A LETHAL FACTOR IN CREPIS EFFECTIVE ONLY IN AN INTERSPECIFIC HYBRID*

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HISTORICAL INTRODUCTION

BABCOCK and COLLINS (1920, a and b) described hybrids between *Crepis capillaris* (L.) Wallr. ($n=3$) and *C. tectorum* L. ($n=4$) which died after developing to the cotyledon stage. Similar results were obtained by NAWASCHIN (1926) but later (1927) he reported a spontaneous *capillaris-tectorum* hybrid which developed normally. He suggested that the phenomenon might be associated with heterozygosity of the parents and later he obtained viable artificial hybrids (unpublished data). *C. capillaris* and *C. tectorum* are taxonomically more closely related than some other species of the genus which produce vigorous interspecific hybrids and it was an interesting result when early attempts to cross them gave inviable seedlings only.

Following the investigations of BABCOCK and COLLINS, Professor BABCOCK's assistant, Mr. C. W. HANEY, in 1924 again crossed these two species, and out of the five populations which he obtained, four contained 69 hybrids all of which died, but a fifth was made up of 40 hybrids, 20 of which died at the cotyledon stage but 20 matured as large vigorous hybrids. Figure 1 shows the parental species and one of these F_1 hybrids at maturity. The hybrids were intermediate or more like *capillaris* in habit of growth but in most other characters were more like *tectorum*. They were nearly sterile.

In the summer of 1926 the writer was given the material to determine if possible whether there was a factorial basis for the phenomenon just de-

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scribed. The investigation was carried out in the laboratories of the Division of Genetics, UNIVERSITY OF CALIFORNIA. The writer wishes to express her thanks to Mr. C. W. HANEY for his advice and assistance in the culture of plants as well as for the data given above. The plan of investigation was suggested by Professor E. B. BABCOCK and it is a pleasure for the

FIGURE 1.—Typical plants of *C. tectorum*, F_1 *C. capillaris-tectorum* and *C. capillaris* at maturity.

writer to acknowledge her indebtedness to him and to Professor J. L. COLLINS for the material and for helpful advice throughout the course of the work.

MATERIALS AND METHODS

Crepis is a genus of the Cichorieae tribe of the Compositae. *C. capillaris*, outstanding among flowering plants for its small chromosome number, belongs to the same section (*Eucrepis*) of the genus as *C. tectorum* (BABCOCK and LESLEY 1926). They differ chiefly in leaf shape, habit of growth, flower color, and shape and size of the achenes.

The *capillaris* plant (X.23.1) used in the cross which gave half viable hybrids was a stray plant picked up in the greenhouse by Mr. HANEY and is probably from one of the European strains. The designation X has been kept for the progeny of this plant throughout the investigation. It gave

rise to a particularly vigorous and early-flowering strain, producing under favorable conditions many branches bearing a large number of heads (figure 1). Most plants fruit well in the greenhouse or outdoors. The *tectorum* plant (T.23.1498-4) was one grown from original seed obtained from the COPENHAGEN BOTANICAL GARDEN, and its progeny have been designated by the accession number 1498. It is a vigorous uniform strain and sets fruit fairly well under bags.

The method of pollination used was a modification of that described by COLLINS (1922). The ligules and stamen tubes were removed from the outer row of florets on a head shortly after these florets opened. The unopened florets were removed and the pollen was washed from the styles with a stream of water from a dentist's chip blower. The head was then encased in a light paper bag to dry and to await pollination when the stigmatic branches should be separated. Pollination was usually carried out on the same or the succeeding day by rubbing the stigmas with opened heads of the plant to be used as a male parent. In the first season of crossing (1927) unprotected heads which had opened only the morning they were used were occasionally selected to provide pollen, but experience showed that even in that short time contamination might have taken place and in later investigations only heads protected by bags were used. The pollinated heads were again bagged and removed when the achenes were mature, about three weeks later.

The number of selfed plants obtained by this method of hybridization with *capillaris* as the female parent was small, averaging a little more than 2 percent in 1927 when 34 pure *capillaris* and 1664 F₁ hybrids were obtained. Seventeen of these *capillaris* plants comprised two whole populations. This does not include the four haploid plants of *C. capillaris* which were found in these cultures. A preliminary note on the occurrence of two of them has been published (HOLLINGSHEAD 1928), and it is hoped to report on them in detail in a later paper. The cross was usually made on *capillaris* since it was early learned that the reciprocal (at least the one involving the 1498 strain of *tectorum*) was only rarely successful and that selfed progeny occurred relatively more often. Only six of the *capillaris-tectorum* hybrids recorded in this paper were from achenes produced on *tectorum* plants. BABCOCK and COLLINS (1920 a and b) showed that the reciprocal hybrids obtained in their investigations were inviable and those obtained by the writer have been grouped together in the data given below.

The progeny of the original *tectorum* plant, T.23.1498-4, were from achenes produced on the plant while isolated from other *tectorum* plants in the greenhouse. All other *tectorum* 1498 seed was taken from bagged, or in

one instance, caged plants. The achenes were planted in sterilized sand and the very young seedlings were transplanted to flats or pots.

INVESTIGATIONS INVOLVING THE 1498 STRAIN OF *TECTORUM*

When the writer took up the work the problem was to determine (1) whether the difference between the normal and abnormal hybrids was due to one or more factors, and (2) if so, from which parent they came. The *capillaris* parent of the hybrid population of which half grew to maturity was also the parent of another population of 57 hybrids all of which died. This indicated that it was perhaps the *tectorum* parent which was responsible for the different behavior of this population. The 1:1 ratio of viable to inviable hybrids suggested that this plant might have been heterozygous for a lethal factor which killed the interspecific hybrid into which it entered. To test this hypothesis it was planned to grow a progeny of this *tectorum* plant and to cross each individual of it to *capillaris*. If the *tectorum* parent had been heterozygous for an interspecific lethal the progeny should be segregating for it and the genotypic constitution of each plant should be indicated by the kind of hybrids it produced when crossed to *capillaris*.

When the investigation was begun in August 1926 there were growing a number of *tectorum* plants, T.26.1498-1 to 30, progeny of this original *tectorum* T.23.1498-4. Most of them were dead or dying but a few, after being cut back, produced some more heads. They were used chiefly as male parents in crosses with *capillaris*, and some hybrid achenes were obtained. Three strains of *capillaris* were used but most of the crossing involved a plant of the X strain. The possibility that the *capillaris* parent might have something to do with the inviability of the hybrid offspring was constantly in mind throughout the early part of the work and this was the chief reason why the X strain, the one involved in the cross which first gave viable hybrids, was the one chiefly used. Evidence to be given later indicated that the *capillaris* plants used had no effect on the viability of the hybrid offspring and in the tables the hybrids are grouped without regard to the *capillaris* parent.

The achenes obtained from these first crosses were planted in December, 1926, but unfortunately the young plants were attacked by red spiders and in a few cases it was difficult to tell whether the seedlings died because of the spiders or whether they were exhibiting the phenomenon which had come to be known as "dying at the cotyledon stage." The results of this preliminary work are given in the first four lines of table 1. It was suspected that those hybrids in the progenies of T.26.1498-26 and T.26.1498-

24 which died owed their death to the spider attack and this was substantiated by investigations to be described later.

Hoping to obtain plants for crossing during the winter months another lot of achenes from the original *tectorum* T.23.1498-4 was planted in August, 1926 and grown in the greenhouse under the numbers T.26.1498-60 to -95 and at the same time some *capillaris* strains were planted. The *tectorum* plants which first sent up flower stalks were attacked by spiders and did not prove to be very vigorous, while the *capillaris* had not yet bloomed. It was decided that conditions were unfavorable for hybridization during the winter and the plants were put outside in the hope of keeping them till spring. Most of them died but a few bloomed late enough in the spring to be available for crossing. The last of the achenes from the original *tectorum* plant were sown in February, 1927, and the plants were grown under the numbers T.27.1498-21 to 40. The population was a vigorous rather uniform one with no outward sign of a lethal factor present in any of the plants.

This provided in June, 1927, a group of *tectorum* plants, progeny of the original T.23.1498-4, each of which was crossed to *capillaris*. An effort was made to obtain at least twenty hybrid achenes from each *tectorum* parent to ensure a progeny large enough to make reasonably valid the indicated parental genetic constitution. As table 1 shows, many more than twenty were obtained in most cases, but low germination in some instances greatly reduced the number of hybrids obtained below the number expected. Variation in percentage of germination characterized the whole investigation and in a few cases the number of hybrids obtained was too small to indicate the parental constitution and these have been omitted in this table.

The results obtained were in agreement with the hypothesis that this population of *tectorum* plants was segregating for a lethal factor effective in an interspecific hybrid but without effect on *tectorum*. The results are summarized in table 1. The hybrids are grouped with respect to the *tectorum* parent and each group will be described as a "population" although in most cases the hybrids in a group were obtained from two or more *capillaris* plants. The footnotes to this table and to those which follow explain why a few hybrids were not classified. The one case here attributed to experimental error is probably due to contamination of heads used for pollination. As the table shows, some *tectorum* plants gave hybrids, all of which lived, indicating no lethal in the parent (*L L*). A larger group gave hybrids, part of which lived and part of which died, indicating a parent heterozygous for the lethal (*L l*). Some gave hybrids, all of which died,

indicating parents homozygous for the lethal (ll). The letters l , for the lethal, and L , for the allelomorph, have been assigned arbitrarily and do not indicate any dominant or recessive relationships.

TABLE 1

F₁ hybrids obtained by crossing progeny of original C. tectorum plant T.23.1498-4 to capillaris.

tectorum PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED ³	LIVED	DIED	GENOTYPE OF tectorum PARENT
T. 26. 1498-26	26	21		18	3	$L L^1$
" " -24	32	13		12	1	$L L^1$
" " -19	14	9		0	9	$l l$
" " -23	18	7		0	7	$l l$
T. 26. 1498-63	98	58		0	58	$l l$
" " -68	39	25		0	25	$l l$
" " -77	37	15		15	0	$L L$
" " -78	24	15		15	0	$L L$
" " -82	43	15		15	0	$L L$
" " -84	40	18	1	17	0	$L L$
" " -86	9	7		5	2	$L l$
" " -88	48	40		0	40	$l l$
" " -91	26	12	1	11	0	$L L$
T. 27. 1498-21	44	39	1	16	22	$L l$
" " -22	45	32		32	0	$L L$
" " -23	47	22		18	4	$L l$
" " -24	29	11		11	0	$L L$
" " -26	27	13		0	13	$l l$
" " -27	54	45		20	25	$L l$
" " -28	26	18		9	9	$L l$
" " -29	23	23		10	13	$L l$
" " -30	32	16	1	7	8	$L l$
" " -31	71	47	1	0	46	$l l$
" " -32	28	21		7	14	$L l$
" " -34	36	30		12	18	$L l$
" " -35	34	22		12	10	$L l$
" " -36	43	23		0	23	$l l$
" " -37	51	30		15	15	$L l$
" " -38	24	14		5	9	$L l$
" " -39	23	8		4	4	$L l$
" " -40	32	12		11	1 ²	$L L$

$LL : Ll : ll$

10: 13: 8

¹ Red spiders attacked the young plants. Progeny tests (see tables 2 and 3) showed the *tectorum* parents were free from the lethal.

² Probably due to experimental error, the chances of obtaining such a ratio from a heterozygous parent being 3 in 1000.

³ Did not survive transplanting.

As noted above two of the *tectorum* plants tested in 1926 gave hybrids most of which lived, and presumably those which died owed their death to red spiders. In order to prove that these two plants were really free from the lethal, progenies of each of them were grown in 1927 and crossed to *capillaris*. The results are summarized in tables 2 and 3. Nine plants of the progeny of T.26.1498-26 gave 148 hybrids, all living, indicating they were free from the lethal. The chance of obtaining nine homozygous plants from a heterozygous parent is only 1 in 512 so that it is most probable that the *tectorum* grandparent of these hybrids, T.26.1498-26, was free from the lethal and it has been so classified. Fifteen plants of the progeny of T.26.1498-24 gave 292 hybrids of which only one died. It was in a population of 25 hybrids and has been attributed to experimental error. A progeny test of its parent, T.27.1498-11 (table 4), showed no evidence of a lethal. These results indicate that the *tectorum* grandparent, T.26.1498-24, was also free from the lethal.

TABLE 2
F₁ hybrids obtained by crossing progeny of T.26.1498-26 to capillaris.

<i>tectorum</i> PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED	LIVED	DIED	GENOTYPE OF <i>tectorum</i> PARENT
T. 27. 1498-41	50	23		23		<i>L L</i>
" " -42	25	17		17		<i>L L</i>
" " -43	21	17		17		<i>L L</i>
" " -45	47	27		27		<i>L L</i>
" " -46	27	7		7		<i>L L</i>
" " -47	14	6		6		<i>L L</i>
" " -48	33	28		28		<i>L L</i>
" " -49	39	15		15		<i>L L</i>
" " -50	20	8		8		<i>L L</i>
Total	276	148		148		

The genotypes of the progeny of the original *tectorum* plant having been established the distribution proved to be 10 *LL* : 13 *Ll* : 8 *ll*. The expected distribution for a single factor difference would be 7.75 *LL* : 15.5 *Ll* : 7.75 *ll*. Such a difference between the actual and the expected as tested by the χ^2 method would occur six times in ten by random sampling and the distribution can therefore be accepted as agreeing with the theoretical expectation.

In order to further establish the conclusion that we were dealing with a simple lethal factor which did not affect the *tectorum* plant bearing it but which caused the death of the interspecific hybrid into which it entered

another season's work was planned. The genotypes of the various *tectorum* plants having been determined and achenes having been obtained from

TABLE 3
F₁ hybrids obtained by crossing progeny of T.26.1498-24 to capillaris.

<i>tectorum</i> PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED ¹	LIVED	DIED	GENOTYPE OF <i>tectorum</i> PARENT
T. 27. 1498- 2	23	9		9		<i>L L</i>
" " - 3	27	16		16		<i>L L</i>
" " - 4	42	14	1 ¹	13		<i>L L</i>
" " - 5	47	27		27		<i>L L</i>
" " - 6	23	22		22		<i>L L</i>
" " - 8	25	10		10		<i>L L</i>
" " - 9	22	12		12		<i>L L</i>
" " -10	35	25		25		<i>L L</i>
" " -11	37	25		24	1 ²	<i>L L</i>
" " -12	59	28	1 ³	27		<i>L L</i>
" " -14	20	18		18		<i>L L</i>
" " -15	37	17		17		<i>L L</i>
" " -16	37	26		26		<i>L L</i>
" " -18	32	18		18		<i>L L</i>
" " -20	45	27		27		<i>L L</i>
Total	511	294	2	291	1	

¹ Abnormal growing point and thick leathery leaves. Died very early.

² Doubtless due to experimental error.

³ Did not survive transplanting.

most of them, two of each genotype were chosen to provide progeny for further work. The six plants and their progenies were as follows:

<i>Genotype</i>	<i>Plant</i>	<i>Progeny</i>
<i>L L</i>	{ T. 27. 1498-11	28H. T. 1498D-1 to-24
	{ T. 27. 1498-15	28H. T. 1498E-1 to-16
<i>L l</i>	{ T. 27. 1498-30	28H. T. 1498F-1 to-24
	{ T. 27. 1498-34	28H. T. 1498G-1 to-32
<i>l l</i>	{ T. 27. 1498-31	28H. T. 1498H-1 to-24
	{ T. 27. 1498-36	28H. T. 1498 I-1 to-16

As many plants as possible of each progeny were crossed to *capillaris* in the summer of 1928. The achenes obtained were sown in the fall of 1928 and the results obtained are summarized in tables 4 to 9.

The progeny of the first *L L* plant, T.27.1498-11, gave 22 hybrid populations containing 249 plants all developing normally (table 4). Seventeen

of these populations contained at least six hybrids, the smallest number from which it is possible to determine the parental genotype with any degree of certainty (the chance of obtaining six viable hybrids from a heterozygous parent is 1 in 64), and these were classified *L L*, while the nature of the other five populations with fewer hybrids was in agreement with the expectation that all the *tectorum* plants of this group were *L L*. The

TABLE 4
F₁ hybrids obtained by crossing progeny of T.27.1498-11 (L L) to capillaris.

<i>tectorum</i> PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED	LIVED	DIED	GENOTYPE OF <i>tectorum</i> PARENT
28H.T.1498D- 1	15	6		6		<i>L L</i>
" " - 2	27	22		22		<i>L L</i>
" " - 3	2	2		2		
" " - 4	15	13		13		<i>L L</i>
" " - 5	14	12		12		<i>L L</i>
" " - 6	27	10		10		<i>L L</i>
" " - 8	18	16		16		<i>L L</i>
" " - 9	10	10		10		<i>L L</i>
" " -10	10	7		7		<i>L L</i>
" " -12	11	9		9		<i>L L</i>
" " -13	29	13		13		<i>L L</i>
" " -14	16	5		5		
" " -15	25	24		24		<i>L L</i>
" " -16	26	17		17		<i>L L</i>
" " -17	19	11		11		<i>L L</i>
" " -18	9	8		8		<i>L L</i>
" " -19	8	5		5		
" " -20	20	14		14		<i>L L</i>
" " -21	23	21		21		<i>L L</i>
" " -22	9	5		5		
" " -23	21	15		15		<i>L L</i>
" " -24	5	4		4		
Total	359	249		249		

progeny of the second *L L* plant, T.27.1498-15, gave 10 hybrid populations including in all 149 hybrids, all normal (table 5). Eight of these populations contained enough hybrids to enable the parents to be classified as normal. This confirms the expectation that plants genetically *L L* give only *L L* progeny and that races were isolated free from the lethal.

The progeny of T. 27.1498-30 (*L l*) were segregating for the lethal as shown by the occurrence again of hybrid populations of three types: all living; part living, part dying; all dying (table 6). The distribution was 6 *L L* : 11 *L l* : 7 *ll* a close approximation to the expected 6 *L L* : 12 *L l*

TABLE 5
F₁ hybrids obtained by crossing progeny of T.27.1498-15 (L L) to capillaris.

<i>tectorum</i> PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED	LIVED	DIED	GENOTYPE OF <i>tectorum</i> PARENT
28H.T. 1498E- 2	32	26		26		L L
" " - 4	19	18		18		L L
" " - 5	2	2		2		
" " - 8	53	46		46		L L
" " -10	10	5		5		
" " -11	15	12		12		L L
" " -12	11	8		8		L L
" " -14	28	17		17		L L
" " -15	24	9		9		L L
" " -16	6	6		6		L L
Total	200	149		149		

TABLE 6
F₁ hybrids obtained by crossing progeny of T.27.1498-30 (L l) to capillaris.

<i>tectorum</i> PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED ¹	LIVED	DIED	GENOTYPE OF <i>tectorum</i> PARENT
28H.T. 1498F- 1	19	6		6	0	L L
" " - 2	24	11		4	7	L l
" " - 3	23	16		10	6	L l
" " - 4	27	12		9	3	L l
" " - 5	22	14		6	8	L l
" " - 6	21	15		0	15	l l
" " - 7	28	13		0	13	l l
" " - 8	17	14		14	0	L L
" " - 9	14	9		6	3	L l
" " -10	26	13		0	13	l l
" " -11	19	14		4	10	L l
" " -12	36	24		11	13	L l
" " -13	33	15		15	0	L L
" " -14	17	6		6	0	L L
" " -15	27	24		13	11	L l
" " -16	31	10		0	10	l l
" " -17		7		2	5	L l
" " -18		14		0	14	l l
" " -19		9	1	0	8	l l
" " -20	28	13		9	4	L l
" " -21	22	18		18	0	L L
" " -22	22	11		11	0	L L
" " -23	24	7		5	2	L l
" " -24	21	11		0	11	l l

L L: L l: l l

6: 11: 7

¹ Did not survive transplanting.

: 6 *ll*. Similarly the progeny of T.27.1498-34 (*Ll*) showed a distribution 4 *LL* : 19 *Ll* : 4 *ll* (table 7). Such a deviation from the expected 6.75 *LL* : 13.5 *Ll* : 6.75 *ll* would occur 11 times in 100 by random sampling and the distribution is therefore in agreement with expectation.

TABLE 7
F₁ hybrids obtained by crossing progeny of T.27.1498-34 (Ll) to capillaris.

<i>tectorum</i> PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED	LIVED	DIED	GENOTYPE OF <i>tectorum</i> PARENT
28H.T. 1498G- 1	20	12		7	5	<i>Ll</i>
" " - 2	26	20		0	20	<i>ll</i>
" " - 3	23	5		2	3	<i>Ll</i>
" " - 5	10	8		3	5	<i>Ll</i>
" " - 7	29	17		17	0	<i>LL</i>
" " - 9	25	7		3	4	<i>Ll</i>
" " -10	23	5		2	3	<i>Ll</i>
" " -11	18	14		9	5	<i>Ll</i>
" " -12	15	13		0	13	<i>ll</i>
" " -13	31	17		9	8	<i>Ll</i>
" " -14	19	4		3	1	<i>Ll</i>
" " -15	43	18		9	9	<i>Ll</i>
" " -16	29	6		6	0	<i>LL</i>
" " -17	45	26		26	0	<i>LL</i>
" " -18	43	13		7	6	<i>Ll</i>
" " -19	33	32	1 ¹	14	17	<i>Ll</i>
" " -20	35	13		7	6	<i>Ll</i>
" " -21	29	19		9	10	<i>Ll</i>
" " -22	13	12		6	6	<i>Ll</i>
" " -23	20	3		1	2	<i>Ll</i>
" " -24	19	8		4	4	<i>Ll</i>
" " -25	21	16		0	16	<i>ll</i>
" " -26	30	13		7	6	<i>Ll</i>
" " -27	30	21	1 ²	20	0	<i>LL</i>
" " -28	21	16		5	11	<i>Ll</i>
" " -30	20	11		9	2	<i>Ll</i>
" " -32	21	7		0	7	<i>ll</i>

LL: *Ll*: *ll*

¹ Did not survive transplanting.

4: 19: 4

² Abnormal, died early.

The progeny of T.27.1498-31 (*ll*) gave 19 hybrid populations containing 157 plants all of which were inviable (table 8). Eleven of these contained enough hybrids to enable the parents to be classified as *ll*. The progeny of T.27.1498-36 (*ll*) gave 14 hybrid populations containing 185 seedlings, all of which died (table 9). Twelve of these contained enough hybrids to enable the parents to be classified as *ll*. Here races were established homozygous for the lethal.

TABLE 8
F₁ hybrids obtained by crossing progeny of T.27.1498-31 (l l) to capillaris.

<i>tectorum</i> PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED	LIVED	DIED	GENOTYPE OF <i>tectorum</i> PARENT
28H.T. 1498H- 2	17	12			12	l l
" " - 3	10	7			7	l l
" " - 4	17	13			13	l l
" " - 5	5	4			4	
" " - 6	9	9			9	l l
" " - 7	17	13			13	l l
" " - 8	12	11			11	l l
" " - 9	14	13			13	l l
" " -11	7	3			3	
" " -12	13	11			11	l l
" " -13	23	9			9	l l
" " -14	4	1			1	
" " -15	27	19			19	l l
" " -16	27	1			1	
" " -17	22	18			18	l l
" " -19	2	2			2	
" " -21	7	5			5	
" " -23	2	1			1	
" " -24	7	5			5	
Total	242	157			157	

TABLE 9
F₁ hybrids obtained by crossing progeny of T.27.1498-36 (l l) to capillaris.

<i>tectorum</i> PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED ¹	LIVED	DIED	GENOTYPE OF <i>tectorum</i> PARENT
28H.T. 1498I- 1	21	8			8	l l
" " - 2	16	3			3	
" " - 3	37	5			5	
" " - 4	22	14			14	l l
" " - 5	22	7			7	l l
" " - 6	6	6			6	l l
" " - 7	29	16			16	l l
" " - 8	27	15			15	l l
" " -10	29	26			26	l l
" " -11	26	11			11	l l
" " -13	31	27			27	l l
" " -14	27	25			25	l l
" " -15	20	16	1		15	l l
" " -16	8	7			7	l l
Total	321	186	1		185	

¹ Did not survive transplanting.

Figures 2, 3, and 4 show three flats of young hybrids whose *tectorum* parents were the progeny of plants of the three genotypes. Figure 2 shows hybrids whose various *tectorum* parents were the progeny of *L L* plants—the hybrids are all developing normally. Figure 3 shows hybrids whose *tectorum* parents were the progeny of *L l* plants. Each kind of hybrid population obtained from a segregating group of *tectorum* plants is represented: all living; part living; part living, part dying; all dying.

FIGURE 2.—*C. capillaris-tectorum* hybrids whose *tectorum* parents were *LL*. A label marks the first plant of a population numbering from below in each row.

Figure 4 shows hybrids whose *tectorum* parents were the progeny of *ll* plants—all are dying at the cotyledon stage.

Table 10 summarizes the distribution of the three genotypes in the original segregating population and in the two just described. The agreement between the total actual and the expected is very close.

It was stated earlier that the *capillaris* parent of a hybrid, so far as has been determined, had no effect on the expression of the lethal. Table 11 shows the nature of eight populations of hybrids classified with respect

FIGURE 3.—*C. capillaris-tectorum* hybrids whose *tectorum* parents were *ll*.

TABLE 10

Distribution of tectorum plants in the three segregating populations investigated.

HETEROZYGOUS tectorum PARENT	SEGREGATING POPULATION	<i>LL</i>	<i>Ll</i>	<i>ll</i>
T. 23. 1498-4	(T. 26. 1498-1 to 91 (T. 27. 1498-21 to 40	10	13	8
T. 27. 1498-30	28H. T. 1498F-1 to 24	6	11	7
T. 27. 1498-34	28H. T. 1498G-1 to 32	4	19	4
	Total	20	43	19
	Expected	20.5	41	20.5

FIGURE 4.—*C. capillaris-tectorum* hybrids whose *tectorum* parents were *ll*.

to their *capillaris* parents. An inspection of the table shows that the various hybrid groups obtained from different *capillaris* parents and the

TABLE 11
Eight hybrid populations classified with respect to their capillaris parents.

<i>tectorum</i> PARENT	<i>capillaris</i> PARENT	HYBRIDS LIVED	HYBRIDS DIED
T. 26. 1648-3	Crane 26-1	2	0
	X 26-2	8	0
T. 26. 1498-68	D 26-8	0	1
	X 27-3	0	2
	X 27H. 8-3	0	7
	X 27H. 21-4	0	15
T. 26. 1498-91	D 26-8	2	0
	X 27-4	2	0
	X 27H. 21-4	7	0
T. 27. 1498-22	Crane 27H. 9-6	6	0
	X 27H. 20-6	26	0
T. 27. 1498-36	Crane 27H. 9-6	0	7
	X 27-4	0	3
	X 27H. 20-6	0	3
	X 27H. 8-11	0	10
T. 27. 1498-37	Crane 27H. 9-6	4	8
	X 27H. 8-5	8	3
	X 27H. 8-3	3	4
T. 27. 1498	D 26-2	0	1
	X 27-3	0	5
	X 27H. 20-6	0	11
	X 27H. 21-4	0	29
T. 27. 1498-34	D 26-3	2	0
	D 26-8	0	1
	X 27H. 20-6	6	7
	X 27H. 8-7	4	8
	X 27-3	0	2

same *tectorum* parent behave similarly with respect to the lethal. There were three strains of *capillaris* involved. The origin of the X strain has been described. *Capillaris* D is an inbred strain from material collected for Professor J. L. COLLINS near Eureka, California. The Crane strain is from a derivative of a cross between D and another inbred strain from the same

locality. The Crane and D strains have less vigorous habit and mature later than X and the Crane strain was segregating for the "chlorina" character described by COLLINS (1924).

It was expected on the basis of a simple lethal factor that the hybrid progeny of heterozygous (*L l*) *tectorum* plants would give a 1:1 ratio of living to dying individuals. In no case, except the one attributed to experimental error (progeny of T.27.1498-40, table 1), was a distribution found which could not be harmonized with such a ratio. In many cases a good 1:1 ratio was obtained in a single population; in many others the number was too small to give any significance to the distribution. On totalling all the populations from *L l* *tectorum* parents the distribution was found to be 346 living to 339 dying, a good 1:1 ratio.

The percentage of germination of the hybrid achenes is of some interest. As may be seen from the tables wide variations occurred. Table 12 shows,

TABLE 12
Percentage of germination of capillaris-tectorum (1498) hybrids grown in the spring and fall of 1928.

	SPRING 1928			FALL 1928			TOTAL		
	ACHENES	GERMI- NATED	PERCENT- AGE	ACHENES	GERMI- NATED	PERCENT- AGE	ACHENES	GERMI- NATED	PERCENT- AGE
Populations from <i>L L</i> parents	1063	572	53.81	822	538	65.45	1885	1110	58.88
Populations from <i>ll</i> parents	326	206	63.19	773	461	59.64	1099	667	60.69
Populations from <i>L l</i> parents	431	295	68.44	729	374	51.30	1160	669	57.67
Total	1820	1073	58.96	2324	1373	59.08	4144	2446	59.02

however, that for large numbers the percentage is rather constant. The data include all the hybrids between *tectorum* 1498 and *capillaris* made in the summers of 1927 and 1928 and grown in the spring and fall of 1928 respectively (omitting 3 populations in table 6 whose seed pots were upset and an unknown number of achenes lost). The average percentage amounts to only 59.02 percent. There is no consistent difference either between the two crops or between hybrid progenies of parents of different genotypes. These data show that there is no differential germination of hybrids with respect to the lethal and this conclusion is confirmed by the 1:1 ratio of living to dying hybrids from heterozygous parents.

The inviable hybrids obtained by BABCOCK and COLLINS in only a few cases developed tiny first leaves; usually development ceased before any trace of leaves was to be seen. This condition characterized most of the inviable hybrids which were obtained in this investigation but some developed further. Figure 5 is a picture of a normal hybrid and six inviable ones

FIGURE 5.—A viable F_1 *C. capillaris-tectorum* F_1 hybrid (centre) and six inviable ones chosen to illustrate various degrees of development to which inviable hybrids attained.

transplanted into a small box from their positions in the flats. The inviable ones were chosen to illustrate the various degrees of development to which the hybrids attained. Figure 6 is a picture of the same box of hybrids a month later. In the interval the first four inviable ones died without developing further, but two continued to produce small granular leaves, darker

green in color and coarser in texture than normal leaves. They were showing signs of coming death when the picture was taken. In only a few cases did the inviable hybrids develop to a stage comparable with these last two

FIGURE 6.—The same box of hybrids a month later.

Three hybrids which had ceased development at the cotyledon stage and two which were obviously abnormal but which had produced a number of leaves were fixed and sectioned for anatomical examination. Normally developing hybrid seedlings of the same age were examined for

comparison. The most striking feature of the inviable hybrids was the occurrence of masses of disintegrating cells which appeared like black slime. This condition was especially characteristic of those seedlings which had ceased development early, being very prevalent in the region just back of the plumule and around the vascular system of the stem and cotyledons. While it was much less prevalent in abnormal hybrids which produced a number of leaves it was more noticeable in them than in normal hybrid seedlings in which there was little or no disintegration. All of the inviable hybrids showed disorganized parenchymatous tissue, the cells being irregular in arrangement and exhibiting striking variations in size and shape which in some cases were probably due to the collapse of intervening cell walls. The plumules of the inviable hybrids which produced no leaves showed several buds in various stages of early development, most of the tissues being still meristematic. The beginnings of differentiation were to be seen in the larger size and vacuolated appearance of some of the cells and in the occurrence of strands of elongated meristematic cells extending upwards through the undeveloped buds. In one plant tracheids were observed extending to within two cell layers of the surface of a bud. These tracheids were much shorter than the recently differentiated tracheids of normal hybrids. The occurrence of tracheids in the meristematic tissue of a very small developing bud is quite abnormal.

The inviable hybrids which developed tiny leaves were still growing when fixed and showed a normal growing point and buds in various stages of development. The shape of the young plant was broad and flat in contrast with the narrower and more upstanding normal hybrid. Irregularity in arrangement and size of the cells of the parenchymatous tissue and the occurrence of small areas of dead cells distinguished them from normal hybrids. Particularly interesting was the occurrence of groups of small cells, sometimes meristematic, which in shape, size, and position resembled axillary buds. In no case did they appear to be developing into leaves. No such structures were seen in normal hybrids.

BABCOCK and COLLINS (1920a) described patches of black slime and irregularities in parenchymatous tissue in their inviable hybrids. Patches of embryonic tissue and of tracheary cells were distributed here and there among the larger vegetative cells. While this latter condition was not observed in these hybrids it could hardly be expected that disorganization causing cessation of development would manifest itself always in the same way and it has been shown above that the various inviable hybrids examined differed noticeably in the degree and kind of irregularities.

INVESTIGATIONS INVOLVING OTHER STRAINS OF TECTORUM

Concurrently with the investigations just described crosses were made in an attempt to discover how widely distributed was the supposed lethal factor in *tectorum*. Achenes from a number of sources obtained over a period of years were sown and as many plants as possible were tested by crossing to *capillaris*. Table 13 gives the sources of the *tectorum* plants used, and the number and kinds of hybrids obtained from them.

TABLE 13
F₁ hybrids obtained by crossing tectorum plants of various origins to capillaris.

ORIGIN OF <i>tectorum</i> PARENT	<i>tectorum</i> PARENT	F ₁ ACHENES	GERMI- NATED	LIVED	DIED
Original seed from Stockholm Botanical Garden	T. 27.1066- 1	13	11	0	11
	" " - 2	20	10	0	10
	" " - 3	24	9	0	9
	" " - 4	19	10	0	10
Ditto	T. 27.1067- 1	21	10	0	10
Original seed? Chelsea Botanical Garden	T. 27.1503- 1	15	13	0	13
	" " - 2	14	13	0	13
	" " - 5	36	22	0	22
Copenhagen Botanical Garden through Nawaschin.	T. 27.1622- 2	8	8	0	8
	" " - 3	11	4	4	0
Ditto	T. 27.1644- 1	12	6	0	6
	" " - 2	22	15	0	15
	" " - 3	7	2	1	1
	" " - 4	14	10	6	4
Original seed from near Tomsk, Siberia.	T. 26.1648- 3	12	10	10	0
	T. 27.1648- 4	12	12	6	6
	" " - 9	27	21	12	9
Original seed from near Kiev.	T. 27.1689- 4	32	23	0	23
Progeny of T. 26.1700-6 (open), original seed from Insula Oland, Sweden.	T. 27.1700- 1a	23	3	3	0
	" " - 3a	22	18	9	9
	" " - 5a	31	18	18	0
	" " - 6a	13	3	3	0
	" " - 8a	10	6	0	6
	" " - 12a	10	10	6	4
Original seed from Upsala Botanical Garden through Berlin.	T. 27.1719- 1	26	15	0	15
Original seed from Stockholm Botanical Garden through Berlin.	T. 27.1726- 1	22	15	0	15

TABLE 13 (continued)

ORIGIN OF <i>tectorum</i> PARENT	<i>tectorum</i> PARENT	F ₁ ACHENES	GERMI- NATED	LIVED	DIED
Original seed from Stockholm Botanical Garden through Berlin.	T.27.1757- 3	11	4	0	4
Original seed from Copenhagen Botanical Garden through Berlin.	T.27.1758- 1	15	7	3	4
	" " - 2	10	6	0	6
	" " - 5	5	1	1	0
Original seed, unknown, through Berlin.	T.27.1760- 1	23	10	0	10
	" " - 2	28	8	0	8
	" " - 3	12	6	0	6
	" " - 4	29	12	0	12
Original seed from Stockholm Botanical Garden.	T.27.1883- 1	31	14	0	14
	" " - 2	11	7	0	7
	" " - 3	19	6	0	6
	" " - 4	28	12	0	12
	" " - 5	16	11	0	11
	" " - 6	9	3	0	3
	" " - 7	9	6	0	6
	" " - 8	20	15	0	15
	" " - 9	7	4	0	4
	" " -10	15	9	0	9

Most of the *tectorum* plants tested produced only inviable hybrids and would be classified as homozygous for the lethal. Two accessions, similar in appearance, obtained from Doctor NAWASCHIN and originally from COPENHAGEN BOTANICAL GARDEN were segregating for the lethal. Two plants of the 1648 strain from Tomsk, Siberia, were heterozygous. The population, T.27.1700-a, appeared to be segregating for the lethal, but since its parent, T.26.1700-6, was open-pollinated and the strain is highly self-sterile the lethal may have been introduced from another strain. A strain from the COPENHAGEN BOTANICAL GARDEN contained both the lethal and its allelomorph. From these results it may be seen that the plants to which the lethal can be traced definitely came either from the COPENHAGEN BOTANICAL GARDEN and are probably of Western European origin or from Tomsk in Central Siberia.

INVESTIGATIONS INVOLVING HYBRIDS BETWEEN TECTORUM AND OTHER SPECIES

These investigations were designed to determine whether the lethal which killed *capillaris-tectorum* F₁ hybrids would also be effective in hybrids between *tectorum* and other *Crepis* species. Table 14 shows the crosses

made and the results obtained. Part of the data on *tectorum-leontodontoides* crosses was kindly supplied by Miss PRISCILLA AVERY who was working with this cross.

TABLE 14
F₁ hybrids between tectorum and other species to show the effect of the lethal.

<i>tectorum</i> PARENT	F ₁ ACHENES	GERMINATED	UNCLAS- SIFIED	LIVED	DIED
28H.T.1498E-4 (L L) × <i>bursifolia</i>	4	2	..	2	0
28H.T.1498E-8 (L L) × <i>bursifolia</i>	6	3	..	3	0
28H.T.1498I-2 (l l) × <i>bursifolia</i>	16	3	..	0	3
T.27.1498-22 (L L) × <i>leontodontoides</i>	7	4	..	4	0
T.27.1498-23 (L l) × <i>leontodontoides</i>	15	10	1 ¹	6	3
28H.T.1498I-2 (l l) × <i>leontodontoides</i>	28	13	..	0	13
28H.T.1498H-15 (l l) × <i>leontodontoides</i>	4	4	..	0	4
T.27.1498-9 (L L) × <i>setosa</i>	13	10	..	10	0
T.27.1498-18 (L L) × <i>setosa</i>	22	10	..	10	0
T.27.1498-29 (L l) × <i>setosa</i>	9	7	..	7	0
28H.T.1498D-18 (L L) × <i>taraxacifolia</i>	3	2	..	2	0
28H.T.1498E-8 (L L) × <i>taraxacifolia</i>	1	1	..	1	0
28H.T.1498E-14 (L L) × <i>taraxacifolia</i>	4	4	..	4	0
28H.T.1498F-4 (L l) × <i>taraxacifolia</i>	9	8	..	8	0
T.27.1498-23 (L l) × <i>taraxacifolia</i>	6	3	..	3	0
28H.T.1498H-2 (l l) × <i>taraxacifolia</i>	3	2	..	2	0
28H.T.1498H-9 (l l) × <i>taraxacifolia</i>	3	2	..	2	0
28H.T.1498H-19 (l l) × <i>taraxacifolia</i>	2	2	..	1	1

¹ Died early.

The table shows that both viable and inviable hybrids resulted from *tectorum-bursifolia* and *tectorum-leontodontoides* crosses and that they occurred in the populations and in the proportions expected if the lethal were effective. The data on *tectorum-setosa* are not quite conclusive but indicate that the factor is ineffective here since seven viable hybrids were obtained from a *tectorum* plant heterozygous for the lethal and the chance of obtaining such a distribution if the lethal were effective is only 1 in 128.

The data on *tectorum-taraxacifolia* indicate the general ineffectiveness of the lethal in these hybrids. A heterozygous *tectorum* gave eight hybrids, all viable, and the chance of this occurring if the lethal were effective is 1 in 256. Four viable hybrids were obtained from *tectorum* parents homozygous for the lethal but from another one, one viable and one typically inviable hybrid were obtained. Whether the lethal occasionally manifests itself or whether this plant died from other causes has not been determined.

DISCUSSION

This is the first reported instance, so far as the writer knows, of a lethal factor which is effective only in an interspecific hybrid. The phenomenon described by SAX (1921) in hybrids between varieties of wheat resembles the one described here more closely than any other with which the writer is familiar. He describes hybrids between Bluestem and Amby, varieties of *Triticum vulgare*, which produced abnormal hybrids while these varieties crossed with other members of the *vulgare* group gave F_1 plants, fully fertile. The abnormal hybrids between these varieties "appeared to develop normally until they reached a height of 15 to 20 cm. They then ceased to increase in height although they were vigorous and stooled excessively. Often as many as 40 or 50 primary culms were formed but in no case did a true culm develop. The plants were observed for five months but did not develop further." In this case the cross was only a varietal one and the plants in question developed further than the inviable interspecific hybrids in this study. SAX suggested that the case could be analyzed by crossing the F_1 of Amby $\times$ Marquis with Bluestem. If a factor similar to the lethal in *Crepis tectorum* were involved, either this cross or the F_1 of Bluestem $\times$ Marquis crossed with Amby should reveal it.

In *Nicotiana* it has been shown by CLAUSEN (BABCOCK and CLAUSEN 1927) that different varieties of a species may give different results with respect to the vigor of hybrids with another species. A series of varieties of *N. Tabacum* were crossed with two varieties of *N. glauca*, one derived from a California source, the other from Argentine. "With the California variety of *N. glauca* the hybrids were uniformly weak with yellowish leaves short internodes, and a total growth not much greater than 2 feet. With the Argentine variety they were exceptionally vigorous with large dark leaves, long internodes and a height ranging from 6 to 12 feet according to the variety of *N. Tabacum* used." It would be of interest to know whether this difference in the F_1 hybrids could be ascribed to simple genetic differences between the varieties of *N. glauca*. Such results warn the investigator against drawing conclusions concerning taxonomic relationship from the viability of interspecific hybrids.

From an evolutionary standpoint there is no evidence as to whether this *Crepis* lethal or its allelomorph is the older. Both were found in Western European and Central Siberian strains, indicating a wide range for each. Since the lethal has no effect on the parental species, and since normal F_1 interspecific hybrids are almost sterile it is difficult to see how it has had any part in the later evolutionary development of the species in-

vestigated. If the lethal is the older its present existence may be a relic from a time when the species concerned were in the process of differentiation and it may have played a rôle in the maintenance of the ancestral stocks.

The nature of the causes of interspecific incompatibility has long been a matter of considerable interest and speculation. Genetic investigations are slowly bringing to light conditions which may constitute these causes. That crossability depends upon the particular parental variety used has been shown by BACKHOUSE (1916) and by GAINES and STEVENSON (1922) in wheat-rye crosses and later investigators (THOMPSON 1926, LEIGHTY and SANDO 1928) have confirmed this knowledge. The investigations of BACKHOUSE showed that the difference between the varieties of wheat in their ability to cross readily with rye might rest on a factor basis. Here the incompatibility between the parental species manifests itself in failure of fertilization or possibly early development but when that has been accomplished the hybrid grows vigorously. The existence of the lethal factor which operates to kill an interspecific hybrid at an early stage in development and the demonstration of its heritability in a simple Mendelian fashion is a point of importance in this connection.

As was pointed out above the designations *l* and *L* for the lethal and its allelomorph are not intended to indicate any dominant or recessive relationship. The fact that the lethal has no effect when present doubly in *tectorum* and that it exhibits its characteristic effect when present singly in the hybrid precludes any decision as to which, if either, is dominant.

Any discussion of the peculiar mode of behavior of this lethal factor must be purely speculative. Its lethal effect appears to be the result of failure of development at a stage when differentiation is the characteristic process. The ineffectiveness of the lethal in *tectorum* might indicate that this failure to develop normally involves some relationship between the gene complexes of the parental species. It has been shown (HOLLINGSHEAD 1928) that a plant will develop in a normal manner with a haploid complex of *capillaris* and it is likely that the same would apply to *tectorum*. It was suggested by BABCOCK (1924) that the mode of development determined by the haploid complex of the one species was incompatible with that determined by the haploid complex of the other. This hypothesis, however, does not explain why there is no apparent incompatibility between the mode of development determined by the *tectorum* complex containing the lethal allelomorph and that determined by the *capillaris* complex, nor between the modes of development of the *tectorum* complexes containing respectively the lethal and its allelomorph. If such an explanation was

the correct one it would mean that the mode of development determined by the *tectorum* complex containing the lethal allelomorph is compatible with either that determined by the *capillaris* complex or by the *tectorum* complex containing the lethal but that the last two are incompatible with each other.

The ineffectiveness of the lethal in *tectorum* might be explained by assuming an inhibitor. The lethal effect in the hybrid could be accounted for by assuming two genes in *capillaris* corresponding to those in *tectorum*, one recessive to the lethal and one dominant to the inhibitor. While without experimental foundation such an explanation is not inconceivable in view of the fact that GOULDEN (1925) and THOMPSON (1928) have found factors inhibiting the effect of dwarfing genes in wheat, and corresponding genes in two species of *Drosophila* have been established (MORGAN, BRIDGES and STURTEVANT 1925). Such an explanation would involve the assumption of the same or similar corresponding genes in the two species (*setosa* and *taraxacifolia*) which give hybrids unaffected by the lethal.

SUMMARY

Interspecific hybrids of *Crepis capillaris* and *C. tectorum* previously investigated developed only to the cotyledon stage. In renewed attempts to secure viable hybrids using different strains of the parental species one hybrid population was obtained of which half matured normally and half were inviable. Investigation showed that the *tectorum* parent had been heterozygous for a lethal factor which halted the development of the hybrid to which it was transmitted at the cotyledon stage. Progeny of the *tectorum* plant were all normal but on crossing the various plants to *capillaris* it was evident that the progeny were segregating for the lethal in a 1 : 2 : 1 ratio. Plants homozygous for the lethal allelomorph (LL) gave only viable hybrids, those homozygous for the lethal (ll) gave only inviable hybrids, and those heterozygous for it (Ll) gave hybrids half viable, half inviable. Progenies from plants of each genotype were grown and their constitution tested by crossing with *capillaris*. All the progeny of LL proved to be LL giving viable hybrids only. Progeny of Ll segregated in a 1 LL : 2 Ll : 1 ll ratio giving hybrid populations of three kinds: (1) all viable, (2) half viable, half inviable, (3) all inviable. All the progeny of ll were ll giving only inviable hybrids.

The viability of the hybrids was independent of the *capillaris* parent used and there was no differential germination with respect to the lethal.

The lethal and its allelomorph have been found in *tectorum* strains from two widely separated localities.

There is evidence that the same lethal is effective in hybrids between *tectorum* and two other *Crepis* species, but hybrids with a third and fourth are unaffected by it.

The lethal may have played a rôle in maintaining ancestral stocks during the early differentiation of the species.

No experimental evidence is available to explain the ineffectiveness of the lethal in the parental species and its effect on an interspecific hybrid but an explanation is proposed which involves an inhibitor of the lethal and corresponding genes in the parental species.

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