Dissemination Pathways of Common Bean (*Phaseolus vulgaris*, Fabaceae) Deduced from Phaseolin Electrophoretic Variability. II. Europe and Africa[1]

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*Phaseolin type, determined by one-dimensional sodium dodecyl sulfate polyacrylamide gel electrophoresis, was used to suggest dissemination routes of common bean (*Phaseolus vulgaris*) cultivars from their areas of domestication to Europe and Africa. In the Iberian Peninsula, 'C' was the most frequent phaseolin type. Only in Chile has a comparably high 'C' frequency been observed previously, indicating that many Iberian cultivars may have been introduced from Chile, or that many Chilean cultivars may have come from the Iberian Peninsula. In Europe (outside the Iberian Peninsula), most cultivars exhibited a 'T' type. The high frequency of this type may be related to the high frequency of green pod cultivars among European cultivars. Most African cultivars exhibited a 'T' or a 'C' type and may have been introduced from Brazil, the Iberian Peninsula, or western Europe. 'T' or 'C' cultivars had larger seeds than 'S' cultivars. The phaseolin patterns of cultivars with different seed types and of early French cultivars are discussed.*

The discovery of the Americas triggered a rapid exchange of crops between the Old and New worlds. In particular, several New World crops—e.g., maize, potatoes, common bean, sunflower, sweet potato, avocado, and cacao—were introduced to the Iberian Peninsula from which they spread to other parts of the world, including western Europe (Simmonds 1976). The first reference to the common bean (*Phaseolus vulgaris* L., Fabaceae) in western Europe was made by Turner (1538) in England; the first description and representation, by Fuchs (1543) in Germany. Further references to the common bean were made by Dodoens (1554) in Flanders; Bock (1546), Heresbach (1570), and Tabernaemontanus (ca. 1590) in Germany; Gerard (1633) and Miller (1754) in England; and Tournefort (1797) in France.

Several centuries after its first introduction in Europe, common bean germplasm consisted of many different cultivars. Based on seed size, shape, color, and growth habit, Martens (1869) defined seven common bean species, each consisting of several divisions or forms. Although this taxonomic treatment is no longer recognized as valid, it gives some indication of the level of phenotypic variability then present.

These early descriptions share a common characteristic: no mention is made of the New World origin of the common bean or from what part of the New World the cultivars of this new crop had been introduced. On the contrary, the common bean was assimilated to a legume species described 1,500 yr earlier by Theophrastus (ca. 300 B.C.), and Dioscorides (first century A.D.). It was thought

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for several centuries to be of Asian origin. Linnaeus (1753), for example, stated that it had originated in India. In the 19th century, Wittmack (1880, 1888a,b) and Gray and Trumbull (1883) argued in favor of an American origin; they identified the legume described by Theophrastus and Dioscorides as cowpea (*Vigna unguiculata* (L.) Walp.), an African species. The close relationship between *Phaseolus* and *Vigna* (and the ensuing morphological similarity) (Maréchal et al. 1978) and the rather vague descriptions in ancient writing may explain the confusion between the two crops.

Little information is available on introduction of the common bean to Africa. Evans (1976) stated that the slave trade took the bean from Brazil to Africa and subsequently inland by trade routes.

Because historical and linguistic sources provide little evidence on the origin and spread of common bean cultivars in Europe and Africa, we gathered genetic data, i.e., phaseolin variability, to attempt to trace their origin to the Middle American or Andean domestication centers.

Genetic data have been used previously to suggest evolutionary patterns of origin and dispersal. Recent examples are the identification of a possible area of domestication for peas (*Pisum sativum* L.) in the Near East (based on chloroplast DNA variability; Palmer et al. 1985) and of multiple origins of sickle-cell anemia (based on restriction fragment polymorphisms at the β-globin locus; Orkin and Kazazian 1984; Pagnier et al. 1984). Based on the existence of protein and enzyme gradients among contemporary human populations in Europe, Ammerman and Cavalli-Sforza (1984) hypothesized that agriculture in Europe was introduced from the Near East through demic diffusion rather than cultural diffusion.

Our own findings indicate that multiple domestications in the common bean have led to small-seeded, 'S' phaseolin cultivars in Middle America; to small-seeded, 'B' phaseolin cultivars in Colombia; and to large-seeded, 'T' (and possibly 'A,' 'C,' and 'H') cultivars in the southern Andes. These results are consistent with other, independently obtained, types of data, e.g., archaeology and history (Gepts 1984; Gepts and Bliss 1986; Gepts et al. 1986).

Genetic data are therefore a valid type of argument—although by no means the only one—to suggest evolutionary patterns of domestication and dispersal. In this article, we present the results of a survey of phaseolin electrophoretic variability among European and African cultivars. From the phaseolin data, we infer the origin of domestication of these cultivars.

MATERIALS AND METHODS

The common bean cultivars included in this study comprised accessions from the Iberian Peninsula collected by C. Leakey and provided by R. Hidalgo H. (Genetic Resources Unit, Centro Internacional de Agricultura Tropical [CIAT], Cali, Colombia); French cultivars provided by H. Bannerot (Institut National de la Recherche Agronomique [INRA], Versailles, France); Dutch cultivars collected by A. Zeven (1979) and supplied by R. Hidalgo H.; two British, one Italian, and one Hungarian cultivar; and African cultivars provided by J. Davis (Bean Program, CIAT, Cali, Colombia) and R. Maréchal (Faculté des Sciences Agronomiques, Gembloux, Belgium); and cultivars from Malawi made available by M. W. Adams (Michigan State University, East Lansing, Michigan, USA) (Table 1).

Phaseolin type was determined by one-dimensional sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS/PAGE) as described by Brown et al. (1981) and Ma and Bliss (1978).

Seed dimensions (length, height, and width) of cultivars homogeneous for seed and phaseolin types were determined as indicated earlier (Gepts et al. 1988).

RESULTS

The sample of cultivars from the Iberian Peninsula originated largely from the germplasm explorations of Dr. C. Leakey in Spain and Portugal (Table 1). Of the 109 genotypes homogeneous for phaseolin type, 43% had a 'C' phaseolin pattern. This is unusually high considering its frequency in tropical America. The 'T', 'S', and 'H' phaseolin types occurred at frequencies of 30%, 26%, and 1%, respectively (Table 2).

Seed types present at high frequencies in the Iberian sample included large, flat, white seeds (e.g., G10146); small, elongated, white seeds (e.g., G10163); and small, round, white seeds (e.g., G10238). All three types had an 'S' phaseolin pattern. Also included were egg-shaped, white seeds (e.g., G10179) and large, elongated, white seeds (e.g., G13043), both types with a 'T' phaseolin pattern; and red to purple seeds (e.g., small: G10153 or elongated: G15240) with a 'C' phaseolin pattern. Accessions with cream-colored seeds with red streaks (e.g., G10166) exhibited either a 'T' or a 'C' phaseolin pattern.

Several seed types in the Iberian sample had been observed previously among the Middle American and Andean cultivars (Gepts and Bliss 1986; Gepts et al. 1986). These include the small, round, white seeds (e.g., G10238), both with an 'S' phaseolin type; egg-shaped, white seeds (e.g., G10179) with a 'T' phaseolin type; cream-colored seeds covered with red streaks (e.g., G10166) and light buff seeds (e.g., G14412) with a 'T' or a 'C' phaseolin pattern.

The sample of 124 cultivars from Europe (excluding the Iberian Peninsula) included entries from France (90) and the Netherlands (30) and two accessions from the United Kingdom, one from Italy, and one from Hungary (Table 1). The 'T' phaseolin type was observed in 72% of the cultivars, the 'S' type in 21%, and the 'C' type in 7% (Table 2).

Among the French common-bean cultivars, 66% had a 'T' phaseolin type, 25% an 'S' type, and 9% a 'C' type. In addition, the distribution of the different phaseolin types varied according to the specific consumption category to which these cultivars belonged: dry beans, green pods with fibers (filet), and green pods without fibers (snapbeans or mangetout). Among the dry bean cultivars, the 'S' and 'T' phaseolin types were represented in approximately equal proportions (Table 3). Generally, large-seeded dry bean cultivars had a 'T' phaseolin type: e.g., the 'Coco' types, such as 'Coco Paimpolais Hervé' and 'Coco Toulonnais Nain'; the 'Flageolet' types, such as 'Flageolet Blanc de Vitry' and 'Flageolet Pleurs'; 'Lingot'; 'Michelet à Longue Cosse'; and 'Soissons Nain à Gros Pied.' Small-seeded dry bean cultivars, on the other hand, tended to exhibit an 'S' phaseolin: e.g., 'Fevette de St. Laud', 'Inépuisable', 'Mogette de Vendée', and 'Prédome Nain.' There were some exceptions, however, to this relationship between seed size and phaseolin type. 'Flageolet Blanc à Longue Cosse', 'Sabre Nain Etoile du Nord', and 'Tarbais' had large seeds and an 'S' phaseolin type. Most of the cultivars grown for their green pods (with or without fibers) exhibited a 'T' phaseolin type (Table 3).

The sample of French common bean accessions included some early cultivars

Table 1. IDENTIFICATION, PHASEOLIN TYPE AND SEED SIZE OF COMMON BEAN CULTIVARS FROM EUROPE AND AFRICA

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a]	and/or Name		Length	Height	Width
1. Africa:	a) Angola:				
NI311	'Alho de Perdiz'	T	12.5	8.8	7.0
NI312	'Chumbo'	T	12.2	6.7	4.9
NI613	'Manteiga'	T	9.4	7.0	5.9
	b) Burundi:				
	'Cerca de Bayumbwe 1'	S	10.7	6.4	5.2
	'Cerca de Bayumbwe 2'	S	11.4	7.1	5.8
	'Cerca de Bayumbwe 3'	C	16.2	8.6	6.2
X716	'Doré de Kirundo'	T	11.7	6.6	5.3
	'Jaune du Mosso'	T	13.2	7.4	6.1
	'Mezcla de 6 líneas'	S	10.7	7.7	6.3
NI681	'Bataaf'	T	12.0	7.2	6.2
X714	'Jaune pointillé'	S	11.2	7.2	5.5
	c) Kenya:				
G1368	'Kisola'	C	15.9	8.0	6.0
G8044	'Wairimu'	S	10.4	6.8	5.8
G8047	GLP10, 'Mwezi Moja'	T	15.3	7.1	5.4
G8049	'Tongmire'	T	11.5	7.9	6.4
G8054	GLP 25	T,C			
	GLP 24	T	13.8	7.3	4.7
	'Naivasha'	T	15.2	7.9	5.6
PI209806	'Yelloweye'	T	12.5	7.7	6.5
	d) Malawi:				
C9a*		S			
C9b	'Chizgama'	T	14.4	9.1	6.5
C9c*		S,T			
C10a-1*	'Sugar Bean'	T			
C10c-1*	'Mkhalasonga'	T,C			
C10d	'Mkhalasonga'	T	14.5	6.8	5.7
C10e-1	'Kanyalubwe'	T	14.3	8.1	6.1
C10f-1	'Kachikwama'	T	14.5	9.0	6.5
C12b-1	'Sugar Bean'	T	16.0	7.8	5.2
C12c	'Katolika', 'Kamchechebe'	S	10.1	6.5	4.7
C12e	'Zituwa'	S	10.6	6.5	5.1
C12f-1	'Zgamanaluwa'	T	16.6	8.6	6.2
C12g	'Chazgama'	T,C			
C12i	'Fipa'	S,C			
C12j-1	'Fipa'	T	15.3	7.8	5.9
C14b	'Mkhalasonga'	C	11.7	7.7	6.5
C23-1		T	11.8	7.4	6.0

Table 1 (contd.):

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a]	and/or Name		Length	Height	Width
C23-2		T	14.2	7.2	5.4
C23b*		T,C			
C23d		T,C			
C27b-1		T	13.5	7.2	5.5
C32-2		T	14.6	7.7	5.8
C32a-1	'Zambia'	T	14.5	7.6	5.9
C32c		T	11.6	7.6	6.2
C32f-1	'Nyanyathi'	T,C			
C32g		T	14.0	7.5	6.0
C32i-1*	'Mzaza'	T			
C32j-1*	'Saaba'	T			
C32k-1		T	13.7	8.6	6.8
C34b*		S,T			
C37b-1*		T,C			
C44b-1		S	9.1	6.1	4.8
C46-5		S	9.6	6.3	4.9
C61-1		S	9.6	6.7	5.8
C64a-1	'Mangulumgulu'	C	13.7	7.5	5.0
C64b-1*		T,C			
C64c-1*	'Mwasipengile'	T			
C64h*		S			
C68b-1*		S,T			
C71-1	'Mbuzi'	T	14.0	8.0	5.9
C71a		T	15.6	7.7	6.2
C71b-1*	'Mwasipengile'	T			
C71c-1	'Shoshi'	T,C			
C71d-1*	'Mangulumgulu'	S,C			
C71e		T			
C71g	'Kabaya'	S	9.9	6.5	4.6
C75-1		T	16.2	8.5	5.5
C78-1*	'Kabagha', 'Chula'	T,C			
C78b	'Maloko'	S,T			
C78c-1*	'Mwasipengire', 'Choshi'	T			
C81-2		T	17.1	7.5	6.1
C87-13		T	15.3	7.6	5.5
C87-4		T	17.0	8.4	6.0
C89-3		S	10.7	7.1	5.0
C90-1		T	11.1	8.0	6.5
C109a*		T			
C109b-1*		T			
C109c-1*		T			
C110-10*		S,T,C			
C115a		T,H			
C115b		T	11.7	8.1	6.5
C115c-1		T	11.8	7.5	5.4

Table 1 (contd.):

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a] and/or	Name		Length	Height	Width
C116b-1*		T,C			
C116c-1*		T,C			
C116d-1*		T			
C117a-1		T	14.3	6.9	5.2
G13825		T	14.0	8.8	7.1
G13827		T	13.4	8.5	7.1
G13835		T	15.3	7.9	6.0
G13856		T	16.5	7.4	5.7
G14288		S	10.9	7.2	5.5
G14353		C	16.1	7.4	5.7
G14366		T	19.7	9.5	6.8
G14367		T	14.0	7.6	5.4
G14368		C	15.7	7.5	6.0
G14376		T	17.6	8.4	5.4
G14466		C	16.8	8.0	5.7
	'Kanzama'	T	14.1	9.0	7.4
	'Lilongwe Market 3'	T	15.5	7.8	6.4
	'MW1039 Climber'	C	16.8	8.1	6.3
	'Ntchisi', 'Malawi 2'	S	11.5	7.3	5.2
	e) Nigeria:				
G8108	'Kabanima'	T,H			
	f) Rwanda:				
	'Mercado de Butare 21'	C	13.3	7.8	6.7
	'Mercado de Butare 22'	C	12.9	6.9	5.1
	'Mutiki 2'	T	14.2	7.8	5.8
NI682	'Uruyumba 1'	T	13.9	7.5	5.2
NI685	'Rusenyinka'	T	16.6	8.6	5.5
	'Nyakchinama'	T	16.5	8.6	5.5
	'Productivo 2'	C	12.3	7.3	6.1
	'Productivo 3'	T	15.0	7.6	5.5
	'Var. 11'	T	14.2	7.8	6.0
	g) Tanzania				
	'Canadian Wonder Mbeya'	T,C			
G13044	'Haricot 373'	S	11.1	6.9	5.2
	'Kiburu Moshi'	S	9.6	5.9	4.0
	'Masusu'	T	13.3	7.1	5.5
	'Masusu Mbozi'	T	13.7	7.3	5.7
	'Mbozi Mixture'	T	13.3	6.9	5.8
	'Mor Local'	S	11.1	7.0	5.4
	'Morogoro Masonga'	C	17.2	8.7	6.5
	'Mwezi Moja'	T	16.4	8.3	6.3
	'Sumbawanga A'	T	12.5	6.8	5.5

Table 1 (contd.):

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a]	and/or Name		Length	Height	Width
	'Sumbawanga C'	S	11.6	6.8	4.6
	'TMO 118'	T	15.8	8.5	6.2
	h) Uganda:				
	'Kabanima'	T	14.8	7.3	6.1
	'Karawa 1/2'	T	13.5	7.0	5.8
	i) Zaire:				
NI8	'Ibundu'	S	11.1	7.7	5.2
	j) Zimbabawe:				
	'Natal Sugar'	T	14.2	7.5	6.4
	k) Zambia:				
	'Chipata Mixture 1'	T	15.9	7.8	5.5
	'Chipata Mixture 2'	T	16.2	7.8	5.4
	'Chula'	T	11.5	7.2	6.4
G13785		T	13.7	8.4	6.5
G13796		T	14.0	9.1	7.0
G14449		T	13.8	8.3	6.9
	'Misamfu'	C	14.2	7.4	5.6
4. Europe:	a) France:				
	'Aiguille Verte'	T	14.1	5.7	5.1
	'Alger Noir Nain'	S,C			
	'Bagnolais Noir'	T	13.7	6.1	5.5
	'Beurre de Corné'	T	15.6	5.9	5.8
	'Beurre Doré'	C	11.3	7.6	6.9
	'Beurre Plein le Panier'	T	15.0	6.6	6.4
	'Blanc Idéal Sans Fil'	T	12.3	6.7	5.9
	'Cabanais'	S	12.5	5.6	4.6
	'Canieu'	T	13.8	7.3	5.9
	'Chevrier d'Etampes'	S	11.8	5.7	4.6
G7633	'Coco Bicolore du Pape'	T	11.6	8.3	6.3
	'Coco Paimpolais No. 7'	T	11.0	8.7	7.8
	'Coco Paimpolais de Guyader'	T	11.9	8.5	7.6
G7635	'Coco Rose'	T	12.6	8.8	6.6
	'Coco Rose de St. Crépin'	T	11.6	8.5	6.9
	'Coco Toulonnais Nain'	T	11.9	8.0	6.6
	'Deuil Fin Précoce'	T	15.4	6.4	4.7
	'Drômois'	T	15.9	5.7	5.9
	'Dubua'	T	12.7	5.9	5.3
	'Du Calaisis'	S	11.2	5.9	5.0
	'Empereur de Russie'	T	12.7	6.6	5.5

Table 1 (contd.):

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a]	and/or Name		Length	Height	Width
	'Enfant de Montcalme'	T	13.4	7.4	6.5
	'Ermitage Sans Fil'	T	14.3	6.3	6.1
	'Extra Fin du Perreux'	T	14.4	6.3	5.4
	'Fevette de St. Laud'	S	11.9	7.5	5.9
	'Fin de Bagnols'	T	15.0	5.8	5.1
	'Fin de Montclar'	T	14.8	5.6	4.9
	'Fin de Montreux'	T	12.7	5.6	4.6
	'Fin des Fins'	T	16.6	6.2	6.0
	'Flageolet Blanc à Longue Cosse'	S	13.7	6.6	5.7
	'Flageolet Blanc de Vitry	T	15.4	6.7	5.4
	'Flageolet Blanc du Nord'	T	15.2	6.9	5.6
	'Flageolet Merveille de France'	S	8.9	5.0	3.5
	'Flageolet Pleurs'	T	17.4	8.2	5.8
	'Giladeau'	T	17.5	6.6	6.6
	'Gloire d'Aubagne'	T	13.0	5.6	5.1
	'Gloire d'Ollainville'	C	12.6	6.9	5.1
	'Gloire de Deuil'	T	16.1	7.4	5.7
	'Gloire de Saumur'	T	11.7	5.0	4.5
	'Gourmandon'	T	12.0	5.9	5.5
	'Gris Deuil'	T	15.7	6.3	5.5
	'Incomparable hâtif'	T	11.0	5.6	4.2
	'Inépuisable'	S	10.5	6.4	4.9
	'Jaune Cent Pour Un'	T	14.3	6.5	5.5
	'Jaune de Chalandray'	S	9.0	5.8	4.5
	'Le Grignonnais'	T	13.7	6.4	5.1
	'Lingot'	T	14.5	6.7	5.3
	'Lingot de Vendée'	T	15.2	6.7	5.5
	'Lyonnais à Longue Cosse'	T	14.4	6.0	4.4
	'Marcelin'	S	10.7	4.8	3.9
	'Marche de Genève'	T	11.1	5.6	5.2
	'Merveille du Marché'	S	14.0	6.7	5.5
	'Métis'	T	14.1	5.8	4.6
	'Métis des Alliés'	T	13.1	6.5	5.2
	'Métis Tigré Rouge et Blanc'	T	18.0	7.7	5.0
	'Michelet à Longue Cosse' (Clause)	T	13.6	7.9	6.4
	'Michelet à Longue Cosse' (Vilmorin)	T	13.5	7.7	6.3
	'Mogette de Vendée'	S	10.1	7.2	5.6
	'Nain de Tous les Jours'	T	14.2	7.0	5.8
	'Noir d'Evian'	C	11.4	6.3	5.3

Table 1 (contd.):

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a]	and/or Name		Length	Height	Width
	'Noir à Ecosser de Chevilly'	C	10.9	8.2	7.2
	'Noir de l'Hermitage'	C	11.7	6.6	4.9
	'Noir Hâtif de Belgique'	S	12.6	6.9	5.9
	'Noir Hâtif de Chateurenard'	S	11.8	5.9	4.9
	'Petit Braisin'	S	12.2	7.8	4.9
	'Petit Potager'	S	14.2	6.2	4.5
	'Phénix'	C	13.4	7.0	6.3
	'Plein le Panier'	C	14.5	6.4	5.9
	'Précoce de Saumur'	T	14.6	6.2	5.0
	'Prédome Nain'	S	7.7	5.5	4.4
	'Princesse Double de Hollande'	S	10.2	6.3	5.3
	'Prodige de Courtry'	T	15.4	7.4	6.2
	'Roi de l'Eté'	C	12.7	6.5	6.3
	'Roi des Belges'	T	14.7	6.8	4.9
	'Sabre Nain Etoile du Nord'	S	13.0	7.8	4.9
	'Sabre Nain Très Hâtif de Hollande'	S	11.9	7.5	5.2
	'Saint André sans Fil'	T	12.9	5.8	4.3
	'Sans Rival'	T	9.5	5.1	4.0
	'Saxa'	T	14.0	5.8	5.3
	'Soissons Nain à Gros Pied'	T	16.0	8.1	6.1
	'Soissons Nain Hâtif'	S	11.4	6.8	4.5
	'Superviolet Clair du Tricastin'	T	15.6	6.4	5.5
	'Tarbais'	S	14.1	9.1	5.4
	'Tardif de Kerfeuteun'	T	12.5	5.5	4.7
	'Très Hâtif d'Etampes'	S	12.0	6.4	5.0
	'Très Hâtif de Massy'	S	12.0	7.3	5.0
	'Triomphe de Farcy'	T	14.6	6.2	5.3
	'Zénith'	T	12.8	5.3	4.6
	b) Hungary:				
G11826	'Mohacsi Lila Furj'	T	11.7	7.6	6.3
	c) Italy:				
G3816	Italia 5	T	16.8	8.4	6.4
	d) Netherlands:				
G10026	'Krombek'	T	13.7	6.8	5.0
G10027	'Eiboon'	T	9.9	7.0	5.9

Table 1 (contd.):

Identification: Number[a]	and/or Name	Phaseolin type[b]	Seed sizes (mm)[c]: Length	Height	Width
G10029	'Walcherse Witte Blanke'	S	9.9	7.2	5.7
G10030	'Eiboon'	T	12.8	7.5	6.0
G10050	'Dikkontjes'	T	13.4	8.4	6.2
G10055	'Berna'	T	12.3	7.3	5.2
G10056	'Berna'	T	12.1	7.4	5.6
G10057	'Kogelboon'	T	10.1	7.3	5.7
G10058	'Kogelboon'	T	11.2	6.1	6.1
G10059	'Noordhollandse Bruine'	T	11.6	6.9	5.7
G10060	Aff. 'Berna'	T	12.0	7.4	5.4
G10061	Aff. 'Berna'	T	11.9	7.2	5.3
G10062	Aff. 'Berna'	T	11.7	7.3	5.3
G10063	'Kogelboon'	T	9.1	6.3	5.0
G10064	'Kogelboon'	T	9.1	7.0	6.0
G10066	Aff. 'Berna'	T	12.1	7.2	5.2
G10069	'Chocolade Bruine Boon'	T	12.9	6.8	5.5
G10070	Aff. 'Berna'	T	12.0	7.1	5.3
G10077	'Rottekeutel'	T	13.5	7.3	5.4
G10081	'Leverkleurige Boon'	T	12.1	8.0	7.5
G10086	'Renka'	T	11.6	7.6	6.4
G10087	'Grootzadige'	T	14.4	8.5	6.7
G10088	'Grootzadige'	T	13.6	8.4	6.0
G10091	'Kleinzadige'	T	11.8	7.7	6.3
G10092	'Transvaalse Bonte met Draad'	S	9.3	6.2	5.3
G10099	'Macedonische Boon'	T	11.6	7.9	6.5
G10100	'Stokkievitsboon'	T	12.7	9.5	7.1
G10101	'Roodbonte Krobben'	T	14.7	7.5	5.7
G10110	'Rode Kievit'	T	12.2	8.0	5.8
G10111	'Citroen'	T	10.9	7.5	6.0
	e) United Kingdom:				
G8131		C	13.6	6.0	5.2
	'Horsehead'	T	14.4	7.4	6.4
5. Iberian peninsula:	a) Portugal:				
G10205	CL0086	T	14.7	7.3	5.3
G10206	CL0087	T	13.1	7.7	5.6
G10209	CL0092	H	12.7	8.6	5.8
G10210	CL0095	S	9.4	5.9	4.9
G10211	CL0096	S	11.3	7.0	4.8
G10213	CL0099	C	12.5	8.1	5.3
G10216	CL0102	C	14.0	8.5	5.8
G10219	CL0105	C	12.4	7.4	5.7
G10229	CL0115	T	15.3	7.2	5.2
G10230	CL0117	C	14.3	7.7	5.5

Table 1 (contd.):

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a]	and/or Name		Length	Height	Width
G10234	CL0121	T	13.7	8.0	5.9
G10238	CL0126	S	9.2	6.4	5.2
G10239	CL0127	S	12.4	7.3	5.5
G10240	CL0130	T	11.6	8.3	6.7
G10241	CL0132	S	15.8	8.9	5.3
G10243	CL0136	T	14.6	7.7	5.8
G10244	CL0137	S,C			
G10245	CL0138	S	12.5	7.4	5.6
G10251	CL0144	S	13.8	8.0	5.4
G10357		T	11.6	7.7	6.0
G10419		C	16.1	8.1	6.5
	b) Spain:				
G7613		T	16.8	8.3	5.7
G10145	CL0001	T	10.7	7.8	6.1
G10146	CL0002	S	15.3	8.9	4.7
G10147	CL0004	S	10.4	7.6	6.0
G10148	CL0005A	C	14.8	7.9	6.2
G10149	CL0007	C	14.3	9.1	6.6
G10153	CL0011	C	10.1	7.2	5.5
G10154	CL0012	C	12.5	8.0	6.1
G10160	CL0020	C	10.3	7.6	5.7
G10161	CL0021	C	10.3	7.8	5.4
G10163	CL0023	S	11.7	6.7	5.1
G10164	CL0024	S	13.1	7.0	4.5
G10166	CL0028	C	11.6	8.5	6.8
G10168	CL0030	C	12.1	9.1	7.3
G10171	CL0038	S,C			
G10172	CL0039	T	10.4	7.6	5.7
G10173	CL0041	C	13.5	9.2	7.3
G10174	CL0045	C	14.5	8.7	6.9
G10176	CL0047	T	13.3	7.2	5.9
G10177	CL0048	C	10.6	8.9	5.9
G10178	CL0051	S	9.6	7.6	6.1
G10179	CL0052	T	11.4	8.0	6.7
G10183	CL0056	C	12.6	9.6	6.9
G10184	CL0057	S	12.1	7.3	5.3
G10185	CL0058	S	12.0	7.4	5.6
G10190	CL0065	C	13.5	8.7	6.6
G10191	CL0066	C	14.6	7.9	6.2
G10193	CL0068	C	13.1	8.0	5.9
G10194	CL0069	C	13.4	8.0	5.5
G10195	CL0070	S	12.8	7.6	5.1
G10199	CL0077	C	13.0	9.1	6.9
G10201	CL0079	C	14.6	8.9	6.8

Table 1 (contd.):

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a]	and/or Name		Length	Height	Width
G11572		S	12.3	7.1	5.6
G13043	'Alubia de Aranjuez'	T	13.8	7.1	5.4
G13135		T	13.7	7.3	4.6
G13161	CL0025A	T	14.1	7.2	6.1
G13936	'Don Timoteo'	C	9.1	7.2	6.4
G14034*	CL0009B	T			
G14405	CL0563	C	13.3	8.1	6.1
G14406	CL0571	C	16.1	9.2	5.7
G14407	CL0572	C	15.6	6.9	5.9
G14408	CL0576	C	12.3	7.7	6.2
G14409	CL0583	C	14.0	9.2	6.9
G14410	CL0588A	T	11.4	8.2	7.0
G14412	CL0596	T	16.3	8.2	6.0
G14413	CL0597	T	16.7	8.3	5.9
G14414	CL0613	S	13.0	8.0	5.5
G14415	CL0636	S	12.3	7.1	5.9
G14416	CL0638	T	13.9	6.9	5.6
G14420	CL0666	C	13.0	8.6	6.1
G14421	CL0676	C	12.7	7.8	5.7
G14422*	CL0679	C			
G14423	CL0685	C	13.7	7.7	6.1
G14425	CL0687	C	13.3	8.2	6.9
G14427	CL0696	C	12.8	9.4	7.6
G14428	CL0698	C	14.2	8.8	6.3
G14429	CL0700	C	12.7	9.7	7.4
G14677		S	12.5	6.8	4.7
G14684	CL0009A	S	11.5	7.7	6.1
G14685	CL0009D	C	10.2	8.6	6.3
G14686	CL0009E	C	10.0	8.4	6.8
G14688	CL0036	C	12.0	8.6	7.3
G14689	CL0037	S	9.5	7.3	6.2
G15229	CL0416	T	12.1	6.2	5.1
G15230	CL0417	S	11.8	7.2	5.5
G15231	CL0419	S	12.6	6.9	5.2
G15232	CL0421	T	13.9	7.3	5.5
G15233	CL0422	T	13.8	7.2	5.7
G15234	CL0423	S	12.5	6.9	5.2
G15235	CL0427	C	11.4	8.1	6.5
G15236	CL0429	S	11.4	6.9	5.3
G15237	CL0436	T	11.4	8.4	7.1
G15239	CL0440	C	13.3	7.3	5.5
G15240	CL0441	C	14.0	7.8	5.5
G15241	CL0442	C	13.9	7.5	5.7
G15242	CL0445	C	13.3	7.3	6.0
G15244	CL0448	C	16.6	8.6	6.8

Table 1 (contd.):

Identification		Phaseolin type[b]	Seed sizes (mm)[c]		
Number[a]	and/or Name		Length	Height	Width
G15245	CL0449	S	13.6	6.9	5.4
G15246	CL0450	S	12.4	7.0	5.6
G15247	CL0451	T	14.4	6.4	6.0
G15248	CL0453	T	13.1	6.7	5.2
G15249	CL0455	T	11.0	6.4	5.4
G15255	CL0486	T	14.4	7.7	5.9
G15256	CL0487	S,T			
G15257	CL0488	T	12.7	5.8	5.1
G15260	CL0502	T	14.3	7.7	6.1
G15261	CL0502	T	14.1	7.1	6.1
G15262	CL0507	T	14.2	7.6	5.9
G15263	CL0509	T	11.0	6.0	5.3
G15265	CL0515	S	9.8	8.0	7.0
G15271	CL0558	S	10.4	6.9	5.7

[a] The asterisk indicates accessions heterogeneous for seed type.
[b] C: 'Contender'; H:'Huevo de Huanchaco'; S: 'Sanilac'; and T: 'Tendergreen' phaseolin types.
[c] Only seed sizes of accessions homogeneous for seed and phaseolin types were included.

from the 18th and 19th centuries (Bannerot, pers. comm.; Cariot 1865; Gibault 1912; Parmentier 1902). In particular, the 'Haricot de Soissons' ('Bean of Soissons') was first mentioned in 1749 by de Combles (Gibault 1912). This group of early cultivars included cultivars grown for dry beans and green pods (with and without fibers). It included equal proportions of 'T' and 'S' phaseolin type cultivars, but only one 'C' phaseolin type cultivar (Table 4).

The sample of 30 Dutch common bean landraces included originated from a germplasm collection of Zeven (1979) in the Netherlands (Table 1). Twenty-eight of these cultivars showed a 'T' phaseolin pattern and two an 'S' pattern. Several landraces mentioned by Zeven (1979) were included in this sample: 'Noordhollandse Bruine,' 'Krombek,' 'Citroen,' 'Stokkievitsboon,' and 'Eiboon' had a 'T' phaseolin type, while 'Walcherse Witte' had an 'S' phaseolin type.

In Africa, the common bean is grown mainly in the East African countries: Ethiopia, Kenya, Uganda, Burundi, Rwanda, Zaire (Kivu province), Tanzania, Malawi, and Zambia. In a sample of 111 cultivars homogeneous for phaseolin type (Table 1), 69% exhibited a 'T' phaseolin type, 19% an 'S' type, and 12% a 'C' type (Table 2). The African sample was characterized by a high diversity of seed types. This was apparent especially in a collection from Malawi. Some of the more frequent types included small, red seeds (e.g., 'Cerca de Bayumbwe 1' from Burundi; C12c from Malawi; and G13044 from Tanzania) and small, white

TABLE 2. FREQUENCY DISTRIBUTIONS OF PHASEOLIN TYPES AMONG COMMON BEAN CULTIVARS FROM DIFFERENT BEAN-GROWING REGIONS OF THE WORLD.[a]

Region	n	Phaseolin type[b]			
		'S'	'T'	'C'	'H'
Iberian Peninsula	109	29 (27)	32 (29)	47 (43)	1 (1)
Western Europe	122	25 (21)	88 (72)	9 (7)	
Africa	111	21 (19)	77 (69)	13 (12)	

[a] Excluding accessions heterogeneous for phaseolin type.
[b] Values represent frequencies and, between parentheses, percentages.

seeds (e.g., C9a and C44b-1 from Malawi), both classes with an 'S' phaseolin type. The 'T' phaseolin cultivars included genotypes with large seeds with a cream-colored background covered by dark speckles (e.g., the 'Mwezi Moja' or 'Chula' type: e.g., G8047 from Kenya; 'Chula' from Zambia; and 'Mwezi Moja' from Tanzania); with large, round, red seeds (e.g., C9b from Malawi; TM0118 from Tanzania; and G13785 from Zambia); with large seeds with a cream-colored background covered by a red mottling (e.g., 'Kabanima' from Uganda; 'Mutiki 2' from Rwanda; and C10f-1 from Malawi); with large seeds with a cream-colored background covered with red streaks (e.g., 'Karawa 1/2' from Uganda; C115b from Malawi; 'Chipata Mixture 2' from Zambia; and 'Natal Sugar' from Zimbabwe). Among the 'C' phaseolin cultivars, zebra-striped seeds were observed (e.g., 'Cerca de Bayumbwe 3' from Burundi; C87-4 from Malawi; and NI685 from Rwanda). One of the most common seed types was the 'Canadian Wonder' type with large, kidney-shaped, dark red to purple seeds, found in cultivars with either a 'T' or a 'C' phaseolin type (e.g., G1368 from Kenya; C23-2 from Malawi; 'Canadian Wonder Mbeya' from Tanzania; and 'Chipata Mixture 1' from Zambia).

Some of these seed types, such as the small red, and small, white-seeded types, or the large-seeded types with a cream background covered either by a red mottling or red streaks, had been observed previously in our Latin American sample. Other types, such as the zebra-striped types, the 'Canadian Wonder' types, the 'Mwezi Moja' types, dark green seed types (e.g., C23-1 from Malawi), and orange seeds covered with red streaks (e.g., 'Butare 21' from Rwanda), appeared to be either unique to Africa or to occur at a high frequency there.

In all the areas, significant differences in seed length, height, and width were

TABLE 3. PHASEOLIN TYPE DISTRIBUTION AMONG CONSUMPTION CATEGORIES OF FRENCH COMMON BEAN CULTIVARS.

Consumption category[a]	n[b]	Phaseolin type		
		'S'	'T'	'C'
Dry beans	34	17 (50)	16 (47)	1 (3)
Green pods (with fibers)	30	4 (13)	24 (80)	2 (7)
Green pods (without fibers)	15	2 (13)	10 (67)	3 (20)
Undetermined	9		7 (78)	2 (22)

[a] According to H. Bannerot (pers. comm.).
[b] Excluding accessions heterogeneous for their phaseolin type.

TABLE 4. CONSUMPTION CATEGORY AND PHASEOLIN TYPE OF EARLY FRENCH COMMON BEAN CULTIVARS.

Cultivar[a]	Consumption category[b]	Phaseolin type
'Empereur de Russie'	GF	'T'
'Enfant de Montcalme'	S	'T'
'Gloire de Deuil'	GF	'T'
'Jaune Cent Pour Un'	GF?	'T'
'Noir Hâtif de Belgique'	GF	'S'
'Prédome Nain'	DB	'S'
'Princesse Double de Hollande'	S	'S'
'Roi de l'Eté'	S	'C'
'Roi des Belges'	GF	'T'
'Sabre Nain Etoile du Nord'	DB	'S'
'Sabre Nain Très Hâtif de Hollande'	DB	'S'
'Saxa'	S	'T'
'Soissons Nain à Gros Pied'	DB	'T'
'Soissons Nain Hâtif'	DB	'S'
'Tarbais'	DB	'S'

[a] According to Cariot (1865), Gibault (1912), Parmentier (1902), and H. Bannerot (pers. comm.).
[b] According to H. Bannerot (pers. comm.); DB = dry bean; GF = green pods with fibers; S = snapbeans.

observed among cultivars with different phaseolin types (Table 5). Multiple comparisons of means by Duncan's Multiple Range Test (Dagnelie 1969) showed that in western Europe and in Africa, the 'T' and 'C' phaseolin cultivars tended to have larger seeds than the 'S' phaseolin cultivars (Table 6), as had been observed previously for cultivars of the Americas (Gepts and Bliss 1986; Gepts et al. 1986). In the Iberian Peninsula, Duncan's Multiple Range Test did not reveal significant differences in seed length and width among 'T', 'C', 'H', and 'S' phaseolin cultivars (Table 6).

DISCUSSION

Contrary to most other regions or countries investigated, the Iberian Peninsula was characterized by a high frequency of 'C' phaseolin patterns. Chile was the only country showing a similar high frequency of 'C' types (Gepts et al. 1986). Several explanations can be offered to account for this similarity. A high proportion of the Iberian cultivars may have been introduced from Chile. These Chilean genotypes might have had a competitive advantage in the Iberian Pen-

TABLE 5. ANALYSES OF VARIANCE OF SEED DIMENSIONS IN RELATION TO PHASEOLIN TYPE FOR COMMON BEAN CULTIVARS FROM DIFFERENT BEAN-GROWING REGIONS OF EUROPE AND AFRICA.[a]

Region	df[b]	F value[c]		
		Length	Height	Width
Iberian Peninsula	3,104	3.69***	16.34***	12.99***
Western Europe	2,119	10.12***	1.44[ns]	9.98***
Africa	2, 97	38.68***	19.05***	14.40***

[a] Excluding accessions heterogeneous for phaseolin or seed type.
[b] df = degrees of freedom of the numerator and denominator, respectively.
[c] *** = significant differences between phaseolin types at the $P = 0.001$ level; ns = no significant differences at the $P = 0.05$ level.

TABLE 6. SEED-SIZE DIFFERENCES BETWEEN CULTIVARS HAVING DIFFERENT PHASEOLIN TYPES IN VARIOUS BEAN-GROWING AREAS OF EUROPE AND AFRICA.[a]

Area	Phaseolin type	Mean seed sizes (mm)[b]		
		Length	Height	Width
Iberian Peninsula	'T'	13.4a	7.4b	5.8a
	'C'	13.1a	8.3a,b	6.3a
	'H'	12.7a	8.6a	5.8a
	'S'	12.0a	7.3b	5.4a
Western Europe	'T'	13.3a	6.9a	5.7a
	'C'	12.5a,b	6.8a	5.9a
	'S'	11.5b	6.6a	5.0b
Africa	'C'	14.6a	7.8a	6.0a
	'T'	14.2a	7.7a	5.9a
	'S'	10.6b	6.8b	5.2b

[a] Excluding accessions heterogeneous for phaseolin or seed type.
[b] For each region and within each column, values followed by the same letter are not significantly different at the $P = 0.05$ level.

insula over genotypes of other origins because of a better photoperiodic adaptation. In Chile the common bean is grown presently in a region stretching from 20° to 40° s. lat. (Cafati 1973), while the Iberian Peninsula extends from 36° to 42° n. lat. (Mexico extends from 15° to 30° n. lat.). On the other hand, present Chilean cultivars could have been introduced from the Iberian Peninsula by immigrants. Further data are needed to distinguish between these possibilities. In particular, a larger sample of Chilean cultivars should be analyzed.

The absence of significant differences in seed length and width among 'T', 'C', 'H', and 'A' phaseolin cultivars in the Iberian Peninsula can be explained possibly as follows. After the discovery of the Americas, both Middle American (small-seeded 'S' phaseolin) and Andean (large-seeded 'T', 'C', and 'H' phaseolin) cultivars were introduced to the Iberian Peninsula. Natural (or artificial?) hybridization between cultivars with different seed sizes may have led to genotypes with intermediate seed sizes. Additional characterization of Iberian cultivars using traits that distinguish Middle American from Andean cultivars may reveal whether the absence of seed size differences is indeed due to hybridization.

The high frequency of 'T' phaseolin patterns observed in western Europe can be explained in several ways. The genotypes that originated in the Andes were better adapted to the cool and short summers of western Europe than the Middle American cultivars. Alternatively, the high frequency of 'T' phaseolin types is due to the high proportion of cultivars grown for their green pods (with or without fibers), a majority of which showed a 'T' phaseolin type (Table 3). A similar observation was made by Brown et al. (1982).

Why then do most green pod cultivars have a 'T' phaseolin type (and should, therefore, have originated in the Andes)? We might hypothesize that the consumption of green pods was unknown in Middle America; no selection would have taken place in that region for cultivars with a reduced fiber content in the pods. However, *Nahuatl*—the language of the Aztecs—has a specific word for green pods: *exotl* (Sturtevant 1919), from which the modern Mexican Spanish word *ejote* is derived. One might also hypothesize that the growth habit, pod characteristics, and climatic adaptation of the Andean cultivars were more favorable for the selection of modern green pod cultivars by Europeans after the introduction of the common bean from the Americas. For example, Andean cultivars tend to have larger pods (correlated with larger seeds) than the Middle American cultivars. Berglund-Brücher and Brücher (1976) observed the fiberless pod trait in "autochthonous native beans" of northern Argentina.

In Africa, most of the cultivars showed a 'T' phaseolin type. Evans (1976) suggested that the common bean had been introduced from Brazil by the Portuguese during the slave trade. In Brazil, however, most of the cultivars showed an 'S' phaseolin pattern. None of the seed types of these 'S' phaseolin cultivars is represented in Africa. The seed type of the Brazilian 'T' phaseolin cultivars resembled some of the seed types observed in Africa (Leakey 1970; Van Rheenen 1979; Westphal 1974). Therefore, it is possible that some of the African cultivars were introduced from the Andes via Brazil. Other sources may have played a role also. Portuguese traders might have introduced common bean cultivars from the Iberian Peninsula. Seed types common to the Iberian Peninsula and Africa include seeds with zebra stripes or with a cream-colored background covered by red streaks or a red mottling. Alternatively, former western European colonial countries may have introduced common-bean cultivars into their colonies. For example, 'Canadian Wonder,' a cultivar with dark red, elongated seeds, became popular in the United Kingdom in the past century (Hedrick 1931). It is now one of the most frequent seed types in some of the eastern African countries, such as Kenya, Malawi, Tanzania, and Zambia.

It appears from our results (Gepts 1984; Gepts and Bliss 1986; Gepts et al. 1986, 1988; present results), that the phaseolin type analyses complement the archaeological, historical, and linguistic data with respect to the domestication and dissemination of common bean cultivars from centers of domestication to other bean-growing regions. In some areas, such as Africa, phaseolin data provide a new outlook on the origin of the common bean cultivars of that continent. The phaseolin-type distributions of any region appear to be influenced by at least three factors: the phaseolin-type distribution of the immediate region of origin, differential environmental adaptations among cultivars of different origin, and differential distribution of phaseolin patterns among consumption categories (i.e., dry bean vs. green pod cultivars).

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Book Review

The Euphorbiales: Chemistry, Taxonomy and Economic Botany. S. L. Jury, T. Reynolds, D. F. Cutler, and F. J. Evans (eds.). Academic Press, Orlando, FL 32887. 1987. 326 pp. $25.00 (paper).

A difficult order of plants is summarized in these proceedings of a joint symposium organized by the Linnean Society of London and the Phytochemical Society of Europe. Delimitation of the Euphorbiales has been disputed by taxonomists for many years, and there is as yet no agreement. It is not surprising, therefore, that this volume contains several, sometimes conflicting, ideas on interrelationships seen from a variety of points of view. "These differences of opinion and approach have vindicated one aim of the symposium by highlighting the present research problems in the Euphorbiales, as well as indicating promising pathways for new advances."

The order contains many species of economic importance. In this regard, papers describing "Members of the Euphorbiaceae in primitive and advanced societies" (R. E. Schultes), "Fuel oils from euphorbs and other plants" (M. Calvin), "New aspects of rubber biosynthesis" (B. L. Archer and B. G. Audley), "Tumor promoters of the irritant diterpene ester type as risk factors of cancer in man" (E. Hecker), and "The chemical constituents and economic plants of the Euphorbiaceae" (A.-F. M. Rizk) are of special value. This scholarly publication adds considerably to our understanding of angiosperms and it is therefore of significance for all those interested in flowering plants.

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