THE ORIGIN OF NEW FORMS IN *RUBUS*

II. THE LOGANBERRY, *R. LOGANOBACCUS* BAILEY

By M. B. CRANE

John Innes Horticultural Institution, Merton

(With Plate V and One Text-figure)

CONTENTS

Introduction

When the loganberry, *Rubus loganobaccus* Bailey, was discovered sixty years ago it was assumed to be a new hybrid, the result of a cross between a blackberry and a raspberry. Subsequently, however, there has been much discussion as to whether it is really a hybrid or only a direct offshoot from the wild blackberry of California, *R. vitifolius*. This difference of opinion, and the conclusions of earlier work at Merton (Crane & Darlington, 1927), led me to undertake a series of breeding experiments to discover which of the above views is the more probable. Seeds of *R. vitifolius* were obtained from California, and in 1934 crosses were made between *R. vitifolius*, *R. idaeus* and other *Rubi*. The results of the breeding work are described and discussed in this report. Many of the plants raised in the experiments have been cytologically examined by my colleague, Dr P. T. Thomas, who gives an account of his studies in a separate paper (Thomas, 1940*b*).

The original story of the origin of the loganberry is probably best told in a communication from Judge J. H. Logan, in whose garden in California the loganberry was raised, to Prof. L. H. Bailey. This communication, quoted below, is dated 1902, and was published by Bailey (1923).

"In August 1881, I planted the seed of the common wild blackberry or dewberry, of California, botanically known as the *Rubus ursinus*,

gathered from plants on one side of which was growing a kind of evergreen blackberry known as the Texas Early, and on the other side of which was growing an old variety of red raspberry. The Texas Early has a growth of cane and leaves similar to the Lawton, although much less vigorous, and in our climate is growing winter and summer. It has a small round berry of more acidity than the Lawton and probably of poorer flavour. The raspberry referred to has been growing in this place for the last forty years and I am unable to ascertain what variety it is, although it is of a type similar to the Red Antwerp. It is not, however, the Red Antwerp as we have been growing it here. From this seed there grew about one hundred plants which were cared for and planted out in the ground. In the summer of 1883 these plants fruited and there appeared one plant which was undoubtedly a cross between the raspberry and the *Rubus ursinus*. The fruit was larger and earlier than the raspberry or any blackberry, except the *Rubus ursinus*, ripening about the middle of May; the appearance of the berry on the surface was something like the raspberry, being less indented and of more even surface than a blackberry; the colour a bright glowing red, becoming very dark and finally, when dead ripe, of a dull purplish-red colour. The berry has a core like the blackberry and parts from the calyx the same as a blackberry. The leaves of the vine are almost identical with the wild *Rubus*, being somewhat larger. The canes are also like the wild *Rubus*, only larger and more vigorous. 'It has the same small sharp spines and, like it, is without adventitious root buds, but multiplies from the stolons or tips or from seed. The fruit, when cooked, has the same rich acidity as the wild *Rubus*, there being only a suggestion of the taste of the raspberry in the cooked fruit, but in the jelly there is a more decided raspberry flavour. This red berry is universally known here as the loganberry."

The assumption of the hybrid origin of the loganberry went unchallenged for several years. Later, however, it came to be disputed, primarily because the high fertility of the loganberry seemed at that time inconsistent with the nature of a hybrid derived from widely distinct parents. Moreover, the types of habit, flower and fruit of the supposed parents failed to reappear in its seedlings, and again, on crossing with other *Rubi*, the dominance of many characters of the loganberry seemed more like the behaviour of a species than like that of a hybrid. For these reasons some authorities came to consider the loganberry as a variety of *R. vitifolius*, and rejected the postulated hybrid origin.

Bailey (1923) is strongly inclined to the opinion that the loganberry is a hybrid, as supposed in the beginning, and in his systematic studies

of the genus gives it specific rank as *R. loganobaccus*. Others, including Darrow (1937), Darrow & Longley (1933) and Hedrick (1925), favour the opposite view and conclude that it is not of hybrid origin.

Varieties of raspberries are of two kinds, the diploids and the tetraploids. The tetraploids have arisen from the diploids during the past eighty years. Morphological differences readily separate the two groups, and there is no doubt that the raspberry described by Logan as "of a type similar to the Red Antwerp", and thought by him to be the male parent of the loganberry, was one of the older diploids.

The species *R. vitifolius*, used in these experiments, is very closely allied to *R. ursinus* if not identical with it. They are both placed in the subgenus *Eubatus* section Vitifolii, and apparently their principal difference is one of hairiness. They are frequently confused and Focke (1914) reduces *vitifolius* to a variety of *ursinus*. Bailey (1923) gives a botanical description of *R. vitifolius* and follows with the statement: "I have not been able to identify any of the named cultivated dewberries with this species as here understood, although I suppose that the Aughinbaugh, once considerably planted in California, belongs here (or possibly to *R. ursinus*)." According to Darrow (1937) the Aughinbaugh is a selection of the wild blackberry or dewberry of California and it was from seed of the Aughinbaugh that the loganberry was raised.

MATERIAL

The following species were used in the experiments:

Species	Chromosome no. $2n$
R. idaeus L.	14
R. idaeus L.	28
R. neglectus Peck	14
R. niveus Thunb.	14
R. loganobaccus Bailey	42
R. vitifolius Cham & Schlechtd.	56

The plants of *R. vitifolius* used in the experiments were raised from seeds collected in California by Dr H. M. Butterfield, who informed me that they came from an area where there was little danger of any natural hybridization. He also stated that the berries collected were of the rounded form and not so long as some found in certain other sections. The plants raised from these seeds were dioecious, being either strictly male or strictly female. Their fruits varied in shape; some were of the rounded form described by Dr Butterfield, others were longer than broad. Differences also occurred in the pigmentation and the amount of waxy bloom on the growth. Some had a heavy covering of bloom, whilst others

were free from it. On the young growth the leaves of all the plants were ternate.

The raspberries used in the experiments were the diploid variety "Superlative" and the tetraploid variety "Hailshamberry". As shown in recent papers (Crane, 1940; Thomas, 1940) the tetraploid raspberries are autotetraploid, and there is every reason for concluding that they have arisen directly from the diploids. Both varieties have hermaphrodite flowers and on the young canes the leaves are 5-pinnate.

The loganberry has hermaphrodite flowers and 5-pinnate leaves on the young growth.

Breeding experiments

The results of the experiments, showing the sex, morphology, and chromosome number ($x=7$) of the parents and seedlings, are summarized in Table I.

TABLE I

Parents					Seedlings					
						Sex				
Family no.		Chromosome no.	Sex	Leaf division	Chromosome no.	♀	☿	♂	Leaf division	% chromosomes from raspberry
4/34	*R. vitifolius* × *vitifolius*	8x 8x	♀×♂	3 3	8x	26	5	35	3	0
2/34	*R. vitifolius* × Loganberry	8x 6x	♀×♂	3 5	7x	24	21	7	3, leaflets more incised than 4/34	14
1/34	Loganberry × *R. vitifolius*	6x 8x	♂×♀	5 3	7x	—	27	2	3, as 2/34	14
3/34	*R. vitifolius* × raspberry	8x 2x	♀×♂	3 5	5x	21	19	—	3, leaflets more incised than 2/34	20
7/34	*R. vitifolius* × raspberry	8x 4x	♂×♀	3 5	6x	—	10	—	5	33
31/37	7/34 17 (selfed)	6x	♀×♂	5	6x	—	45	—	5	33
15/13	Loganberry (selfed)	6x	♀×♂	5	6x	—	53	—	5	33
Many fams.	Raspberry × raspberry	2x 2x	♀×♂	5 5	2x	—	All*	—	5	100
,,	Raspberry × raspberry	4x 4x	♀×♂	5 5	4x	—	All	—	5	100

* As shown in previous papers (Crane & Lawrence, 1931; Lewis, 1939) sex forms occur in the raspberry, and as detailed in recent papers (Crane and Thomas, 1940) a proportion of the seedlings in Family 7/34 had fifty-six chromosomes and were of asexual origin and one had thirty-five chromosomes, but none of these occurrences essentially affect the investigation with which we are concerned. From the chromosome number, morphology and genetics of the seedlings detailed in Table I, it is concluded that they all arose by normal sexual reproduction.

In the leaf division columns in the table, 3 = ternate and 5 = 5-pinnate leaves.

In the family 4/34, *R. vitifolius* ♀×♂, twenty-six of the seedlings had female flowers, thirty-five male flowers, and the flowers of five were

classed as hermaphrodite. In these five plants the female organs were normal, but the male were only partially or feebly developed. On the fruiting growth the leaves were lobed or ternate and on the young growth (turions) the leaves were ternate. Of the fifty-two plants in family 2/34, *R. vitifolius* × loganberry, twenty-four were female, twenty-one hermaphrodite and seven male. On the young growth the leaves were ternate but the leaflets were more deeply incised than in the *R. vitifolius* family 4/34.

In the reciprocal family 1/34, loganberry × *R. vitifolius*, twenty-seven seedlings were hermaphrodite and two male. The leaves were ternate and incised as in family 2/34. In family 3/34, *R. vitifolius* × diploid raspberry, twenty-one of the plants were female and nineteen hermaphrodite. The leaves on the young growth were ternate, but more deeply incised than those in families 1 and 2/34. As a rarity, an occasional plant in families 1, 2, 3 and 4/34 developed a leaf with five more or less distinct leaflets. The plants of sexual origin in family 7/34, *R. vitifolius* × tetraploid raspberry, were all hermaphrodite and the leaves on the young growth were 5-pinnate.

Family 31/37 was raised from selfing one of the sexually reproduced plants in family 7/34. All the plants in this family had hermaphrodite flowers, and 5-pinnate leaves on the young growth like their parent. The plants in family 15/13, loganberry selfed, were all hermaphrodite with 5-pinnate leaves.

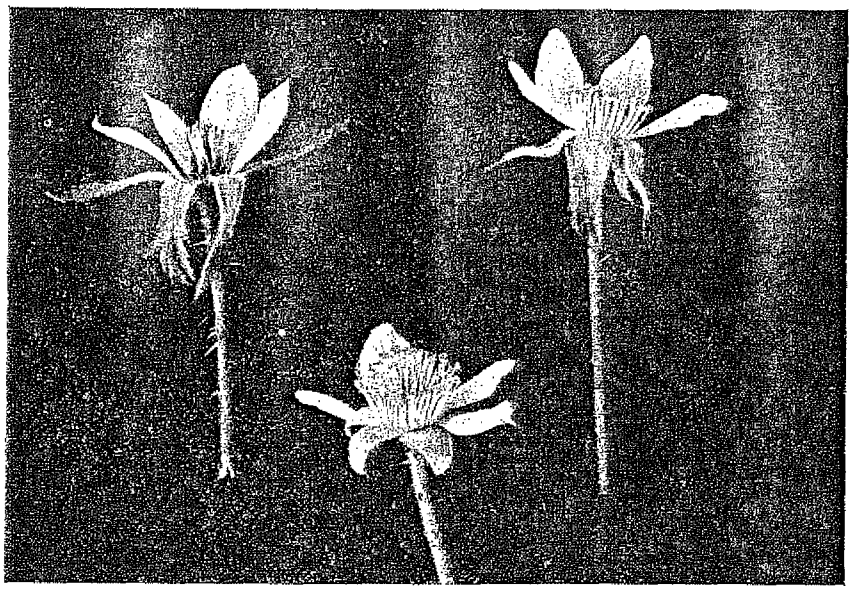
In breeding experiments at Merton with tetraploid raspberries, including the Hailshamberry, the seedlings have all had hermaphrodite flowers and 5-pinnate leaves on the young growth. In the diploid raspberries, however, some varieties are homozygous for hermaphroditism and 5-pinnate leaves. Others are heterozygous and segregated for hermaphrodite, male and female flowers. The hermaphrodite and female forms have 5-pinnate leaves, but in the male forms the leaves have only three leaflets (see Crane & Lawrence, 1931; Lewis, 1939).

In all the above families segregation occurred for such characters as pigmentation of growth and prickles, waxy bloom on the stems, hairiness and other minor characters, and in family 4/34, *R. vitifolius* ♀ × ♂, the length of the fruit varied considerably. In the heptaploid families 1 and 2/34 and the pentaploid family 3/34, the plants were highly sterile, and in consequence the fruits formed were usually imperfect.

Families were also raised from crossing the loganberry with *R. neglectus* and *R. niveus*. As shown in an earlier paper (Crane & Darlington, 1927) these hybrids were extremely sterile.

Inheritance of sex

As previously mentioned, in family 4/34, *R. vitifolius* ♀ × ♂, the five plants classed as ☿ were intersexes rather than true hermaphrodites; the female organs were normal, but those of the male were only slightly developed. If these five plants are included in the female class we have 31 ♀ to 35 ♂, which approximates to a 1 : 1 ratio.



Text-fig. 1. *A* = female flower of *R. vitifolius*. *B* = male flower of *R. vitifolius*. *C* = hermaphrodite flower of 6*x* hybrid. These flowers are from three seedlings of family 7/34 (*R. vitifolius* 8*x* × *R. idaeus* 4*x*). *A* and *B* are 8*x* apomictic segregates, and *C* is 6*x* and of sexual origin.

In the family raised from *R. vitifolius* ♀ × loganberry ☿, there were approximately equal numbers of ♀ and ☿ plants, plus a few males. In the reciprocal cross, where *R. vitifolius* was used as the ♂ parent, no females occurred, two were males and the remaining twenty-seven were hermaphrodites. Again when *R. vitifolius* ♀ was crossed with diploid raspberry, ☿, one-half of the seedlings were female and one-half hermaphrodite. The reciprocal cross, diploid raspberry × *R. vitifolius*, entirely failed. When *R. vitifolius* ♀ was crossed with the tetraploid raspberry, ☿, family 7/34, the sexual offspring were all ☿ (see Text-fig. 1).

As described in an earlier paper (Crane, 1940), a number of plants occurred in family 7/34 which were of asexual (apomictic) origin. These plants were typically *R. vitifolius*, like their mother, but some were female and some were male (see Text-fig. 1). This strongly suggests that in *R. vitifolius* the female is the heterozygous sex.

Dominance in polyploids

In polyploid plants, including *Rubus*, the phenomenon of dominance is often obscure and genetic analysis difficult owing to the intergradation of characters. Dominance is used here to mean character dominance and presumably depends on complex reactions rather than strict single gene reactions. When, however, we know the chromosome constitution of parental forms, and particularly when we know how the parents themselves have arisen, we begin to understand why the expression of dominance is essentially variable in polyploids. In this connexion the inheritance of the leaf characters of *Rubus* studied in these experiments is of interest. As shown in Table I, there is a gradation from the ternate leaf to the pinnate leaf with five distinct leaflets. If we accept the hybrid origin of the loganberry, we then find, as shown in the last two columns of the table, that this gradation is directly correlated with the proportion of chromosomes derived from the pinnate-leaved raspberry. Thus in hybrids where one-seventh of the chromosomes are derived from the 5-pinnate-leaved raspberry and six-sevenths from the ternate-leaved *R. vitifolius*, the hybrid plants are ternate, but the leaves are more deeply lobed than those of *R. vitifolius*. When one-fifth of the chromosomes are derived from the raspberry the hybrids are still ternate, but the leaves are more deeply incised than in the one-seventh case. With one-third raspberry chromosomes, the leaves of the hybrid are 5-pinnate like those of the raspberry. Other examples of intergradation of characters and change of dominance correlated with the proportion of parental chromosomes have occurred in our breeding work with other species of *Rubus*. For example (Crane & Darlington, 1927), when we crossed the widely different species *R. rusticanus* $2x$ with *R. thyrsiger* $4x$, most of the F_1 were $3x$ and very similar to their $4x$ male parent. One of the F_1 seedlings, however, was $4x$, the result of an unreduced germ-cell of its $2x$ parent taking part in fertilization. This plant, with fourteen instead of seven *rusticanus* chromosomes, was very similar to its $2x$ female parent.

Review of the evidence of origin

If the loganberry is a hybrid as originally supposed, it should be possible to remake it by means of suitable crosses between the presumed parents, and to make such crosses was the purpose of these experiments.

Before reviewing the results of the experiments, it may be of value to recall the principal characters of the species and forms used in the breeding work.

The leaves of *R. vitifolius* are ternate, and the sexes are borne separately, some plants being male and others female. The fruits are generally small and variable in shape. Some plants have a rounded form of fruit, whilst others have fruits which are much longer than broad. The somatic chromosome number of the species is 56.

In the loganberry the leaves are 5-pinnate, the flowers hermaphrodite and the fruits large and elongated. The somatic chromosome number is 42. There are therefore very pronounced differences between *R. vitifolius* and the loganberry in sex, morphology and chromosome number. These differences in themselves make it difficult to accept the view that the loganberry arose directly from *R. vitifolius*.

In the raspberry, *R. idaeus*, the leaves are 5-pinnate, the flowers hermaphrodite and the fruits comparatively large. The somatic chromosome number of most varieties is 14, a few being tetraploid, $4x=28$. We therefore see that the loganberry and raspberry, although different in chromosome number, are alike in their sexual condition and in the morphology of their leaves.

The plants in family 3/34, *R. vitifolius* × diploid raspberry, are in several respects different from the loganberry. They differ in leaf morphology and chromosome number and are highly sterile and unproductive of fruit. Nevertheless, in most characters they are intermediate between their parents. In family 7/34, *R. vitifolius* × tetraploid raspberry, however, the leaves of the plants of sexual origin are 5-pinnate, the flowers are hermaphrodite, fertile and productive of fruit, and the fruits of some are large and elongated. Their somatic chromosome number is 42. We therefore see that in all these major characters the hybrids are like the loganberry.

The fruits of the seedlings are not quite so large as those of the loganberry, but this I think is readily accounted for on the assumption that the named variety of *R. vitifolius*, "The Aughinbaugh", had larger fruits than the seedlings of *R. vitifolius* used in these experiments. As previously mentioned, the Aughinbaugh, the mother of the loganberry,

was selected from the wild and the size of the fruit would undoubtedly have been a major consideration in the selection. The F_2, family 31/37, raised from *R. vitifolius* × tetraploid raspberry, bred true in respect of the sex of the flowers and the 5-pinnate leaves, and there is no approach to the parental forms. Variation in size of fruit is of a similar order to that in families I have raised from selfing the loganberry. The plants in this family which have been examined by Dr Thomas are also hexaploid, $6x = 42$, like the loganberry. All these facts agree with the originally postulated hybrid origin, and at the same time they contradict the view that the loganberry could have arisen as a direct offshoot of the wild blackberry of California.

There is no doubt that the raspberry similar to Red Antwerp, which was supposed by Judge Logan to be the male parent of the loganberry, was a diploid. We have seen from family 3/34 that *R. vitifolius* × diploid raspberry gives pentaploid plants which are highly sterile and morphologically unlike the loganberry. When a tetraploid raspberry is used, however, the plants are hexaploid, fertile, productive of fruit and also morphologically like the loganberry. It is therefore reasonable to assume that an unreduced germ cell of the diploid raspberry took part in fertilization to give rise to the loganberry. The loganberry, that is, with $6x = 42$, has twenty-eight chromosomes derived from *R. vitifolius* and fourteen derived from the raspberry. Many cases are on record of unreduced germ cells of raspberries and other *Rubi* taking part in fertilization and giving rise to new fertile forms (Crane & Darlington, 1927). One of these, the Veitchberry $4x = 28$, was raised from *R. rusticanus* $2x = 14$, × raspberry, and like the loganberry it breeds nearly true, and in our breeding work at Merton unreduced germ cells of the raspberry have frequently taken part in fertilization (Lewis, unpublished).

One, and perhaps the most prominent, objection which has been advanced against accepting the postulated hybrid origin of the loganberry is that it is highly fertile and breeds nearly true; that is to say, although its seedlings are variable there is no approach to either parental form. Such an objection is untenable, and at the present time calls for no elaborate discussion. It is of course true that in hybrids from widely distinct forms, such as the parents of the loganberry, we are more familiar with the occurrence of sterility than of fertility, and when hybrids are fertile there is commonly much diversity in the progeny and an approach to the parental forms. But during the last decade, as a result of world-wide genetical and cytological research, we have become acquainted with many virtually true-breeding new forms and species which have

arisen from hybridization accompanied by chromosome duplication (see Crane & Lawrence, 1938; Crane, 1940). In many cases hybridization has been accompanied by complete duplication of the chromosomes to give rise to the new species, but in some cases the new species have arisen from hybridization and unilateral chromosome duplication, and this is presumably what occurred in the case of the loganberry, where the raspberry parent may be taken to have furnished a non-reduced germ cell.

In repeating the cross, if only the diploid raspberry had been available, we should have had to wait until one of the rare unreduced germ cells took part in fertilization; but as the raspberry already exists in the tetraploid as well as in the diploid form, it was possible to use a tetraploid variety in the cross and so provide an unlimited number of diploid germ cells. This, as we have seen, solved the problem. As the details in Table I and the figures in Pl. V show, the cross *R. vitifolius* × tetraploid raspberry gave hybrids which in morphology, chromosome number, sex and fertility closely match the loganberry; and like the loganberry they breed practically true. The fact that their fruit size does not quite range up to that of the loganberry does not detract from the plausibility of the hybrid view; rather it adds to it, for, as mentioned earlier, one would naturally suppose that the cultivated variety of *R. vitifolius* grown by Logan to have had larger fruits than those of the wild seedlings we used, and to have handed on large size to their hybrid progeny.

Darrow & Longley (1933) have raised other objections and made some highly speculative suggestions. First they suggest that *R. loganobaccus* is a haploid species derived from *R. ursinus* and *R. macropetalus*, but since *R. ursinus* is 8*x*, and *R. macropetalus* 12*x*, it is difficult to see how the loganberry which is 6*x* could have arisen in such a way from hybridization between these two species. They conclude, however, that the loganberry arose from a wild form which they have themselves designated as *R. loganobaccus*, but they state: "The Logan differs from the wild *R. loganobaccus* in its hermaphrodite flowers and red fruit." There is, therefore, a gross difference between *R. loganobaccus* as described by Darrow & Longley and the loganberry, *R. loganobaccus* Bailey. The former, as defined, is prevailingly unisexual, whereas the loganberry is hermaphrodite, and this and the difference in fruit colour, as we have seen, are two of the principal characters which separate the loganberry from *R. ursinus* and its allied species or variety *R. vitifolius*. It does not seem necessary to pursue this question.

The whole series of blackberry-raspberry crosses we have made at Merton, in which varying proportions of raspberry chromosomes are

included, show behaviour which is in complete agreement with the hybrid origin of the loganberry, and there can now be no doubt that the loganberry is a hybrid as originally supposed by the raiser, Judge J. H. Logan.

SUMMARY

1. Although the loganberry arose as recently as 1881, the details of its origin are in dispute. It has been held (1) that the loganberry is a hybrid, the result of a cross between a blackberry and a raspberry, and (2) that it is not a hybrid but a "direct derivative" of the wild blackberry or dewberry of California, *Rubus vitifolius*. The present experiments were planned to decide between the two theories.

2. From crossing *R. vitifolius*, 8*x*, with *R. idaeus*, 4*x*, a hybrid was obtained which in morphology, chromosome number, sex and fertility closely match the loganberry; like the loganberry it is hexaploid and nearly true-breeding.

3. Crosses made between *R. vitifolius*, *R. idaeus*, 2*x*, and the loganberry, in which *R. vitifolius* and *R. idaeus* chromosomes were brought together in different proportions, gave results which are also in agreement with the hybrid view.

4. The only conclusion which can be reached from the experiments is that the loganberry is a hybrid as originally supposed, derived from an unreduced male germ cell of a raspberry, which is known to correspond to the diploid type, and a normal reduced germ cell of the blackberry.

5. The breeding data suggest that in *R. vitifolius* the female is the heterozygous sex.

6. The effects of introducing different proportions of parental chromosomes into hybrids are correlated with differences in morphological and other characters. This results in the intergradation of characters, a common feature of polyploids, and sometimes in a change of dominance.

ACKNOWLEDGEMENT

I am indebted to Mr A. Gavin Brown for assistance in the breeding work.

REFERENCES

BAILEY, L. H. (1923). "Quidam Rubi Cultorum." *Gentes Herbarum*, **5**, 152–8.

CRANE, M. B. (1940). "Reproductive versatility in *Rubus*, I." *J. Genet.* **40**, 109.

—— (1940). "The origin and behaviour of cultivated plants." *The New Systematics* (ed. J. S. Huxley). Oxford.

CRANE, M. B. & DARLINGTON, C. D. (1927). "The origin of new forms in *Rubus*. I." *Genetica*, **9**, 241–78.

CRANE, M. B. & LAWRENCE, W. J. C. (1931). "Inheritance of sex, colour and hairiness in the raspberry, *Rubus idaeus* L." *J. Genet.* **24**, 243–55.

—— —— (1938). *The Genetics of Garden Plants*, 2nd ed. London: Macmillan.

DARROW, G. M. (1937). "Blackberry and raspberry improvement." *Yearb. U.S. Dep. Agric.* pp. 496–533.

DARROW, G. M. & LONGLEY, A. E. (1933). "Cytology and breeding of *Rubus macropetalus*, the logan and related blackberries." *J. agric. Res.* **47**, 315–30.

FOCKE, W. O. (1914). *Bibl. bot., Stuttgart*, heft 83, 79.

HEDRICK, U. P. (1925). *The Small Fruits of New York*. Albany, N.Y.

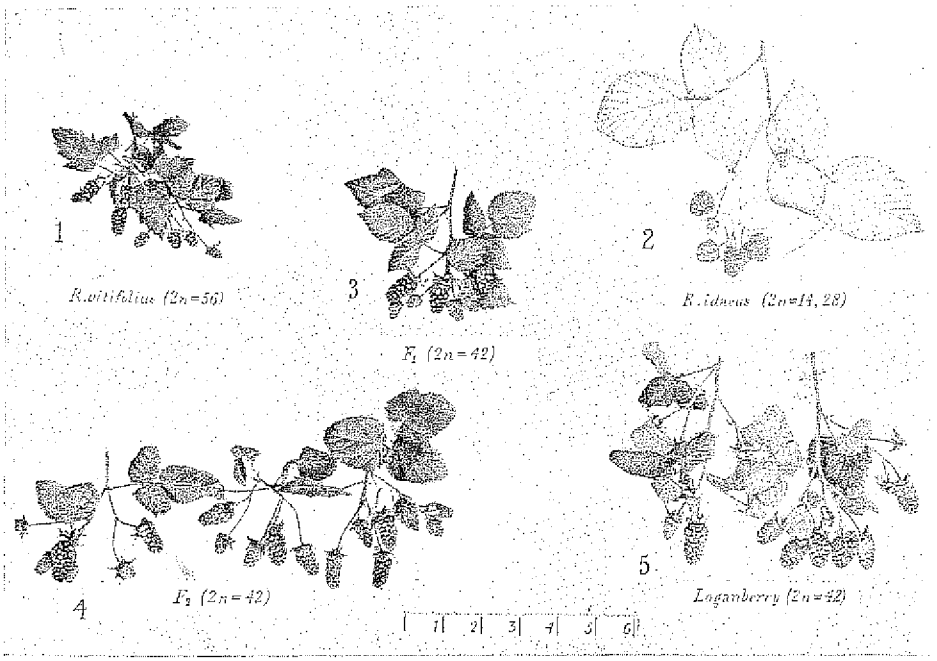
LEWIS, D. (1939). "Genetical studies in cultivated raspberries. I. Inheritance and linkage." *J. Genet.* **38**, 367–79.

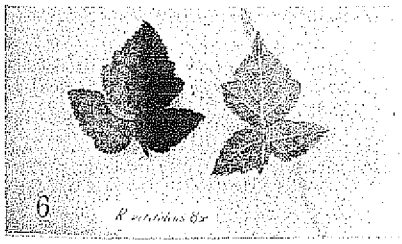
THOMAS, P. T. (1940*a*). "Reproductive versatility in *Rubus*. II." *J. Genet.* **40**, 119.

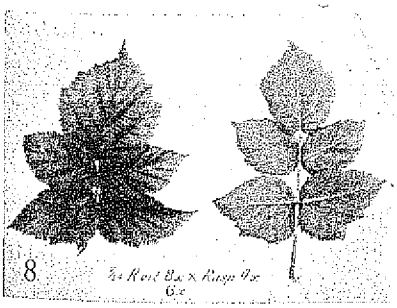
—— (1940*b*). "The origin of new forms in *Rubus*. III." *J. Genet.* **40**, 141.

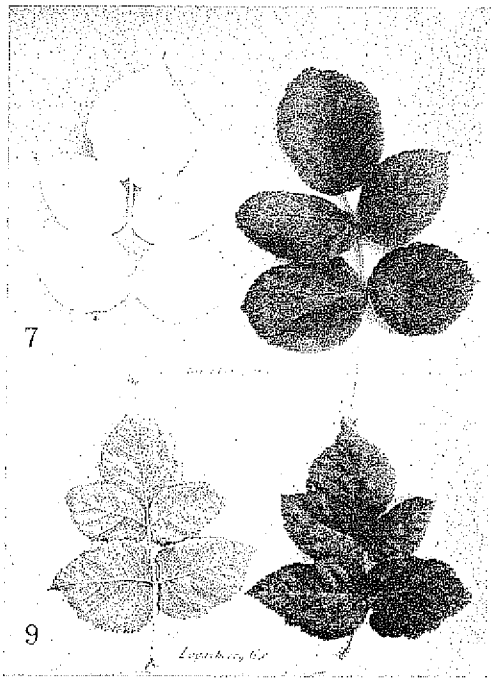
EXPLANATION OF PLATE V

Fig. 1. Fruits of *R. vitifolius*, showing round and elongated forms.
Fig. 2. Fruits of *R. idaeus*.
Fig. 3. Fruits of F_1 6*x* hybrid from *R. vitifolius* 8*x* × *R. idaeus* 4*x*.
Fig. 4. Fruits of F_2 from *R. vitifolius* × *R. idaeus* 4*x*.
Fig. 5. Fruits of *R. loganobaccus*.
Fig. 6. Leaves of *R. vitifolius*.
Fig. 7. Leaves of *R. idaeus* 4*x*.
Fig. 8. Leaves of F_1 6*x* hybrid from *R. vitifolius* 8*x* × *R. idaeus* 4*x*.
Fig. 9. Leaves of *R. loganobaccus*.


1
R. wilfolius (2n=56)
3
F1 (2n=42)
2
R. idaeus (2n=14, 28)
4
F2 (2n=42)
5
Loganberry (2n=42)


6


8


7
9