THIRD CONSPECTUS OF GENETIC VARIATION WITHIN *VICIA FABA* (1986)

FABIS

Faba Bean
Information Service

INTERNATIONAL CENTER FOR AGRICULTURAL RESEARCH
IN THE DRY AREAS (ICARDA)

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ICARDA
P.O. Box 5466, Aleppo, Syria
Telex: 331206 SY; 331208 SY; 331263 SY
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DAMASCUS OFFICE
Hamed Sultan Bldg., First Floor
Abdul Kader Ghazali Str.,
Abu Roummaneh (Next to Al-Malki Circle)
P.O. Box 5908
Damascus, Syria
Tlx 412924 ICARDA SY
Tel 420482, 420483, 331455

CAIRO OFFICE
15 G, Radwan Ibn El-Tabib Str.,
11th Floor, Giza,
P.O. Box 2416
Cairo, Egypt
Tlx 091-21741 ICARD UN
Tel 728099, 723564, 724358

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Rue Bashir El-Kassar,
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Tlx 22509 LE
Tel 813303, 804071

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El-Menzah, Tour C-D, 7th Floor,
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2049 Ariana, Tunisia
Tlx 14066 ICARDA TN
Tel 230225

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c/o Arid Zone Research Institute,
Pakistan Agriculture Res. Council,
P.O. Box 362
Quetta, Pakistan
Tlx 7836 CTO QT PK
Tel 73248

Cover: The diagram on the cover is the outline of Fig 1 from the paper by Kenton Ko and Neil A. Strauss (see pages 8-21) showing the physical map of the *Vicia faba* chloroplast genome.

CONTENTS

INTRODUCTION

In 1981 FABIS published the first edition of 'Genetic Variation within *Vicia faba*' With slight revision it was republished by Chapman (1984). Since then, with the active encouragement of ICARDA, the list has been completely revised. To avoid confusion with its predecessors and to simplify subsequent updating the authors adopted a new title and incorporated the year of publication.

A new feature is the inclusion of the description in Part I of the *Vicia faba* chloroplast genome by Professor Ko, to whom the authors express their gratitude. In any further revision we hope a similar treatment for the mitochondrial genome would by then be possible. In the meantime, we are pleased to include in Part II the contribution from Briquet, Goblet, Poutry, Flamand and Faber of the molecular analyses of *Vicia faba* cms and other cytoplasms. Part III comprises the revised table from earlier editions.

The present revision records published variation up to the end of 1985, plus variation reported at the Third International *Vicia faba* Review Meeting at Gatersleben in April of that year. The conspectus now includes isozyme variants and seed amino acid content and the list of organisms with which *Vicia faba* interacts has been further extended.

While it is inappropriate in this publication to attempt to systematise continuous variation, one can recognise three lacunae of present interest. These are in regard to difference of varietal response to fertiliser levels, to pesticide damage and to differences in *in vitro* culture. In regard to the latter, however, see Busse (1986).

The authors in compiling this revision sought information particularly about anti-digestants and favism-inducing factors. It is evident both that useful variation exists and that the search should continue and with advancing chemical analytical techniques perhaps geneticists should turn their attention more to the basis of inheritance of these deletorious substances. We would particularly endorse the view of Hussein and Saleh (1983) for a co-operative approach involving the plant breeder, food technologist and nutritionist to the problem of favism.

Whether one's self-description is that of geneticist, breeder, cytologist or cytogeneticist, the recent paper by Schubert, Rieger and Michaelis (1986) is required reading since it provides an authoritative account of the remarkable extent to which *Vicia faba* chromosomes can be experimentally manipulated. In this conspectus we have in regard to chromosome manipulation only two objectives. The first is to report chromosome alteration that is phenotypically detectable in living plants and the second is to interest breeder and cytologist in what the other is doing since the influence of cytogenetics so conspicuous in wheat breeding, for example, has only recently begun in faba beans to become apparent.

Criteria used in the present list

1. **Availability** This is understood to mean 'known to exist' rather than 'available for distribution .
2. **Citation** To include all journal references would have added unjustifiably to the length of the conspectus and the following convention is adopted in regard to Part III. Dates not in parentheses indicate how recently a variant was described. Dates in parentheses together with authors appear in the bibliography. These are restricted to reviews or papers that present important synopses.

Named individuals are cross-referenced to the appended list of addresses of scientific establishments.

3. **Authenticity** Every effort has been made to ensure the accuracy of the information included here, but in many cases the list deals with areas of variation in need of re-examination or further investigation. Our approach in this connection has been that of editors rather than arbitrators.

4. **Genetic status of variation** Not all variation can be resolved into single gene units nor should it be assumed that what is most frequently seen is necessarily dominant. The commonplace situation is underlined. Where known or suspected, pleiotropy is indicated, and that associated with white flowers merits re-examination as to its extent.

5. **Chromosomes** Several systems of nomenclature have been proposed and the one adopted here, as previously, is that used by Schubert, Rieger and Michaelis (*ibid*).

6. **Other *Vicia* species** No reference to other *Vicia* species has been included since *Vicia faba* appears to be genetically isolated with little prospect of this being modified in the near future.

Future priorities

Linkage Systematic study of linkage remains a central need and the accumulating stocks of genetic and chromosome variants and the emerging molecular techniques make this increasingly feasible.

New variation 1. Anti-digestants and favism-inducing substances

These have already been referred to and the need to search for new variation is emphasised.

2. Disease and pest resistance A surprise in recent years

has been the discovery of ILB 938 *Botrytis* resistance in Andean *Vicia faba* (Robertson 1984) and it may be that populations of the crop there might reveal other useful attributes. Clearly, too, greater understanding is required of resistance mechanisms and their genetic basis.

3. Determinate beans In view of their importance and obvious interest, several points deserve emphasis. It is for example essential to distinguish between segregant forms of the original Svalof mutant ti-1 and newer mutants for the same character, a point sometimes not fully grasped.

   The original mutant ti-1 allowed the synthesis of alternative phenotypes and to test whether its shortcomings could be diminished by segregating it in different genetic backgrounds. It is worth stressing that there are now alternative mutants available and listed here, and a strong case exists for them to be tested collaboratively in a wide range of contrasted sites.

   These alternative mutant forms differ in various ways and Ti-g obtained in Gottingen, for example, is dominant. Another recessive, ti-5 is only semi-determinate. There seems little doubt that careful study of these forms would enhance our understanding of the physiology and agronomy of the crop and improve the prospects for the development of good determinate varieties.

4. Male sterility Male sterility in *Vicia faba* is more than ordinarily complex. In addition to the normal distinction between nuclear and cytoplasmic male

sterility two other matters cause difficulty. The first is in regard to symbols. Cytoplasmic variants are referred to as cms and their restorers as Rf but the separate identities of Rf1, Rf2 and Rf3 and their loci and allelic relations are obscure. Secondly, the involvement of a cytoplasmic particle in cms 447 but not cms 350, which only some workers believe to be dodder-transferable, makes its status uncertain.

It was in regard to male sterility, more than any other topic, that we felt an authoritative review was needed and we commend the undertaking to our peers as a matter both important and interesting.

5. Salt tolerance The feasibility of breeding for 'salt tolerance' in faba bean is perhaps due now for critical re-appraisal and is in any case inseparable from irrigation policy.

6. Flower colour The locus and allelic relations for flower colour and spotting have been explored by Moreno, Martin and Cubero (1981) and attention is drawn to comments in that section of the Table.

Centralisation The need to maintain a central collection of authentic genetic stocks remains of course important and a legitimate claim on resources. The crop out-pollinates and assumptions made on the basis of cereal line propagation are inappropriate. This does not always seem to be appreciated.

FABIS Publication of new data in FABIS has facilitated the present updating and it is urged that workers will continue to do this.

It is increasingly realised that two or three generations per year of *Vicia faba* (under properly controlled conditions and using appropriate phenotypes) is a feasible rate of genetic turnover. Added to this, the diversity available and the manipulability of the chromosomes give the possibility of a broader genetic understanding for this species.

Concluding comments The original intention in compiling the list of genetic variation was that it would benefit not only breeders but their colleagues in related disciplines, and so it has proved, providing the incentive for the current revision. In response to our enquiry, we found that the format adopted originally was welcomed and is mostly unchanged. We do however welcome suggestions for improvement.

Apart from this conspectus and its predecessors, three international *Vicia faba* cytogenetics review meetings have been held, and - except for the inaugural one - their proceedings are now published. A fourth review meeting is planned. To this extent therefore the systematic progress of *Vicia faba* genetics and breeding seems assured.

We thank all those who have so readily assisted us, not least ICARDA for financial support, hoping that workers will find this conspectus at least as useful as its predecessors.

S. Ward*
G.P. Chapman

*Overseas Crops Service, Department of Biological Sciences, Wye College, Wye, Ashford, Kent. TN25 5AH.

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The Chloroplast Genome of *Vicia faba*

Kenton Ko and Neil A. Strauss
Department of Botany, University of Toronto
Toronto, Ontario, Canada M5S 1A1

Although photosynthesis occurs entirely within the chloroplast, two distinct genomes code for the different proteins that are part of this complex process. The nucleus contributes the largest proportion of chloroplast proteins. Nuclear encoded proteins are translated in the cytosol of the cell and transported into the chloroplast. The chloroplast genome, although small in comparison to the nuclear genome, codes for 80 - 100 polypeptides that play important roles in photosynthesis.

The molecular forms of all chloroplast chromosomes examined so far are remarkably similar. They consist of a double-stranded, circular DNA molecule containing 130,000 to 155,000 nucleotide pairs. The general organisation of the chloroplast genome is highly conserved among the majority of vascular plants. It consists of a sequence of 22,000 to 25,000 nucleotide pairs that is repeated once in an inverted configuration. The inverted, repeated sequences are separated by two unique sequences of unequal size. The larger single copy sequence has 12,000 to 30,000 nucleotide pairs.

The organisation of the *Vicia faba* chloroplast genome differs greatly from the chloroplast genomes of most vascular plants. *Vicia faba* is a member of a small group of legumes that has lost one of the inverted, repeated sequences. The deletion of one entire segment of inverted repeats is accompanied by a reduction in the genome size of

17,000 - 20,000 nucleotide pairs. The resultant length of chloroplast DNA in *V. faba* is estimated to be 123,000 base pairs (Ko *et al* 1983)

In the absence of a large number of polysynthetic mutants that can be genetically mapped to the chloroplast chromosome, physical maps are necessary to provide reference points for the analysis of the chloroplast DNA; restriction endonucleases which recognise specific, short DNA sequences provide convenient and reproducible reference points for this type of mapping. The physical map of the *V. faba* chloroplast genome which has been constructed using renaturation studies (Koller and Delius, 1980) and Southern blot hybridisation (Ko *et al*, 1983) is shown in Fig. 1.

The *V. faba* chloroplast genome codes for one set of ribosomal RNAs and at least 31 tRNA species (Koller and Delius, 1980; Ko *et al*, 1983; Sun *et al*, 1984; Mubunbila *et al*, 1984). To date, a total of eighteen chloroplast genes that code for identified polypeptides have been located on the chloroplast chromosome. Their locations have been determined using gene specific probes constructed from heterologous sources, such as spinach, pea, mung bean and tobacco chloroplast DNA (Ko *et al*, 1984; Shinozaki *et al*, 1984; Ko *et al*, 1983). The current list of structural genes located on the chloroplast chromosome of *V. faba* is found in Table 1. Their positions and directions of transcription are indicated on the physical map (Figure 1).

Chloroplasts cannot survive by themselves even though the chloroplast genome has the capacity to code for 80 - 100 polypeptides. It has already been demonstrated that none of the protein complexes of either the light or dark reactions of photosynthesis is encoded exclusively in the chloroplast genome. In fact, the nuclear genome

codes for the majority of the proteins found in the chloroplast. Nuclear encoded proteins are imported into the plastid and assembled with chloroplast encoded polypeptides into functional complexes.

The simplest protein complex that typifies nuclear and chloroplast interaction is the chloroplast enzyme ribulose-1,5-biphosphate carboxylase/oxygenase. The enzyme is composed of eight identical large subunits (ls) coded by the chloroplast genome and eight small subunits (SS) coded by the nuclear DNA. The SS is translated as a larger precursor in the cytoplasm, recognised by the chloroplast and imported through both membranes. The SS precursor contains an additional peptide sequence at its N-terminus that is necessary for importation and processing by a specific soluble endoprotease. Once processed, the SS is assembled into the holoenzyme. The assembling process is not yet fully understood.

The genes encoded by the two compartments differ in many respects. Nuclear genes are inherited through classical Mendelian genetics; the chloroplast genome undergoes non-Mendelian, uniparental (predominantly maternal) inheritance. Unlike nuclear genes, which are present in low copy number and usually part of a gene family, chloroplast genes are present in multiple copies of a single gene because of the polyneny of the chloroplast genome. The expression of nuclear and chloroplastic genes also differ. The transcriptional and translational properties of the chloroplast genes are predominantly prokaryotic in character in contrast to the eukaryotic features of nuclear gene expression. This is clearly seen in the different chemicals that inhibit translation in the chloroplast or in the cytosol. Chloroplast translation is inhibited by prokaryotic antibiotics like chloramphenicol and spectinomycin; cycloheximide inhibits translation in the cytosol.

Introns are frequently found in nuclear genes and are generally considered to be a characteristic property of eukaryotic genes. Chloroplast genes that code for polypeptides in vascular plants are generally not interrupted by intervening sequences, except in a few reported cases. Introns have recently been found in the ribosomal protein gene, *rpl 2*, of *Nicotiana debneyi* (Zurawski *et al.* 1984) and in the gene coding for the CF_0 subunit I of ATP synthase in wheat and spinach (Bird *et al.* 1985; Westhoff *et al.* 1985). A systematic search for introns in the *Vicia faba* chloroplast genome (Koller and Delius, 1984; Bonnard *et al.* 1984) showed that almost all hybrids found were uninterrupted; a maximum number of six possible introns were observed.

Studies on the structural rearrangements that distinguish the chloroplast DNA of *V. faba* from those of most vascular plants reveal interesting evolutionary differences. In *V. faba*, the region corresponding to the surviving inverted repeated segment is divided into two widely separated parts of the chloroplast genome. The inverted repeat-large single copy junction, represented by the *rps19-rpl2* genes, is located in the P1/S3a/X6 region. A polypeptide gene that is normally located in the middle of the inverted repeat sequence, is found as one copy within the K7a fragment of *V. faba*. The end of this surviving inverted repeat segment is marked by the position of the $tRNA^{Leu}$ gene which is normally found in the middle section of typical inverted repeat. The rest of the inverted repeat region, that contains the rRNA cistrons, is contained within the P3/P6 area (Palmer and Thompson, 1982; Ko *et al.*, 1983; Shinozaki *et al.* 1984).

The region corresponding to the small single copy sequence of the typical chloroplast genome has also been rearranged into at least two distinct areas. Cross-hybridization studies using probes constructed from the small single copy sequence of *Nicotiana tabacum* (Shinozaki *et*

al. 1984), *Vigna radiata* (Palmer and Thompson, 1982) and *Brassica napus* (Ko *et al.*, unpublished data) show that the corresponding areas were located in the K7a/K5 and K3 regions. Surprisingly, hybridization studies using relatively small fragments reveal that the loss of the inverted repeated sequence has also been accompanied by a loss of at least one third of the typical small single copy region (Ko *et al.*, unpublished data). Unlike the loss of a repeated sequence this deletion represents a real loss of unique genetic material.

Despite the deletion of one inverted repeat and part of the small single copy region, all the genes identified so far in *Spinacia oleracea* have also been found in *Vicia faba*. A minimum of four inversions is responsible for the gene order changes relative to the order characterized in spinach and *Brassica* (Figure 2). The ancestral gene order represented by the mung bean chloroplast DNA differs from spinach by an 50 kilobase pair inversion. The inversion in mung bean reverses the gene order between *psbA* and *petA* and places the *rbcL-atpB,E* genes next to *psbA* and the *atpH*, *atpA* genes next to *petA*. A second inversion in *Vicia faba* appears to involve a fragment covering the area from the 5' end of the 16S rRNA gene to the 3' of *atpE* gene. This inversion changes the gene order with respect to the 16S-23S rRNA cistron; genes initially located on one side of the ribosomal RNA cistron are moved to the other side. Two smaller inversions within this fragment reverses the *psbA-rbcL-atpB,E* gene order with respect to the ribosomal RNA cistron. The *atpB,E* genes are close to the 23S rRNA instead of *psbA*. The smaller inversion also resulted in the separation of the once co-linear small single copy region.

The continuing analysis of chloroplast genes will provide further insights into gene structure and expression. This information will also set the basis for investigating the function of this organelle and its co-operation with the nucleo-cytoplasmic compartment. The

V. faba chloroplast genome offers an unique system to study many aspects of chloroplast molecular biology. Its restructured chromosome provides an opportunity to study the sequences involved in recombination and chromosomal rearrangement, and to assess the role these sequences play in the evolution of the chloroplast genome. Additionally, the defined structure of the *V. faba* chloroplast genome provides a system for the investigation of the function of the inverted repeat regions in chloroplast DNA.

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Table 1. List of chloroplast DNA encoded genes

Structural RNA	
	23S, 16S, 4.5S ribosomal RNA
	31 transfer RNAs
Ribosomal proteins	
	2 subunits - L2, S19
Membrane proteins	
ATPase synthase	- α, β, ϵ subunits of CF_1
	- I and III subunits of CF_0
Photosystem I	- two P700 chlorophyll conjugated apoprotein
Photosystem II	- 51kd and 44kd chlorophyll a apoprotein
	- cytochrome b_{559}
	- 32kd herbicide-binding protein
Cytochrome b_6/f	- cytochrome f
	- cytochrome b_6
	- subunit 4
Stromal proteins	
	Large subunit of ribulose-1,5-bisphosphate carboxylase

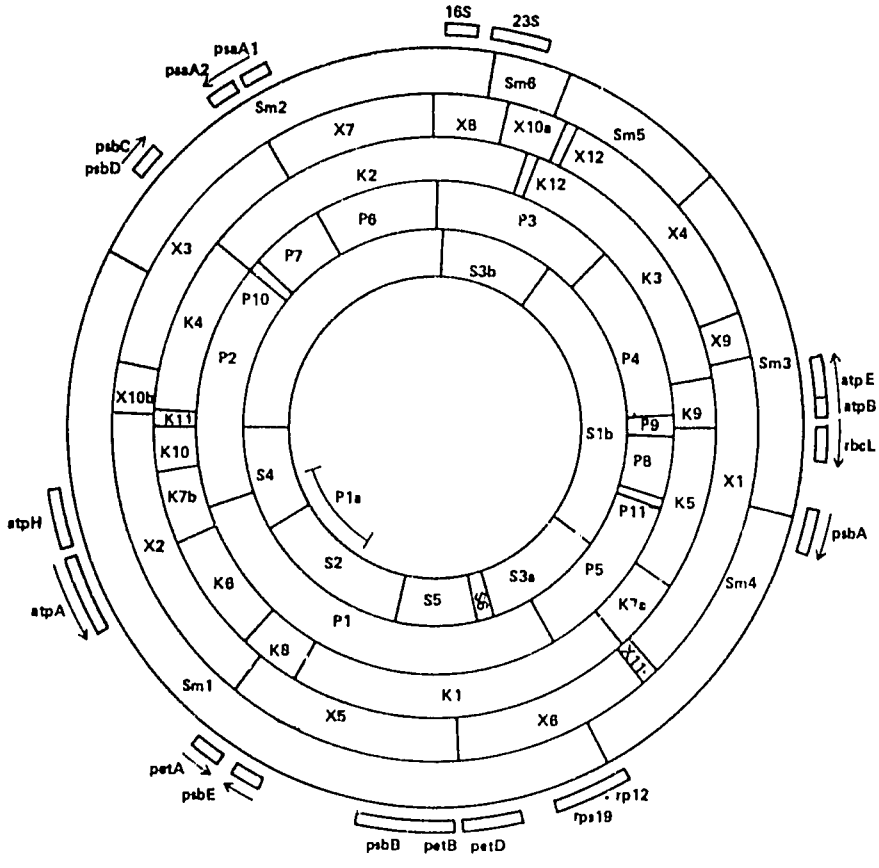


Fig. 1. Physical map of the *Vicia faba* chloroplast genome. The map shows restriction sites, starting from inside the map, for Sal I (designated S fragments), Pst I (designated P fragments), Kpn I (designated K fragments), Xho I (designated X fragments) and Sma I (designated Sm fragments). The location and orientation of genes are indicated. The fragment marked Pla is one of the fragments cloned to complete the clone bank (see Ko *et al.* 1983). The map of Sal I sites was determined by Keller and Delius, 1980. Gene designations: *rbcL* - the large subunit of ribulose-1,5-bisphosphate carboxylase; *atpA, atpB, atpE, atpH* - the alpha, beta, epsilon and proton-translocating subunits, respectively, of the ATP synthase; *psaA1 psaA2* - the two P700 chlorophyll a apoproteins of photosystem I; *psbA, psbB, psbC, psbD* and *psbE* - genes for the 32 kd herbicide-binding, 51 kd chlorophyll a-binding, 44 kd chlorophyll a-binding, "D2" and cytochrome b_{559} proteins, respectively, of photosystem II; *petA, petB* and *petD*- cytochrome f, cytochrome b_6 and subunit 4 components, respectively, of the cytochrome B6/f complex; *rp12* and *rps19* - putative chloroplast ribosomal protein genes homologous to *E. coli* ribosomal proteins L2 and S19, respectively

Fig. 2. A stepwise model for the evolution of the *Vicia faba* chloroplast genome. The model illustrates the five steps leading to the organization observed in *Vicia faba*. Molecule A represents the ancestral chloroplast genome typified by spinach. A 50 kbp inversion within the large single copy region of molecule A resulted in the arrangement found in the mung bean-type chromosome (molecule B). Molecule C represents the loss of one of the inverted repeated sequences from a mung bean-like ancestor yielding the alfalfa-type genome (Palmer *et al.* 1984; Palmer, unpublished data). Three subsequent inversions (numbered steps 1-3) resulted in the organization observed in the present-day *Vicia faba* chloroplast chromosome. The gene designations have been explained in the legend of Figure 1. Four transfer RNA genes have also been included. They are designated: trnL(CAA) - $tRNA^{Leu}_{CAA}$; trnL(UAG) - $tRNA^{Leu}_{UAA}$ and trnF - $tRNA^{Phe}$. The arrows marked by HindI4, BamI2,Bam4 and BamI3 are not gene designations. They indicate position and relative orientation of blocks of sequences. The hollow triangle points to the position of the BamI3 block (in molecules A and B) and, upon its subsequent deletion, it points to the fusion site (in molecules C-F). The solid triangles in molecule F indicate the location of recombination/inversion sites.

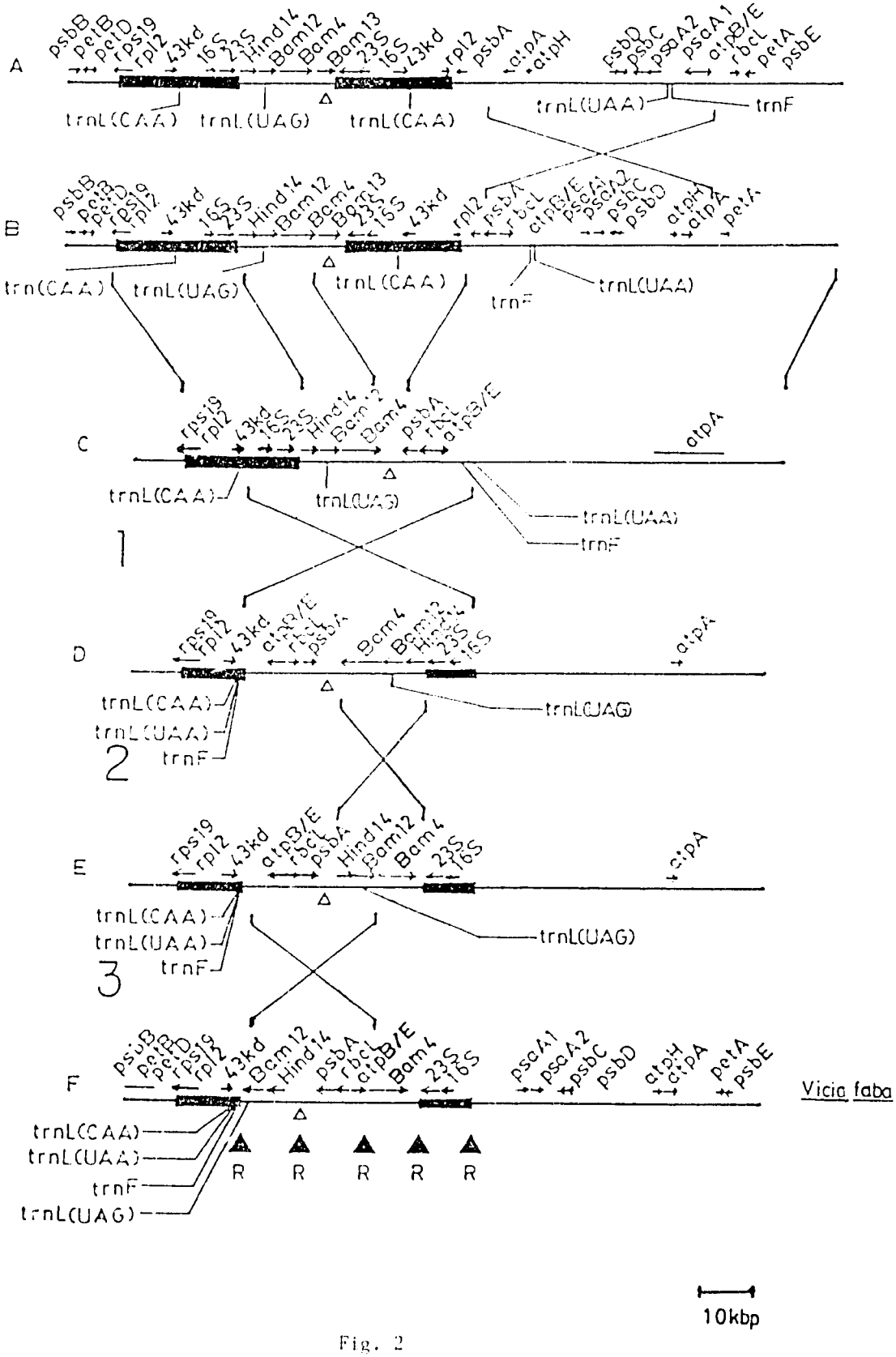


Fig. 2

Molecular analysis of *Vicia faba* L. cytoplasms.

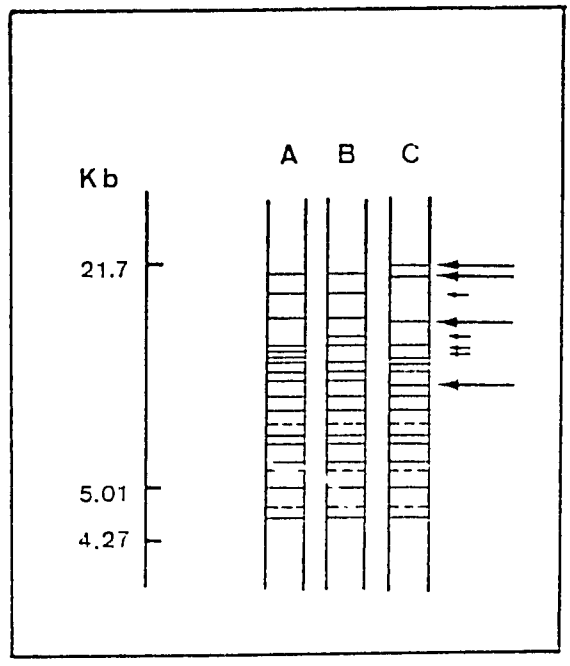
Laboratoire d'Etude de l'Heredite Cytoplasmique, Universite de Louvain
Faculte des Sciences Agronomiques, Place Croix du Sud, 1, 1348 Louvain-la-Neuve, Belgium
M. Briquet, J.-P. Goblet, M. Boutry, M.-C. Flamand, A.-M Faber

Genotype Nuclear	Genotype Mitochondrial	Phenotype	Mitochondrial DNA (+ EcoRI)	Mitochondria plasmids (Sizes in base pairs)	Mitochondrial variant polypeptides (Mp in K daltons)	Cytoplasmic spherical bodies	Origin
Ad23	N	Fertile	Type A	1700F-1420	26	-	G. Duc, INRA (Dijon) France
Ad23	447	Sterile	Type B	1700F-1420 1700S	24	+	G. Duc
Ad23 x HG115	447	Fertile	Type B	1700F-1420 1700S	24 + 26	-	G. Duc
Ad23(Revert)	447	Fertile	Type B	1700F-1420 1700S	24 + (26)*	-	G. Duc
123	N	Fertile	Type A	1700F + 1420	...	-	G. Duc
123	447	Sterile	Type B	1700F + 1420 1700S	...	+	G. Duc
123 x Hg115	447	Fertile	Type B	1700F + 1420 1700S	...	-	G. Duc
123(Revert)	447	Fertile	Type B	1700F + 1420 1700S	...	-	G. Duc
135	N	Fertile	Type A	...		-	G. Duc
135	447	Sterile	Type B	...	24	+	G. Duc
Ad23	421	Sterile	Type B	...	24 + (26)*	+	G. Duc
241	421	Sterile	Type B	...	24 + (26)*	+	G. Duc
G58	421	Sterile	Type B	...	24	+	G. Duc
G58	N	Fertile	Type A	1700F-1420	26	-	P. Berthelem, INRA (Rennes), France

G58	447	Sterile	...	...	24 + (26)*	+	P. Berthelem
G58	350	Sterile	Type B	1700F-1420 1700S-1540	24 + (26)*	-	P. Berthelem
OR-BEN	350	Fertile	Type A	1700F-1420	(26)*	-	P. Berthelem
G58 x HG115	350	Fertile	Type B	1700F-1420 1700S-1540	(24)* + 26	-	P. Berthelem
127	N	Fertile	Type A	1700F-1420	26	-	G. Duc
127	35[illegible]	Sterile	Type B	1700F-1420 1700S-1620	24	-	G. Duc
196	N	Fertile	Type C	1700F-1420	26	-	G. Duc
196	350	Sterile	Type B	1700F-1420 1700S	24	-	G. Duc
GG-140	N	Fertile	...	...	26	-	P. Berthelem
GG-140	350	Sterile	...	...	24	-	P. Berthelem
GG-140(Revert)	350	Fertile	...	...	24 + (26)*	-	P. Berthelem
232	N	Fertile	...			-	G. Duc
232	350	Sterile	...	1700F + 1420 1700S		-	G. Duc
228	N	Fertile	...	1700F + 1420		-	G. Duc
228	350	Sterile	...	1700F + 1420 1700S		-	G. Duc

- Mitochondiral DNA analysis was performed by horizontal agarose gel electrophoresis of Eco RI. DNA digests as described previously (Boutry, M and Briquet, M., 1982, Eur. J. Biochem. 127, 129-135). Plasmid analysis was carried out using ^{32}P-labeled mitochondrial plasmids as a probe (Goblet, J.-P. et al., Current Genetics, 1985, in press). Mitochondrial polypeptides was analysed by SDS-polyacrylamide gel electrophoresis followed by autoradiography (Boutry, M. et al., 1984, Plant Mol. Biol. 3, 445-452).

(*) : asterisks indicate a less intense band of the polypeptide on the autoradiography.



Schematic diagrams of the three different types of Eco RI digests of mitochondrial DNA of Vicia faba drawn from the electrophoretic pattern obtained on agarose gel.

A: normale fertile cytoplase
B: sterile cytoplasm
C: normal fertile cytoplasm of the 196 normal fertile line.

Short arrow indicate the bands specific either to normal (N) cytoplasm or to male sterile cytoplasm. Long arrows point specific bands found in the 196 normal fertile line.

N.B. this list is based on information currently available and is subject to periodic revision.

feature	variation (the commonplace situation is underlined)	locus and dominance relations	origin	chromosome ascription
LEAF	bi- to multifoliate during life cycle			
	unifoliate (obligate)	un-a_2^1	induced, X-irradiation, 800 Or. 1958 Sjodin [52]	
	(obligate)	un-a_5	spontaneous, obtained from Gottschalk 1961	
	(obligate)	un-a_6	Spontaneous, isolated in breeding material, 1966	
	(obligate)	un-a_7	spontaneous, isolated in breeding material, 1966	
	(obligate)	un-a_8	induced, MMS.0.05% 1965	
	(obligate)	un-a^1	induced, neutrons, 140 rad. 1966	
	(transnormal)	un-bc^1	spontaneous, found in Bohuslan, Sweden, 1961 Sjodin [52]	
	grey-green colour			
	bluish variant of above			
	variegated		X-irradiation, 750 rad. Errico [40] and co-workers 1984. Associated with dicentric chromosome (see under KARYOTYPE).	
	chlorotic		PBI line S45, 1982 Bond [59]. Possible link with spherical bodies associated with cms 447 male sterility.	
	chlorotic (uniform, yellow-green)		induced, EMS 1.2% from cv. Aquadulce, Filipetti [42] 1983	
LEAFLET	larger about 10cm. x 5cm.			
	smaller, about 6cm. x 3cm.			
	oblong shape (leaflet width/length ratio 0.41)		spontaneous, in progeny of variegated mutant, Filippone [42] 1984	
	leaflet half normal width, rounded		induced, gamma ray 8 Krad. from cv. Violetta di Policoro, [42] Filipetti, 1983	
	leaflet half normal width, pointed		induced, EMS 1.2% from cv. Manfredini, Filipetti [42] 1983	

feature	variation (the commonplace situation is underlined)	locus and dominance relations	origin	chromosome ascription
LEAFLET (cont.)	greatly enlarged		induced, gamma rays 8 Krad. from cv. Violetta di Policoro, Filipetti [42] 1983	
			N.B. Martin [49] and co-workers have also reported variations in leaflet morphology associated with trisomics. (See under KARYOTYPE).	
TENDRIL	not more than 2cm., not subdivided			
	longer than 2cm., (subdivision?)			
STIPULE	small			
	large			
	greatly enlarged		induced, gamma rays 8 Krad. from cv. Violetta di Policoro, Filipetti [42] 1983 (in mutant with enlarged leaflet)	
	serrate			
	spotted			
	unspotted	sp-a	see floral mutants	
	unspotted	sp-b	(pleiotropy)	
STEM	indeterminate with axillary inflorescences	Ti		
	determinate with terminal inflorescence	ti-1	neutrons 35 rd. Sjodin [52]	long arm c'some V, Sjodin
		ti-4	mutagen treatment, Steuckardt	
	determinate with terminal inflorescence		induced, gamma rays 8 Krad. from cv. Violetta di Policoro, Filipetti [42] 1983	
	determinate with terminal inflorescence		induced, EMS 1.2% from cv. Aquadulce, Filipetti [42] 1983	

feature	variation (the commonplace situation is underlined)	locus and dominance relations	origin	chromosome ascription
STEM (cont.)	semideterminate with terminal inflorescence	ti-5	spontaneous mutant Cubero [49]	
	semideterminate with terminal inflorescence	Ti-g?	spontaneous mutant Frauen [30] (dominant)	
	(Note: Brimo [30] (1983) reports a) determinate habit controlled by two nonallelic genes ti - 1, tp (topless) b) semideterminants possess different alleles at ti locus, designated ti-s1, ti-s2, ti-s3, Ti-s. Ti-s is dominant over ti-1 and Ti (indeterminant). When homozygous, tp is epistatic to Ti-s, producing determinant form.)			
	tall			
	compact (short internodes giving dwarf appearance)	dw-1	from Bond [59] 1964 from var. Compacta	
		dw-2	spontaneous Svalof 1970	
		dw-3	INRA spontaneous mutant from a double restorer line HG 115C Berthelem [21]	
		dw-4?	X-ray mutant from cv. Fribo, 1972, Dietrich [26]	
		dw-5?	induced EMS 1.2% from cv. Aquadulce, Filipetti [42] 198	
	main stem with one to three side branches			
	main stem with many (up to 15) side branches. Associated with terminal flowering.			
	anthocyanins present	Rs		
	anthocyanins absent giving green stem.	rs	PBI Cambridge. Line 349 Bond [59]. (rs condition occurs in Triple-White pleiotropy)	
	erect			
	decumbent			
	± prostrate		Dijon collection, France (Picard [21])	

feature	variation	locus and dominance relations	origin	chromosome ascription
STEM (cont.)	basal branching			
	high incidence of branches arising from higher nodes			
INFLORESCENCE				
	axillary	(see ti above)		
	terminal			
	multiflowered (up to 10 or 12)			
	one or two flowered		as in subsp. paucijuga	
	pedicels arising close to base of peduncle			
	pedicels arising more than 2cm. from base			
	elongated peduncle		induced EMS 1.2% from cv. Aquadulce Filipetti [42] 1983	
	asynchronous flowering (within inflorescence			
	synchronous flowering		reported by Gates 1980 (Durham)	
	precocious flowering (neotonous)		reported by Chapman and Peat 1978 (Wye)	

(Note: Smith [56] reported inbred *V. faba* lines with independent vascular supply to each flower as opposed to commercial cultivars with 2nd/3rd and other flowers connected. Inbred lines less susceptible to flower drop in reponse to stress, resulting in a higher level of pod setting, 1982)

feature	variation	locus and dominance relations	origin	chromosome ascription
FLOWER	Note: Flower colour variants, often striking, tend to be included in lists of variation. Only the most distinctive and stable are of value, however, and there is an urgent need to identify these. Moreno et al (1981) proposed a scheme for flower colour based on three gene loci and using different gene symbols to those adopted earlier. A logical step now would be to extend, if possible, this interpretation using the defined mutants of earlier workers. Since the flower components together manifest substantial genetic variation, their relevance for linkage studies and varietal identity is self-evident (S.W. and G.P.C.)			
	ground colour off-white			short arm
	violet	dp-a1	EI 0.0031% 1958	c'some I
	violet	dp-a2	X-irradiation, 1956	(satellite
	dark brown	dp-a3	X-irradiation, 1956	c'some)
	dark brown	dp-a4	X-irradiation, 1956	(Sjodin)
	dark brown	dp-a5	X-irradiation, 1956	
	dark brown	dp-a6	X-irradiation, 1956	
	pink standard, violet wings	dp-a7	X-irradiation, 6000r. 1958	
	light pink standard, brown wings	dp-a8	X-irradiation, 8000r. 1957	
	pink standard, brown wings	dp-a9	EI 0.0031% 1959	
	light pink standard, brown wings	dp-a10	EI 0.0062% 1959	
	violet standard, brown wings	dp-a11	EI 0.025% 1959	
	violet	dp-a12	EI 0.025% 1959	
	dark brown	dp-a13	EI 0.025% 1959	
	dark brown	dp-a14	X-irradiation 7000r. 1959	
	violet	dp-a15	X-irradiation 7000r. 1959	
	dark brown	dp-a16	X-irradiation 7000r. 1959	
	dark brown	dp-a17	spontaneous, from Bohuslan 1961	
	violet	dp-a18	spontaneous, from Bohuslan, 1961	
	dark brown	dp-a19	neutrons, 132 rad. 1961	
	pink	dp-a20	spontaneous, obtained from Bond [59] (9311/1/1/1, 1963)	
	dark brown	dp-a21	spontaneous, obtained from Bond [59] (9311/1/2/3, 1963)	
	violet	dp-a22	spontaneous, obtained from Bond [59] (51/3 x 9311), 1963	
	scarlet	dp-a23	spontaneous, obtained from Bond [59] (C5/2/12/1), 1963	

feature	variation (the commonplace situation is underlined)	locus and dominance relations	origin	chromosome ascription
FLOWER (cont.)	dark brown	dp-a24	spontaneous, obtained from Bond [59] (C8/2/2/1/1/1), 1963	
	dark brown	dp-a26	spontaneous, obtained from Rowlands (VI 63/8), 1964	
	dark brown	dp-a27	spontaneous, obtained from Rowlands, (CI) 1964	
	dark brown	DP-A28	spontaneous, obtained from Rowlands, (C8), 1964	
	solid yellow	dp-a29	spontaneous, obtained from Rowlands (IV 63/2) 1964	
	yellow wing spots	dp-b1	spontaneous, obtained from Rowlands (VI 6309) 1964	
	greyish brown	dp-a31	gamma rays, 9000r. 1967	
	dark brown	?	gamma rays, 8 Krad. from cv. Violetta du Policoro, Filipetti [42] 1983	
	wing petals spotted, standard dark striped			
	wing spots irregular, less intense	ww	spontaneous, Moreno [49], 1981 (Locus independent of "short internodes" and of the two loci for white flower, but linked with Sjodin's topless mutant?)	
	unspotted (=white flower)	sp-a1	spontaneous, obtained from [59] Bond, 1963	
	unspotted	sp-a2	spontaneous, obtained from Rowlands (Ch 170) 1964	
	unspotted	sp-b1	spontaneous, obtained from Rowlands Triple White, 1964	
	unspotted	sp-b2	spontaneous, obtained from Rowlands VI 6302, 1964	
	unspotted	sp-b3	spontaneous, obtained from Rowlands VI 6301, 1964	
	unspotted	sp-b4	spontaneous, obtained from Picard [21], 1968	

feature	variation	locus and dominance relations	origin	chromosome ascription
FLOWER (cont.)	unspotted	?	gamma rays, 8 Krad. from cv. Violetta di Policoro, Filipetti [42], 1983	
	(Note: Picard [21] suggests unspotted character (i.e. white flower) governed by two recessive genes; linked to low seed tannin - see also under SEED).			
	flowers 2.5 - 3.5cm. long flowers less than 2.5cm long			
	enlarged flower		gamma rays, 8 Krad., from cv. Violetta di Policoro. Associated with enlarged leaflets and stipules. Filipetti [42], 1983	
	leguminous keel present separated or diverging keel petals exposing the stigma (sometimes associated with "unifoliate" character			
	open flower closed flower			
	partially closed flower	cf	spontaneous? Poulsen [10], 1977	
	anthers yellow-grey anthers black, no pollen		spontaneous in offspring derived from Ad23 x cms 447 cross, Thiellement [22] 1980	
	anthers black, white pollen		spontaneous in offspring derived from Ad23 x cms 447 cross, Thiellement [22] 1980	

feature	variation	locus and dominance relations	origin	chromosome ascription
POLLEN	pale grey white		spontaneous in offspring derived from Ad23 x cms 447 cross, Thiellement [22] 1980	
	yellow		spontaneous? Thiellement [22], 1982	
	prolate	Po		
	round	po-1*	X-ray, 4000r. *See later note on tetraploidy.	
	triangular	?	reported by Graman [8] in two i_7 lines, 1982.	
	round-triangular	po-3	MS 0.01%	
	fertile		Graman [8] reports varietal differences in levels of non-viable pollen grains (up to 30.8% in Maris Bead), 1982	
	nuclear genetic male sterility	ms-1	PBI spontaneous, from Bond [59] 1963	
	nuclear genetic male sterility	ms-2?	INRA. Selected lines from Berthelem [21]	
	nuclear genetic male sterility	Ms-d	Duc [21], 1985. In M_2 obtained by EMS 1.5% from cv. Diana. (Note: "Ms-d" since this mutant is dominant and was discovered by the Dijon group - the suffix signifies origin (S.W. & G.P.C.)	
	cytoplasmic male sterility	cms 447	PBI, Spontaneous, Bond [59], 1966. Associated with presence of RNA-containing cytoplasmic spherical bodies, which are not present in male fertile 447 plants, restorer lines or in restored sterile plants.	
	cytoplasmic male sterility	cms 350	INRA. Spontaneous, Berthelem [21], 1970. Goblet [21] reports supercoiled DNA molecule of 1540 bp in male-sterile 350, not found in fertile cytoplasm or in cms 447, 1985.	

feature	variation	locus and dominance relations	origin	chromosome ascription
POLLEN (contd.)	cytoplasmic male sterility	cms 417	INRA Berthelem [21], 1981. From cms 447/Ad 23F line, induced BE 0.5% + MSE 2.5%	
	cytoplasmic male sterility	cms 421	INRA. Duc [21], 1978. From cms 447/ Ad 23F line, induced BE 0.5% + MSE 2.5%.	
	intermediate male fertility		Thiellement [22], 1979. In hybrids Ad23 x cms 447.	
	maintainer 447		INRA, Berthelem [21]. From selected lines Ad 23F, G62, 245-17, 29E.	
	maintainer 350		INRA, Berthelem [21]. Selected line G58.	
	restorer 447	Rf1	PBI, Bond [59]. Selected lines S45, LCF. INRA, Berthelem [21]. Selected lines G8 G85, Ad20, Po74.	
	restorer 350	Rf2	INRA, Berthelem [21]. Selected line 6A with gametophytic determinism.	
	restorer 350	Rf3	INRA, Berthelem [21]. Selected lines G77, G78, G84, Bob 7, Bob 13, 47D, S129B.	
	double restorer 447 and 350	Rf1, Rf3	INRA, Berthelem [21]. Selected lines HG115N, G108.	

Note: Duc (1984) reports that in crosses between cytoplasmically male-sterile lines and near isogenic maintainers a) stability in the proportion of male-sterile progeny was recessive to instability and reciprocal effects were observed, b) variability existed in the degree of sterility in the progenies of 6 genotypes backcrossed with cms 447. Correlation of degree of sterility of maternal plant with that of progeny was observed.

feature	variation	locus and dominance relations	origin	chromosome ascription
CARPEL (at flowering)	partial self-compatibility			
	self compatible auto fertile		Lord [65] et al. report autofertility in cv. Afghan related to stigma structure (low papillae, thin cuticle). 1984	
	auto sterile		Line T2 reported by Lord [65]; has longer papillae, thicker cuticle than autofertile lines. 1984.	
	partial autofertility		Line T51 reported by Lord [65]: intermediate between T2 and T51. 1984	
	four ovuled			
	one or two ovules		some Ethiopian material	
	five to seven ovules		some *major* x *minor* crosses reported by Poulsen [10], 1980.	
	eight or more ovules		some *V. faba major* selections.	
CARPEL (at maturity)	erect (*V. faba minor*)			
	pendent (*V. faba major*)			
	horizontal			
	straight			
	curved		some *V. faba major* cultivars	
	with felty indumentum			
	without felty indumentum			
	dehiscent			
	indehiscent			
	enlarged		induced, gamma rays 8 Krad. from cv. Violetta di Policoro; associated with enlarged leaflet, stipule and flower. Reported by Filipetti [42]. 1983.	

feature	variation	locus and dominance relations	origin	chromosome ascription
SEED	<u>about 1cm. long, bolster-shaped</u> down to 0.5cm. long, bolster-shaped up to 2.5cm. long, flattened (Note: Higgins and Evans [58] in "Systems for Cytogenetic Analysis in *Vicia faba*" (1984) include the following characters for cultivar identification:- <u>Seed shape</u>: circular/elliptic/square/oblong/ovate <u>Seed dimpling</u>: absent/present).			
	<u>"black" seeded</u> (Sometimes regarded as very dark brown or dark violet)	Sc-1	isolated in X-irradiated material, 1956	Long arm c'some II (Sjodin)
		Sc-2	isolated in X-irradiated material, 1956	
		Sc-3	isolated in EI-treated material, 0.125% 1958	
		Sc-4 - Sc-7	isolated in X-irradiated material, 1956	
		Sc-8	isolated in X-irradiated material, 400 r. 1956	
		Sc-9, Sc-11 - Sc13	isolated in X-irradiated material, 1956	
		Sc-14	isolated in X-irradiated material, 8000r. 1956	
		Sc-16	isolated in EI-treated material, 0.05% 1969	
		Sc-17	isolated in X-irradiated material, 1957	
		Sc-18	wild form from Italy, obtained from Gatersleben, 1961	
		Sc-29	Kiemes Schwartze Pferdebohne, obtained from Gatersleben, 1961	

feature	variation	locus and dominance relations	origin	chromosome ascription
SEED (cont.)	"black" seeded (cont.)	Sc-41	isolated in X-irradiated material, 6000r. 1967	
		Sc-42	isolated in MMS-treated material, 0.02%, 1967	
		?	Higgins [58] describes cv. "Vesuvio" as black-seeded 1981	
	violet seeded	V-1	isolated in Primus, 1959	
		V-3	isolated in Primus, 1959	
		V-4	obtained from Botanic Garden, Moscow, 1962	
		V-5	obtained from Botanic Garden, Moscow, 1962	
		V-6	obtained from Rowlands (AD99) 1964	
		V-7	obtained from Bryssine, Rabat, 1964	
			Polish cultivars	
	buff seeded yellow seeded		collections at Dijon, France	
	green seeded	y-1	wild from China, obtained from Gatersleben, 1961	
		y-2	obtained from Rowlands (Ch193) 1964	long arm
		y-3	Japan through FAO 1965	c'some IV
		y-4	obtained from Bond [59], Line 349, 1968	(Sjodin)
		y-5	obtained from Bond [59] "Staygreen", 1968	
	red seeded	r-1	obtained from Rowlands (AD96), 1964	
		r-2	obtained from Picard [21] (D1434), 1967	
			also red-spotted forms in collections at Dijon, France	
	white seeded		reported by Martin [49] in line VFM 15 from Ethiopia 1982	
	unspeckled speckled		Ricciardi [43] et al. report speckled form shows monofactorial dominance over uniform or unspeckled pigmentation 1982	
	unstriped striped		South American collections at Dijon, France (Picard [21])	

feature	variation	locus and dominance relations	origin	chromosome ascription
SEED (cont.)	(Note: Ricciardi [43] et al. (1985) suggest that segregation of a multiallelic series at two independent loci accounts for observed segregation rations in *V. faba* seed coat colour. Epistatic effects remain to be explored).			
	unhooked (i.e. without cotyledon bulges)		Ho	
	tough testa papery testa semi-naked	sn	spontaneous, Poulsen [10]	
	incomplete testa (i.e. palisade layer lacking in parts of testa)	it	mutant form reported by Poulsen [10], 1982	
	long narrow hilum 1mm. x 4-5mm. small hilum 0.5mm x .3mm.	Hi-1 Hi-2		
	round hilum long hilum 1mm. x 6mm.	Hi-3 Hi-4		
	black hilum colourless hilum	n	Fyfe 1951	
	dormant non-dormant		Khare and Singh [37] report dormancy dominant over non-dormancy, controlled by single gene, 1984.	
	high percentage of hard seeds low percentage of hard seeds		up to 22.8% in some lines reported by Salih [51] cvs. Sudanese Triple White, Kambal, Salih	
	(Short cooking time - related to soft seeds?) (Long cooking time - related to hard seeds?)			

feature	variation	locus and dominance relations	origin	chromosome ascription
SEED (cont.)	low oil content		Haro [49] et al. report lines with less than 0.2% lipid, 1980.	
	high oil content			
	low protein (to 15%)			
	medium protein (25-30%)			
	high protein (to 45%)		El Sayed [53] et al. report some ICARDA lines with 30-34%, 1982 Barratt [57] reports crude protein levels in the following lines: Gilletts Longpod 38.7%; Dacre D 34.5%; GOTT 25/7/3 34.4%; *V. faba* 240 34.1%. 1982	
	low sulphur amino acid			
	high sulphur amino acid			
	(Note: a number of authors have reported a negative correlation between seed protein content and proportion of sulphur amino acids, especially lysine, methionine and cysteine. See Griffiths (1983). Mitkees and Hassan (1983) reported on the inheritance of content of some amino acids. Variation between cultivars in legumin: vivilin ratios and in legumin composition has also been reported; see Maplestone et al. (1985).			
	> 2% tannin			
	< 2% tannin		Hussein and Saleh [17] report low tannin in cvs. Compacta Dwarf, Lux, and line R.12, 1983. Poulsen [10] reports creation of low tannin population by transfer of white flower/low tannin gene to cv. Francks Ackerperle, 1982.	
	low trypsin inhibitor (< 3.0 units/g)		reported by Hussein [17] in cvs. Erfordia, Poecnvyje, 1983.	
	high trypsin inhibitor (> 4.0 units/g)		reported by Hussein [17] in cv. Diane, 1983.	

feature	variation	locus and dominance relations	origin	chromosome ascription
SEED (cont.)	Favism: the metabolism of favism is not fully explored but the alkaloid glucosides vicine and convicine are believed to be significant in inducing favism in genetically susceptible humans. The significance of dihydroxyphenylalanine (DOPA) remains unclear. (S.M.W and G.P.C.)			
	high convicine (> 0.5%)		Lattanzio [42] reports high levels in cv. Gemini, 1983 Hussein [17] reports high levels in family 402, 1985 Pitz [5] reports high levels in lines PI 222129, PI270056 1981	
	low convicine (<0.3%)		Lattanzio [42] reports low levels in lines MG 106364, MG 103259, 1983 Pitz [5] reports low levels in cvs. Maxine, Maris Bead, 1981 Gardiner [6] reports low levels in lines CH 360/125/1, Minor/3, 1982.	
	low convicine (< 0.2%)		Hussein [17] reports very low levels in cvs. Giza 2, Double White, 1985	
	high vicine (> 0.7%)		reported by Lattanzio [42] in cv. Gemini, 1983 reported by Hussein [17] in cvs Giza 1, Rebaya 40, 1985 reported by Pitz [5] in cvs. Columba, Norislandski, 1981 reported by Gardiner [6] in cvs Diana, Herz Freya, Maxine, 1982	
	low vicine (< 0.5%)		reported by Lattanzio [42] in cvs. Korunde, line MG 103271, 1983 reported by Hussein [17] in cv. Roumy, 1985 reported by Gardiner [6] in lines PI 223304/2, PI 223304/3, 1982 Bjerg [11] also reports low glucosides in material of Algerian origin, 1985	

feature	variation	locus and dominance relations	origin	chromosome ascription
ROOT	nodulated			
	non-nodulated?		Brunner [2] reports small variability among mutants derived from cv. Wieselburger in % nitrogen derived from fixation, 1981.	
	normal rooting depth			
	deep rooting		evidence that certin Mediterranean lines can extract soil moisture from a greater depth than normal	
WHOLE PLANT				
	photoperiod sensitive			
	photoperiod insensitive			
	vernalisation sensitive		winter beans	
	vernalisation insensitive		spring beans	
	frost susceptible		most lines of *V. faba*	
	frost resistant		U.K. and French winter varieties and many West Asian lines e.g. ILB 1813 and ILB 1814, Syria, ICARDA	
	highly frost susceptible		cvs. Hudeiba 72, Sudan; Giza 4, Egypt.	
	drought susceptible		Heringa [35] reports late ripening lines and cvs. more susceptible (e.g. Colomba) 1984.	
	drought tolerant		Heringa [35] reports some lines and cvs. drought tolerant, 1984.	
	susceptible to water-logging			
	resistant to water-logging		Dodds [44] reports cvs. Aquadulce, Daffa more resistant, 1983.	
	sensitive to soil salinity		Salem [12] reports Giza 1, Giza 3 especially sensitive, 1982.	
	less sensitive to soil salinity		the following workers have reported some tolerance of soil salinity: Khondekar [33] in cvs. Verde Ante, Con Amore, Skladia, 1984. Pocsai [36] in cv. Webo, 1983. Salem [12] in Diana, Ackerperle, 1982.	

feature	variation	locus and dominance relations	origin	chromosome ascription
WHOLE PLANT (cont.)	very early leaf fall		Kittlitz [31], 1985.	
	yellow senescent (i.e. yellowish colour throughout growing period, early, low yielding)	vs	mutant form governed by single recessive gene, reported by Poulsen [10], 1982	
	flowering on low nodes	Lfp	Lfp is epistatic over Efd.	
	flowering on high nodes	lfp	lfp lfp is late, but actual position affected by vernalisation and long days.	
	early flower development	Efd	Lfp - efd shows early initiation but delayed development, giving intermediate appearance.	
	later flower development	efd	Lfp - Efd - is early with little response to photoperiod or vernalisation (e.g. cv. Colossal). Reported by Fattah [64], 1986.	

feature	variation	locus and dominance relations	origin	chromosome ascription
ISOENZYMES	(Note: a number of workers have reported variation between lines and cultivars of *V. faba* in the banding patterns obtained from electrophoresis of isoenzymes and polypeptides. See Hill-Cottingham (1983) for further details. The genetic basis for the inheritance of such variation has been investigated in some cases, as listed below. S.M.W. and G.P.C.)			
	alcohol dehydrogenase		controlled by 2 loci, one with clear segregation	
	aspartate aminotransferase		possibly two loci, with clear segregation at one	
	superoxide dismutase		controlled by 2 loci, segregation in one	
	phosphoglucomutase		clear segregation in one locus, less well-defined in second locus the above all reported by Mora [50] et al., 1983	
	non-specific esterase		reported by Peat and Adham [64] to be controlled by 3 genes A with two alleles B and C each with three alleles. 1984.	
	glutamate-oxaloacetate-transaminase		reported by Suso and Moreno [50] to be controlled by one locus with two alleles, 1982.	

feature	variation	locus and dominance relations	origin	chromosome ascription
KARYOTYPE*	diploid			
	tetraploid	po-1 ?	Poulsen [10], 1977 Bourgeois [21], following colchicine treatment, 1980.	
	normal six bivalent formation			
	asynaptic		Martin [49].	
	partially asynaptic		reported by Linnert [28] in mutants A8, A16, 1981.	
	trisomics		Note: trisomics are not available from diploid x tetraploid crosses backcrossed to diploid. Martin and Barcelo [49] (1984) describe some trisomics in *V. faba* An alternative approach to trisomics is that of Schubert, Rieger and Michaelis [27] (1986). Trisomic plants are not easily maintained and there is a case for an alternative approach to gene mapping. (S.M.W. and G.P.C.)	
	transmissable dicentric chromosome		reported by Errico [40] et al. in a variegated mutant 1984.	
	chromosome I 9% longer than normal (longer centromeric region)		reported by Filippone [42] et al. in an oblong-leaf mutant, 1984.	
	translocations		these entries derive mostly from Gatersleben. See Schubert, Rieger and Michaelis (1986)	
	A I^s - III^l			
	C I^l - VI^l		*chromosomes are numbered I to VI following Michaelis and Rieger (1959, 1968).	
	D I^s - III^s		l = long arm	
	E IV^l - V^l		s = short arm	
	F II^l - III^s			

feature	variation	locus and dominance relations	origin	chromosome ascription
KARYOTYPE (cont.)	translocations (cont.)			
	G I^S - II^l		Note: capital letters indicate primary changes. Secondarily, two separate lines can then be hybridised and appropriate selections made for double translocations, thus: AN, GN, KN HD, FD, DP, DM, DN, JE, GJ, BF, AC, DC, KC, NC, AP, AH. A further cycle of crossing can then lead to such combinations as NDF, NDH, PAN and NDP.	
	H III^l - IV^l			
	J I^S -V^S			
	K I^S - VI^l			
	L II^l - III^l in. A			
	P III^l - V^S in. B			
	inversions			
	B V^S - V^l (pericentric)			
	M I^S - I^l (pericentric)			
	N I^S - I^S (paracentric)			
	pericentric inversion in chromosome I		Reported by Ramsay [55], spontaneous in ICARDA lines BPL 1192, ILB 950, 1985.	
	banding			

Note: banding as a means of chromosome recognition has not yet in *V. faba* been associated with variant DNA composition and at this stage, therefore, we feel unable to give it extended treatment.
S.M.W. and G.P.C.

organisms with which *Vicia faba* interacts	locus and dominance	resistance relations
ANGIOSPERMS *Orobanche crenata* *Orobanche aegyptiaca*		Nasseb [16] reports that the Egyptian line F402, and ICARDA lines BPL472 and 561 show some resistance apparently associated with slower root growth and a more compact root system, 1981. Kasasian reports cv. Express shows tolerance, 1973. Cubero [49] reports some resistance in lines VF115, VF172, 1980. Abdalla [15] reports variation among *V. faba* landraces in response of different characters to *Orobanche* infection, 1982. Nassib [16] suggests that Egyptian landraces in particular represent important sources of resistance, 1981. Cubero [49] reports: - greater susceptibility in major vars. than in equina or minor - greatest resistance in paucijuga races - population differences in major genetic systems governing resistance - intra-population differences based on minor genetic systems associated with seed size - overall partially dominant system for susceptibility; resistance recessive, 1983. Abdalla also reports resistance recessive, and genetically complex. Abdalla [15] also reports variation among *V. faba* genotypes in reactions to glyphosphate used to control *Orobanche*, 1983.

organisms with which *Vicia faba* interacts		locus and dominance	resistance relations
BACTERIA	*Rhizobium leguminosarum*		Strains shown to vary in nodule effectiveness with particular *V. faba* materials. Lawes et al. P.B.S. Wales
		sym-1	Duc [21] reports recessive gene of Indian origin inducing inefficient symbiosis with Dijon *Rhizobium* strains, 1985.
	Xanthomonas spp.		
	Pseudomonas spp. *Erwinia* spp.		
FUNGI	*Alternaria tenuis* *Alternaria alternata*		Gurha [39] et al. report some resistance in 2 Japanese and 1 Indian cultivars 1981.
	Aphanomyces eutiches		Lamari [4] and co-workers report resistant selections, 1984.
	Ascochyta fabae	Af-1 Af-2 Af-3 Af-4 Af-5 Af-6	Resistance genes Af-1, Af-2 and Af-6 confer resistance to more than one isolate. Material was derived from a variety of sources and was analysed by Bernier [4] and co-workers, 1985. The following workers have also reported resistance: Berthelem [21] in selected winter lines 29H, 29W, 29M,1985. Bond [59] in vars. Bulldog, Banner, Buccaneer, 1980. Cubero [49] in cv. Alameda, 1984. Furgal-Wegrzycka [45] in vars. Beryl, Komprima and others 1984. Golubev [66] in cvs. Pikuloichskie 1, Burshtynskie 56 and others, 1982. Hanounik and Malika [53] in Syrian selections 14434-1, 14986-3, and in BPL 2485, 1983, 1984. Jellis [59] in winter-hardy inbred line IB18-1/3, 1985 Tomasszewski [45] in cv. Jasny II, 1983. Zakrzewska [47] in some lines and cvs., including dwarf determinates and early lines, 1983. Steiner et al. [31] also report variation amongst cvs in levels of seed infection, 1983

organisms with which *Vicia faba* interacts		locus and dominance	resistance relations
FUNGI	*Botrytis fabae*		Harrison [61] reported on role of *B. cinerea* in chocolate spot disease: incidence of *B. cinerea* lesions increases at lower but steadier rate over U.K. growing season then *B. fabae*, but *B. cinerea* benomyl-tolerant, 1984 The following workers have reported levels of resistance to *Botrytis* spp. Abdel-Hak [16] in some X-ray mutants, 1983. Furgal-Wegrzycka [45] in cvs. Beryl, Komprimo and others 1984. Gondran [38] in synthetic line Survoy, 1983 Hanounik [53] in cvs. Giza 1, Giza 3 and some ICARDA lines, especially ILB 938, 1983 (Note: this line has elsewhere been referred to as NEB 938 and BPL 1179). Khalil et al. [16] in lines ILB 938, 249/804/80, RC 39/80, 1984 Nassib [16] in Giza 3 and other ARC lines, 1984 Robertson [53] in lines derived from ILB 438 (=BPL 710) and ILB 938; selections also found with multilocational resistance in material from Canada, Egypt, Syria and U.K., 1984. Tomaszewski [45] reports moderate resistance in some lines, 1983 El-Hosary et al. [20] report complete dominance for resistance in an F_2 cross NA 112 x Romi, 1984 Note: 40 mar, Bailiss and Chapman (1986) have shown that for both *Botrytis* species symptoms are more severe in virus infected plants and pointed out implications for screening *Botrytis* resistance (S.M.W. and G.P.C.)
	Cercospora spp. *Cylindrocarpon* sp. *Erysiphe* spp. *Fusarium avenaceum* *F. acuminatur* *F. culmorum* *F. equiseti* *F. fabae* *F. oxysporum* *F. solani f.sp. fabae*		Mohamed [16] reports some resistance to fusarium wilt in Giza 3 and Fam. 402, 1982. Steinkardt [25] reports some fusarium resistance, apparently polygenic, in some lines, 1985.

organisms with which *Vicia faba* interacts		locus and dominance relations	resistance
FUNGI (cont.)	*Gibberella zeae*		
	Leveillula taurica		
	Microsphaera penicillata		
	Mycosphaerella pinodes		
	Peronospora viciae		
	Phoma medicaginis var. pinodella		
	Phytophthora megaspora		
	Pythium spp.		
	Rhizoctonia solanii		Mohamed [16] reports some resistance to *Rhizoctonia* in Fam. 402, line 63/1051, 1982.
	Sclerotinia sclerotiorum		
	S. trifoliorum		
	Sclerotium rolfsii		
	Stemphylium botryosum		
	Thielaviopsis basicola		
	Uromyces fabe (= *Uromyces viciae fabae*)	Fr-1 Fr-2 Fr-3 Fr-4 Fr-5 Fr-6 Fr-7 Fr-8 Fr-9	Resistance genes Fr-2, Fr-4, Fr-7 confer resistance to more than one rust isolate. Bernier [4] and co-workers report presence of resistance genes in a number of lines and cultivars, 1983. The following workers have also reported levels of resistance: Abdel-Hak [16] in some gamma ray mutants, 1983 Cubero [49] in cv. Alameda, 1984 Furgal-Wegrzycka [45] in cvs. Beryl, Komprimo and others 1984 Hanounik [53] in Sel. 80 LAT 15563-3, 1983 Khalil and Nassib [16] in ILB 938, Reina Blanka, 249/803/80 and 249/804/80, 1984 Mohamed [16] in ILB 938, M288, M311, M299, M300 and other ARC lines, 1982 Rashid and Bernier [4] also report slow-rusting lines, including 2N6, 2N29, 2N43, 2N122, ILB 938 and some crosses, 1985

organisms with which *Vicia faba* interacts		locus and dominance relations	resistance
INSECTS	*Acyrthosyphon pisum*		Lowe [62] et al. report red and green strains with differing fecundity etc. Muller [31] reports yellow strain, 1984
	Aphis craccivora *Aphis fabae*		Partial resistance in var. Rastatt reported by Miller [59]. Bond [59] and Holt [59] also report resistance in line 14 derived from Rastatt, 1980, 1981. Some resistance in ICARDA lines, especially BPL1076 reported 1981 Geissler [24] reports partial resistance in some lines,; also vars. Friba and mutant 3945 less attractive in sucking tests, 1983. Birch [61] reports some resistance in cvs. Herra, Reina Mora, Line 14 and Throws MS. No clear difference in resistance between vars. major, minor, equina, 1984.
	Aphis gossypii *Apion aethiops* *Apion vorax* *Aulacorthum solani* *Bruchus dentipes* *Bruchus elnairensis* *Bruchus rufimanus* *Caliothrips sudnensis* *Callosobruchus maculatus* *Callosobruchus chinensis* *Empoasca fabae* *Euscelidius vriegatus* *Heliothis armigera* *Liriomyza congesta* *Liriomyza hidobrensis* *Liriomyza trifolii*			

organisms with which *Vicia faba* interacts		locus and dominance relations	resistance
INSECTS (cont.)	*Lixus algirus*		
	Macrosihum euphorbiae		
	Megoura viciae		
	Myzus persicae		
	Phyllophaga crinita		
	Resseliella spp.		
	Sitona hispidulus		
	Sitona limossus		
	Sitona lineatus		
	Sitona scifrons		
	Spodoptera exigua		
	Taenothrips spp.		

organisms with which *Vicia faba* interacts		locus and dominance relations	resistance
NEMATODES	*Ditylenchus dipsaci*		Hooper [60] reports no known resistant *V. faba*, 1983 Same author reports different races of this nematode. Steiner [31] et al. reports variation amongst *V. faba* cvs. in levels of seed infestation, 1983.
	Heterodera gottingiana *Meloidogyne spp.* *Merlinius brevidens* *Pratylenchus spp.* *Radopholus similis* *Rotylenchus reniformis* *Siddiqia maximus* *Tylenchorhynchus dubius*		
VIRUS	alfalfa mosaic bean common mosaic bean leaf roll		Rollwitz [23] reports tolerance in some lines, 1982.
	bean yellow mosaic	bym-1 bym-2	Schmidt [24] et al. reports two recessive complementary genes for resistance following crosses between susceptible cv. Fribo and other susceptible lines with resistant line A., 1985. Rohloff [32] reports two sources of resistance to two different strains of bean yellow mosaic virus: in one, gene recessive and homozygosity established; in second, gene may be recessive, 1984. Bernier [4] et al. report resistance in some selections and inbred lines, especially 2N138, 1984. Steuckardt [26] reports resistance in some lines; resistance apparently semi-dominant, 1985.
	bean yellow veinbanding broad bean fireblight broad bean mild mosaic broad bean mosaic		Viruses causing mosaic-type symptoms in *V. faba* but with particle features distinct from those in bean yellow mosaic have been reported in Algeria and India. (See review article by Cockbain in "The Faba Bean", ed. Hebblethwaite, 1983).

organisms with which *Vicia faba* interacts		locus and dominance relations	resistance
VIRUS (cont.)	broad bean mottle		
	broad bean necrosis		
	broad bean red blotch		
	broad bean ringspot		
	broad bean severe chlorosis		
	broad bean stain		
	broad bean true mosaic		Rollwitz [23] reports tolerarce in some lines, 1982.
	broad bean vein chlorosis		
	broad bean β		
	broad bean V		
	broad bean wilt		Rollwitz [23] reports tolerance in some lines, 1982.
	clover yellow vein		
	cowpea mosaic		
	cucumber mosaic		
	dolichos ringspot mottle		
	pea early-browning		
	pea enation mosaic		Schmidt [24] et al. report resistant lines, 1984.
	subterranean clover red leaf		
	tomato spotted wilt		
	turnip mosaic		
	vicia cryptic		
	watermelon mosaic		
	white clover mosaic		

MYCOPLASMAS Mycoplasma-like organisms have been reported by Jones [60] et al. to be present in the phloem sieve elements of *V. faba* from the Sudan showing phyllody, 1984.

Alivizatos [34] reports corn stunt spiroplasma in *V. faba*, 1984.

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APPENDIX 1 : LIST OF SCIENTIFIC ESTABLISHMENTS

AUSTRALIA

1. South Australian Department of Agriculture, Adelaide, S.A. 5000, Australia.

AUSTRIA

2. IAEA Laboratory, Seibersdorf, Austria.

BELGIUM

3. Laboratoire d'Etude de l'Heredite Cytoplasmique, Universite Catholique de Louvain, 1348 Louvain-de-neuve, Belgium.

CANADA

4. Department of Plant Science, University of Manitoba, Winnipeg. Manitoba, Canada.
5. Department of Crop Sciences, Saskatchewan University, Saskatoon, Saskatchewan, Canada.
6. Research Station, Agriculture Canada, Agassiz, British Colombia, Canada.

CZECHOSLOVAKIA

7. Katedra biologickych zakladu rostlinne vyroby, Ustav geneticy a slechteni VSZ, Prague-Suchdol, Czechoslovakia.
8. Vyoska skola zemedelska Praha, provozne ekonomicka fakulta, 37005 Ceske Budejovice, Czechoslovakia.

DENMARK

9. Breeding station "Maribo", 4960 Holeby, Denmark.
10. Danish Plant Breeding Ltd., Boelshoj, Denmark.
11. Department of Crop Husbandry, Royal Veterinary and Agricultural University, Copenhagen, Denmark.

EGYPT

12. Faculty of Agriculture, Alexandria University, Alexandria, Egypt.
13. Radiobiology Department, Nuclear Research Centre, Atomic Energy Establishment, Cairo, Egypt.
14. Department of Botany, University Ain-Shams, Cairo, Egypt.
15. Faculty of Agriculture, Cairo University, Giza, Egypt.
16. Field Crops Research Institute, Agricultural Research Centre, Orman, Giza, Egypt.
17. National Research Centre, Giza, Egypt.
18. Faculty of Agriculture, Mansoura University, Mansoura, Egypt.
19. Faculty of Agriculture, Menoufia University, Shebin El-Kom, Egypt.
20. Agronomy Department, Faculty of Agriculture, Moshtohor, Zagazig University, Egypt.

FRANCE

21. INRA, Station d'Amelioration des Plantes, B.V. 1540, 21034 Dijon Cedex, France.
22. INRA, Laboratoire d'Amelioration des Plantes, Universite de Paris-Sud, 91405 Orsay Cedex, France.

GERMAN DEMOCRATIC REPUBLIC

23. Institut fur Pflanzenzuchtung, Gulzow-Gustrow, G.D.R.
24. Institut fur Phytopathologie, Aschersleben, G.D.R.
25. Sektion Biologie, Wilhelm-Pieck-Universitat, DDR-2500, Rostock, G.D.R.
26. Veg. Pflanzenproduktion Gotha Friedrichswerth, Gotha 8, Pfarrstr. 8, G.D.R.
27. Zentralinstitut fur Genetik und Kulturpflanzenforschung der Akademie der Wissenschaften, DDR-4325, Gatersleben, G.D.R.

GERMAN FEDERAL REPUBLIC

28. Institut fur Angewandte Genetik, Freie Universitat Berlin, G.F.R.
29. Institut fur Angewandte Genetik, Universitat Hannover, Herrenhauser Strasse 2, D-3000 Hannover 21, G.F.R.
30. Institut fur Pflanzenbau und Pflanzenzuchtung, Universitat Gottingen, Gottingen, G.F.R.
31. Institut fur Pflanzenzuchtung, Saatgutforschung und Populationsgenetik, Universitat Hohenheim, 7000 Stuttgart 70, G.F.R.
32. Institut fur Virusrankheiten der Pflanzen der Biologischen Bundestalt, D-3300, Braunschweig, G.F.R.
33. Institute of Crop Science, Technical University, 1000 Berlin. 33, G.F.R.

GREECE

34. Benaki Phytopathology Institute, Kiphissia, Athens, Greece.

HOLLAND

35. Foundation for Agricultural Plant Breeding, P.O. Box 117, 6700 AC Wageningen, Holland.

HUNGARY

36. Agrartudomanyi Egyetem, Mosonmagyarovar 9201, Hungary.

INDIA

37. Department of Plant Breeding and Genetics, Jawaharlal Nehru Agricultural University, Jabalpur, India.
38. Division of Plant Sciences, Meerut University, Uttar Pradesh, India.
39. IARI, Kanpur, Uttar Pradesh, India.

ITALY

40. Cattedra di Miglioramento Genetico delle Piante Coltivante, Universita di Napoli, Portici, Italy.
41. Centro Miglioramento Genetico Ortaggi C.N.R., Portici, Napoli, Italy.
42. Centro di Studio sull'Orticoltura Industriale, C.N.R., Via Amendola, 165/A 70126-Bari, Italy.
43. Plant Breeding Institute, University of Bari, Bari, Italy.

MEXICO

44. Centro de Investigacion y de Estudios Avanzados del IPN., Apartado postal 629, 36500 Iraputo, Mexico.

POLAND

45. Instytyt Hodowli Poslin i Nasiennictwa, AR-T, Olsztyn, Poland.
46. Zaklad Doswiadczalny HiAR, Batazek, Poland.
47. Zaklad Immunologii Roslin iHAR, Radzikow, 05-870 Blonie pod Warszawa, Poland.

SPAIN

48. Centro Regional de Andalucia, Instituto Nacional de Investigaciones Agrarias, Apartado 240, Cordoba, Spain.
49. Escuela Tecnica Superior de Ingenieros Agronomos, Departamento de Genetica, Apartado 3048, Cordoba, Spain.
50. Instituto Nacional de Investigaciones Agrarias, Unidad de Leguminosas, Cordoba, Spain.

SUDAN

51. Hudeiba Agricultural Research Station, P.O. Box 31, Ed-Damer, Sudan.

SWEDEN

52. Swedish Seed Association, S-26800 Svalof, Sweden.

SYRIA

53. ICARDA, P.O. Box 5466, Aleppo, Syria.

UNITED KINGDOM

54. Bayfordbury Research Laboratories, Hertford, Herts., U.K.
55. Department of Agricultural Botany, Plant Science Laboratories, Whiteknights, University of Reading, Reading, U.K.
56. Department of Botany, Durham University, South Road, Durham, U.K.
57. Long Ashton Research Station, Bristol, U.K.

UNITED KINGDOM (cont.)

58. National Institute of Agricultural Botany, Cambridge, U.K.
59. Plant Breeding Institute, Trumpington, Cambridge, U.K.
60. Rothamsted Experimental Station, Harpende, Herts., U.K.
61. Scottish Crop Research Institute, Invergowrie, Dundee, U.K.
62. University of Wales, Cardiff, U.K.
63. Welsh Plant Breeding Station, Plas Gogerddan, Aberystwyth, U.K.
64. Wye College, Ashford, Kent, U.K.

UNITED STATES

65. Department of Botany and Plant Science, University of California, Riverside, CA92521, U.S.A.

USSR

66. VIR, Leningrad, USSR.
67. Vsesoyuznyi institut zernobobvykh ku'tur, Orel, USSR.