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BUD MUTATIONS IN THE POTATO AND THEIR CHIMERICAL NATURE.

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(With Seven Text-figures and a Colour-plate.)

THE present investigation was suggested to the author by the study of a remarkable form of potato plant (discovered in 1920 by P. S. Gussev on one of the plots of the Kostroma Experiment Field), which had evidently arisen through bud mutation.

The most characteristic feature of this "Kostroma mutant" is the peculiar and strongly marked dissection of the leaf blade (Fig. 1). The flowers under natural conditions are abortive and drop in the bud stage. But by availing ourselves of the method devised by E. Uspensky, research assistant at the Korenevo Experiment Station, we were able in 1926 to obtain two perfectly developed flowers. As distinct from the normal rotate corolla, these flowers had their corolla dissected up to the base of the stamens (Fig. 1 *a*). The tubers differed in no way from normal ones.

The "Kostroma mutant" was propagated by means of tubers during six consecutive years and proved perfectly constant, all of its vegetative offspring being distinguished by the same characteristic peculiarities as the original plant.

From time to time, however, on different individuals of the mutant, clone leaves were observed bearing one or two perfectly normal leaflets (Fig. 2). Sometimes one of the longitudinal halves of the leaf showed a normal division into major and minor leaflets, while the other half preserved its peculiar abnormal structure. Leaves with normal leaflets may occur on separate plants in greater or smaller number—usually not more than two to three per plant—but most frequently they are entirely absent. Attempts to select types within the mutant clone showing a greater tendency to form normal leaflets failed.

The appearance of normal leaflets on the abnormal form suggested that this form might be an instance of the natural formation of a chimaera.

Fig. 1. *Kostroma mutant*; *a*, flower.

It was supposed that the mutation process which had given rise to this form, and had evidently originated in the growing point of the sprout, had affected only the cells composing the outer layers of the plant tissues. As to the inner tissues, the process had not affected them, and they were perfectly normal. In the process of growth, the normal internal tissue may in some cases break through the external abnormal one, thus causing the deformed leaves to bear normal leaflets.

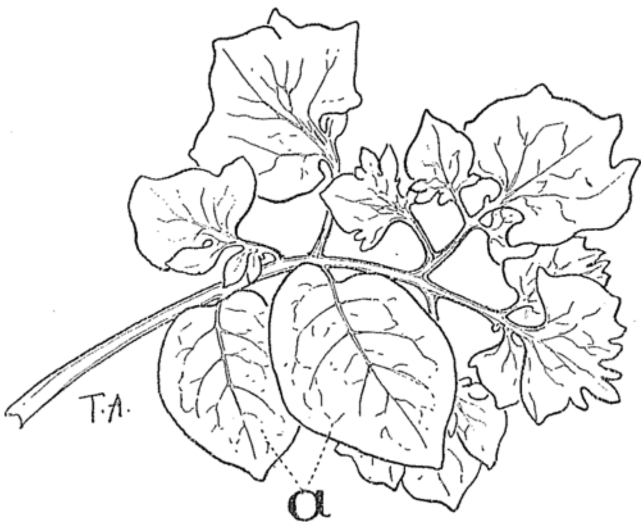


Fig. 2. Normal leaflets on leaves of the *Kostroma mutant*; *a*, normal leaflets.

It thus seemed reasonable to suppose that by cutting away the external layers of cells changed through mutation, and causing the bud to form entirely from the internal normal tissues of the plant, it might be possible to induce the formation of normal shoots from the "Kostroma mutant." For this purpose 20 tubers of the mutant were selected, and all of their eyes removed a month before being planted in the field. It was supposed that they would form new buds from the deeper cell layers which had remained untouched by the mutation process, and that these buds would give rise to perfectly normal plants.

The results bore out our expectations. Out of 20 tubers with eyes removed, 10 gave rise to perfectly normal plants. The remainder either produced no sprouts whatever and perished (2 tubers), or gave rise to plants showing the former abnormalities (this may evidently be explained by the fact that the eyes had not been cut out deeply enough, or that by chance some lateral buds had not been removed in the operation).

Twenty-four control tubers whose eyes had not been cut produced, as might have been expected, only plants of the original abnormal form.

The experiment may be claimed as confirming the supposed chimerical nature of the "Kostroma mutant."

The question then arose whether the other bud mutations of the potato may not be of the same chimerical character, and whether many common potato varieties may not actually be chimaeras. To elucidate this question experiments were carried out in the following year, 1926, with a series of potato varieties that for one reason or another might be regarded as possible chimaeras.

In order to remove certain sources of error the experiments were carried out on a somewhat modified method. The tubers of each given variety were cut into two longitudinal halves, from one of which all eyes were removed, while the other half remained intact. After this the halves were tied together, and so kept until the moment of planting. The plot intended for the experiment was marked out by furrows at right angles to each other, and at the points of intersection holes were made. At the moment of planting the thread holding the tuber together was cut, and the halves with their eyes removed were planted in the furrow to the right, while the intact halves were placed in that to the left. Thus, the scheme of the planting may be represented as follows:

Variety A		Variety B		Variety C	
Eyes removed	Eyes not removed	Eyes removed	Eyes not removed	Eyes removed	Eyes not removed
Half of tuber No. 1	Half of tuber No. 1	Half of tuber No. 1	Half of tuber No. 1	Half of tuber No. 1	Half of tuber No. 1
,, No. 2	,, No. 2	,, No. 2	,, No. 2	,, No. 2	,, No. 2
,, No. 3	,, No. 3	,, No. 3	,, No. 3	,, No. 3	,, No. 3
and so on	and so on	and so on	and so on	and so on	and so on

In cutting the eyes, as well as in planting, the condition was strictly observed that at any given moment only the two halves of the same tuber should be in an untied condition. Owing to this precaution the possibility of mixing up the halves of different tubers was entirely excluded. From fear that the marked dessication of the tuber halves might check the formation of new buds, several whole tubers of each variety, with their eyes removed, were also planted.

The eyes were cut with a sharp scalpel to a depth of 0·5–1 mm. With shallow eyes the author confined herself to slightly scraping off the outer tissues. The removal of the eyes was performed on March 6th, while planting took place on May 25th. Until the moment of planting, all tubers were kept in a cellar under the usual conditions of storage.

The cutting of the eyes, as well as the planting, was carried out by the author of the present paper in person, and the harvest of the crop was superintended by her.

As above stated, the experiment of removing the eyes was carried out on a number of varieties in 1926. All our investigations have been conducted at the Korenevo Potato Section of the Moscow Agricultural Experiment Station. The results obtained are set forth below.

1. "KOSTROMA MUTANT."

The "Kostroma mutant" behaved as follows:

8 halves, eyes not removed, gave rise to	8 abnormal plants
8 halves, eyes removed, gave rise to	1 *normal* plant 7 died
6 tubers, eyes removed, gave rise to	2 abnormal plants 3 *normal* ones 1 of *intermediate* type

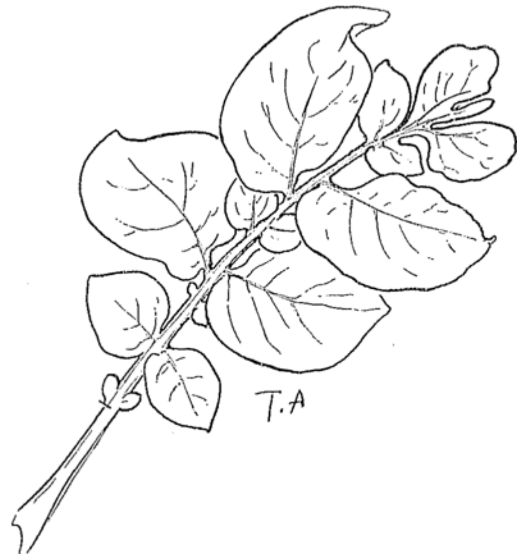


Fig. 3. Leaf with traces of abnormal dissection, obtained from a tuber of the "Kostroma mutant" with the eyes removed.

The upper leaves of the last plant showed the usual normal structure, while on the lower leaves the unpaired segment exhibited traces of abnormal dissection (Fig. 3). In this case, the external mutated layers had evidently not been completely removed, and a few remaining cells had induced the phenomenon of monstrosity. On the whole, the "chimerical" structure of the "Kostroma mutant" may be considered as established. The normal plants which in 1926 grew from the tubers of the "Kostroma mutant" developed so well that they could be easily identified as belonging to the variety *Imperator* (Richter), one of the most widely spread in U.S.S.R.

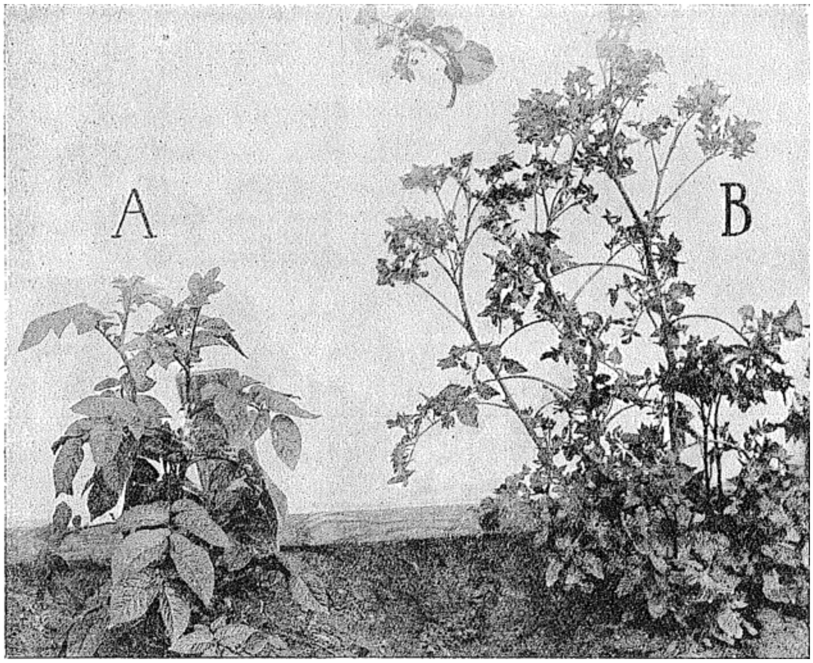


Fig. 4. Two plants grown from two halves of one and the same tuber of the "Kostroma mutant." A, normal form grown from the half with removed eyes. B, monstrous form grown from the half with eyes not removed.

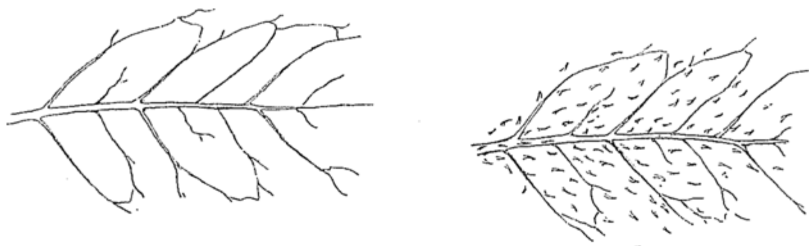
Fig. 4 shows the normal and monstrous forms produced by the two halves of the same tuber.

The causes which brought about this peculiar bud mutation in the variety *Imperator* are up to the present unknown to us.

2. "Voronesh mutant."

This form was found by Miss M. Bogoslovskaja on the fields of the Voronesh Agricultural Institute, among sowings of the variety *Wohltmann* and was afterwards kindly placed at the author's disposal. The mutant plant was distinguished by a complete absence of bristle-hairs on all its organs (Fig. 5 *a*). Glandular hairs were observed in normal number. The vegetative progeny of this mutant repeated, on the whole, the original form, being likewise devoid of bristle-hairs. From time to time, however, individual leaflets on some plants showed a normal pubescence. In single cases the appearance of whole shoots and even plants with normal pubescence was observed.

Another peculiarity of the "Voronesh mutant" was the structure of its flowers. In the majority of plants the corollas were normally rotate and of purple colour, similar to those of the variety *Wohltmann*, but in some plants the flowers were white and the corollas dissected up to the base of the stamens, as in the "Kostroma mutant." From the general



a *b*

Fig. 5. Part of leaf surface of "Voronesh mutant," *a*; and of normal form, *b*.

habit of the plant, the structure of the leaf blade, the colour and shape of the tubers, the "Voronesh mutant" is strongly suggestive of the variety *Wohltmann*, and is, in all probability, a bud mutation of the latter.

From analogy with the "Kostroma mutant," it might be assumed that in this case also the structure of the mutant plant was of a "chimerical" character.

The results obtained by removing the eyes provided confirmation of this view:

8 halves, eyes not removed, produced	7 glabrous plants 1 *pubescent*[1] plant
8 halves, eyes removed, produced	3 *pubescent* plants 5 died
3 tubers, eyes removed, produced	2 *pubescent* plants 1 of *intermediate* type

In the last case the stems from some eyes were pubescent, and from others were smooth.

The corolla of one of the glabrous plants was dissected and white in colour, while in all other plants, no matter whether glabrous or pubescent, only normal rotate corollas of purple colour were observed.

[1] As mentioned above, in the progeny of the "Voronesh mutant" *from time to time* normal pubescence of the plant is observed.

In the two instances described above the modifications were observed in the aerial portions of the plants, while in the instances given below mutation shows itself chiefly in the colour of the tubers.

3. Bovinia (Plate I, fig. 1).

This variety is fairly common in U.S.S.R.; it possesses white tubers with large red patches peculiar to the eyes, which are of deeper colour than the ground. Not unfrequently, however, on separate plants of this variety, tubers of an almost continuous white colour may be found. The red patches are then reduced to scarcely perceptible minute speckles; the eyes are colourless[1].

Such tubers, when planted apart, give rise to plants showing likewise almost entirely white tubers. But from time to time, among their offpsring, mottled tubers with dark eyes are met with, which in their turn also produce plants with mottled tubers. Thus, either form—the mottled and the white one—being to a certain degree constant when propagated vegetatively, may occasionally give rise to the other.

This phenomenon suggests the idea that one form is a chimerical sport from the other.

The removal of the eyes led to the following results:

A. *Bovinia mottled-tubered.*

14 halves, eyes not removed, produced	14 plants with mottled tubers
14 halves, eyes removed, produced	2 plants with mottled tubers 1 plant with mottled and *white* tubers 11 plants died
6 tubers, eyes removed, produced	2 plants with mottled tubers 2 plants with mottled and *white* tubers 2 plants died

Thus, in three plants the occurrence of white[2] tubers was observed, though not more than 1–2 tubers per plant. In this restricted number white tubers may be rather frequently met with in the progeny of the mottled *Bovinia* even under natural conditions; therefore their appearance can be scarcely attributed to the removal of the eyes.

B. *Bovinia "white"-tubered.*

The author had at her disposal only four tubers of this form, which produced the following results:

[1] From the author's investigation (Asseyeva (1 and 2)) the colour of the eyes is a very constant systematic feature, and in the case given the transition from coloured eyes to colourless ones indubitably bears the character of mutation.

[2] Like the original white-tubered *Bovinia*, the white tubers obtained always exhibited small red splashes.

3 halves, eyes not removed, gave rise to	1 plant with white tubers 2 plants died
3 halves, eyes removed, gave rise to	3 plants with *mottled* and white tubers
1 tuber, eyes removed, gave rise to	1 plant with white tubers

The three plants which produced both mottled and white tubers gave them in the following proportions:

1st plant	—20 white and 3 mottled tubers
2nd ,,	—26 ,, 6 ,, ,,
3rd ,,	— 6 ,, 8 ,, ,,

In this case, the appearance of mottled tubers must probably be ascribed to the removal of the eyes, as under natural conditions only a small percentage of the plants belonging to the progeny of the white-tubered *Bovinia* produce mottled tubers, the number of the latter not exceeding 1 or 2 per plant.

The scantiness of the material at our disposal allows of no definite conclusions, though the following supposition appears probable.

Bovinia with mottled tubers is the original form showing the faculty of repeated mutation to the white-tubered form. The white-tubered sport is of a chimerical character, and when propagated vegetatively often sports the inner component with mottled tubers. The removal of the eyes facilitates the process of such sporting.

4. MERVEILLE D'AMÉRIQUE (Plate I, fig. 2).

This variety was obtained under this name from Vilmorin. Its behaviour is very similar to that just described in the case of *Bovinia*. Here also two forms may be observed: (A) tubers red, self-coloured, with eyes darker than the ground; (B) tubers red with yellow patches round the eyes; eyes colourless. When vegetatively reproduced both forms are, on the whole, fairly constant, but, from time to time, on the plants of the mottled form, self-coloured tubers may occur, and conversely self-coloured forms occasionally give mottled tubers.

The author had only self-coloured tubers at her disposal. The removal of the eyes gave the following results:

4 halves, eyes not removed, produced	4 plants with self-coloured tubers
4 halves, eyes removed, produced	2 plants with self-coloured tubers 2 plants with *mottled* tubers
4 tubers, eyes removed, produced	4 plants with self-coloured tubers

It is probable that the appearance of mottled tubers is due to the removal of the eyes. In this case, as in that of *Bovinia*, it must be assumed that the mottled form is the original one, while the self-coloured is its chimerical mutation. The material at our disposal, however, is very scanty and requires further testing. Besides, it must be borne in mind that *Merveille d'Amérique* belongs to the little investigated group of the so-called South American potatoes, distinguished from our common varieties by many characters.

The changes induced by the removal of the eyes in *Bovinia* and *Merveille d'Amérique* may also be observed in these varieties under natural conditions, and the influence of the removal of the eyes shows itself only in the greater frequency of these changes. Therefore the experimental results from the two last varieties are not altogether convincing.

Much better evidence was obtained in the following cases.

5. Mindalny (Almond) (Plate I, fig. 3).

The variety known under this name is grown on a large scale in the region of Moscow[1]. It has white tubers slightly tinged with pink near the eyes. Not infrequently however, on individuals of this variety, tubers with blue-purple patches are found. If the patch does not extend over the eye, the offspring of the tuber will give rise to the usual white-tubered plant. But if the patch extends over the eye, the shoots developing from it will bear tubers that are either purple-coloured with dark eyes and small white splashes, or white with purple eyes and minute purple speckles. Eyes not touched by the purple patch will produce the usual white tubers with pink eyes. When further propagated vegetatively all three forms prove constant.

The phenomenon evidently bears the character of bud mutation. It is worth noting that the tendency to mutation in *Mindalny* is very strongly developed, though less than in *Bovinia* and *Merveille d'Amérique*. Approximately, 2–3 plants out of 100 show single tubers with purple patches, but in the majority of cases these patches do not extend over the eyes.

In order to elucidate the interrelation of the white-tubered and the purple-tubered forms of *Mindalny*, the eyes in both cases were removed. The white *Mindalny* remained unchanged, while the purple one reverted to the form with white tubers. Thus, the chimerical nature of the latter was revealed.

A. *Mindalny, normal* (with white tubers).

14 halves, eyes not removed, produced	14 plants with white tubers
14 halves, eyes removed, produced	9 plants with white tubers 5 died
10 tubers, eyes removed, produced	8 plants with white tubers 2 died

[1] In foreign collections this variety has not been met with.

B. *Mindalny, mutant* (with purple tubers).

4 halves, eyes not removed, produced	4 plants with purple[1] tubers
4 halves, eyes removed, produced	2 plants with *white* tubers 2 died
2 tubers, eyes removed, produced	2 plants with purple tubers

6. WOHLTMANN (Plate I, fig. 4).

The variety *Wohltmann* normally shows red tubers and purple flowers. In 1922, in addition to normal red tubers, one plant bore 2 white tubers with red splashes. The vegetative offspring of these mottled tubers was constant in exhibiting mottled tubers and white flowers. In 1926 the same mutation was met with in another clone of the variety *Wohltmann*. Evidently, in this variety also, mutation shows a tendency to repeat itself, but its percentage is much lower than in the preceding varieties.

Here also removal of the eyes revealed the chimerical nature of the sport.

A. *Wohltmann, normal* (with red tubers).

2 halves, eyes not removed, produced	2 plants with red tubers
2 halves, eyes removed, produced	2 plants with red tubers
2 tubers, eyes removed, produced	2 plants with red tubers

B. *Wohltmann, mutant* (with mottled tubers).

2 halves, eyes not removed, produced	2 plants with mottled tubers
2 halves, eyes removed, produced	1 plant with *red* and with mottled tubers 1 died
3 tubers, eyes removed, produced	2 plants with *red* and with mottled tubers 1 plant with *red and with white tubers*

The appearance of normal red tubers in the progeny of the mottled *Wohltmann* is evidently the result of the removal of the eyes. But the appearance of the pure white tubers was, in the author's opinion, not connected with the operation of removing the eyes. It is more probable that the shoot on which they were formed arose from another eye having accidently remained and that this shoot was either of the nature of a fresh mutation, or else was due to some rearrangement of the tissues involving the sub-epidermal as well as the epidermal layer. Further investigations of the white-tubered mutation of *Wohltmann* will probably enable us to solve the question with more certainty. The stem carrying white tubers differs sharply from all the others by a complete absence of anthocyanin, though similar to them in all other characters.

[1] More exactly, two plants showed purple tubers with white patches, while two had white tubers with purple patches and eyes. These colour distributions were merely repetitions of those obtaining in the plants from which they were raised.

7. Switez (Plate I, fig. 5).

The normal colour shown by the tubers of this variety is white. In 1921, a plant was observed which, along with white tubers, produced two red ones with small white splashes. When planted out apart, these tubers gave rise to a constant offspring with red mottled tubers.

The removal of the eyes in the normal form led to no change, while in the mutant the same operation induced reversion to the original form. Consequently, in this case also the sport is of a chimerical nature.

A. *Switez, normal* (with white tubers).

3 halves, eyes not removed, produced	3 plants with white tubers
3 halves, eyes removed, produced	3 plants with white tubers
3 tubers, eyes removed, produced	3 plants with white tubers

B. *Switez, mutant* (with red tubers).

4 halves, eyes not removed, produced	4 plants with red tubers
4 halves, eyes removed, produced	4 plants with red tubers
3 tubers, eyes removed, produced	2 plants with red tubers 1 plant with red and with *white* tubers

In all the instances described above (1–7) we were dealing with forms which arose by mutation. In the following two cases (8 and 9) the origin by mutation can only be suggested as a probability.

8. Triumph and Noroton Beauty (Plate I, fig. 6).

Both varieties are of American origin and identical in their foliage, but differ sharply in the colour of the tubers: in *Triumph* they are red with dark eyes, while *Noroton Beauty* shows tubers of a light pink colour with red eyes and minute sparse red splashes. This led us to suppose that one variety is a bud mutation of the other, and possibly of chimerical nature. The removal of the eyes caused no change in *Triumph*, while *Noroton Beauty* produced self-coloured red tubers, in other words, turned into *Triumph*.

A. *Triumph* (with red tubers).

8 halves, eyes not removed, produced	8 plants with red tubers
8 halves, eyes removed, produced	5 plants with red tubers 3 died
3 tubers, eyes removed, produced	3 plants with red tubers

B. *Noroton Beauty* (with mottled tubers).

8 halves, eyes not removed, produced	8 plants with mottled tubers
8 halves, eyes removed, produced	2 plants with mottled tubers 3 plants with *red* tubers 3 died
4 tubers, eyes removed, produced	2 plants with mottled tubers 1 plant with mottled and with *red* tubers 1 died

Hence, *Triumph* must be recognised as the original form, and *Noroton Beauty* as its chimerical bud sport.

9. L'INSTITUT DE BEAUVAIS AND TCHUGUNKA (CAST IRON) (Plate I, fig. 7).

The variety *L'Institut de Beauvais*[1] is grown on a large scale in U.S.S.R., and in some provinces almost the whole acreage under potatoes is occupied by this crop. Wherever grown, it is followed by its invariable attendant *Tchugunka*[2]. Both varieties differ sharply from one another in the colour of flowers and tubers. *L'Institut de Beauvais* has white flowers and white tubers with pink eyes. The flowers of *Tchugunka* are blue, its tubers being of purple colour with dark eyes and white splashes. In all other characters, however, the varieties are exactly similar. This once more suggests that one of the varieties is a bud sport of the other, and may possibly be of a chimerical nature. Removal of the eyes once more confirms this supposition—*Tchugunka* turns into *L'Institut de Beauvais*. The latter variety is evidently the original one, and *Tchugunka* its chimerical bud sport.

A. *L'Institut de Beauvais* (with white tubers).

10 halves, eyes not removed, produced	10 plants with white tubers
10 halves, eyes removed, produced	1 plant with white tubers 9 died
18 tubers, eyes removed, produced	11 plants with white tubers 7 died

B. *Tchugunka* (with purple tubers).

6 halves, eyes not removed, produced	6 plants with purple tubers
6 halves, eyes removed, produced	2 plants with purple tubers 2 plants with *white* tubers 2 died
9 tubers, eyes removed, produced	4 plants with purple tubers 3 plants with *white* tubers 2 died

10. QUARANTAINE VIOLETTE (Plate I, fig. 8).

This variety was so named in the collection received from Vilmorin. It has blue-purple tubers with splashes of a dirty pink, and red-purple sprouts, thus showing the simultaneous presence of blue and red pigment, a fact never before observed in potatoes[3]. All varieties with purple, or with mottled purple tubers have blue-purple sprouts. The only known

[1] It was obtained under this name from Vilmorin.

[2] "Tchugunka" is a local name. This variety was not met with in foreign collections.

[3] Exceptions are the cases of bud mutation, as for instance the appearance of purple-blue splashes on white tubers with pink eyes observed in the variety *Mindalny* (see above).

exception to this rule is the variety *Quarantaine violette* whose chimerical nature is revealed by the results given below.

4 halves, eyes not removed, produced	4 plants with mottled tubers (*i.e.* purple with pink splashes)
4 halves, eyes removed, produced	{1 plant with *pink* tubers {3 died
2 tubers, eyes removed, produced	2 plants with *pink* tubers

The pink-tubered variety obtained through the removal of the eyes in *Quarantaine violette* was evidently identical with the variety *Rose* of Vilmorin's collection.

The chimerical nature of *Quarantaine violette* does not explain, however, the contradiction between the colour of the tubers and that of the sprouts. It may be assumed, of course, that the outer modified cell layers carrying the factor for blue-purple colour do not extend over the whole surface of the tuber, being as it were, interrupted in the place where the eye is situated; indeed, the eyes of the variety *Quarantaine violette* are always observed in the pink patches of the tuber, and not in the purple ones. But if this assumption is true it is unlikely that such sprouts, of which all cells lack the factor for blue-purple colour, should again give rise to tubers with blue-purple splashes.

Another instance of the disturbance of absolute correlation is the chimaera of *Bovinia* described above. All potato varieties fall into two groups: those with coloured eyes and those with colourless ones. In the former case, the pedicel always exhibits a strongly marked ring of pigment at the point of articulation, while in the latter no such ring is to be seen. But chimaeras form exceptions to this rule. When *Bovinia* with mottled tubers and dark coloured eyes mutates to a form with white tubers and colourless eyes, the newly arisen form retains the pigment ring on the pedicel peculiar to the original form.

In others of the chimaeras described, a disturbance of the correlation between the colour of the stems and that of the tubers is to be observed. Varieties with dark-coloured tubers have, as a rule, stems strongly suffused with pigment. In the cases described above, however, when the white-tubered form turns into one with coloured tubers, the colour of the stems does not change, remaining either pure green (*Switez*) or faintly coloured (*Mindalny*, *Tchugunka*, etc.). In the case now under discussion the disturbance of correlation, which is not of an absolute character, is not so striking. We have not been able so far to find a reliable explanation of the disturbance of the usual correlation in chimaeras. One circumstance, however, is worth noting. While the pigmentation of the stem depends on the cells of the sub-epidermal layer and not on those of the epidermis, the colour of the tuber is conditioned by both, epidermis as well as sub-epidermal layer taking part in the formation of the tuber periderm with its anthocyan cells (Esmarch (8)). Further anatomical investigations will probably lead to a definite solution of the question.

11. LOCAL PURPLE VARIETY (Plate I, fig. 9).

This variety has been found in the local potato crops and has purple tubers with light-coloured eyes and white splashes. As it possesses fertile pollen it readily produces seeds when self-pollinated. All seedlings obtained from these seeds have *white* tubers. This striking contradiction between the colour of the parent and that of its progeny can be explained only by the chimerical nature of the plant. In other words, it must be supposed that the outer cell layers contain the total of factors necessary for the appearance of purple colour, while the inner tissues—those forming the sexual elements included—lack one or several of these factors. This view is supported by the fact that some plants produced from the adventitious buds (artificially induced by removing the eyes), had white tubers.

2 halves, eyes not removed, produced	2 plants with purple tubers
2 halves, eyes removed, produced	1 plant with purple and with *white* tubers 1 died
7 tubers, eyes removed, produced	5 plants with purple tubers 1 plant with *white* tubers 1 died

Besides *Local Purple*, several of the other varieties described above were genetically investigated in 1926. But before stating the results of the investigation, we think it necessary to give a short survey of our modern knowledge in regard to the genetical nature of the potato.

According to Salaman (19, 20), the red colour of the tubers depends on two factors **D** and **R**, and appears only when both are present, *i.e.* in the presence of the combination **DR**. The purple (blue) colour depends on the factor **P** and appears only when the latter is brought together with **DR**, *i.e.* in the presence of the combination **PDR**. The author of the present paper (Asseyeva (1)) also distinguishes the factor $\mathbf{R}_1$, closely related to the factor **R**. $\mathbf{R}_1$ with **D**—combination $\mathbf{DR}_1$—gives only a faint pink colour[1], while with **PD**—combination $\mathbf{PDR}_1$—it produces an intense purple colour.

Besides the factors for "general" colouration of the tubers, the

[1] Further on, in describing segregation, tubers with such colour will be ranked with the white ones.

author(1) considers that there is a factor for the colour of the eye, **A**, which is active only in the presence of **D**. The combination **DA** develops white tubers with pink eyes, while the combinations **DRA** and **PDRA** produce red or purple tubers respectively, both with dark eyes. In the absence of **A**, the eyes will be of a light colour or altogether colourless[1].

The varieties in which the above-mentioned combinations are not contained, produce white tubers. The sprouts of varieties from which **P** is absent are *red*-purple, while varieties with **P** exhibit *blue*-purple sprouts (Asseyeva(1)).

Of the varieties described above those genetically investigated were: *Local Purple*, *Noroton Beauty*, *Switez* (normal and mutant form), *L'Institut de Beauvais* and *Tchugunka*. For the majority of them the genetical formula could be established. An exception is formed by the two last varieties for which only the formula of the "general" colour was ascertained, that of the colour of the eyes remaining unknown.

The segregation results are given in the table A.

From this table (p. 17) it is clear that in spite of the sharp difference in the colour of such varieties as *Switez*—the normal and the mutant—on the one hand, and *L'Institut de Beauvais* and *Tchugunka*, on the other, segregation proceeds in a precisely similar way. The mutation, though changing the colour of the tuber, does not affect the sexual cells. In other words, the genetical analysis is one more proof of the chimerical nature of the varieties investigated.

It must be noted, that in many cases the mutation shows a tendency towards the appearance of a dominant character. The varieties *Quarantaine violette*, *Local Purple*, and the mutants of *Mindalny* and *Switez*, are plus-mutations, but since the mutation is confined to the epidermal cell layers its dominant character cannot directly be tested by genetical methods.

One circumstance is worth nothing. All seedlings obtained as the result of segregation, invariably bore self-coloured tubers, while all chimerical parental forms had mottled tubers. It is only with the help of one of the following hypotheses that this mottling may be explained.

(1) The unequal peeling off of the periderm cells of the tuber may expose the internal tissues unaffected by the mutation process, and consequently possessing another complex of colour factors.

(2) Owing to the fact that the cells of the epidermis, as well as those of the sub-epidermal tissue, take part in the formation of the tuber

[1] Between factors **A** and **R** linkage relations were observed.

TABLE A.

Segregation for Colour of Tubers.

Names and constitutions of the parental varieties ♀	♂	Absolute number of all seedlings	Actual and theoretical ratio of seedlings with different tuber colour	Remarks
Local Blue	(Self-pollinated)	318	All white-tubered	Av. for 6 families
PpDd	,,	—	,,	—
Local Blue	Alma	97	3·14 *p* : 12·86 *wh*	Av. for 2 families
$PpDdr_1r_1$	**$ppDdR_1r_1$**	—	3 : 13	—
Noroton Beauty	Fürstenkrone	89	5·47 *r** : 1·52 *wh** : 8·81 *wh*	Av. for 2 families
DdRrAA	**ddRraa**	—	6 : 2 : 8	—
Switez normal	(Self pollinated)	124	All white-tubered	Av. for 2 families
Switez mutant	,,	258	,,	Av. for 3 families
Rr	**Rr**	—	,,	—
Switez normal	Fürstenkrone	252	All white-tubered	Av. for 2 families
Switez mutant	,,	84	,,	—
Rr	**Rr**	—	,,	—
Switez mutant	Alma	85	4·90 *r* : 11·10 *wh*	—
ddRr	**Ddrr (R_1r_1)**	—	4 : 12	—
L Institut de Beauvais	Fürstenkrone	144	3·45 *r** : 4·22 *wh** : 8·33 *wh*	Av. for 2 families
Tchugunka	,,	107	4·04 : 4·33 : 7·63	—
Ddrr...?	**ddRr**	—	4 : 12	—
L'Institut de Beauvais	Alma	66	6·70 *wh** : 9·30 *wh*	—
Tchugunka	,,	86	6·06 : 9·94	—
Dd...?	**Dd**	—	16	—

N.B. Conventional designations of tuber colour: *p* = purple; *r* = red; *wh* = white; * = eyes coloured.

periderm, the latter may partly consist of cells not modified by the mutation process, *i.e.* showing another complex of colour factors.

It can readily be understood that neither in the one nor in the other case will this mottling be transmitted through the seeds.

As far as we can judge, the colour of the tubers that is of a chimerical character is, as a rule, always mottled. An exception is formed by *Merveille d'Amérique* (form A-red, self-coloured tubers)[1].

The chimerical mottling of the tubers must not be confused with the mottling conditioned by hereditary characters. The latter case may be illustrated by *Bovinia*, with mottled tubers, and the mottled *Merveille d'Amérique*. In these two varieties the arrangement of the patches is

[1] It must be pointed out once more that *Merveille d'Amérique* belongs to the group of South American potatoes, differing in many respects from our common varieties.

in close connection with the eyes. In the first variety the eyes are situated in the coloured areas of the skin, in the second, on the contrary, in the colourless ones[1]. In cases where mottling indicates the chimerical nature of a variety, the patches show a tendency to be situated on the "eye-brows." As far as one may judge, the colour of the eyebrows corresponds to the genetical formula of the colour of the sub-epidermal layer. This question, however, requires further investigation.

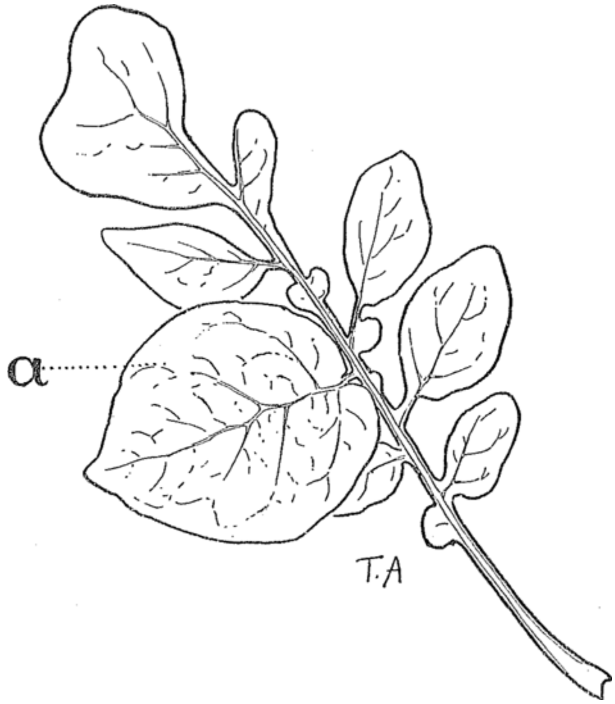


Fig. 6. Leaf of bud mutation of variety *Alma*; *a*, normal leaflet.

Besides the varieties described above, whose chimerical character might have been suspected for one reason or another, and which indeed proved to be chimaeras, controls were made in several cases where no such idea suggested itself. Removal of the eyes, indeed, caused no changes in the plants produced by tubers of these varieties which were as follows:

[1] It must be kept in mind that in our common potato varieties the selfed colour of the tuber is dominant to the mottled one, while in the South American varieties the selfed colour is, on the contrary, recessive to mottling (Asseyeva (1)).

Blaue Riesen (Paulsen)	—purple tubers	with	dark eyes
Perkun (Dolkowski)	— ,,	,,	light ,,
Granat	—red	,,	dark ,,
The Daughter of Early Rose	— ,,	,,	light ,,
Fürstenkrone (Richter)	—white	,,	pink-purple sprouts
Maercker (Richter)	— ,,	,,	blue-purple ,,

All these varieties have self-coloured tubers.

Fig. 7. Bud mutation of the variety *Imperator*.

In 1927 we propose to carry out the experiment of removing the eyes on a larger scale, and to amplify it by including an anatomical investigation of the chimaeras. In all probability, we shall be able to reveal the chimerical nature of at least 30 varieties. The majority of them belong to the commonly cultivated potato varieties[1], though others,

[1] Among their number are the varieties of Thiele—*Geheimrat Appel* and *Magdeburger Blaue*—which he asserts are graft-hybrids, but which probably originated by bud mutation.

found as single plants in crops of potatoes, bear the character of monstrous mutation, as for instance, plants of the varieties *Alma* (Cimbal) and *Imperator* (Richter) free from pubescence. The former of these two varieties is also distinguished by an irregular structure of the leaf blade (Fig. 6). Of great interest is another monstrous form of *Imperator* found in 1927 in different parts of the province of Moscow. As distinct from the "Kostroma mutant," which also belongs to the variety *Imperator*, this form is distinguished by a leaf blade which is only slightly dissected (Fig. 7).

It is very interesting to compare the results of the present investigation with other recorded cases of bud mutation in potatoes.

Many instances of mutation in the potato plant are mentioned in the literature, but unfortunately most of the data come from practical crop-growers and the descriptions are, therefore, not always sufficiently clear and detailed.

The most diverse characters of the potato plant are subject to mutation.

Colour of the tuber. The transition of purple and of red into mottled and into white; the appearance of purple patches on red tubers; the change of white and of mottled into purple and into red were observed. Very often the mottled character of the mutation colour is recorded.

Structure of the tuber skin. The modification of the smooth skin into a "russet" one, and the reverse change that of russet into smooth are recorded.

Shape of the tubers. Since this character is much subject to fluctuating variation under the influence of environmental conditions, it is difficult to single out the real mutational changes in the shape of the tuber. However, undoubted cases of transition from a round (recessive) shape to an elongated (dominant) one have been recorded.

Colour of the flowers. The change of purple into white has been recorded, and this is not infrequently correlated with the change of the self-coloured tubers into mottled ones.

Shape of the corolla. The occurrence of a star-shaped corolla instead of the normal rotate one has been observed.

Shape of the leaf. The variations of the leaf blade are frequently more of the nature of monstrosities. Such are the mutations: "raspberry-leaf," "tomato-leaf" described by Dorst (6), "simple leaved" and other forms mentioned by Folsom (9). Both authors record the occurrence of normal leaflets on these abnormal leaves.

Variations of the leaf blade showing no character of monstrosity have also been observed, such as the change of a broad-leaved form into a narrow-leaved one.

Colour of the leaves. Various types of albinism have been described, *e.g.* variegated leaves, fading of the leaf-margin, general paler colour.

Colour of the stem. Decrease of stem pigmentation has been recorded, the colour of the tuber diminishing simultaneously[1].

Besides the morphological mutations enumerated above, bud mutations affecting the physiological character of the potato have been observed: productivity, degree of immunity, faculty of sexual reproduction, etc. Characters such as these are of little use for the study of mutations, as they are strongly influenced by environmental conditions.

The morphological mutations described have much in common with the material investigated by the author. The tendency of the vegetative offspring to revert to the original form, observed in many of these mutations, strengthens our right to assume that these sports, at least in the majority of cases, if not always, are of a chimerical nature. Theories as to the chimerical character of bud variations in the potato have been advanced by Dorst (6), Rudno (17) and Bukassov (4).

A singular theory is set forth by Salaman (18). His material, thoroughly worked up from every point of view, is of great interest and worth dwelling upon.

The initial variety, *Arran Victory*, has purple tubers with dark (?) eyes. In 1919 McKelvie discovered three tubers of this variety showing a variation in colour:

(1) half white, half purple;
(2) light pink, with dark purple eyes and tip;
(3) white with purple splashes at tip and base.

The vegetative offspring of all three tubers was reared through five generations under strict control of McKelvie and afterwards of Salaman.

The progeny of mutations 1 and 2 consisted of plants carrying mottled tubers whose ground was white in the first case, being in the second of a light purplish pink. But from time to time, in the progeny of mutation 1 tubers occurred suggestive of mutation 2, and reversely, in the progeny of mutation 2, tubers were met with recalling mutation 1. In all other characters both clones were perfectly similar to one another, as well as to the original normal type of *Arran Victory*.

Mutation 3 gave rise to an offspring partly with mottled and partly with purely white tubers. The white-tubered plants differed from the

[1] The decrease of colour in the tubers, however, may be frequently not accompanied by a diminished pigmentation of the haulms (see p. 14).

normal *Arran Victory* also in many other characters: shape of tubers, shape and colour of leaves, pigmentation of stem.

The original form, as well as its mutations, were crossed with a white-tubered seedling. Segregation in regard to tuber colour showed the following figures:

Mother plant		Number of seedlings of different tuber colour with $N = 16$*			Absolute number of seedlings
Name	Colour of tubers	Purple	Red	White	
Arran Victory	Purple self-coloured	5·92	3·36	6·72	38
Mutation 2–A	Purplish-pink ground with dark purple patches	5·60	8·00	2·40	20
,, 2	,, ,,	5·92	4·16	5·92	27
,, 2–A	,, ,,	4·48	4·32	7·20	49
,, 1	White ground with dark purple patches	1·28	2·40	12·32	13
,, 3–A	Purely white	—	—	16·00	13

* In the original work the numerical relations are given with $N = 100$: here the value of N is taken as that of the number of combinations in dihybrid segregation $= 16$.

The patches in the parental form of mutations 2–A and 1–A occupied 50–70 per cent. of the tuber surface, those in mutation 1, 15 per cent. The colour of mutation 2 was not exactly described; Salaman supposes that in this case the size of the patches was somewhat less than in mutation 2–A.

All seedlings obtained as the result of segregation, carrying purple and red tubers, were *self-coloured*.

In Salaman's opinion the figures mentioned above support the view that in this case we are not dealing with a simple Mendelian segregation. He supposes that the pigmentation of the mutationally changed tubers and of their vegetative offspring is of a "mosaic" character, and that the ovules of these plants show a corresponding character. In other words, Salaman holds that, in each of these plants, the somatic as well as the sexual cells carry different colour factors, and in a different percentage, which shows itself in the size of the patches.

The author of the present paper thinks, however, that in the given case we are in the presence not of a "mosaic" but of a periclinal arrangement of the cells with different hereditary factors. In mutations 2–A, 2, 1–A the sexual cells are situated in layers not yet affected by the mutation process and the sexual generation is similar to the progeny of the initial *Arran Victory*. The deviations observed may be sufficiently explained by the scantiness of the material. In the mutation 3–A the sexual cells are evidently deprived of the necessary complex of colour factors. It is possible that this mutation is no longer of a chimerical structure, *i.e.* that it has originated exclusively from modified cells, devoid of factors for purple colour. The fact, however, that in this clone tubers occasionally show small purple splashes "usually slightly hollowed," makes one suppose that the deeper layers are still formed by cells containing factors for purple colour. In any case the sexual cells already lie in the modified layer.

As regards mutation 1, the mutation probably embraces deeper cell layers than in the three preceding mutations, though less deep than in mutation 3–A. It is possible that the germ cells arise on the margin between type and mutant tissue, and that some are of one kind and some of the other. It is more probable, however, that here also *all* sexual cells are affected by the mutation, but that the latter is of a somewhat different character than in mutation 3–A.

It would be very interesting to observe the influence of the removal of the eyes on the mutations described.

In conclusion we wish to mention the investigations of Bateson on *Bouvardia* and *Pelargonium*. Some varieties of these plants when propagated by means of root cuttings give rise to plants with a flower colour dissimilar from that of the top cuttings. Bateson supposes that such a plant is a periclinal chimaera. Sometimes on such plants shoots are formed in a natural way, exhibiting the character of the inner component. With sexual reproduction only the characters of this inner component are transmitted.

These facts suggest that a chimerical structure in plants propagated vegetatively is by no means a rare occurrence, and that probably many cultivated varieties of such plants are chimaeras. The author supposes that the overwhelming majority of bud mutations give rise to chimaeras.

For potatoes this supposition may be regarded as sufficiently proved experimentally, since in the author's investigations all bud mutations, taken at random, proved to be chimaeras. It would be interesting to carry out similar investigations in other plants[1]. Theoretically, the supposition as to the chimerical nature of bud mutations is quite plausible if we admit that the original mutation process takes place only in one of the cells of the growing point of the shoot. As a rule such a cell gives rise not to the whole plant, but only to the one or to the other layer or group of cells[2], so that a periclinal or sectorial chimaera

[1] Chittenden's recently published paper (5) contains many facts similar to our own in regard to other plants.

[2] An exception may be formed by buds arisen on the root.

is formed. If the author's idea is true that bud variations are as a rule of a chimerical nature, care is needed when studying in them the results of mutation. It must be borne in mind that the new character confined to 1–2 cell layers cannot always manifest itself in a perfectly normal way. And our conception of the actual state of such mutations will be as imperfect and as relative as would be our idea of the tomato if we were to study its characters exclusively on Winkler's graft-hybrid *Solanum tubingense*.

Summary.

Bud mutations in potatoes are on the whole of not infrequent occurrence, though their frequency varies in different varieties. In some varieties these mutations occur constantly (*Bovinia*, *Merveille d'Amérique*), in others they are less frequent (*Mindalny*), in the third they are very rare (*Wohltmann*), or appear only in single cases (*Switez*).

The mutations are sometimes gain- and sometimes loss-mutations. In other instances they may give rise to monstrous forms.

All investigated bud mutations are of the character of periclinal chimaeras, *i.e.* only the outer cell layers are modified.

Some of the common potato varieties have also proved to be chimaeras. This makes us suppose that at some time they have originated by bud mutation.

The chimerical structure of the mutations investigated has been proved in two ways:

(1) when the eyes were removed from the tuber of the mutant, the new buds that had formed in deeper layers produced plants recalling not the mutationally modified parents, but also the original form from which the mutant had arisen;

(2) the characters of the mutant are not transmitted through seed, and its offspring are exactly similar to the progeny of the original variety[1].

The results of segregation are given on p. 17, the tabulated results of the removal of the eyes are represented in the subjoined table:

[1] The existence of chimerical mutations whose characters are transmitted through the seeds is, however, perfectly admissible. This will take place when the mutation process embraces the sub-epidermal layer from which the sexual cells develop.

Names of investigated varieties	Halves with eyes not removed Number of plants			Halves with eyes removed Number of plants			Tubers with eyes removed Number of plants		
	Not modified	Modified	Died	Not modified	Modified	Died	Not modified	Modified	Died
1. "Kostroma mutant"	8	.	.	.	1	7	2	4	.
2. "Voronesh mutant"	7	1	.	.	3	5	.	3	.
3. Bovinia white	1	.	2	.	3	.	1	.	.
4. Merveille d'Amérique (red)	4	.	.	2	2	.	4	.	.
5. Mindalny, mutant	4	.	.	.	2	2	2	.	.
6. Wohltmann, mutant	2	.	.	.	1	1	.	3	.
7. Switez, mutant	4	.	.	4	.	.	2	1	.
8. Noroton Beauty	8	.	.	2	3	3	2	1	1
9. Tchugunka	6	.	.	2	2	2	4	3	2
10. Quarantaine violette	4	.	.	.	1	3	.	2	.
11. Local Purple	2	.	.	.	1	1	5	1	1

In chimaeras the disturbance of the correlations usual in the potato —and often of absolute correlations—is observed. Chimerical tubers are, as a rule, always mottled. Both phenomena may be explained to a certain degree by the peculiar anatomical structure of chimaeras.

In the descriptions of bud mutations of the potato to be found in the literature there are many indications which make us suspect the chimerical nature of these sports. It is very probable that bud mutations of the potato, and possibly also those of other plants, are, as a rule, of a chimerical character.

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EXPLANATION OF PLATE I.

Transformation of a mutationally modified form into a normal one, induced by the removal of the eyes from the seed tuber:

1 *a*. *Bovinia*, white-tubered	→	1 *b*. *Bovinia*, mottled-tubered.
2 *a*. *Merveille d'Amérique*, self-coloured	→	2 *b*. *Merveille d'Amérique*, mottled.
3 a_1 and a_2. Mutant of *Mindalny*	→	3 *b*. *Mindalny*, normal.
4 *a*. *Wohltmann*, mutant	→	4 *b*. *Wohltmann*, normal.
5 *a*. *Switez*, mutant	→	5 *b*. *Switez*, normal.
6 *a*. *Noroton Beauty*	→	6 *b*. *Triumph*.
7 *a*. *Tchugunka*	→	7 *b*. *L'Institut de Beauvais*.
8 *a*. *Quarantaine violette*	→	8 *b*. *Rose*.
9 *a*. *Local Purple*	→	9 *b*. (Not named.)

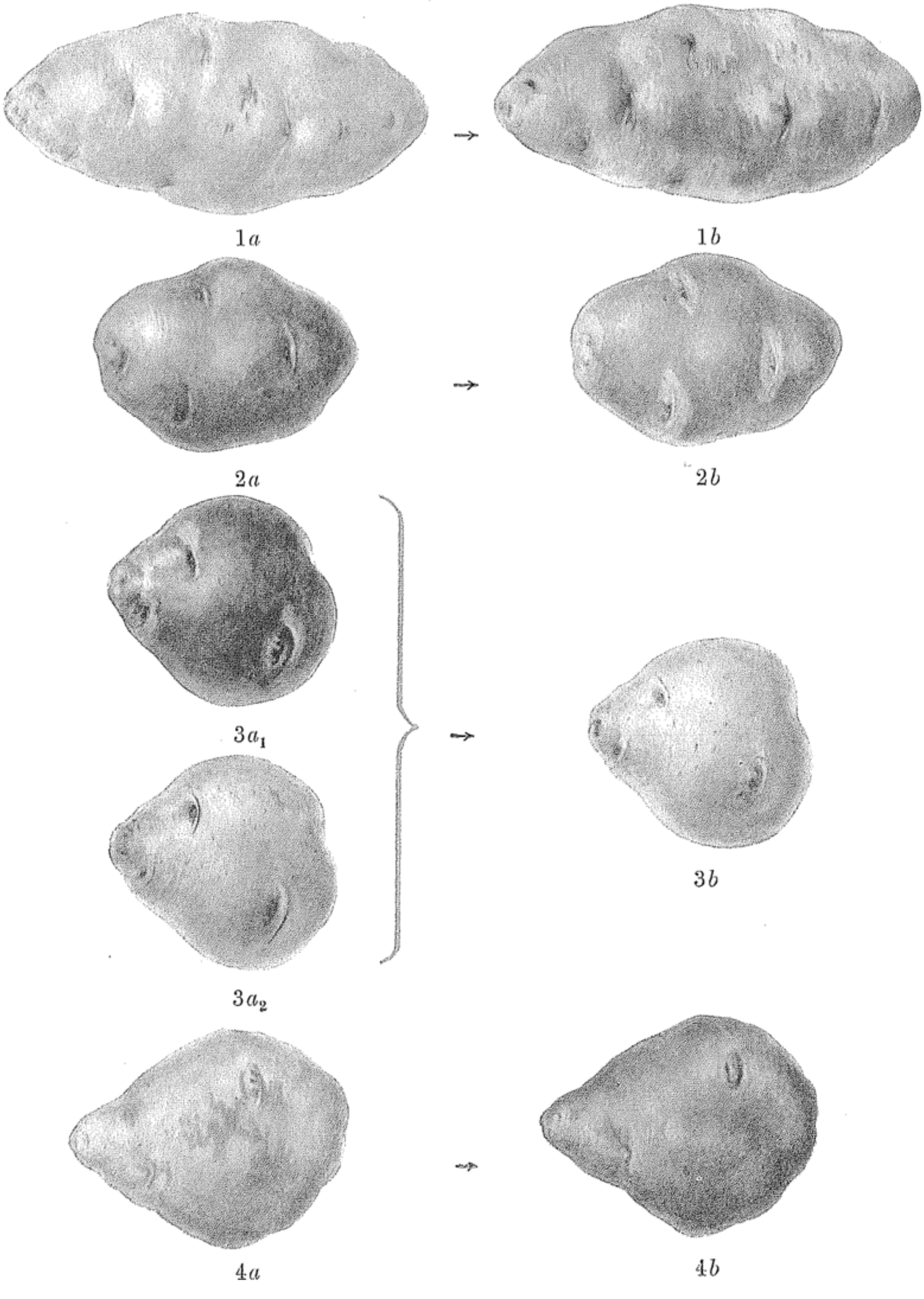

1a
1b
2a
2b
3a₁
3a₂
3b
4a
4b

PLATE I

5a

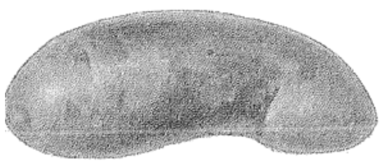
5b

6a

6b

7a

7b



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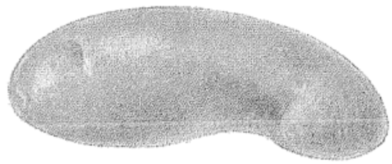

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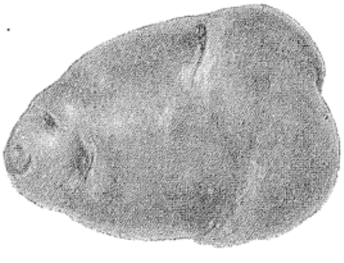

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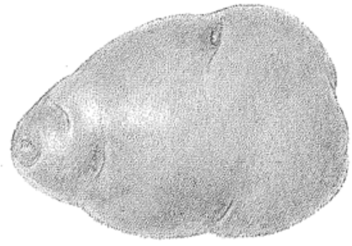

9a