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Inheritance of Green Variegation and Other New Variants of *Collinsia heterophylla*

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ABSTRACT

Six new genetic variants, extending the described genome of *Collinsia heterophylla* Buist. (2N=14) to over one hundred gene loci, are: (1) carpophyllous, *cp*, with fused leaf pairs terminating the growth of main axis; (2) umbellate, *la*, with tetra- and/or hexamerous whorls of vegetative leaves and an umbellate inflorescence of 6-30 flowers; (3) dwarf, *dw*, with a 3.5-7 cm long stem; (4) fringed, *fr*, with deeply cut leaf margin; (5) semidominant mottling, *M*, with leaves densely sprinkled with whitish streaks; (6) green variegation, *vag*, with light-green and dark-green sectored leaves, controlled by a reversible recessive nuclear gene transferable to the offspring through male and female gametes. In addition, two new alleles of the *vao* (orange variegation) locus are reported: (1) vao^{g} allele (in stable and reversible form), and (2) vao^{a}, a nonreversible allele producing nearly white (alba) cotyledons and leaves or orange cotyledons and leaves with a white margin. Finally, an additional allele, z^{c}, of the toothless (*z*, zahnlos) locus, has been identified, causing, in homozygotes, complete adaxial fusion (clasping) of cotyledons thus precluding stem formation.

INTRODUCTION

Ongoing efforts to find more genetic variants of *Collinsia heterophylla* Buist. (Scrophulariaceae), to be applied in studies of genetic homologies between 21 species of the genus *Collinsia* Nutt., have been rewarded by encountering nine new mutants (in cultures grown in a greenhouse without use of mutagens). Six of the new variants, introduced below, are controlled by alleles of hitherto unknown and three by alleles of previously identified gene loci. The addition of six to 95 previously reported genes (GoröiË 1957, 1973, 1977, 1994; GoröiË and Kerby 1996; Hiorth 1930, 1931, 1933; Rai and Garber 1960; Rasmuson 1920) extends the described genome of *C. heterophylla* to 101 gene loci.

MATERIALS AND METHODS

Seeds used in these experiments were from prior Collinsia cultures (GoröiË 1977, 1993, 1994), originally obtained from Denholm Seed Co., Lompoc, California.

Dry seeds, kept at -5° C for two days, were planted directly into 3 1/2 inch pots filled with a mixture of commercial potting soil and vermiculite (3:1 by volume). The percentage of seed germination under these conditions was essentially the same as when seeds were germinated on moist filter paper in Petri dishes kept at 10° C for 5-7 days (method used in my previous investigations).

Because of high population density (8 seeds per pot) some fertilizer was applied by watering plants (once every two weeks) with a solution of one teaspoonful of Miracle-Gro (15-30-15) per gallon of water.

The hybridization method employed in my investigations has been recently described (GoröiË 1994). The Chi-square method, using Yates' term for cultures with two phenotypic classes and a sample size less than 50, was used to test the fitness of the phenotypic segregation ratios.

ORIGIN OF VARIANTS AND HYBRIDIZATION RESULTS

Growth habit variants

Carpophyllous, *cp*. Two cultures (h8861, h8864) both being progenies of selfings of hybrids involving two sibling plants, brought forth carpophyllous plants which are characterized by adaxial fusion of vegetative leaf pairs forming a tubular structure. When primordia of the first leaf pair fuse (the earliest expression), stemless seedlings result which die in the cotyledonous stage (Fig. 1B). Formation of carpophyllous tubes (Fig. 1D) by repeated fusion of leaf pairs of the stem and/or branches (Collinsias have a decussate leaf arrangement) terminates the expansion of the main axis and induces growth of the secondary and/or tertiary branches thus giving the mutants a profusely branched habit. The most delayed expression of carpophylly is the formation of a fertile, usually actinomorphic, terminal flower on the main stem (Fig. 1C).

Most of the extensively branched carpophyllous (*cp*/*cp*) plants never bloomed; those that produced flowers were self-pollinated and crossed with wild type (*Cp*/*Cp*) plants. Offspring of self-fertilized carpophyllous plants were either stemless or exhibited one or more carpophyllous (tube) structures, and were more or less profusely branched. The hybrid (*Cp*/*cp*) plants, however, were wild type, and, upon selfing and backcrossing, produced progenies segregating into wild type and carpophyllous plants in monohybrid ratios establishing carpophyllous as a monogenic recessive trait (Table 1).

Dwarf, *dw*. Among 17 offspring of a self-fertilized plant (culture h90268) 11 plants were dwarf (Fig. 1E), having dark-green, stiff leaves, densely clustered on a 3.5-7 cm long stem (at flowering time) in contrast to the wild type sibling plants having 45-50 cm tall stem.

Because of the dwarf mutants' greatly reduced capacity for expansion of the hypocotyl during seed germination, it was necessary to dig out some seedlings lest they die due to the exhaustion of their food supply before reaching the light. At maturity the number of leaf pairs of dwarfs was the same as in the wild type sibling plants, but their internodes were so short that the overlapping leaves mostly hid the stem from sight.

The offspring of selfed and intercrossed mutants were all dwarf. The reciprocal crosses between dwarf (*dw*/*dw*) and wild type (*Dw*/*Dw*) plants produced wild type hybrid (*Dw*/*dw*) plants, and these, when self-fertilized and backcrossed, produced progenies segregating into wild type and dwarf plants in monohybrid ratios (Table 1) establishinig dwarf as a monogenic recessive trait.

Umbellate, *la*. The umbellate mutant first appeared among the offspring of a self-fertilized plant (h79271-4, culture h8095). No genetic analysis ensued until the mutant reappeared in cultures h93110 and h93235 both featuring the h79271-4 plant in their pedigree. The umbellate plants had (1) dark-green leaves arranged in tetra- and/or hexamerous whorls instead of the decussate (wild type) pattern and (2) an umbellate inflorescence of 6-30 bracts with as many, or fewer, flowers having a short corolla with concave side lobes of the lower lip, a deeply split upper lip and a humped corolla tube (Fig. 1F).

The umbellate pleiotropic mutants lagged behind in size relative to their wild type sibling plants, not because of a reduced rate of growth, but because they skipped elongation of the selected internodes. In some umbellate seedlings the cotyledonous node and the first leaf node were united into a tetramerous whorl; in all mutants the subsequent leaf nodes were joined in pairs or threes forming tetra- and/or hexamerous whorls of leaves separated by internodes of the wild type length. In the region of the peduncle the inhibition of internode elongation became complete, so that the tri-, tetra-, and pentamerous verticillate inflorescence of the wild type was condensed into an umbellate, terminal head (Fig. 1F).

Reciprocal crosses between umbellate (*la*/*la*) and wild type (*La*/*La*) plants produced wild type offspring. The F_2 and backcross progenies segregated into wild type and umbellate plants in typical monohybrid ratios (Table 1), establishing umbellate as a monogenic recessive trait controlled by pleiotropic gene *la*.

Leaf morphology variants

Fringed, *fr*. In culture h8855 a plant appeared having deeply cut (fringed), partly double serrate leaf margin (Fig. 1A). Reciprocal crosses made between the fringed (*fr*/*fr*) and wild type (*Fr*/*Fr*) plants yielded wild type offspring. The F_2 and backcross progenies segregated into wild type and fringed plants in statistically acceptable monohybrid ratios (Table 1) establishing fringed as a monogenic recessive trait.

Hiorth (1930) described a similar recessive variant he called crinkled (kraus, *k*) having somewhat wavy, partly double serrate leaves and, in addition, concave (not flat) side lobes of flower's lower lip with a diluted violet color, and a greatly reduced fertility. None of the additional features were observed in the fringed (*fr*) mutant.

That the *fr* gene is not a member of the multiple allelic *Lm* (leaf margin) locus (GoröiË, 1977) was supported by the observation that the crenate (Lm^c/Lm^c) leaved *Fr*/*fr* heterozygotes produced, upon selfing, fringed offspring with round-tipped fringes (Lm^c/Lm^c *fr*/*fr*), the dentate (Lm^d/Lm^d) leaved *Fr*/*fr* heterozygotes produced offspring with pointed fringes (Lm^d/Lm^d *fr*/*fr*), and the double heterozygotes (Lm^c/Lm^d *Fr*/*fr*) produced three types of fringed plants: with round-tipped, intermediate, and pointed fringes.

Mottling, *M*. Leaves of this mutant exhibited whitish streaks spread over the entire blade or were clustered in sectors (Fig. 1G). The most severley mottled plants simulated symptoms of a viral infection and had strap-like leaves and distorted growth habit (zig-zag stem).

Progenies of self-fertilized mottled plants were conspicuously mottled and contained many moribund individuals. Reciprocal crosses between mottled (*M*/*M*) and wild type (*m*/*m*) plants produced offspring with mildly mottled leaves, or, in some cases, offspring with a few barely detectable white streaks. The F_2 progenies of hybrids (*M*/*m*) segregated into wild type and mottled plants in statistically acceptable monohybrid ratios (Table 1). Mottling (*M*) behaved as a semidominant trait with variable expressivity.

On the other hand, the appearance of white streak clusters in one region of the leaf blade and the formation of nonmottled sectors in another part may point to the reversibility of the *M* gene to the wild type *m* by a transposable element.

Toothless, *z*. Among 13 offspring of two self-fertilized sibling plants (h8408-6, -8) four seedlings appeared having their cotyledons (petioles and blades) adaxially fully fused (clasped) preventing stem formation by blocking the expansion of epicotyl. The wild type sister plants of these stemless mutants were self-fertilized and (some of them) produced seedlings with clasping cotyledons. A few of these clasping cotyledon (z^c) seedlings managed to produce a stem with leaves having a smooth (nonserrate) margin (Fig. 2A) simulating Hiorth's (1930) *z* mutant which is characterized by a nonserrate-leaf margin and flowers lacking two protuberances (hence, toothless, i. e. zahnlos) on the upper lip at the entrance of the corolla tube.

Clasping cotyledon mutants bred true. Reciprocal crosses between wild type plants (*Z*/*Z*) and clasping cotyledon (z^c/z^c) mutants produced wild type offspring having spreading (open) cotyledons and serrate leaves, which, when self-fertilized and backcrossed, produced wild type (spreading) cotyledon and clasping cotyledon seedlings in 3:1 and 1:1 ratios respectively (Table 2). These results established that clasping cotyledon (z^c) is a monogenic recessive trait.

To find the allelic relationship between clasping cotyledon gene z^c and Hiorth's toothless gene *z*, crosses have been made using clasping cotyledon (z^c/z^c) plants as female and toothless (*z*/*z*) plants as pollen parents (the latter having spreading cotyledons and being practically female sterile). These crosses produced toothless offspring having spreading cotyledons and leaves with a nonserrate margin (z^c/z), which, upon selfing, produced seedlings with spreading (open) and clasping cotyledons (both classes with nonserrate leaves) in 3:1 ratio (Table 2). The backcrosses of z^c/z (spreading cotyledons) and z^c/z^c (clasping cotyledons) plants produced seedlings with spreading and clasping cotyledons (all with nonserrate leaves) in 1:1 ratios (Table 2), confirming the allelic nature of z^c and *z* genes.

The action of z^c gene differs from *z* allele in its ability to fully fuse cotyledons and in having no deleterious effect on fertility. The penetrance of z^c/z^c genotype in some cultures was incomplete (about 95%). The fact that z^c gene surfaced in a *Z*/*Z* genetic line

suggests that it originated by mutation of a dominant *Z* allele rather than from a mutated recessive *z* allele.

Variegation variants

Orange variegation, *vao*. Among 44 offspring of two self-pollinated green-leaved sibling plants (h92120-2, -9), 14 individuals had orange leaves resembling pure breeding orange plants of the orange variegation (*vao*) mutant - a reversible nuclear recessive variegation (GoröiË and Kerby, 1996) - except they had green cotyledons (vao^g) at emergence from the soil (which turned orange in 14 days) in contrast to *vao* which has orange cotyledons at emergence.

Reciprocal crosses between vao^g/vao^g orange plants and typical *vao*/*vao* orange plants produced orange plants (vao^g/vao) having green cotyledons at emergence. The progenies of self-fertilized vao^g/vao hybrids segregated into orange plants with green cotyledons at emergence (vao^g/vao^g, vao^g/vao) and orange plants having orange cotyledons at emergence (*vao*/*vao*) in 3:1 ratiois (Table 3), evidence that the vao^g gene is allelic to *vao* gene and dominant over it.

In progeny of 19 offspring of a self-fertilized orange (vao^g/vao^g) mutant (h9362-3), 16 plants had green cotyledons at emergence and developed orange leaves, but three plants had nearly white (alba) cotyledons (with a tinge of orange), developed three pairs of tiny, nearly white leaves and died.

Sister plants of the three alba (vao^a) mutants were selfed, intercrossed, and reciprocally hybridized with the wild type (*Vao*/*Vao*) and orange (*vao*/*vao*) plants. Some of the selfed sister plants (vao^g/--) produced only orange plants (vao^g/vao^g) but most of them produced orange (vao^g/vao^g, vao^g/vao) and alba (vao^a/vao^a) plants (Fig. 2B) in a 3:1 ratio (Table 3). Sibling plants, which produced orange and alba offspring when selfed, produced the same phenotypes when intercrossed.

The reciprocal crosses of alba heterozygotes (vao^g/vao^a) with the wild type (*Vao*/*Vao*) produced only wild type offspring of Vao/vao^g and Vao/vao^a genotypes, which, upon selfing, produced progenies segregating in 3:1 ratios for wild type and orange, and wild type and alba, respectively (Table 3).

A few alba plants (vao^a/vao^a) survived until flowering stage and were used as pollen parents in backcrosses with vao^g/vao^a and Vao/vao^a hybrids producing orange plants with green cotyledons (vao^g/vao^a) and alba (vao^a/vao^a), and wild type (Vao/vao^a) and alba (vao^a/vao^a) respectively in 1:1 ratios (Table 3). Alba plants of the backcrosses survived in higher numbers than alba seedlings of the selfed hybrids and produced, upon selfing, viable seeds.

Crosses between vao^g/vao^a and *vao*/*vao* plants produced only orange offspring (vao^g/vao, vao^a/vao) with green cotyledons at emergence. The vao^g/vao hybrids produced upon selfing only orange-leaved offspring - 3/4 with green, 1/4 with orange cotyledons (Table 3). The vao^a/vao hybrids backcrossed with *vao*/*vao* plants produced orange-leaved offspring with green cotyledons at emergence (vao^a/vao) and orange leaved offspring with orange cotyledons at emergence (*vao*/*vao*) in 1:1 ratios (Table 3).

These hybridization experiments established the *vao*^{g} and *vao*^{a} genes as members of the multiple allelic *vao* locus.

In the presence of *Ac*, an independent (from *vao*) dominant activator for *vao* gene reversion (GoröiË and Kerby, 1996), the *vao*^{g} and *vao g*enes revert to *vao*^{gR} and *vao*^{R} respectively producing the wild type green sectors in stems and leaves (Fig. 2C).

Crosses between male alba (*vao*^{a}/*vao*^{a}) plants and female orange variegated (*vao*^{gR}/*vao*^{g} and *vao*^{R}/*vao*) plants (with orange and green sectored leaves) carrying *Ac*, produced hybrids (*vao*^{g}/*vao*^{a} *Ac*/-- and *vao*/*vao*^{a} *Ac*/--) having orange and green sectored leaves. These hybrids were self-fertilized and produced a total of 145 offspring: 109 had orange and green sectored leaves (that is, all exhibited *vao*^{gR} or *vao*^{R} gene reversion), 36 were alba, none exhibiting any green sectors on cotyledons or leaves (that is, no *vao*^{aR} were present), indicating that the *vao*^{a} alelle is not amenable for reversion, or that the *vao*^{a} is coupled with another (in this case the nonfunctional) factor required for reversion.

Green variegation, *vag*. Three of 11 offspring of a self-fertilized wild type plant (h87174-2, culture h8885) exhibited subdued light-green sectors on their leaves (Fig. 2C). These green variegated (*vag*) mutants bred true, and, when reciprocally crossed with wild type plants, produced wild type offspring. The F_2 and backcross progenies of these hybrids (*Vag*/*vag*) segregated into green plants and green-light-green-sectored ones in 3:1 and 1:1 ratios respectively (Table 4), establishing the green variegation as a recessive trait controlled by a nuclear gene (*vag*) transferable to the offspring through male and female gametes.

The greeen variegation (*vag*) is the fourth type of variegation unconvered in *C. heterophylla* that is controlled by a recessive nuclear gene transferable to offspring through the female and male gametes; the other three being: orange (*vao*), white (*vaw*), and blending (*vab*, see below) variegation reported by GoröiË and Kerby (1996).

The light-green sectors of green variegation (*vag*/*vag*) mutants appeared on cotyledons and leaves of 3-4 week old seedlings. The shape and number of light-green sectors on the leaves of siblings varied from plant to plant, but were more or less uniform on leaves of individual plants. The variability of color sectoring is best explained by considering reversibility of the *vag* gene (possibly by a transposable element - Delool and Tilney-Bassett, 1986; Martinez-Zapater, 1993; Nevers et al., 1986). The localization of green and light-green areas in cotyledons and the first pair of leaves seems to set the pattern for distribution of color sectors higher up the stem. Retention of the same coloration pattern along the stem (Fig. 2D) suggests that the *vag* gene reversion occurred in the cells of the developing embryo prior to seed germination, and that the green sectors of leaves resulted from mitotic propagation of apical cells of the stem carrying reverted *vag*^{R} gene.

Because no stable, true breeding, pure light-green (without green sectors) *vag*/*vag* strain has as yet been isolated, no distinction is made in writing genetic formulae between the nonreverted *vag* allele that produces light-green, and the reverted *vag*^{R} allele that produces wild type green coloration. In other words, all green variegated (*vag*/*vag*) plants of this report carried nonreverted and reverted *vag* alleles.

The green variegated mutants (*vag*/*vag*) were crossed with orange variegation (*vao*/*vao*) mutants (Fig. 2C) producing *Vag*/*vag Vao*/*vao* dihybrids exhibiting wild type green leaves. The F_2 progenies of these dihybrids segregated into wild type, green variegated, and orange variegated plants in a 2:1:1 ratio, indicating that the *vag* and *vao* genes were nonallelic and linked in repulsion phase (Table 4).

A cross between *Vagvao*/*vagVao* (wild type dihybrid) and *vagVao*/*vagvao* (green variegated plant heterozygous for orange variegation) produced a progeny of wild type, green variegated, and orange variegated plants in the expected ratio of 1:2:1 (Table 4).

A green variegated plant heterozygous for orange variegation (vag^R/*vag Vao*/*vao*) was self-pollinated and produced 23 offspring: 17 were green variegated (vag^R/*vag Vao*/--) having light-green and green sectored leaves, and 6 were double variegation plants (vag^R/*vag* vao^R/*vao*) exhibiting both green and orange variegation symptoms.

Some chimeric leaves of the double variegation plants exhibited four types of color sectors: green, light-green, orange, and light-orange. This four color pattern can be explained as follows: cells of green sectors (vag^R/-- vao^R/--) must have carried at least one reverted allele of each variegation gene; light-green sectors (*vag*/*vag* vao^R/--) were expressed in the overlapping areas with green sectors where the nonreverted *vag* gene pair diluted the green to light-green; orange sectors (vag^R/-- *vao*/*vao*) appeared in tissues where green of the reverted vag^R gene could not be expressed because of the action of the nonreverted allelic pair of the *vao* locus producing orange; and light-orange sectors (*vag*/*vag vao*/*vao*) were observed in areas where orange coloration produced by the nonreverted *vao* allelic pair, was diluted by the action of the nonreverted *vag* allelic pair. These light-orange sectors turned pale-yellow or white in aging leaves.

A cross between two green variegated plants, both heterozygous for orange variegation (vag^R/*vag Vao*/*vao* x vag^R/*vag Vao*/*vao*), produced 17 green variegated plants (vag^R/*vag Vao*/--) and 4 orange plants (vag^R/*vag vao*/*vao*) exhibiting light-orange and orange sectors (indicating the presence of reverted vag^R) but no light-green and green sectors (indicating the absence of *vao* gene reversion). The absence of vao^R genes may be explained by (1) *vao* genes' escape from reversion by chance (unlikely), (2) by the irreversibility (stable form) of the *vao* present (such allele has been isolated, GoröiË and Kerby, 1996), or (3) by the fact that the mechanism for reversion of the *vag* and *vao* genes is not the same (requiring different transposons and/or activators).

To test the allelic relationship between *vag* and *vab* (blending variegation exhibiting yellow-green and green sectored leaves with blending borders between color sectors; GoröiË and Kerby, 1996), a cross has been made between a green variegated (*vag*/*vag*) plant and blending variegation (*vab*/*vab*) plant (Fig. 2C) producing wild type offspring. The numbers of individuals in three phenotypic classes of the F_2 of *Vag*/*vag Vab*/*vab* dihybrid were: 23 wild type green (*Vag*/--*Vab*/--), 14 green variegated (*vag*/*vag Vab*/--), and 10 plants with blending variegation (*Vag*/-- *vab*/*vab*), indicating the nonallelic nature of *vag* and *vab* genes and their close linkage (also corroborating linkage of *vab* and *vao* genes reported by GoröiË and Kerby, 1996 - for *vag-vao* linkage see above).

SUMMARY

From 9 variants reported in this article 3 concern the growth habit of plants: (1) carpophyllous (*cp*) is established as a monogenic recessive trait expressed either as a stemless cotyledon lethal, as a profusely branched plant, or as a plant with a terminal flower on the main stem and (in some cases) on branches; (2) dwarf (*dw*) is established as a monogenic recessive trait, characterized by a powerful inhibition of all internodes in the vegetative as well as the reproductive part of the stem; (3) umbellate is controlled by a recessive highly pleiotropic gene *la*, inhibiting the expansion of alternate internodes which results in mainly tetramerous (or hexamerous) whorls of vegetative leaves and a terminal umbel-like inflorescence.

Three described variants concern leaf morphology: (1) fringed (*fr*) is a monogenic recessive trait characterized by a deeply cut leaf margin; (2) mottling with whitish streaks on leaves, also associated with a tendency to distort the leaf and stem morphology when inbred, is controlled by a semidominant gene *M*; (3) clasping cotyledon mutant, characterized by complete fusion of cotyledons (stemless) and formation of nonserrate leaves by individuals that manage to produce a stem, is controlled by an additional recessive allele z^c of the toothless (zahnlos) locus *z*.

Of the three nuclear recessive variegation variants, presented in this paper, green variegation is controlled by a reversible gene of a newly identified *vag* locus, and the remaining two are controlled by alleles of previously identified orange variegation locus *vao*: (1) vao^g allele, that produces seedlings with green cotyledons at emergence, exists in the reversible as well as the stable (true breeding) form; (2) vao^a allele, which produces white or orange-tinged cotyledons and orange leaves with white margins, behaves as a nonreversible (stable) gene.

Green (*vag*) and orange (*vao*) variegtions are nonallelic to the reversible blending variegation (*vab*), but both are closely linked to it.

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Table 1: Phenotypic segregation of the F_2 and backcross (BC) progenies of hybrids of new genetic variants of *Collinsia heterophylla* (expected ratios: F_2 3:1, BC 1:1).

Variant	Gene	No. cultures	Progeny	Dominant	Recessive	Total	Chi-square	P
Carpophyllous	*cp*	5	F_2	181	50	231	1.387	.2
		2	BC	21	14	35	1.028	.3
Dwarf	*dw*	5	F_2	248	70	318	1.513	.2
		2	BC	52	51	103	0.010	.9
Umbellate	*la*	5	F_2	161	41	202	2.383	.1
		2	BC	43	38	81	0.308	.5
Fringed	*fr*	5	F_2	100	33	133	0.003	.9
		2	BC	20	19	39	0.000	--
Mottling	*M*	5	F_2	103	26	129	1.615	.2

Table 2: Phenotypic segregation of the F_2s and backcrosses (BC) involving alleles of the toothless (*z*) locus of *Collinsia heterophylla* (expected ratios: F_2 3:1, BC 1:1, BC* 2:1:1).

Genotype/ Cross	No. cultures	Progeny	Wild type open cotyl., *Z*	Toothless, open cotyl., *z*	Toothless, clasping cotyl., z^c	Chi-square	P
Z/z^c	6	F_2	294	--	103	0.189	.7
Z/z^c x Z/z^c	1	F_2	52	--	19	0.118	.7
Z/z^c x z^c/z^c	1	BC	24	--	25	0.000	--
Z/z^c x z/z^c	1	BC*	29	14	14	0.017	.9
z/z^c	2	F_2	--	52	15	0.244	.5
z/z^c x z^c/z^c	2	BC	--	17	13	0.534	.3

Table 3. Phenotypic segregation of selfed (F_2) and backcrossed (BC) hybrids involving *Vao*, *vao*, *vao*^{a}, and *vao*^{g} alleles of orange variegation locus of *Collinsia heterophylla* (expected ratios: F_2 3:1, BC 1:1).

			Orange leaves					
Genotype or Cross	No. cultures	Progeny	Wild type	Green cotyl.	Orange cotyl.	Alba	Chi-square	P
Vao/vao^g	3	F_2	72	20	--	--	0.521	.3
vao/vao^g	3	F_2	--	49	14	--	0.259	.5
vao/vao^a *x vao/vao*	2	BC	--	46	51	--	0.258	.5
vao^g*/vao*^{a}	3	F_2	--	95	--	40	1.543	.2
vao^g*vao*^{a} *x vao*^{a}*/vao*^{a}	3	BC	--	24	--	25	0.000	--
Vao/vao^a	3	F_2	76	--	--	21	0.581	.3
Vao/vao^a *x vao*^{a}*/vao*^{a}	1	BC	8	--	--	8	0.000	1
Vao/vao^a *x vao*^{g}*/vao*	2	BC	22	24	--	--	0.022	.8
Vao/vao^g *x vao*^{g}*/vao*^{a}	1	BC	18	17	--	--	0.000	--

Table 4. Phenotypic segregation of the F_2 and backcross (BC) progenies of monohybrids and dihybrids involving green (v*ag*) and orange (*vao*) variegation mutants of *Collinsia heterophylla* (ratios: monohybrid F_2 3:1, BC 1:1; dihybrid *F_2 2:1:1 instead of 9:3:3:1 because of close linkage of *vag* and *vao* in repulsion phase).

Genotype or Cross	No. cultures	Progeny	Wild type	Green varieg.	Orange varieg.	Total	Chi-square	P
Vag/vag	6	F_2	107	26	--	133	2.108	.1
Vag/vag x vag/vag	2	BC	30	26	--	56	0.286	.5
vag/vag x Vag/vag	2	BC	11	11	--	22	0.000	1
Vag/vag Vao/vao	8	*F_2	126	53	67	246	1.740	.4
vagvao vagVao ---------- x ---------- *vagVao vagvao*	1	[a]BC	14	27	15	56	0.107	.9

[a]Expected ratio in absence of crossing-over between *vag* and *vao* 1:2:1.

Figure 1. Genetic variants of *Collinsia heterophylla*. A. Fringed, *fr*. B-D Phenotypic expressions of carpophyllous, *cp*: B. Cotyledon lethal; C. Actinomorphic terminal flower; D. Termination of growth of main axis by formation of a carpophyllous tube and secondary branches. E. Dwarf, *dw*, with flower buds. F. Umbellate, *la*. G. Dominant mottling, *M*.

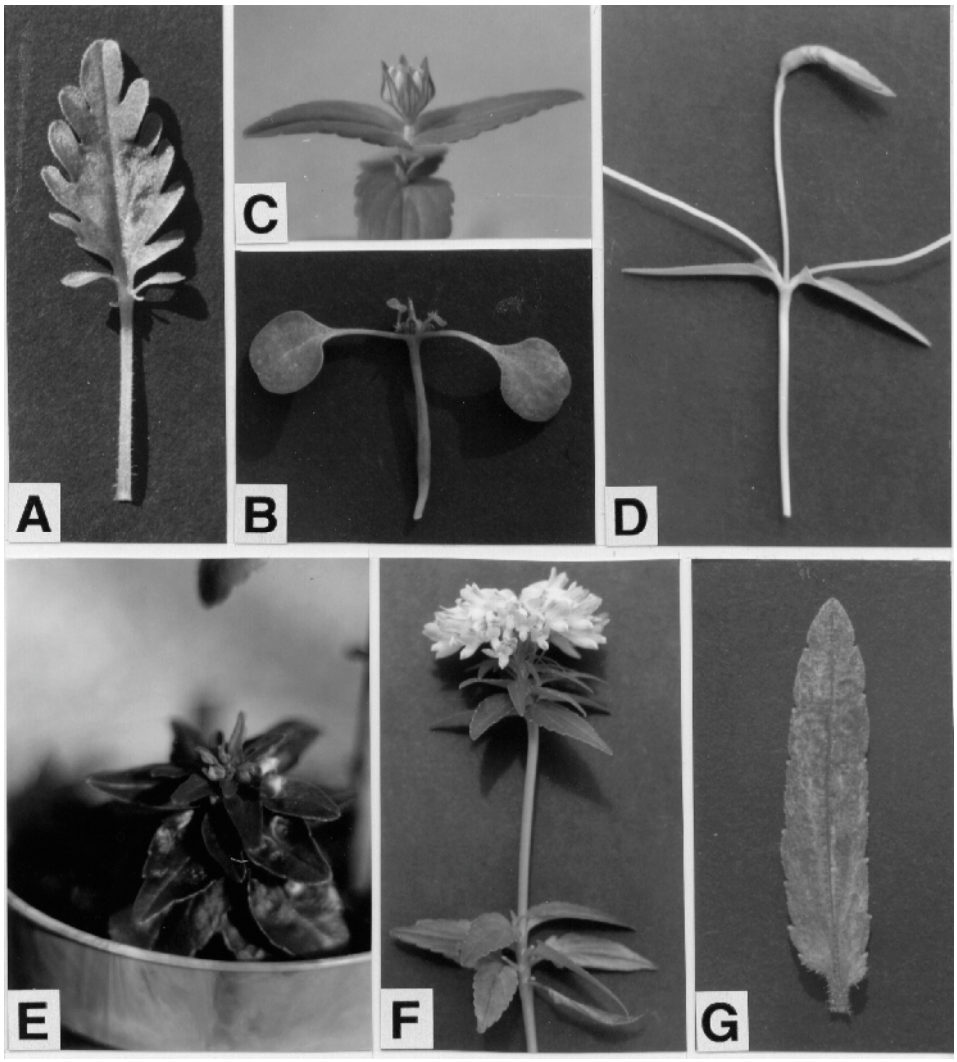

Figure 2. Genetic variants of *Collinsia heterophylla*. A. Clasping cotyledons (zahnlos), z^c: adaxially fused cotyledons (left), nonserrate leaf (right). B. Alba, vao^a, seedling. C. Leaves of variegation mutants: orange, *vao* (left); blending, *vab* (middle); green, *vag* (right). D. Leaves of the 6-th (horizontal) and 7-th (vertical) pair of a green variegation (*vag*) mutant exhibiting major green sectors on one side of stem (notice green coloration of adjacent halves of leaves in the upper left quadrant of the picture).