

MUTANT RACES DERIVED FROM *OENOTHERA LAMARCKIANA SEMIGIGAS*

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INTRODUCTION

The progeny of *Oenothera Lamarckiana semigigas* splits up into numerous mutant types, among which the prominent ones are seen to repeat the external features of the old mutated races of *Oe. Lamarckiana* more or less clearly. Besides these, deviating types are observed, but as a rule the deviations are small and do not constitute really new characters. They are to be considered as the result of different combinations of the same elementary changes.

The question arises, whether these mutants are also like the older races in their hereditary characters. If this is so, they may be considered as belonging to the same general types and as identical with them in the special cases. The *semigigas* would then have to be considered simply as due to a sevenfold mutation or to the simultaneous production of the seven main derivatives lately distinguished by BOEDIJN and myself for *Oe. Lamarckiana*, and of their secondary forms (DE VRIES and BOEDIJN 1923).

This problem could be solved by means of the cultivation of the second generation of the mutants described in previous articles. These were derived from three crosses, made in 1922, on a biennial specimen of *Oe. (lata* × *Lamarckiana) semigigas*. For one of these the pollen of *Oe. (biennis* × *Lamarckiana) velutina* was used and for the offspring of this

cross the external features of each type have been described and the chromosomes counted for every individual by BOEDIJN and myself (1924 a, b, p. 258). For the two others I have chosen the pollen of *Oe. Lamarckiana* mut. *tardescens* and of *Oe. Lamarckiana* mut. *blandina*. *Tardescens* has pure *velutina* pollen and the offspring behave like those of the first-named cross. In the pollen of *Oe. blandina* (synonym: *Oe. Lamarckiana* mut. *velutina*) the characteristic lethal factor of the *velutina* type is absent, and therefore the corresponding seeds, which are ordinarily barren, are viable here, producing a large part of the progeny in consequence of their preferential fertilization (DE VRIES 1924 a). For these two crosses the chromosomes of the mutants have not been counted, and they are grouped in the following tables according to their external marks and to the condition of their offspring.

After self-fertilization in 1923 some of the mutants of *Oe. semigigas* produced a sufficient supply of seeds, while others gave only a small harvest. Only the first category could be used for the present purpose, and cultures of about 60 individuals were derived from them, wherever possible, in 1924. Almost all of these plants have flowered, with the exception of a small part of specimens of the *Lamarckiana* type, when this was indubitably clear in the stage of rosettes of root leaves.

The different constituents of the cultures have been counted in this stage and afterwards during the summer, especially shortly before flowering and in the flowering and fruiting condition. The general results of these separate countings will be given in the tables. These deal with representative members of five of the seven main classes and with some of their secondary forms. In the categories of *lata* and *pallescens* no plants have given a useful amount of seeds, but the tables may suffice to warrant the general conclusions.

Oenothera Lamarckiana semigigas MUT. *scintillans*

From the cross of *Oe. semigigas* with *Oe. (biennis* × *Lamarckiana) velutina* studied by BOEDIJN and myself (1924 b, p. 261) I had two, and from that with *Oe. tardescens*, three plants of *Oe. scintillans* (1924 b, p. 224), all of them of a very pure type. They proved to be sufficiently fertile after self-fertilization and about sixty specimens of the offspring of each were cultivated and counted during the flowering period. The two first-named parent plants had 15 chromosomes, but for the three others the number has not been determined. The cultures showed exactly the same splitting as is known for the old race of *Oe. Lamarckiana* mut. *scintillans*. The main types were *scintillans*, *Lamarckiana* and *oblonga*.

Moreover, there were barren seeds which amounted to 34 percent in the first culture, and a small number of mutants.

The countings on the beds are given in table 1. No. 1 and No. 2 were derived from the cross with *velutina*, Nos. 3 to 5 from that with *tardescens*.

TABLE 1
Oenothera semigigas mut. *scintillans*. Second generation.

<i>Scintillans</i> PARENT	TOTAL	<i>Lamarckiana</i>	<i>Scintillans</i>	<i>Oblonga</i>	MUTANTS
No. 1	58	52	2	3	1
No. 2	38	32	2	4	0
No. 3	60	48	4	7	1
No. 4	60	41	7	9	3
No. 5	60	51	4	3	2
Total	276	224	19	26	7
Percentage		81	7	9	3

For my race of the same name the figures are, in the main, 70 percent *Lamarckiana*, 18 percent *scintillans*, 10.5 percent *oblonga* and 1.5 percent mutants (DE VRIES 1924 c). The conformity is thus seen to be as close as might be expected. The mutants were of the ordinary types, namely, *hamata* on the first bed, one *semigigas* in each of the last three beds and *liquida*, *pulla* and *palescens* in cultures No. 4 and No. 5.

Oenothera semigigas MUT. *cana*

From the cross with *velutina*, already cited, we had eight specimens of *cana*, all of them with 15 chromosomes and of a pure type. Six plants produced a sufficient supply of seeds, but with only a small germinating power. All of the seeds were sown and all of the seedlings planted out. Counted during the flowering period they gave the results presented in table 2.

TABLE 2
Oenothera semigigas mut. *cana*. Second generation.

<i>Cana</i> PARENT	TOTAL	<i>Lamarckiana</i>	<i>Cana</i>	MUTANTS
No. 1	59	28	20	11
No. 2	23	12	9	2
No. 3	28	16	7	5
No. 4	27	13	9	5
No. 5	6	3	3	0
No. 6	5	1	4	0
Total	148	73	52	23
Percentage		49	35	16

For my race of *cana* the corresponding numbers were almost the same, namely, 62 percent *Lamarckiana*, 33 percent *cana* and 5 percent of mutants (DE VRIES 1916 a, pp. 254, 256). Of the mutants in the cultures of 1924 a relatively large number were dwarfs, namely, 8 in the first, and 5 in the fourth, experiment, or 14 and 15 percent. This fact is easily explained by assuming that their parent plants in 1923 were half-mutants for this character and split according to the ordinary rules. The remaining mutants were *pallescens*, *spatulata*, *hamata* in No. 1, *oblonga* in No. 2 and No. 3, and four *auricula* in No. 3. Besides those given in our table, there was a *cana* with 15 chromosomes, which produced 154 seedlings, almost all of which showed the type of the parent plants, only two having the marks of *Oe. Lamarckiana*. Moreover, there was a large amount of barren grains (76 percent). I also sowed the seeds of two specimens of *cana linearis* derived from the cross of *Oe. semigigas* × *blandina*. As was to be anticipated, they produced the type *blandina laeta* instead of *Lamarckiana*, and of this 25 and 17 specimens out of a total of 66 and 60, and besides these 30 and 39 plants of the type of *blandina*. The remainder were 8 and 4 *cana linearis*, 2 *pallescens* and 1 *spatulata*. These figures are therefore to be considered as a corroboration of the main result.

Oenothera semigigas MUT. *liquida*

From the cross with *velutina*, I selfed five plants out of the seven of *liquida* of a pure type and with 15 chromosomes (DE VRIES 1924 b, p. 261). There was some difference in their spikes; that of one plant (No. 1) was as compact as in my old race, while the four remaining specimens (Nos. 2 to 5 of the table) had looser racemes. The same difference was seen among four plants from the cross with *tardescens* (DE VRIES 1924 b, p. 224), of which one (No. 6) had a dense spike and three (Nos. 7 to 9) a loose spike. This variation, however, did not seem to have any influence on the genetic constitution, as will be seen from table 3.

For Nos. 2 to 5 the number of barren seeds has been determined and found to be 61, 75, 86 and 81, or on the average 76 percent. This is rather a high figure, but for my race of *liquida* it was almost exactly the same, namely, 78 percent (DE VRIES 1916 b, p. 261). Besides these, the constitution of my race was, on the average, 67 percent *Lamarckiana*, 32 percent *liquida* and 1 percent mutants (DE VRIES 1916 a, pp. 268-269), agreeing sufficiently with the figures of table 3. In the cultures of 1924 the mutants were for a large part *oblonga*, and besides these, one *pallescens*, one *hamata*, one *nanella*, six *pulla*, one *semigigas* and some belonging to types not yet described.

Oenothera semigigas MUT. *spathulata*

Among the mutants of *Oe. semigigas* × *velutina* four specimens of *spathulata* with 15 chromosomes and of a pure type have been recorded (DE VRIES 1924 b, p. 261). They had, however, no good pollen and were therefore fertilized by means of *Oe. blandina*. This change from the

TABLE 3

Oenothera semigigas mut. *liquida*. Second generation.

<i>Liquida</i> PARENT	TOTAL	<i>Lamarckiana</i>	<i>Liquida</i>	MUTANTS
No. 1	29	24	4	1
No. 2	60	47	7	6
No. 3	59	49	8	2
No. 4	60	52	6	2
No. 5	60	47	10	3
No. 6	60	49	7	4
No. 7	61	43	12	6
No. 8	58	39	12	8
No. 9	59	32	16	11
Total	507	382	82	43
Percentage		76	16	8

ordinary method of self-fertilizing must result in two main changes in the progeny. Instead of specimens of the type of *Lamarckiana*, the well known hybrid, *Oe. (Lamarckiana* × *blandina*) *laeta*, must arise, and instead of the barren grains of *velutina* × *velutina*, viable seedlings with the characters of *Oe. blandina* must be found. According to the preferential fertilization of this latter (DE VRIES 1924 a) the *blandina* plants will occur in relatively too high numbers. There were still some empty grains, reaching 30 to 52 percent of the harvest, but these were evidently due to the weak condition of the type. The offspring of the four mutants flowered for the larger part in 1924 and yielded the figures of table 4.

TABLE 4

Oenothera semigigas mut. *spathulata* after fertilization by *Oenothera blandina*.

<i>Spathulata</i> PARENT	TOTAL	<i>Laeta</i>	<i>Blandina</i>	<i>Spathulata</i>	MUTANTS
No. 1	58	13	40	3	2
No. 2	63	0	47	5	11
No. 3	68	11	41	10	6
No. 4	59	20	21	15	3
Total	248	44	149	33	22
Percentage		18	60	13	9

In my previous race of *Oe. spathulata* × *blandina* I counted 25 percent of barren grains, and among the viable germs I observed 30 percent *laeta*, 52 percent *blandina*, 18 percent *spathulata* and very few mutants (DE VRIES 1924 b, p. 213). The constitution of the mutants from *semigigas* may therefore be considered as sensibly the same as that of the race. The mutants in the cultures of 1924 were 1 *lata*, 3 *auricula*, 2 *hamata*, 1 *liquida*, and in the second and third experiment 10 plants of a uniform but new type, with small, rounded and shiny leaves.

Oenothera semigigas MUT. *hamata*

Under this name I have described a very rare mutant, which, however, originated from different strains (DE VRIES 1924 b, p. 216). The same type is, curiously enough, not at all rare among the mutants from *Oe. semigigas*. From the cross with *velutina* I had two flowering specimens of a pure type and with 15 chromosomes (DE VRIES 1924 b, p. 261), which gave, after self-fertilization, a progeny whose constitution is shown in table 5.

TABLE 5
Oenothera semigigas mut. *hamata*. Second generation.

<i>Hamata</i> PARENT	TOTAL	<i>Lamarckiana</i>	<i>Hamata</i>	MUTANTS
No. 1	58	48	9	1
No. 2	3		2	1
Total	61	48	11	2
Percentage		79	18	3

My race of this name had given, as an average from two generations, 82 percent *Lamarckiana* and 31 percent *hamata*, besides about one-half of barren seeds. The constitution of the new mutants was, therefore, sufficiently the same as that of the race. Both were splitting mutants of the ordinary dimorphic type. The mutants were, in 1924, one *liquida* and one of the form of *diluta*.

Oenothera semigigas MUT. *pulla*

This type, which has not been remarked until very recently, is now easily recognized in the phase of the rosettes as well as during the time of flowering (DE VRIES 1924 b, p. 229; DE VRIES and BOEDIJN 1924 b, pp. 261, 266, fig. 2). It reaches half the height of the parent species, is hardly branched and has long, narrow, conical flower-buds with a reddish tinge. It is rich in pollen and in seeds. In the table given by BOEDIJN and myself (1924 b, p. 261) five specimens with 15 chromosomes and of a pure type

have been mentioned. I have self-fertilized them in 1923 and got in the next summer the results shown in table 6.

TABLE 6
Oenothera semigigas mut. pulla. Second generation.

<i>Pulla</i> PARENT	TOTAL	<i>Lamarckiana</i>	<i>Pulla</i>	MUTANTS
No. 1	88	40	33	15
No. 2	125	106	17	2
No. 3	135	123	10	2
No. 4	158	127	25	6
No. 5	155	132	17	6
Total	661	528	102	31
Percentage		80	15	5

I have made a control experiment with my race of this name, which originated directly from *Oe. Lamarckiana*, and which is to be described elsewhere, and found as an average from the offspring of two parent plants, 34 percent *Lamarckiana*, 40 percent *pulla*, and 26 percent of mutants. The constitution is thus sufficiently proven to be the same in both cases. The amount of barren grains was 50 percent for the race and 38 percent (27 to 48 percent) as an average for the five specimens referred to. The mutants of 1924 were 2 *albida*, 5 *oblonga*, 7 *auricula*, 7 *cana*, 4 *pallescens*, 1 *spathulata* and 5 *nanella*. Evidently they showed the same range as the ordinary mutants from *Oe. Lamarckiana* and no other types occurred. Like the primary forms of the six other main classes, the *pulla*, which is the only trisomic mutant in the central group, is a dimorphic form, giving one-half of empty seeds and reproducing from the other half, partly its own type, and partly that of the parent species.

MUTANTS OF THE TYPE SESQUIPLEX

In a previous article I have proposed this name for those mutants which have about one-half of empty seeds, but are constant and uniform in their living progeny (DE VRIES 1923 a). Their genetical constitution is usually either (mutant + *laeta*) × *laeta*, or (mutant + *velutina*) × *velutina*. They are dominant, the mutated gametes reproducing the race, whereas *velutina* × *velutina*, and *laeta* × *laeta* give the barren grains.

Among the mutants from *Oe. semigigas* such *sesquiple*x forms rarely occur, or perhaps are not always easily recognized. I selected two of them with 15 chromosomes, namely, *oblonga* and *auricula* (DE VRIES 1924 b, p. 261) for self-fertilization. Moreover, two specimens of *cana* with a deviating type, but with the same number of chromosomes (DE

VRIES 1924 b, p. 261) were found, after self-fertilization, to have a uniform progeny, besides a few mutants, and therefore to belong to this category. For convenience's sake I shall distinguish them by the name of *cana sesquiflex*. They reached about one-half the height of normal *cana* and had thicker fruits, which were almost like those of *Oe. Lamarckiana*. The results are in table 7.

TABLE 7
Sesquiflex mutants of *Oenothera semigigas*. Second generation.

MUTANTS	TOTAL	<i>Oblonga</i>	<i>Auricula</i>	<i>Cana Sesquiflex</i>	MUTANTS
<i>Oblonga</i>	84	83	1
<i>Auricula</i>	57	..	57
<i>Cana sesquiflex</i> ..	59	56	3
<i>Cana sesquiflex</i> ..	58	54	4
Total	258	83	57	110	8
Percentage					3

The amount of barren grains was, for *oblonga*, 69 percent, for *auricula*, 52, and for *cana sesquiflex*, 73 and 81 percent. Since the non-mutated gametes must have been of the *velutina* type, which is usually preferred during fertilization (DE VRIES 1924 a), these numbers must be considered as being too high, and as pointing to the expected figure of one-half of barren seeds. Setting aside these and the mutants, the four lines were found to be uniform. The mutants were 1 *albida*, 1 *scintillans* and 3 *oblonga*.

16- AND 17-CHROMOSOME MUTANTS OF *Oenothera semigigas*

All of the mutants of *Oe. semigigas* dealt with in the above tables and descriptions had 15 chromosomes in their nuclei, as far as investigated. Besides them, I succeeded in getting a sufficient harvest from four specimens with 16 or 17 chromosomes, derived from the cross *Oe. semigigas* × (*biennis* × *Lamarckiana*) *velutina* and from two plants of the *cana* type, from the cross *Oe. semigigas* × *tardescens*, which behaved like them in their progeny, but whose chromosomes, unfortunately, have not been counted. If the doubling of the chromosomes may be considered as an indication of a specific mutation, we should conclude that in the 16- and 17-chromosome mutants, two or three chromosomes, respectively, were in this condition. And if the application of the law of probability to the distribution of the mutations among the egg-cells of *Oe. semigigas*, as proposed by BOEDIJN and myself (1924 b), holds good in these instances, we must

expect that among the progeny of such plants the two or three mutated types, respectively, might separate and be seen each for itself. This is, however, not always the case. The dominant type is repeated in about the expected percentage, but the second form is either absent, or concealed in a few specimens among the other mutants, or shows in too small figures. Only in one instance it was plentiful, as will be seen in table 8. The third type, to be expected from the 17-chromosome mutants, has not shown itself clearly in the experiments here to be recorded. It seems probable that the second and third type suffer in a larger degree from the mortality of the germs within the seeds of *Oe. semigigas*, which is different for different categories, as will be shown elsewhere. But why this should be so, remains an open question.

In table 8 the type of the parent plants is introduced as "main type," while of the other types, aside from *Lamarckiana*, that form is considered to be a "second type," which occurred in the largest number of individuals. The remainder are given under the head of "mutants." In this table the mutants are given for each of the cultures, since they might include a

TABLE 8

16- and 17-chromosome offspring of Oe. semigigas. Second generation.

PARENTS	NUMBER OF CHROMOSOMES	TOTAL	<i>Lamarckiana</i>	MAIN TYPE	SECOND TYPE	MUTANTS	TOTAL MUTANTS
<i>Liquida</i> ...	16	81	26	4 <i>liquida</i>	42 <i>oblonga</i>	1 <i>albida</i> , 1 <i>auricula</i> , 1 <i>semigigas</i> , 6 <i>pulla</i>	9
<i>Pulla</i> ...	16	59	25	29 <i>pulla</i>	..	1 <i>albida</i> , 1 <i>auricula</i> , 1 <i>pallescens</i> , 2 <i>nanella</i>	5
<i>Pulla</i> ...	17	60	39	18 <i>pulla</i>	..	1 <i>auricula</i> , 1 <i>semigigas</i> , 1 <i>nanella</i>	3
<i>Auricula</i> ..	17	55	..	51 <i>auricula</i>	4 <i>oblonga</i>	0
<i>Cana</i>	77	39	21 <i>cana</i>	5 <i>auricula</i>	1 <i>albida</i> , 2 <i>oblonga</i> , 8 <i>nanella</i> , 1 <i>rubrinervis</i>	12
<i>Cana</i>	57	13	26 <i>cana</i>	12 <i>auricula</i>	1 <i>albida</i> , 3 <i>pallescens</i> , 1 <i>spathulata</i> , 1 <i>nanella</i>	6

third type in one or more of the four last-named cultures. The number of chromosomes was 16 in the first two and 17 in the following two parent plants. The *nanella* and *rubrinervis* are mutants of the central group, having only 14 chromosomes; therefore, they cannot be included in this discussion. The other mutants were *albida*, *auricula*, *pulla*, *pallescens*, *oblonga*, *spathulata* and *semigigas*. The chance of finding a "third type" among the progeny of No. 3 and No. 4 is, however, very small, since

there occurred only one trisomic mutation, namely, *auricula* in one of them, and none in the other. It is to be noted that the second types of our table are secondary forms of the class of *scintillans*, and that for the *pulla*, also, *auricula* has been observed among the mutants, although only in one individual for each. Perhaps the viability for second types is the largest in this group, as it has often been for *scintillans* itself and for its secondary forms in analogous experiments. In experiment No. 5 eight dwarfs have been observed, or about 10 percent, and this points to the condition of the parent plant as that of a half-mutant for this factor, as has been discussed above under the head of, *Oe. semigigas* mut. *cana*.

I have cultivated the offspring of a cross, *Oe. pulla* × *blandina*, in which the female parent had also 16 chromosomes. Among 60 offspring, however, here also no second type was seen. There were 8 *pulla* and no mutants, the remaining 52 individuals having the characters of *Oe. (Lamarckiana* × *blandina*) *laeta*, as was to be expected.

Among the offspring of *Oe. semigigas* × *blandina* I self-fertilized two beautiful plants of *hamata* and had a second generation of 58 and 59 individuals, respectively. Among these, 6 and 11 were like the parent, but 10 and 8 were *cana*, which might be considered as a second type and thus give a corroboration of the conclusions given above. There were 23 and 5 *blandina-laeta* and 16 and 25 *blandina*, as might be expected. In the first culture there were three mutants (*lata*, *palescens* and *nanella*) and in the second, 10 dwarfs, pointing to a condition of a half-mutant for this factor in the parent plant, as discussed under the head of "*cana*."

INTERCHROMOSOMAL CORRELATIONS

Almost all the cultures described above produced a large number of mutants besides the main types. The percentages did not essentially differ from those of *Lamarckiana*, and the same forms were present in almost every single instance, although the size of the experiments was too small for the expectation of complete series. But all of the primaries occurred, namely, *lata*, *scintillans*, *cana*, *liquida*, *palescens*, *spatulata* and *pulla*, also both the accessories, *albida* and *oblonga*. Nor did *semigigas* fail, and *nanella* occurred either as such or as half-mutants (as in the experiment with *cana*). From this we may conclude that the activation of one of the primaries or accessories in one of the chromosomes does not change the mutability of the others. This condition remains the same as it has been found in the parent species, *Oe. Lamarckiana*.

In this respect the trisomic or specific mutations are essentially different from the homogeneous or homozygotic types, previously described

(DE VRIES 1923 c, p. 221). *Oe. blandina*, *Oe. deserens* and *Oe. decipiens* have produced, until now, almost no mutations, even in cultures of a large size. If crossed with one another, the progeny also shows no mutability, either in the first or in the second generation. Over 350 mostly flowering hybrids have been studied for each of the two, embracing the six possible combinations. Here, therefore, is a clear proof of interference, especially when we compare this absence of mutability with the mutability shown in the tables of the present article. Of the homogeneous mutations mentioned, *Oe. blandina* belongs to the class of *velutina*, but *Oe. decipiens* and *Oe. deserens* to that of *laeta*. All of them lack both the zygotic lethals which are characteristic for the parent species. The factor-complexes of all three must be assumed to be represented in the central pair of chromosomes, which also carries the lethal factors, as BOEDIJN and I (1923, 1924b) have shown. Those complexes are of a recessive nature. From this we see that the operative condition of these recessives in the central chromosome hinders the mutability of the lateral ones in producing its types. In other words, there exists an interchromosomal correlation between the central rod and the lateral ones, which is absent between the lateral rods among themselves.

The latent condition of the mutability of *Oe. Lamarckiana gigas* discovered by means of double crossing (DE VRIES 1924b) may be due to such a form of correlation, and this would point to the possibility of some degree of latent mutability existing in numerous other cases, where plants have been considered until now as immutable.

14-CHROMOSOME OFFSPRING OF *Oenothera semigigas*

These have ordinarily the type of *Oe. Lamarckiana* and should be expected to come true to their type after self-fertilization. This proved to be true in the cultures of the offspring of three such plants and of two others, whose chromosomes had not been counted. Each experiment embraced about 60 flowering individuals. Mutants or aberrant types were not seen in the first-named three lines, but included in the two others, 1 *auricula* and 1 *cana* in the first, and 2 *lata*, 3 *albida*, 2 *scintillans* and 2 *cana* in the second instance. Leaving these aside, all of the 300 plants were uniform and pure *Lamarckiana*.

Among the offspring of *Oe. semigigas* × *tardescens* I had noted one plant which had the external marks of *Oe. rubrinervis* (DE VRIES 1924 b, p. 225). I sowed its seeds after fertilization and had in 1924 a progeny of 59 plants, 54 of which were like the parent and as brittle as my race of that name, while five were mutants (2 *oblonga* and 3 *liquida*).

CONCLUSION

The offspring of *Oe. semigigas*, after fertilization with the pollen of a *velutina* type (*biennis* × *Lamarckiana-velutina*, *tardescens* or *blandina*), shows the same hereditary constitution as the corresponding older races. The dimorphic mutants split into *Lamarckiana* and their own type (*scintillans*, *cana*, *liquida*, *spathulata* and *pulla*), the *sesquiflex* forms give a uniform progeny besides about one-half of empty seeds (*oblonga*, *auricula*, and the new form *cana sesquiflex*). Derivatives with 14 chromosomes also give a uniform offspring, with some mutants. Those with 16 or 17 chromosomes might be expected to split into two or three forms each, but they repeat their main type and give a second one only rarely and then mostly in very small numbers of individuals.

All in all, the mutants derived from *Oe. Lamarckiana semigigas* are genetically constituted, as far as investigated, exactly like the corresponding mutant races, directly sprung from the parent species. Interchromosomal correlations have not been found between them.

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