

LIST OF GENES - *Phaseolus vulgaris* L.

The original comprehensive gene list was prepared by S.H. Yarnell (Bot. Rev. 31:247-330, 1965) and published in the BIC 8:4-20, 1965. An updated list was prepared by M.H. Dickson and associates and published in the BIC 25:109-127, 1982. The next update (BIC 32:1-15, 1989) was prepared by M.J. Bassett, involving extensive additions, corrections, revisions, and style changes. Subsequent updates (BIC 36:vi-xxiii, 1993; BIC 39:1-19; and BIC 47:1-24) were prepared by M. J. Bassett. Updates were completed by T.G. Porch in 01/2008, 12/2009, 02/2011, and 10/2013; by K.E. Bett in 02/16; by P. Miklas in 11/17, 03/21, and in BIC 65 (2022).

Coordination of Genes and Gene Symbol Nomenclature - BIC Genetics Committee.

The Genetics Committee is a sub-committee of the Bean Improvement Cooperative that organizes and coordinates activities that deal with *Phaseolus* genetics. The committee has served as a clearinghouse for the assignment and use of gene symbols. The committee also maintains the **Guidelines for Gene Nomenclature (last published in the Annual Report of the Bean Improvement Cooperative in 1988, 31:16-19 and supplemented in 1999, 42:vi)**. The committee also evaluates materials submitted for inclusion in the Genetics Stocks Collection of the Plant Introduction System (for those rules see 1995 BIC 38:iv-v).

We strongly recommend that any researcher conducting studies of potentially new, qualitatively inherited traits of common bean submit the manuscript to the committee prior to publication (concurrent submission can be made to the genetics committee and the journal). The committee will evaluate the data to determine 1) if sufficient evidence exists to establish the inheritance hypothesis, 2) whether any issue of potential allelism of the trait has been met, and 3) whether the proposed gene symbol has been previously assigned to another gene. The evidence must include 1) data from one generation to formulate a hypothesis, 2) data from subsequent generations to test that hypothesis, and 3) molecular data including linkage and physical mapping to support naming new genes within or near known gene clusters (e.g. the *Co-1* cluster on Pv01). The population sizes used must be sufficiently large to distinguish (with statistical significance) among potential segregation hypotheses.

For example, during 2020, the symbol p^{sd} with supporting data was submitted to the committee for approval, which was granted.

The following is the review process for new traits and gene symbols:

- a. The committee will evaluate the data to determine:
 - i. if sufficient evidence exists to establish the inheritance hypothesis
 - ii. whether any issue of potential allelism of the trait has been met
 - iii. whether the proposed gene symbol has been previously assigned to another gene
- b. The evidence must include:
 - i. data from one generation to formulate a hypothesis
 - ii. data from subsequent generations to test that hypothesis
 - iii. for hyper-variable pathogens: family mean testing (F2:3 progenies, or recombinant inbred lines – RILs), and use of multiple, specific races of the pathogen to separate effects of individual genes in gene clusters

- iv. molecular marker data and genetic linkage map and physical map (preferred) positions when available with available resources for such determinations detailed in “genomic resources” section below. When associating an annotated gene with a gene symbol include the gene model and reference genome.
- c. Lastly – parent, germplasm line, or cultivar source of new genes accepted by the committee must be made publically available via seed deposit with the U.S. National Plant Germplasm System - Plant Introduction Station in Pullman, WA, as a Genetic Stock (this enables others to access the gene source for subsequent allelism tests, genetic studies, etc.). This requirement is unnecessary for well known and easily accessible materials.

Genomic resources – as genomic resources have improved for *Phaseolus*, they have correspondingly been useful to characterize (physical position, candidate genes, sequenced-based mutant alleles) and discern new and existing genes. There are now multiple reference genomes available for alignment of marker and sequence data to assist in locating genes to specific regions of the genome.

- Andean Landrace Chaucha Chuga (G19833; Schmutz et al. 2014) version 2.1, is available on Phytozome 13 (https://phytozome-next.jgi.doe.gov/info/Pvulgaris_v2_1).
- The reference assembly and annotation for the race Durango pinto genotype UI 111 is available at Phytozome 13 (https://phytozome-next.jgi.doe.gov/info/PvulgarisUI111_v1_1).
- The Guatemalan race genotype Labor Ovalle is available at Phytozome 13 https://phytozome-next.jgi.doe.gov/info/PvulgarisLaborOvalle_v1_1).
- The Mesoamerican race genotype 5-593 is now available as well https://phytozome-next.jgi.doe.gov/info/PvulgarisLaborOvalle_v1_1
- The BAT 93 (race Mesoamerican) was released (Vlasova et al., 2016).
- The interspecific genotype OAC Rex (race Mesoamerican + tepary) is also available on a different site (<http://www.ncbi.nlm.nih.gov/sra/?term=OAC+Rex>).
- Frijol Bayo (dom. Tepary) is available at https://phytozome-next.jgi.doe.gov/info/Pacutifolius_v1_0, and W6 15578 (wild tepary) at https://phytozome-next.jgi.doe.gov/info/PacutifoliusWLD_v2_0).
- The assembly and annotation of Lima bean G27455 (Garcia et al., 2021) is also available at Phytozome 13 (https://phytozome-next.jgi.doe.gov/info/Plunatus_V1).

In addition to reference genomes WGS data for hundreds of accessions (eg. Lobaton et al., 2018; Wu et al., 2020) also exists and can be useful for gene identification and characterization as well; however, to date, centralized access to resequencing data sets is unavailable. But that is changing with the development of the Legume Information System (LIS) platform– excerpt from Parker et al. [(2021) BIC 64:65-66.] “LIS offers a continuously updated, highly integrated platform for comparing genetic and phenotypic data among distinct genomes assemblies and species. Recent updates in the data deposition system (available at https://legumeinfo.org/submit_data) now facilitate the process of adding QTL mapping or GWAS data to the repository. Resources include genome browsers, tools for accessing gene annotation and expression data, trait and map databases, and numerous comparison tools. The portal now includes example data sets that can be used as templates for future submissions. Under this proposal, submission by the authors of QTL mapping and GWAS results to LIS as a

routine part of the publication process in *Phaseolus* is strongly encouraged. These data can be reviewed by LIS developers and rapidly incorporated into the database.”

The BIC website ‘Genetics’ section http://www.bic.uprm.edu/?page_id=91 has a new Beyond SCARs Table for trait-linked snps and indels converted to tm-shift assays (see Soler-Garzón et al., BIC v65: this issue). Please submit gene-linked markers with utility for MAS to add to this list.

Questions or comments should be addressed to the chairperson of the committee:
Phillip Miklas, USDA-ARS: phil.miklas@usda.gov

GENE LIST

- Acc* *Accompanying* colors, i.e., the formerly "pleiotropic effects of R^{st} on the color of pods, the top edge of the standard, and the hypocotyl" (Prakken 1974).
- ace* *acera* (Latin): produces shiny pod (Yen 1957). *Ace* is linked to *V* (Bassett 1997a), which is located on Pv06 (McClellan et al. 2002).
- Adk* structural gene for *adenylate kinase* enzyme (Weeden 1984).
- Am* *amaranth*: with *No* and *Sal* geranium flower color, and scarlet flower with *Beg No Sal* (Lamprecht 1948b, 1961a). Scarlet flower (Fan 1, 43C; Royal Hort. Soc. fans) is expressed by *Sal Am V^{mf}* (or *v*), and *Sal Am v* expressed oxblood red seed coats (vs. mineral brown) due either to a pleiotropic effect of *Am* or a very closely linked dominant gene (Bassett 2003b). *Am* has no expression with *sal*, and *Am* is located 9 cM from *V* (Bassett 2003b) on Pv07 (McClellan et al. 2002).
- Amv-1* high level resistance to a strain of *alfalfa mosaic virus* (Wade and Zaumeyer 1940).
- Amv-2* resistance to the same strain of *alfalfa mosaic virus* as for *Amv* (Wade and Zaumeyer 1940).
- Ane* *Anebulosus* (Latin): produces nebulosus-mottling on testa (Prakken 1977a); observable only in $c^u J$ and $C/c^u J$ backgrounds. Not allelic with *V* or *R*, but linked to *B* (Lamprecht 1964). This trait is more commonly known as strong (grayish brown) vein pattern of seed coats (Bassett, editor).
- aph* *aphyllus* (Latin): plants are sterile and have only two (unifoliate) leaves and 4 to 6 nodes. (Lamprecht 1958).
- Arc* *arcus* (Latin): with *Bip* gives virgarcus seed coat pattern, with *bip* gives virgata; *arc* with *Bip* gives *arcus*, with *bip* gives bipunctata; extends seed coat color in partly colored seeds (Lamprecht 1940b). The arcus pattern is also expressed by $t z Bip J Fib$; possible allelism between *Arc* and *Fib* has not been tested (Bassett and McClellan 2000; Lamprecht 1940b), whereas *J* and *Fib* are not allelic (Bassett 2001).
- arg* *argentum* (Latin): with *Y* produces a "silver" or greenish gray pod (Lamprecht 1947b), formerly *s* (Currence 1930, 1931); *arg* with *y* gives a white pod (Currence 1931; Lamprecht 1947b).
- Arl (Arc)* structural gene for the seed protein *arcelin* (Osborn et al. 1986).
- asp* *asper* (Latin): very dull (non-shiny) seed coat that is slightly rough textured due to the pyramidal shape of the outer epidermal palisade cells (Lamprecht, 1940c). With $P C J G B V$, *asp* seed coats had only 19% of the total anthocyanin content (delphinidin 3-*O*-glucoside, petunidin 3-*O*-glucoside, and malvidin 3-*O*-glucoside) compared with *Asp*; this was achieved by *asp* changing the size and shape of the palisade cells of the seed coat epidermis, making the cells significantly smaller than with *Asp* (Beninger et al. 2000). *Asp* is located Pv07 (Miklas et al. 2000).
- B (Br, Vir)* as used by Lamprecht (1932a, 1939, 1951a); the greenish brown factor of Prakken

(1970). Similar or equivalent genes, according to Feenstra (1960), are the *C* of Tschermak (1912), the *D* of Shull (1908), the *E* of Kooiman (1920), the *H* of Shaw and Norton (1918), and the *L* of Sirks (1922). Smith (1961) used the gene symbol *Br* for *B*, according to Prakken (1972b). Lamprecht (1932b) used the gene symbol *Vir* for the effects of segregation at *B* in the genotype *P C j g B/b v*, according to Prakken (1970). The interactions of *B* with nearly all combinations of genes for seed coat color were summarized by Prakken (1972b). With *P C J G V Asp*, the *B* gene acts to regulate the production of precursors of anthocyanins in the seed coat color pathway above the level of dihydrokaempferol formation (Beninger et al. 2000). With *P C J G v Asp*, the *B* gene acts to regulate the production of astragalin and kaempferol 3-*O*-glucoside (Beninger et al. 1999). *B* is very tightly linked (Kyle and Dickson 1988) to the virus resistance gene *I* on Pv02 (Freyre et al. 1998; Vallejos et al. 2000).

- bc-u^d* strain-*unspecific* complementary gene, giving resistance to certain strains of *bean common mosaic virus* (BCMV/BCMNV) only when together with one or more of the strain-specific resistance genes. Originally named *bc-u* by Drijfhout (1978b) but renamed by Soler-Garzón et al. (2021b) to reflect Durango race origin and absence from host groups (HG) 2, 4, 5, 7 and presence in HG-10. A basic Leucine Zipper (bZIP) transcription factor protein is the candidate gene for *bc-u*. bZIP protein gene Phvul.005G124100 (G19833 v2.1) carries a unique non-synonymous mutation at codon 14 in the first exon (Pv05: 36,114,516 bases), resulting in a premature termination codon that causes a nonfunctional protein. A marker for this mutation is listed in the Beyond SCARs table (http://www.bic.uprm.edu/?page_id=91).
- bc-1* alone provides resistance to pathogroup PG-1 strains and combined with *I* gene provides protection (localized vein necrosis - VN) to NL-8 strain (PG-3). Combined with *bc-u^d* it provides resistance to PG-2, -3, and -5, and combined with *I* gene and *bc-u^d* it provides VN resistance to PG-6 (NL-3 strain) (Soler-Garzón et al. 2021a). A marker linked with this gene on Pv03 is listed in the Beyond SCARs table (http://www.bic.uprm.edu/?page_id=91). Gene was first described by Drijfhout (1978b).
- bc-2* combined with *bc-u^d* gives resistance to BCMV and BCMNV except PG-7, and combined with *bc-4* provides resistance to all BCMV (except PG-5) but not BCMNV (Soler-Garzón et al. 2021b). Phvul.011G092700 (G19833 v2.1), a vacuolar protein-sorting 4 (Vps4) AAAC ATPase endosomal sorting complexes required for transport (ESCRT) protein, is the *bc-2* candidate gene. Two different variants within the candidate gene are noted *bc-2^[UI 111]*, contains a 10-kb deletion, and *bc-2^[Robust]* consists of a single nucleotide polymorphism (SNP) deletion. Markers for these different variants are listed in the Beyond SCARs table (http://www.bic.uprm.edu/?page_id=91). Gene was first described by Drijfhout (1978b).
- bc-3* with *bc-u* gives resistance to all strains of BCMV (Drijfhout 1978b). This gene is located on Pv06 (Johnson et al., 1997).
- bc-3²* Previously *cyv*, conditions resistance to *clover yellow vein virus*. Allelic to *desc*, *cvy*, and *bc-3*, located on Pv06, and linked to PveIF4E (Hart and Griffiths, 2013).
- bc-4* when combined with *bc-2* provides resistance to all BCMV (except PG-5) but not BCMNV (Soler-Garzón et al. 2021b). Gene model Phvul.005G125100, a Vps4 AAAC ATPase ESCRT protein, was identified as the candidate gene for *bc-4* gene, and a marker for the putative causal mutation is listed in the Beyond SCARs table

http://www.bic.uprm.edu/?page_id=91).

<i>Bcm</i>	confers temperature-sensitive resistance to <i>blackeye cowpea mosaic virus</i> . Tightly linked, if not identical, to the <i>I</i> gene for resistance to bean common mosaic virus (Kyle and Provvidenti 1987; Provvidenti et al. 1983).
<i>Bct (Ctv-1)</i>	a gene conditioning resistance to <i>beet curly top virus</i> discovered by Schultz and Dean (1947). The <i>Ctv-1</i> symbol was proposed by Provvidenti (1987) and updated to <i>Bct</i> by Larsen and Miklas (2004). <i>Bct</i> is located between the <i>Phs</i> and <i>Asp</i> loci on Pv07 (Miklas et al. 2000).
<i>Bdm</i>	confers resistance to <i>Bean dwarf mosaic virus</i> (BDMV) through the blockage of long-distance movement in the phloem (may or may not be associated with a hypersensitive response) (Seo et al. 2004).
<i>Beg</i>	with <i>P v</i> (Line 214), gives <i>begonia</i> red flower color by fully dominant action, but with <i>P v^{lae}</i> , expresses partial dominance for <i>begonia</i> red flower (Lamprecht 1948b). Allelism of <i>Beg</i> with <i>Sal</i> was not tested (Bassett 2003b).
<i>bgm</i>	(<i>syn with bgm-1</i>) confers resistance (prevents a chlorotic response) to bean golden yellow mosaic virus (BGYMV) (Velez et al. 1998), found in A429 (Urrea et al., 1994), and located on Pv03 (Blair et al., 2007). A mutation (5 bp deletion) in the NAC (No Apical Meristem) domain transcriptional regulator superfamily protein gene model Phvul.003G027100 (G19833 v2.1) corresponds with the recessive <i>bgm</i> resistance allele (Soler-Garzón et al. 2021c). A marker for the causal mutation is listed in the Beyond SCARs table (http://www.bic.uprm.edu/?page_id=91).
<i>bgm-2</i>	from DOR 303 confers resistance (prevents a chlorotic response) to BGYMV (Velez et al. 1998).
<i>bgm-3</i>	from <i>P. coccineus</i> confers resistance to leaf chlorosis in the presence of BGYMV (Osorno et al. 2007).
<i>Bgp</i>	prevents pod deformation in the presence of BGYMV (may require <i>bgm</i> for expression) and found in DOR 482 ('Don Silvio') (Acevedo-Román et al., 2004).
<i>Bgp-2</i>	from <i>P. coccineus</i> prevents pod deformation in the presence of BGYMV (Osorno et al. 2007).
<i>bic</i>	<i>bic</i> confers bicolor flowers (colored banner and white wings) and dark olive brown seed coat (Bassett and Miklas 2007).
<i>Bip</i>	<i>bipunctata</i> (Latin): <i>Bip</i> and <i>bip</i> combine with <i>Arc</i> and <i>arc</i> to form seed coat patterns based on the hilum; extends seed coat color in partly colored seeds (Lamprecht 1932d, 1940b). Genotype <i>t z bip</i> expresses the bipunctata pattern of partly colored seed coats; whereas <i>t z Bip</i> expresses virgarcus pattern (Bassett 1996c; Schreiber 1940). <i>Bip</i> is linked to <i>J</i> and is located on Pv10 (McClellan et al. 2002).
<i>bip^{ana}</i>	Anasazi pattern of partly colored seed coats is expressed by genotype <i>t Z bip^{ana}</i> ; whereas <i>t z bip^{ana}</i> expresses the Anabip pattern (Bassett et al. 2000).
<i>blu</i>	<i>blue</i> flower color mutant (Bassett 1992a).
<i>Bpm</i>	confers resistance to <i>bean pod mottle virus</i> (Thomas and Zaumeyer 1950); symbol proposed by Provvidenti (1987).
<i>Bsm</i>	confers resistance to <i>bean southern mosaic virus</i> (Zaumeyer and Harter 1943); symbol proposed by Provvidenti (1987).
<i>By-1</i>	confers strain-specific resistance to pea mosaic virus, a strain of <i>bean yellow mosaic virus</i> (Schroeder and Provvidenti 1968).
<i>By-2</i>	strain-unspecific gene for temperature sensitive resistance to <i>bean yellow mosaic virus</i> (Dickson and Natti 1968).
<i>C</i>	with <i>P z j g b v</i> , sulfur-white or primrose yellow testa; no color in the hilum ring

- (Lamprecht 1932a, 1939, 1951a, 1951b; Tjebbes and Kooiman 1922b). According to Feenstra (1960), this *C* is the equivalent of the *B* of Tjebbes (1927), of Kooiman (1920), and of Sirks (1922), and the *Cm* of Prakken (1934). From the early 20th century until the present, the regulation of color and pattern expression (especially in seed coats, but also in other plants organs, e.g., flowers, pods, petioles and stems) at *C* has had dual characterization as both a series of alleles at a locus and a series of very tightly linked genes in one chromosome region (Prakken, 1974). Plant introduction (PI) lines with various seed coat patterns were identified and demonstrated to be allelic (Troy and Hartman 1978). The interactions of *C* and *J* were summarized by Prakken (1972b). *C* is located on Pv08 (McClellan et al. 2002).
- C/c* inconstant (ever-segregating) mottling with color genes (Lamprecht 1932a, 1939; Prakken 1940-1941; Shaw and Norton 1918; Tschermak 1912). According to Prakken (1974), the "complex *C* locus" includes 6 tightly linked loci, including *M*, *Pr*, *Acc*, *C/c*, *R*, and *Cst*.
- c^{cr}* superscript *cr*, *completely recessive*: the heterozygote *C/c^{cr}* shows the pure dark pattern color *C/C*, without mottling as in *C/c* and *C/c^u* (Nakayama 1965).
- C^{cir}* superscript *cir*, *circumdatus* (Latin): lateral accumulation of medium sized spots on the testa (Lamprecht 1947a).
- C^{ma}* (*M*, *R^{ma}*) responsible for constant (not heterozygosity dependent) (superscript *ma*) *marbling* of the seed coat; the colors depend on other genes (Emerson 1909a; Shull 1908; Smith 1939, 1947; Tschermak 1912). Later interpreted to be an allele of *R* and re-designated *R^{ma}* (Lamprecht 1947a). *M* was originally used by Shull (1908) for inconstant mottling. *M* with *Ro* and *V* produces marbling of the pod (Lamprecht 1940a, 1951b). According to Prakken (1974), *C*, *R*, and *M* are 3 distinct but very closely linked loci that are included in the "complex *C* locus."
- C^r* indistinct, inconstant mottling of the seed coat (Lamprecht 1940a, 1947a; Smith 1939).
- C^{res}* superscript *res*, *resperus* (Latin): sprinkled or speckled seed coat (Lamprecht 1940a, 1947a).
- C^{rho}* superscript *rho*, *rhomboidus* (Latin): rhomboid spotting of the testa (Lamprecht 1947a; Troy and Hartman 1978).
- Cst* superscript *st*, *striping* on seed coat and pod (Kooiman 1931; Lamprecht 1939; Sirks 1922; Smith 1939; Tjebbes and Kooiman 1919b; Tschermak 1912); considered by Lamprecht (1947a) to be due to *Rst*. The *Cst* allele in 'La Gaude' has the pleiotropic effect of producing blackish violet zebra-like veins on the standard petal of the flowers (Prakken 1977a).
- [*Cst R Acc*] (*Aeq*) with *v*, also "darkens" the tip of the banner petal (Prakken 1972b and 1974), i.e., the otherwise white standard has a red tip; the genes *R* and *Acc* are tightly linked within the "complex *C* locus" (Prakken 1974); the *Terminalverstärkung der Blütenfarbe* character of Lamprecht (1961a) does not require his *Uc*, *Unc* genes to account for its highly variable penetrance (color intensity).
- c^u* (*inh*, *i_e*) superscript *u*, *unchangeable*: produces a creamish testa (Feenstra 1960); the modifier genes *G*, *B*, and *V* do not change the pale background color of *P J c^u* (Prakken 1970). With *v^{lse}*, *c^u* blocks production of flavonol glycosides; with *V*, *c^u* blocks production of flavonol glycosides and anthocyanin (Feenstra 1960).
- [*c^u Prpⁱ*] (*Prp*, *c^{ui}*, *Nud*) with *T P V* produces cartridge buff seed coats, with very tight genetic linkage to a syndrome of anthocyanin (superscript *i*) *intensification* effects: *purple* flower buds, *intense purple* flowers, *purple* pods, *purple* petioles and stems, and a

blush of *purple* on leaf lamina as found in 'Royal Burgundy' (Bassett 1994a; Kooiman 1931); a series of purple pod "alleles" exist at the complex *C* locus (Bassett 1994a; Okonkwo and Clayberg 1984). The same anthocyanin intensification syndrome has been reported repeatedly (but incompletely), each time with a new gene symbol: *Nud* by Lamprecht (1935e), *c^{ui}* by Nakayama (1964), and *Prp* by Okonkwo and Clayberg (1984).

- [*c^u prpst*] (*prpst*) with *T P V* produces cartridge buff seed coats with very tight genetic linkage to green pods with *purple* (superscript *st*) *stripes* as found in Contender (Bassett 1994a).
- [*C Prp*] (*Prp, Ro*) with *T P J B V* produces black seed coats and purple pods as found in 'Preto 146' (Bassett 1994a).
- c^v* a completely recessive *c* that does not show heterozygous mottling and has no effect on seed coat color except with *V*, producing a grayish brown with *G B V* (Bassett 1995b).
- [*C R*] (*R*) with *P*, produces a *red* seed coat (Emerson 1909b; Lamprecht 1935a; Tjebbes and Kooiman 1921) that has been variously described as light vinaceous (Tjebbes and Kooiman 1921), light purple vinaceous (Lamprecht 1947a), and deep oxblood red (Smith 1939), the differences possibly due to modifying genes. The flowers are red (Tjebbes and Kooiman 1922b). It does not affect the color of the hilum ring (Lamprecht 1939). *R, R^{cir}, R^r, R^{res}, R^{rho}*, and *r* are allelic, according to Lamprecht (1947a); but Prakken (1977b) has shown that *Cst* patterns can exist without the *R* locus red color. Therefore, the striping, marbling, and other patterns are more correctly designated as properties of the *C* locus, and the bracket notation, [*C R*], is used to indicate two genes with nearly unbreakable linkage (Bassett 1991b). The interactions of [*C R*] with other genes controlling seed coat color were summarized by Prakken (1972b).
- [*C r*] (*r*) with appropriate modifier genes gives white seed coat (Emerson 1909b; Lamprecht 1940a, 1947a).
- Ca* *caruncula* (Latin): expresses a stripe pattern, originating at the caruncula and extending away from the hilum (Lamprecht 1932c and 1934a).
- Cam* confers temperature sensitive resistance to *cowpea aphid-borne mosaic virus*. Tightly linked, if not identical, to the *I* gene for resistance to bean common mosaic virus (Kyle and Provvidenti 1987; Provvidenti et al. 1983).
- Cav* *Caruncula verruca* (Latin): causes a wrinkling of the testa radiating from the caruncula (Lamprecht 1955). The heterozygote is less distinct.
- cc* *chlorotic cup* leaf mutation (Nagata and Bassett 1984).
- chl* pale green *chlorophyll* deficiency (Nakayama 1959a).
- cl* *circumlineatus* (Latin): in partly colored seed coats, each of the color centers and even the smallest dots are bordered by (circumlineated) a sharp precipitation-like line (Prakken 1972b).
- cml* *chlorotic moderately lanceolate* leaf mutant (Bassett 1992c).
- Co-1 (A)* an anthracnose [*Colletotrichum lindemuthianum* (Sacc. & Magnus) Lams.-Scrib.] resistance gene discovered by McRostie (1919) and found in the Andean variety Michigan Dark Red Kidney. *Co-1* is located (Kelly et al. 2003) on Pv01 (Zuiderveen et al., 2016). The gene symbol base *Co* was proposed for all anthracnose resistance genes by Kelly and Young (1996). A comprehensive review of the genetics of anthracnose resistance in common bean is available (Kelly and Vallejo 2004; Ferreira et al., 2013).

- Co-1*² an anthracnose resistance gene discovered by Melotto and Kelly (2000) and found in 'Kaboon'.
- Co-1*³ an anthracnose resistance gene discovered by Melotto and Kelly (2000) and found in 'Perry Marrow'.
- Co-1*⁴ an anthracnose resistance gene discovered by Alzate-Marin et al. (2003a) and found in AND277 (Gonçalves-Vidigal et al. 2011).
- Co-1*⁵ an anthracnose resistance gene from 'Widusa' discovered by Gonçalves-Vidigal and Kelly (2006).
- Co-2 (Are)* an anthracnose resistance gene discovered by Mastenbroek (1960) and found in the Middle American differential variety Cornell 49242. *Co-2* is located on Pv11 (Adam-Blondon et al. 1994).
- Co-3 (Mexique 1)* an anthracnose resistance gene discovered by Bannerot (1965) and found in the Middle American variety Mexico 222. *Co-3* is located on Pv04 (Rodríguez-Suarez et al. 2004).
- Co-3*² an anthracnose resistance gene found in the Middle American variety Mexico 227 (Fouilloux 1979).
- Co-3*³ an anthracnose resistance gene first described by Geffroy et al. (1999) in the variety BAT93. The *Co-3*³ gene was previously named *Co-9* and subsequently found to be an allele of *Co-3* (Gonçalves-Vidigal et al., unpublished; Mendez-Vigo et al. 2005; Rodríguez-Suárez et al. 2004). *Co-3*³ is also present in the differential variety PI 207262 (Alzate-Marin et al. 2003c) and is located on Pv04 (Geffroy et al. 1999).
- Co-3*⁴ an anthracnose resistance gene previously named *Co-10* and described in the variety Ouro Negro (Alzate-Marin et al., 2003b). Tightly linked to *Phg-3* and located on Pv04 (Gonçalves-Vidigal et al. 2013).
- Co-3*⁵ an anthracnose resistance gene previously named *Co-7* and described in the Middle American differential variety G2333 (Young et al. 1998). The allele is located on Pv04 (Sousa et al., 2014).
- Co-4 (Mexique 2)* an anthracnose resistance gene discovered by Bannerot in 1969 (Fouilloux 1976, 1979) and found in the Middle American differential variety TO. *Co-4* is located on Pv08 (Kelly et al. 2003; Oblessuc et al., 2015).
- Co-4*² an anthracnose resistance gene found in SEL 1308 and G2333 (Young et al. 1998).
- Co-4*³ an anthracnose resistance gene found in PI 207262 (Alzate-Marin et al. 2002).
- Co-5 (Mexique 3)* an anthracnose resistance gene discovered by Bannerot in 1969 (Fouilloux 1976, 1979) and found in the Middle American differential variety TU and G2333, SEL 1360 (Young et al. 1998).
- Co-5*² an anthracnose resistance allele of *Co-5* found in G 2333, SEL 1360 and MSU 7-1 (Vallejo and Kelly 2009; Sousa et al. 2014).
- Co-6* an anthracnose resistance gene discovered by Schwartz et al. (1982) and found in the Middle American differential variety AB136. *Co-6* is located on Pv07 (Kelly et al. 2003; Mendez de Vigo 2002). It is likely that *Co-6* is located within *Co-5* gene cluster (Campa et al., 2017).
- co-8* an anthracnose resistance gene first described in differential variety AB136 (Alzate-Marin et al. 1997).
- Co-11* is an anthracnose resistance gene from 'Michelite' (Gonçalves-Vidigal et al. 2007).
- Co-12* an anthracnose resistance gene from cultivar 'Jalo Vermelho' described in Gonçalves-Vidigal et al. (2008).
- Co-13* an anthracnose resistance gene from landrace 'Jalo Listras Pretas' described in Gonçalves-Vidigal et al. (2009) is located on Pv03 (Lacanallo and Gonçalves-Vidigal

- 2015).
- Co-14* an anthracnose resistance gene from cultivar 'Pitanga' described in Gonçalves-Vidigal et al. (2012) was mapped to Pv01 (Gonçalves-Vidigal et al., 2016).
- Co-15* anthracnose resistance gene from Corinthiano on Pv04 linked to STS marker g2685 described in Sousa et al. (2015).
- Co-16* anthracnose resistance gene from Crioulo 159 on Pv04. Likely distinct from *Co-3* (Coimbra-Gonçalves et al. 2016).
- Co-17* anthracnose resistance gene from SEL1308 on Pv03 (Trabanco et al., 2015). Line SEL1308, derived from a backcross of cultivar G2333 (Talamanca*2/G2333; Young and Kelly, 1996).
- cr-1 cr-2* complementary recessive genes for crippled morphology, i.e., stunted plants with small, crinkled leaves (Coyne 1965; Finke et al. 1986).
- Crg* this *complements resistance gene* is a factor necessary for the expression of *Ur-3*-mediated bean rust resistance and is located on Pv08 (Kalavacharla et al. 2000).
- cry* *crypto-dwarf*: a dwarfing gene; with *Fin* intermediate height (Nakayama 1957); with *la* produces long internodes resulting in slender type of growth in bush (*fin*) but not in tall (*Fin*) forms (Lamprecht 1947b).
- cs* *chlorotic stem* mutant (Nagata and Bassett 1984).
- Ct* for *curved pod tip* shape; *ct* for straight pod tip (Al-Mukhtar and Coyne 1981).
- ctv-1 ctv-2* confer resistance to beet *curly top virus* (Schultz and Dean 1947); symbol proposed by Provvidenti (1987).
- Da* straight pod (Lamprecht 1932b).
- Db* polymeric with *Da* for straight pod (Lamprecht 1932b, 1947b). [Polymeric genes have identical functions (expression) but different loci].
- dgs (gl, le)* *dark green savoy* leaf mutant (Frazier and Davis 1966b; Nagata and Bassett 1984). According to Nagata and Bassett (1984), *dgs* is synonymous with the *wrinkled leaf* mutant of Moh (1968) and the *gl (glossy)* of Motto et al. (1979); also synonymous with the *le (leathery leaf)* of Van Rheenen et al. (1984).
- dia* *diamond* leaf mutant (Nagata and Bassett 1984). Leaflets are angular, slightly chlorotic, thick, and reduced in area.
- Diap-1* structural gene for *diaphorase* enzyme (Weeden and Liang 1985).
- Diap-2* structural gene for *diaphorase* enzyme (Sprecher 1988).
- diff* *diffundere* (Latin): with *exp* gives completely colored testa except for one end of the seed; *diff* with *Bip Arc* gives maximus phenotype, with *bip Arc* gives major phenotype; extends seed coat color in partly colored seeds (Lamprecht 1940b).
- dis* *dispaes* (Latin): mottled or striped flower of scarlet runner bean (Lamprecht 1951c).
- DI-1 DI-2 (DL₁ DL₂)* complementary genes for *dosage-dependent lethality* and developmental abnormality; *DI DI DI-2 DI-2* is lethal, *DI dl DI-2 DI-2* and *DI DI DI-2 dl-2* are sublethal, *DI dl DI-2 dl-2* is temperature dependent abnormal, and *DI DI dl-2 dl-2*, *dl dl DI-2 DI-2*, *DI dl dl-2 dl-2*, *dl dl DI-2 dl-2*, and *dl dl dl-2 dl-2* are normal; *DI* inhibits root development and *DI-2* inhibits shoot development (Shii et al. 1980). *DI-1* is located on linkage group 11 and *DI-2* is located on linkage group 2 (Hannah et al., 2007).
- do* *dwarf out-crossing* mutant (Nagata and Bassett 1984). Out-crossing rates up to 56% are observed due to delayed pollen dehiscence (Nagata and Bassett 1985).
- ds (te)* *dwarf seed*: produces small seeds and short pods with deep constrictions between the seeds; cross pollination with *Ds* gives normal size seeds and pods on *ds/ds* plants, breaking the usual dominance of maternal genotype over embryo genotype

- for seed size development (Bassett 1982); the xenia effect was first described by Tschermak (1931) and the trait was named *tenuis* (Latin) for "narrow" pod by Lamprecht (1961a).
- dt-1^a dt-2^a* *daylength temperature*: produce early, day-length neutral flowering with complex temperature interactions (Massaya 1978).
- dt-1^b dt-2^b* *daylength temperature*: control flowering response to short days with complex temperature interactions; *dt-2^b* causes increased production of branches (Massaya 1978).
- dw-1 dw-2* duplicate genes causing *dwarf* plant (Nakayama 1957).
- Ea Eb* polymeric genes for "flat" pod, elliptical in cross-section vs. *ea eb* round pod (Lamprecht 1932b, 1947b; Tschermak 1916).
- Est-1* structural gene for most anodal *esterase* enzyme (Weeden and Liang 1985).
- Est-2* structural gene for second most anodal *esterase* enzyme (Weeden and Liang 1985).
- exp* *expandere* (Latin): with *diff* gives solid color to seed coat except for one end of the seed, giving minimus and minor phenotypes (Lamprecht 1940b).
- F* confers resistance to the *F* strain of anthracnose found in variety Robust (McRostie 1919); 'Robust' is extinct, but it was a parent of variety Michelite, which has not been fully characterized for anthracnose resistance although close to *Co-1* type (Kelly, personal communication).
- Fa* basic gene for pod membrane (Lamprecht 1932b).
- fast* *fastigate* shape of seed (Lamprecht 1934a).
- Fb Fc* supplementary genes for pod membrane (Lamprecht 1932b).
- fa fb fc* weak pod membrane; pod may be constricted (Lamprecht 1932b); may give 9:7, 15:1, or 63:1 ratios (Lamprecht 1932b, 1947b).
- fd* *delayed flowering* response under long days (Coyne 1970).
- Fe-1 Fe-2* *Ferrum* (Latin): complementary dominant genes controlling resistance to leaf chlorosis due to iron deficiency in plants grown on calcareous soils (Coyne et al. 1982; Zaiter et al. 1987).
- Fib* *fibula* arcs, with *t*, white arcs (bows) expressed in the corona zone of seed coats, together with *expansa* partly colored pattern (Bassett 2001; Bassett and McClean 2000).
- Fin (fin)* *Finitus* (Latin): indeterminate vs. *fin* determinate plant growth (Lamprecht 1935b; Rudolf 1958); long vs. short internode; later vs. earlier flowering. *Fin* is 1 cM from *Z* (Bassett 1997c) and located on Pv01 (Koinange et al. 1996; Freyre et al. 1998).
- Fop-1* confers resistance to the Brazilian race of *Fusarium oxysporum* f. sp. *phaseoli* (Ribeiro and Hagedorn 1979).
- Fop-2* confers resistance to the U.S. race of *Fusarium oxysporum* f. sp. *phaseoli* (Ribeiro and Hagedorn 1979).
- Fr* a *fertility restoring* gene (Mackenzie and Bassett 1987) for the cytoplasmic male sterility source derived from CIAT accession line G08063 (Bassett and Shuh 1982). Restoration is partial in *F*₁, complete and irreversible in fertile *F*₂ segregants, i.e., the gene alters the mitochondrial DNA, deleting a fragment of at least 25 kilobases in restored plants (Mackenzie et al. 1988; Mackenzie and Chase 1990).
- Fr-2* a *fertility restoring* gene that is derived from CIAT accession line G08063 and that restores fertility without deleting the same mitochondrial DNA fragment affected by *Fr* (Mackenzie 1991).
- G (Flav, Ca, Och)* The yellow-brown factor of Prakken (1970). The equivalent of *C* of Shaw and Norton (1918). Prakken (1970) believed that Lamprecht (1951a) genes *Flav*, *Ca*, and

- Och* are synonyms for *G*. The interactions of *G* with other combinations of seed coat color genes are summarized by Prakken (1972b). *G* is located on Pv04 (McClellan et al. 2002).
- Ga* *gametophyte* factor, which achieves complete selection for pollen carrying *Ga*, i.e., no pollen carrying *ga* achieves fertilization (Bassett et al. 1990).
- gas* *gamete-sterile*: causes both male and female sterility (Lamprecht 1952b).
- glb* *glossy bronzing* leaf mutant (Bassett 1992c).
- Gpi-c1* structural gene for *glucose phosphate isomerase* enzyme, i.e., the more anodal of the two *cytosolic* isozymes (Weeden 1986).
- Gr* in the presence of *ih*, produces *green* dry pod color; in the presence of *lh*, produces tan dry pod color; *gr* in the presence of *ih* or *lh*, produces tan dry pod color (Honma et al. 1968).
- gy* *greenish yellow* seed coat, usually with *P [C r] gy J g b v* (or *v^{lae}*) *Rk* of the Mayocoba market class, but also expressed with *G b v* or *G B v* (Bassett et al. 2002a). A second gene (tentative symbol *Chr*) is necessary to express greenish yellow color in the corona (with *g b v^{lae}*) and hilum ring with *g b v^{lae}* or *g b v* (Bassett 2003c). *Gy* is either closely linked to *C* or is part of the 'complex *C* locus' on Pv08 (Bassett et al. 2002a).
- Hbl* (*L_{HB-1}*) controls expression of *halo blight* tolerance in *leaves* (Hill et al. 1972).
- Hbnc* (*SC_{HB-1}*) controls expression of *halo blight* tolerance resulting in *nonsystemic chlorosis* of leaves (Hill et al. 1972).
- Hbp* (*PD_{HB-1}*) controls expression of *halo blight* tolerance in *pods* (Hill et al. 1972).
- hmb* controls expression of sensitivity to the *herbicide metobromuron*, where *Hmb* expresses metobromuron insensitivity (Park and Hamill 1993).
- Hss* *hypersensitivity soybean*: confers a rapid lethal necrotic response to soybean mosaic virus (SMV) that is not temperature sensitive (Kyle and Provvidenti 1993).
- Hsw* *hypersensitivity watermelon*: confers temperature sensitive resistance (lethal hypersensitivity) to watermelon mosaic virus 2. Very tightly linked, if not identical, to the *I* gene for bean common mosaic virus (Kyle and Provvidenti 1987).
- Ht-1 Ht-2* (*L-1 L-2*) genes of equal value for height of plant (Norton 1915). They also increase length of seed (Frets 1951).
- I* confers temperature sensitive resistance to bean common mosaic virus. Tightly linked, if not identical, to *Bcm*, *Cam*, *Hsw*, and *Hss* (Ali 1950; Kyle et al. 1986; Kyle and Provvidenti 1993). The *I* gene (or the complex *I* region) conditions resistance and/or lethal necrosis to a set of nine potyviruses, BCMV, WMV, BICMV, CAbMV, AzMV, ThPV, SMV, PWV-K, and ZYMV (Fisher and Kyle 1994). *I* has a nearly terminal position on Pv02 (Vallejos et al. 2000).
- la lb* parchmented vs. *ia* tender pod (Lamprecht 1947b). Flat or deep (elliptical cross-section) vs. round pod (Lamprecht 1932b, 1947b, 1961a).
- ian-1 ian-2* (*ia*) *indehiscent anther* where the heterozygote produces partial indehiscence (Wyatt 1984); currently, two unlinked mimic genes can produce indehiscent anther (Wyatt, personal communication).
- lbd* *leaf-bleaching dwarf* mutant (Bassett 1992c).
- ico* *internodia contracta* (Latin): internodes 4-7 cm long instead of the normal 8-11 cm (Lamprecht 1961b).
- lgr* (*lh*) *inhibits* the action of *Gr*, conferring tan dry pod color in the presence of *Gr* or *gr* (Honma et al. 1968).
- ilo* *inflorescentia longa* (Latin): 5-7 long internodes in the inflorescence instead of the

	usual 2-3 (Lamprecht 1961b).
<i>ip</i> (<i>i</i> ₁)	<i>inhibits</i> the action of <i>P</i> with respect to the color of the hypocotyl (Nakayama 1958).
<i>iter</i>	<i>iteratus-ramifera</i> (Latin): with <i>ram</i> produces triple branched inflorescence (Lamprecht 1935b, 1935d).
<i>iv</i> (<i>i</i> ₂)	<i>inhibits</i> the action of <i>V</i> with respect to the color of the hypocotyl; is lethal with <i>v</i> ^{jae} (Nakayama 1958).
<i>iw</i>	<i>immature white</i> seed coat in the presence of <i>p</i> (Baggett and Kean 1984).
<i>J</i> (<i>Sh</i>)	With <i>P</i> , gives light yellow-brown or pale ochraceous buff testa (Lamprecht 1933), Rohseidengelb testa (Lamprecht 1939), raw silk testa (Lamprecht 1932a, 1951a) and the same color to the hilum ring (Lamprecht 1951a; Prakken 1934). The equivalent of the <i>Sh</i> of Prakken (1934) (Lamprecht 1960; Prakken 1970). Similar to <i>Asp</i> (Lamprecht 1940c) only in seed coat shininess (Bassett 1996b). It causes seed coats to glisten and to darken with age (Lamprecht 1939). <i>J</i> is linked to <i>Bip</i> and is located on Pv10 (McClellan et al. 2002).
<i>j</i> (<i>mar</i>)	Expresses “immature” seed coat colors, viz., paler and highly variable (seed to seed) along the ventral (darker relative to dorsal) to dorsal surface transition, for whatever combination of other seed coat color genes are present (Bassett 1996b; Prakken 1972b). <i>j</i> produces dull (mat) seed coat (Prakken 1940-41), nearly white corona with <i>Z</i> , and nearly white corona and hilum ring with <i>z</i> (Bassett 1996b; Bassett et al. 1996b). Same as <i>mar</i> of Lamprecht (1933) for a broad band of color about the hilum. With <i>j</i> , no leuco-anthocyanidins are synthesized and production of anthocyanins and flavonol glycosides is low (Feenstra 1960).
<i>j</i> ^{ers} (<i>ers-2</i>)	The <i>j</i> ^{ers} allele (from ‘Early Wax’) differs from <i>j</i> expression: <i>TZj</i> ^{ers} fails to express the margo pattern of <i>TZj</i> , <i>Tzj</i> ^{ers} fails to express the margo <i>z</i> pattern of <i>Tzj</i> , and <i>tZj</i> ^{ers} fails to express marginata of <i>tZj</i> ; but <i>tZj</i> ^{ers} and <i>tZj</i> express white seed coats (Bassett 1997d; Bassett et al. 2002b). <i>T/tz/zj/j</i> ^{ers} in a <i>PCJGBV</i> background expresses reverse margo pattern (Bassett et al. 2002b).
<i>Ke</i>	<i>potassium utilization efficiency</i> (Shea et al. 1967).
<i>la</i>	<i>Lamm</i> : with <i>cry</i> gives long internode; <i>la</i> with <i>Fin</i> is dwarf; <i>la cry fin</i> is slender (Lamprecht 1947b).
<i>Lan</i>	<i>lanceolate</i> leaf mutant; <i>Lan/Lan</i> is usually a zygotic lethal, and survivors are dwarfs that do not flower; <i>Lan/lan</i> segregates 2:1 (lanceolate to normal) in selfed progeny (Bassett 1981).
<i>Ld</i>	<i>leaf distortion</i> resembling phenoxy herbicide injury, with interveinal clearing, slight chlorosis, necrotic scarring of the midrib, altered leaf shape, and extra leaflets (Rabakoarihanta and Baggett 1983).
<i>Lds</i> (<i>Ds</i>)	<i>Ld suppressor</i> (Rabakoarihanta and Baggett 1983).
<i>Lec</i>	structural gene for the seed protein <i>lectin</i> or phytohemagglutinin (Osborn et al. 1986).
<i>Li</i> (<i>L</i>)	<i>long</i> vs. <i>li</i> short <i>internodes</i> (Lamprecht 1947b; Norton 1915).
<i>lo</i>	plants have a short inflorescence (Lamprecht 1958).
<i>lr-1 lr-2</i>	the double recessive genotype produces <i>leaf rolling</i> of trifoliolate leaves through the third or fourth nodes, ending in stem and apical necrosis and death of the plant (Provvidenti and Schroeder 1969).
<i>Me</i>	structural gene for <i>malic enzyme</i> (Weeden 1984).
<i>Mel</i> (<i>Me</i>)	confers nematode resistance to <i>Meloidogyne incognita</i> (some isolates of race 1), <i>M. javanica</i> , and <i>M. arenaria</i> (Omwega et al. 1990).
<i>Mel-2</i> (<i>Me-2</i>)	confers nematode resistance to <i>Meloidogyne incognita</i> race 1 (isolates to which

- Mel* is susceptible), race 2 and race 3, but is susceptible to *M. javanica* and *M. arenaria* (Omwega and Roberts 1992).
- mel-3 (me-3)* confers temperature sensitive nematode resistance (resistant at 26 C but susceptible at 28 C) to the same species, races, and isolates as with *Mel-2* (Omwega and Roberts 1992).
- Mf* *mancha na flor* (Portuguese): brownish-violet blotch on the base of the standard flower petal (Vieira and Shands 1969).
- mi, mia* micropylar stripe pattern (Lamprecht 1932c and 1934a); both 3:1 and 15:1 segregation were observed.
- Mic (Mip)* *micropyle inpunctata* (Latin): small dots near the micropyle (Lamprecht 1940c).
- miv* *minor intervallis* (Latin): end of seed flattened and a short distance between funicles (Lamprecht 1952a).
- Mrf* *Mosaico rugoso del frijol* (Portuguese): confers immunity to bean rugose mosaic virus (Machado and Pinchinat 1975).
- Mrf²* *Mosaico rugoso del frijol* (Portuguese): confers the localized lesion type of resistance to bean rugose mosaic virus; the order of dominance in the allelic series is *Mrf*>*Mrf²*>*mrf* (Machado and Pinchinat 1975).
- mrf* *mosaico rugoso del frijol* (Portuguese): confers susceptibility (systemic infection) to bean rugose mosaic virus (Machado and Pinchinat 1975).
- ms-1* an induced mutant for genic *male sterility*, where no pollen is produced but female fertility is unimpaired (Bassett and Silbernagel 1992).
- Mue* structural gene for *methyumbelliferyl esterase* (Garrido et al. 1991).
- mu* *mutator* locus that produces mutations of *us* to *Us*, thus giving normal green leaf sectors in yellow leaves due to *us mu*, where the ratio of normal to variegated plants is 15:1 (Coyne 1966).
- Nag* structural gene for *N-acetyl glucoseaminidase* enzyme (Weeden 1986).
- Nd-1 Nd-2 (D-1 D-2)* additively control the variation in *node* number on the main stem of determinate beans and additively control the number of days to flowering (Evans et al. 1975).
- nie* an induced mutation for *ineffective nodulation* by *Rhizobium* (Park and Buttery 1994).
- nnd (sym-1)* an induced mutation for *non-nodulation* by *Rhizobium*, i.e., lacking capacity for *symbiosis* (Pedalino et al. 1992).
- nnd-2* an induced mutation for *non-nodulation* by *Rhizobium* (Park and Buttery 1994).
- No* with *P v*, expresses Light *Nopal* Red (light salmon with brownish tinge) flower color and much darker reddish color of flower buds by pleiotropic action; with *P V*, expresses Pure *Nopal* Red flower; *No* action is fully dominant; *No* is linked (31 cM) to *Fin* (Lamprecht 1948b, 1961a). Allelism of *No* with *Sal* was not tested (Bassett 2003b).
- nts (nod)* *nitrogen tolerant supernodulation*: an induced mutation that permits abundant nodulation in the presence of high nitrogen (Park and Buttery 1989).
- ol* *overlapping leaflets* mutant (Bassett 1992c).
- P* basic color gene (Emerson 1909a; North and Squibbs 1952; Prakken 1934; Schreiber 1934; Shaw and Norton 1918; Shull 1908; Skoog 1952). *P* without color genes is colorless as is *p* (Lamprecht 1939; Smith 1939). According to Feenstra (1960), *P* is the equivalent of the *A* of Tschermak (1912), of Kooiman (1920), and of Sirks (1922). *P* is located on Pv07 (Erdmann et al. 2002; Koinange et al. 1996; Vallejos et al. 1992) with physical position reported by McClean et al., 2018) as a member of

	clade B of subclass IIIf of plant basic helix–loop–helix (bHLH) proteins.
p^{sd}	is an allele of the <i>P</i> (Pigment) gene with order of dominance $P > P^{sd} > p$ (Islam et al., 2020). It replaces the <i>sd</i> gene (symbol) that conditions the slow darkening seed coat trait in pinto (Elsadr et al. 2011) and carioca beans (Alvares et al., 2019).
p	white seed coat and flower (Emerson 1909a). Ten gene pool-specific p alleles conditioned the white seed phenotype, and each causative mutation affected at least one bHLH domain required for color expression (McClellan et al., 2018).
p^{gri} (<i>Gri</i> , v^{pal})	superscript <i>gri</i> , <i>griseoalbus</i> (Latin): p^{gri} with <i>C J B V</i> produces grayish white (blubber white) seed coat without a hilum ring, giving the dominance order $P > p^{gri} > p$ (Bassett 1994b; Lamprecht 1936); p^{gri} with <i>C J B V</i> produces flowers with very pale lavender wing petals and two dots of violet on the upper edge (center) of an otherwise near white standard petal (Bassett 1992b); formerly a second basic color factor like <i>P</i> (Lamprecht 1936). Lamprecht (1936) speculated that the flower color observed with p^{gri} segregation must be due to an undiscovered new allele (tentatively v^{pal}) at <i>V</i> . p^{stp} superscript <i>stp</i> , <i>stippled</i> seed coat and white flowers with a narrow, violet banner tip and pale violet periphery (2-3 mm) on the wing petals (Bassett 1996a, 2003a).
p^{hbw}	stippled seed coat (different from p^{stp}) and violet flowers with the lower (superscript <i>hbw</i>) <i>half</i> of the <i>banner</i> petal <i>white</i> (Bassett 1996a, 2003a).
p^{mic}	self-colored seed coat except for a white (superscript <i>mic</i>) <i>micropyle</i> stripe and violet flowers without pattern (Bassett 1998, 2003a).
pa	<i>pale green leaves</i> (Smith 1934).
pc	<i>persistant green pod color</i> (Dean 1968).
pg (pa_1)	<i>pale-green</i> foliage mutant (Wyatt 1981).
<i>Pha</i>	structural gene for the seed protein <i>phaseolin</i> (Osborn et al. 1986).
<i>Phg-1</i>	confers resistance to angular leaf spot in the common bean cultivar AND 277. <i>Phg-1</i> is linked to <i>Co-1</i> ⁴ on Pv01 (Carvalho et al. 1998; Gonçalves-Vidigal et al. 2011).
<i>Phg-2</i>	confers resistance to angular leaf spot from Mexico 54 and is located on Pv08 (Sartorato et al. 2000; Namayanja et al. 2006).
<i>Phg-2</i> ²	confers resistance to angular leaf spot from BAT332 (Namayanja et al. 2006).
<i>Phg-3</i>	confers resistance to angular leaf spot from Ouro Negro and located on Pv04 (Corrêa et al. 2001; Faleiro et al. 2003; Gonçalves-Vidigal et al. 2013).
<i>Phg-4</i>	confers resistance to angular leaf spot previously reported as the major QTL ALS4.1 on Pv04, present in the common bean line G5686 (Mahuku et al. 2009; Keller et al. 2015; Souza et al. 2016).
<i>Phg-5</i>	confers resistance to angular leaf spot previously reported as the major QTL ALS10.1 on Pv10, present in the common bean lines G5686 and CAL143 (Oblessuc et al. 2012, 2013; Keller et al. 2015; Souza et al. 2016).
<i>Pkp-1</i>	resistance from PI 181996 to soybean rust (SBR), caused by the fungus <i>Phakopsora pachyrhizi</i> (Souza et al. 2014).
<i>Pmv</i>	confers incomplete dominance for resistance to <i>peanut mottle virus</i> (Providenti and Chirco 1987).
<i>ppd</i> (<i>neu</i>)	<i>photoperiod-insensitive</i> gene found in ‘Redkloud’ with a syndrome of effects (Wallace et al. 1993); an allele-specific associated primer is now available for <i>ppd</i> (Gu et al. 1995); probably the same locus as <i>Neu</i> ⁺ for short day vs. <i>neu</i> for day <i>neutral</i> flowering response to length of day of Rudorf (1958). The red/far-red photoreceptor gene PHYTOCHROME A3 (PHYA3) was identified as the <i>ppd</i> gene on Pv01 (Kamfwa et al., 2015; Weller et al., 2019).

- Pr* Preventing the "flowing out" of red color (Prakken 1972b, 1974); *pr* with pattern alleles at *C* and *R* allow the red color in the dark pattern color zones to "flow out" into the light pattern color areas, producing various light red hues such that the contrast between the dark and light pattern colors is very small; tightly linked to the *C* locus.
- Prpⁱ-2* a gene controlling (superscript *i*) intensified anthocyanin (*purple*) expression syndrome (not linked to *C*) in flower buds, corolla, pods, stems and leaf lamina (Bassett 2005).
- prc* (*pc*) progressive chlorosis mutant (Nagata and Bassett 1984); redesignated *prc* (Awuma and Bassett 1988).
- Prx* structural gene for peroxidase enzyme, i.e., the most cathodal of the peroxidase isozymes (Weeden 1986).
- Pse-1* (*R1*) a halo blight resistance gene described by Walker and Patel (1964) and reported as the *R1* gene by Teverson (1991) and Taylor et al. (1996); present in the halo blight differential variety Red Mexican UI-3. *Pse-1* is located on linkage group 10 and confers resistance to pathogen races 1, 5, 7 and 9 (Miklas et al., 2009).
- Pse-2* (*R2*) a halo blight resistance gene described by Teverson (1991) and Taylor et al. (1996) as present (as *R2*) in the halo blight differential variety A43 (ZAA12). Confers resistance to races 2, 3, 4, 5, 7, 8, and 9 and is located on Pv10 (Miklas et al. 2011).
- Pse-3* (*R3*) a halo blight resistance gene described by Teverson (1991) and Taylor et al. (1996) as present (as *R3*) in the halo blight differential variety Tendergreen. *Pse-3* confers hypersensitive resistance response to races 3 and 4 and is completely linked with the *I* gene locus on Pv02 (Fourie et al. 2004; Teverson 1991).
- Pse-4* (*R4*) a halo blight resistance gene discovered by Teverson (1991) and Taylor et al. (1996) to be present (as *R4*) in the halo blight differential variety Red Mexican UI-3.
- pse-5* (*R5*) a halo blight resistance gene described by Teverson (1991) and Taylor et al. (1996) as present (as *R5*) in the halo blight differential variety A43 (ZAA12) and conditioning recessive resistance to race 8. Miklas et al. (2011) observed that this gene cosegregated with *Pse-2* on Pv10.
- Pse-6* a halo blight resistance gene identified in BelNeb-RR-1, conditioning resistance to races 1, 5, 7 and 9 and located on Pv04 (Miklas et al. 2014).
- punc* *punctatus* (Latin): causes dotting of the testa (Lamprecht 1940c).
- ram* *ramifera* (Latin): branched inflorescence (Lamprecht 1935b).
- Rbcs* (*rbcS*) small subunit of the *rubisco* enzyme (Weeden 1984).
- rf-1* reclining foliage due to downward slanting petioles (Bassett 1976). *Rf-1* is linked (11 cM) to *V* (Bassett 1997a), and *V* is located on Pv06 (McClellan et al. 2002).
- rf-2* reclining foliage mutant due to downward slanting petioles (Bassett and Awuma 1989).
- rf-3* reclining foliage mutant due to downward slanting petioles (Bassett and Awuma 1989).
- rfi* (*i*) reclining foliage inhibitor: recessive epistatic factor to *rf-1* and *rf-3* (Bassett 1976; Bassett and Awuma 1989).
- Rfs* (*m*) reclining foliage suppressor: dominant suppressor of *rf-1* (Bassett 1976).
- Rk* red kidney: the *Rk* allele does not express testaceous (pink) color of light red kidney beans (Gloyer 1928; Smith 1939) or garnet brown color of dark red kidney beans (Smith and Madsen 1948); interactions of *rk* and *rk^d* with *C*, *D* (now *Z*, Bassett et al. 1999b), *J*, *B*, and *V* (using Prakken's symbols) were investigated (Smith 1961). According to Prakken (1972b), *Rk* is linked (28 cM) to *B*, which is located on Pv02

- (Kyle and Dickson 1988; Vallejos et al. 2000).
- rk* *red kidney*: with *m* or *c* (now *c^u*), *rk* expresses testaceous (pink) seed coat color; with *M* (red/buff marbled pattern), *rk* modifies cartridge buff expression to testaceous (Smith 1939, 1947); *rk* is dominant over *rk^d* (Smith and Madsen 1948); *rk* has no expression with *j* (Lamprecht 1961c; Smith 1961).
- rk^d* (*lin*) *red kidney* (superscript d) *dark*: with *r* (now *c^u*) and *J*, *rk^d* expresses garnet brown testa (Smith and Madsen 1948); *rk^d* has no expression with *j* (Smith 1961). With *P v* (or *v^{ae}*) and either *T/-* or *t/t/*, *rk^d* always gives red veins in the wing petals, whether clear or faint (Prakken 1972a, b); in some genetic backgrounds the red veins are “incompletely recessive”, i.e., *Rk/rk^{cd}* gives very faint red veins (Prakken 1972b). The red color of red kidney beans (all recessive alleles) is expressed by proanthocyanidins although three yellow flavonol glycosides are also present in the seed coats (Beninger and Hosfield 1999).
- rk^{drv}* *red kidney* (superscript drv) *dark red vein*: with *P v*, a spontaneous mutant of the *rk^d* gene expressing red wing petal veins that are “expanded” (larger in diameter and diffuse) compared to those of *rk^d*, creating the illusion of pale pink flowers when viewed at one meter or more (Bassett 2004).
- rk^{cd}* *red kidney* (superscript cd) *convertible dark*: *C rk^{cd}* expresses garnet brown seed coats, whereas *c^u rk^{cd}* expresses pink (testaceous) seed coats; thus, expression at *rk^{cd}* (from ‘NW 63’) is a function of interaction with *C* (Bassett and Miklas 2003).
- rk^p* *red kidney* (superscript p) *pink*: *rk^p* (from ‘Sutter Pink’) expresses consistently very weak pink color under humid growing conditions, unlike *rk* from ‘Redkloud’ (Bassett and Miklas 2003).
- rn-1 rn-2* (*r rN*) together confer resistance to *root-knot nematode*, where 2-4 dominant alleles give susceptible reaction and 1 dominant allele gives intermediate resistance in a 11:4:1 ratio (Barrons 1940).
- rnd* *round leaf mutant with lateral leaflet tips rounded* (Nagata and Bassett 1984).
- Sal* with *P*, *Sal* expresses *salmon* red flower color and a reddish tinge to the testa; scarlet red flower is expressed with *Sal Am Beg No* (Lamprecht 1948b). *Salmon* red flower color (Fan 1, 52C or D; Royal Hort. Soc. fans) is expressed by *Sal am V^{mf}* (or *v*), and scarlet flower (Fan 1, 43C; Royal Hort. Soc. fans) is expressed by *Sal Am V^{mf}* (or *v*) (Bassett 2003b). *Sal Am v* expressed oxblood red seed coats (vs. mineral brown tinged with red) due either to a pleiotropic effect of *Am* or a very closely linked dominant gene (Bassett 2003b), and *Am* has no expression with *sal* (Bassett 2003b).
- sb* *spindly branch* mutant; the stems are thinner and more highly branched than normal (Awuma and Bassett 1988).
- sb^{ms}* *spindly branch* (superscript ms) *male sterile* mutant; allelic with *sb*; anthers are atrophied and produce no viable pollen, but there is no loss of female fertility (Bassett 1991a)
- sb-2* *spindly branch* mutant; the stems are thinner and more highly branched than normal (Bassett 1990).
- sb-3* *spindly branch* mutant; the stems are thinner and more highly branched than normal (Bassett 1990).
- sil* *silver* colored leaves and severe plant stunting under high intensity light in the field; no stunting under glasshouse culture (Frazier and Davis 1966a; Nagata and Bassett 1984).
- Skdh* structural gene for *shikimate dehydrogenase* enzyme (Weeden 1984).

<i>sl</i>	<i>stipelless lanceolate</i> leaf mutant (Nagata and Bassett 1984) gives a lanceolate leaf form with loss of stipels from the terminal leaflet.
<i>Smv</i>	confers incompletely dominant resistance to <i>soybean mosaic virus</i> (Provvidenti et al. 1982).
<i>St</i>	<i>stringless</i> pod; <i>st</i> gives a complete string (Prakken 1934); has modifiers.
<i>Sur</i>	<i>Sursum versus</i> (Latin): causes leaves and petioles to point downward (Lamprecht 1937) with pulvinule rotated 180E. See X ^{su} .
<i>sw-1 sw-2</i>	the double recessive genotype produces <i>seedling wilt</i> (Provvidenti and Schroeder 1969), i.e., epinasty of primary leaves, necrosis of terminal bud, and death of the plant in primary leaf stage.
<i>T</i>	self-colored seed coat and colored flowers (Emerson 1909a; Lamprecht 1934b; Shaw and Norton 1918). <i>T</i> is located Pv09 (McClellan et al. 2002).
<i>t (z-1)</i>	a seed coat pattern gene required for all partly colored seed coat patterns; has pleiotropic expression for white flowers (Schreiber 1934; Shaw and Norton 1918) and green cotyledons and hypocotyls (Prakken, 1972b). Early reports of interactions of <i>t</i> with <i>Z</i> and <i>z</i> (Lamprecht 1934b; Sax 1923; Shaw and Norton 1918) were later extended to <i>t</i> interactions with <i>Z</i> , <i>J</i> , and <i>Bip</i> (Bassett 1994c, 1996b and c, 1997c and d; Bassett et al. 2000, 2002b; Lamprecht 1940b; Schreiber 1940).
<i>t^{bp}</i>	superscript bp for <i>blue pattern</i> . A seed coat gene from G07262 that conditions blue patterned flowers in the presence of <i>Prpⁱ-2</i> described by Bassett and Miklas (2009).
<i>t^{cf}</i>	superscript cf, <i>colored flower</i> : a seed coat gene (from PI 597984) for partly colored patterns without pleiotropic expression for white flowers; necessary for expression of the two-points pattern (Bassett et al. 1999a).
<i>Th-1 Th-2</i>	genes of equal value for seed <i>thickness</i> (Frets 1951).
<i>Tm</i>	confers immunity to <i>tobacco mosaic virus</i> (Thompson et al. 1952).
<i>To</i>	cell wall fiber (Prakken 1934).
<i>top</i>	<i>topiary</i> plant architecture; a spontaneous mutant with determinate habit (terminal bud is reproductive); dark green leaves on shortened rachis, petiolules, and petioles that cause overlapping leaflets held close to the stem (Guner and Myers 2000).
<i>Tor (T)</i>	<i>torquere</i> (Latin): twining habit vs. <i>tor</i> non-twining (Norton 1915; Lamprecht 1947b); confers phytochrome-controlled climbing habit in indeterminate bush bean types (Kretchner et al. 1961; Kretchmer and Wallace 1978).
<i>Tr</i>	<i>testa rupture</i> (Dickson 1969); an incompletely dominant gene with 25-30% penetrance.
<i>tri</i>	<i>tricotyledonae</i> (Latin): produces three cotyledons (Lamprecht 1961b) with 40-50% penetrance.
<i>trv</i>	confers resistance to <i>tobacco ringspot virus</i> (Tu 1983); symbol proposed by Provvidenti (1987).
<i>Ts</i>	<i>temperature-dependant string</i> formation (Drijfhout 1978a); <i>St ts</i> is without string, <i>St Ts</i> expresses incomplete string, and <i>st Ts</i> and <i>st ts</i> have complete string.
<i>tw</i>	<i>twisted</i> pod character produces pod rotation that is highly variable, from slight to more than 360 degrees in snap bean germplasm (Baggett and Kean 1995).
<i>uni</i>	<i>unifoliata</i> (Latin): unifoliolate leaves; complete sterility (Lamprecht 1935c); this material is lost, and no allelism tests were made with other unifoliolate mutants before <i>uni-1</i> was lost.
<i>Uni-2</i>	a dominant mutation for <i>unifoliolate</i> true leaves (Garrido et al. 1991).
<i>uni^{nde}</i>	induced mutation with <i>unifoliolate</i> leaves with (superscript nde) <i>node dependent expression</i> ; partial fertility and shows reversion to normal leaflet number at higher

- nodes (Myers and Bassett 1993).
- uni^{nie}* *unifoliolate* leaves with (superscript nie) *node independent expression* (natural mutant); completely female sterile but male-fertile and shows consistently strong expression of the unifoliolate trait at higher nodes (Myers and Bassett 1993).
- Ur-1* rust [*Uromyces appendiculatus* (Pers.) Unger var. *appendiculatus*] resistance gene discovered by Ballantyne (1978) and found in the Middle American source 'B1627'. Kelly et al. (1996) proposed using the *Ur* symbol as a base for all rust resistance genes.
- Ur-2* rust resistance gene discovered by Ballantyne (1978) and found in the Middle American source 'B2090'.
- Ur-2²* rust resistance allele at the *Ur-2* locus discovered by Ballantyne (1978) and found in the Middle American source 'B2055'.
- Ur-3* rust resistance gene discovered by Ballantyne (1978) (see also Ballantyne and McIntosh 1977) and found in the Middle American sources 'Aurora', 'Mex 235', 'Nep-2', and '51051', albeit with slightly different reaction profiles across a differential set of races for each source (Miklas et al, 2002). *Ur-3* is linked to the *Co-2* gene and has a nearly terminal position on Pv11 (Miklas et al. 2002; Kelly et al. 2003).
- Ur-4 (Up-2, Ur-C)* rust resistance gene originally discovered by Ballantyne (1978) as *Ur-C* and rediscovered by Christ and Groth (1982) as *Up-2*. *Ur-4* is an Andean gene found in 'Early Gallatin' and is located on Pv06 (Miklas et al. 2002).
- Ur-5 (B-190)* block (cluster) of eight tightly linked rust resistance genes (*Ur-5A* through *Ur-5H*) found by Stavely (1984) and present in the rust differential variety Mexico 309. *Ur-5* is located on Pv04 (Miklas et al. 2002) in the vicinity of other resistance genes (Kelly et al. 2003).
- Ur-6 (Ur_a, Ur-G)* rust resistance gene originally discovered by Ballantyne (1978) as *Ur-G* and rediscovered by Grafton et al. (1985) as *Ur_a*. *Ur-6* is an Andean gene present in 'Olathe' and the rust differential variety Golden Gate Wax. *Ur-6* is independent of *Ur-3* and located on Pv11 (Miklas et al. 2002).
- Ur-7 (R_{B11})* rust resistance gene discovered by Augustin et al. (1972) and found in the Middle American varieties GN 1140 and Pinto US-5. *Ur-7* is independent of *Ur-3* and *Ur-6* and located on Pv11 (Park et al. 2003).
- Ur-8 (Up-1)* rust resistance gene discovered by Christ and Groth (1982) and found in the Andean variety U.S. #3.
- Ur-9 (Ur_p)* rust resistance gene discovered by Finke et al. (1986) and found in the Andean variety Pompadour Checa. *Ur-9* is located on Pv01 (Miklas et al. 2002) near the *Co-1* locus (Kelly et al. 2003).
- Ur-10 (URPR1)* rust resistance gene discovered by Webster and Ainsworth (1988) and found in snap bean varieties Cape and Resisto.
- Ur-11 (Ur-3²)* originally a rust resistance allele at the *Ur-3* locus discovered by Stavely (1990), but later found to be tightly linked with *Ur-3* (Stavely 1998). *Ur-11* is located on Pv11 (Miklas et al. 2002).
- Ur-12* gene conditioning adult plant resistance (APR) to bean rust discovered by Jung et al. (1998) that is initially expressed at the fourth trifoliolate leaf stage or later. *Ur-12* is found in the Andean variety Pompadour Checa and is tentatively located at a terminal position on Pv07 (Jung et al. 1998; Miklas et al. 2002).
- Ur-13* rust resistance gene discovered by Liebenberg and Pretorius (2004) and found in the Andean sugar bean variety Kranskop; however, the gene appears to be of

	Middle American origin and is carried by variety Redlands Pioneer (Liebenberg and Pretorius 2004). <i>Ur-13</i> is located on Pv08 (Miene et al., 2005).
<i>Ur-14</i>	adominant gene in Ouro Negro on Pv04 conditioning resistance to rust, described by Souza et al. (2011).
<i>us</i>	<i>unstable</i> gene that mutates to <i>Us</i> in presence of <i>mu</i> to produce green leaf sectors in a yellow leaf background due to <i>us mu</i> , resulting in variegation (Coyne 1966).
<i>V (Bl)</i>	with <i>P</i> produces pale glaucescens testa without a hilum ring (Lamprecht 1939). The color ranges from pale violet to black depending upon other color genes present (Lamprecht 1932a; Prakken 1934, 1972b). According to Prakken (1972a) the <i>Bl</i> of Smith (1939) is the same as <i>V</i> . <i>Bl</i> with the basic color factors produces purple-violet seed coat (Smith 1939; Tjebbes and Kooiman 1921, 1922a), changes oxblood red to purple (Smith 1939), and is responsible for bluish tints to plant colors (Tjebbes and Kooiman 1921). <i>bl</i> with appropriate genes produces red seed coat (Tjebbes and Kooiman 1922a). According to Feenstra (1960), <i>V</i> is the equivalent of the <i>B</i> of Shull (1908) and of Tschermak (1912), the <i>F</i> of Kooiman (1931), the <i>G</i> of Shaw and Norton (1918), and the <i>Z</i> of Sirks (1922). <i>V</i> is located on Pv06 (McClellan et al. 2002). <i>V</i> encodes flavonoid 3'5' hydroxylase (F3'5'H), a P450 enzyme required for the expression of dihydromyricetin-derived flavonoids in the flavonoid pathway (McClellan et al., 2022).
<i>V^{wf}</i>	a gene with the seed coat color properties of <i>V</i> but with the pleiotropic effect of (superscript wf) <i>white flower</i> color; a gene derived from <i>P. coccineus</i> (Lamprecht line M0137, now PI 527845), permitting black seed coats and scarlet or vermilion flowers in nature (Bassett 1997b).
<i>v^{lae} (Cor)</i>	superscript lae, <i>laelia</i> (Latin): with <i>T P</i> gives <i>laelia</i> (pink) flowers and rose stem (Lamprecht 1935e); with <i>P C J G B</i> produces mineral brown seed coats with the black corona character; expresses dark corona (purple to black) with numerous other genotypes (Bassett 1995a). The <i>Cor</i> locus of Lamprecht (1934a, 1936) is a synonym for <i>v^{lae}</i> .
<i>v</i>	white flowers, and with <i>P C J G B</i> , produces mineral brown seed coat (Lamprecht 1935e).
<i>var</i>	<i>variegated</i> : environment-sensitive gene, in combination with <i>mu</i> and <i>us</i> produces yellow lethal plants in a ratio of 63 normal:1 variegated (Coyne 1966).
<i>vi (vir_i)</i>	<i>virescent</i> foliage mutant (Grafton et al. 1983).
<i>wb</i>	with <i>T P V</i> , gives flowers with a <i>white banner</i> petal and wings of pale violet; the gene is from the <i>P. coccineus</i> PI 273666 (Bassett 1993a).
<i>Wmv</i>	confers resistance to <i>watermelon mosaic virus 2</i> (Kyle and Providenti 1987; Providenti 1974).
<i>X^{su}</i>	<i>ex parte</i> (superscript su) <i>sursum versus</i> (Latin): causes the leaves and petals to point downward (Lamprecht 1961b); effect is similar to <i>Sur</i> , but pulvinule is rotated only 90E.
<i>Xap-1</i>	Single dominant gene resistance to <i>Xanthomonas axonopodis</i> from PR0313-58 that co-segregates with SAP6 QTL on Pv10 (Zapata et al., 2011)
<i>y</i>	with <i>Arg</i> , produces <i>yellow wax</i> pod; with <i>arg</i> , the pod is white; <i>Y</i> with <i>Arg</i> produces green pod; <i>Y</i> with <i>arg</i> gives a greenish gray (silvery) pod (Currence 1931; Lamprecht 1947b).
<i>Z (D) (ers)</i>	<i>zonal</i> partly colored seed coat patterns are expressed with <i>t z</i> (Tschermak 1912, as interpreted by Lamprecht 1934b). With <i>t</i> , the <i>Z</i> locus interacts with <i>Bip</i> to express a wide range of partly colored seed coat patterns (Lamprecht 1934b, 1940b). The <i>L</i> of

Schreiber (1940) was found to be allelic with *J* (Bassett et al. 2002b); hence, all the partly colored patterns controlled by interactions (with *t*) of *Z* and *L* (Schreiber 1940) are really interactions of *Z* with *J*. Similarly, the *mar* gene of Lamprecht (1933) was found to be allelic with *j* (Bassett 1996b); hence, the interaction of *t* with *j* expresses marginata pattern (Bassett 1994c), which is the equivalent of the *t Z L* of Schreiber (1940) for marginata. Similarly, the new allele *j^{ers}* (Bassett 1997d) is now recognized to be *j^{ers}* (Bassett et al. 2002b). The *D* gene for hilum ring color was found to be allelic with *Z* (Bassett et al. 1999b). Thus, hilum ring color is controlled by the interaction of *J* and *Z* (Prakken 1970), where colorless hilum ring is expressed by *z j*. Thus, *Z* and *J* have dual roles, 1) color expression of the hilum ring and 2) major roles in the expression of partly colored seed coats. A review of partly colored seed coat patterns with illustrations and genotypes is available (Bassett and McClean 2000). *Z* is located on Pv03 (McClean et al. 2002).

z^{sel} superscript sel, *sellatus* (Latin): with *t*, *z^{sel}/z^{sel}* expresses *sellatus* pattern and *z^{sel}/z* expresses piebald pattern (Bassett 1997c; Lamprecht 1934b; Tschermak 1912).

z with *t Bip*, expresses virgarcus pattern; with *t bip* expresses bipunctata pattern (Bassett 1996c). For other interactions see Bassett and McClean (2000).

Znd gene found in the variety Matterhorn for resistance to soil deficiency of Zn (Singh and Westermann 2002).

APPENDIX – Obsolete symbols removed from list

- A* basic color factor, producing yellow-brown (Kooiman 1931; Sirks 1922; Tjebbes and Kooiman 1922b; Tschermak 1912). It is the equivalent of *P*, which has priority.
- A* indeterminate versus determinate, *a*, plant habit (Emerson 1916; Norton 1915). Symbol superseded by *Fin* (Lamprecht 1935b).
- A, B, C* schematic genes contributing to the length and number of internodes (Emerson 1916). Also used as schematic genes contributing to hybrid vigor (Malinowski 1924).
- A, B, C, D* schematic genes each contributing 1 cg to a minimum seed weight (Sirks 1925).
- Aeq* *Aequicoloratus* (Latin): with *P T E Uc Unc* and *Rst* or *R^{ma}* darkens the banner petal (Lamprecht 1935e, 1948a); with *Sal* the effect is similar to *V* (Lamprecht 1948b).
- an* appears to have the functions of *P* (Hilpert 1949).
- av, sv, iv* confer resistance to bean common mosaic virus (Ali 1950; Petersen 1958).
- B* originally a "blackener", producing anthocyanin with the basic color gene *P* = *A* (Shull 1908; Sirks 1922; Tschermak 1912). According to Feenstra (1960) this gene is the equivalent of the *G* of Shaw and Norton (1918), the *F* of Kooiman (1920), the *Z* of Sirks (1922), and the *V* of Lamprecht (1932a) and Prakken (1934). It is the equivalent of Feenstra's *C* (1960).
- bc-u* strain-unspecific complementary gene, giving resistance to strains of bean common mosaic virus (BCMV) only when together with one or more of the strain-specific resistance genes (Drijfhout 1978b).
- bc-1²* with *bc-u* gives resistance to BCMV strains NL1, NL2, NL7, and NL8 (Drijfhout 1978b).
- bc-2²* with *bc-u* gives resistance to BCMV strains NL1, NL2, NL5, NL6, NL7, and NL8 (Drijfhout 1978b).
- B I* hypothetical genes for testa vein color and orientation (Sarafi 1974). Data not sufficient to establish new genes (Bassett, editor).
- Br* According to Prakken (1972a), the *Br* of Smith (1947, 1961) is the same as *B*. *Br* with *P Rk* produces brown seed coat (Smith 1947), *br* with *P Rk* green seed coat, *br* with *P rk* pink seed coat (Smith 1947).
- C R* hypothetical genes for seed coat color where *C* gives cream, *R* gives red, *C R* produces milky phenotypes, and *r c* produces pink (Sarafi 1974). The real genotypes probably involve the *Rk* locus and its modifiers (Bassett, editor).
- Ca* with color genes, *caruncula* stripe (Lamprecht 1932c). Prakken (1970) believed this gene is a synonym for *G*.
- Can* According to Prakken (1972a), *D* is the equivalent of *Can* or *Ins* of Lamprecht (1939). *Can* with color genes gives a whitish (Speckweiss) testa (Lamprecht 1939) or blubber white (Lamprecht 1951a), with a yellowish brown hilum ring (Lamprecht 1939).
- Co-7* an anthracnose resistance gene found in the Middle American differential variety G2333 (Young et al. 1998) was renamed *Co-3⁵*.
- Co-9* Replaced by the *Co-3³* gene symbol.
- Co-10* An anthracnose resistance gene described by Alzate-Marin et al. (2003b) in the variety Ouro Negro. It is located on linkage group 4 (Freyre et al. 1998), and has been renamed *Co-3⁴*.
- cyv (by-3)* Confers high level resistance to *clover yellow vein* virus, formerly known as the

- severe, necrotic, or pod-distorting strain of bean yellow mosaic virus (Provvidenti and Schroeder 1973; Tu 1983); symbol proposed by Provvidenti (1987). Renamed *bc-3²*.
- def* *defectus* (Latin): gene *def* is a synonym for *gy* (Bassett, editor). The hypothesis of Prakken (1972b) was that the interaction of *G/g* with *def* produced zonal variability of greenish yellow expression on seed coats. Whereas the seed coat color expression of *gy* was falsely attributed to *G b v* and *g b v*. The hypothesis of Bassett et al. (2002) is that the interaction of (*C J*) *G* or *g* (*b v*) with *gy* expresses greenish yellow seed coat with variable expressivity. Thus, Prakken (1972b) attributed the instability of *gy* expression to a separate and non-existent gene *def* and attributed the greenish yellow color of *gy* to *C J g b v*, whereas the latter genotype has only shamois expression.
- E* intensifier with color genes (Tjebbes and Kooiman 1922b).
- e* *E* required for complete coloring of seed coat (Emerson 1909b); the action of *e* is hypostatic on *t*, producing much reduced partial coloring of seed coat and required for the soldier series of seed coat patterns (Emerson 1909b; Lamprecht 1934b; Leakey 1988; Sax and McPhee 1923; Smith 1939). The only published data (Sax and McPhee 1923) supporting the existence of this gene is too preliminary and inadequate to establish the gene.
- Epi Hyp* interspecific genes for *epigeal* and *hypogeal* cotyledons in *P. vulgaris* and *P. coccineus*, respectively (Lamprecht 1945, 1957). Lamprecht's model with *Epi* and *Hyp* giving 9 distinct phenotypes for cotyledon attachment position has been superseded by a quantitative model (Wall and York 1957).
- ers, ers-2* *erasure*: genes restricting partly colored seed coat patterns, now known to be synonyms for *z* and *j^{ers}*, respectively (Bassett 1997d; Bassett and Blom 1991; Bassett et al. 2002b).
- Ext Int* interspecific genes for *external* and *internal* stigma positions in *P. coccineus* and *P. vulgaris*, respectively (Lamprecht 1945). Lamprecht's Mendelian model with the *Ext* and *Int* loci giving 9 distinct phenotypes for stigma form has been superseded by a quantitative model (Manshardt and Bassett 1984).
- F* was used as a color gene by Shaw and Norton (1918) with basic genes and their *C* for yellow to produce coffee-brown. It was also used similarly by Kooiman (1931) with *C* for yellow or orange-brown plus *E*, producing coffee brown, to give black (*A B C E F*). The combinations *A B F*, *A C F*, and *A D F* had pale lilac flowers (Tjebbes and Kooiman 1922b) perhaps the equivalent of *v^{lae}*. The gene is no longer recognized.
- Fcr, Fcr-2* formerly (Bassett 1993b), complementary genes for *flower color restoration* with *t*; but *t^{cf}* is now known to express flower color normally (no white flower effect) while expressing (with *Z*, *Bip*, and *J*) partly colored seed coat patterns (Bassett et al. 1999a).
- Flav* has a light yellow influence (Lamprecht 1951a) on seed coat color; previously considered to be recessive (Lamprecht 1939). Prakken (1970) believed this gene is a synonym for *G*.
- H* described by Shaw and Norton (1918) as producing light brown or olive. Considered by Feenstra (1960) as the equivalent of the *D* of Shull (1908), the *C* of Tschermak (1912), the *E* of Kooiman (1931), the *L* of Sirks (1922), the *B* of Lamprecht (1939), the *B* of Prakken (1934), the *B* of Feenstra (1960), and the *Bl* of Smith (1939).

<i>ie</i>	similar to the action of <i>ip</i> ; also inhibits the action of <i>B</i> and <i>G</i> (Nakayama 1959b); considered by Lamprecht (1961c) to be equivalent of <i>c</i> .
<i>inh</i>	<i>inhibeo</i> (Latin): inhibits the action of <i>V</i> on seed coat colors (Lamprecht 1940c).
<i>Ins</i>	According to Prakken (1972a), <i>D</i> is the equivalent of <i>Can</i> or <i>Ins</i> of Lamprecht (1939). <i>Ins</i> with appropriate factors gives light buff (Lamprecht 1939) or raw silk (Lamprecht 1951a) testa; has a hilum ring.
<i>L</i>	<i>Löschungsfaktor</i> (German): inhibits (or <i>limits</i>) the partial coloring of the testa; with <i>t</i> , producing an entirely white testa (Schreiber 1934). <i>L</i> and <i>I</i> combine with <i>Z</i> and <i>z</i> to produce several color patterns (Schreiber 1940). <i>L</i> is a synonym for <i>J</i> (Bassett et al. 2002b); Schreiber's (1940) <i>L</i> is exactly equivalent to <i>j</i> .
<i>lin</i>	<i>lineatus</i> (Latin): produces red veins in wing petals (Lamprecht 1935e). According to Prakken (1972a), red veins in wing petals are a pleiotropic effect of the testa color gene <i>rk^d</i> .
<i>Mst</i>	causes striping of the seed coat (Smith 1947); redesignated <i>Rst</i> (Lamprecht 1947a).
<i>mar</i>	<i>margo</i> (Latin): broad colored zone around hilum ring (Lamprecht 1933).
<i>Ms In-ms</i>	<i>Ms</i> confers <i>male sterility</i> and <i>In-ms</i> inhibits action of <i>Ms</i> , restoring pollen fertility; <i>in-ms Ms</i> is lethal (Mutschler and Bliss 1980). Without translocation heterozygosity to account for the semisterile class, the validity of the model is questionable (Ashraf and Bassett 1986).
<i>Nud</i>	<i>Nudus</i> (Latin): with <i>P</i> , gives purple, waxy stem and crimson flowers (Lamprecht 1935e). <i>Nud</i> is a synonym for [<i>c^u Prpⁱ</i>] (Bassett 1994a; Bassett, editor).
<i>Och</i>	with <i>P C j</i> , gives <i>ochre</i> yellow tints such as ochraceous, Hell Lohfarben, light tawny brown, tawny olive to clay (Lamprecht 1933, 1939); has colored hilum ring (Lamprecht 1939); epistatic to <i>Vir</i> (Lamprecht 1939). Prakken (1970) believed this gene is a synonym for <i>G</i> .
<i>P</i>	(schematic) increases vigor with <i>A B C</i> (Malinowski 1924).
<i>Pur</i>	obsolete symbol for <i>V</i> (Lam-Sanchez and Vieira 1964; Okonkwo and Clayberg 1984), originally <i>Pur Ro</i> has a deep <i>purple</i> pod (Lamprecht 1951b).
<i>R</i>	(schematic) increases vigor with <i>A B C</i> (Malinowski 1924).
<i>Ro</i>	<i>Rosa</i> (German): the <i>Ro</i> of Lamprecht (1951b) and Lam-Sanchez and Vieira (1964) is synonymous with the <i>Prp</i> of Bassett (1994a) and Okonkwo and Clayberg (1984). With <i>Pur</i> (<i>V</i>), gives dark purple pod; with <i>pur</i> (<i>v</i>), gives <i>rose</i> pod color (Lamprecht 1951b). Lam-Sanchez and Vieira (1964) report <i>Ro V</i> gives dark purple pod and <i>Ro v</i> gives red pod; Okonkwo and Clayberg (1984) report <i>Ro</i> as a second locus, along with <i>Prp</i> , giving purple pods.
<i>S</i>	(schematic) increases vigor with <i>A B C</i> (Malinowski 1924).
<i>sd</i>	slow darkening seed trait. Two genes controlling slow darkening with <i>J</i> epistatic to <i>sd</i> . Presence of the dominant allele <i>J</i> results in a tendency to darken, while <i>sd</i> , is responsible for how quickly a seed coat will darken (Elsadr et al. 2011). <i>sd</i> was found to be conditioned by an allele at the <i>P^{sd}</i> locus (Islam et al., 2020).
<i>Uc Unc (I₁ I₂)</i>	<i>uni coloris</i> (Latin): with appropriate genes, darken the banner petal (Lamprecht 1948a); either <i>Uc-uc</i> and <i>Unc-unc</i> (Lamprecht 1948a) or <i>I₁-i₁</i> and <i>I₂-i₂</i> (Nakayama 1958) for the presence or not of anthocyanin in hypocotyl and stem. According to Prakken (1972b), both of these gene pairs are synonyms for genes in the "complex <i>C</i> locus", e.g., <i>Unc</i> is the equivalent of <i>Str</i> .
<i>v^{pal}</i>	with <i>P</i> , gives clear light red flowers (Lamprecht 1936); later shown to be a pleiotropic effect of <i>p^{eri}</i> (Bassett 1992b, 1994b).

<i>Vir</i>	with <i>P Gri C virescens</i> or greenish shades on the testa (Lamprecht 1933); among these are Russgrun or olive black. Prakken (1970) believed that <i>Vir</i> is a synonym for <i>B</i> .
<i>Ws</i>	confers resistance to <i>Whetzelinia</i> (now <i>Sclerotinia sclerotiorum</i>). Gene is no longer in use (Abawi et al. 1978).
<i>X x</i>	early designation for inconstant mottling of the seed coat (Emerson 1909a); now <i>C c</i> (Lamprecht 1940a).
<i>Z</i>	constant mottling of the seed coat (Tjebbes and Kooiman 1919a); now <i>C^{ma}</i> or <i>R^{ma}</i> .
<i>Z-1</i>	self-colored seed coat (Tschermak 1912); the equivalent of <i>T</i> .
<i>Z-2</i>	pigment extender (Tschermak 1912); the equivalent of <i>Z</i> .

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