A new version of pea linkage group 5

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Within the past few years considerable revision of the Lamprecht-Blixt pea genetic map has occurred. Not only have certain markers been located more accurately, but significant segments of the linkage map have been rearranged. Recently linkage groups 5 and 7 were combined to form a new linkage group 5 (2, 11), although the first genetic data indicating linkage between genes *gp – coch – tl* were obtained in the sixties by Wellensiek (12) and Marx (3). Nowadays, there is considerable evidence that in the standard karyotype the genes *bt – r – tl – coch – gp – Fs* are located on a single chromosome which corresponds to the new linkage group 5. However, many of the well known genetic markers, clearly assigned to this linkage group, have not been located precisely, and the gene order on linkage group 5 is still uncertain.

Previously we localised gene *His1* coding for the fraction of histone H1 with the lowest electrophoretic mobility (5, 6), the gene for the major pea seed albumin component, *Sca* (or SA-K9) (6, 9), and the protease inhibitor gene cluster, *lp* (7), near the *r – tl* segment of group 5. Our colleague O.G. Smirnova localised a new legumin fraction, *Lg-u,* near the *His1* gene (8). Over the past several years we have carried out a number of crosses which permit more precise relative placement of some markers in linkage group 5, including genes *bt, det, coch, curl, gp,* and *cri.* We present the results here. The data were analysed using the program LINKAGE-1.

Wiatrowo line Wt-11745 (*wsp, Bt, Det, r, Tl, His1^{s}, coch, Sca^{s}*) was crossed with our tester line RT-2 (*Wsp, bt, det, r, tl^{w}, His1^{ss}, Coch, Sca^{f}*). The joint segregation data for the F_2 population are presented in Table 1. Note that gene *wsp* segregates independently of all other markers involved in the analysis, in agreement with a suggestion that gene *wsp* is not a part of linkage group 5 (group 7 in Lamprecht's nomenclature) but forms with some other markers a segment of one of the satellite chromosomes (2).

The results in Table 1 clearly indicate the following gene order:

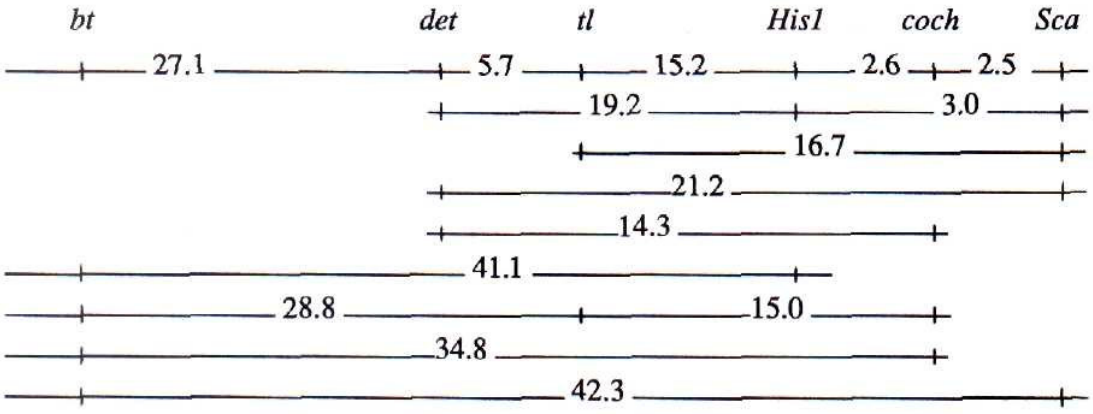


Table 1. Joint segregation data obtained from the F_2 of cross Wt-11745 *(Bt, Det, tl^w, His1^s, Sca^s, coch, wsp)* x RT-2 *(bt, det, Tl, His1^{ss}, Scd^f, Coch, Wsp).*

Genes		Phase	Number of progeny with designated phenotype[1]									Joint seg.	Recomb.	SE
			A/B	A/h	A/b	h/B	h/h	h/b	a/B	a/h	a/b	χ^2	frac.	
bt	*det*	C	137	--	23	--	--	--	20	--	20	24.1****	27.1	3.8
bt	*tl*	C	50	85	25	--	--	--	2	20	18	21.4****	28.8	3.7
bt	*His1*	C	45	78	37	--	--	--	4	24	12	5.7	41.1	4.2
bt	*coch*	R	118	--	42	--	--	--	36	--	4	4.8*	34.8	6.1
bt	*Sca*	C	43	80	37	--	--	--	4	25	11	5.1	42.3	4.2
det	*tl*	C	60	105	5	--	--	--	1	5	45	163.2****	5.7	1.6
det	*His1*	C	58	93	19	--	--	--	1	18	32	63.3****	19.2	2.9
det	*coch*	R	116	--	54	--	--	--	50	--	1	18.6****	14.3	6.6
det	*Sca*	C	55	94	21	--	--	--	0	22	29	52.0****	21.2	3.0
tl	*His1*	C	57	15	3	23	87	13	0	14	39	183.8****	15.2	1.8
coch	*tl*	C	53	104	19	--	--	--	1	19	57	105.2****	15.0	2.4
tl	*Sca*	C	55	18	3	21	87	15	0	18	36	160.7****	16.8	1.8
coch	*His1*	C	54	116	5	--	--	--	1	0	75	224.1****	2.6	1.0
His1	*Sca*	C	73	7	0	2	112	2	0	4	51	418.7****	3.0	0.8
coch	*Sca*	C	54	119	3	--	--	--	0	4	74	222.3****	2.5	1.0
wsp	*bt*	R	116	--	32	--	--	--	44	--	8	0.9	44.0	5.6
wsp	*det*	R	126	--	40	--	--	--	44	--	11	0.4	46.7	5.2
wsp	*tl*	C	41	94	58	--	--	--	13	28	18	0.0	50.4	3.9
wsp	*His1*	C	42	92	57	--	--	--	13	24	22	1.3	47.6	3.9
wsp	*coch*	C	138	--	55	--	--	--	38	--	21	1.1	45.8	4.9
wsp	*Sca*	C	43	94	56	--	--	--	11	29	19	0.4	47.8	3.9

[1] A,a - first gene; B,b - second gene; h - heterozygous. Where both genes are dominant, the capital letter stands for the dominant allele. Where the second gene is codominant, capital A stands for the dominant allele of the first gene and capital B for an allele of the second gene which is in coupling with A. Where both genes are codominant, the capital letter stands for an allele of the first parent. *,**,***,**** $p < 0.05$, 0.01, 0.001 and 0.0001, respectively. Data were analysed by the LINKAGE-1 program.

Table 2. Joint segregation analysis for genes binding the *r-tl* and *gp* segments of linkage group 5.

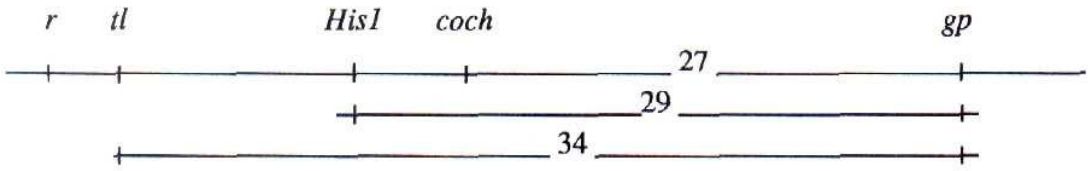
Genes		Number of progeny with designated phenotype[1]									Joint seg.	Recomb.	SE
		A/B	A/h	A/b	h/B	h/h	h/b	a/B	a/h	a/b	χ^2	frac.	
a) F_3[2]: SGR "coch"(*R, Tl, His1^{ss}, Scd^f, coch, Gp*) x NGB-1238 (*r, tl^w, His1^s, Sca^s, Coch, gp*)													
coch	*tl*	60	136	8	--	--	--	1	14	54	163.7****	8.9	1.8
coch	*r*	140	--	64	--	--	--	68	--	1	25.4****	12.5	5.9
coch	*His1*	67	135	2	--	--	--	0	5	64	237.2****	2.6	1.0
r	*tl*	62	145	1	--	--	--	0	5	60	240.9****	2.2	0.9
tl	*His1*	56	5	1	10	129	11	0	6	55	362.7****	6.4	1.1
r	*His1*	66	130	12	--	--	--	0	10	55	167.5****	8.3	1.7
coch	*gp*[3]	25	--	17	--	--	--	7	--	1	2.3	26.9	12.9
gp	*His1*	4	21	7	--	--	--	1	7	10	5.9*	28.7	7.4
gp	*r*	7	17	8	--	--	--	2	7	9	3.3	34.4	7.9
gp	*tl*	7	17	8	--	--	--	2	7	9	3.3	34.4	7.9
b) F_2: RT-1 (*r, tl^w, His1^f, Sca^f, Curl*) x NGB-5558 (*R, Tl, His1^s Sca^s, curl*)													
Sca	*r*	22	7	0	4	53	5	0	7	29	136.2****	9.5	1.9
Sca	*tl*	23	6	0	3	55	4	0	6	30	153.9****	7.8	1.7
curl	*Sca*	36	61	0	--	--	--	0	1	29	121.5****	0.8	0.8
Sca	*His1*	26	3	0	1	60	1	0	4	32	203.7****	3.6	1.2
r	*tl*	25	1	0	1	65	1	0	1	33	229.8****	1.6	0.8
curl	*r*	34	59	4	--	--	--	0	8	22	69.2****	10.1	2.8
r	*His1*	22	4	0	5	58	4	0	5	29	156.2****	7.4	1.7
curl	*tl*	34	60	3	--	--	--	0	7	23	77.5****	8.4	2.5
tl	*His1*	23	3	0	4	60	3	0	4	30	175.6****	5.7	1.5
curl	*His1*	33	63	1	--	--	--	0	4	26	100.8****	4,1	1.8

[1] The same designation as in Table 1.
[2] F_3 progeny of 3 heterozygous F_2 plants from this cross.
[3] Only one of the 3 F_3 families was heterozygous for gene *gp*.
*,**,***,**** $p < 0.05$, 0.01, 0.001 and 0.0001, respectively.

The significant linkage between gene *bt* and genes surrounding gene *r* is in agreement with earlier work. As had been shown by Folkeson in his experiments involving translocation line L-25, the recombination fraction for *r – bt,* T – *bt* and T – *r* was 33.9 ± 2.3, 23.2 ± 2.99 and 3.1 ± 0.93, respectively (1).

The gene order in segment *tl – His1 – coch – Sca* was obtained after phenotypic analysis of individual recombinant plants. The presence of two double-crossover plants recombinant in both the *tl – His1* and *His1 – coch* (or *coch – Sca*) segments, can explain the observed slight nonadditivity in this region.

The position of gene *coch* was confirmed in a cross between our gamma-ray induced mutant line SGR-"coch" and NGB-1238. A cross between SGR-"coch" and line Wt-11745 (*coch*) showed both mutants were allelic. Unfortunately, due to root disease only a few F_2 plants were obtained in cross SGR "coch" x NGB-1238. Thus the genetic analysis was carried out on the combined F_3 progeny of three F_2 plants heterozygous for genes *r*, *tl, His1* and *coch* (Table 2). One of these F_3 families showed segregation for *gp.* This enabled us to estimate the linkage and orientation of gene *gp* and the *r – tl* segment. Considering the data concerning the relative position of the markers near gene *r* given above, the following scheme is proposed:



The position of *det* was also confirmed by segregation data (Table 3) obtained from testcross: F_1 (Svoboda x OS-1) x RF-3. The genotypes of these lines are: Svoboda (*det, tl, His1*^{s}, *Sca*^{s}), OS-1 (*Det, tl, His1*^{ss}, *Sca*^{f}), and RT-3 (*det, Tl, His1*$^{ss}_{y}$ *Sca*^{f}). The position of *curl* was verified by the cross NGB-5558 (*curl, R, Tl, His1*^{s}, *Sca*^{s}) x RT-1 (*Curl, r, tl*^{w}, *His1*^{ss}, *Sca*^{f}). The segregation data for this cross are presented in Table 2b. Recombination data and results of crossover analysis (not shown) revealed the following gene order:

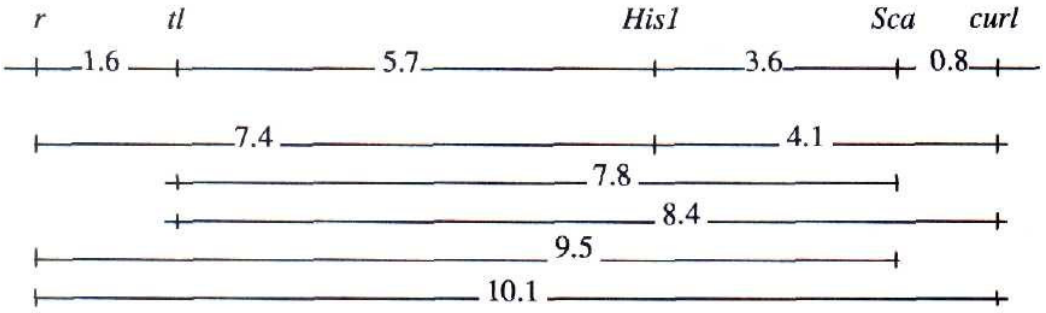


Table 3. Joint segregation data for genes *His1, Sca, Tl* and *det* obtained from the testcross F_1 (Svoboda x OS-1) x RT-3.

Genes		Phenotype classes[1] H-H	T-H	H-T	T-T	Joint seg. χ^2	Recomb. frac.	SE
His1	*Sca*	36	3	2	27	49.2****	7.35	3.17
His1	*det*	2	26	37	3	49.2****	7.35	3.17
His1	*tl*	0	39	27	2	60.2****	2.94	2.05
Sca	*det*	4	24	34	6	33.4****	14.71	4.29
Sca	*tl*	2	36	25	5	42.9****	10.29	3.69
det	*tl*	26	2	1	39	56.5****	4.41	2.49

[1] T = homozygous for the tester genotype; H = heterozygous.
**** $P < 0.0001$

Table 4. Joint segregation data a) for genes *r* and *tl* and markers *gp* and *cri,* and b) for markers in the *gp-Fs* segment of linkage group 5.

Genes		Number of progeny with designated phenotype[1] A/B	A/h	A/b	h/B	h/h	h/b	a/B	a/h	a/b	Joint seg. χ^2	Recomb. frac.	SE
a) F_2: NGB-1238 (*r, tl^w, gp, Cri*) x SGE-182 (*R, Tl, Gp, coch*)													
cri	*gp*	58	--	44	--	--	--	24	--	1	13.4***	15.6	8.6
cri	*r*	42	45	16	--	--	--	5	9	7	4.3	36.1	5.1
cri	*tl*	42	54	22	--	--	--	4	15	10	6.4*	36.6	4.7
gp	*r*	17	34	21	--	--	--	3	18	23	8.6*	33.1	5.1
gp	*tl*	21	41	20	--	--	--	4	18	23	10.9**	32.7	4.9
r	*tl*	45	2	0	1	52	1	0	1	22	218.9****	2.0	0.9
b) F_2: NGB-1238 (*gp, cp, U, fs*) x SGE-185 (*Gp, Cp, u, Fs*)													
Fs	*cp*	53	--	9	--	--	--	5	--	2	0.9	32.2	7.1
Fs	*gp*	48	--	12	--	--	--	5	--	3	1.3	37.6	7.8
Fs	*U*	24	--	39	--	--	--	7	--	1	7.0**	16.8	11.5
cp	*gp*	62	--	10	--	--	--	4	--	9	19.4****	20.6	5.0
cp	*U*	22	--	36	--	--	--	9	--	2	7.2**	23.3	11.3
gp	*U*	21	--	32	--	--	--	9	--	6	2.0	39.3	10.1

[1] The same designation as in Table 1.
*,**,***,**** $P < 0.05$, 0.01, 0.001 and 0.0001, respectively.

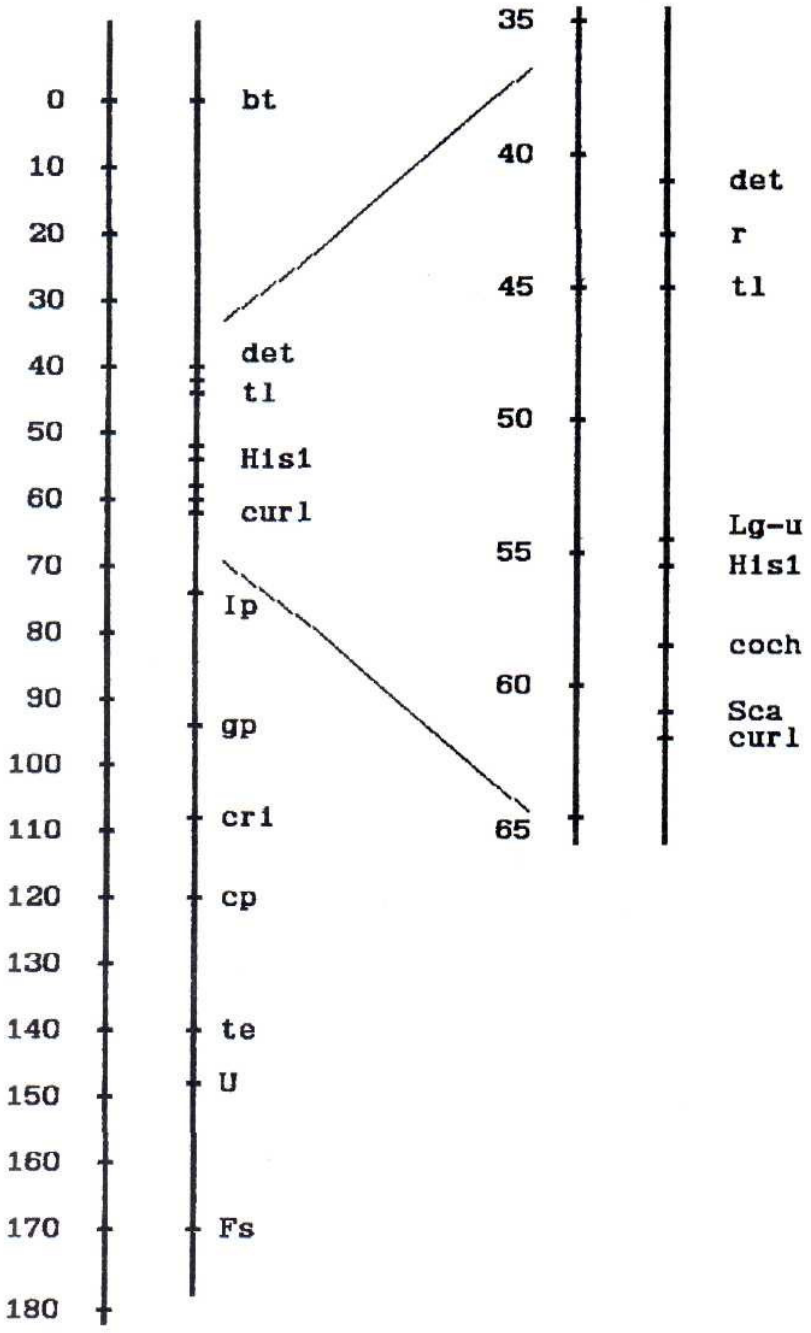


Fig. 1. Map of pea linkage group 5.

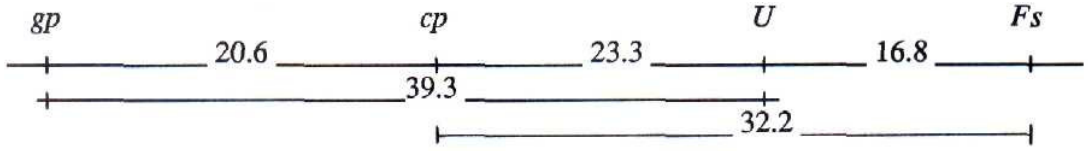
We conclude that, in contrast to the last version of the pea genetic map (10, 11), genes *det* and *curl* are located on the different ends of the *r – tl* segment and the whole segment *r – tl – His1 – coch – Sca – curl* is inverted in relation to other markers belonging to this group.

In two other crosses, the positions of genes *cri, gp, cp, Fs* and *U* were estimated (see Table 4). Our EMS-induced line SGE-182 displays a *crispa* phenotype due to a mutation which showed allelism with gene *cri* in a cross with line NGB-1297 (*cri*). In the cross NGB-1238 x SGE-182 significant evidence of linkage between *r – tl* and *gp* was obtained. The results given in Table 4a indicate the following gene order:

--r --2.0-- *tl* ----------32.7--------- *gp* ----- 15.6-----*cri*--

These results are in accordance with those of Murfet (4).

Table 4b and the next scheme show data for genes *gp, cp, Fs* and *U* obtained in cross NGB-1238 x SGE-185.



According to data given above we propose a new version of the pea linkage group 5 map as shown in Fig. 1.

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