Allelism Tests Involving Two Genes, *ers* and *ers-2*, that Restrict Partly Colored Seedcoat Expression in Common Bean

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ABSTRACT. An inheritance study was conducted with genetic stocks constructed in the genetic background of the recurrent parent 5-593, a Florida dry bean (*Phaseolus vulgaris* L.) breeding line with black seeds and purple flowers and genotype *P T z l⁺*. The genetic stocks, *t ers ers-2 BC₃ 5-593* (pure white seeds), *t virgarcus BC₃ 5-593*, and *t BC₂ 5-593* self-colored were constructed by backcrossing selected recessive alleles for partly colored seedcoats into 5-593. The cross *t ers ers-2 BC₃ 5-593* x *t BC₂ 5-593* self-colored was studied in *F₁*, *F₂*, and *F₃*. The observed data supported the hypothesis that *ers* is a synonym for *z* and that *ers-2* is a synonym for a new allele (*l^{ers}*) at the *L* locus. The cross *t ers ers-2 BC₃ 5-593* x *t virgarcus BC₃ 5-593* was studied in *F₁* and *F₂* progeny, and the results confirmed the hypothesis of allelism between *ers* and *z*. 'Thuringia' (pure white seedcoats) with genotype *P t z L* was crossed with *t ers ers-2 BC₃ 5-593*, *t virgarcus BC₃ 5-593* and *t BC₂ 5-593* self-colored. The cross 'Thuringia' (*P t z L*) x *t ers ers-2 BC₃ 5-593* was studied in *F₁* and *F₂* and supported the hypothesis that *l^{ers}* is an allele at *L*. The results of the other two test crosses are discussed. The gene *ers-2* is a new recessive allele at *L*, for which the new symbol *l^{ers}* is proposed. Thus, the dominance order at the *L* locus is *L* > *l⁺* > *l^{ers}*, where *l⁺* is the null allele at *L* found in 5-593. The *l⁺* allele does not restrict the colored area of a partly colored seedcoat and is hypothetically the wild-type allele at *L*.

Bassett and Blom (1991) demonstrated that the white seedcoat of 'Early Wax' snap bean was produced by the action of three recessive genes, *t ers ers-2*. The *t* allele is needed for expression of any partly colored seedcoat pattern, i.e., where part of the seedcoat is colored and the remainder is pure white (Leakey, 1988). The action of *ers* (with *t*) blocked color expression in the seedcoat in all areas except those close to the hilum, whereas the action of *ers-2* (with *t ers*) produced pure white seedcoats (Bassett and Blom, 1991). It was speculated that the *ers* gene may be a synonym for the *z* of Lamprecht (1934) and Schreiber (1940), but the classification of the segregating materials was not sufficient to establish that relationship. It was also speculated that the *ers-2* gene may be an allele at the *L* locus of Schreiber (1940), where Schreiber's erasure allele *L* is dominant and the erasure allele *ers-2* acts recessively (Bassett and Blom, 1991). An allelism test with one of the varieties used by Schreiber (1940) that carries *L* was needed, but earlier attempts to obtain seed of such varieties were unsuccessful. Also, a stock expressing the virgarcus pattern of partly colored seeds was needed for an allelism test with *ers*, preferably one adapted to Florida field conditions. A *t z virgarcus BC₃ 5-593* stock was subsequently developed (Bassett, 1996) and was used in experiments reported below.

This paper presents the results of an inheritance investigation into possible allelism between the genes *ers* and *ers-2* and genetic stocks carrying *z l⁺* or *z L*.

Materials and Methods

In 1985 a program was initiated at the Florida Agricultural Experiment Station to backcross various individual recessive

genes, or combinations of recessive genes, for seedcoat colors and patterns into the recurrent parent, 5-593, which is a Florida dry bean breeding line. The genotype of 5-593 is *T Mar [C r] D J G B V Rk*, which produces shiny, unpatterned black seeds and purple flowers (Bassett, 1994). The genetic tester stocks *t ers ers-2 BC₃ 5-593* and *t BC₂ 5-593* self-colored were produced during the investigation of the inheritance of the unusual genotype for pure white seedcoats found in 'Early Wax'. The development of the genetic tester stock 't virgarcus BC₃ 5-593' was described in detail in Bassett (1996) and has the partly colored seedcoat pattern, virgarcus (Fig 1).

Seeds of the variety 'Thuringia' (accession PHA 1105/86) were obtained from the genebank at the Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, D-06466, Germany. The genotype of 'Thuringia' is *P t z L* (Schreiber, 1940). 'Thuringia' has white flowers due to *t* and pure white seedcoats due to *P t z L*.

In 1994 the cross *t ers ers-2 BC₃ 5-593* x *t BC₂ 5-593* self-colored was made and an *F₂* population of 63 plants was grown in

Fig. 1. A ventral view (left) and a side view (right) of the virgarcus pattern of partly colored seedcoat produced by genotype *t/t z/z l⁺/l⁺*.

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Fig. 2. Six views showing the range of variability of the ambigua pattern of partly colored seeds produced by the genotype *t/t Z/Z l⁺/l⁺*.

the greenhouse in Winter 1995. The F_3 progenies were grown in the field at Gainesville in Spring 1995. Data were taken on the seedcoat colors and patterns in F_1 , F_2 , and F_3 .

In 1994 two test crosses were made, viz., *t ers ers-2 BC₃ 5-593* $\times$ *t virgarcus BC₃ 5-593* (*t z l⁺*) and 'Thuringia' (*P t z L*) $\times$ *t ers ers-2 BC₃ 5-593*. Data were taken on the flower color and seedcoat patterns in the F_1 and F_2 progenies of both test crosses, and the F_2 populations were grown in the field at Gainesville in Spring 1995. In 1994 two additional test crosses were

Fig. 3. A ventral view (left seed) and two side views (right seeds) showing the range of variability of the expansa pattern of partly colored seeds (with fibula arcs) produced by the genotype *t/t Z/Z l⁺/l⁺*.

made, viz., 'Thuringia' $\times$ *t virgarcus BC₃ 5-593* and 'Thuringia' $\times$ *t BC₂ 5-593* self-colored. Data were taken on the seedcoat patterns of the F_1 progenies grown in the greenhouse in Winter 1995.

Results and Discussion

The F_1 progeny from the cross *t ers ers-2 BC₃ 5-593* $\times$ *t BC₂ 5-593* self-colored produced F_2 seed with the ambigua pattern seedcoats (Fig. 2). The F_2 progeny from *t ers ers-2 BC₃ 5-593* $\times$ *t BC₂ 5-593* self-colored was classified originally into five phenotypic classes, viz., first a combination of self-colored, expansa (Fig. 3), and ambigua classes (those classes could not be unambiguously classified), followed by four separate classes, intermedia (Fig. 4), virgarcus, weak virgarcus (Fig. 5), and pure white (data presented below). It was necessary to make F_3 progeny tests of the 63 F_2 plants to develop sufficient evidence to support a genetic model for the observed segregation and to classify the F_2 as fully as possible (F_3 and F_2 data presented below) (Table 1).

Fig. 4. A ventral view (left seed) and a side view (right seed) of the intermedia pattern of partly colored seeds produced by the genotype *t/t Z/z l^{ers}/l^{ers}*.

Fig. 5. Five ventral views showing the range of variability of the weak virgarcus pattern of partly colored seeds produced by the genotype *t/t z/z l⁺/l⁺*.

Table 1. Genetic model for the F_2 and F_3 from the cross $t\text{ers}\text{ers-2 BC}_3\text{ 5-593 } (t\text{z l}^{\text{ers}}) \times t\text{ BC}_2\text{ 5-593 self-colored } (t\text{Z l}^+)$.

Expected segregation in F_2			
Genotypes	Frequency	Phenotypes	Expected segregation in F_3
$Z/Z\text{ l}^+/\text{l}^+$	1/16	Expansa ^z	All expansa ^z
$Z/Z\text{ l}^+/\text{l}^{\text{ers}}$	2/16	Expansa	All expansa ^y
$Z/Z\text{ l}^{\text{ers}}/\text{l}^{\text{ers}}$	1/16	Expansa ^y	All expansa ^y
$Z/z\text{ l}^+/\text{l}^+$	2/16	Ambigua-1	3 exp/amb ^x :1 virgarcus
$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	4/16	Ambigua-2	10:2:1:2:1 ^w
$Z/z\text{ l}^{\text{ers}}/\text{l}^{\text{ers}}$	2/16	Intermedia	1 exp:2 inter:1 white ^x
$z/z\text{ l}^+/\text{l}^+$	1/16	Virgarcus	All virgarcus
$z/z\text{ l}^+/\text{l}^{\text{ers}}$	2/16	Weak virgarcus	1 virg:2WV:1 white ^x
$z/z\text{ l}^{\text{ers}}/\text{l}^{\text{ers}}$	1/16	Pure white	All pure white

^zSome of plants with $Z/Z\text{ l}^+/\text{l}^+$ will have self-colored seedcoat, the genetics of which is unknown.^yThe genotype $Z/Z\text{ l}^{\text{ers}}/\text{l}^{\text{ers}}$ may have a limiting effect on the extension of the colored zone, but the classification is ambiguous.^xExp = expansa, amb = ambigua, inter = intermedia, virg = virgarcus, WV = weak virgarcus.^wThe ratio is 10 expansa or ambigua:2 intermedia:1 virgarcus:2 weak virgarcus:1 pure white.Table 2. Segregation for seedcoat colors or partly colored patterns in the F_3 progenies of 63 randomly selected F_2 progeny from the cross $t\text{ers}\text{ers-2 BC}_3\text{ 5-593 } (t\text{z l}^{\text{ers}}) \times t\text{ BC}_2\text{ 5-593 self-colored } (t\text{Z l}^+)$.

Plot no.	Genetic hypothesis of F_2 parent	Seedcoat colors or patterns with genotypes					χ^2 (ratio tested)	P value
		Self-c/exp/amb ^z $Z/Z\text{ -/- or } Z/z\text{ l}^+/\text{l}^+$	Inter-media $Z/z\text{ l}^{\text{ers}}/\text{l}^{\text{ers}}$	Virgarcus $z/z\text{ l}^+/\text{l}^+$	Weak virgarcus $z/z\text{ l}^+/\text{l}^{\text{ers}}$	Pure white $z/z\text{ l}^{\text{ers}}/\text{l}^{\text{ers}}$		
5-316	$Z/Z\text{ -/-}$	41						
5-317	$Z/Z\text{ -/-}$	53						
5-319	$Z/Z\text{ -/-}$	46						
5-321	$Z/Z\text{ -/-}$	66						
5-322	$Z/Z\text{ -/-}$	79						
5-324	$Z/Z\text{ -/-}$	71						
5-328	$Z/Z\text{ -/-}$	34						
5-349	$Z/Z\text{ -/-}$	55						
5-350	$Z/Z\text{ -/-}$	68						
5-353	$Z/Z\text{ -/-}$	73						
	Total	586						(3:1)
5-318	$Z/z\text{ l}^+/\text{l}^+$	29		9			0.035	0.85
5-320	$Z/z\text{ l}^+/\text{l}^+$	47		10			1.690	0.19
5-323	$Z/z\text{ l}^+/\text{l}^+$	58		16			0.451	0.50
5-325	$Z/z\text{ l}^+/\text{l}^+$	21		10			0.871	0.35
5-326	$Z/z\text{ l}^+/\text{l}^+$	54		24			1.385	0.24
5-327	$Z/z\text{ l}^+/\text{l}^+$	26		8			0.039	0.84
5-345	$Z/z\text{ l}^+/\text{l}^+$	55		26			2.177	0.14
	Total	290		103			0.306	0.58
							(10:2:1:2:1)	
5-348	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	45	14	4	9	4	2.526	0.64
5-351	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	28	9	2	6	3	1.967	0.74
5-352	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	45	7	4	16	3	6.067	0.19
5-354	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	50	6	1	6	2	6.631	0.16
5-355	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	51	15	5	11	2	4.019	0.40
5-356	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	44	12	7	11	4	2.226	0.69
5-357	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	50	9	7	13	4	1.819	0.77
5-358	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	43	11	4	9	9	4.611	0.33
5-359	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	85	23	9	16	11	2.333	0.68
5-360	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	93	14	5	13	12	5.061	0.28
5-361	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	38	9	2	8	0	5.007	0.29
5-362	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	49	2	4	10	5	6.137	0.19
5-363	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	68	12	6	12	3	2.192	0.70
5-364	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	39	12	1	3	5	7.893	0.10
5-365	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	32	3	2	5	3	2.076	0.72
5-366	$Z/z\text{ l}^+/\text{l}^{\text{ers}}$	51	8	9	12	1	7.119	0.13

The genetic model rests on the hypotheses that *ers* is a synonym for the well-known *z* gene and that *ers-2* is a new recessive allele (l^{ers}) at the *L* locus (Table 1). The F_3 progenies were classified into the same five phenotypic classes described above for the F_2 . However, the F_2 parents can now be grouped into seven genetic classes because it was possible to separate two distinct genotypes for ambigua from the former combined self-colored/expansa/ambigua class (Table 2). The segregation observed in F_3 progenies derived from each of the heterozygous F_2 parents corresponded with the expected segregation ratios (Tables 1 and 2). The only anomaly was the highly disturbed segregation in plot 5-339, for which no explanation can be given.

With the additional information derived from the F_3 progenies, a classification of the F_2 into seven genetic classes was possible (Table 3). There was a surplus (nonsignificant) of F_2 plants in the pure white class and a shortage (nonsignificant) of F_2 plants in the expansa class. This was probably due to a disturbance (nonsignificant) in the segregation at the *Z* locus (Table 3). Although the above segregation disturbance is technically nonsignificant, in a larger F_2 the disturbance would probably have achieved significance and deserves comment.

The F_1 progeny from the test cross *t ers ers-2* BC₃ 5-593 × *t virgarcus* BC₃ 5-593 (*t z l⁺*) produced seed with the weak virgarcus seedcoat pattern (Fig. 5) (data not shown). In previous work (Bassett and Blom, 1991) the weak virgarcus pattern was called eye. The genetic hypothesis for the F_1 plants with the weak virgarcus pattern is *t/t z/z l⁺/l^{ers}*, where *ers* is considered a synonym for *z* and l^{ers} is a new symbol for *ers-2*. The F_2 progeny of the cross *t ers ers-2* BC₃ 5-593 × *t virgarcus* BC₃ 5-593 (*t z l⁺*) produced only three phenotypic segregation classes, viz., the two parental classes and the weak virgarcus class produced in the F_1 (Table 4). Most of the F_2 progenies fit a 1:2:1 ratio for the classes virgarcus, weak virgarcus, and pure white, respectively (Table 4). The genetic model for the data is that segregation occurred at the *L* locus, where the virgarcus parent (*t z l⁺*) carried the null allele (l^+) at the *L* locus, and the pure white parent (*t z l^{ers}*) carried the recessive allele for erasure (l^{ers}) at the *L* locus (Table 4). The superscript plus sign in the gene symbol l^+ denotes the wild-type allele at the *L* locus, a speculative hypothesis. Two of the F_2 progenies, 5-212 and 5-217, did not fit the 1:2:1 segregation ratio, and no genetic model was found to account for the apparently disturbed segregation (Table 4).

Table 2. Continued.

Plot no.	Genetic hypothesis of F_2 parent	Seedcoat colors or patterns with genotypes					χ^2 and (ratio tested)	<i>P</i> value
		Self-c/exp/amb ^z <i>Z/Z -/-</i> or <i>Z/z l⁺-</i>	Inter-media <i>Z/z l^{ers}/l^{ers}</i>	Virgarcus <i>z/z l⁺/l⁺</i>	Weak virgarcus <i>z/z l⁺/l^{ers}</i>	Pure white <i>z/z l^{ers}/l^{ers}</i>		
5-367	<i>Z/z l⁺/l^{ers}</i>	39	7	3	8	4	0.272	0.99
5-368	<i>Z/z l⁺/l^{ers}</i>	36	8	4	4	3	1.611	0.81
5-369	<i>Z/z l⁺/l^{ers}</i>	46	9	4	11	10	5.720	0.22
	Total	932	190	83	183	88	1.397	0.85
							(1:2:1)	
5-338	<i>Z/Z l⁺/l^{ers}</i>	16	28			15	0.186	0.91
5-339	<i>Z/Z l⁺/l^{ers}</i>	40	47			15	12.88	0.002
5-340	<i>Z/Z l⁺/l^{ers}</i>	19	38			17	0.162	0.92
5-341	<i>Z/Z l⁺/l^{ers}</i>	19	33			21	0.781	0.68
5-347	<i>Z/Z l⁺/l^{ers}</i>	16	24			20	2.933	0.23
	Total	110	170			88	4.7609	0.09
5-342	<i>z/z l^{ers}/l^{ers}</i>			81				
5-343	<i>z/z l^{ers}/l^{ers}</i>			47				
5-344	<i>z/z l^{ers}/l^{ers}</i>			46				
5-346	<i>z/z l^{ers}/l^{ers}</i>			41				
	Total			215			(1:2:1)	
5-329	<i>z/z l⁺/l^{ers}</i>			5	18	9	1.500	0.47
5-330	<i>z/z l⁺/l^{ers}</i>			18	18	15	4.765	0.09
5-331	<i>z/z l⁺/l^{ers}</i>			14	32	12	0.759	0.68
5-332	<i>z/z l⁺/l^{ers}</i>			9	30	15	2.00	0.37
5-333	<i>z/z l⁺/l^{ers}</i>			16	27	12	0.600	0.74
5-334	<i>z/z l⁺/l^{ers}</i>			14	29	12	0.309	0.86
5-335	<i>z/z l⁺/l^{ers}</i>			10	23	15	1.125	0.57
5-336	<i>z/z l⁺/l^{ers}</i>			13	40	17	1.886	0.39
5-337	<i>z/z l⁺/l^{ers}</i>			13	28	16	0.333	0.85
	Total			112	245	123	0.713	0.70
5-370	<i>z/z l^{ers}/l^{ers}</i>					40		
5-371	<i>z/z l^{ers}/l^{ers}</i>					37		
5-372	<i>z/z l^{ers}/l^{ers}</i>					37		
5-373	<i>z/z l^{ers}/l^{ers}</i>					31		
5-374	<i>z/z l^{ers}/l^{ers}</i>					23		
5-375	<i>z/z l^{ers}/l^{ers}</i>					43		
5-376	<i>z/z l^{ers}/l^{ers}</i>					38		
	Total					249		

^zThis class is a composite of three classes, viz., Self-c = self-colored, exp = expansa, and amb = ambigua, because those classes could not be classified without ambiguity. The genotype of self-colored and expansa is *Z/Z -/-*, and the genotype of ambigua is *Z/z l⁺/l⁺* or *Z/z l⁺/l^{ers}*.

Table 3. Segregation for seedcoat colors or partly colored patterns in the F_2 from the cross *t ers ers-2 BC₃ 5-593* (*t z l^{ers}*) $\times$ *t BC₂ 5-593* self-colored (*t Z l⁺*).

Phenotypic class	Frequency		χ^2 (4:2:4:2:1:2:1)	<i>P</i>
	Observed	Expected		
Expansa ^z	10	15.75	2.099	
Ambigua-1	7	7.88	0.097	
Ambigua-2	19	15.75	0.671	
Intermedia	5	7.88	1.050	
Virgarcus	4	3.94	0.001	
Weak virgarcus	9	7.88	0.161	
Pure white	9	3.94	6.509 ^y	
	63		10.587	0.10 ^y

^zSome of the expansa class expressed self-colored seedcoats, the genetics of which is unknown in a *t/t* background.

^yThe surplus of the pure white seed class is probably due to disturbed segregation (nonsignificant) at *Z*. For *Z/Z* = 10, *Z/z* = 31, and *z/z* = 22, the χ^2 (1:2:1) = 4.587; *P* = 0.10. For *l⁺/l⁺* = 11, *l⁺/l^{ers}* = 28, and *l^{ers}/l^{ers}* = 14, the χ^2 (1:2:1) = 0.509; *P* = 0.78.

The cross 'Thuringia' $\times$ *t ers ers-2 BC₃ 5-593* produced F_1 plants with white flowers and pure white seedcoats (data not shown). The F_2 progeny (125 plants) of the cross 'Thuringia' $\times$ *t ers ers-2 BC₃ 5-593* produced only plants with white flowers and pure white seedcoats (data not shown). Those results are interpreted to mean that the two parents are allelic at *t*, *z*, and *L*, with the understanding that 'Thuringia' carries the *L* allele and *t ers ers-2 BC₃ 5-593* carries the *l^{ers}* allele at the *L* locus.

In summary, the genetic stock *t ers ers-2 BC₃ 5-593* has been demonstrated to carry the recessive gene substitutions *t*, *z*, and *l^{ers}*. Thus, the genotype *t z l^{ers}* produces the white seedcoat found in 'Early Wax', which was previously reported (Bassett and Blom, 1991) to result from *t ers ers-2*. The former gene *ers* is now known to be a synonym for *z*, and the former gene *ers-2* is now known to be a new allele at the *L* locus, for which the new gene symbol *l^{ers}* is proposed. Schreiber (1940) has already demonstrated that *L* is fully dominant to *l* (now *l⁺* to distinguish it from *l^{ers}*). Thus, the dominance order at the *L* locus is *L* > *l⁺* > *l^{ers}*, where the null allele at *L* found in 5-593 is given the proposed new symbol *l^{*}*.

The test cross 'Thuringia' (*P t z L*) $\times$ *t virgarcus BC₃ 5-593* (*P*

Table 4. Segregation for seedcoat patterns in the F_2 from the cross *t ers ers-2 BC₃ 5-593* (pure white seed coats, *t z l^{ers}*) $\times$ *t virgarcus BC₃ 5-593* (*t z l⁺*), where the hypothetical genotype of the F_1 is *t/t z/z l^{ers}/l⁺* due to allelism of *ers* with *z* and *ers-2* with the *L* locus.

Plot no.	Virgarcus <i>l⁺/l⁺</i>	Weak virgarcus <i>l⁺/l^{ers}</i>	Pure white <i>l^{ers}/l^{ers}</i>	Ratio tested	χ^2	<i>P</i>
5-213	12	17	12	1:2:1	1.195	0.55
5-214	12	20	9	1:2:1	0.463	0.79
5-215	13	27	5	1:2:1	4.644	0.10
5-216	15	18	9	1:2:1	2.571	0.28
5-218	7	30	8	1:2:1	5.044	0.08
5-219	8	21	16	1:2:1	3.044	0.22
5-220	8	16	16	1:2:1	4.80	0.09
	75	149	75	1:2:1	0.003	0.998
5-212	2	22	14	1:2:1	8.526	0.014
5-217	3	21	14	1:2:1	6.790	0.03
	5	43	28	1:2:1	15.237	<0.001

Table 5. The genetic model for partly colored seedcoats of Schreiber (1940).

Genotypes ^z	Pattern names		Description
	Schreiber	Lamprecht (1934)	
<i>Z/Z L/L</i>	Marginata	Laciniata	Dark hilum ring and caruncula stripe
<i>Z/Z L/l</i>	Ambigua A	Minimus to Maximus	See Fig. 2
<i>Z/Z l/l</i>	Expansa	Minimus	See Fig. 3
<i>Z/z L/L</i>	Laciniata	Unipunctata	Dark spot at caruncula
<i>Z/z L/l</i>	Intermedia	(None)	See Fig. 4
<i>Z/z l/l</i>	Ambigua B	Minimus to Maximus	See Fig. 2
<i>z/z L/L</i>	Erasa	Pure white	No color pattern
<i>z/z L/l</i>	Erasa	Pure white	No color pattern
<i>z/z l/l</i>	Restricta	Virgarcus	See Fig. 1

^zAll genotypes also have *t/t*, which is required for any pattern of partly colored expression.

$t z l^*$) produced F_1 progeny with pure white seedcoats due to $P t z L/l^*$. Thus, the L gene is fully dominant to l^* , which agrees with the results of Schreiber (1940) (Table 5). The test cross 'Thuringia' ($P t z L$) $\times$ $t BC_2$ 5-593 self-colored ($P t z l^*$) produced F_1 progeny with the partly colored seedcoat pattern intermedia due to $P t Z/z L/l^*$, which agrees with the results of Schreiber (1940) (Table 5). Thus, the stock of 'Thuringia' used in the above experiments appears to have the same genotype reported by Schreiber (1940), and the allelism test results for L and l^{ers} in this paper can be regarded with confidence.

Schreiber (1940) found (Table 5) that two different genotypes produced the ambigua pattern, and two different genotypes produced ambigua in the present work (Table 1). Schreiber's (1940) ambigua B (Table 5) has the same genotype as my ambigua-1; but his ambigua A has genotype $Z/Z L/l$ (Table 5), whereas my ambigua-2 has genotype $Z/z l^*/l^{ers}$ (Table 1). The genotype $Z/Z l/l$ (same as $Z/Z l^*/l^*$) produced the expansa pattern, and $z/z l/l$ produced the restricta (virgatus) pattern (same as $z/z l^*/l^*$) in the

work of Schreiber (1940) and in the present work. Thus, every relevant comparison of the present work is consistent with that of Schreiber (1940).

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