

THE GENETIC SYSTEM OF CULTIVATED DIPLOID POTATOES

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Cultivated diploid potatoes ($2n = 24$) are indigenous to the Andes of South America, where they are grown at altitudes between about 6,500 and 14,000 ft. They occur from Venezuela in the north to northern Argentina in the south.¹

The first study of a collection of cultivated diploids was made by Juzepczuk and Bukasov (1929), who recognized seven species. Hawkes (1944) discarded one of these species but added four more when classifying the material of the Commonwealth Potato Collection. Recently he has revised this classification and reduced the total number of species from ten to a possible four, stating that "hybridization experiments between species or putative species taken in most cases to the F_2 generation, have given results agreeing on the whole with the concept of larger specific units in *Solanum*" (Hawkes, 1956). The present position is summarized at the foot of the page.

In the main, we shall use the Latin epithets of the earlier classification (Hawkes, 1944) to refer to our material, because these are the names that prevail in the

literature. They are printed in Roman letters and without initial capitals to signify that they are used informally; where necessary, they are abbreviated to the following three-letter combinations: ajh, asc, crd, chu, gon, kes, phu, ryb, stn, and yab to denote ajanhuiri, ascasabii, cardenasii, churuspi, goniocalyx, kesselbrenneri, phureja, rybinii, stenotomum, and yabari, respectively. The cytogenetical data on which Hawkes's (1956) revised classification was based have not been published. We propose to show in this paper that the variability of the cultivated diploids is continuous and that the genetic system of the group does not justify the recognition of "species."

We have had three lots of cultivated diploid potatoes to work with: (1) the Commonwealth Potato Collection comprising about 80 clones; this collection was part of the material used by Prof. J. G. Hawkes for his taxonomic studies; (2) 21 clones collected in Peru and sent by Dr. H. J. Toxopeus of the Plant Breeding Institute, Wageningen; and (3) about 220 clones collected by the authors during a four-months' expedition to the Andes, when they were able to supplement laboratory studies with field observations.

¹ One or two clones from Chiloé thought to be diploids by Brücher (1959) were re-collected by the authors and on counting, their chromosome numbers proved to be tetraploid.

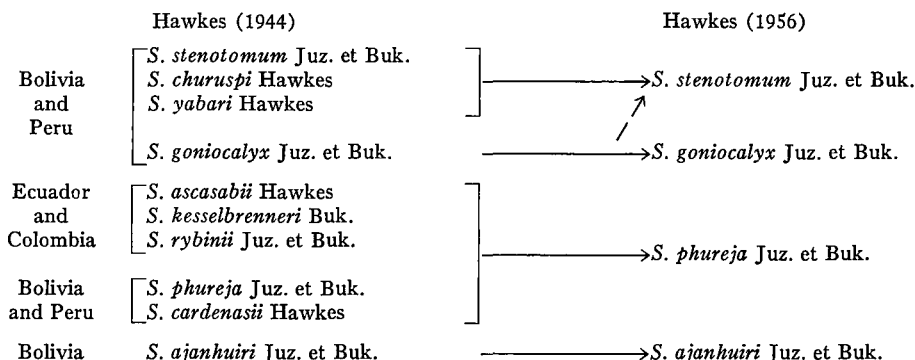


TABLE 1. *Meiosis in cultivated diploids*

C.P.C. parental clones ¹	Cells with			Br. + f
	12 ^{II}	11 ^{II} + 2 ^I	10 ^{II} + 4 ^I	
ryb 979 × stn 234.2	16	4	0	
ryb 979 × phu 1310	18	2	0	
ryb 979 × yab 1797	19	1	0	
gon 436 × stn 854	17	3	0	
gon 1500 × yab 1496b	18	1	1	+
gon 1500 × ryb 979	20	0	0	
stn 249.2 × crd 1776	20	0	0	+
ajh 232 × yab 1490	18	2	0	

¹ Members of the Commonwealth Potato Collection which is maintained at this Institute.

THE BREEDING SYSTEM

The cultivated diploids are very variable, and students of potato taxonomy have had great difficulty in defining criteria by which species could be separated. The position is, of course, that the taxonomy of the group cannot be divorced from an appreciation of both its breeding system and its management in cultivation.

Meiosis in F_1 hybrids between diploid cultivars is usually fairly regular (Swaminathan and Howard, 1953). Typical metaphase data are given in table 1. Although meiosis is regular, there is a considerable degree of pollen sterility in clones and their hybrids. Whether this arises from cryptic structural hybridity of the chromosomes or from a combination of cytological and physiological causes is not known. There are no cytogenetical barriers to crossability between "species," but it is evident that a considerable wastage of reproductive potential is tolerated in this, a vegetatively propagated crop.

Diploid cultivated potatoes are sexually fertile and are outbreeders exclusively, the flowers being visited by bees, species of *Bombus* (*Fervidobombus*) and *Melipona*. The breeding system is determined by gametophytic incompatibility. Three investigators have examined it previously. Carson and Howard (1942) used only four plants of rybinii, too few to give a reasonable likelihood of observing four fertility groups. Choudhuri (1944) found that a cross rybinii × kesselbrenneri produced berries with many seeds but that the recip-

rocal cross failed. Bains (1951) tried to classify a progeny of 19 plants of rybinii and found three plants that did not belong to any of the four groups into which the remainder fitted. We have analyzed 25 plants of an inter-clonal cross of rybinii (ryb 1311 × ryb 979); they were classifiable into four intra-sterile, inter-fertile groups of 5, 7, 6, and 7 plants: say S_aS_c , S_aS_d , S_bS_c , and S_bS_d , respectively. Likewise, 24 plants of the cross (kes 836 × ryb 2212) × stenotomum were classified without any anomaly into four inter-fertile intra-sterile groups of 6, 3, 8, and 7 plants. Three other families, ryb 979 × kes 836, ryb 979 × ryb 2211, and acs 827 × ryb 2211, each gave two intra-sterile, inter-fertile groups of 14 : 10, 8 : 2, and 7 : 5 plants, respectively. The parents were assumed to have one allele in common, and this was confirmed by using the technique mentioned below to examine pollen tubes in styles. These data show clearly that incompatibility is based on a simple series of oppositional factors (S -alleles), and they seem to function as well in crosses between as within "species," i.e., rybinii, kesselbrenneri, ascasabii, and stenotomum.

THE DISTRIBUTION OF INCOMPATIBILITY ALLELES

In a semi-compatible mating, about half the pollen tubes grow down the style without hindrance whereas the remainder are stopped at varying distances within the distal one-third. The tips of the arrested tubes swell irregularly, a behavior which

is readily seen about 48 hours after pollination in styles stained in acid fuchsin and light green (Darlington and La Cour, 1942). We have used this technique to determine the distribution of certain *S*-alleles.

First consider gonicalyx: according to Hawkes (1956), this "species" is a "northern derivative of *S. stenotomum* with large white or pink flowers and red calyx base." Gonicalyx is very popular in Peru where it is known as "Papa amarilla." There is such a thriving and organized trade in its tubers, both for "seed" and for local consumption, that one is led immediately to wonder if it is basically a single clone. We have evidence that this is so. Seven collections of gonicalyx studied by Hawkes (1944), described as being "more or less identical, differing only in very minor details from each other" and seven others were crossed cyclically. Only the crosses with gon 1514 as one parent, and two crosses 2014 $\times$ 436 and 214 $\times$ 2026, were successful: all others failed. The simplest explanation of these data is that all the collections except gon 1514 had the same *S*-allele constitution; but two matings were successful owing to pseudo-compatibility. The 13 inter-incompatibles had white flowers and tubers, but the flowers of gon 1514 were red and its tubers self red. All except two of the 13 collections were discarded several years ago, but stylar preparations of crosses of the two survivors have confirmed that they have the same *S*-allele constitution, say S_1S_2 .

The occurrences of S_1 and S_2 were determined in 21 clones of gonicalyx recently obtained from Peru, almost twenty years after the clones just described (table 2). It may be concluded from these tests that gonicalyx is a mixture of a few clones in which the white flowered one predominates.

Second, consider phureja: this name as used by Hawkes (1956) embraces clones which are "distinguished by the sparsely pubescent leaf, which is shiny in the living state, and rather irregular calyx with lanceolate lobes. Tubers yield in three to

TABLE 2. *The preponderance of the white flowered clone S_1S_2 in collections of gonicalyx*

<i>S</i> alleles	Flower color	
	White	Red
S_1S_2	13	2
S_1S_x or S_2S_x	2	1
S_xS_y	0	3

four months under short-day conditions and possess no dormancy period." The name includes clones which used to be called *ascasabii*, *boyacense*, *cardenasii*, *kes-selbrenneri*, *phureja*, and *rybinii* (Hawkes, 1944). Its members are distributed mainly in the northern Andes, from Venezuela to northern Peru.

We have used a member of this group, ryb 979, which was collected in Pasto market, Ecuador, as a tester to determine the distribution of its two *S*-alleles, S_{11} and S_{12} which, as table 3 shows, are very common. Their relative frequencies were determined by using two other testers, ryb 2211 ($S_{11}S_x$) and ryb 128/17 ($S_{12}S_y$). Table 3 shows that whereas S_{11} preponderates in Colombia, the two alleles are equally frequent in Ecuador. These two populations of clones are separated geographically by a fifty-mile-wide strip of scrubland in the north of Ecuador, in which potatoes are not grown.

Third, consider *stenotomum*: again the name is from Hawkes's (1956) revised classification and includes clones which used to be called *churuspi* and *yabari*. Members of the group occur mainly on the altiplano in southern Peru and Bolivia, being particularly frequent in the basin of Lake Titicaca. We have tested 68 clones for the presence of either S_{11} or S_{12} , the two alleles that are so common in *phureja*; eight contained one or other of the two (table 3). In a smaller sample of 25 clones, six had either S_1 or S_2 , alleles which are typical of gonicalyx. One or two of these clones would have been identified at one time as *S. yabari*.

These analyses show that some *S*-alleles are distributed throughout the geographical range of the cultivated diploids, which

TABLE 3. *The distribution of alleles S₁₁ and S₁₂*

		<i>S</i> ₁₁ or <i>S</i> ₁₂		Clones with		
		Present	Absent	<i>S</i> ₁₁	<i>S</i> ₁₂	not identified
phureja	Venezuela	3	1	2	0	1
	Colombia	74	28	42	11	21
	Ecuador	26	16	12	14	0
stenotomum ¹	Peru	7	21	6	1	0
	Bolivia	6	34	2	2	2

¹ Includes a few non-dormant clones.

therefore share a common breeding system and are, at least potentially, panmictic.

THE ANTHOCYANINS

The best known series of genes in cultivated diploids is that concerned with anthocyanins, and its members are found in all the "species" of cultivated diploids.

Type of anthocyanin.—So far, three independent loci, designated *P*, *R*, and *Ac*, are known to be concerned with anthocyanin production. Gene *P*, which is epistatic to *R*, controls the production of delphinidin in both flower and tuber; because of methylation, however, the visible pigment is petunidin when gene *Ac* is present, as mentioned below. The flowers of *P* genotypes are blue. Locus *R* is peculiar to cultivars and must have been established under human selection following the domestication of tuberous wild species. The gene *R* controls production of cyanidin in the flower and pelargonidin in the tuber. The flowers of *ppR*— genotypes are red. An allele *R*^{pw} in the homozygous phase suppresses cyanidin in the flowers and pelargonidin in the tuber. In *ppR*^{pw}*R*^{pw} genotypes, if the tubers are colored, they contain only peonanin, the *p*-coumaryl

5-glucoside 3-rhamnosylglucoside derivative of peonidin (Dodds and Long, 1955; Harborne, 1960).

Locus *Ac* is associated with three effects: (1) acylation of the anthocyanin molecule with *p*-coumaric acid; (2) the attachment of a glucose residue in the 5 position and (3) methylation. The gene *Ac* behaves as a simple Mendelian dominant (table 4). Homozygous *acac* plants can usually be distinguished by the deeper color-tones of their flowers whether blue or red, but they are most readily identified by means of chromatograms; their deacylated pigments have lower *R_F* values than when acylated (Harborne, 1960).

Anthocyanin patterns.—The distribution of anthocyanin on the individual appears to be determined by a genetic system common to all cultivated diploids. Up to the present, three loci *B*, *I*, and *F* have been identified; they are closely linked and probably in the order given. In their homozygous recessive phases *ii* and *ff*, loci *I* and *F* inhibit anthocyanin formation to give unpigmented tubers and flecked flowers, respectively. Locus *Ac* appears to be independent of locus *F* (table 5). In the presence of alleles *B*^c and *B*^d, which have

TABLE 4. *Segregation at the Ac locus*

C.P.C. parents		FLOWERS				
		Blue <i>PRAc</i>	Deep blue <i>PRac</i>	Red <i>pRAc</i>	Deep red <i>pRac</i>	Ratio
ryb 1311 × yab 1490	] <i>ppRRAc</i> × <i>ppR</i> [—] <i>acac</i> red deep red			64	59	1 : 1
ryb 1311 × F ₁ (yab 1492 × stn 1878)				19	20	1 : 1
stn 267 × phu 1310	<i>PPRRAc</i> × <i>PpR</i> [—] <i>Acac</i> blue blue	47	18			3 : 1

TABLE 5. Joint segregations at the Ac and F loci

C.P.C. parents		Self		Flecked		Ratio
		Red <i>ppRAcF</i>	Deep red <i>ppRacF</i>	Red <i>ppRAaff</i>	Deep red <i>ppRacaff</i>	
F ₁ (ryb 1311 × ryb 2211) × ryb 1311	<i>ppRRAcacFf</i> × <i>ppRRAcacff</i> self red flecked red	32	11	23	10	3:1:3:1

been observed only in the phureja group, anthocyanin occurs on the cotyledonary node of the embryo and shows as a spot through the testa of the seed (Dodds and Long, 1956).

The character "spectacle."—Clones occur in which the colored tubers are "spectacled," that is pigment does not occur around the eyes. The genetics of this character have not been described previously but our data suggest that it is inherited in a simple Mendelian way.

The tubers obtained from F₁ hybrids between three rybinii clones and certain backcrosses are recorded in table 6. The three clones were ryb 979 and ryb 2211, both with self-colored tubers, and ryb 2205 with unpigmented tubers. In this last clone, a flush of anthocyanin sometimes develops on the tubers in certain environments. When this happens, the pigment traces the faint outlines of spectacles round the eyes.

Tubers of a selfed progeny of ryb 979

were either self-colored or unpigmented (table 6 in Dodds and Long, 1955). The genotype of ryb 979 may be designated *Ii* where *I* is an allele which controls the development of pigment over the entire surface of the tuber; in the homozygous recessive *ii*, tubers are unpigmented. The cross between ryb 979 and ryb 2211 has been discussed elsewhere (Dodds and Long, 1956); ryb 2211 proved to be homozygous *II*, and spectacles did not appear in any of the progeny. When either of these two clones is crossed with ryb 2205, spectacled tubers occur in the F₁ progeny (table 6). Evidently ryb 2205 is heterozygous for a factor which controls the appearance of spectacle. As all the selfed progeny of ryb 2205 had unpigmented tubers like their parent, we may suppose that the factor for spectacle can act only in the presence of the allele *I*. That the character spectacle is determined by an allele of *I*, say *i^{sp}*, can be deduced from the data in table 7; plants

TABLE 6. Segregation for the character spectacle

C.P.C. parentage			Tubers			Ratio	$\chi^2[n]$	<i>P</i>
			Self <i>II, Ii</i>	Spectacle <i>Ii^{sp}</i>	White <i>ii, ii^{sp}, i^{sp} i^{sp}</i>			
—	ryb 979 × self	<i>Ii</i> × <i>Ii</i>	78	0	18	3:0:1	2.00 [1]	0.2 -0.1
51/128	ryb 2205 × self	<i>ii^{sp}</i> × <i>ii^{sp}</i>	0	0	48	0:0:1		
—	ryb 979 × ryb 2211	<i>Ii</i> × <i>II</i>	143	0	0	1:0:0		
—	ryb 979 × ryb 2205	<i>Ii</i> × <i>ii^{sp}</i>	42	29	66	1:1:2	3.45 [2] ¹	0.2 -0.1
51/124	ryb 2205 × ryb 2211	<i>ii^{sp}</i> × <i>II</i>	62	41	0	1:1:0	4.30 [1] ¹	0.05-0.02
<i>Backcrosses</i>								
51/124/36	× ryb 2211	<i>Ii^{sp}</i> × <i>II</i>	59	56	0	1:1:0	0.08 [1]	0.8 -0.7
51/124/42			30	24	0	1:1:0	0.67 [1]	0.5 -0.3
51/124/80			54	45	0	1:1:0	1.0 [1]	0.3 -0.2
51/124/90			39	0	0	1:0:0		
51/124/93	× ryb 979	<i>Ii</i> × <i>II</i>	40	0	0	1:0:0		
51/124/94			96	0	0	1:0:0		
51/128/23			37	0	25	1:0:1	1.25 [1]	0.3 -0.2
51/128/20			21	18	29	1:1:2	1.74 [2]	0.5 -0.3

¹ Unthrifty *ym ym* segregants may have misclassified.

TABLE 7. *Absence of spectacles in the cross ii × Ii^{sp}*

	Tubers		χ^2 1:1
	Self <i>Ii</i>	White <i>ii, ii^{sp}</i>	
ryb 1311 × 54/64/6 ¹	24	23	14.14 ³
54/41/13 ² × 54/64/10	55	22	
kes 1776 × stn 1558	45	37	

¹ 54/64/6 = stn 267 × phu 1310.² 54/41/13 = (ryb 2205 × self) × ryb 979.³ An unthrifty progeny.

with spectaclled tubers do not occur in the F_1 's of crosses between plants with spectaclled tubers and those with unpigmented tubers without the spectacle factor in the genotype.

Confirmation that i^{sp} is an allele of I was obtained by using the characters spectacle and seed spot for the joint classification of progenies in appropriate crosses. Spotted seeds gave plants with self colored tubers, and spectacles were observed only on the tubers of plants from spotted seeds, a behavior that agrees with expectation if the parental genotypes are as given in table 8.

Gene distributions.—Table 9 shows the frequency distributions of some color phenotypes in 220 clones of diploids. Blue pigmented clones (P) are less common in the northern region than in the south, whereas the position with respect to the relative frequencies of alleles R and R^{pw} is the reverse, R being less frequent in the south. The alleles I and i are both common and about equally frequent throughout the geographical range. Alleles i^{sp} and f are distributed throughout the range but are

comparatively rare; only about 10% of samples had spectaclled tubers, and about 7% had flecked flowers. No homozygous $acac$ individuals were collected at the northern end of the geographical range but, in contrast, alleles B^c and B^d were confined to this sector.

THE DISTRIBUTION OF THE RECESSIVE ALLELES Ym AND Nl

Deleterious recessives often segregate in F_2 and backcross progenies of cultivated diploids. We have examined the distribution of two such alleles which occur in the tester clone ryb 979 collected in Ecuador. This double heterozygote $YmymNlnl$ (ym : yellow margin; nl : narrow leaflet) was crossed with our diploids and 20 plants of each hybrid progeny were raised.

Allele ym .—Seedlings homozygous for ym are indistinguishable from normal seedlings until the second or third leaf has appeared. Thereafter all leaflets have a glossy appearance and yellowish margins. In the adult, leaflets are smaller and rounder than in normal seedlings and the flowers too are smaller in all their parts.

TABLE 8. *Joint segregation of seed spot and spectacle in F_1 families*

Parental genotypes ¹	F_1 seed	F_1 tubers			χ^2 [2] 2:1:1	P
		Self blue	Spectacle	White		
$p\bar{p}RR\frac{bi}{bI} \times P\bar{P}RR\frac{bI}{B^c i^{sp}}$	spot no spot	0 68	24 1 ²	36 2 ²	2.77	0.3–0.2
$p\bar{p}R^{pw}R^{pw}\frac{B^d I}{bi^{sp}} \times P\bar{p}RR\frac{bI}{bi}$	spot no spot	23 0	0 8	0 11	1.73	0.5–0.3

¹ See Dodds and Long (1956).² Probably misclassified "spots."

TABLE 9. Percentages of color phenotypes

			Percentage of samples from			
			Colombia	Ecuador	Peru	Bolivia
Pigments	Blue	$P----$	18	41	33	76
	Red	$--R^1-$	98 ²	97	83	72
Flowers	Flecked	$----ff$	8	0	11	5
Tubers	Selfed Spectacle	$I-$	46	61	58	47
		Ii^{sp}	10	7	8	14
		ii	44	32	33	39
	White	ii				
		ii^{sp} $i^{sp}i^{sp}$				

¹ Recognized in blue colored clones by chromatography.

² Differences $100 - 98 = 2$, $100 - 97 = 3$, $100 - 83 = 17$, and $100 - 72 = 28$ are frequencies of $--R^{pw}$ R^{pw} .

The expressivity of the gene is high, its effects being readily observable. They vary in intensity, however, according to the genetic background; in the same cross, some of the recessive homozygotes may be very unthrifty dwarf plants only a few inches tall and fail to flower, whereas others may be almost as vigorous as normal plants though with smaller flowers. The allele was observed only in clones from the northern end of the distribution (table 10).

The possibility that the heterozygote might be selected preferentially was examined as follows: 30 normal-looking F_1 seedlings from each of two crosses of the type $YmYm \times Ymy m$ between unrelated rybinii collections were planted in a randomized block in the field, and tubers from each surviving plant were weighed separately. Subsequently the genotype of each plant with respect to ym was determined. Out of the 52 tested plants, 20 were heterozygous ($Ymy m$) with a mean yield

per plant of 20.5 (± 1.47) oz, and 32 were homozygous ($YmYm$) with a mean yield per plant of 14.3 (± 1.23) oz. Thus the yield of the heterozygotes was significantly greater than that of the homozygotes ($P < 0.01$). It may be suggested that the heterotic effect on yield of that part of the chromosome which contains the Ym locus has led to the preferential selection of heterozygotes and hence to their high frequency in cultivation.

In all but one instance, crosses in which ym was segregating have given straightforward 3 : 1 ratios (table 11). The exception, 49 normal to 21 $ymym$ plants, was the progeny of a cross between two normal F_1 hybrids from crosses between different pairs of rybinii clones. Six normal looking plants were selected at random, and on testing they proved to be heterozygous $Ymy m$. As 20 seedlings had died at the cotyledon stage, it seems likely that, in two of the four parental clones, ym is linked to

TABLE 10. Frequencies of $Ymy m$ and $Nlnl$ heterozygotes : clones tested by examination of families outcrossed by tester stock

	Clones tested	$Ymy m$	$YmYm$	$Nlnl$	$NlNl$
Venezuela	4	2	2	0	4
Colombia	82	35	47	11	71
Ecuador	24	18	9	10	14
Peru	21	0	18	3 ¹	18
Bolivia	24	0	24	0	24

¹ Three non-dormant clones from Huancabamba, in the extreme north of Peru.

TABLE 11. Segregation for *ym* in *phureja* collections

Cross	No. of families	Frequencies		Ratio	χ^2 * [D.f.]
		<i>YmYm</i> <i>Ymym</i>	<i>ymym</i>		
<i>Ymym</i> × <i>Ymym</i>	10	819	237	3 : 1	3.68 [1]

* Heterogeneity $\chi^2[9] = 11.18$; slight deficiency of *ymym* phenotypes in seven of the families.

a recessive lethal in the repulsion phase, the cross being:

$$\frac{Yml}{ymL} \times \frac{Yml}{ymL} \rightarrow \frac{Yml}{Yml} (20) : \frac{Yml}{YmL} (49) : \frac{ymL}{ymL} (21)$$

This situation leads to a preponderance of heterozygotes even in the absence of selection for heterosis.

Allele nl.—Seedlings with genotype *nl**nl* emerge from the soil and open their cotyledons in step with other genotypes (*Nl*—), but the true leaves develop more slowly and the leaflets are narrower: the plants tend to be unthrifty as seedlings but they grow away from this weakness and come into flower about a month later than normal seedlings. The allele occurs only in clones of *phureja* (table 10). It behaves as a simple recessive; our data on the joint segregation of *nl* and *ym* give no evidence of linkage (table 12).

EXPERIMENTAL TAXONOMY

Hawkes (1956) retains four species of diploid cultivars in his revised classification of the tuber-bearing solanums. We have grown progenies from crosses within four of these “species” to see if their patterns of variability differ. There were five families of *stenotomum*, five of *phureja*, four of *goniocalyx*, and two of *yabari* in the

field at Bayfordbury. Each family consisted of a hundred seedlings and they were grown in rows of 20 plants randomized in five blocks. No progeny of *ajanhuiri* was included owing to lack of material. We have five clones in the Commonwealth Potato Collection which have been referred to this “species.” They have the distinctive pale blue flowers of genotype *P-R^{pw}R^{pw}* (Dodds and Long, 1955), and this characteristic may have been partially responsible for the recognition of the “species” (cf. *S. yabari* mentioned below); it has no other distinctive characters that we can recognize.

Parental clones of *stenotomum* and *phureja* were selected at random from our comparatively large collection, and it is probably safe to assume that they were not related. This is not so, however, with *goniocalyx* and *yabari*. We now realize that these “species” are each mixtures of a few clones which are probably closely related; for example, the *S*₁*S*_x and *S*₂*S*_x clones of *goniocalyx* in table 2 could be *F*₁ hybrids between *S*₁*S*₂ and *S*_x*S*_y, and the two red flowered *S*₁*S*₂ clones are probably *F*₂ or backcross hybrids. The four progenies of *goniocalyx* were from crosses between clones of constitution *S*₁*S*₂ and *S*₁ (*S*₂) *S*_x(*S*_y), and they showed about 40% de-

TABLE 12. Joint segregation of *ym* and *nl*

Cross	No. of families	Progeny				Ratio	χ^2 [n]
		<i>Ym</i> — <i>Nl</i> —	<i>ymym</i> <i>Nl</i> —	<i>Ym</i> — <i>nl</i> <i>nl</i>	<i>ymym</i> <i>nl</i> <i>nl</i>		
<i>Ymym Nnl</i> × <i>Ymym Nnl</i>	2	138	54	41	16	9 : 3 : 3 : 1	1.64 [3]
<i>Ymym nl</i> <i>nl</i> × <i>ymym Nnl</i>	2	55	46	85	35	1 : 1 : 1 : 1	24.99*[3]
<i>Ymym Nnl</i> × <i>Ymym nl</i> <i>nl</i>	1	22	8	14	6	3 : 1 : 3 : 1	1.81 [3]
<i>Ymym Nnl</i> × <i>ymym Nnl</i>	1	39	28	13	13	3 : 3 : 1 : 1	2.17 [3]

* Heterogeneity $\chi^2[3] = 12.20$; highly significant. Probably misclassification between *Ym*—*nl**nl* and *ymym nl**nl*.

pauperate seedlings such as dwarfs, partial chlorotics, and "blinds." It seems reasonable to assume that the unthriftness observed in gonicalyx resulted from inbreeding depression and provides further evidence of the close relationship of the parental clones. The genetic structure of gonicalyx is that which would be expected under the present agricultural regime. Known as "Papa amarilla," gonicalyx is grown in fairly uniform stands for the markets of Lima. Invariably there are other diploids at hand to supply pollen and, although a considerable amount of weeding is usually done, selection is not rigorous enough to exclude chance seedlings. They might be expected to become established occasionally and to contribute tubers to the harvest. Thus both botanical and agricultural considerations clearly show that gonicalyx is a cultivar and not a "species."

The "species" formerly called *S. yabari* was abolished by Hawkes (1956) after the senior author had shown (unpublished) that most of its members were homozygous for the simple Mendelian recessive *ac* and so had a distinctive flower color. Some members were transferred to *S. stenotomum* and others to *S. gonicalyx*.

There are left for consideration the two "species" phureja and stenotomum. The most obvious differences between them are in distribution and physiology. Phureja is grown from Venezuela to north Peru, mainly in the valleys at between 6,500 and 11,000 ft. It has a definite place in the potato culture of this region, being known to the peasants as "Papa chaucha" (early potato). They grow the clones mainly for home consumption, and can identify them when asked to do so. The plants mature in three to four months and the tubers are not dormant. In contrast, stenotomum occurs on the altiplano of southern Peru and Bolivia, particularly in the basin of Lake Titicaca. Its members have no separate identity in the sense that they are grown with the triploid and tetraploid cultivars, forming part of a general mixture in the

field. The geographical separation of the two groups is not absolute inasmuch as a few phureja-like cultivars do occur in the valleys of south Peru and Bolivia and clones of stenotomum have been collected in northern Peru (Ochoa, personal communication).

Variability was studied in the progeny of these two groups by measuring seven characters in each plant (table 13): leaf dissection, leaf hairs (two characters used as taxonomic criteria), leaflet index, pedicel abscission, length of calyx, flowering time, and tuber production. All these characters varied very significantly between families, with the exception of length of calyx tube ($P = 1-5\%$). Significant differences were observed between phureja and stenotomum only in flowering time and leaf dissection. The mean time of flowering was earlier in the phureja families than in the others and, indeed, early flowering in phureja is correlated with its characteristic early maturity. Nevertheless, for the three characters time of flowering, leaf dissection, and leaflet index (a character with differences between "species" of borderline significance, $P = 1-5\%$) the segregation in families was so wide that even when we used a conservative estimate of the range of segregation, family mean $\pm$ standard deviation, there was still a well-marked overlap between "species" (table 13). Sparse pubescence has been regarded as a particularly valuable character by which to recognize phureja (Hawkes, 1956), but our counts did not show any significant differences between "species."

DISCUSSION

Breeding system.—The breeding system of cultivated diploids is based on a common series of *S*-alleles and there are no cytogenetic barriers to the crossability of different clones. There is no dearth of opportunities to cross. Dr. C. Ochoa has now shown that the distributions of phureja and stenotomum overlap considerably in north Peru (collections of stenotomum occur in Ochoa Herbarium nos. 1880 to

TABLE 13. *Variation in diploids*

A = range of family means

B = range from lowest family mean -S to highest mean +S

Character ¹		phu	gon	yab	stn
Leaflet index	A	56-68	62-64	56-59	48-60
	B	49-76	53-72	50-66	43-68
Leaf dissection	A	12-18	19-21	20-22	19-31
	B	7-25	12-28	14-28	14-40
Leaf hairs	A	21-66	33-80	45-90	29-46
	B	12-80	22-135	19-113	2-87
Pedicel abscission	A	49-61	52-56	52-55	47-62
	B	41-66	41-64	45-62	41-69
Flowering time	A	71-74	80-92	75-80	76-79
	B	64-78	73-101	72-87	68-85
Calyx tube	A	38-43	42-46	39-40	36-44
	B	33-49	36-51	34-45	31-50

¹ Measured

Using mature leaves:

Leaflet index: $\frac{\text{breadth}}{\text{length}}$ leaflet, percentage.

Leaf dissection: number of lateral and interjected leaflets.

Leaf hairs: hairs on upper surface in 10 microscope fields; total area 7.85 sq mm.

Pedicel abscission: length below abscission/total length.

Calyx tube: length of tube/total length, percentage.

Flowering time: days from sowing to first fully opened flower.

Tuber production: number $\times$ size on arbitrary scales.

1962, from the Departments of Huanuco, Ancash, Libertad, Cajamarca and Amazonas; nos. 950 to 951 (*stenotomum*), nos. 944 to 955 (*goniocalyx*), no. 949 (*yabari*), and *phureja* were collected on the same farm). Of southern Peru, in the vicinity of Marcapata, he writes (1956): "... in the same plot, relatively small in area, one can meet *S. stenotomum*, *S. goniocalyx*, *S. Yabari*, *S. Juzepczukii* and *S. curtilobum* in a most heterogeneous mixture of varieties and forms and with the greatest opportunity for cross pollination" (Authors' translation). We too have encountered similar mixtures in Bolivia and noted the presence of pollinating bees. If the cultivated diploids are indeed panmictic, it is not surprising to find them showing a range of variability that is continuous. This variability has been evolved by selection during the course of domestication. It

may be assumed that certain components of the main population were favored, selected, and raised to the status of cultivars by vegetative propagation. The most extreme example of this effect is *goniocalyx*; basically it appears to be a single white flowered clone in that part of Peru where it is grown as a cultivar called "Papa amarilla." Less extreme is the example of the northern diploids. These are all similar in being non-dormant but, nevertheless, are very variable.

Group phureja.—The western side of South America is dominated by the Andes with its vast series of high valleys. In the bottoms of the valleys and along their lower slopes, coffee, sugar cane, rice, bananas, and maize are grown. At about 6,500 ft or somewhat higher, the tropical crops are replaced by wheat, barley, beans, onions, and potatoes. At this altitude and

up to 10–11,000 ft many of the valleys have mild climates free from frost. Two or even three crops of diploid potatoes are grown in a year. This is possible because diploid cultivars have been selected which do not undergo a period of dormancy. These genotypes have been called *rybinii*, *kesselbrenneri*, *boyacense*, and *ascasabii* when collected in Venezuela, Colombia, and Ecuador; and *cardenasii* and *phureja* if collected in the valleys of Bolivia.

In the diploids of the northern *phureja* complex there is a marked preponderance of alleles S_{11} and S_{12} , such as would be expected if the *S* locus were linked to another locus with agricultural significance, for example, dormancy. An alternative suggestion is that *phureja* was evolved from a small nucleus of original material but this does not seem likely. The group varies at the *P*, *R*, *F*, *I*, and *B* loci and, although S_{11} and S_{12} are common, the number of other alleles at the *S* locus is not low. In the field experiment, *phureja* families showed no signs of inbreeding depression such as was observed in *goniocalyx*. Variability in flowering time was less in the *phureja* than in the *stenotomum* families (average standard deviation 3.47 as compared with 6.12; $P = 0.1$ – 1.0%), but in all other characters the two “species” were equally variable. Thus it would appear that the early maturity and short dormancy characteristics of *phureja* have been selected under a regime of assortative mating in an otherwise variable population.

If the genetic control of non-dormancy is simple, it seems reasonable to suppose that the character would be established relatively quickly in cultivars; whereas if complex, the process would take longer. The formal genetics of dormancy has not yet been studied but, however the character originated, it would be developed and retained by a combination of sexual reproduction and vegetative propagation. The evolutionary influence of these two processes would depend on the level of agricultural development; the less care given to weeding, the greater would be the

chance of a self-sown seedling reaching maturity to contribute tubers to the harvest; agricultural advance would bring the recognition, maintenance, and distribution of clones. These conflicting influences are detectable at the present day. Although the use of common names such as “*negra*,” “*blanca*,” and “*morada*” may be regarded as a step towards the awareness of clones, mixtures are commoner in the fields than pure stands, if indeed the latter ever occur. We often saw a mixture of more than six kinds of tubers in the harvest from a single plot.

The *phureja* group is distinct in two other genetical ways; by the frequency of heterozygotes *Ymym* and the occurrence of the alleles B^c and B^d which in the presence of *P* produce a band of pigment external to the leaf axis. As yet, however, the group is not sufficiently genetically isolated to be regarded as a separate species. It is no more than an assemblage of cultivars which in morphological and culinary characters meets the requirements of the local people.

Group stenotomum.—Travelling upwards, eventually one emerges on to the altiplano, undulating land of about 12,000 ft and subject to frost and snow. The most mixed cultivations of potatoes are found on the altiplano surrounding Lake Titicaca: diploids, triploids, tetraploids, and pentaploids can be seen growing together in fields that border the lake. Many of these cultivars have similar growing periods. This and the similar appearance of their tubers is reflected in the markets of, for example, La Paz. We have taken tubers which have proved to be diploid, triploid, and tetraploid from the same heap on a vendor's stall. The planting season is from August to September and harvests may be taken from January until June. The climate is suitable for only one crop and, as would be expected, the potatoes undergo a period of dormancy. In the past, diploid potatoes collected from this region have been called *S. ajanhuiri*, *S. churuspí*, *S. goniocalyx*, *S. stenotomum*, and *S. yabari* but, in reality,

TABLE 14. *A classification of cultivated potatoes*¹

Species	Ploidy	Group	Main distribution	Origin	Remarks
<i>S. tuberosum</i>	2x	[Stenotomum Phureja]	(1) Central Peru and Bolivia (2) Venezuela to northern Peru	From unknown wild diploid species	Includes Subgroup Goniocalyx Includes Subgroup Amarilla
	3x	Chaucha	(3) Central Peru and Bolivia	From crosses of (1) and (2) by (4)	Mixed with (1) and (4) in the field
	4x	[Andigena Tuberosum]	(4) Venezuela to northern Argentina (5) Europe and North America	Doubling of chromosome numbers of (1) and (2) Selection from (4)	
<i>S. × juzepczukii</i>	3x		(6) Central Peru and Bolivia	From crosses between (1) and <i>S. acaule</i>	Few and unimportant. Usually mixed with (1) and (4)
<i>S. × curtilobum</i>	5x		(7) Central Peru and Bolivia	Crosses between (4) and (6)	Few and unimportant. Usually mixed with (1), (4), and (6)

¹ From Dodds (in press).

they are all members of a large variable group of cultivars.

Classification.—This study of cultivated diploids shows that they share the same genetic system and that the application of the concepts of formal taxonomy to potatoes is more confusing than helpful. This outlook has led one of us to propose a simplified classification for cultivated potatoes (Dodds, in press), in accordance with the *International Code of Nomenclature for Cultivated Plants*.

With the exception of two hybrids, *S. × juzepczukii* and *S. × curtilobum*, all cultivated potatoes share a common heritage. This basic similarity is indicated in the system of classification by including all these potatoes under the same latin name—*Solanum tuberosum* L. In essential, the system is concerned with a hierarchy of categories within this large and variable species. The most important category is that of ploidy, which has three levels: Ploidy 2×, Ploidy 3×, and Ploidy 4×. In this study we have been concerned with the diploids. As shown in table 14, they are divided into two groups. Some clones of Group stenotomum are slender plants with narrow leaflets and so are quite distinct in the field, even though their tubers are like those of certain tetraploids. On the altiplano of southern Peru and Bolivia, tubers of Groups Stenotomum, Chaucha, and Andigena are often grown together, harvested together, and sold together. The character which best identifies diploids of Group phureja is non-dormancy of tubers, but it must be remembered that some triploids and more rarely tetraploids are equally non-dormant.

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SUMMARY

Cultivated diploid potatoes occur in the Andes from Venezuela to northern Argentina. They are obligate crossbreeders with a single series of oppositional factors controlling the incompatibility reaction. Some of the S-alleles are found throughout this geographical range.

Six loci concerned with the occurrence and patterning of anthocyanins are members of a genetic system controlling pigmentation, a system that is basically the same in all cultivated diploids.

No evidence was obtained from an analysis of the variability of seedling progenies that parental differentiation has reached the level of speciation. The greatest diversity of cultivars (clones) is in the highlands of southern Peru and Bolivia. Elsewhere, other cultivars or groups of cultivars are grown according to local preferences; notably a group of quicker maturing, non-dormant selections in Ecuador and Colombia.

These data are subsumed under a simple classification of cultivated potatoes.

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