* the estimate will not exceed some tens of thousands i. e., from the time the South-eastern coast of Sweden emerged from the sea. This estimate could be still smaller, dating from the time of the species introduction by man. This is a case of a natural experiment on the effect of isolation of distinct populations in different periods. The influence of the length of the isolation period and of different environments upon the degree of taxonomic differentiation can therefore be investigated. It is also an example of the influence of man upon the youngest evolutionary history of the genus *Geum*.

RESULTS OF CYTOGENETIC INVESTIGATIONS

To obtain an accurate comparison of *G. molle* and the Swedish and Spanish *G. hispidum*, the plants were cultivated for several years, under the most uniform conditions possible, in Warsaw Botanical Garden. *G. molle* was grown from seeds received from Sofia (Bulgaria) and collected from natural sites around this town. The Swedish *G. hispidum* originated from seed taken from a herbarium specimen in Göteborg Botanical Garden, collected by Sterner in Ryssby near Kalmar in the province Småland in Sweden. The Spanish *G. hispidum* was grown from seed received from prof. A. Bolos of Barcelona, which had been collected on a natural site in Hilari near Sacalm, Catalonia. In Warsaw the plants were propagated from seed several times, then crossed in all possible combinations.

Observation of the cultivated plants showed *G. molle* to differ from both the Spanish and Swedish *G. hispidum* in a whole series of morphological characteristics eg. the shape of basal leaves, the type of hairiness, the length and branching of shoots, the shape, the colour and dimensions of petals, the flowering period and a whole series of other traits. The differences are not particularly important, but they are sufficiently distinct to make the separation of two species easy. Seed formation after cross pollinating *G. molle* and *G. hispidum* is quite normal in the reciprocal crosses. Reciprocal F_1 hybrids are identical. Average fertility values for the pollen and the seeds of these crosses were:

Fertility in percent	Pollen	Seeds
F_1 <i>G. molle</i> $\times$ <i>G. hispidum</i> Spanish	54,2	56,3
F_1 <i>G. molle</i> $\times$ <i>G. hispidum</i> Sweden	55,9	54,2

A cytological analysis showed the $2n$ number to be 42 in *G. molle* as well as in the Spanish and Swedish *G. hispidum*. The hybrids between *G. molle* and *G. hispidum* showed a completely normal course of meiosis with 21 bivalents in MI in the majority of PMC's. In some PMCs 2 to 6 univalents may be found and the corresponding smaller numbers of bivalents. The results of the investigation of FMCs at MI gave the following results:

Number of PMCs with configuration of	21_{II}	$20_{II} + 2_I$	$19_{II} + 4_I$	$18_{II} + 6_I$
<i>G. molle</i> $\times$ <i>G. hispidum</i> Spanish	112	4	4	2
<i>G. molle</i> $\times$ <i>G. hispidum</i> Swedish	56	6	1	

It can be seen that the degree of chromosome conjugation is almost the same in both hybrids. As has already been reported (Gajewski 1957) the parental traits segregate quite clearly in the F_2 generation of the

hybrid *G. molle* $\times$ *G. hispidum* (Swedish). This can be most easily seen in the shapes of the basal leaves (Fig. 7). The F_2 generation between *G. molle* and *G. hispidum* from Spain showed the same type of segregation.

Fig. 7. Basal leaves from different F_2 plants of the hybrid *G. molle* $\times$ *G. hispidum* (Sweden) showing clear segregation. Extreme types are nearly identical with parental species *G. hispidum* (left) and *G. molle* (right)

There was also a clear segregation of the fertility of the F_2 plants. Quite a number of plants were as fertile as parental species:

Fertility of seeds in percent	0	20	40	60	80	100
F_2 <i>G. molle</i> $\times$ <i>G. hispidum</i> (Spain)	—	35	52	15	11	
F_2 <i>G. molle</i> $\times$ <i>G. hispidum</i> (Sweden)	2	20	23	13	2	

The segregation of the other characters of the hybrid *G. molle* $\times$ *G. hispidum* have already been reported (Gajewski 1957).

To summarize, one can assert on the basis of comparison and cytogenetic analysis that the *G. molle* and *G. hispidum* underwent a clear morphological differentiation. The differences are small but concern most vegetative and floral organs. The continual mode of segregation of the differential traits shows that the differences are probably based upon a series of slight mutations with a cumulative effect. Along with morphological differentiation a genetico-physiological differentiation took place,

causing a decrease in the fertility of hybrids inspite of the highly normal conjugation of chromosomes.

At first sight, populations of the Spanish and Swedish *G. hispidum* grown under similar conditions, seem identical and differences between them are difficult to distinguish. The differences in the shape of basal leaves are not apparent (Fig. 8). Under cultivation the Swedish *G. hispi-*

Fig. 8. Basal leaves of *G. hispidum* from Sweden (upper row) and from Spain (lower row)

dum was stronger on the average, having longer and often more branched stems and slightly smaller flowers than the Spanish *G. hispidum*, observations directly opposite to those noted by Bolle. The stronger amongst the Spanish *G. hispidum* individuals, however equalled the Swedish plants. None the less after a close scrutiny of larger populations cultivated side by side, a whole series of slight differences becomes apparent eg. shape and dentation of leaves and leaf stipules, hairiness, sometimes in the flowering time. These differences are very slight difficult to measure, even to describe. Perhaps the differences in the petal dimensions were the clearest:

Petal length in mm:	5	6	7	8	9	n	M	$\pm m$
<i>G. hispidum</i> (Spain)		4	38	70	2	114	7,6	0,05
<i>G. hispidum</i> (Sweden)	2	40	54	10	2	108	6,7	0,13
Petal width in mm:	5	6	7	8	9	n	M	$\pm m$
<i>G. hispidum</i> (Spain)	4	82	25	3		114	6,2	0,06
<i>G. hispidum</i> (Sweden)	2	72	30	4		108	6,3	0,06

It can be seen from the figures above that the differences in petal measurements are slight and significant only in the case of petal length. The same type of differences may be expected of course, between local but distinct populations in either Sweden or Spain and does not denote at all that the Spanish and Swedish populations have actually become differentiated. Similar, even less tangible differences concern still other traits of the studied plants. Photographs of herbarium specimens of whole plants and basal leaves are given for comparison in figs.

Both forms of *G. hispidum* were crossed reciprocally. The seed set after crossing is perfectly normal. Reciprocal hybrids are identical, and quite uniform. A total of 300 F_1 hybrids were grown to maturity. The plants were strong and of vigorous growth. Since the differences between the parental forms are very slight the hybrids can hardly be distinguished from their parents. For comparison petal measurements of both F_1 populations are given below:

Petal length in mm:	5	6	7	8	9	n	M	$\pm m$
F_1 <i>G. hisp.</i> (Sweden) $\times$ <i>G. hisp.</i> (Spain)		1	59	60	1	121	7,5	0,05
F_1 <i>G. hisp.</i> (Spain) $\times$ <i>G. hisp.</i> (Sweden)		4	46	59	3	112	7,6	0,06
Petal width in mm:	5	6	7	8	9	n	M	$\pm m$
F_1 <i>G. hisp.</i> (Sweden) $\times$ <i>G. hisp.</i> (Spain)	2	30	88	1		121	6,7	0,04
F_1 <i>G. hisp.</i> (Spain) $\times$ <i>G. hisp.</i> (Sweden)	2	48	59	3		112	6,5	0,07

It can be seen from these figures that petal measurements in both hybrids are nearly the same. It may be of interest that the petal width in the hybrids seems to exceed petal width of the parental forms. The pollen fertility of the hybrids is normal. Average pollen fertility estimated, on the basis of forty slides, with ab. 200 pollen grains counted on each, was $93,4 \pm 1,2\%$ for the hybrid *G. hispidum* Sweden $\times$ *G. hispidum* Spain and $91,5 \pm 0,9\%$ for the reciprocal hybrid.

Seed fertility of the F_1 hybrids however, was clearly lower than fertility of the parental forms. The figure for the F_1 *G. hispidum* Sweden $\times$ *G. hispidum* Spain came to $82,0 \pm 1,2\%$ and to $77,4 \pm 2,1\%$ for the reciprocal cross, whilst the seed fertility figures in the parental forms came to, $93,5 \pm 0,9\%$ for the Spanish plants and $95,3 \pm 0,7\%$ for the Swedish plants. The above values represent an average of measurements for 10 plants, 3 fruit heads per plant after free pollination. The material was collected from plants growing in adjacent plots, at the same time. There can be no doubt that in spite of normal pollen fertility of the F_1 hybrids there is a statistically significant decrease in seed fertility of ab. 10—15%.

F₂ generations were obtained through intercrossing of F₁ plants in both reciprocal hybrids. The populations looked rather uniform and the plants were vigorous. The plants could hardly be distinguished from F₁ hybrids. Unfortunately a strong mildew infection occurred in summer, resulting in the death of some of the plants before seed set and causing others to show a decreased fertility on account of the fungal infection. Pollen and seed fertility estimations carried out on the healthier plants, indicated, as in the F₁ hybrids, normal pollen fertility and decreased seed fertility in most plants, with values from 70 to 85%. Some of the F₂ plants however, show high seed fertility 85—95%, similar to that of parental forms.

Cytological analysis of both reciprocal F₁ hybrids showed a normal course of meiosis with 21 bivalents at MI in all PMCs. 2 or 4 univalents were found in few cells only. The course of AI and of the second meiotic division was quite normal.

DISCUSSION

Geographical isolation is one of the factors contributing to the formation of new taxonomic units. Sub-populations of the original uniform population, separated from each other by distances which make gene exchange impracticable may differentiate, due to the mutation process and differently acting selective factors. The degree to which such a differentiation may proceed is certainly dependent on many very different factors. The first of these would be the cytogenetical nature of the given taxon. If it is genetically very uniform, composed of but a small number of biotypes, then even a long-lasting isolation will not bring about a greater differentiation. Likewise if the isolated populations are geographically distant but existing under similar climatic conditions and in similar communities, which show only inconsiderable changes over large periods of time, then chances for the differentiation of new species would also be small. Species with a bipolar distribution are good examples of species with large disjunctions, dating from distant geological periods, yet morphologically very close as e. g. *Draba incana* or *Saxifraga magellanica*, also numerous forest species, are common to North America and eastern Asia, separated from very ancient times. The last mentioned grow in forests of both continents where the floral composition and microclimatic conditions are very similar, not having undergone any major change since the Tertiary period. Many other similar examples of large disjunctions within the limits of one species may be found. cf. Good's (1953) text book of plant geography. Unfortunately in most cases a cytogenetical

analysis is lacking superficially identical species may be differentiated at least from genetical-physiological point of view.

One could, of course, compose a much longer list of species with disjunctive distribution forming pairs or groups of vicarious varieties, races or closely related species. Here too the cytogenetic nature of such taxa is only very poorly known. It is possible that in some cases, due to a wide geographical separation, distinct populations of the same species have been described as separate species, as in the case of *G. albarraciense* and *G. hispidum*. Comparative cytogenetical and taxonomical studies of taxa with different types of disjunctions, will undoubtedly play a significant role in the study of the evolutionary mechanisms in nature. The relationship of the rate and degree of morphological and cytogenetical differentiation to the extent and age of the disjunction, size and type of the isolated population, ecological and geographical conditions of the site occupied by these populations, requires thorough study.

Finally the most recent period of plant evolution linked with man's domination on earth, creates new conditions for the study of the influence of isolation and environment on the differentiation of plant species, often transported by man to new continents. It is frequently possible to establish the time of the occurrence of a given isolation, the size of the initial population, which may be of the outmost importance for the study of the rate and mode of differentiation. It is of uttermost significance, that the great experiment being carried out by mankind in changing our vegetation should be earnestly followed and studied from the very beginning.

The present work is a small contribution to this line of research. It has already been attempted to demonstrate that the subgenus *Eugeum* of the genus *Geum* L. represents the youngest stage in the evolution of this genus. The whole subgenus probably has its origin in the Mediterranean region. In the course of spreading, due to isolation, forms of this subgenus underwent differentiation into numerous species often maintaining their chromosome homology and potential ability for gene exchange. Genetical and physiological differentiation in this group did not always keep pace with the degree of morphological differentiation. Man played a considerable role in the present distributional pattern of the *Eugeum* species.

The group of closely related taxa under discussion is an example of these processes. It seems highly probable that *G. molle* and *G. hispidum* represent two vicarious species which arose as a result of an old disjunction, whilst the separated population of *G. hispidum* in Sweden results from a relatively recent introduction of this species by man from Spain. In this case the degree of morphological and cytogenetical differen-

tiation is to some extent proportional to the time the disjunction lasted. Whereas in the first case one may consider the differentiation to have proceeded to the stage of distinct species, in the second case the disjunctive populations can at the most be regarded as varieties within a species. As the differences are probably based on numerous small mutations, it seems that the process of differentiation is of a continuous nature and is in a certain sense dependent on the time factor. Small morphological differences insignificant at first or the inconspicuous decrease in hybrid fertility, may increase with time until distinct species arise. In any case, the Swedish *G. hispidum* is not at the moment an endemic member of the Scandinavian flora. Neither has it been definitely shown that the established differences between the Swedish and Spanish plants are of greater consequence than possible differences between populations originating from distinct mountain ranges in Spain. This point would require additional study. Undoubtedly however, further observation of the fate of this species in Scandinavia can assist the study of the influence of isolation upon the formation of new taxonomic units.

CONCLUSIONS

1. *G. molle* Vis. et Panc from the Balkan Peninsula and *G. hispidum* Fr. from the Iberian peninsula form a pair of nearly related vicarious species. Both species differ morphologically in a whole series of traits. The hybrids among them show a nearly normal course of meiosis in PMCs but the seed and pollen fertility are lowered to a 50% level.

2. *G. hispidum* Fr. outside in Spain occurs also in Sweden. The differences between the two populations are very small. It is suggested that *G. hispidum* was introduced to Sweden by man, where it occurs on sites very young geologically.

3. Both *G. hispidum* populations inspite of considerable disjunction are little differentiated morphologically and cytogenetically. Meiosis in hybrids is normal, their pollen fertility is high and only a small ($\pm 15\%$) decrease in seed fertility was noted.

4. The disjunction between *G. molle* and *G. hispidum* from Spain is much older than the disjunction between the Spanish and Swedish *G. hispidum* localities. In keeping with the duration of the disjunction in the first case, the differentiation has proceeded to a stage, which can be accepted as on the species level, whilst in the second case the differences are at the most of the variety rank. The differentiation may be a continuous process in nature and is to a certain degree proportional to the length of duration of the isolation period.

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