

THE INHERITANCE OF COLOUR AND OTHER CHARACTERS IN THE POTATO.

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INTRODUCTION.

THE experiments here described were begun in the spring of 1906 and are still being continued; the work has been carried on in my garden at Barley in Hertfordshire. Although the subject material of this research was my own choice, at the time it was determined on I was quite ignorant of the very special advantages as well as disadvantages which the Potato offers for the Mendelian student. To Professor Bateson and Professor Punnett I owe a debt of gratitude for the encouragement they have always given me and the time they have so kindly devoted to examining and criticising my work.

The potato plant as grown domestically in England is a perennial, that is to say, it is raised from tubers vegetatively year by year. Most of our varieties bear flowers, but only a very small proportion set seed; this peculiarity will be considered more fully later, and has already been dealt with in detail⁽¹⁾.

The potato flower bears five anthers (sometimes six or seven) arranged in a cone through whose apex projects the stigma. The anthers dehisce at their distal extremities, the pollen, when there is any, falling on to the knob-shaped stigma which projects but a short distance beyond the cone's apex.

When cross fertilizations are made, the flower which is to act as the female parent is emasculated before the bud is open while both anthers and stigma are still unripe.

The flowers are borne as a cyme, on axial stalks, each bloom having a short stem about an inch long, and at a distance of half an inch

¹ The numbers in brackets refer to the Bibliography.

below the base of the flower there occurs a ring of cork. In all potatoes the flowers have a great tendency to separate at this point from their stems: the tendency is more marked in those flowers where the anthers are sterile. If such a flower is used as the female parent the chances of a successful cross fertilization are somewhat less good than if the fertilization is made on one with fertile anthers owing to this habit of separation. In all potato plants, however, when grown out in the open, successful fertilization, be it "selfing" or "crossing," is a hazardous undertaking, and I personally do not succeed in getting more than about 5% of the individual flowers I handle to set seed.

Once the ovary begins to swell there is little fear of separation taking place at the cork ring, indeed the stem gradually thickens and carries the berry late into the autumn.

All my work has been carried on without placing the flowers in bags. The reasons for not adopting special precautions were that when bagged the flower invariably drops, that bees and the like never approach a potato flower though a small fly often lives in the bottom of the corolla, that the flower is constructed for self-fertilization, and that the quantity of pollen is so scanty as to render fertilization by the wind in the highest degree improbable. Each year I have sterilized a number of flowers and purposely left them unpollinated, in no instance has any fertilization taken place. In two instances out of some hundreds so treated the ovaries swelled till they attained a diameter of 3/16 in., but they contained no seed and dropped.

Although the potato, owing to its scanty pollen, its frequent sterility, and its delicate flower, is not an ideal subject for Mendelian research, it does still offer to the experimentalist one redeeming character. An individual plant can always be "carried on" by means of its tubers into the next season's work, and whether it be for the sake of comparison or for the purposes of further fertilization this property is of the utmost service.

The Scope of the Observations. Attention has been concentrated mainly on the heredity of characters of the tubers, for the haulm or foliage of the potato plant, though variable in habit of growth, size, shape, texture and colour, does not lend itself readily to this type of work. The foliage more especially is so variable in different parts of the same plant, whilst the differences between one type of foliage and another, however apparent, are so difficult to define that except in one instance, which will be considered later in detail, I have not made out anything sufficiently definite.

The colour of the stem is always correlated in some degree with that of the tuber, but whereas one meets with innumerable white-tubered plants, yet, as far as my experience goes, in all of these some colour may be found, if not in the stem, then in the shoot which emerges from the tuber in spring.

Very definite Mendelian segregation of colour in the stem occurs when the black or deep purple pigment, such as is seen in "Congo," is introduced, but in the case of the red- and white-tubered plants the quality of the pigment being constant, it is the quantity that varies and that is not readily to be measured. In one family of 100 seedlings I ascribed values to the colour as seen in the stem. The parent was a plant with a medium quantity of pigment in the stem. The degrees of pigmentation in the stems of the seedlings were divided into "strong," "medium," and "weak," and the numbers in each class bore to each other as nearly as possible the relation of 1 strong : 2 medium : 1 weak.

The absence of distinct and definable gradations between the various degrees of colour, as well as the possible personal bias in the classification, is my reason for not publishing the results of the observations on colour in stem and foliage which were made in every individual plant during the four years' work covered by this paper.

Observations on the colour of the flowers have been made, but only in the case of seedlings of the potato known as Lindsay's *etuberosum* has anything of interest been observed: a description of the phenomena in the flowers is given in the section dealing with this peculiar variety.

Observations on the pollen have disclosed some interesting facts in connection with heredity of sterility and have confirmed East's⁽⁶⁾ observation of the relation between amount and viability of pollens.

The incidence of disease (*Phytophthora infestans*) has been closely watched, but only in the case of the Lindsay tuber, *q.v.*, has anything definite been observed.

The fact that there has been till now no really immune variety to work with has prevented any headway being made in this direction.

The Material used. All the observations, excepting those dealing with the peculiar variety already described by Sutton⁽⁶⁾, and known as Lindsay's *etuberosum*, have been made with ordinary domestic varieties. The most useful of all the potatoes employed has been Sutton's "Flourball," which indeed gives the key to the understanding of them all. The black pigment was introduced by the potato known as the "Congo," a potato which is of a deep blue-black both within and without and which is used domestically for salads. One variety which

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proved of value was a white kidney potato known as "Record." It was brought out by Messrs King, of Coggeshall, but it has entirely gone out of cultivation as far as could be ascertained, not only in England generally, but in my garden also, and my notes of its characters are unfortunately not very full.

I give here a list of the domestic varieties I have used.

In self and cross fertilization.

For observations on pollen.

A. Flourball (Sutton).	B. Varieties in list A.	
Record (King).	Ringleader.	
Congo.	Supreme.	
Reading Russet.	Dutch Cornwall.	
Red Fir Apple.	Peckover.	
Queen of the Valley.	The Dean.	
Bohemian Pearl.	Purple Eyes.	
Sole's Kidney.	Up-to-Date.	
Early Regent.	Duke of York.	
Prof. Maerker.		
<i>S. etuberosum.</i>	<i>S. commersonii</i>	} species.
	<i>S. tuberosum</i>	
	<i>S. verrucosum</i>	
	<i>S. maglia</i>	

Several other varieties were used in class A without success.

STERILITY OF ANTHERS. CONTABESCENCE.

Darwin (5), in considering the origin of sterility, describes a condition not uncommonly found amongst plants of various families in which the anthers are more or less twisted up or aborted and contain no pollen. Darwin called this condition "contabescence," and described how it might be propagated by layers, cuttings, etc., and even by seed.

Gaertner first observed the condition and described a similar change affecting the female organ (6).

Bateson described in the Sweet Pea a similar phenomenon and found it recessive to fertile anthers (7).

The potato "Record," which possesses no pollen in its anthers, was crossed by Sutton's "Flourball," which possesses abundant pollen: 20¹ of the 32 F¹ plants which bore flowers not one of which contained any

¹ In 1910 26 of the F¹ plants flowered and they were all sterile.

pollen. Two individuals of the F^1 family were fertilized by a derivative of "Flourball A," very rich in pollen, and gave rise to 39 plants, 19 of which bore pollen and 20 bore none: the expectation on the assumption that sterility is dominant being here equality.

In the "Congo" potato the anthers are entirely devoid of pollen, though they are not usually aborted or crippled. A plant of this variety was crossed by a "Flourball" seedling, and out of 18 F^1 plants which flowered, 8 had abundant pollen and 10 had none: here again the expectation was equality, "Congo" being heterozygous in sterility.

Two F^1 plants possessing abundant pollen were selfed, and of 44 plants examined, 41 possessed pollen and 3 possessed but a few grains of immature pollen. Why these plants should not have borne a fair quantity of pollen seeing that the F^2 parents must have been recessives and should have bred true, it is not possible to say. All three examples came out of one family.

A second cross with "Congo," viz. by "Reading Russet," gave only a small F^1 family, three plants bearing flowers, two containing pollen, and one none.

Similar results were obtained in the cross "Red Fir Apple" and "Reading Russet," F^1 being part pollen producers, part sterile, whilst F^2 , from the pollen bearing F^1 , gave 9¹ plants all pollen producers.

The flower of the "Red Fir Apple" is heliotrope in colour and the anthers are aborted.

"Queen of the Valley" has heliotrope flowers with sterile anthers. Crossed by "Flourball" one plant gave a series of F^1 plants of which some bore pollen and others none, although exact notes as to their characters in this family were not taken. One of the F^1 plants was crossed by a "Bohemian Pearl" seedling, and gave rise to a long line of pollen producers.

The heredity of male sterility in the potato is obviously the converse of that described by Bateson in the Sweet Pea, for the condition here is distinctly dominant. Bateson found it partially coupled with green axils in certain families. In the case of the potato, the only evidence of sterility being coupled with any other character was of a negative sort. Working with a large number of established varieties as well as with those plants which arose in the course of this work, I never found a plant possessing pale heliotrope flowers that had other than sterile and contabescent anthers, whilst those that were further tested proved

¹ In 1910 22 more F^2 plants flowered and all possessed pollen in the anthers.

to be heterozygous as regards sterility of anthers. No connection was observed between the condition of the male and female organs.

The presence of pollen in the anther being as we have seen a recessive character, it is of some interest to note how it behaves in selfed families. Unfortunately these pollen observations were not begun till 1909, although the breeding experiments began in 1906. Still a good deal of information may be extracted from the early notes.

Thus, in 1906, a red-tubered seedling derived from a "Flourball" plant in 1904, was "selfed," and gave rise to a large number of seedlings. One white-tubered plant (*D*) was reserved. From this a further generation was bred, and from this again another, so that in this case the family has been handed through five generations, and in all the anthers have had abundant pollen though the quality of the pollen was bad.

Two other lines, *A* and *G*, derived from "Flourball," have been bred through three and four generations respectively, and the recessive character, viz. presence of pollen in the anther, has remained true.

The occurrence of spontaneous sterility, due to absence of pollen, has already been mentioned as having taken place in the F^2 generation of the family "Congo" \times "Flourball"; it has also been observed in some other families where it was unexpected, but in all these cases it has occurred in normal and not deformed or strictly "contabescent" anthers. It is possible that "contabescence" is not a simple character but that absence of pollen and deformity of anther are due to separate factors between which exists an intimate linking.

The relations between quality and quantity of pollen and the shape of pollen in varieties and species of *Solanum* are discussed elsewhere (9).

HEREDITY OF CHARACTERS IN THE HAULM.

The difficulties in relation to haulm characters have already been adverted to; although to experts constantly reviewing crops of well-grown varieties it becomes comparatively easy to diagnose a variety by the general appearance of the foliage, and by inspection to designate at once such and such a potato as an "Up-to-Date" variety, or a "Ringleader" type, and so forth, yet if one closely compares any two foliages, taking corresponding specimens from various parts of the plant, it will be found very difficult to describe any constant differentiating character between any two varieties; there are differences no doubt,

but they do not admit of such definition as to fit them for Mendelian analysis.

The cross of "Red Fir Apple" and "Reading Russet" was made in 1906 for the purpose of tuber colour observations, and in 1909 a large family of some 120 individuals of F^2 plants were raised.

The "Red Fir Apple" has a somewhat distinctive foliage, the leaves are relatively small, ovate with sharp apices, peculiarly soft and silky to the touch, and, in addition, have a character which entirely distinguishes them from "Reading Russet" and most other varieties. The leaf has a peculiar twist in its axis, this twist being seen in all the upper leaves and often down to the lowest when the plant is 18 inches high or more.

The condition of leaf twist here in question must be clearly distinguished from that which occurs as a pathological condition in many varieties; in such cases the plants are dwarfed, the stems shrunk, the axes of the branches very shortened, and the leaves on them crowded together. The individual leaves also are much twisted, crenate and small.

In the "Red Fir Apple" the twist is less violent, it is not associated with crenation, and the plants are thoroughly healthy, vigorous and of good size.

"Reading Russet" possesses a much coarser foliage, the leaves are big, broad, blunt, flat, smooth, hard and coarse; the green colour is of a deeper shade than in "Red Fir Apple."

The four F^1 plants which were examined were intermediate as regards shape and texture of foliage, but resembled "Red Fir Apple" shape rather than "Reading Russet"; no twist in the leaf axis was observed.

In F^2 an analysis was made of the plant's foliage characters as seen in the table below.

The characters taken are all leaf ones.

"Reading Russet" shape.	Broad and blunt leaf.
" " texture.	Few stiff hairs, glazed surface to leaf.
"Red Fir Apple" shape.	Ovate, sharp apex to leaf.
" " texture.	Soft and silky.
Twist.	Twist in the axis of the leaf.
Intermediate shape.	Leaf shape neither "Reading Russet" nor "Fir Apple" in type, but resembling more closely the latter.
" " texture.	Softer than "Reading Russet" and harder than "Fir Apple."

FOLIAGE OF F^2 GENERATION.

"Reading Russet" texture.	"Reading Russet" shape	10	} 11
" " " "	Intermediate shape	1	
Intermediate texture.	"Reading Russet" shape	4	
" " " "	Intermediate shape	40	
" " " "	"Fir Apple" shape	12	
"Fir Apple" texture.	Intermediate shape	9	
" " " "	"Fir Apple" shape	42	
Total number of F^2 plants		118	
Twist in leaf		27	

In considering these figures it must be remembered that it is a matter not only of considerable difficulty to classify the living plants according to the shape and texture of their leaves, but that the personal element is paramount in such a classification. More particularly do such remarks apply to the consideration of texture and to the intermediate forms. Certain features, however, are readily and unmistakably recognized; these are the twist in the axis of the leaf and to a lesser degree "Reading Russet" shape.

The intermediate form of leaf is much more like the "Fir Apple" leaf than the "Reading Russet," and the former may therefore be considered dominant, whilst the twist in its leaf is recessive.

If the "Reading Russet" shape and texture are recessive, then it should occur combined in the F^2 family in the ratio of 1:15 and here it is 1:12.

The twist in the leaf occurred 27 times out of 118, that is practically in the ratio of 1:3, and it was associated 23 times with the "Red Fir Apple" shape, the remaining four having intermediate shapes and none showing "Reading Russet" shape.

Allowing again for the difficulty in distinguishing the intermediate form from "Fir Apple" shape and texture, it would seem to be a fact that this peculiar twist in the leaf is definitely linked up with the "Fir Apple" characters of shape and texture. None of the eleven plants possessing "Reading Russet" shape showed the slightest sign of a twist. The same consideration leads one to believe that "Reading Russet" texture is coupled up with "Reading Russet" shape; ten out of eleven times it is recorded as being so linked whilst the eleventh

time "Reading Russet" texture was united to intermediate shape, which might possibly be an error of observation.

These observations demonstrate at least that such fleeting and difficult characters as leaf shape and texture in the potato segregate in the sexual generation.

This year¹ a fresh F^2 family of this cross is being raised, and close attention will be paid to their foliage character.

THE SHAPE OF THE TUBERS.

No character seemed at first sight more elusive and less likely of solution in respect to its heredity than that of shape. Whenever I spoke to experts I was told that from the best "kidney" types you could pick out "rounds," and that exhibitors had won prizes both for "rounds" and for "kidneys" from one and the same potato.

East (5) notes four cases where originally "long" tubered varieties produced as bud sports rounded tubers; in two cases these "round" tubers reproduced themselves vegetatively true to "roundness," while the other two relapsed in the following season.

The oval varieties he notes as producing on single plants entire crops of very elongated tubers, which however did not grow true in subsequent years.

My observations would lead me to think that these bud sports in "kidney" and oval potatoes are quite common and are to be explained by their heterozygous composition as regards "roundness."

A frequent cause of trouble in dealing with the shapes of tubers is the nomenclature. The terms used to describe the different shapes are sufficient for the purpose of the gardener, but they connote no scientific accuracy.

Where the cylindrical potato ends and the kidney begins, where the latter ceases and the "pebble" starts, and where both merge into the round is a problem which it would be hopeless to attempt to solve by the mere classification of tubers.

It is only by the isolation of a type and its fixation as pure when bred sexually that the problem can be solved.

In describing the shape of a potato, two points can be regarded as

¹ In 1910 out of 71 F^2 seedlings on Aug. 3rd 6 showed the "Fir Apple" twist, on Aug. 23rd 14 had developed it.

fixed, viz. the point from which the tubers grow out from the stolon, and the most distal point from that, which in 19 out of 20 cases coincides with the central of the crown of eyes at the distal end. It is from this eye that the earliest and strongest shoot grows out. The line between these two points is the long axis, the breadth and depth are respectively the greatest measurements in each direction measured at right angles to the long axis and to each other. Adopting the conventional terms for potato shapes, the names long, kidney, pebble, and round appear to have the following meanings:—

A long potato is one in which the long axis is between $1\frac{1}{2}$ and $2\frac{1}{2}$ times the greatest breadth, and the depth is equal to the breadth. The ends are either blunt, as in the "Congo," giving the tuber a cylindrical appearance, or they are pointed as in *B*, Plate XXIV.

A kidney potato is one in which the length is usually between $1\frac{1}{3}$ times and twice the breadth, and the depth is considerably less than the breadth, giving the tubers a flattened appearance which is characteristic. The measurements of three specimens, unselected, of well-known "kidneys" are:—

"Myatt's Ashleaf":

	Length. Inches	Breadth. Inches	Depth. Inches	Ratio
(1)	2, 12/16	1, 9/16	1, 3/16	=44 : 25 : 19
(2)	3	1, 7/16	1, 3/16	=48 : 23 : 19
(3)	2, 4/16	1, 7/16	1, 2/16	=36 : 23 : 18

"Sutton's Ideal":

(1)	2, 7/16	1, 8/16	1, 4/16	=39 : 24 : 20
(2)	2, 5/16	1, 10/16	1, 4/16	=37 : 26 : 20
(3)	2, 4/16	1, 7/16	1, 4/16	=36 : 23 : 20

"Table Talk":

(1)	3, 1/16	1, 14/16	1, 6/16	=49 : 30 : 22
(2)	3	2	1, 9/16	=48 : 32 : 25
(3)	3, 1/16	1, 15/16	1, 8/16	=49 : 31 : 24

"Sir John Llewellyn":

(1)	3	1, 10/16	1, 2/16	=48 : 26 : 18
(2)	2, 13/16	1, 10/16	1, 4/16	=45 : 26 : 20
(3)	2, 11/16	1, 13/16	1, 7/16	=43 : 29 : 23

The Lapstone Potato is a bluntly elliptical or oval potato which is much broader than it is deep.

The Pebble Shape. This term includes a vast number of rather irregularly shaped tubers—tubers for the most part obtusely elliptical and almost as broad as they are long.

Below are some typical specimens:—

“Reading Russet,” see Plate XXI.

	Length	Breadth	Depth	Ratio
(1)	2, 6/16	1, 15/16	1, 7/16	=38 : 31 : 23
(2)	1, 15/16	1, 12/16	1, 3/16	=31 : 28 : 19
(3)	1, 15/16	1, 13/16	1, 8/16	=31 : 29 : 24

“Flourball,” see Plate I.

(1)	1, 15/16	2, 1/16	1, 8/16	=31 : 33 : 24
(2)	2, 3/16	2, 9/16	1, 13/16	=35 : 41 : 29

Round Potatoes. The tubers are practically globular, as in “Windsor Castle.”

An examination of these different descriptions is enough, almost in itself, to convince one of their artificiality, but when one comes to close quarters with them by breeding various pure lines and by crossing, one is soon convinced of the fact.

If Plate I, seedlings of “Flourball,” be now examined, it will be seen that it is easy to pick out¹

Longs	Nos. 14, 48, 135.
Kidneys	„ 21, 87, 88, 123.
Pebbles	„ 74, 90, 91, 154, 179;

but a close inspection shows a number of tubers which might be described as round, but which are not globular. They are short, and as deep as they are wide, such as Nos. 40, 89, 92, 112, 132, 138, 155, 156, 162, 185—10 individuals out of a total of 43.

If now we turn to Plates II, III, IV, V we shall find a family of 100 individuals all bred from one of these peculiarly shaped tubers (A). The whole family present a striking uniformity of appearance and similarity to the parent. Exceptions, however, there are, and they are figured in full in Plates IV and V.

Turning to these plates we see photographed all the available tubers from each of these individual plants, and it will be at once seen that each individual plant in Plate IV contains striking examples of this “round” type amongst its tubers.

¹ It should be said that the representatives of the individual plants here shown are when there are ovals and others more resembling “rounds” present on the same root, always the oval. The bias in favour of the “longs” as against the “rounds” has been purposely made in the composition of all the plates, in order that the recessive “round,” when present, shall be free from the suggestion that it is only a variant form of the dominant “long.” If therefore the effect to the eye be less convincing the deductions that are drawn rest on a firmer basis.

On Plate V, Nos. 67, 87, 91, 94, only further illustrate the fact that though certain tubers of a plant in this family may be more or less oval, yet other tubers on the same plant will be found to be of this peculiar "round" type.

One exception, however, stands out, and this is No. 100, which is definitely unlike the parent type and all its 100 other sister plants.

It is possible that it arose from a stray tuber and does not belong to this series at all—a view that has some plausibility, seeing that two years before "Flourball" seedlings were grown on this ground. Efforts are being made this year (1910) to obtain selfed seed from this plant.

On Plate VI a further illustration (*G* family) of this "round" type of potato is seen; it arose from a "Flourball" plant, but not the same one as the line *A*.

Seed from four of these plants has been saved and a batch of seedlings of *G*⁴ were planted in October 1909 and hurried forward; on April 26, 1910, they were examined and all the seedlings bore tubers, varying from $\frac{1}{4}$ to $\frac{3}{4}$ in. diameter, true "rounds" in shape. Those of the *G*³ seedlings which have formed tubers have also developed typically "round" ones¹.

It thus appears that there is a certain definite type of "round" potato that can be extracted from Sutton's "Flourball," and which can be bred sexually pure through at least two generations after having been isolated.

Before following further the evidence as regards the heredity of this type and its behaviour when crossed with other types, it will be best to discuss more fully its shape and variations.

The tuber shape, which is under consideration and which for the purposes of my work I have called "round," is to be found white, or coloured as red or black.

No relation has in the course of this research been shown to exist between shape of any kind and the pigmentation either of haulm or tubers.

The "round" tubers may be furnished either with "deep" or "fleet" eyes. It will be shown later that depth of the eye is itself a character inherited on Mendelian lines, and my experiments fail to show any relationship between depth of eye and shape of tuber. The size of the tuber is of course variable, but I have not found, however one may have

¹ Aug. 29, 1910. Although the *G* family has not been completely harvested there is evidence that the *G*³ family consists of three "longs" to one "round," and that the *G*¹ and *G*⁴ families are pure to "roundness."

bred it, this type of "round" potato assuming large proportions; few examples with a diameter over 2 inches occur, although oval and kidney from the same original parent stocks may be of large size and weight.

A typical specimen of this "round" type is represented by the first tuber of *G*⁶, Plate VI. The tuber is apple-shaped, its upper or proximal end as well as its distal or crown end is depressed, and the height is less than either its width or its depth. The actual dimensions are:—

Length	Breadth	Depth	Ratio
1, 5/16	2, 2/16	1, 1/16	= 21 : 34 : 17

One of the tubers of the parent *A* has the following measurements:—

Length	Breadth	Depth	Ratio
1, 5/16	2, 2/16	1, 1/16	= 21 : 34 : 17

The most characteristic feature is the stumpiness of the tuber in relation to its breadth.

Potatoes are raised commercially by the vegetative method, thus a crop of "Magnum Bonums" raised to-day should be regarded as merely an offshoot—a cutting so to speak—of a seedling raised some time before the year 1876. In other words the tens of thousands of tons which in the past 34 years have been grown of this stock are for scientific purposes merely replicas of a particular tuber of a particular individual, and hence the continuity through the intervening years of the variety's characters. Tubers that are grown by this vegetative means, within limits, reproduce themselves in their original shape more or less exactly, though I think, and hope to prove, that the degree to which a potato reproduces its shape vegetatively depends in large measure on its gametic constitution.

It may therefore be confidently expected that whilst a crop raised from a typical "round" such as *A* by vegetative means will remain perfectly true to type (and this indeed has been proved in the case of *A* itself, by growing it in 1908 and 1909), a crop raised say from the fifth tuber of No. 67, Plate V, might produce tubers more or less uniform and unlike the type *A*. A family raised by seed from any of the individuals, however aberrant in shape, will probably produce a set of seedlings at least as uniform as the family *A* itself.

The variation of this "round" type, if grown vegetatively, so far as my experience goes, is very slight or indeed none at all. The variations of the type as raised sexually by seed are slight but definite, being

towards greater length and approaching the pebble shape. In diagram the type and extreme variation may be represented as below :—

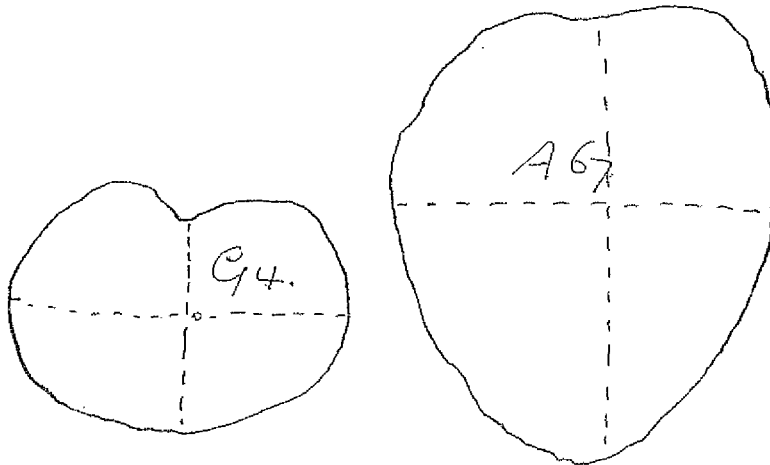


Fig. 1. These drawings are tracings of sagittal sections of potatoes—the long and transverse axes are shown—the depth cannot be shown.

Height and breadth are here represented, the depth being relatively great.

The “round” type is not a potato that recommends itself for its beauty or its economic qualities as regards shape; its merit is derived from the fact that there is very good reason to regard it as a gametically pure type, and that “roundness” in the sense in which it has been used here is a simple Mendelian character. The further evidence in support of this thesis will appear as we proceed to discuss other shapes.

A seedling of “Flourball” was selfed in 1906, and in 1907 a large number of seedlings were raised from it, one only of which was again selfed in 1907. The plant was carried forward by tubers to 1908, 1909 and 1910. In both 1907 and 1908 it produced seed, but in these two years only four plants came to maturity, and they produced the tubers numbered in Plate VII, *D*¹, *D*², 1908, *D*¹ and *D*², 1909. The seedlings from 1909 seed have not yet formed their tubers.

The tubers of plant *D* are quite unlike the “rounds” of the *A* family, they are oval and more or less kidney-shaped. The offspring of these, only four in number (excluding the seedlings now growing), comprise distinct types.

D^2 , 1908, a long pyriform tuber.

D^2 , 1909, cylindrical tubers tending to kidney shape.

D^1 , 1908, oval or blunt kidney with a sister tuber nearer circular.

D^1 , 1909 " " " "

The numbers in this case are all too small to draw precise deductions; all that can be said is that D does not represent a fixed type, that, on selfing, it gives both longs and ovals.

In 1908 this same D was crossed by A , and on Plate VIII the family is shown, or rather two families, because two D plants (D^1 and D^2) both grown from tubers of the original D of 1907 were fertilized by pollen of A .

A glance at the plate is enough to show that one has here two types of tubers, the "round" that we have already discussed on the one hand, and a series of ovals and kidneys on the other. The "rounds" are:

Nos. 3, 4, 5, 8, 13, 14, 15, 16, 18, 19.

3, 6, 7, 8, 10, 12, 14, 18, 19, 20, 21, 22, 28.

That is, 10 out of 19 in the first family, and 13 out of 30 in the second family. Total, 23 out of 49.

One has, in other words, "rounds" and not "rounds" in practically equal numbers; and it must be remembered that one counts here only those as "rounds" which come well up to the standard already given for a typical "round" such as either A , G^1 or G^6 .

The result of this cross admits of a direct Mendelian interpretation, for inasmuch as A is pure to "roundness," D must be heterozygous in that character—a fact which was already strongly indicated before. And the "non-rounds" must be all heterozygous in shape. If now one examines more closely the "non-rounds," one sees that they are made up of good kidneys such as Nos. 1 ($D^1 \times A$), and 1, 4, 11 and 26 of ($D^2 \times A$); of cylindricals, such as 5 and 23 ($D^2 \times A$), while the remainder are ovals and pebbles difficult to place, but which include among themselves abundant examples of the same shape as the parent D .

The experiment therefore as portrayed in Plate VIII is capable of being interpreted as meaning, not only that an oval "pebble" such as shape D is heterozygous as to "roundness," but that a true kidney and a true cylindrical may also be heterozygous in the same degree. Further, if "roundness" (i.e. shortness of axis) is the one allelomorph here in action, then "non-roundness" or length is the other. Later evidence

will be given proving that there is a tuber shape true to length, but before bringing this evidence forward it will be necessary to discuss a little further the nature of the kidney and the shapes which are heterozygous.

Plate X shows a family derived from the cross of H^1 , a kidney whose origin will be described later, and the typical "round" A . The "rounds" can be picked out most readily.

The typical "rounds" are:

Nos. 4, 6, 7, 16, 17, 19, 22, 25, 26, 27, 29, 30, 34, 35, 36,
38, 39, 40, 42, 45, 49,

i.e. 21 out of 44, practically half.

A kidney potato of so typical a shape as H^1 is therefore heterozygous in shape, and length, and must clearly be dominant to "roundness." Excellent specimens of kidneys occur in the family, and they must also be heterozygous.

It is interesting to note that No. 46 is more or less cylindrical, and that it is heterozygous and probably a merely variant form of kidney.

The hybrid nature, in regard to shape, of the kidney may be regarded as settled, that of the pebble follows as a necessity, but we have in support two sets of crosses.

A pebble-tubered plant H^{10} was crossed by the same "round" A as has been used before (see Plate XI). H^{10} is a typical pebble tuber and another of the same root-crop can be seen on Plate IX. The family, consisting of 47 individuals, is seen at once to break up into two types, the "round" and the ovals of different degrees.

The "rounds":

Nos. 1, 2, 3, 4, 10, 11, 13, 13A, 15, 17, 18, 19, 26A, 29,
31, 32, 33, 34, 40, 46, 48, 49.

22 out of 47 are all typical.

Emerging from this union of pebble and "round" occur really good kidney tubers such as 26, 38 and 41, as good or better than those produced in the family $H^1 \times A$, where the parent was a typical kidney.

The next cross, and perhaps the most convincing, is represented in Plate IX. It was made between a kidney potato, "Record" on the one hand, and the pebble-shaped "Flourball" on the other. The offspring number 32, of which Nos. 12, 13, 18, 21, 24, 25, 26, 30 are all typical "rounds"; i.e. 8 out of 32, or 1:4, the expected proportion

if both the kidney and the pebble-shaped parent are heterozygous as regards shape, i.e. "length," and amongst the dominants some are excellent kidneys, others pebbles. No. 3 is interesting because it shows on one and the same root a cylindrical potato and a pebble, a form which has just been shown to be heterozygous.

The arguments and the evidence in support of them, as to the heredity of the tuber shapes have, so far, all turned on the fact that there exists a variety of "round" potato which is recessive and breeds true; at the same time all examples that have been so far brought forward contain directly "Flourball" blood. It might therefore be supposed that the whole structure of my contentions rest on this keystone—this "Flourball" derivative—and that if this latter be removed the argument and deductions would fall to the ground. It becomes necessary, therefore, at this stage to describe an experiment entirely free from such an objection, at least as far as I am aware. A cross was made in 1906 between "Red Fir Apple" and "Reading Russet." "Reading Russet" is a pebble-shaped potato and "Red Fir Apple" a long cylindrical. F^1 was not examined critically for shape; the note as to the 117 young seedlings raised in 1907 is that about one-quarter bore "round" tubers, of these only nine survived, and only five of them were reared in 1909. Four individuals are shown in Plate XXI, and the fifth one, which was omitted, was a long-shaped tuber. On the whole the evidence is rather in favour of F^1 being a mixture of "longs" and "rounds" in the proportion of 3 : 1, but of the F^1 "rounds" we have no examples. The F^2 generation, however, is represented by 120 individuals contained in the two families $L^{1(a)}$ and $L^{1(b)}$, both derived from the selfing of a kidney-shaped F^1 plant.

The first family, $L^{1(a)}$, consists of 60 individuals; of these 52 are represented in Plate XXII, and of the eight missing, five were long and three "round." When the plate is examined, and still more the actual individuals, the "rounds," such as we have already become accustomed to, are to be found at once, and the following typical examples are seen, Nos. 1, 2, 22, 35, 37, 46, 47, 49, 61, 63 and 64, which in addition to the three not figured, makes the total of 14 out of 60 or nearly 1 : 3.

The second family, $L^{1(b)}$, Plate XXIII, affords some very striking examples of typical "rounds" such as Nos. 6, 47, 52. The family contains 59 tuber-bearing individuals, and of these Nos. 6, 10, 17, 19, 22, 24, 29, 30, 33, 40, 47, 52, 54, 61 are typical "rounds," i.e. 14 out of 59 or 1 : 3.

In the two families containing 119 tuber-bearing individuals, 29 are "round," that is 1 in 3, as would be expected in an F^2 family from a heterozygous parent in which "roundness" was recessive.

It remains now to consider the evidence bearing on the existence and nature of the dominant shape in its pure form. So far, it has been shown that length of tuber is dominant and that the degree of dominance is variable, i.e. the hybrid form is not constant, the heterozygous tubers varying from a long kidney to an ovoid. On Plates XXII and XXIII, amongst the long tubers are undoubtedly pure dominants, but which exactly they are, and how to distinguish them from the impure dominants with certainty nothing but breeding experiments could determine.

It is, however, significant that by selecting those individuals whose tubers were the most uniformly long, it was found that out of the 119 members of the *L* family already described there were 34, or a little more than one-quarter, that could be picked out as being probably pure in respect to length.

Fortunately better evidence is to hand in respect to individuals homozygous in the character of length.

A potato, called "Sole's Kidney," yielded abundant seed in 1906, in 1907 several hundred seedlings were planted¹, and they all came true to type, viz. a long attenuated kidney, see Plate XXVI. One of these seeded and 50 seedlings were raised in 1909, and every one of these were long kidney form, see Plate XXVI. It would seem, therefore, that this potato *C*, "Sole's Kidney," is a pure dominant as regards length.

Another kidney, "Bohemian Pearl," was sown in 1907 and a very large number of seedlings (family *B*) raised; these were not examined very critically in respect to size and shape, but were noted as being uniformly long and pyriform: one selfed naturally, and of the five seedlings raised three bore long tubers, and two bore oval tubers, Plate XXV. These ovals are distinctly flattened and are not "rounds." They have been grown in 1909 and have retained their shape. Had there been any appreciable number of oval or "round" tubers in the first batch of 300 seedlings raised in 1907 it would undoubtedly have been noted; on the contrary, my own and my gardener's impression is that nothing but "longs" occurred. There is in my mind but very little doubt that the stock *B* is pure to length. Efforts are being made to self the oval tubered plants this season.

¹ I was presented with several hundred of the seed of both these stocks by the Manager of the Cambridge University Farm.

In 1908 a cross was effected between a pebble-shaped tuber (M^5 , Plate XXIV) and a seedling of the family B carried on by tuber from 1907¹. The issue of this union forms a striking example of the effect of crossing a heterozygous by a dominant long. The whole family of 39 individuals is without exception long or oval, and includes the most elegant kidney and one or two cylindricals, see Plate XXIV.

In three experiments cylindrical potatoes were employed as the female parent. In the first "Red Fir Apple," a cylindrical, was crossed by "Reading Russet." There is good reason to believe that the F^1 family really consisted of three "longs" and one "round," though the small number of survivors, viz. 11 in the first season, does not assist one to any definite conclusion. Those of the F^1 family which survived 1909 are shown on Plate XXI. "Red Fir Apple," though long and cylindrical, is therefore in all probability heterozygous as regards length. It is of interest that, since it has been cultivated in my garden, it has become shorter and broader and less cylindrical; on the other hand "Congo," which was used in the second and third experiment, maintains its truly cylindrical shape. Plates XII and XXV.

In the second experiment "Congo" was crossed by a "Flourball" seedling of 1906. The "Congo" tubers are typically cylindrical, the seedling "Flourball" was not especially described², but the F^1 series, see Plate XXIX, consisting of 29 individuals, all of which bore kidney-shaped tubers, is evidence that the "Flourball" seedling's parent must have been "round" and that "Congo" must be a pure dominant; for if neither of these suppositions are true, then we should have expected pure "rounds," which are conspicuously absent, or if the "Flourball" seedlings were pebble or heterozygous in shape, then half of the K seedling family should be pure "longs," which they are not. F^2 families were raised from K^6 and K^9 , both elongated and more or less kidney-shaped. The following proportion of "rounds" and "longs" occurred:

	Rounds	Longs
Family K^6	65	210
Family K^9	13	69
	<hr/> 78	<hr/> 279

¹ The B line planted in 1908 from the pollen of which this cross was made, was grown from long tubers arising both from the plant which gave the seed ball in 1908 and from its sister plants, sown indiscriminately.

² The absence of a description of shape implies that it was "round" or "pebble" shaped and not markedly distinct from the parent "Flourball."

i.e. 1 : 3.6. The families are illustrated in Plates XIII, XIV, XV, XVI, XVII, XVIII, XIX, XX.

In the third experiment "Congo" was crossed by "Reading Russet." Only four F^1 plants survived, and the tubers of these, Plate XII, are elongated, but here again the numbers are not large enough to draw conclusions from.

The dominant character of length in the tubers has been isolated or identified in the potato *C*, and is represented by a very elongated kidney; in *B*, where it is more pyriform; and in "Congo," where the ends of the tubers are blunted and the tuber has a cylindrical appearance.

It is not improbable, as was suggested earlier, that the allelomorphic pair to the character manifested in the "round" potato is length of axis, and that the kidney and cylindrical shapes, though inseparable with respect to length, are dependent on other factors governing shape besides that governing the length of the main axis.

The dominance of the long potato tuber over the short is analogous to the dominance of the giant over the dwarf plant, as Mendel showed in the Pea Family. This dominance probably rests on the same anatomical basis, viz. the respective length and number of internodes involved. Tubers are borne on underground stems, called stolons, and the eyes may be regarded as buds or nodes, so that the number of eyes present may represent the number of internodes condensed into the length of a tuber. A study of the tubers from this point of view is not yet complete, but it is quite clear that as a general rule the "round," i.e. short axis potatoes, have less eyes than the long axis ones, i.e. they represent fewer internodal lengths.

It has already been shown that the dominance of length is not equal in degree: sometimes the heterozygote is of the most attenuated form, but more often an intermediate shape is assumed varying from kidney to pebble and oval. The ordinary kidney of fair breadth is probably always an heterozygote.

The Variations in the Shape of Tubers. The amount of variation has already been indicated in the case of the "round" potato; in the "long" it is rather less. If "*C*" and "Congo" be taken as pure "longs," then, accepting the typical well-grown tuber of each sort, it is apparent that they are as to their proportion between length and breadth much the same, and the form is fairly uniform.

By far the greatest variation in shape, both amongst the individual members of the same family and the several tubers of the

same individual, is met with in the case of the heterozygous variety.

The examples of heterozygous potatoes which have been tested, viz. "Flourball" D^1 , H^1 , H^{10} , K^a , K^b and L^1 , varying as they do from kidney to pebble, testify to this.

The degree of variation in the shape of tubers of some given sort is in itself very variable, but I think it would be acknowledged that the kidney types vary most. A striking example of this is shown on Plate XXVIII, reproduced by permission of Messrs Sutton, where a kidney potato, "Superlative," is photographed in the clamp, and whilst the majority of the tubers are kidneys, a large percentage are best described as pebbles.

The variety H^1 , Plate X, so clearly demonstrated to be heterozygous, is a remarkably uniform kidney shape, but out of less than half-a-bushel it is possible to pick out potatoes varying from a very long to an obtuse ellipse, Fig. 2.

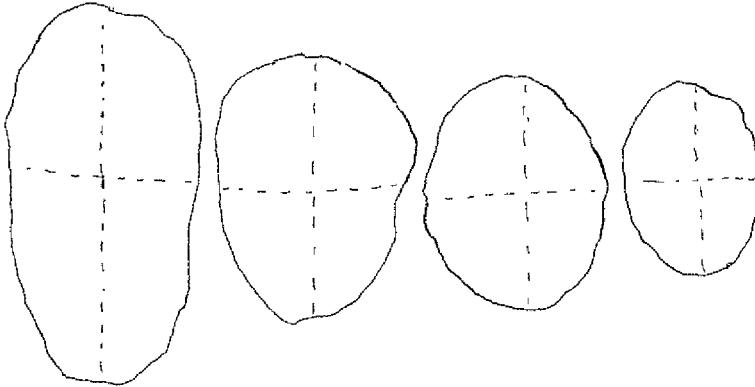


Fig. 2. These drawings are tracings of sagittal sections of potatoes of the individual H^1 . The long and transverse axes are shown. The depth is less than the transverse diameter.

THE DEPTH OF THE EYE.

The potato tuber has scattered on its surface buds from which grow the shoots; the buds are known as "eyes."

The potato eye consists essentially of two parts, a central spot or shoot, and an overhanging ridge or brow which is curved, and whose concavity always points downwards or distally.

The eye is recognized to occur in two forms and is known as either

"shallow" or "deep." The "shallow" eye is a superficial eye, i.e. the central growing point is not depressed but is level with the general surface of the tuber and the brow is but very slightly marked.

Typically "deep" eyes are those of "Congo" and most of the family *K* ("Congo" × "Flourball" seedling) and *A*¹⁰⁰, whilst typically "shallow" eyes are seen in *A*²⁷; *H*¹ × *A*, Nos. 5, 37, 41. The "shallow" eye is a distinctive and an easily recognized feature. Briefly the "deep" eye is dominant to the "shallow," and the heterozygous "deep" eye is never quite so "deep" as the typically "deep" one. In "Flourball" the eye is "deep" but not remarkably so; of its seedlings 14 out of 43 were definitely "shallow." In the family *A*, of 98 seedlings 21 were "shallow," and *A* the parent may be regarded as having the standard impure "deep" eye.

The *D*¹ × *A* families contain 16 "shallow"- and 33 "deep"-eyed individuals.

The *H*¹ × *A* families contain 22 "shallow"- and 71 "deep"-eyed. *K*⁹ is a further example of an impure dominant "deep"-eyed potato. Of the 73 seedlings of this family 23 are "shallow" and 51 "deep."

Two *F*² families were raised from the cross of "Red Fir Apple" × "Reading Russet." These two families differ a little in respect to the eyes. Both were raised respectively from sister tubers of the individual *F*² plant (*L*¹). Both parent plants grown from these tubers had "shallow" eyes, one family, *L*¹⁽⁶⁾, consists of 54 individuals, all of which carry "shallow"-eyed tubers. In the other family, *L*¹⁽⁹⁾, Plate XXIII, out of 55 individuals 5 (Nos. 4, 15, 51, 52, 59) must be described as medium, i.e. the eye is distinctly depressed and the brow is evident, though not heavily developed. The only other "shallow"-eyed potato that was selfed was "Bohemian Pearl," all the individual plants which have arisen from it that have come under my notice are "shallow"-eyed. Of the first generation there were some hundreds, of the second only five.

If all the families arising out of matings of impure dominant eyes be put together, we obtain the following:

	Shallow	Deep
"Flourball" seedling selfed	14	29
<i>A</i>	21	77
<i>D</i> ¹ × <i>A</i>	16	33
<i>H</i> ¹ × <i>A</i>	9	39
<i>H</i> ¹⁰ × <i>A</i>	9	36
<i>K</i> ⁹	22	51
Total ...	91	to 265

This is almost exactly 1 : 3.

K^6 is an example of a pure "deep"-eyed potato; all the 284 seedlings of which are "deep"-eyed.

This family, K^6 , further illustrates a curious phenomenon. Certain individuals, such as $K^{6(2)}$, Nos. 28, 84 and 95, appear at first sight to be "shallow"-eyed. When, however, they are examined with their sister tubers from the same plant, it will be seen that the "shallowness" is only present at those points where an outgrowth or protuberation is taking place: elsewhere in the same tuber or on its sisters, the eyes are "deep" $K^{6(6)}$. No. 28 is apparently "shallow," but here also outgrowths are just beginning. A true "shallow"-eyed potato is "shallow" in every tuber of the plant and a true "deep" is equally "deep" in every tuber. The heterozygote is more variable and, though "deepness" is dominant, the eye is often shallower than in the tubers of a pure dominant "deep" eye.

The potato "eye" is therefore, like shape, a distinct character inherited on Mendelian lines.

THE COLOUR OF TUBERS.

The colour is due to the presence of pigmented cell sap in the cells of the superficial layers. The white skinned or, more correctly, yellow skinned tuber, owes its colour on the one hand to the presence of the cork in the upper layer of the corky tissue, and on the other to the absence of any red or purple pigment. The red potato contains a vermilion pigment in solution and the black potato, which is in reality an intense purple, derives its colour from a deep blue purple sap pigment which, seen under the microscope in contrast with the red, is quite distinct.

It was pointed out in the Introduction that potatoes of all colours, including the whitest—with white flowers—showed more or less purple pigment in the shoots, arising from the tubers in spring, if not in the haulm also. Vilmorin (10), in his catalogue of all the known varieties, makes three classes in which the tubers possess white shoots; it is probable that small deposits of pigment were overlooked. Out of the 1200 separate and distinct varieties he describes some 45 as having white shoots. Often the pigment occurs in punctate deposits which need a lens to distinguish them clearly, but the pigment is unmistakably present. From this fact it would seem clear that all tubers, coloured or not, possess the chromogen base, i.e. using the notation

employed in the Mendelian analysis by Bateson, Miss Saunders and others, all potatoes possess the factor *C*. Miss Wheldale, who has very kindly examined many of my tubers from this point of view of pigment analysis, confirms this view. If, then, colour can be present in the haulm and even in the shoot and still not be developed in the tuber, it would seem that there must be some factor which acts as a "developer" of pigment, and in its absence the tuber is white (yellow). The supposition that this factor might be an inhibitor of colour is negated by the fact that white are recessive to coloured tubers.

It is necessary now to observe how the potato plant behaves in actual breeding experiments.

The white potato breeds true.

Several hundred, about 600 in all, of seedlings of "Bohemian Pearl" and "Sole's Kidney," both white potatoes, were raised, and all the plants that bore tubers at all carried white ones only.

A "Bohemian Pearl" seedling was selfed and gave a half-dozen white-tubered seedlings.

A "Sole's Kidney" gave 300 white-tubered seedlings, and one of these selfed and produced fifty seedlings, all of which were white-tubered.

A white-tubered variety (*D*) extracted from "Flourball" has been bred now through three generations and gives rise to nothing but white-tubered plants.

The variety "Early Regent" sown this season has produced 125 white-tubered plants and none carrying coloured tubers.

The Colour Composition of the Red Potato. If seedlings of "Flourball" be grown and these, after harvesting, divided up in respect to colour, it will be found that red-tubered plants are to white as 9 : 7.

The numbers in my experiments were :—

	1907	271 Red plants		217 White
June 1909	71	"		60 "
Oct. 1909	24	"		19 "
Aug. 13, 1910 ¹	54	"		44 "

Total	420	"	:	340 "
Ratio	9	"	:	7.09 "

¹ There are still about 100 plants to be harvested.

The ratio 9 : 7 is one very well-known in Mendelian analysis and is evidence of the interaction of complementary factors belonging to separate pairs of allelomorphs.

Now if R be considered the factor which in presence of the developer D converts the chromogen into a red pigment, then the zygotic composition of "Flourball" should be written $RrDd$, which will on selfing give plants with the following composition :—

$$\begin{aligned} 9 \text{ } RD &= \text{Reds} \\ 3 \text{ } Rd &= \text{Whites} \\ 3 \text{ } Dr &= \text{Whites} \\ 1 \text{ } dr &= \text{White} \end{aligned}$$

Further, it will be seen that there are five kinds of white and four of red plants, viz.—whites of the composition :—

$$Rrdd, ddrr, RRdd, rrDD, rrdD,$$

and reds of the composition,

$$RRDD, RrDd, RrDD, RRdD.$$

Of the red it is at present only possible to distinguish three kinds, viz.,

$RRDD$, $RrDD$, or $RRdD$ and $RrDd$. Of these $RrDd$ we know as the parent or type, the pigmentation of which is weak.

$RrDD$ or $RRdD$ has been raised twice out of "Flourball" seedlings, and each case has given red and white tubered seedlings in the proportion 3 : 1. Thus,

Family A	70 red	27 white
„ G	12 „	5 „

The colour of the tuber $RrDD$ is distinctly stronger than the colour of the ordinary "Flourball." There is good reason to hope that the type $RRDD$ will be isolated this season : such a potato will breed true to red. "Reading Russet," a pale red, selfed in 1909 and planted out this year, already gives evidence of a 9 : 7 ratio. Amongst the whites no certain distinction has yet been made between the possible kinds, nor have two whites been yet successfully mated ; an experiment which when the two whites contain, one the R factor and the other the D respectively, will probably give rise to a coloured potato¹.

¹ This year, 1910, a large number of crosses between various whites have been effected.

"Flourball" has therefore yielded three types of potato which have been identified by reason of their gametic qualities, namely, two reds, one giving reds to whites in the ratio 9 : 7, another red to white in the ratio 3 : 1, and a white variety.

In order to elucidate further the colour factors the white variety *D* was crossed by the 3 : 1 red variety *A* and the result was

27 Red to 22 White.

This ratio is presumably to be taken as approaching equality, as 9 : 7 ratio would be here impossible.

If the formula of *A* be *RrDD* then this particular white potato must be *rrDD*; similarly if *A* be *RRDd* then the white variety must be *RRdd*. It is here assumed that *A* = *RrDD*, and the family *D* therefore will be represented by *rrDD*, it could of course be equally well *rrDd*.

A cross of peculiar interest was made between "Flourball" and a potato called "Record" which, although of attractive appearance, was of such frail constitution that it has entirely died out everywhere. The result of the cross was a family *H*. Of the 30 individuals which lived through the following years 19 were white and 11 red. The numbers are small, but enough at least to show that the whites are in a very distinct majority. If the notes of the *H* family be examined from its first origin, one finds that there were 28 whites to 12 reds and two with no tubers, and that the mortality has taken place amongst the white and tuberless.

The formula for "Flourball" was shown to be *RrDd*, and there are two possible formulas for a white potato which would, in union with "Flourball," give rise to a family having a majority of whites. They are *rrdd* and *rrDd* respectively;—the first would give a family of three whites to one red; the second would give a family of five whites to three reds. The numbers in the *H* family are not large enough to decide with certainty which formula for "Record" is the more correct. We have seen that the mortality affected those plants which were either white tuber bearers or tuberless, and that the approximation of the final result of two whites and one red is due to this mortality amongst the whites. Whether it is possible that plants pure to the absence of pigment factors are more weakly than others cannot, on the present evidence, be asserted, but the facts suggest such a possibility.

Two white-tubered members of the *H* family were crossed by the red potato *A*, whose gametic composition we may assume to be *RrDD*,

seeing that on selfing it gives three red and one white. The results were different in each case—

$H^1 \times A$ gave	29 red	19 white
$H^{10} \times A$ „	18 „	27 „
Total	47 „	46 „

In either case it is possible that larger numbers would have shown a nearer approach to equality.

It must however be noted that the family $H^{10} \times A$, had far less pigment in its stem than $H^1 \times A$, and that the possible results of mating whites with reds of A 's composition are equality, if the white is $rrDD$ or $rrdd$, or three red to one white if $Rrdd$.

One other cross was made between a pale red and a white-tubered plant.

“Queen of the Valley” was crossed by a red seedling of “Flourball” and the F^1 generation consisted of seven red to three white. One of these a pale red, M^3 , was crossed by a white seedling of the white “Bohemian Pearl” B . Forty-one seedlings grew and 38 survived to form tubers. Of these

19 had red and 19 had white tubers.

This result of equality suggests that the composition of the two parents may have been—(M^3) $RrDd \times (B)$ $rrDD$. M^3 is probably $RrDd$ and not $RRDD$, $RrDD$, etc., because it is a particularly feeble red and might therefore be assumed to have the least possible factors that would give a red.

Two reds, one very deep red, viz. “Red Fir Apple,” and the other a weak one, “Reading Russet,” were crossed. “Reading Russet” has now been selfed, and this year we shall learn its composition, but its colour is weak like that of “Flourball,” and it has probably the same gametic composition, viz. $RrDd^1$. “Red Fir Apple” is of a very deep colour and might be $RRDd$. The F^1 raised were 117 seedlings, but only 11 of them came to maturity, viz. eight red, and three white, indicating, as would be expected from the union, a 3 : 1 ratio.

$$RRDd \times RrDd = 3 \text{ red} : 1 \text{ white.}$$

Two plants arising both from tubers of the same individual of the F^1 family, viz. L^1 and L^4 , were selfed and produced in the F^2 generation large families in which the ratio of red and white was 3 : 1.

¹ The 1910 seedlings of “Reading Russet,” so far as yet harvested, are divided into 14 red-tubered plants and 10 white-tubered.

The numbers in the latter are not conclusive in themselves, because only selections of these families were actually planted out; but amongst the young seedlings, before planting out, there were 23 red to 8 white and the appearance of the harvested selections fully bear out the suggestion of a 3 : 1 ratio.

Purple Coloured Tubers.—The “Congo” potato is a cylindrical potato of almost a black colour, the pigment extending within the tuber somewhat irregularly. The “Congo” flower, which is white with a purple tinge at the base of the petals, is completely sterile in the male organs, and it was therefore only used as a mother plant.

Two crosses were made—

1. *Congo* × *Reading Russet*. There were eight seedlings and only four survived until the late autumn of 1906, of these

Two were black like “Congo,”

Two bright red.

But on July 25, 1907, there was a fifth plant with white tubers which died out subsequently.

The numbers are too small to make any deduction as to ratios, but there is one factor of great importance which stands out, viz.—that out of a union of a deep purple and weak red, there have segregated out deep purple (black), bright red and white.

The next cross was—

Congo × *Flourball Seedling*. This cross was effected in 1906. The “Flourball” seedling was a stray plant growing in one of the experiment lines containing “Ringleader” and was used as pollen parent. “Ringleader” itself did not flower that year. Except that it was a red tubered variety nothing further can be told about it, as it was unfortunately not preserved. Its pollen was used in the cross with “Queen of the Valley” and, as has been mentioned before, it is probable, for the reasons already given, that it was a red of the formula $RrDD$ or $RRDd$.

The F^1 generation contained 29 plants and these were

13 Black tubers.

12 Red tubers.

4 White tubers.

Here again the important features are the complete segregation and the appearance of the white tubers.

Before discussing the possible constitution of “Congo,” it will be best to consider the F^2 generation.

In 1908 two of the F^1 plants, viz. K^6 and K^9 both selfed and large families were planted; those of K^6 did well, the K^9 family fared badly in the wet summer of 1909.

K⁶ Family. K^6 , Plate XXIX, is a black (i.e. deep purple) potato. Several seedballs were collected from the plants, and one coming from a plant $K^{6(6)}$ was planted in its entirety. Originally 301, there were harvested but 160 seedlings. The tubers of the F^2 family separate at once into blacks, reds and whites in the proportion of 77 black, 29 red, 54 white; the reds are either quite pale and similar to "Flourball" or "Reading Russet," or they have more purple colour and resemble "Red Fir Apple."

Of the whites about one-sixth (9 in 54) are quite pure, i.e. no tinge of colour can be seen in the tubers or eye before sprouting, whilst the remainder may have a trace of colouring usually purple, in the eye or the skin and more especially in any scars following a wound by fungous disease or other lesion. Such pigment is minute in quantity and often needs a lens to demonstrate its presence. The reds are roughly of two kinds, a deep strong group, and a pale. The proportion between these is 23 deep red, and 6 pale red, and they can be classed fairly readily into these main groups. The blacks are all alike, viz. deep purple. In considering the factors which underlie the phenomena of colour in the red- and white-tubered potatoes we assumed the presence of the two factors R and D . The purple potato is obviously bringing a fresh factor besides these into the field and this new or "purpling" factor can be called P .

If K^6 has the gametic formula Pp, Rr, Dd , then on selfing we should get plants or biotypes with the following gametic constitutions:

27	plants of the composition	PRD	= purple.
9	"	"	PR = white (tinged).
9	"	"	RD = red.
9	"	"	PD = white.
3	"	"	R = white.
3	"	"	D = white.
3	"	"	P = white.
1	"	"	prd = white.

The numbers for the K^6 family are:—

	Purple	Red	White
Calculated numbers ...	73	24	75
Actual Numbers ...	77	29	54

The results¹ are sufficiently close to give one some confidence that the phenomena are correctly represented by the assumption of the factors PR and D that have been supposed to be at work.

The sister family K^9 adds additional evidence of a strong nature. Several lots of seed of K^9 plants were sown and in all some 300 seedlings raised. The majority were however planted in selections and therefore are of no use for quantitative purposes. All the groups, however, coincided in one feature—none produced a single red tuber; and the evidence from the selected groups strongly favour the view that purples to whites were as 9 : 7, whilst the groups that were planted in full give 26 : 14. The parent plant of such a family must be homozygous in the purpling factor and heterozygous in its two other colour factors. To K^9 , therefore, should be given the zygotic formula PP, Rr, Dd .

Having considered K^6 and K^9 , we can now turn back to the original cross and the F^1 family. The F^1 family consisted of 13 purple, 12 red, 4 white. It is obvious that as regards P , "Congo" must be heterozygous, further we knew the "Flourball" seedling was red and therefore contained RD . If we represent the cross

$$\text{"Congo" } PpRrDD \times \text{"Flourball" seedling } RrDD$$

we get 12 purple, 12 red, 8 white.

The result of these experiments on colour inheritance would seem to be (1) that whilst colour may be present in the stem to any degree, a special developer D is necessary to bring it out in the tuber, (2) that redness is dependent on a separate factor R , (3) that purple is dependent on a further one P , and (4) that the purple colour cannot be developed except in the presence of all three factors PRD .

In all the experiments there has been much to suggest that the degree of the "redness" is due to the homozygous condition or otherwise of the plant as regards both R and D , but the evidence has not been given in full because the classification into shades of "redness" would be too empirical and dependent on personal judgment. In one group the distinction was clearly made out, viz. in the family A where the formula was shown to be $RrDD$ (or $RrDd$) the deep reds were to the remaining reds as 24 to 48, whilst in the K^6 group the reds were 23 deep red to 6 pale red. Amongst the blacks (purple) no distinction could be made.

¹ If the disproportionate mortality of the whites be remembered, the actual numbers will be seen to be not so far removed from the calculated ones. Thus the number of whites, had the mortality in all classes been equal, would be 66 instead of 54.

SOLANUM ETUBEROSUM.

The plant with which I have worked is identical with that used by Mr Sutton⁽⁸⁾ and described and figured so fully by him. I obtained my tubers from Kew, whence it was sent to me with the name of "Maglia," though the misnomer was realized later. Mr Sutton has been good enough to see my plants growing, and has no hesitation in confirming that they are the same as his own obtained from Mr Lindsay of Edinburgh Botanical Gardens and which he has described under the name of "*etuberosum*." The Rev. Aikman Paton's supply of *etuberosum* was derived from mine, and his results, as far as they are published, confirm mine in many particulars.

It is not necessary to decide as to whether this plant is the one originally described by Lindley in 1834 as *etuberosum*; the general feeling is that it is not the same, but that it is a plant of the greatest interest is none the less true though its name be a borrowed one.

The contention of Sutton⁽⁸⁾ that *S. etuberosum* is the parent plant of our domestic varieties has been considered by me in an earlier paper⁽⁹⁾. Wittmack⁽¹²⁾ has also discussed this question, and though I do not share his opinion that *etuberosum* is an ordinary *S. tuberosum* variety I, nevertheless, agree with him that there is no reason to regard it as the parent type of our domestic varieties.

The *etuberosum* plant is a low growing one with very light green leaves which are of a different tone to any other I have had growing in my garden. It rather suggests the dusty appearance of the olive. The haulm spreads at its lower end, sending out lateral branches parallel to the ground.

The average size of the leaf is $2\frac{1}{4}$ inches by 1 inch; the surface is soft and rather woolly; the veins are marked, but the leaf not curled or rugose. Compared with most domestic varieties the nodes of the stem would be considered short, but they are, in proportion to the rather dwarf-like habits of the variety, about normal in length.

Pigment in the stem is red, patchy, extending feebly into the petioles, and visible in the axils. The flowers occur in close clusters, and are of an extremely beautiful lilac, which, viewed from above, has a peculiarly soft appearance. This is due to the fact that the pigment is on the under surface of the petal, that is outside when the flower is closed. This lilac colour differs considerably from the heliotrope seen commonly in domestic varieties. The anthers are delicate and form

a close cone similar to that seen in the various true wild species, and through the apex projects a short style ending in a simple knob. The anther contains abundant pollen.

The corolla is very definitely wheel-shaped, the tips of the petals recurve; they are rather sharp and hairy, and the calyx is hairy and its five processes are long.

The tubers are borne on rather long stolons. They are white and round, but the shape (Plate XXVII) is not typical of "round" as we have met it before in this paper. The tubers are irregular, neither oval nor long, but are often depressed at various points, so that although the general shape is round, the actual circumference is not necessarily circular.

The size is variable. When the tubers were first cultivated here they were not more than $1\frac{1}{4}$ inches in diameter; in 1909 I had some up to 3 inches in diameter.

The taste is bitter.

In 1906 Mr Sutton informed me that he had for over 20 years tried to self and cross this variety and had failed. In that year, however, a plant bore one berry. I, also, after repeated trials, in 1906 succeeded in making a cross. In 1907 Mr Sutton again obtained selfed berries, and some tubers I had sent to the North of Scotland set seed naturally and crosses were made. Hence, after over 20 years of observed sterility, this variety suddenly flowers out into fertility in Reading, Scotland and North Herts, which, as we shall see, has cost it dear. The tubers in both 1906 and 1907 showed no variation, except a slightly enlarged size. In 1908 when the plant first set seed naturally in Barley, it was noticed that the tubers of one plant had a slight violet tinge in the skin in places; this plant set seed in addition to one other, and 30 of the seedlings came from this plant. There is no evidence that the seedlings are, as a whole, different from those which did not show this vegetative variation.

The fertilization of the plants took place naturally, but at a date when all the other potato plants in my garden had ceased flowering and when some *F*¹ "Congo" crosses, which were close by, had already formed good-sized berries.

Immunity to Disease. (*Phytophthora infestans*.) During the culture of this variety in Reading it was noted for its immunity to disease. In my garden it was in

1906. Perfectly immune from disease in haulm and tubers.
Three hybrid seeds only obtained.

1907. Very slight touch of disease on haulm, none in tuber.
No seed.
1908. Slight disease in haulm, none in tuber. Set seed freely.
1909. No disease in haulm on September 3, but some later,
considerable disease in tubers. No Seed.
1910. Some disease in haulm in August. Selfed and crossed
seed.

The incidence of disease amongst the seedlings was remarkable, those attacked by disease were in some cases consumed away and all of them, excepting one which was but very slightly touched in the haulm and quite free in the tuber, were most seriously damaged. Out of 40 seedlings 34 were diseased and six were untouched, to these might be added the one only just touched by disease on a leaf or two, making seven. The ratio of 33 : 7 is of course suggestive of a 3 : 1 ratio. Resistance to disease being, as Biffen⁽²⁾ found in the case of wheat, a recessive. Further careful observation will be needed before anything more definite can be asserted. It is a most striking fact that although the parent *etuberosum* plant was for 20 years and upwards noted for its immunity to disease, yet directly its sexual life begins that immunity goes. The chain of events, the fact that the F^1 family contains a number of immune plants, suggests that with the onset of sexual activity some disturbance in the mechanism by which the plant had hitherto secured its immunity to *Phytophthora* had occurred—and that the dominantly susceptible state of the plant apparently heterozygous in this respect, has as it were been uncovered and its true nature laid bare.

The immune seedlings in 1910 demonstrated afresh their resistance to *Phytophthora*. The *etuberosum* seedlings were so planted that on either side of an immune plant was a susceptible one, whilst immediately behind was a row of ordinary domestic potatoes. The susceptible seedlings and the ordinary potatoes were devastated by disease. Before the end of July the haulms of both these latter were destroyed. Up till the beginning of September the immune plants were unscathed. Signs were not wanting that the immune plants had been attacked but had successfully withstood the enemy. Pale spots were seen on some of the green leaves during the height of the disease, whilst on these spots on a few fading leaves colonies of *Cladosporium epiphyllum* were found. The presence of the bright green healthy immune plants

standing out in the midst of the blackened and diseased débris which marked the site of their destroyed neighbours formed a very striking picture. Successful crosses have been made this year between the immune seedlings and domestic varieties.

The Flower. It has been already noted that the flower of this potato is of a very delicate lilac and that the pigment is on the under surface. The petal is entirely self-coloured; there is neither an intensification or a weakening of the general tone in the central region of the petal, as one so commonly finds in potato flowers.

The flowers of the seedlings offer considerable variations. Of the 40 plants 20 flowered, and of these—

Nine plants were exactly like the parent, i.e. uniform colouring on under surface;

Two plants were similar to parent but double the intensity of colour;

Three plants had the same general colouring as the parent, but with a deep-coloured tongue in the middle of the petal, and in one it was noted (probably true for all) that the colour in the tongue was both in the upper and in the lower coats of the petal;

Three plants had white flowers with purple tongues in the centre of the petal, the colour in the tongue being on the upper surface;

Three plants were pure white.

The sequence of the diverse flowers can be readily explained on the following hypothesis—that we have two pairs of characters at work—

- | | |
|---|--|
| A. Colour. | a. Colour absence. |
| B. Uniform distribution of colour on under surface. | b. Distribution of colour in a pattern on upper surface. |

We then get—

- | | |
|--------------------|------------------------------------|
| 6 : <i>Bb. Aa.</i> | = Parent type. |
| 2 : <i>Bb. AA.</i> | = „ „ with deeper-coloured tongue. |
| 1 : <i>AA. BB.</i> | = „ „ but deeper colour. |
| 3 : <i>A. b.</i> | = White with coloured tongue. |
| 3 : <i>a. B.</i> | = White. |
| 1 : <i>ab.</i> | = White. |

The numbers are too small to lay much stress on an explanation such as the one given, but the phenomena fall readily into line.

Shape of Tuber. The tubers of *etuberosum* are, as already mentioned, "round"—the seedlings comprise both "rounds" and "longs," and amongst the latter are kidneys. The numbers are 18 round, 14 long. It is evident that the "roundness" of *etuberosum* is of a quite different order and with a different hereditary value to that of the domestic varieties, and moreover, it is obvious that the "round" here is dominant to the "long," whereas in the domestic types it was recessive.

The Eyes. The eye of the parent tuber is "shallow" and very insignificant. The seedlings can, as regards the tuber eye, be at once divided into "deep" and "shallow."

These are 26 "shallow" to 8 "deep."

"Shallow" eye is therefore clearly dominant: in the domestic variety it is as clearly recessive.

The Colour of the Tuber. It will be remembered that, although the *etuberosum* tuber is white, yet in 1908 certain tubers were noted to have shown a slight purplish tinge. It is not therefore surprising to find that the seedlings are varied in colour and that the parental white is a dominant.

The colours of the seedling tubers are white and deep purple. The latter are identical in colour to those purple tubers dealt with in the earlier part of this paper.

The numbers of the different colourings are—

White	13	} 25.
White tinged	12	
Deep purple (black)	13.	

The numbers suggest that purple is a recessive character and that white is a simple dominant. In the domestic varieties the reverse is true. No reds were formed.

Crosses with Domestic Varieties. In 1906 I succeeded in effecting a cross with "Queen of the Valley." Three seedlings only grew, and they all died out. Mr Paton^o crossed *etuberosum* by the white kidney "Duchess of Cornwall," and he obtained 13 seedlings, the colour of 12 of which he describes, viz.

9 white, 2 purple, 1 red,

showing the dominance of white. It is of further interest to note that he describes the shape of ten of them. Eight are "round" and two are "long" (kidney and oval), again showing the dominance of the *etuberosum* type of "roundness."

Crosses with S. etuberosum and maglia.

Sol. *etuberosum* × Sol. *maglia* (deep purple)

One seedling white tuber.

Sol. *maglia* × Sol. *etuberosum*.

One seedling white tuber.

Here again the "white" of *etuberosum* is dominant to the purple of the recognized species *maglia*.

The relation of S. etuberosum to other potatoes. Although the name "etuberosum" has been used in this paper, it has been done rather for convenience than with any idea of establishing its identity with the species described by Lindley.

Whether *S. etuberosum* is to be classed with the domestic varieties or as a native species is a question that may have an increasing importance. It has been shown in this paper that in respect to such important characters as shape, eye and colour of tuber it behaves in a diametrically opposite way to the domestic varieties, and it is, therefore, likely that it is distinct from them. On the other hand, its white is dominant to the *maglia* purple, and its own purple is also recessive; so that in respect to this character it certainly more closely resembles *maglia*.

The flower of *etuberosum* is much smaller and more compact than that of the domestic potato, and is much more like the wild *S. etuberosum* and *S. maglia*, and its scheme of colour as described here has no parallel amongst the domestic varieties.

There would seem, therefore, to be no adequate reason at all for classing *S. etuberosum* amongst domestic varieties; on the other hand, it has certain characters akin to those of recognized specific types, such as *S. maglia*.

It has been suggested that the diversity of the *S. etuberosum* seedlings shows it clearly to be a hybrid. That may be, but we can feel at least equally sure that its parents are not domestic varieties.

CONCLUSIONS.

Very briefly the following conclusions have been reached in this paper.

Domestic Varieties.

1. The twist of leaf, as seen in "Red Fir Apple," is a recessive character.

2. Length of tuber is dominant to "roundness."
3. Depth of "eye" is dominant to "shallowness."
4. Purple is dominant to red in the tubers.
5. Red is dominant to white, but is dependent on the presence of two factors in addition to a chromogen.
6. *S. etuberosum* is not subject to the same laws of dominance as the domestic varieties of potatoes.
7. That amongst the seedlings of *S. etuberosum* occur some which are at present immune to the attacks of *Phytophthora infestans*.
8. That immunity to the attacks of *Phytophthora infestans* is in *S. etuberosum* a recessive character.
9. *S. etuberosum* may be a hybrid and, if so, its parents are possibly native species.

I take this opportunity of tendering my thanks to my head gardener, Mr E. Jones, for the assistance he has rendered, and the great care he has shown in the raising of the seedlings.

DESCRIPTION OF PLATES.

PLATE I.

Tubers of seedlings of Sutton's "Flourball" selfed. "Rounds" are—Nos. 40, 89, 92, 118, 132, 138, 155, 156, 162, 165.

PLATE II.

Family of seedlings of parent *A* selfed. The majority of the tubers are normal "rounds"; the least typical "round" has been chosen to represent each individual root. On Plates IV. and V. can be seen the sister tubers of the more abnormally shaped "round" tubers.

PLATE III.

A family continued.

PLATE IV.

All the available tubers of each root crop are shown of those individuals who vary from the typical "round." In all cases one or more typical "rounds" occur in each root crop.

PLATE V.

Same as Plate IV. No. 100 is probably a stray plant and not a member of this family.

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PLATE VI.

The *G* family, consisting of six individuals with their root crops are shown. G^1 , G^5 and G^6 are more or less typically "round."

PLATE VII.

The *D* family—Top row—Three tubers of parent plant. D^1 and D^2 , 1908, are the seedlings raised in 1908 from *D* (1907) selfed. D^1 and D^3 , 1909, are seedlings raised in 1909 from *D* (1907) selfed.

PLATE VIII.

Seedlings of the family raised from cross *D* × *A*. The family consists of half "rounds" and half "non-rounds." The "rounds" are Nos. 3, 4, 5, 8, 13, 14, 15, 16, 18, 19, and 3, 6, 7, 10, 12, 14, 18, 19, 20, 21, 22, 28.

PLATE IX.

Seedlings of the family raised from the cross "Record" × "Flourball." "Record" is a kidney, "Flourball" a pebble-shaped potato (neither parents shown). One quarter of the seedlings are "rounds," viz., Nos. 12, 13, 18, 21, 24, 25, 26, 30.

PLATE X.

Seedlings of the family raised from the cross H^1 (F^1 of family *H*, Plate IX) × *A*. Half the seedlings are "round," viz.: Nos. 4, 6, 7, 16, 17, 19, 22, 25, 26, 27, 29, 30, 34, 35, 36, 38, 39, 40, 42, 45, 49.

PLATE XI.

Seedlings of the family raised from the cross H^{10} (F^1 of family *H*, Plate IX) × *A*. Half the family are "rounds," viz.: Nos. 1, 2, 3, 4, 10, 11, 13, 13A, 15, 17, 18, 19, 26A, 29, 31, 32, 33, 34, 40, 46, 48, 49.

PLATE XII.

Family *J* raised from the cross "Congo" × "Reading Russet." The fifth seedling, a long white-tubered one, died out and is not shown here.

PLATES XIII—XVIII.

The family raised from the individual K^6 (F^1 of "Congo" × "Flourball" seedling, see Plate XXIX). This family for convenience has been divided into sub-families K^6 , K^6 , etc., according to the particular seedball from which the seedlings were grown. "Rounds" are to "longs" as 1 : 3 in this series, and the eyes are all deep with the exceptions noted in the text.

PLATES XIX, XX.

The family raised from selfing K^9 (F^1 of "Congo" × "Flourball" seedling, see Plate XXIX) the "rounds" are rather deficient, viz.: 13 to 60; the eyes are deep to shallow, 3 : 1.

PLATE XXI.

The family *L*, raised from the cross of "Red Fir Apple" × "Reading Russet." In the *F*¹, No. *L*⁷, a kidney has been omitted.

PLATES XXII, XXIII.

*F*², family raised from *L*¹, selfed. The rounds are 1 in 4, viz.: Nos. 1, 2, 22, 35, 37, 46, 47, 49, 61, 63, 64 (Plate XXII). Five long- and three round-tubered individuals have been omitted. In Plate XXIII the "rounds" are Nos. 6, 10, 17, 19, 22, 24, 29, 30, 33, 40, 47, 52, 54, 61.

PLATE XXIV.

The family raised by crossing *M*² (*F*¹ of "Queen of the Valley" × "Flourball" seedling) × "Bohemian Pearl" long-tubered seedling. Nos. 2 and 20 which in the plate look "round" are in reality much flattened and are clearly not rounds. Two other typical long members of this family have been omitted.

PLATE XXV.

Examples of tubers, not from individual roots, of *B*.

"Bohemian Pearl" seedlings long and oval.

"Congo." The long tubers are much more common than the stunted.

"Red Fir Apple." The tubers in 1909 were all more or less stunted as shown in the Plate.

PLATE XXVI.

C, 1907, one of the seedlings of "Sole's Kidney."

C, 1909, representatives of 4 seedlings of *C*, 1907.

PLATE XXVII.

Family raised from selfing Lindsay's *etuberosum*. The long-tubered seedlings are here in the minority. The ravages of the disease are clearly seen.

PLATE XXVIII.

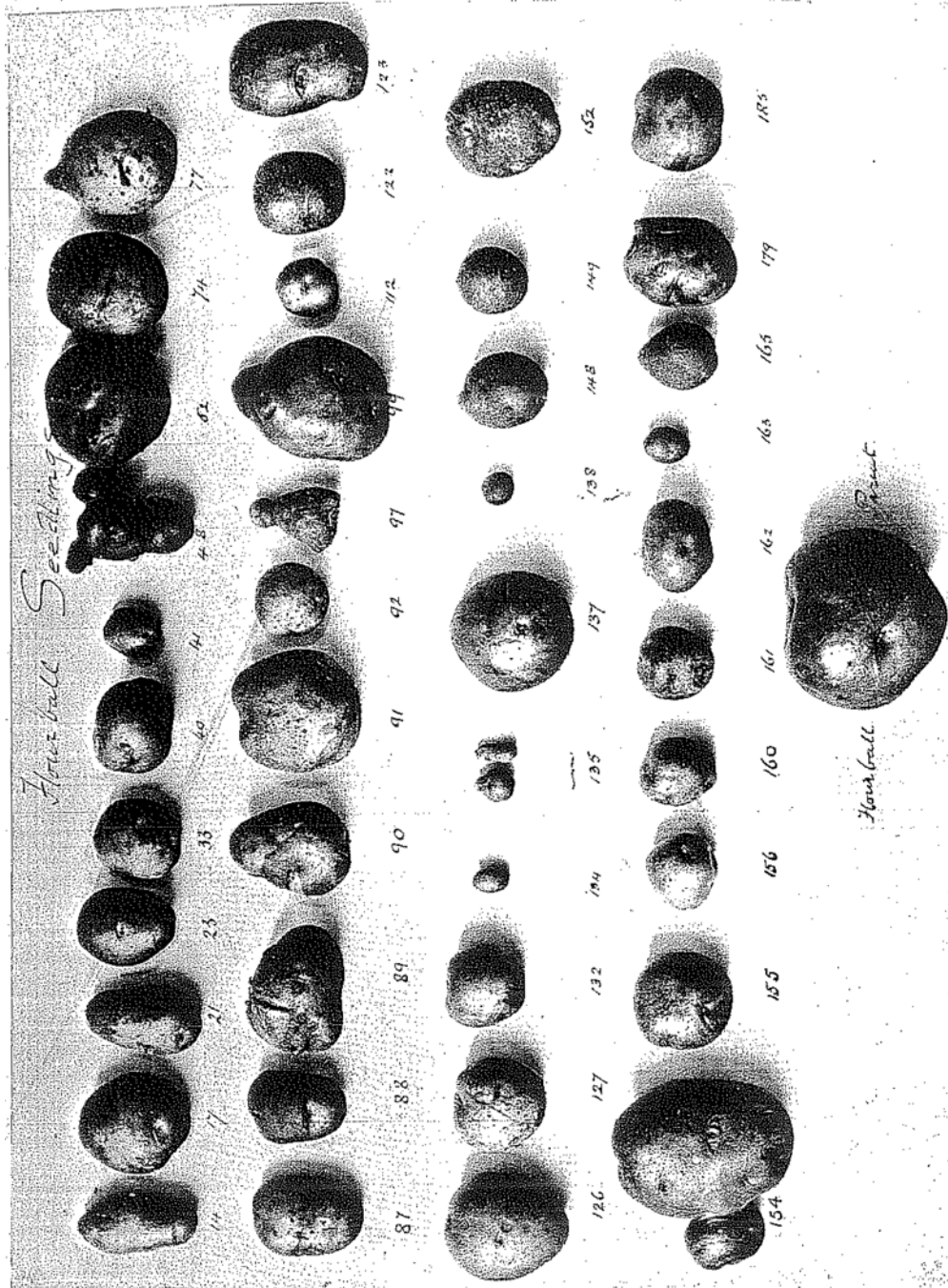
(Reproduced by kind permission of Messrs Sutton of Reading.) The kidney potato "Superlative" in clump. The variability of shape amongst the kidney and pebble-shaped tubers is very marked.

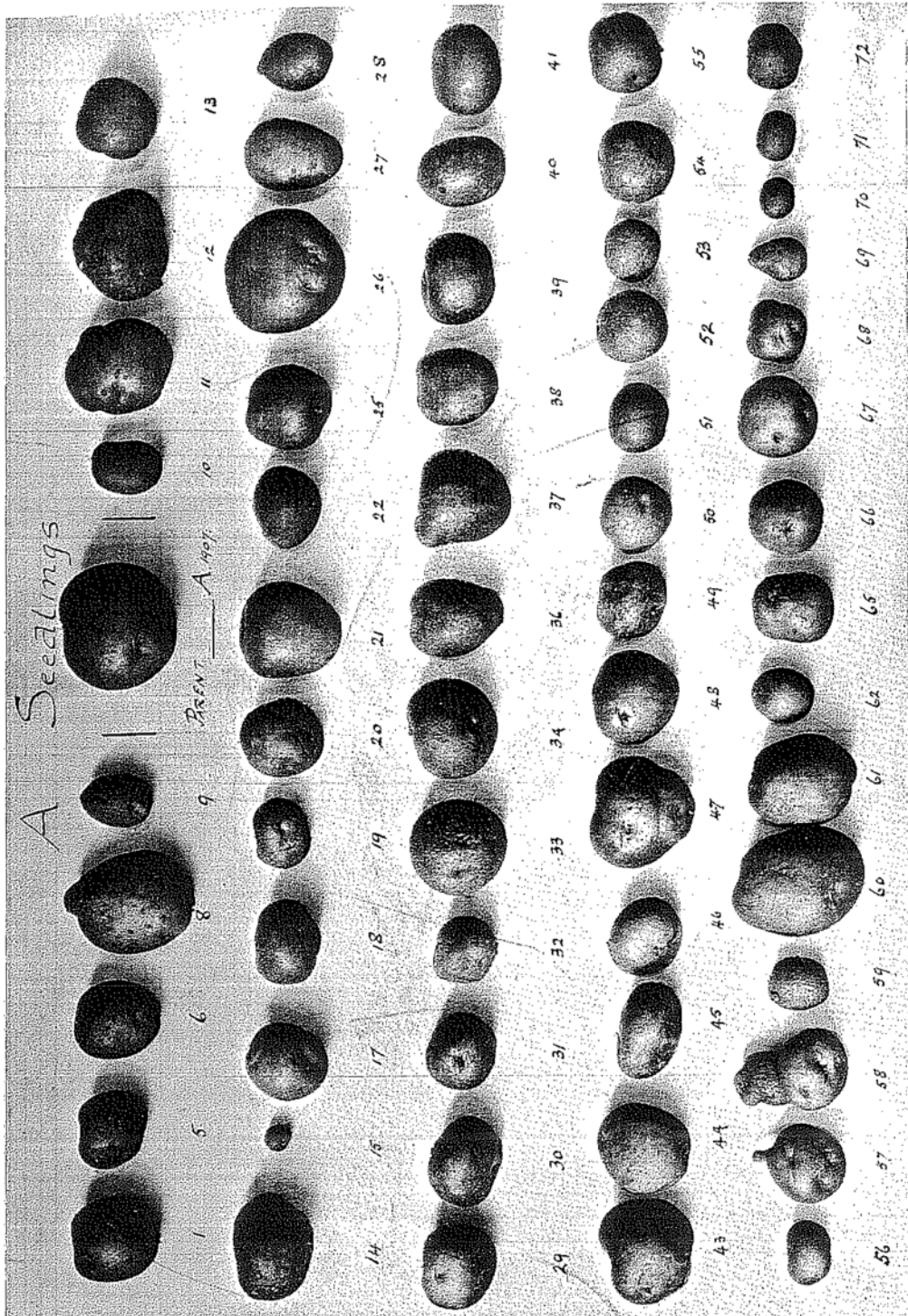
PLATE XXIX.

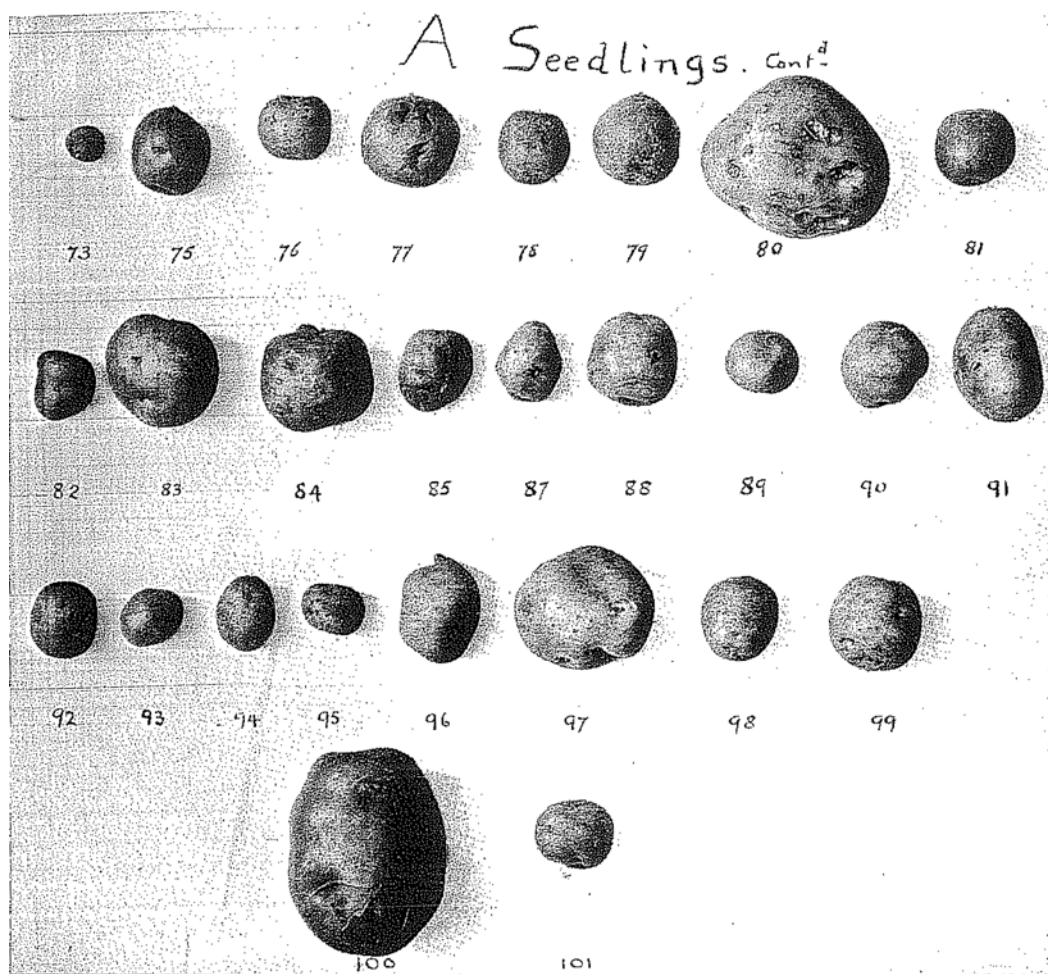
The *F*¹ family raised by crossing "Congo" × "Flourball." The segregation of the colours Purple, Red and White are well-shown. The shapes are all "long" and the eyes all "deep," demonstrating the dominance of these characters.

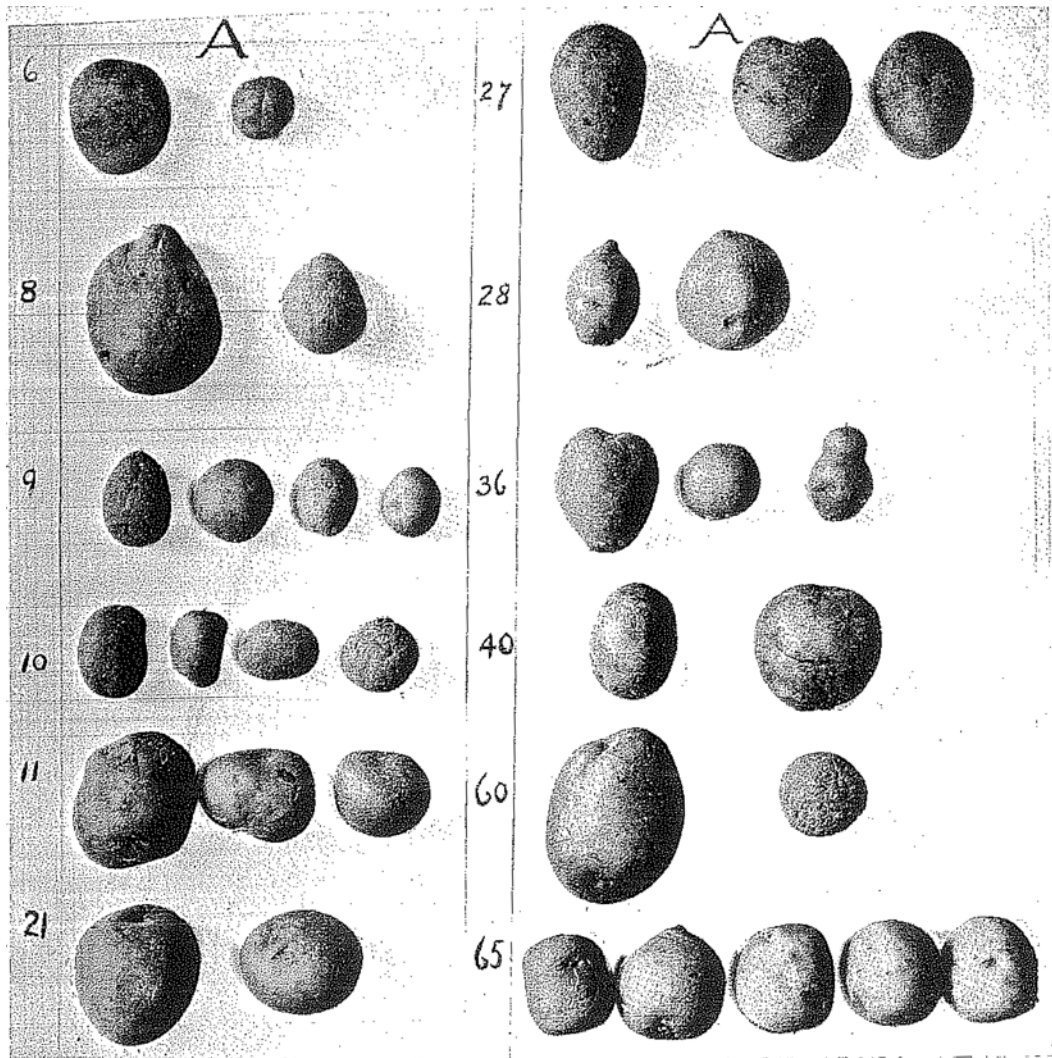
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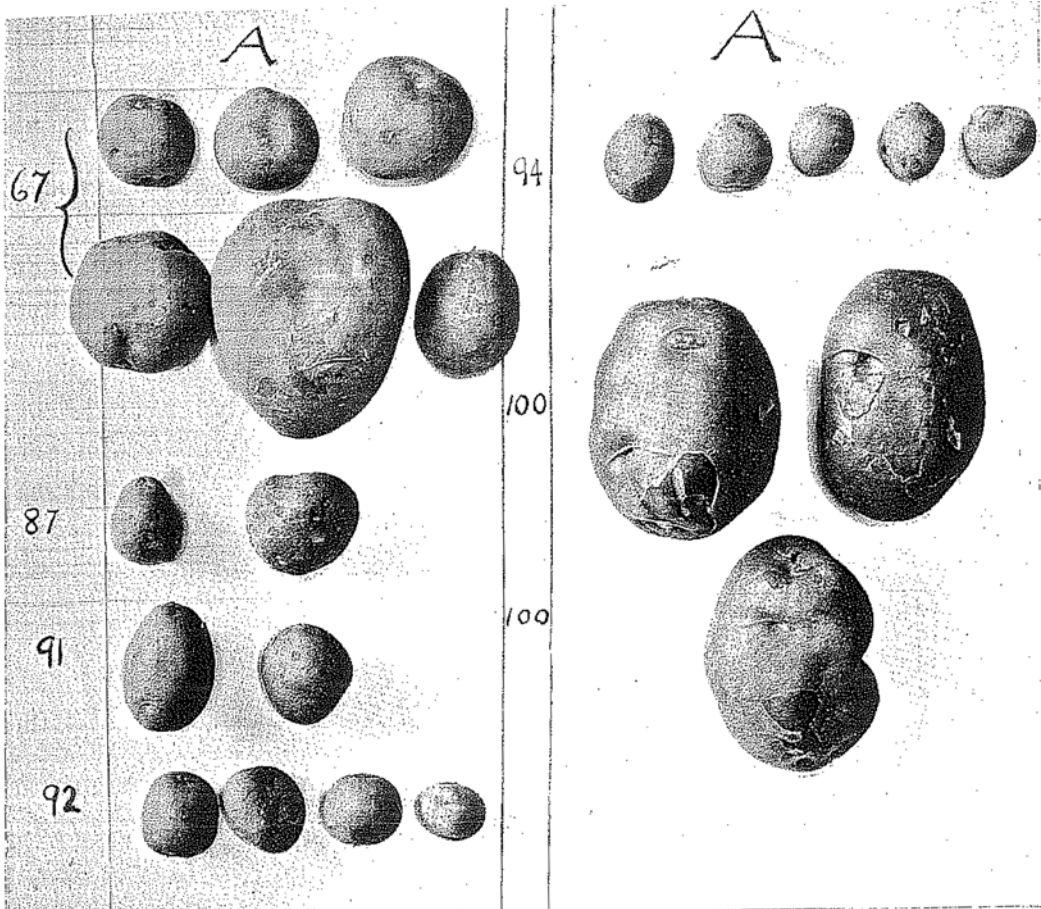
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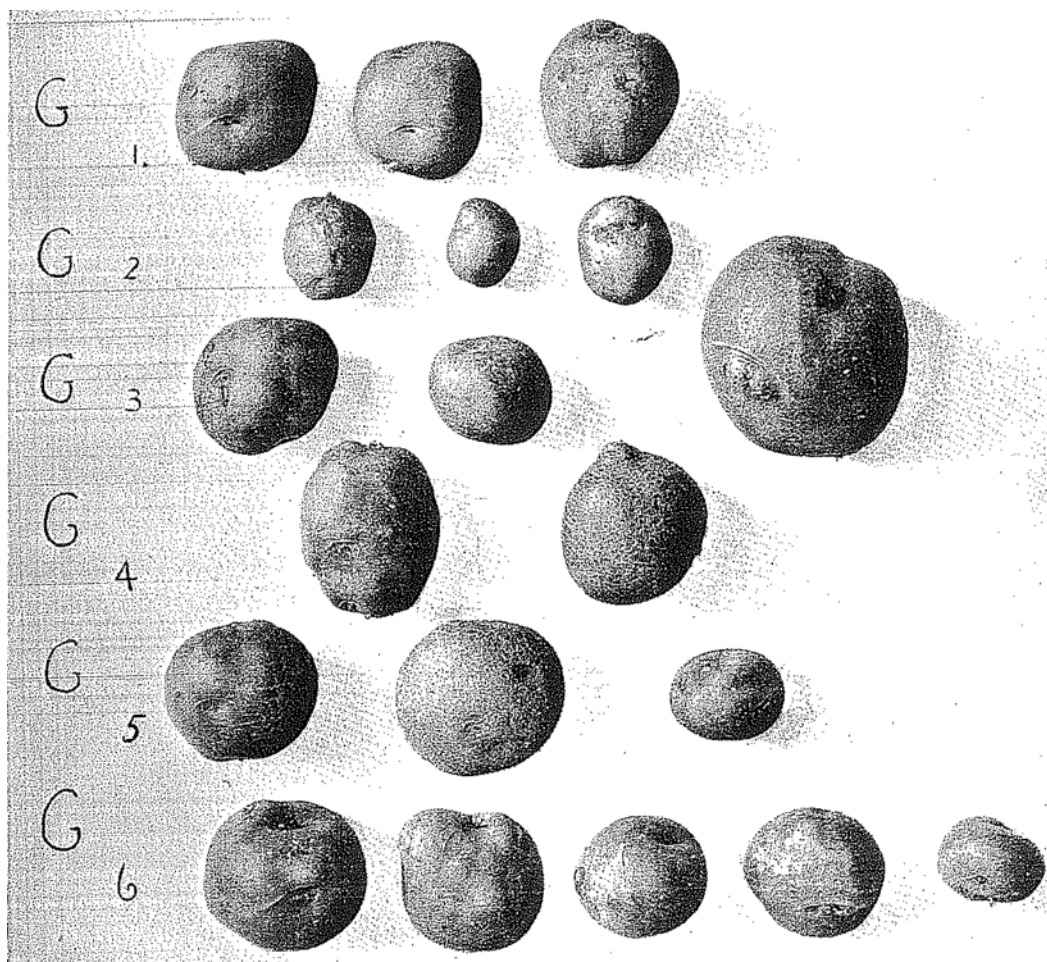


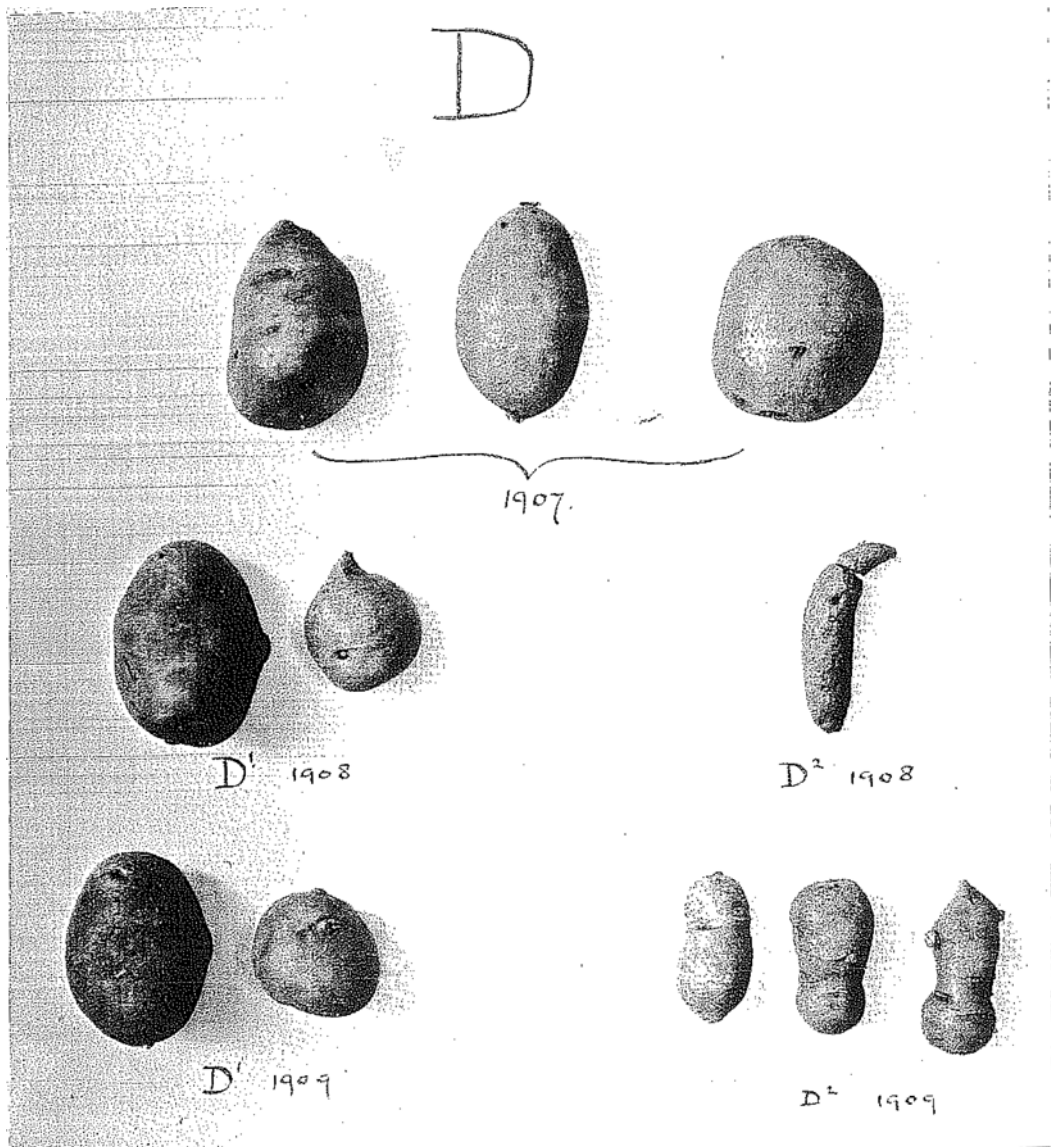


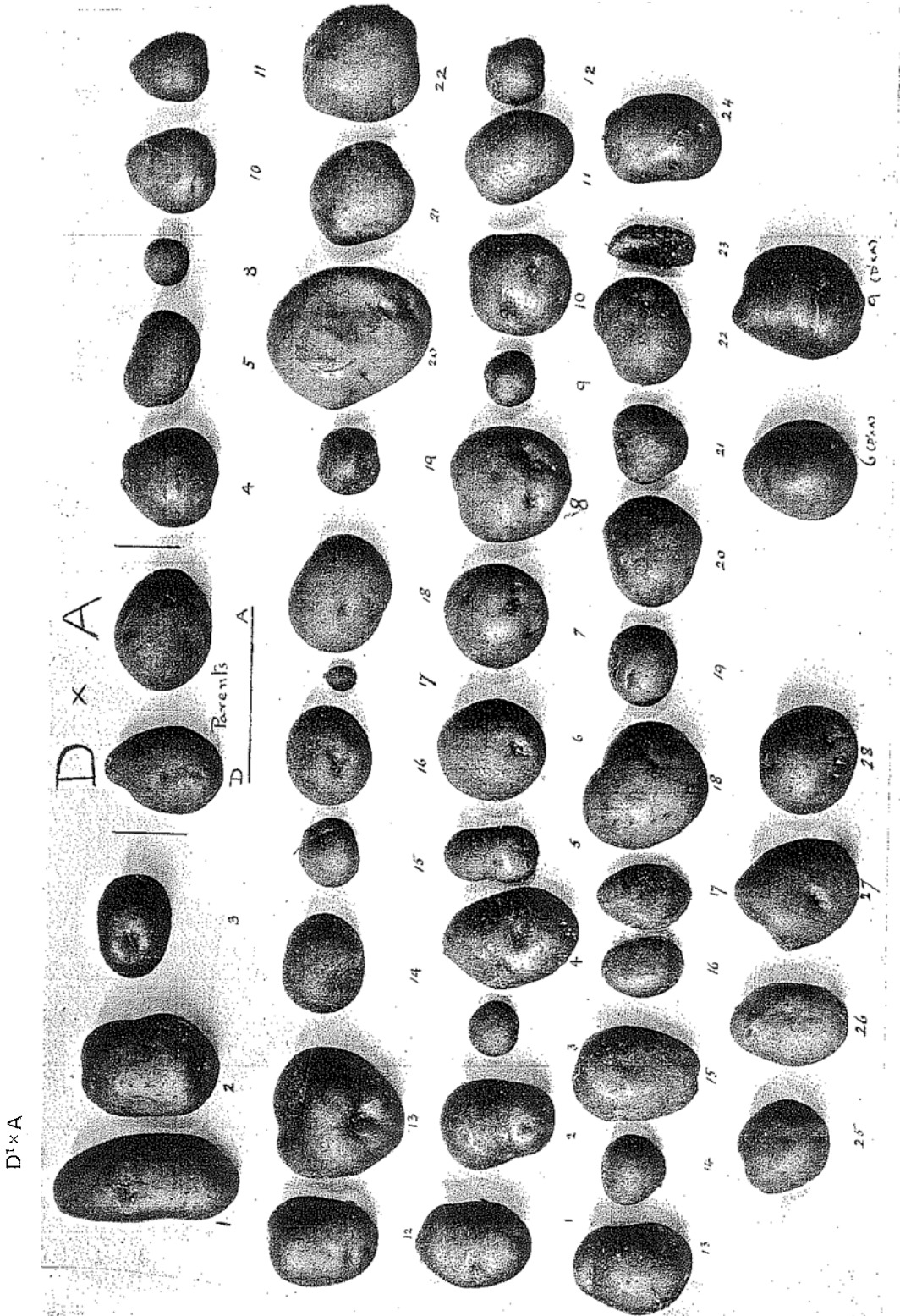


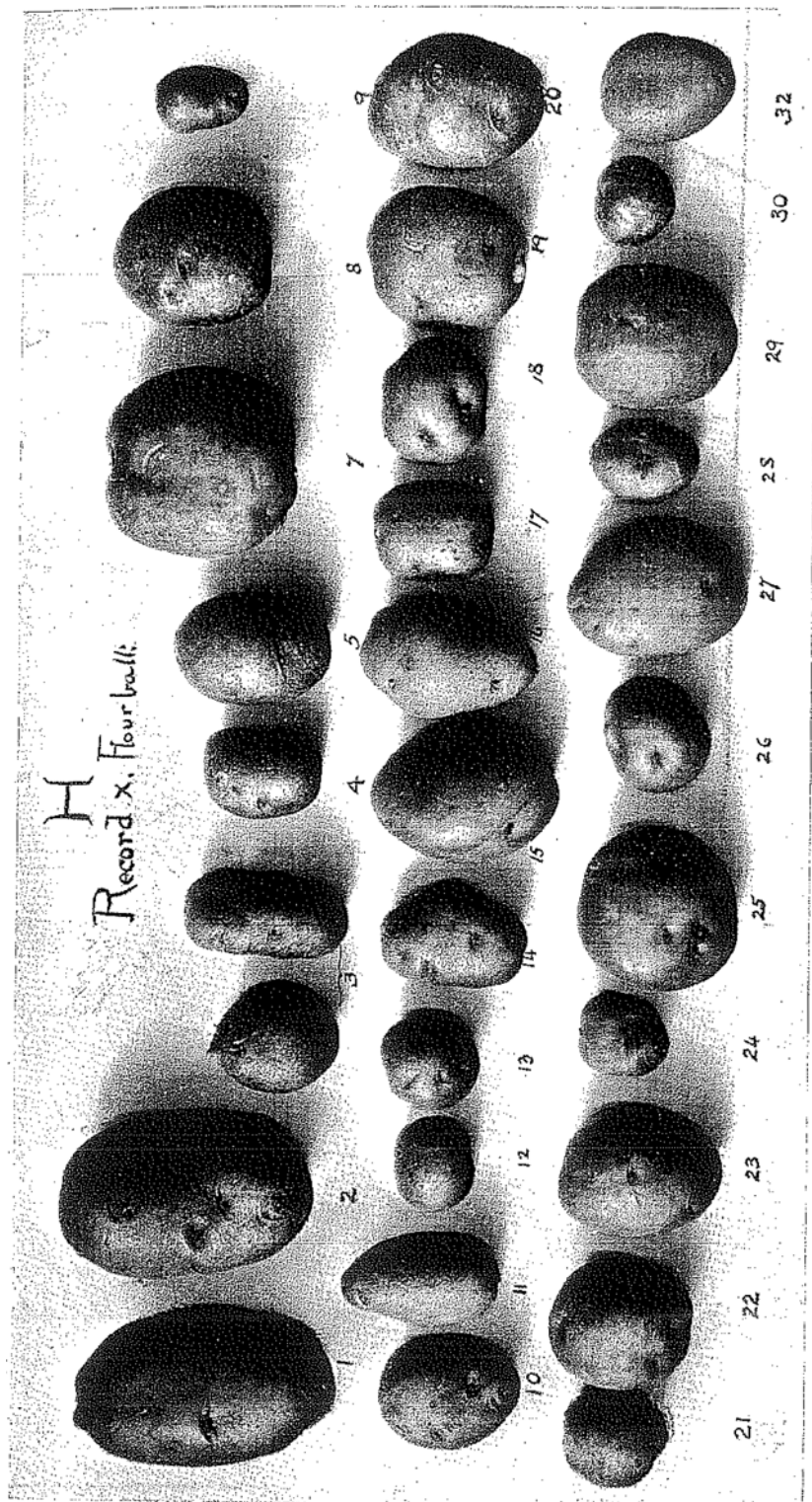


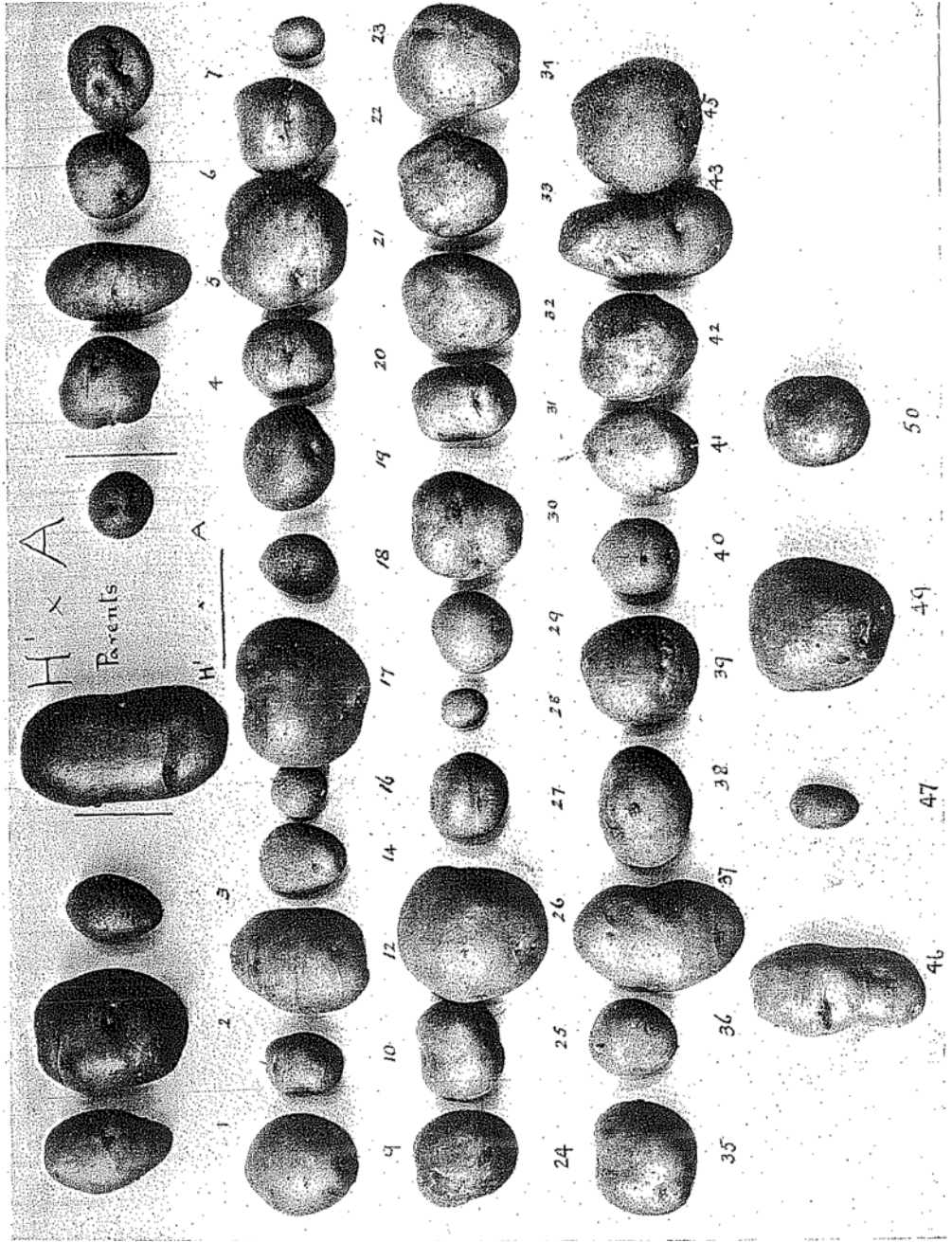


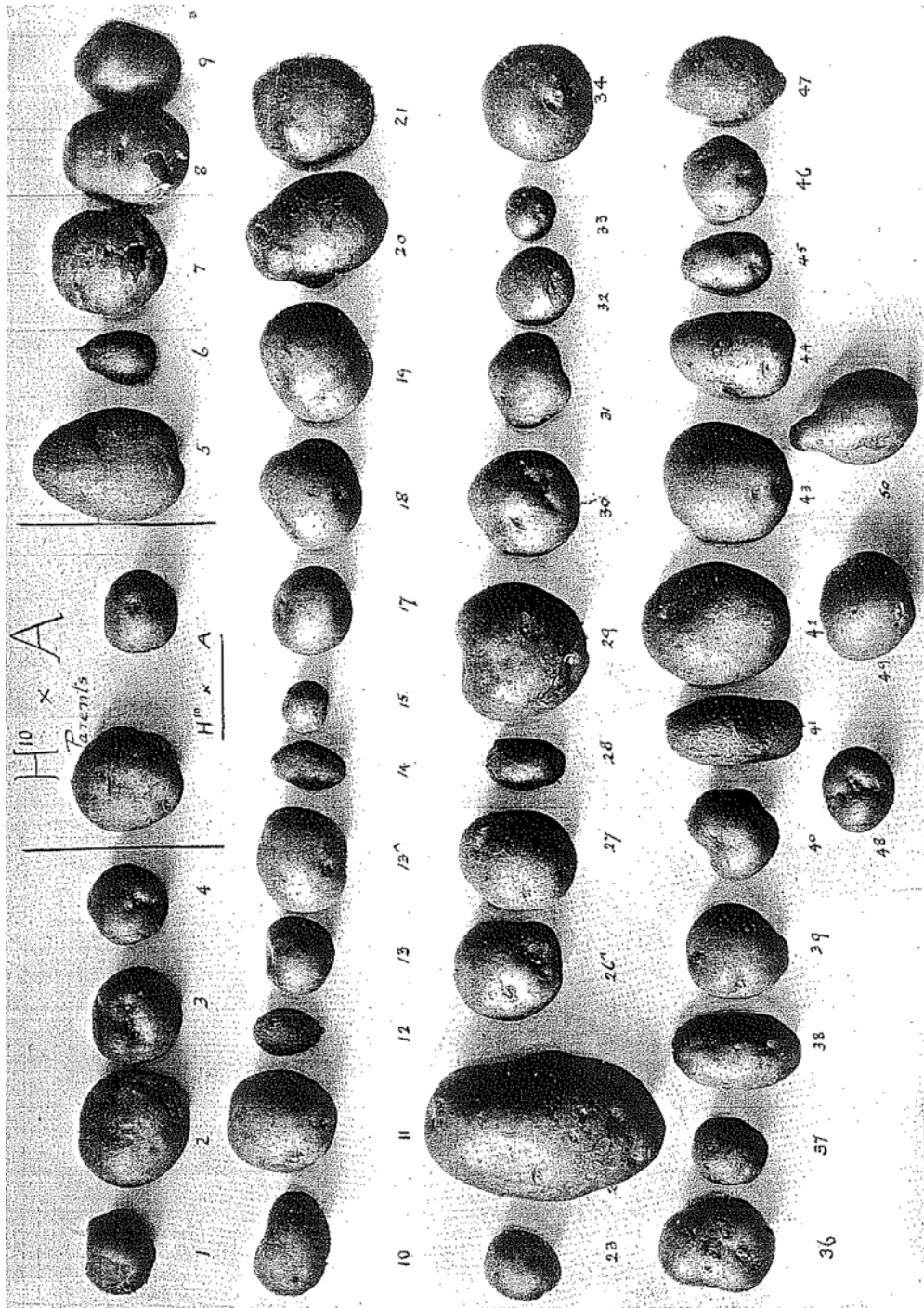


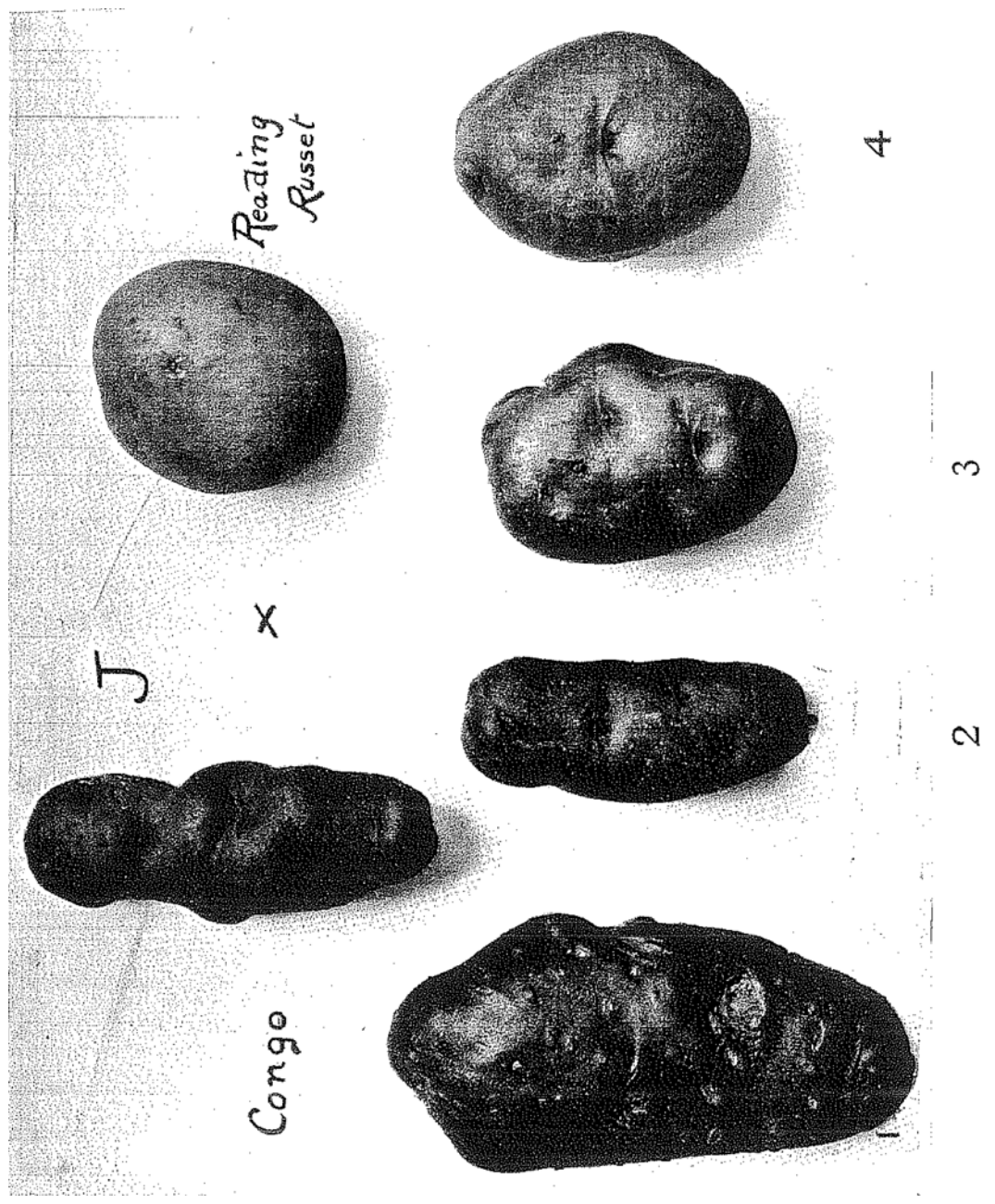


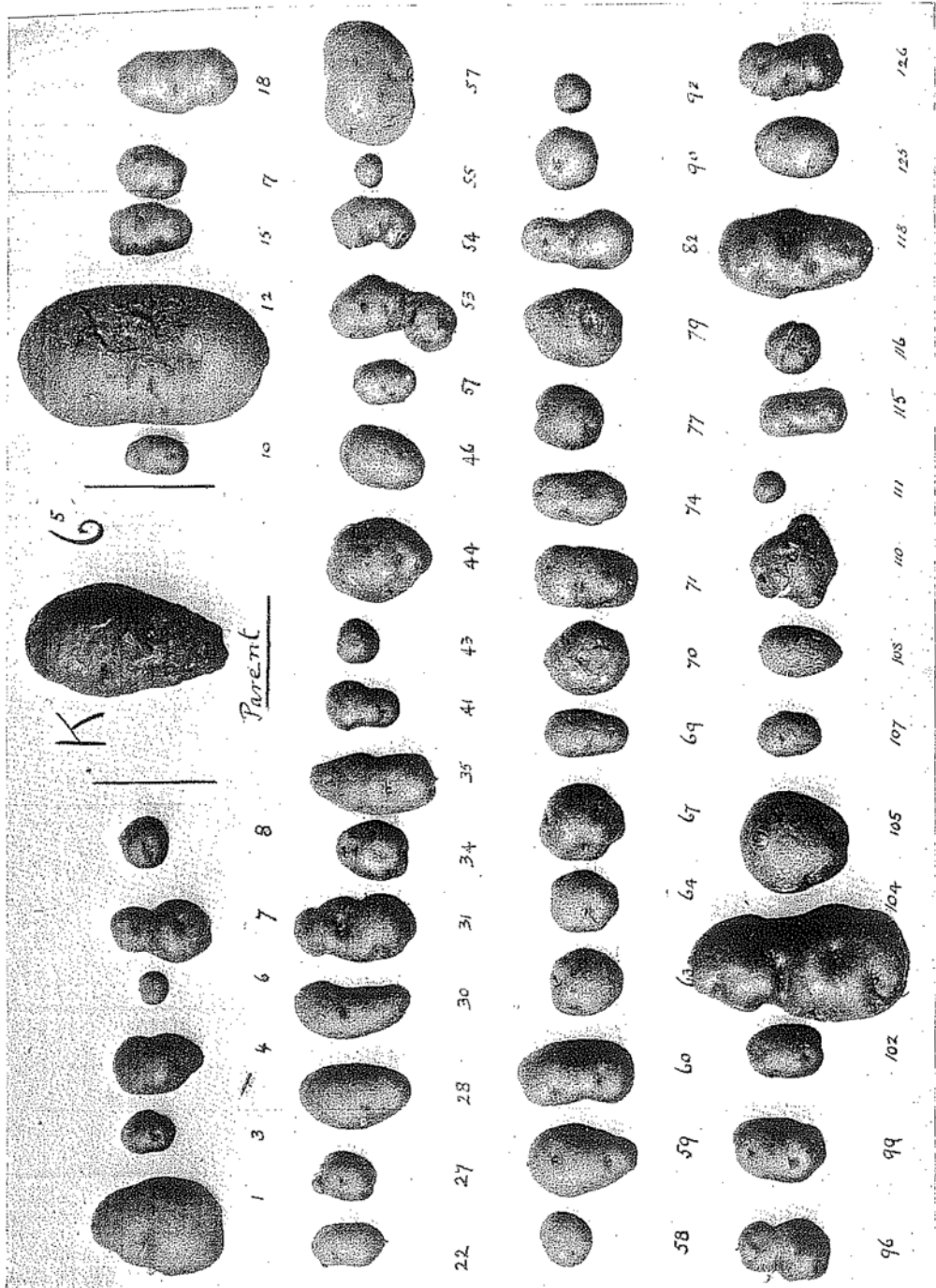


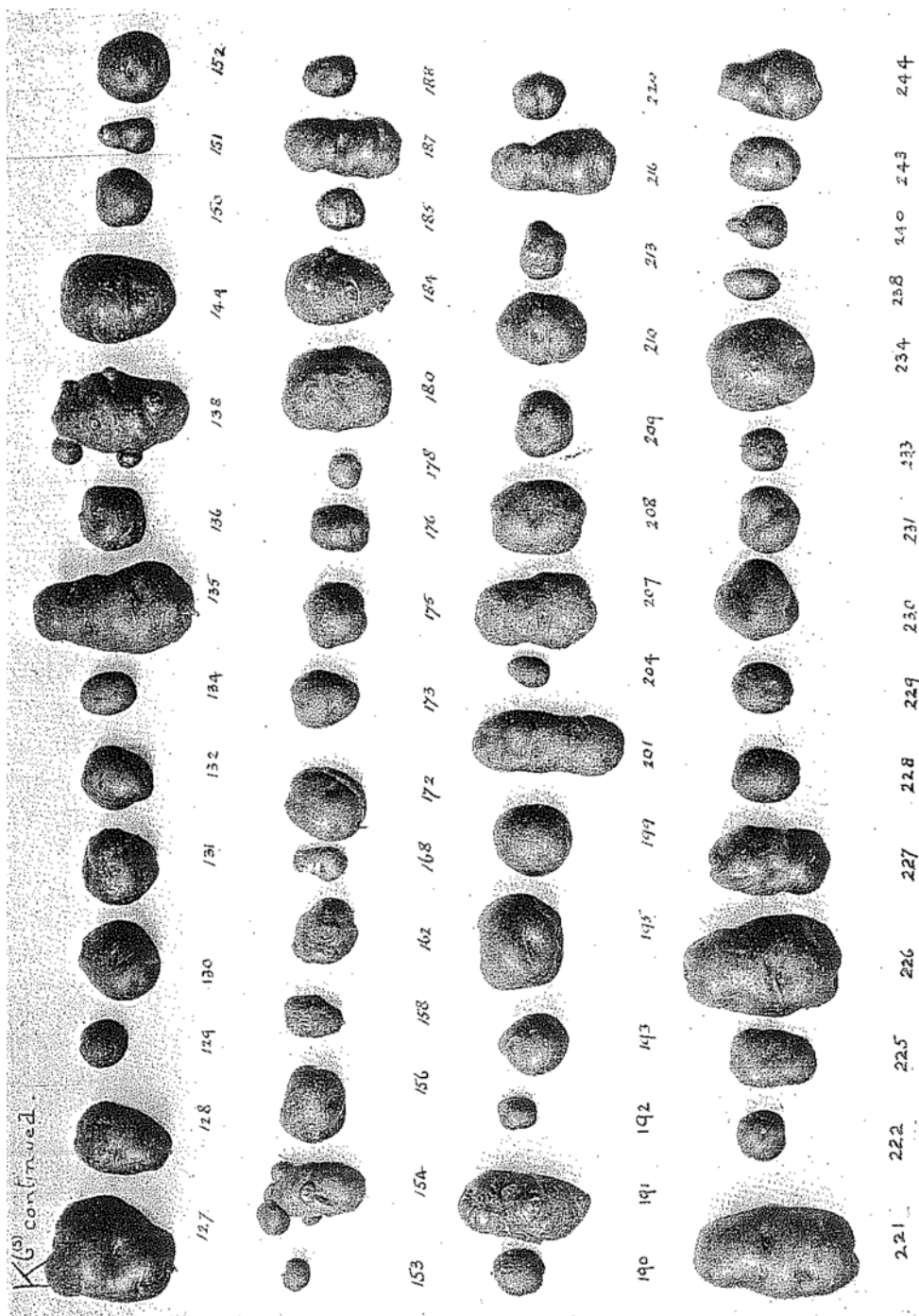


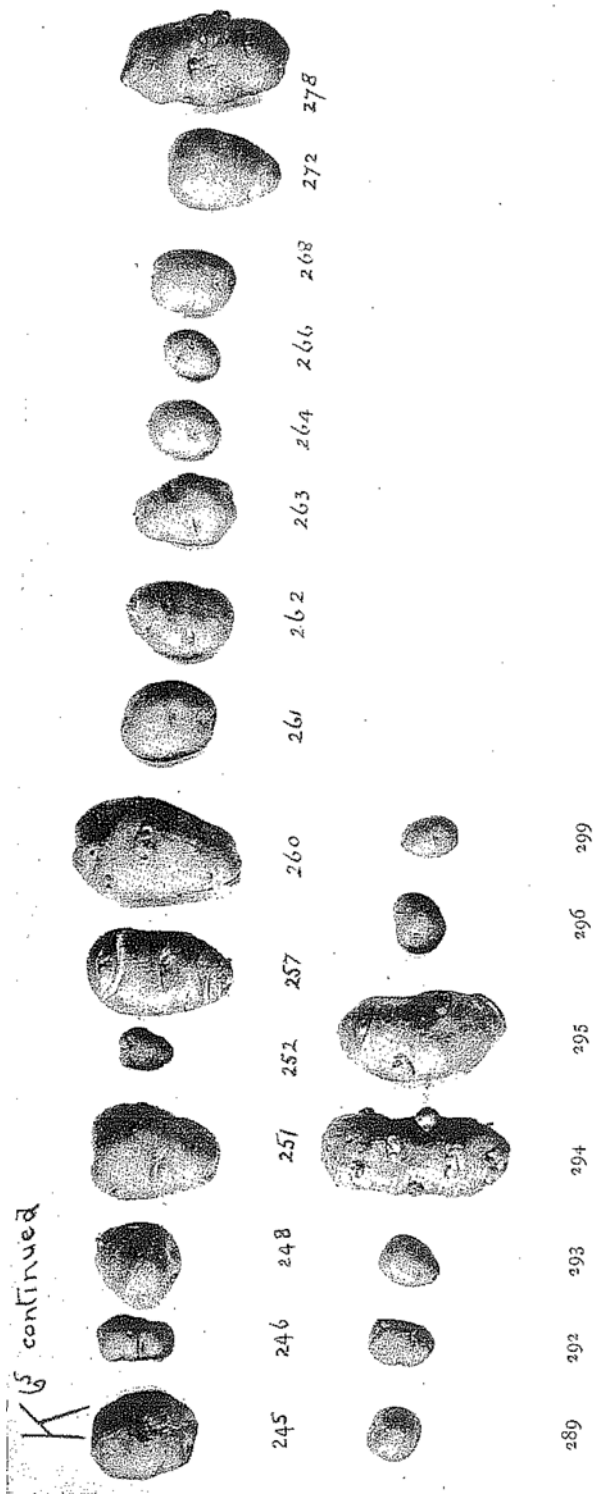


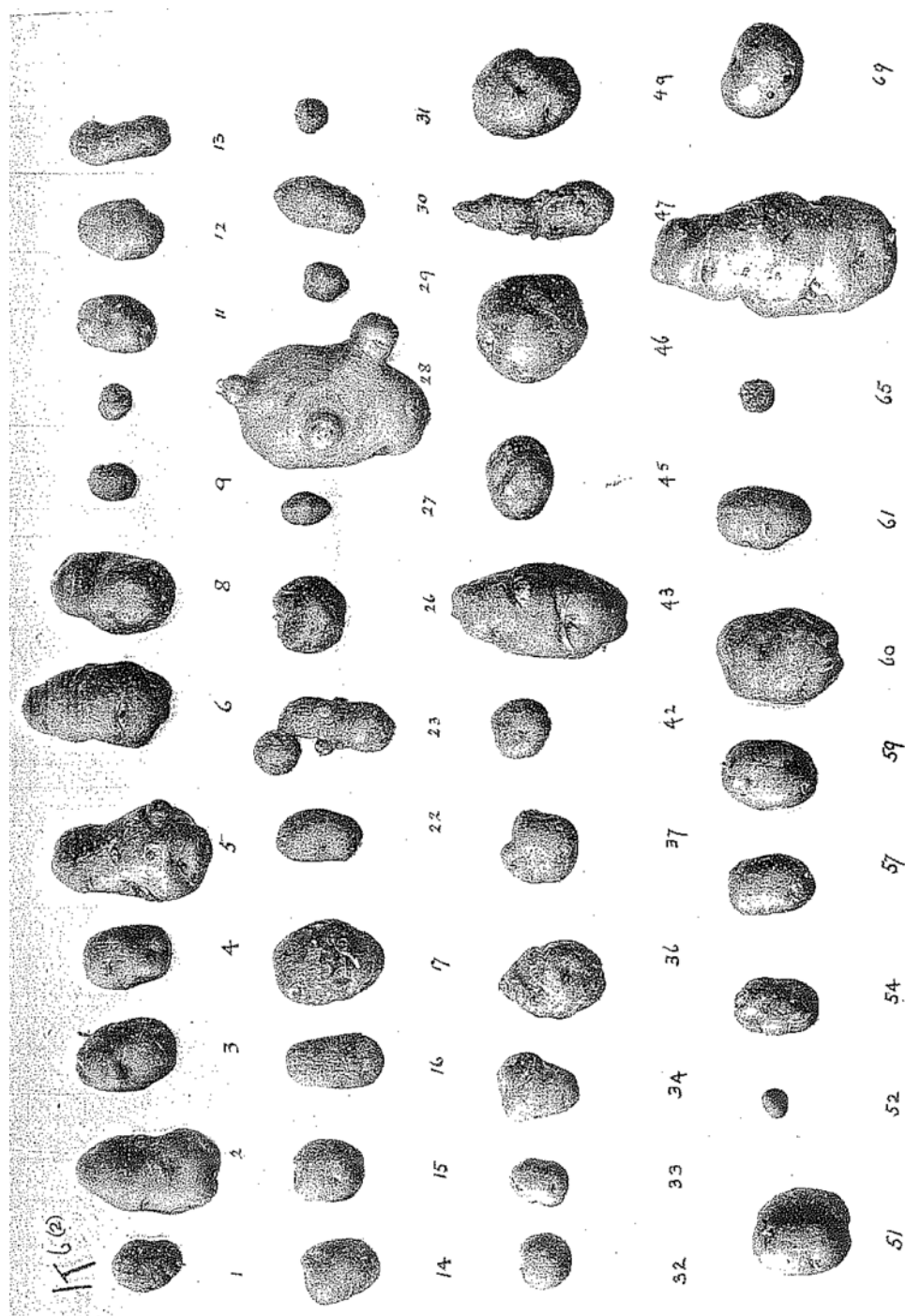


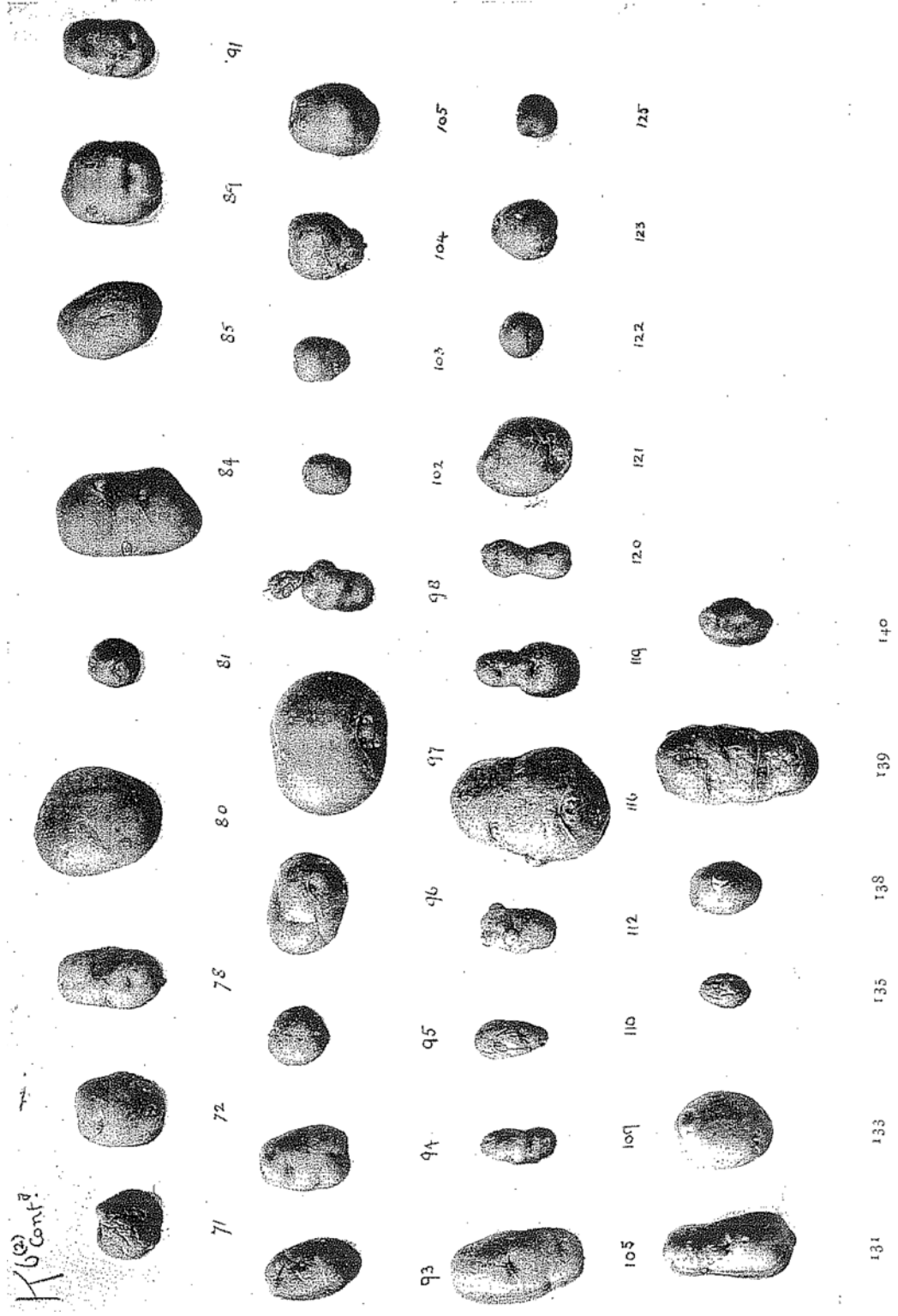




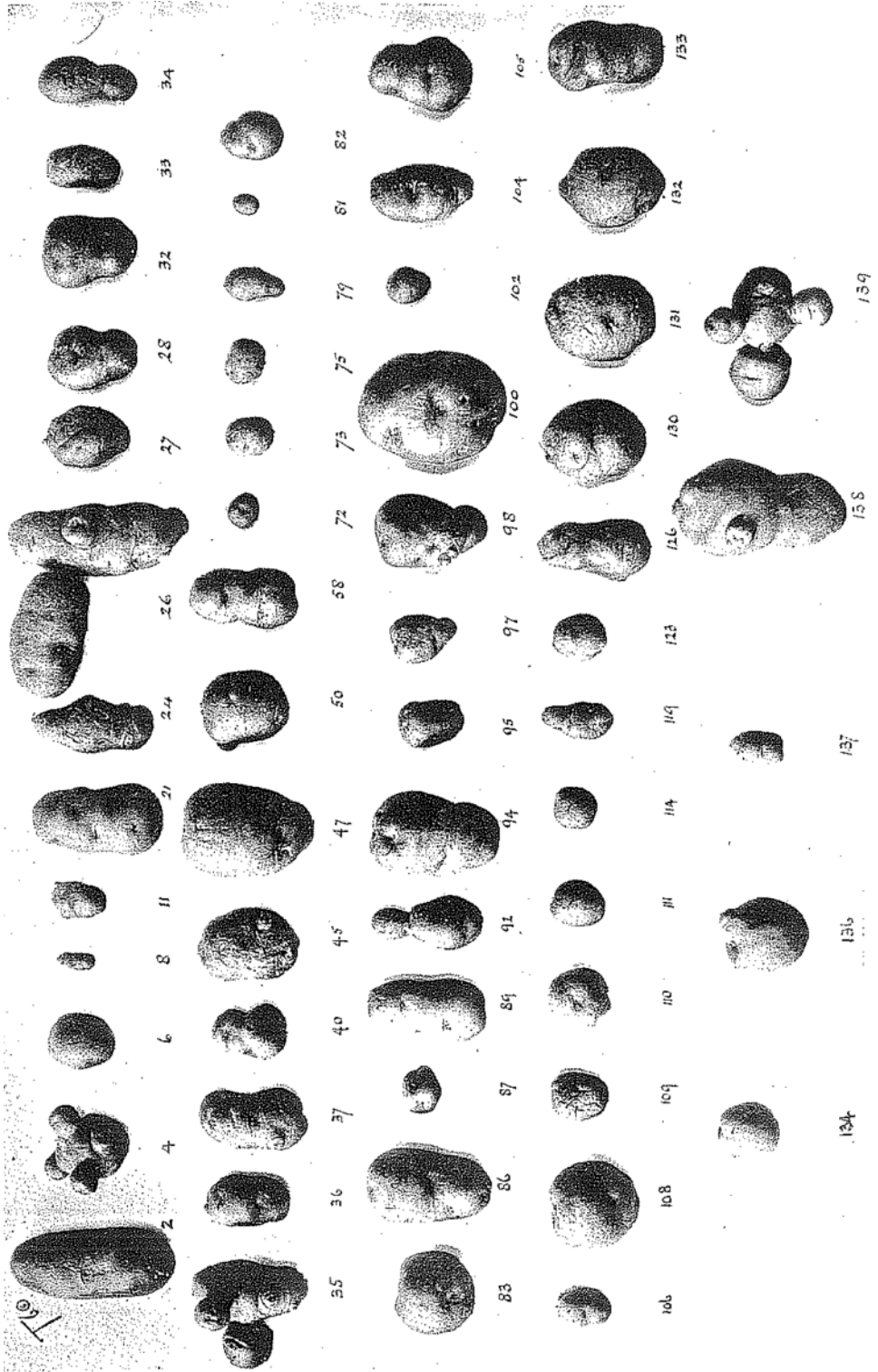


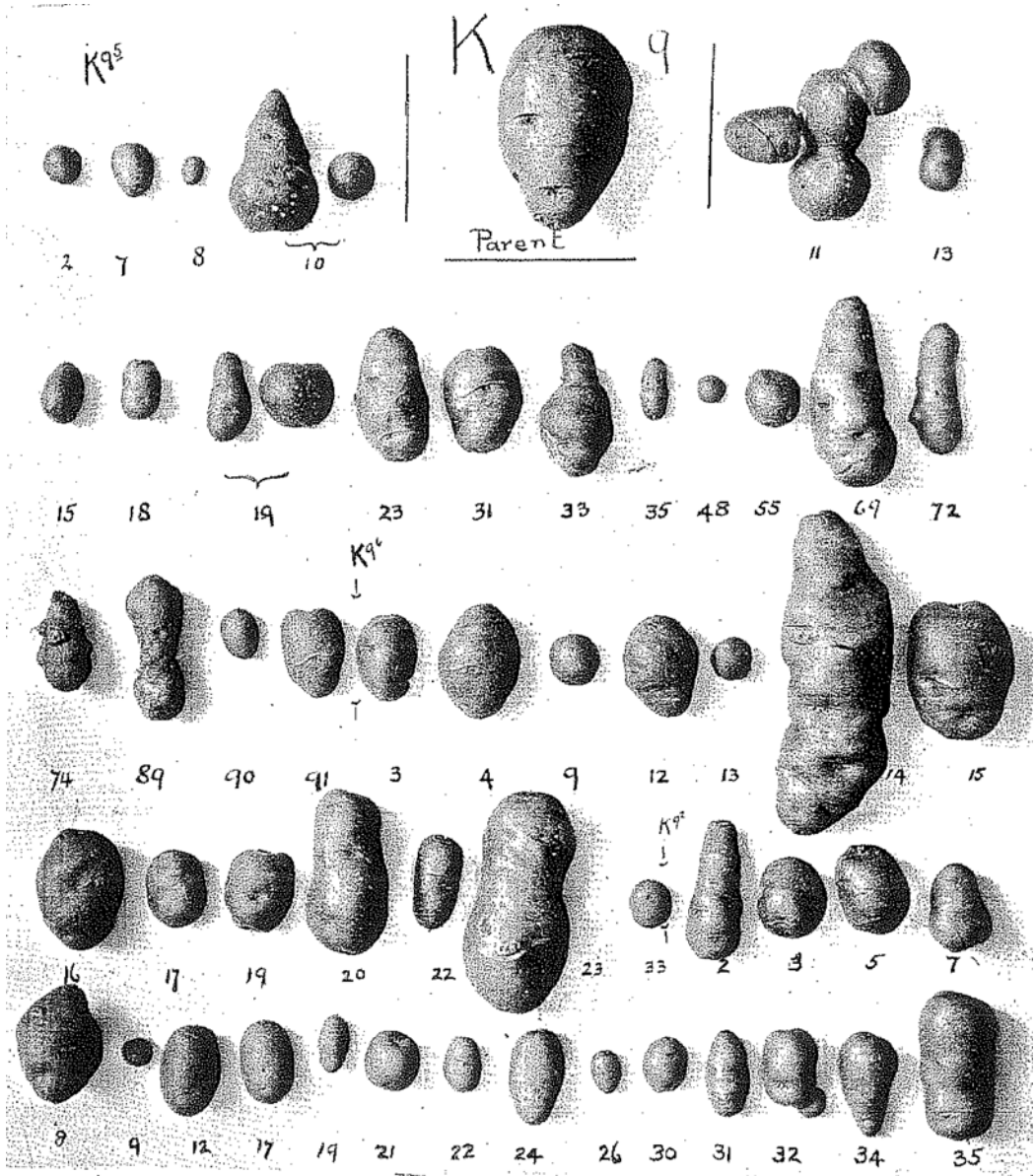






X6⁽⁹⁾







Line L

Firapple.

Reading Russet

Parents.



F₁.

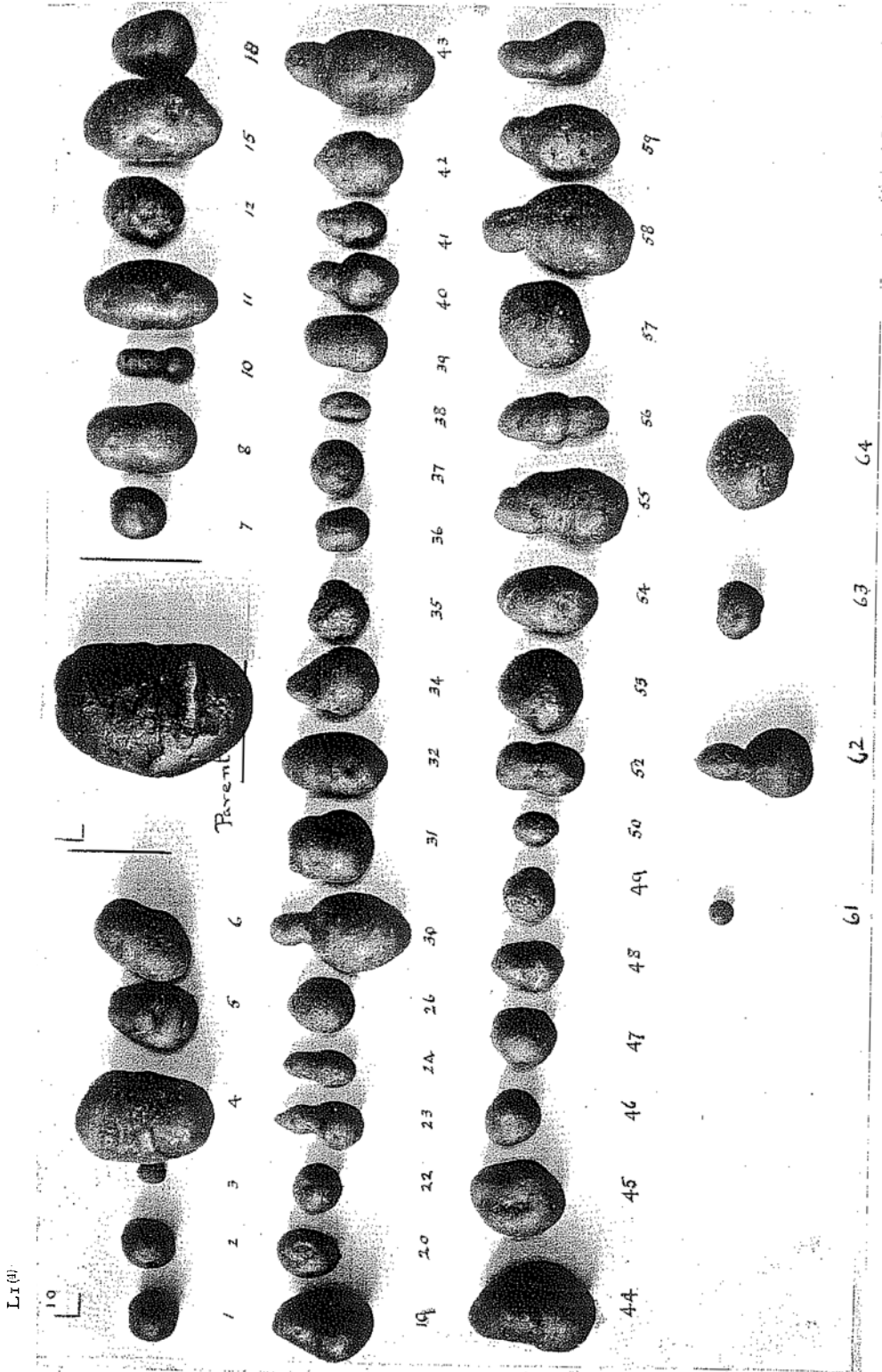


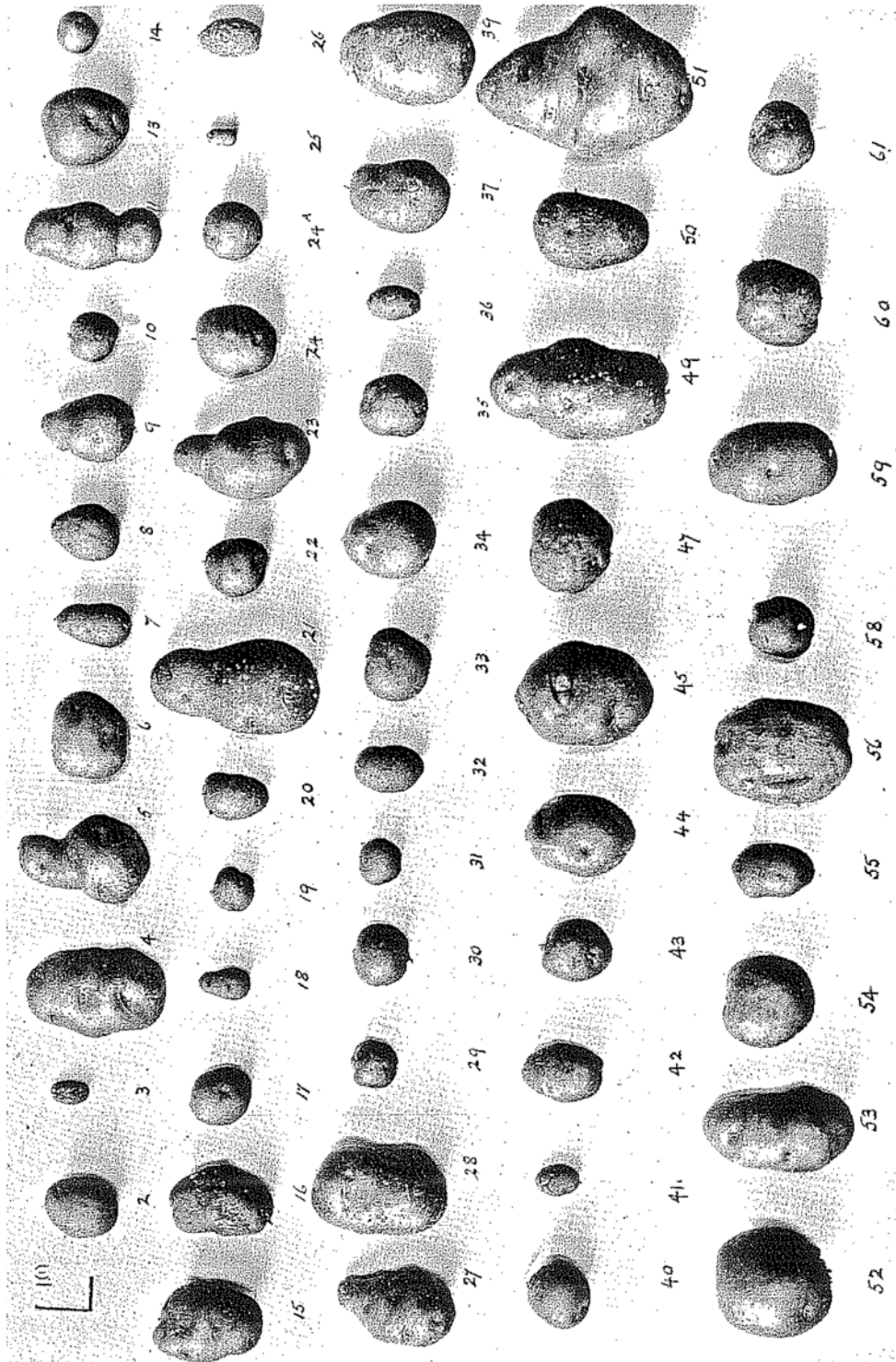
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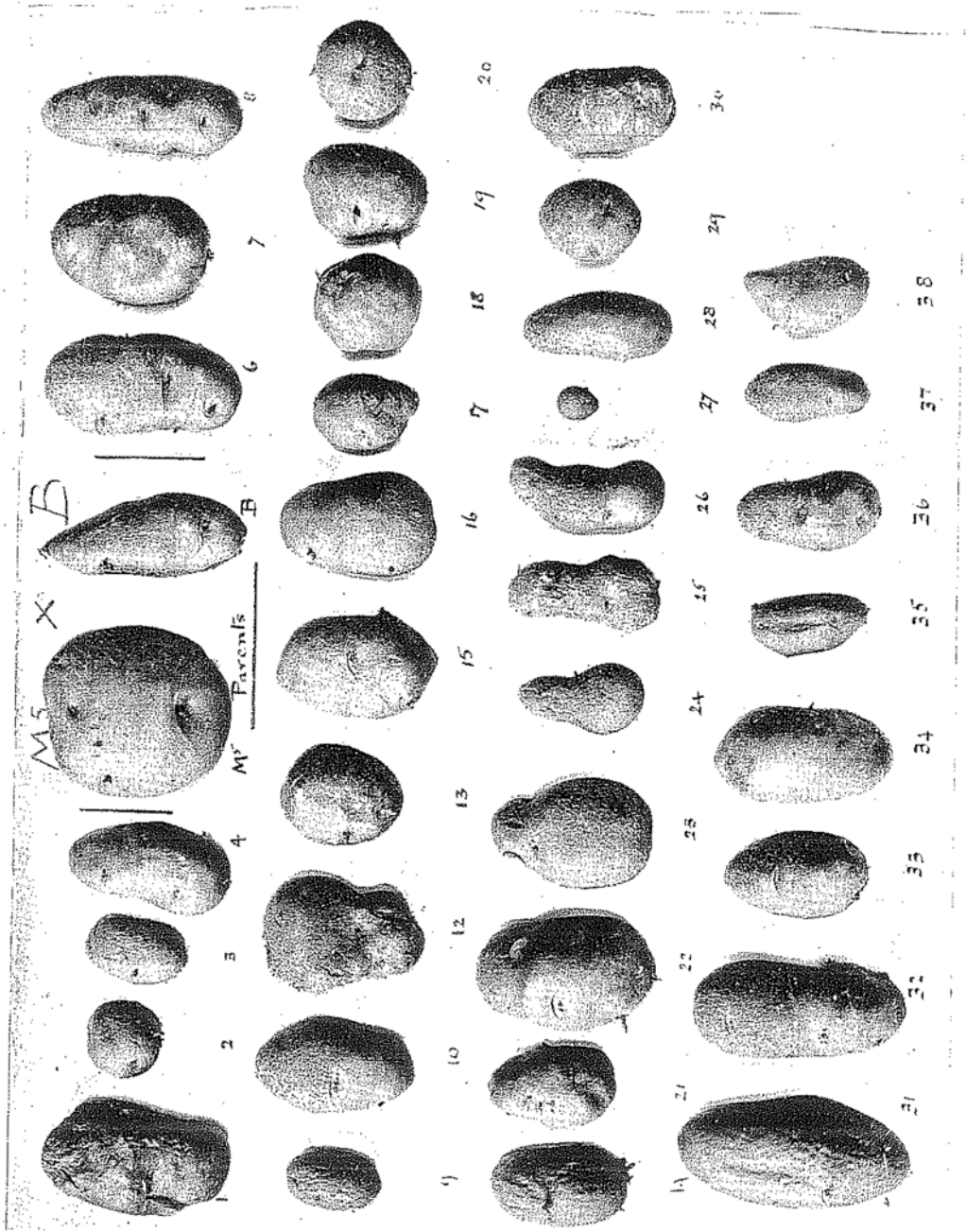
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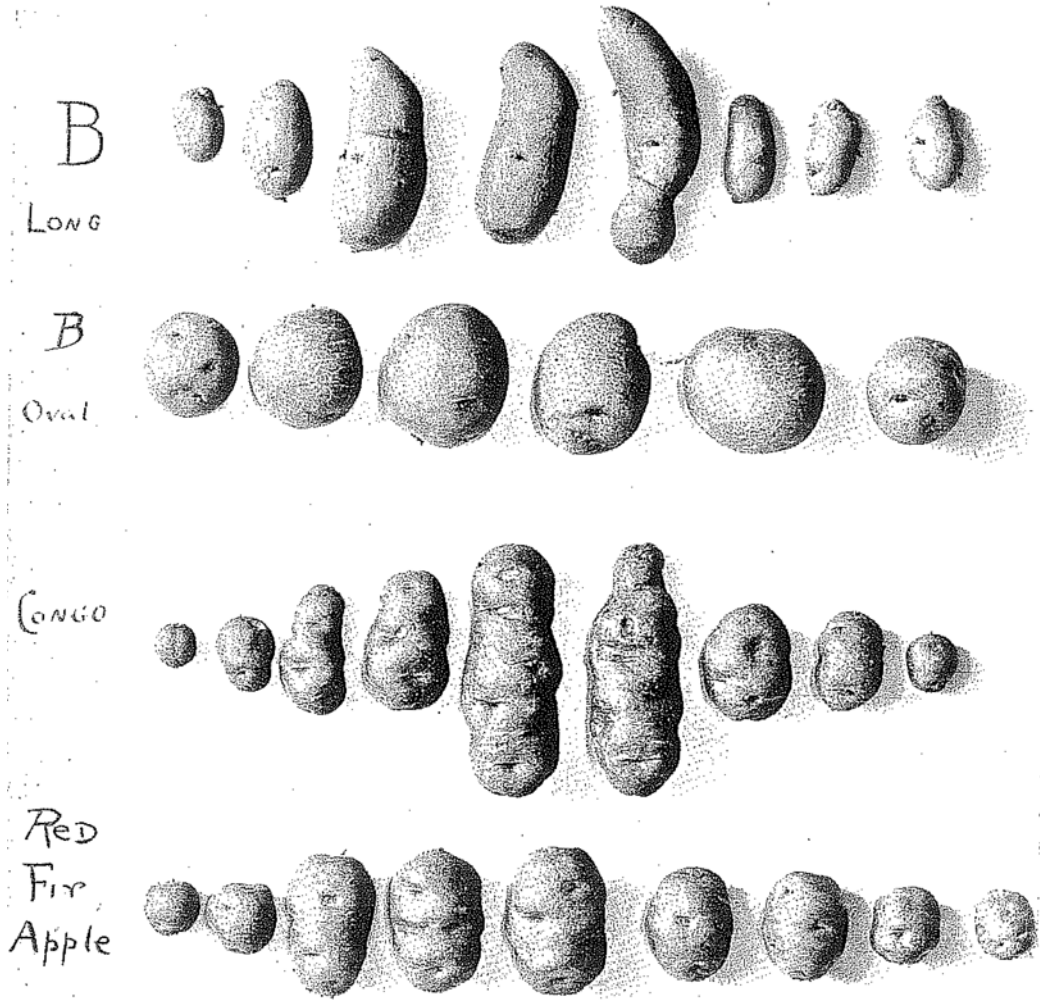
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6.









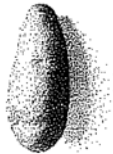
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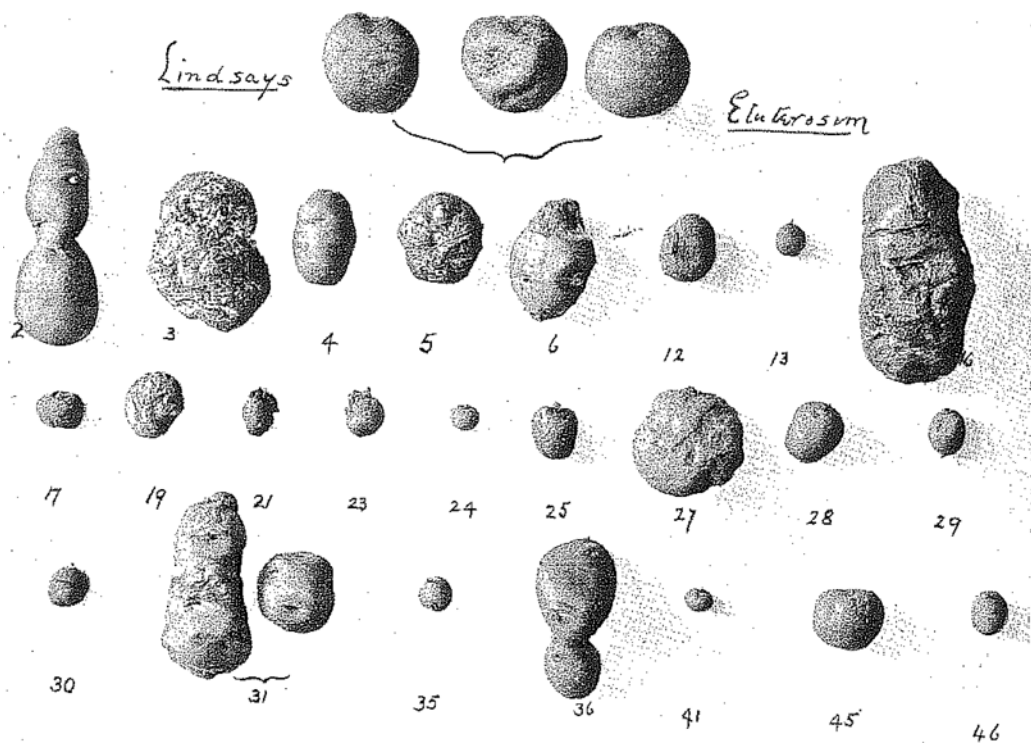
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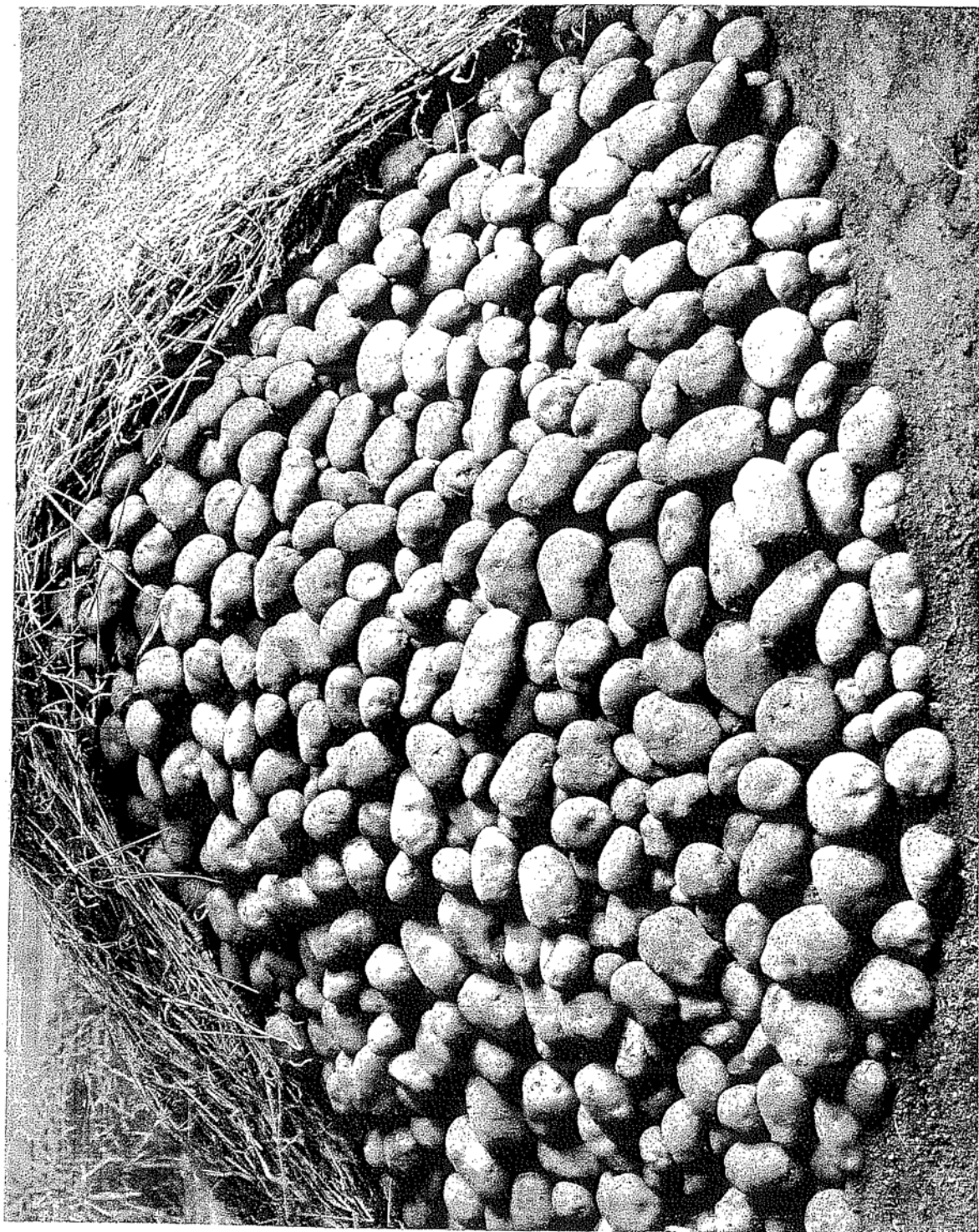


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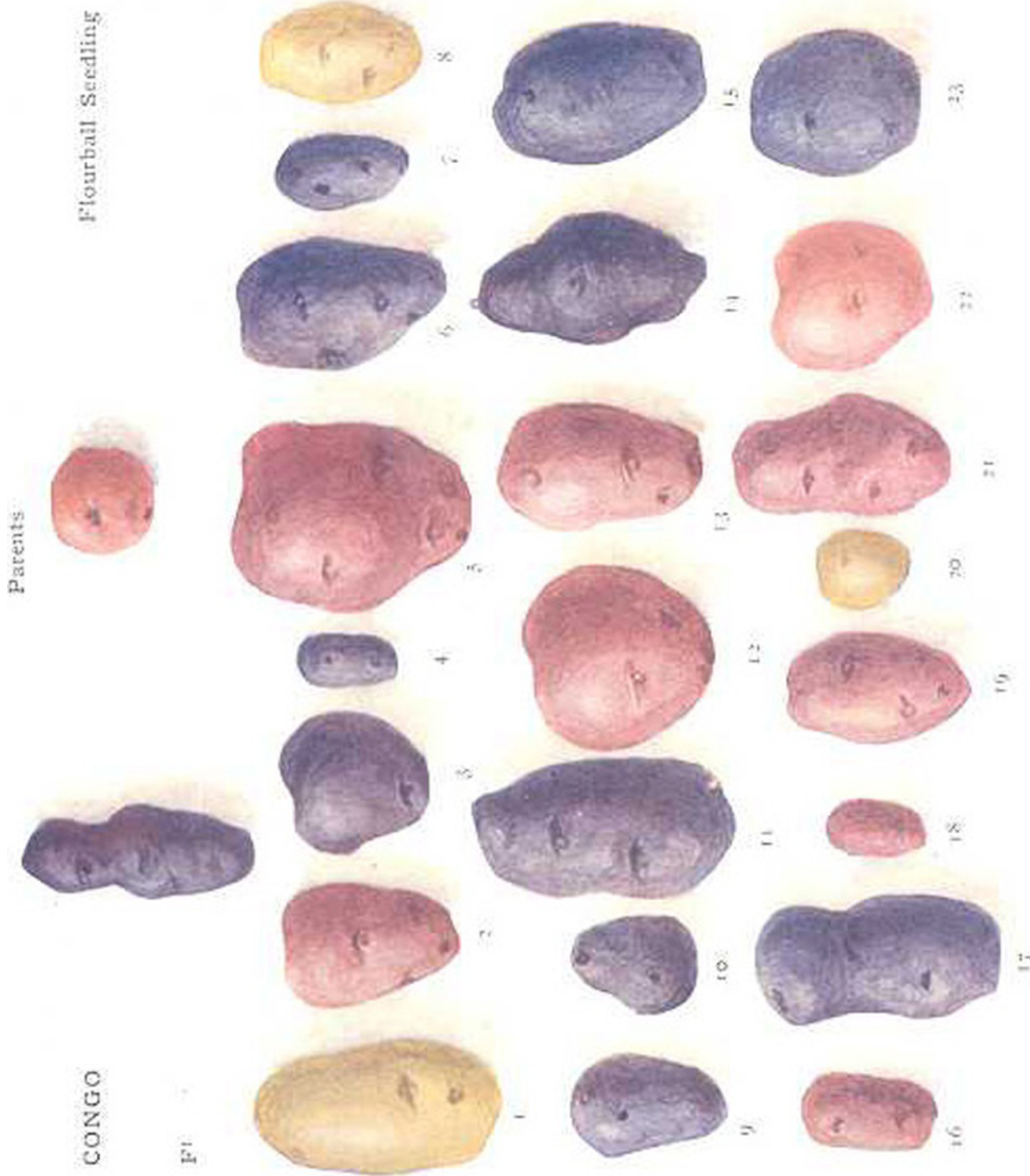
seedlings 1909







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CONGO

Flourball Seedling

Parents

Pt