OBSERVATIONS ON THE ORIGIN OF *PHASEOLUS POLYANTHUS* GREENMAN[1]

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Schmit, Véronique *(Genetic Resources Unit, Centro Internacional de Agricultura Tropical, Apartado Aéreo 6713, Cali, COLOMBIA. Present address: Unité de Phytotechnie Tropicale, Faculté des Sciences Agronomiques, B-5030, Gembloux, BELGIUM) and* **Daniel G. Debouck** *(CIAT-IBPGR Research Programme, Centro Internacional de Agricultura Tropical, Apartado Aéreo 6713, Cali, COLOMBIA. Present address: International Board for Plant Genetic Resources, Research Programme, Via delle Sette Chiese 142, 00145 Rome, ITALY).* OBSERVATIONS ON THE ORIGIN OF *PHASEOLUS POLYANTHUS* GREENMAN. *Economic Botany 45(3):345–364. 1991. Total seed protein variability in a sample of 163 entries of year-bean (*Phaseolus polyanthus*), including wild, feral and cultivated forms of the whole range of distribution in Latin America was studied using 1-dimensional SDS/PAGE and 2-dimensional IEF-SDS/PAGE. Ten different patterns were observed in this crop. Eight of these are found in the Mesoamerican materials, the other two of those in the northern Andes. The highest diversity is found in the wild ancestral forms present in central Guatemala with six patterns. The 'b' pattern predominant in all Mesoamerican cultivated materials is also present at low frequency in Colombia. The 'k' pattern, predominant in the northern Andes, is present in Costa Rica. These results together with information on indigenous names for the crop suggest that there is a single gene pool domesticated from a wild ancestor still present in Guatemala, and distributed afterwards to the northern Andes, but with a clinal genetic drift from Mesoamerica to the Andean region.*

Observaciones sobre el origen del Phaseolus polyanthus Greenman. La variabilidad de la proteína total en una muestra de 163 materiales de frijoles de Phaseolus polyanthus *que incluye formas silvestres, escapadas y cultivadas de toda su distribución en América latina ha sido estudiada usando la técnica de electroforesis en una dimensión y en dos dimensiones después del punto isoeléctrico. Se encontraron diez patrones diferentes en este cultivo, ocho en Mesoamérica y otros dos en los Andes del Norte. La mayor diversidad (seis patrones) se encontró en las formas silvestres ancestrales presentes en el centro de Guatemala. El patrón 'b' dominante en todos los materiales cultivados mesoamericanos es también presente con baja frecuencia en Colombia. Al revés, el patrón 'k' dominante en los Andes del Norte ya lo es en Costa Rica. Estos resultados junto con la información lingüística tradicional sugieren que se trata de un solo acervo genético. También indican que se domesticó este cultivo a partir de una forma silvestre ancestral aún presente en Guatemala. Sugieren en fin una distribución posterior hacia los Andes del Norte donde una deriva genética empieza de manifestarse con relación a Mesoamérica.*

Key Words: bean, linguistic evidence, *Phaseolus* domestication, *Phaseolus polyanthus, Phaseolus* taxonomy, seed protein.

Phaseolus beans have been a major source of inexpensive proteins for the American Indians since at least 6000 years B.P. in Mesoamerica (Kaplan 1981; Kaplan and Kaplan 1988; MacNeish 1964), and 8000 years B.P. in the southern Andes (Kaplan and Kaplan 1988; Lynch et al. 1985; Pearsall 1978; Tarrago 1980). There is now little doubt, taking recent biochemical evidence into account, that beans were domes-ticated in several independent places in the Americas from wild plants that the American Indians found there (Debouck et al. 1989d; Gepts and Debouck 1991; Gepts et al. 1986). Although one can reasonably infer that the American Indian farmers knew about wild *Phaseolus* species and perhaps used them as they still sometimes do today (Table 1), apparently only five groups of beans were actually domesticated.

Probably because of their importance, beans were given several names by early American Indian farmers (see Table 2 for a brief survey of

TABLE 1. USE OF WILD *PHASEOLUS* BEANS BY CONTEMPORARY INDIGENOUS PEOPLES.

Species	Use	Ethnic group, and place	Source
P. acutifolius	food	Seri, Sonora	Nabhan and Felger 1978
P. augusti	food	Huanca, Junín	Debouck 1987
P. coccineus	food	Tzotzil, Chiapas	Delgado Salinas 1988
P. coccineus	medicine	Cakchiquel, Sololá	same
P. maculatus	food, medicine	Tarahumara, Chihuahua	Nabhan et al. 1980
P. vulgaris	food	Mam, Huehuetenango	McBryde 1945
P. vulgaris	food	mestizo, Catamarca	Brücher 1954
P. vulgaris	food	Quechua, Junín	Debouck et al. 1989c

contemporary names of two bean species; see also: Delgado Salinas 1988; Schmit 1988 for *P. coccineus* L. and related taxa; Gepts and Debouck 1991 for *P. vulgaris* L.; Nabhan and Felger 1978 for *P. acutifolius* Asa Gray).

Many botanists (e.g., Evans 1980; Lackey 1981; León 1987) recognize four cultigens in that genus, which includes some 36 species (Delgado Salinas 1985) principally distributed in Mesoamerica, namely: *P. vulgaris, P. coccineus, P. lunatus* L. and *P. acutifolius*. From the very beginnings of systematic botany, the first three taxa have not been questioned (they appeared unchanged in subsequent treatments by De Candolle, Bentham, Hassler and Piper); in some way one could say that formal scientific nomenclature went along with folk tradition. The tepary bean, *P. acutifolius,* was formally described first from one of its wild relatives (Gray 1850), the relationship with the cultivated material being established later (Freeman 1913).

As revealed by germplasm explorations (Berglund-Brücher and Brücher 1974; Debouck and Soto 1988; Hernández X. et al. 1959), indigenous peoples of the cool and humid highlands of Mesoamerica and the northern Andes have long been growing a fifth bean (see Fig. 1 for the distribution of the cultivated material presently registered in the World *Phaseolus* collection at CIAT). Environmental conditions in those regions have prevented them from growing the lima bean and the tepary bean, but have not excluded the common and the scarlet runner beans together with the fifth cultivated bean in certain areas. That bean has been morphologically described elsewhere (Delgado Salinas 1985; Hernández X. et al. 1959), displaying different intermediate traits between the common and the scarlet runner beans. These differences together with results from crossing studies were judged significant enough by most authors (Baudet 1977; Delgado Salinas 1985; Hernández X. et al. 1959; Maréchal et al. 1978; Smartt 1973) to justify a special taxonomic rank. That rank is however still controversial (specific: Schmit and Baudoin 1987; or subspecific: Delgado Salinas 1985; Maréchal et al. 1978). The exact origin of that bean as well as its taxonomic rank remain to be resolved (Piñero and Eguiarte 1988; Smartt 1973). We will use the name *P. polyanthus* Greenman for it and we explain later our reasons for using that particular name and species rank.

TABLE 2. NATIVE NAMES GIVEN TO *P. COCCINEUS* AND *P. POLYANTHUS* IN PLACES OF MEXICO AND GUATEMALA WHERE THEY ARE USUALLY GROWN TOGETHER.

Place and language	Names		Source
	P. coccineus	*P. polyanthus*	
Puebla, Totonaco	Shanshana	Xuyumel	(1)
Puebla, Nahuatl	Ayocote	Acaletl	(2)
Chiapas, Tzeltal	Botíl	Botíl	(2)
Chiapas, Tzotzil	—	Ibis	(2)
San Marcos, Mam	Chomborote	Dzich	(3)
Huehuetenango, Mam	Chomborote	Ixich	(3), (4)
Chimaltenango, Cakchiquel	Piloy	Piloy, Piloya	(2), (3)
Alta Verapaz, Quichil	Piloy	Piloya, Piligue	(3)

(1) Delgado Salinas 1988; (2) Hernández X. et al. 1959; (3) Debouck 1986 and field notes; (4) Standley and Steyermark 1946.
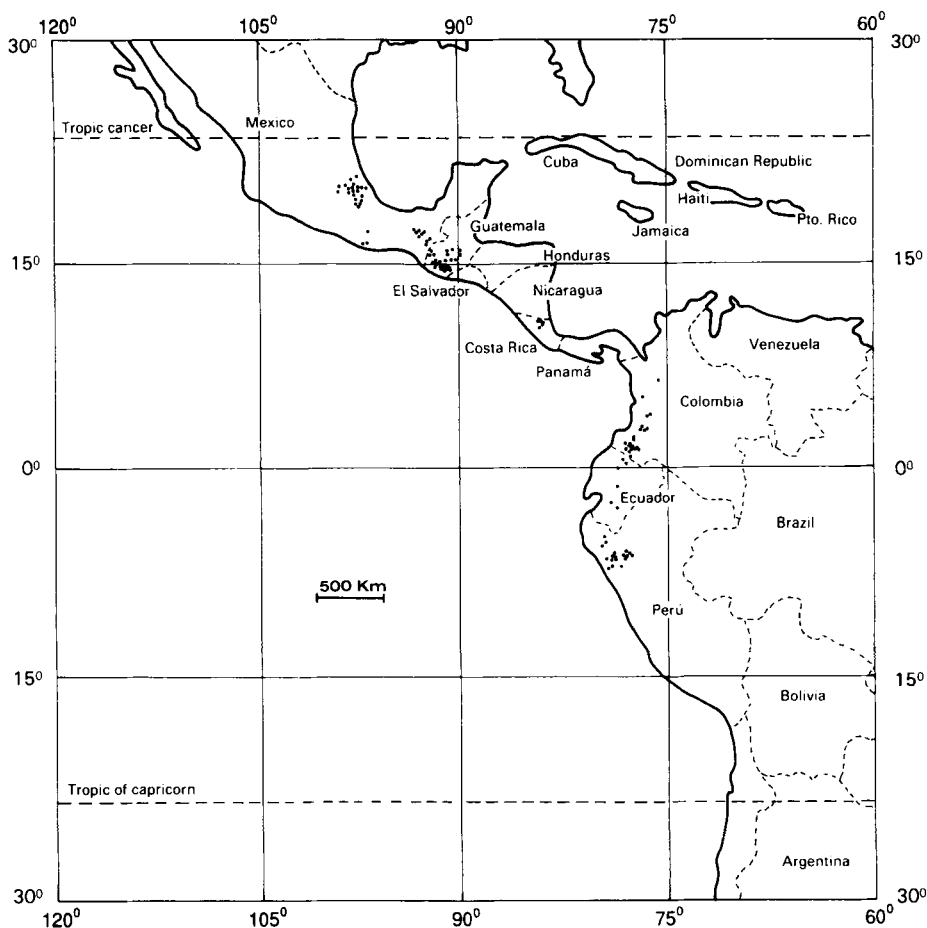
Fig. 1. Distribution of seed accessions of cultivated *P. polyanthus* present in the World *Phaseolus* Collection of CIAT.

On the basis of new data, we report here on: 1) the taxonomic status of this fifth cultivated bean, discussing both its nomenclature and genetic relationships; 2) the discovery of a wild bean in Guatemala which might be its ancestral form; 3) the status of the weedy forms frequently found in Central America and the northern Andes; and 4) the results of an analysis of the total seed protein using 1-dimensional sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS/PAGE) and 2-dimensional isoelectric focusing (IEF-SDS/PAGE) for several materials of different biological status from Mesoamerica and the northern Andes.

MATERIALS AND METHODS

The origin, identification and biological status of the 163 *P. polyanthus* entries used in this study are indicated in Table 3. All entries derive from the World *Phaseolus* germplasm collection currently maintained at CIAT, Cali, Colombia, from which seeds can be obtained freely on request. Care was taken to exclude materials collected in markets. One-dimensional SDS/PAGE has been run on a total of 356 individuals for these 163 entries.

The protein of a 30 mg sample of crude seed cotyledon ground with mortar and pestle was extracted in 1 ml of 0.4 M NaCl buffered to pH 2.4 (following a methodology defined by Brown et al. 1981a). Centrifugation was carried out at 14 000 rpm for 12 min. Equal volumes of supernatant and cracking buffer were mixed and boiled 5 min before being applied on the gel. Cracking buffer used was 62.5 mM Tris-Cl pH 6.8, 2 mM EDTA, 2% SDS, 40% sucrose and 1% bromophenol blue.

Gels for SDS-PAGE of phaseolin were pre-

TABLE 3. ORIGIN, IDENTIFICATION AND BIOLOGICAL STATUS OF THE 163 *P. POLYANTHUS* ENTRIES STUDIED.

Entry	Biological status	Origin	Phaseolin pattern	Alt (m)	Location		100 seed weight
G35015	C	MEX Veracruz	b		97.19W	19.48N	61.0
G35020	C	MEX Veracruz	b		96.29W	20.04N	59.0
G35141	C	MEX Veracruz	b		97.14W	19.46n	66.0
G35403	C	MEX Veracruz	b		97.02W	19.09N	82.9
G35434	C	MEX Veracruz	b	1700	97.03W	18.44N	84.3
G35458	C	MEX Veracruz	b	1944	97.19W	19.48N	90.5
G35654	C	MEX Veracruz	b	1750	97.05W	18.41N	68.0
G35054	C	MEX Hidalgo	b		98.20W	20.06N	62.0
G35056	C	MEX Hidalgo	b		98.20W	20.06N	58.0
G35058	C	MEX Hidalgo	b		98.20N	20.06N	59.0
G35059	C	MEX Puebla	b		98.03W	20.11N	50.0
G35060	C	MEX Puebla	b		98.03W	20.11N	88.2
G35061	C	MEX Puebla	b		98.03W	20.11N	56.8
G35062	C	MEX Puebla	b		98.03W	20.11N	61.0
G35063	C	MEX Puebla	b		98.03W	20.11N	64.0
G35136	C	MEX Puebla	b		97.22W	19.49N	75.0
G35338	C	MEX Puebla	b	1720	97.24W	19.54N	86.2
G35348	C	MEX Puebla	b	1660	97.35W	19.54N	83.2
G35349	C	MEX Puebla	b	1710	97.36W	19.58N	75.7
G35350	C	MEX Puebla	b	980	97.31W	20.32N	79.5
G35351	C	MEX Puebla	b	2025	97.31W	20.32N	75.3
G35380	C	MEX Puebla	d		97.58W	20.19N	73.4
G35452	C	MEX Puebla	b		97.35W	19.54N	78.2
G35453	C	MEX Puebla	b	885	97.31W	20.32N	74.0
G35460	C	MEX Puebla	b	980	97.39W	19.56N	61.0
G35462	C	MEX Puebla	b		97.38W	19.56N	77.0
G35467	C	MEX Puebla	b		97.38W	19.56N	76.0
G35472	C	MEX Puebla	b		97.35W	19.59N	72.0
G35473	C	MEX Puebla	b		97.35W	19.59N	74.2
G35481	C	MEX Puebla	b		97.35W	19.54N	73.0
G35004	C	MEX Oaxaca	b		90.13W	15.03N	67.0
G35122	C	MEX Oaxaca	b	2103	96.24W	17.00N	53.4
G35337	C	MEX Oaxaca	b	1600	96.53W	18.10N	78.7
G35414	C	MEX Oaxaca	b		96.30W	16.09N	76.0
G35415	C	MEX Oaxaca	b		96.30W	16.09N	78.5
G35420	C	MEX Chiapas	b	2150	92.40W	16.45N	81.5
G35428	C	MEX Chiapas	b		92.22W	16.50N	79.0
G35432	C	MEX Chiapas	b	2350	92.31W	16.49N	89.0
G35433	C	MEX Chiapas	b	2100	92.31W	16.49N	81.0
G35442	C	MEX Chiapas	b	2000	92.22W	16.50N	82.7
G35513	C	MEX Chiapas	b		92.40W	16.45N	81.4
G35515	C	MEX Chiapas	b		92.40W	16.45N	80.0
G35516	C	MEX Chiapas	b		92.43W	16.45N	70.0
G35524	C	MEX Chiapas	b		92.41W	16.47N	78.9
G35527	C	MEX Chiapas	b	2113	92.40W	16.45N	93.0
G35528	C	MEX Chiapas	b		92.43W	16.45N	78.7
G35529	C	MEX Chiapas	b		92.43W	16.45N	84.0
G35535	C	MEX Chiapas	b	1420	92.02W	16.07N	58.0
G35538	C	MEX Chiapas	b		92.02W	16.07N	68.0
G35559	C	MEX Chiapas	b	1980	92.31W	16.49N	76.0
G35560	C	MEX Chiapas	b	1980	92.31W	16.49N	98.0
G35563	C	MEX Chiapas	b, h	1760	92.22W	16.50N	93.0
G35632	C	MEX Chiapas	e	1400	91.52W	16.19N	80.0

<div align="center">TABLE 3. CONTINUED.</div>

Entry	Biological status	Origin	Phaseolin pattern	Alt (m)	Location		100 seed weight
S29924	W	GTA	e				38.4
S29925	W	GTA	f				29.2
DGD1684	C	GTA Huehuetenango	b	2450	91.28W	15.23N	63.0
DGD1685	C	GTA Huehuetenango	b	2450	91.28W	15.23N	60.0
DGD1686	C	GTA Huehuetenango	b	2450	91.28W	15.23N	60.0
G35569	C	GTA Huehuetenango	b	1500	91.46W	15.39N	60.0
DGD1650	C	GTA San Marcos	b	2670	91.49W	15.05N	67.0
DGD1652	C	GTA San Marcos	b	2650	91.49W	15.05N	70.0
DGD1660	C	GTA San Marcos	b	2570	91.49W	15.05N	70.0
DGD1661	C	GTA San Marcos	b	2560	91.49W	15.05N	71.0
G35083	C	GTA Totonicapan	b	2438	91.22W	14.55N	75.0
G35100	C	GTA Quiche	b	1981	91.07W	14.57N	78.2
G35034	C	GTA Quezaltenango	b	2333	91.31W	14.50N	89.4
G35035	C	GTA Quezaltenango	b	2333	91.31W	14.50N	75.0
G35336	C	GTA Quezaltenango	b	2475	91.31W	14.50N	87.3
G35631	C	GTA Quezaltenango	b	2500	91.31W	14.50N	88.0
G35041	C	GTA Retalhuleu	b	239	91.41W	14.32N	68.0
DGD1601	E	GTA Chimaltenango	b	2320	90.48W	14.36N	90.0
DGD1631	W	GTA Solola	b, c, g	1680	91.10W	14.46N	25.0
S26187	E	GTA Solola	b				25.5
G35616	C	GTA Baja Verapaz	b		90.26W	15.05N	55.0
G35008	C	GTA Alta Verapaz	b		89.59W	15.35N	26.0
G35617	C	GTA Alta Verapaz	b		90.19W	15.29N	42.0
DGD1605	E	GTA Sacatepequez	b	1920	90.44W	14.33N	57.0
DGD1608	W	GTA Sacatepequez	a	1550	90.42W	14.29N	19.0
DGD1622	W	GTA Sacatepequez	b	1940	90.50W	14.33N	23.6
DGD2444	E	GTA Sacatepequez	b	1730	90.51W	14.33N	30.0
G35036	C	GTA Sacatepequez	b	1530	90.44W	14.33N	57.3
G35042	C	GTA Sacatepequez	b	1530	90.44W	14.33N	74.8
DGD2458	E	GTA Guatemala	b	1730	90.35W	14.25N	42.8
DGD2460	W	GTA Guatemala	b	1800	90.35W	14.26N	28.0
G35614	C	GTA Jalapa	b		89.54W	14.38N	35.0
G35001	C	CRA	b				57.0
S23347	C	CRA	k				97.7
S23348	C	CRA	b				83.4
DGD2121	E	CRA San Jose	k	2000	83.58W	09.41N	53.0
DGD2138	E	CRA San Jose	b, k	1560	84.07W	09.52N	53.0
G35724	C	CRA San Jose	k				91.6
S23087	C	CRA San Jose	k				89.8
G35262	C	CRA Cartago	k	1650	83.52W	09.50N	64.8
G35728	C	CRA Cartago	k				92.5
S23351	C	CRA Cartago	k				75.4
S23353	C	CRA Cartago	k				79.6
S23354	C	CRA Cartago	k				106.9
S23358	C	CRA Cartago	k				60.7
G35317	C	VNZ Merida	k	3000			63.6
G35622	C	VNZ Merida	k		71.08W	08.24N	52.0
G35270	C	CLB	k				60.0
G35630	C	CLB	k				48.1
ANDES13	E	CLB Antioquia	k				90.0
G35359	C	CLB Antioquia	k		75.21W	05.58N	69.0
DGD2653	E	CLB Risaralda	b, k	2160	76.57W	05.07N	62.4
S26141	C	CLB Caldas	k	1840	75.56W	05.16N	67.7
G35360	C	CLB Valle	k				57.0

TABLE 3. CONTINUED.

Entry	Biological status	Origin	Phaseolin pattern	Alt (m)	Location	100 seed weight
G35372	C	CLB Valle	k		76.17W 03.33N	58.0
S24892	C	CLB Valle	k	1800	76.07W 03.25N	67.7
S24898	C	CLB Valle	k	2000	76.27W 03.40N	72.0
DGD602	E	CLB Cauca	k	1850	76.32W 02.28N	68.9
G35306	C	CLB Cauca	b		76.40W 02.20N	58.0
G35383	C	CLB Cauca	k	2470	76.32W 02.27N	63.0
G35625	C	CLB Cauca	k	2360	76.28W 02.20N	22.0
G35628	C	CLB Cauca	k	2540		65.0
S30313	C	CLB Huila	k		75.48W 01.59N	75.6
DGD1271	C	CLB Narino	k	2500	77.18W 01.15N	72.0
DGD1279	C	CLB Narino	k	1960	77.23W 01.18N	69.2
DGD1281	E	CLB Narino	k	1750	77.24W 01.26N	53.8
DGD1294	C	CLB Narino	k	1890	77.23W 01.23N	41.2
DGD1297	E	CLB Narino	k	2360	77.21W 01.18N	64.2
DGD1298	C	CLB Narino	b	2160	77.22W 01.19N	64.6
DGD1314	C	CLB Narino	k	1590	77.36W 01.18N	63.4
DGD1320	C	CLB Narino	k	2350	77.39W 01.08N	37.0
DGD1367	E	CLB Narino	k	2110	77.13W 01.33N	55.6
DGD1394	C	CLB Narino	b	2170	76.58W 01.31N	66.5
DGD1406	C	CLB Narino	b	2270	77.29W 01.59N	74.8
DGD1407	C	CLB Narino	k	2270	77.29W 01.59N	86.0
DGD1411	E	CLB Narino	k	2640	77.32W 00.40N	41.5
S24895	C	CLB Narino	b	2550		51.5
S24899	C	CLB Narino	k			60.0
DGD1424	C	CLB Putumayo	k	2010	76.50W 01.12N	58.0
DGD1425	C	CLB Putumayo	k	2010	76.50W 01.12N	60.0
G35373	C	CLB Putumayo	k	2000	76.55W 01.13N	57.0
DGD2657	C	ECD Imbabura	k	2400	78.09W 00.33N	77.4
DGD2721	E	ECD Carchi	k	2120	77.56W 00.24N	68.0
DGD2754	C	ECD Azuay	k	2440	78.56W 02.46S	56.7
DGD2770	E	ECD Chimborazo	k	1710	78.58W 02.16S	54.0
DGD2775	C	ECD Tungurahua	k	2080	78.32W 01.17S	65.0
DGD2779	C	PER Lambayeque	k	2185	79.24W 06.16S	63.3
DGD2800	C	PER Piura	k	1820	79.26W 05.15S	56.8
DGD2851	C	PER Piura	k	2100	79.27W 05.15S	62.6
DGD2853	C	PER Piura	k	1700	79.35W 05.23S	50.5
DGD713	C	PER Cajamarca	k	2180	78.31W 07.19S	44.3
DGD813	C	PER Cajamarca	k	2240	78.57W 07.07S	51.1
DGD1257	C	PER Cajamarca	k	2650	78.15W 06.54S	62.2
DGD1264	C	PER Cajamarca	k	1850	78.31W 06.16S	83.5
DGD1841	E	PER Cajamarca	k	2220	78.37W 06.26S	63.8
DGD1877	E	PER Cajamarca	k	2340	78.38W 06.27S	63.1
DGD1885	C	PER Cajamarca	k	2430	78.38W 06.27S	59.9
DGD1985	E	PER Cajamarca	k	2160	78.42W 06.14S	82.4
DGD2785	C	PER Cajamarca	k	1350	79.06W 06.53S	59.0
S29921	C	PER Cajamarca	k			54.3
DGD1212	E	PER Amazonas	k	2000	77.43W 06.15S	68.7
DGD1258	E	PER Amazonas	k	2430	77.48W 06.34S	57.8
DGD1259	E	PER Amazonas	k	1820	77.55W 06.20S	56.5
DGD1260	E	PER Amazonas	k	2050	77.32W 06.14S	59.0
DGD1261	E	PER Amazonas	k	2490	77.35W 06.13S	59.3
DGD1262	E	PER Amazonas	k	2030	77.43W 06.15S	61.7
DGD1263	E	PER Amazonas	i	1810	77.32W 06.13S	49.6
S22656	C	PER Amazonas	k			75.4

TABLE 3.   CONTINUED.

Entry	Biological status	Origin	Phaseolin pattern	Alt (m)	Location	100 seed weight
S25050	C	PER Amazonas	k			65.0
S25051	C	PER Amazonas	k			52.0

MEX = Mexico, GTA = Guatemala, CRA = Costa Rica, VNZ = Venezuela, CLB = Colombia, ECD = Ecuador, PER = Peru; C = cultivated, E = escaped, W = wild.

pared in a vertical slab apparatus. The slab gels used were 1.5 mm thick with 13.5% acrylamide in the running gel and 4% acrylamide in the stacking gel. Electrophoresis was performed in a 25 mM Tris-glycine buffer pH 8.3 with 0.1% SDS at 70 V until the tracking dye reached the separating gel; afterwards the voltage was increased to 180 V. The total run was about 12 hours (according to a methodology described by Hussain et al. 1988).

The gels were stained overnight with a Coomassie blue solution (0.25%) and excess of stain was removed by rinsing the gel with a destaining solution of methanol, acetic acid and distilled water (6:1:14). Two-dimensional IEF-SDS/PAGE was carried out as described by Anderson (1988). Phaseolin was silver stained following Blum et al. (1987) except that 4 g of sodium carbonate were used.

Voucher specimens have been deposited in BR, COL, MICH, US, USCG.

RESULTS

1. TAXONOMIC STATUS OF THE CULTIVATED FORM

Information from Folk Tradition

We will first consider the indigenous names of the two cultigens *P. coccineus* and *P. polyanthus* in those areas where both are grown (Table 2). Those names can be considered as representative since with the exception of the Sierra de Juárez in Oaxaca, Mexico (Hernández X. et al. 1959) and the Sierra de las Minas, in El Progreso, Guatemala (D. G. Debouck, personal observations, 1987), most of the places where *P. coccineus* and *P. polyanthus* are still grown sympatrically are listed. In most cases the two taxa are given different indigenous names. De Candolle (1883) favored the linguistic argument after careful checks when establishing the origin of cultivated plants. Because of the different names, it could be inferred that several groups of American Indians noticed morpho-physiological differences sepa-

rating both cultigens. For instance, when visiting the Sierra de Cuchumatanes, Huehuetenango, Guatemala in 1985, the Mam Indians pointed out to one of us (D. G. Debouck, personal observations, 1985) that *P. polyanthus* has to be handled as an annual crop because of killing frosts while *P. coccineus* will sprout spontaneously from March onwards. That difference is due to the presence of tuberous, perennial, conical root in *P. coccineus*. The root of *P. polyanthus* is large, fibrous, somewhat thickened and fleshy, but not tuberous. *P. polyanthus* differs from *P. coccineus* for the following characters (also reported by Delgado Salinas 1988): epigeal germination (hypogeal in *P. coccineus*), large, somewhat divergent, purple or white wings (large, somewhat overlapping, scarlet or white wings in *P. coccineus*), long, ciliate, narrow bracteoles exceeding the calyx (highly variable in size, shape and pilosity in *P. coccineus*), capitate, terminal stigma (always extrorse in *P. coccineus*), and large, rounded seeds with large orbicular hilum and frequently split placental tissue (small, elliptic, entire hilum in *P. coccineus*).

Table 2 shows the multiplicity and originality of names which we interpret to mean that the different ethnic groups have grown the two cultigens over a long time (since pre-Columbian times according to Hernández X. et al. 1959). Interestingly enough, Torres (1985) notes from the Chroniclers that in pre-Hispanic Mexico of nahuatl influence, *P. coccineus* was called "ayecocimatl" and *P. polyanthus* possibly "tepecimatl."

Outside of the areas with optimal environmental conditions for *P. polyanthus* or when asking mestizos, names become variable. In Suchitepéquez, on the Pacific slopes of the Cordillera Volcánica, Guatemala, sieva beans (*P. lunatus*) which progressively replace *P. polyanthus* are alternatively called "ixtapacál" or "piloy" (McBryde 1945; Standley and Steyermark 1946). "Juruna" is a common name given to *P. polyanthus* in Jalapa, Guatemala (Hernández X. et

TABLE 4. LATIN NAMES GIVEN CHRONOLOGICALLY TO THE FIFTH *PHASEOLUS* CULTIGEN WITH ORIGIN AND STATUS OF THE TYPE MATERIAL.

Name	Author	Year	Origin and status of material
Phaseolus dumosus	MacFadyen	1837	Jamaica; weedy
Phaseolus polyanthus	Greenman	1907	Mexico, Veracruz; weedy
Phaseolus flavescens	Piper	1926	Colombia, Caldas; weedy
Phaseolus harmsianus	Diels	1937	Ecuador, Tungurahua; weedy
Phaseolus coccineus ssp. *darwinianus*	Hernández X. & Miranda	1959	Mexico, Puebla; cultivated
Phaseolus coccineus ssp. *polyanthus*	Maréchal, Mascherpa & Stainier	1978	—

al. 1959) where it is occasionally grown (Debouck 1988). But that name is applied to *P. lunatus* by the Pocoman Oriental Indians also of Jalapa (Debouck 1988). *P. polyanthus* is frequently grown in the humid Cordilleras of Colombia above 1600 masl and is called there "cacha" or "petaco" (Hernández X. 1970; Schmit 1988; see also Table 6). *P. coccineus* is just present in some parts of Antioquia, Nariño and the upper Putumayo where it is called "petaco de año," "de vida" and "torta" respectively (Debouck, personal observations, 1985; Schmit 1988). Again, rural inhabitants distinguish between *P. coccineus* and *P. polyanthus*. One should, however, remember when considering these names that *P. coccineus* has most probably been introduced into Colombia, perhaps through Antioquia. In southern Colombia, "de vida" and "torta" are also common names for the large seeded lima beans, *P. lunatus* (Debouck, personal observations, 1985).

Information from Botanical Descriptions

We summarize chronologically in Table 4 the different Latin names given to the fifth *Phaseolus* cultigen as well as the biological status of the beans from which the original descriptions were most probably made. As stated by Delgado Salinas (1985), *P. dumosus* may well serve as a type for it. Four facts prevent us using the name of *P. dumosus*, however: the description of the pedicels is unclear in the original description by MacFadyen (1837); the number of seeds per pod is six in *P. dumosus* while it is usually three or four in Mesoamerican *P. polyanthus*; the absence of details about the hilum, a striking character of *P. polyanthus*, in an otherwise fairly good description; and finally the lack of any reference specimen deposited in a herbarium. That situ-

ation led to confusion: *P. dumosus* was later considered as a synonym of *P. lunatus* (Smartt 1973; van Eseltine 1931). Perhaps these authors were misled by the origin of *P. dumosus,* thinking that a Caribbean island was more likely to be the habitat for a tropical variant of *P. lunatus.*

On the other hand, *P. polyanthus* is an appropriate name because it has a type specimen (in GH) and a good description, although in Greenman's publication of 1907 there are no indications about root system, mature pod and seed. In Piper's paper (1926), in the group "*Phaseolus coccineus* and its allies," there is a possibility that *P. leucanthus* is also a *P. polyanthus,* however "pedicellar glands prominent"—a common trait of the American *Vigna* (Maréchal et al. 1978)—would prevent it being considered as *Phaseolus.* *P. flavescens,* described in the same group in the same paper and originally found in the region of Great Caldas, Colombia, would be another synonym of *P. polyanthus*; the fact that the distribution of weedy *P. polyanthus* is discontinuous through the Isthmus of Panama does not imply that we are automatically dealing with another species in the northern Andes. The same observation would be a fortiori valid for *P. harmsianus* since the distribution of *P. flavescens* in the Central Cordillera of the Andes is nearly continuous (see Fig. 1)! Again the lack of any reference herbarium specimen for *P. harmsianus* induced misconception: the Brüchers said in 1976 that Diels considered *P. harmsianus* as the progenitor of *P. vulgaris.*

One merit of the Hernández X. et al. (1959) study has been to draw attention to the presence of another bean crop in the fields of indigenous farmers and to propose an origin for it. After a biosystematical and cytological study, they concluded that the fifth cultigen was a natural hybrid

TABLE 5. LIST OF WILD AND WEEDY *P. POLYANTHUS* FOUND RECENTLY IN GUATEMALA.

Collection number	Department, District	Longitude	Latitude	Altitude masl
Wild forms:				
1608	Sacatepéquez, Santa María de Jesús	90°42'W	14°29'N	1550
1622	Sacatepéquez, San Miguel Dueñas	90°51'W	14°33'N	1940
1631	Sololá, Panajachel	91°10'W	14°46'N	1680
2460	Guatemala, Amatitlán	90°35'W	14°26'N	1800
Weedy forms:				
2444	Sacatepéquez, San Miguel Dueñas	90°51'W	14°33'N	1730
2458	Guatemala, Amatitlán	90°35'W	14°25'N	1730

between *P. coccineus* and *P. vulgaris* deserving the subspecific rank, and named it *P. coccineus* ssp. *darwinianus*. The idea that *P. vulgaris* and *P. coccineus* were interbreeding to some extent in Guatemala was put forward by the Russians Ivanov and Bukasov (according to Carter 1946). According to the scheme proposed by the Mexican researchers, the hybrid would have had *P. coccineus* as the female parent. Artificial crosses between *P. vulgaris* and *P. coccineus* have been attempted by more than a dozen researchers since Fermond's pioneering experiments (1855) and have had partial success when *P. vulgaris* was used as female (see Hucl and Scoles 1985; Smartt 1979, for reviews). The reciprocal cross with *P. coccineus* as the seed parent although difficult (Smartt 1970) has been made possible with the aid of embryo rescue techniques (Alvarez et al. 1981; Shii et al. 1982) and nutrient solution applied on the stigmatic surface (Ibrahim and Coyne 1975). Inbred progeny usually turns back to parental cytoplasm phenotypes with little introgression in the long run (Manshardt and Bassett 1984; Smartt 1970; Wall 1970; Wall and York 1957); crippled plants were also observed in the progeny (Alvarez et al. 1981; Smartt 1970; Thomas 1964).

These results from artificial crosses between modern cultivated genotypes would thus indicate that there is at the present time little probability of producing stable plant material resembling *P. coccineus* ssp. *darwinianus*. Either the fifth bean cultigen was produced by a cross between the two parental species when they were not too distant (perhaps as wild forms: Evans 1980; and below), or it has a different origin. Another possibility would be to consider *P. polyanthus* as a variant of *P. coccineus* without re-

ferring to any hybrid status. Some evidence to support this has recently been presented by Piñero and Eguiarte (1988) and will be discussed later on. According to that scheme, these authors logically keep the name *P. coccineus* ssp. *polyanthus* proposed by Maréchal et al. (1978). But in following this treatment, one would have to accept that the year-bean—the only vernacular name in English for cultivated *P. polyanthus* found so far (MacFadyen 1837)—has evolved from the wild scarlet runner, evidence of which is still lacking. Given this and the rule of anteriority in formal nomenclature, the less confusing name for the fifth cultigen for the time being is *Phaseolus polyanthus* Greenman.

2. DISTRIBUTION OF THE WILD FORM IN GUATEMALA

In 1978, Vakili and Freytag (Dr. George Freytag, pers. comm.), looking for wild forms of *P. coccineus* in Guatemala, discovered plants (VF-78-Guat. 47) with lavender colored flowers resembling wild *P. polyanthus*, in a forest between Patzicia and Panajachel, in the Department of Sololá. Another population was found the same year by Rolando Cojulun (Co-78-Guat.6) between San Andres Semetabaj and Panajachel, also in Sololá. During two field explorations carried out in 1985 and 1987 in search of new *Phaseolus* germplasm, Debouck and co-workers confirmed these early findings (Table 5 and Fig. 2) with four additional collections from other places (Debouck 1986, 1988; Debouck and Soto 1988). It is known by rural inhabitants as "piligue de monte" and serves as occasional forage for horses of loggers (D. G. Debouck, personal observations, 1987).
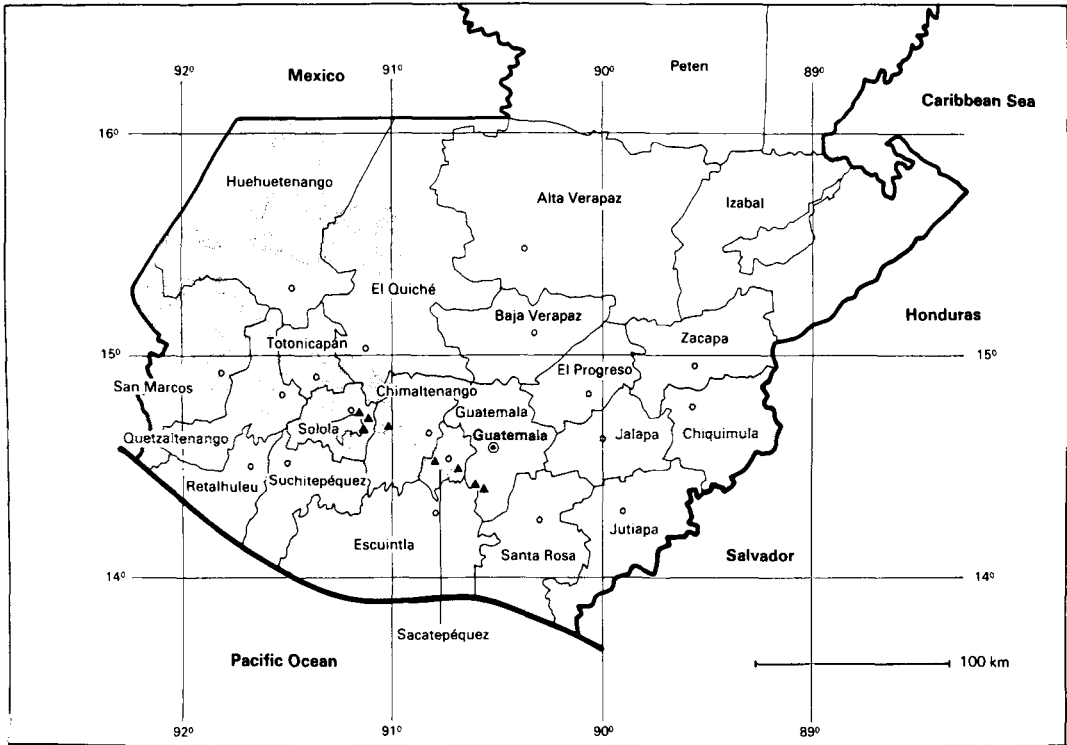
These plants are understory vines up to 10 m

Fig. 2. Distribution of the wild *P. polyanthus* in Guatemala on the basis of available records. The dotted area corresponds to the tropical montane rain forest.

high growing in one of the numerous variants of the montane rain forest (according to the vegetation classifications by Beard 1944; Breedlove 1973; Steyermark 1950; Wagner 1964). Such a forest has two tree strata of about 20 m and 10 m high; it contains vines such as *Ipomoea* sp., *Cucurbita* sp., and *Passiflora* sp. The trees generally have simple, mesophyllous leaves, are covered with numerous epiphytes (mainly Bromeliaceae) and grow in deep, rich, organic soils, derived from late Tertiary and Pleistocene volcanic ash.

The habitat range of wild *P. polyanthus* extends from 1500 to 1900 masl. From indirect sources (Anonymous 1972) and the type of vegetation, one could expect there an average temperature of 16–22°C and 2000–3000 mm rainfall/year with a drier period from December to March. As can be seen in Fig. 2, that habitat is partly contiguous to the tropical montane rain forest as defined elsewhere (Anonymous 1983). The other bordering forest is a less humid variant of the montane rain forest called "Bosque húmedo montano bajo subtropical" (Anonymous 1983).

The distribution of wild *P. polyanthus* is extremely narrow on the basis of the present findings and would be concentrated only in central southwestern Guatemala (an area between 90°30′W and 91°30′W, and 14°30′N and 14°50′N), since the following transects explored in the same part of Guatemala in order to find more populations have so far yielded none: Quezaltenango-Almolonga-Zunil-Sta María de Jesús, San Marcos-Palo Gordo-San Rafael Pie de la Cuesta-El Rodeo, Tejutla-San Miguel Ixtahuacán, Totonicapán-Malacantancito and Guatemala-Mataquescuintla.

3. Presence of Weedy and Feral Forms

In 1987, in central Guatemala, two populations of apparently wild *P. polyanthus* (*DG Debouck & JJ Soto* # 2444 in Sacatepéquez and # 2458 in Guatemala; see Table 5) were found in two areas of disturbed natural vegetation (clearings of the primary tropical rain montane forest). The first one, # 2444, was growing close to the wild population found in 1985 (# 1622) and had white flowers; its 100 seed weight was 30 g. The second one, # 2458, had lavender flow-
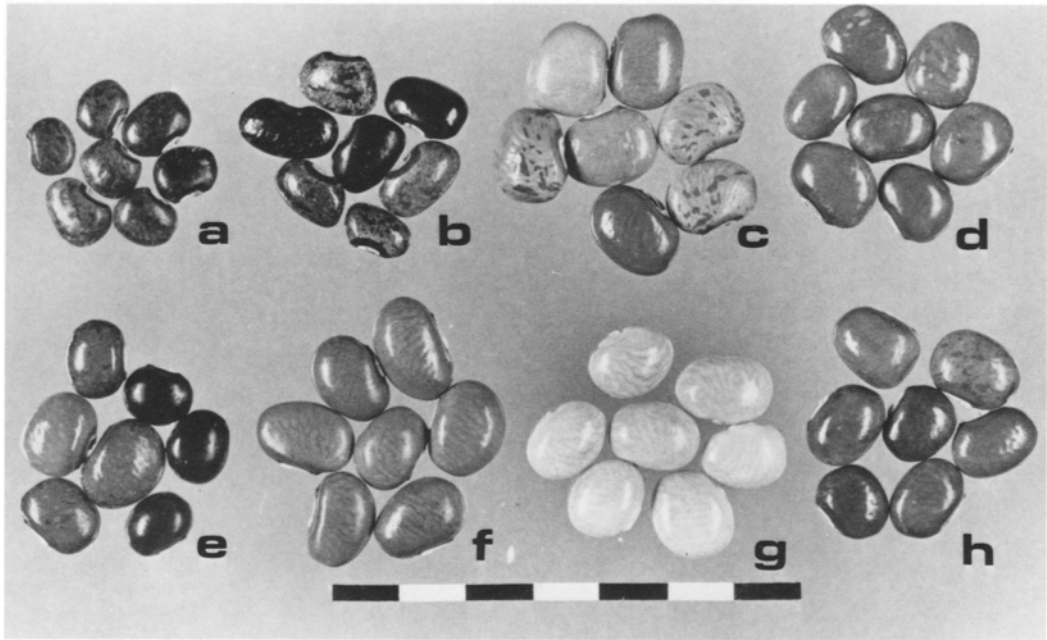
Fig. 3.   Seeds of different populations of *P. polyanthus* with different biological status and from different origins. Upper row: **a**: wild, DGD-1631, from Guatemala; **b**: weedy race, DGD-2458, from Guatemala; **c**: escaped, DGD-2653, from Colombia; **d**: escaped, DGD-1877, from Peru. Lower row, all cultivated: **e**: DGD-1685, from Guatemala; **f**: DGD-1650, from Guatemala; **g**: DGD-1406, from Colombia; **h**: DGD-2779, from Peru (scale: one bar = 1 cm).

ers and larger seeds (100 seed weight 43 g; see Fig. 3b) than the normal wild type (100 seed weight 24 g; see Fig. 3a), with different color backgrounds: bayo, pink, brown and solid black. These variants could be explained by the natural variation within natural wild populations (this would be the case with # 2444 if we assume that the slight increase in seed weight is not significant), or could be interpreted as the result of natural crossing with cultivated *P. polyanthus* growing in the vicinity.

The increase in seed size and the number of color variants in # 2458 would favor the second hypothesis. *P. polyanthus* has indeed been reported as a preferentially allogamous species (Schmit and Baudoin 1987) and cultivated *P. polyanthus* was observed in the vicinity of the wild populations during our field work, namely in Aldea Chimachoy, Paramos, Chimaltenango, within a 4–8 km radius of the wild population # 1622.

In our view, populations # 2444 and 2458 should be considered as weedy races resulting from natural crosses between wild and cultivated forms. It should be noted that they were distrib-

uted on the edge of the wild habitats where slash-and-burn agriculture is still practiced (Debouck 1988; Sanders 1985). We would thus have a "wild-weed-crop complex" for this crop similar to that observed for *P. vulgaris* in the Andes (Debouck et al. 1989c) and for *P. lunatus* in northern Peru (Debouck et al. 1987).

Beside these weedy races, scattered groups of *P. polyanthus* can be found in Mesoamerica growing wild in different kinds of secondary vegetation replacing the montane rain forest. They have white or lilac flowers, and yellow or chestnut seeds, but differ little from the same races often cultivated nearby by the American Indians and rural mestizos. These populations could be named feral. They have been observed in Veracruz, Mexico (Piper 1926), in Chimaltenango and Sacatepéquez, Guatemala (D. G. Debouck, personal observations, 1985) and in San José, Costa Rica (D. G. Debouck, personal observations, 1987).

A similar situation prevails in northern South America. There between 1600 and 2400 masl, in the variants (almost everywhere disturbed) of the montane rain forest, small populations of *P.*
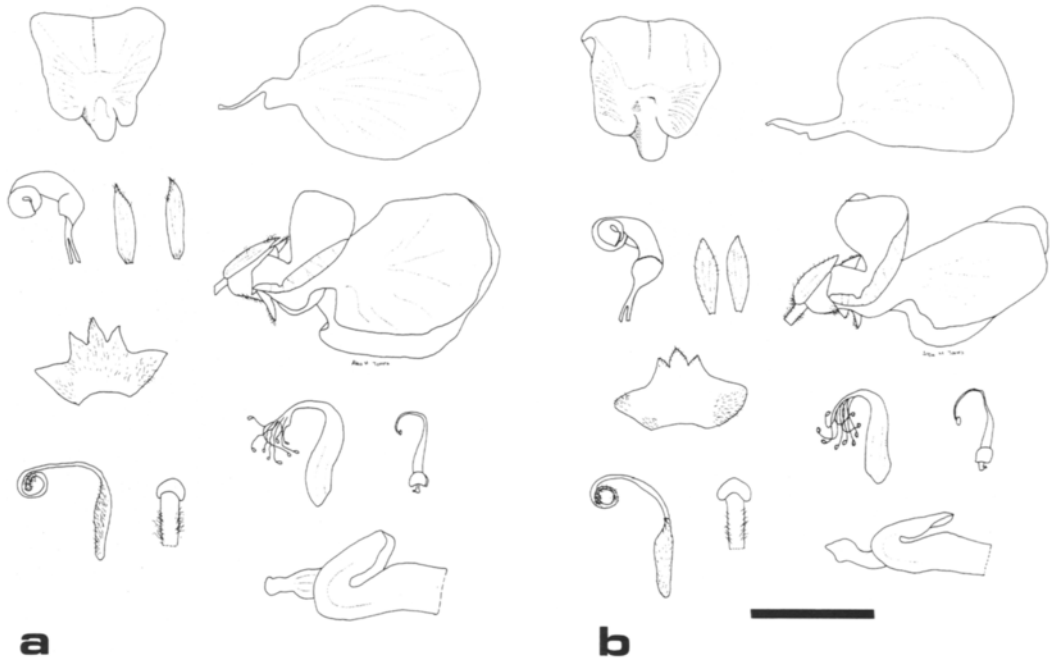
Fig. 4. Floral parts of: a, *P. flavescens* (*D. G. Debouck & V. Schmit 2653, from the type locality in Colombia*), and b, wild *P. polyanthus* (*D. G. Debouck & J. J. Soto 1631, from Sololá, Guatemala*). Scale: bar = 1 cm, for all parts excepting stigma tip and base of vexillar stamen.

polyanthus with white flowers and yellow seeds can be observed. They are present in the western Cordillera of Venezuela as "murutungo" beans (Berglund-Brücher and Brücher 1974). On the slopes of the Cerro Tatamá, between the departments of Choco and Risaralda in Colombia (the type locality of *P. flavescens*), we found *P. polyanthus* # 2653 (see Fig. 3c) growing wild in old secondary rain forest with *Cecropia* (Debouck and Schmit 1989).

The flowers of the *P. flavescens* form and the wild Guatemalan type are shown in Fig. 4a and 4b respectively. They are almost identical, with minute differences in the lower lip of the calyx and in the basal part of the wing. In Ecuador, *P. polyanthus* is found growing wild in recent clearings of the primary rain forest west of Nono in Pichincha province (Debouck et al. 1989b) as well as around the Tungurahua volcano (D. G. Debouck, personal observations, 1989, and Diels 1937). In Peru, it is distributed along the eastern slopes of the Andes, from the palm rain forest in Amazonas (D. G. Debouck, personal observations, 1985) down to the banks of the Urubamba River in northern Cuzco (Debouck 1987). On the western slopes of the Andes, its distri-

bution as an escaped plant starts in Piura and reaches to southwestern Cajamarca (D. G. Debouck, personal observations, 1989). There, because of the effects of the Humboldt current, the western mountainous ranges are less humid and feral *P. polyanthus* often behaves as an annual, senescing and drying after the first seed set.

The presence of escaped, feral *P. polyanthus* in secondary rain forest in South America, the morphological similarity between this type and the cultivated types, as well as the vernacular names in the Andean region (see Table 6) especially south of Colombia, all point to an introduction from elsewhere. The linguistic argument would support a recent introduction from Colombia southwards into the Andean region, down to northern Cuzco. Alternatively, one could hypothesize a more ancient introduction from Mesoamerica into Colombia. At this stage, what needs to be determined is: 1) whether the wild form found in Guatemala is similar to the cultivated Mesoamerican *P. polyanthus* or not, and 2) whether the feral forms found in South America (a good prototype of which might be *P. flavescens* from Colombia) are different from that particular wild Mesoamerican form.

TABLE 6.   VERNACULAR NAMES OF *P. POLYANTHUS* IN THE ANDEAN REGION.

Country, province	Name	Source
Venezuela, Merida	Murutungo	Berglund-Brücher and Brücher 1974
Colombia, Antioquia	De Vida	Schmit 1988
Colombia, Risaralda	Petaco	Debouck and Schmit 1989
Colombia, Valle	De Vida	Schmit 1988
Colombia, Huila	Cacha	Hernández X. 1970
Colombia, Cauca	Cacha, De la tierra	Schmit 1988
Colombia, Nariño	De(l) año, torta	Debouck, pers. observ., 1985
Colombia, Putumayo	Tranja	Debouck, pers. observ., 1985
Ecuador, Ibarra	Popayán	Debouck et al. 1989b
Ecuador, Chimborazo	Frejol perenne	Diels 1937
Ecuador, Cuenca	Dauleño	Debouck, pers. observ., 1989
Peru, Piura	Toda la vida	Debouck, pers. observ., 1989
Peru, Amazonas	Toda la vida	Debouck, pers. observ., 1985
Peru, Cajamarca same	Toda la vida, jaeno, forastero	Schmit 1988; Debouck, pers. observ., 1985
Peru, Junín	Frijol colombiano	Debouck 1987
Peru, Apurimac	Pacay colombiano	Debouck 1987

4. BIOCHEMICAL ANALYSES

The gels in 1-dimensional SDS-PAGE (Fig. 5, 6, 7) show four major proteinic fractions with molecular weights of around 45, 33, 28, and 24 kd. According to what has been observed in *P. vulgaris* (Brown et al. 1981b; Osborn 1988) and *P. coccineus* (Durante et al. 1989), these fractions were tentatively classified as phaseolin, lectin I, lectin II and albumin respectively.
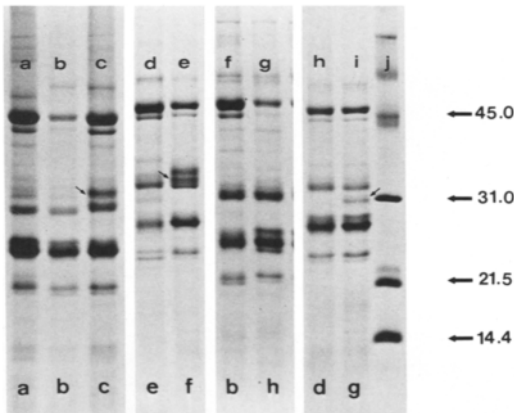
Fig. 5. One-dimensional SDS/PAGE gels of total seed protein of *P. polyanthus*: patterns of Mesoamerica. **a**: 'a', wild, DGD-1608, from Guatemala; **b**: 'b', wild, DGD-1622, from Guatemala; **c**: 'c', wild, DGD-1631, from Guatemala; **d**: 'e', wild, S29924, from Guatemala; **e**: 'f', wild, S29925, from Guatemala; **f**: 'b' and **g**: 'h', both of cultivated, G35563, from Mexico; **h**: 'd', cultivated, G35380, from Mexico; **i**: 'g', wild, DGD-1631, from Guatemala; **j**: protein marker.

Our results in 1-dimensional SDS-PAGE (Fig. 5, 6, 7 and Table 3) show first the great similarity between all populations of the range of distribution independent of their origin and biological status. The small variation in 1-dimensional patterns for the four major proteinic fractions allowed us to classify the 356 individuals of the 163 accessions of *P. polyanthus* into ten different patterns (Tables 3 and 7). The seed storage protein patterns of *P. polyanthus* were classified using the Roman alphabet as they differ from the phaseolin patterns described elsewhere for the common bean (Gepts et al. 1986), for the tepary bean (Schinkel and Gepts 1988) and for the lima bean (Maquet et al. 1990). Eight patterns, classified as 'a' to 'h' (Fig. 5) are present in all accessions from Mesoamerica, and in two accessions from Colombia. Two patterns, called 'k' and 'i', are present in the northern Andes and in the majority of accessions from Costa Rica. Frequencies of patterns as well as countries of origin are given in Table 7. It is obvious that pattern 'b' is dominant in Mesoamerica (present in 115 of the 127 individuals from Mexico, Guatemala and Costa Rica), while the 'k' pattern is dominant in the northern Andes (present in 145 of the 154 individuals from Venezuela, Colombia and Peru). The 'b' pattern is also dominant in the wild ancestral populations of Guatemala, which definitively display the highest number of patterns (Fig. 5a to e). Finally one should note that the 'i' pattern (Fig. 6b), the second most common pattern in the Andean region, is dis-
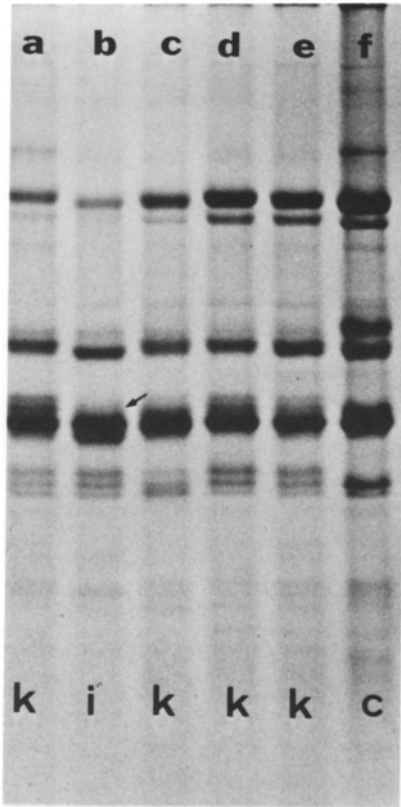
Fig. 6. One-dimensional SDS/PAGE gels of total seed protein of *P. polyanthus*: patterns of the Andes. **a**: 'k', escaped, DGD-1261, from Peru; **b**: 'i', escaped, DGD-1263, from Peru; **c**: 'k', escaped, DGD-1411, from Colombia; **d**: 'k', escaped, DGD-1367, from Colombia; **e**: 'k', escaped, DGD-1281, from Colombia; **f**: 'c', wild, DGD-1631, from Guatemala.

Fig. 7. One-dimensional SDS/PAGE gels of total seed protein of *P. polyanthus*: comparison between the Andes and Mesoamerica: **a**: wild P. vulgaris, DGD-1962, from Peru; **b**: 'k', cultivated, S26141, from Colombia; **c**: 'k', cultivated, S30313, from Colombia; **d**: 'k', escaped, DGD-1841, from Peru; **e**: 'k', DGD-1877, escaped, from Peru; **f**: 'k', escaped, DGD-1985, from Peru; **g**: 'b', escaped, S26187, from Guatemala; **h**: 'e', wild, S29924, from Guatemala; **i**: 'f', wild, S29925, from Guatemala; **j**: 'b', cultivated, G35403, from Mexico; **k**: 'b', cultivated, G35420, from Mexico; **l**: 'g', wild, DGD-1631, from Guatemala; **m**: protein marker.

P. polyanthus (Fig. 8d). One will note that in 2-dimensional IEF-SDS/PAGE, there is also a one polypeptide difference between the wild *P. polyanthus* of Guatemala and the weedy form of Colombia (compare Fig. 8a with Fig. 8b).
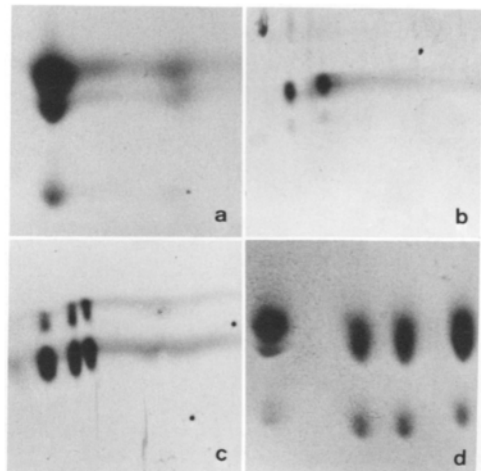
played by a single accession from the department of Amazonas, Peru.

The phaseolin fraction is not at all polymorphic in the different populations of *P. polyanthus* in 1-dimensional SDS-PAGE. It consists of two bands of around 48 and 45 kd, similar to the beta and gamma bands found in *P. vulgaris* (Bliss and Brown 1983; Osborn 1988). The phaseolin pattern found in *P. polyanthus* in this study is indeed somewhat similar to the pattern 'Inca' described for wild *P. vulgaris* (Koenig et al. 1990) from western Cajamarca, Peru. In 2-dimensional IEF-SDS/PAGE (Fig. 8) however, it lacks one polypeptide that is present in the wild *P. vulgaris* from Cajamarca (compare Fig. 8a and 8b with Fig. 8c). Further confirmation of that difference in the phaseolin type is obtained when analyzing a 50% mixture of the extracts of *P. vulgaris* and

Fig. 8. Two-dimensional IEF-SDS/PAGE gels of phaseolin of *P. polyanthus* (**a**: DGD-1631, wild, from Guatemala; **b**: DGD-2653, escaped, from Colombia) and of *P. vulgaris* L. (**c**: DGD-1962, wild, from Peru), and of a 50% mixture of the same extracts of *P. polyanthus* (DGD-1631) and *P. vulgaris* (DGD-1962) (**d**).

TABLE 7. GEOGRAPHIC FREQUENCY DISTRIBUTION OF SEED PROTEIN PATTERNS AMONG *P. POLYANTHUS* MATERIALS.

Country	Status	Accessions	Patterns										Individuals	%*
			a	b	c	d	e	f	g	h	k	i		
MEX	C	53		83		1	1			1			86	24.2
GTA	C	21		30									30	8.5
	E	4		4									4	1.1
	W	7	13	31	5		1	1	1				52	14.6
CRA	C	11		2							9		11	3.1
	E	2		1							18		19	5.3
VNZ	C	2									11		11	3.1
CLB	C	27		5							61		66	18.5
	E	7		3							21		24	6.7
ECD	C	3									14		14	3.9
	E	2									2		2	0.6
PER	1	14									27		27	7.6
	E	10									9	1	10	2.8
Total		163	13	159	5	1	2	1	1	1	172	1	356	
%*			3.6	44.6	1.4	0.3	0.6	0.3	0.3	0.3	48.3	0.3		

MEX = Mexico, GTA = Guatemala, CRA = Costa Rica, VNZ = Venezuela, CLB = Colombia, ECD = Ecuador, PER = Peru; C = cultivated, E = escaped, W = wild; * = % of total number of individuals.

The lectin I fraction displays two bands, the thicker of which is around 32 kd, in most accessions. One variant, the 'c' pattern (Fig. 5c), has been found in only one wild population, DGD-1631, from Sololá, Guatemala. Another variant with three polypeptides, called 'f' (Fig. 5e and 7i), has been found in a single individual of a Guatemalan wild form. Finally, the lectin I fraction offered another variant, 'g', with a polypeptide of 31 kd (Fig. 5i and 7l); again it was found only in the wild population DGD-1631.

The lectin II fraction usually displays four or five bands (with a major protein concentration at around 27 kd), according to whether there are two or three bands in the albumin fraction respectively. There is a single exception to this general observation: the 'i' pattern found in a single accession, DGD-1263 of Amazonas, Peru (Fig. 6b), which lacks the upper band of 28 kd.

The most striking difference that can be related to geographic origin, which allowed us to separate the Mesoamerican and the Andean materials, can be observed in the albumin fraction. The Mesoamerican beans commonly have two groups of polypeptides of about 24 kd, while the North Andean types have three. Only eight individuals, representing six accessions from Colombia, displayed two bands, while none from Mesoamerica but eleven accessions from Costa Rica displayed three bands. Interestingly enough,

one of these six accessions is DGD-2653, found at the type locality of *P. flavescens*.

DISCUSSION

Three points emerge from these results. First, the wild form discovered in Guatemala and the cultivated forms present either in Mesoamerica or in the northern Andes are so similar at the morphological, ecological and biochemical levels that one can conclude that the former is the ancestor of that cultigen, thus adding a fifth cultigen to the genus *Phaseolus* sensu stricto (Maréchal et al. 1978). The sole morphological differences are in seed and perhaps pod characteristics, pointing out the wild and ancestral status of the Guatemalan material; a parallel evolution can be observed in the other four bean cultigens (for *P. vulgaris*: Delgado Salinas et al. 1988; Brücher 1988; for *P. lunatus*: Baudoin 1988; Debouck et al. 1987; for *P. coccineus*: Delgado Salinas 1988; and for *P. acutifolius*: Nabhan and Felger 1978). On the basis of the characters indicative of evolutionary changes mentioned by Smartt (1988), particularly the relative difference in seed size between the ancestral form and its derived cultigen, one could consider *P. polyanthus* a species with a higher unrealized evolutionary potential than the other four bean cultigens.

Second, the above-mentioned similarity raises the question of the origin of the wild ancestor of

P. polyanthus. Three hypotheses can be considered. First, some genetic affinities between wild *P. polyanthus* and wild *P. vulgaris* or wild *P. coccineus* (V. Schmit, unpublished results) cannot rule out the hypothesis of Hernández X. et al. (1959) that this taxon results from a cross between *P. coccineus* and *P. vulgaris.* Indeed the three wild forms, without being fully sympatric, can be found in natural vegetation in central Guatemala (above San Miguel Dueñas in Sacatepéquez: D. G. Debouck, personal observations, 1985, 1987) within a radius of 12 km from each other. But natural introgression has not so far been reported to occur between these three wild taxa in that part of Guatemala. On the other hand, Evans (1980) claimed that *P. coccineus* and *P. vulgaris* would cross more easily as wild than as cultivated parents, even when using *P. coccineus* as female. Was the product of these crosses similar to wild *P. polyanthus* and was it genetically stable? Unfortunately that aspect was not then considered in the crossing program (Miranda Colin and Evans 1973). Another explanation to be considered after the results presented by Piñero and Eguiarte (1988) is that *P. polyanthus,* this time as a wild form, would be a variant of wild *P. coccineus.* The dendrogram presented by Sullivan and Freytag (1986) after an electrophoretic analysis of several *Phaseolus* species with the use of SDS/PAGE on seed protein, also shows a high similarity index between *P. polyanthus* and different wild forms of *P. coccineus.* As further support for this hypothesis, one should mention the natural hybrids between cultivated *P. polyanthus* and *P. coccineus* discovered by one of us (D. G. Debouck, personal observations, 1985) in the upper Putumayo, Colombia. According to that scenario, *P. coccineus* is becoming a heterogeneous species with subspecies such as *glabellus* (Piper) Delgado (Delgado Salinas 1988), and *polyanthus* (Greenm.) M.M.S. (Maréchal et al. 1978), which are quite distinct from each other. Worth mentioning here is the fact that subspecies *glabellus* lacks most of the phaseolin present in other taxa of the *P. coccineus* complex (Schmit and Debouck 1990). Is *P. coccineus* not too heterogeneous vis-à-vis species such as *P. angustissimus* A. Gray, *P. esperanzae* Seaton, *P. filiformis* Bentham, *P. microcarpus* Mart.? A third possibility overlooked so far is to consider a common phylogeny for the three taxa, *P. vulgaris, P. coccineus* and *P. polyanthus,* that is they would have evolved as wild forms, long before bean

domestication, from a common ancestor, either still present somewhere in Mesoamerica and uncollected so far or already extinct. This possibility gains some support when the existence of other related taxa within the *P. coccineus* complex is taken into account such as the recently collected and identified *P. costaricensis* (G. F. Freytag, pers. comm.; Debouck et al. 1989a). Natural hybrids have also been observed between the latter and *P. polyanthus* (Debouck et al. 1989a). According to this scheme, *P. vulgaris* would have separated very early from the bulk of *P. coccineus* with later separations of *P. glabellus* and then *P. polyanthus.* Separations are still taking place today within the *P. coccineus* complex. One way to decide between these three hypotheses would be to use a common set of clones (random genomic or cDNA) for RFLP mapping on organelles DNAs (chloroplast or mitochondrial DNA) because they are maternally inherited. We would thus avoid skewed information due to outcrossing, frequent in this group of plants (Delgado Salinas 1985; Schmit and Baudoin 1987).

Third, as judged on electrophoretic patterns, the variability is higher in the few wild forms collected so far than in the cultivated ones. Pattern 'b', predominant in the wild forms, is also predominant in all cultivated forms present in Mesoamerica, a clear indication that the Mesoamerican *P. polyanthus* derive from the wild ancestor present in Guatemala. The fact that two additional patterns ('d' and 'h') displayed by two cultivated accessions from Mexico are absent in the wild ancestor is in our view more an indication that the analysis of these wild forms has been so far insufficient rather than the result of a particular kind of genetic diversity present in the cultigen and absent in the wild progenitor. Taking this into account, one could claim that there is also a "founder effect" (as defined by Ladizinsky 1985) in the year-bean, that is a reduction of genetic variability upon domestication, as has already been described in other bean species (for *P. vulgaris*: Gepts et al. 1986; Gepts and Debouck 1991; Debouck and Tohme 1989; for *P. lunatus*: Debouck et al. 1989d; for *P. acutifolius*: Schinkel and Gepts 1988). A substantial part of genetic diversity would thus have been left behind in the wild, even if the existence of a wild-weed-crop complex has reduced the founder effect, as has been suggested for *P. vulgaris* in the Andes (Debouck et al. 1989c).

The predominant 'k' pattern in the Andes is lacking in the wild forms of Guatemala. That difference consists of one additional polypeptide group in the lectin II and albumin fraction. This is the sole difference between the Andean beans and the Mesoamerican ones, since the most common morphotype in the Andes, with yellow seeds and white flowers (Delgado Salinas 1988), is also present in Mesoamerica (compare Fig. 3f with 3h). There is thus no correlation between that morphotype and the electrophoretic pattern 'b' or 'k'. Furthermore it should be noted that the 'k' pattern is already present in the Costa Rican materials, particularly in the escaped ones. There, as in Colombia, the 'b' pattern is still present but at a low frequency. This could be interpreted thus: as we move from Guatemala southwards through the montane rain forest where *P. polyanthus* can maintain itself in clearings, etc., the 'k' pattern increases in frequency perhaps because it is more competitive in those environmental conditions. Similar clinal variation has been observed in wild barley for seed storage protein (Nevo et al. 1983) and allozymes (Nevo et al. 1979) and for allozymes in *Avena barbata* (Clegg and Allard 1972) and wild common bean (Koenig and Gepts 1989) in relation to environmental parameters.

A higher number of morphological variants is present in the cultigen in Mesoamerica than in the northern Andes. This fact, together with the information on vernacular names, points to a domestication in Guatemala and a subsequent diffusion towards the humid highlands of Chiapas, Oaxaca, Puebla and Veracruz, and towards Costa Rica and the northern Andes. The vernacular names currently used in some parts of Ecuador and Peru (see Table 6) even suggest a post-Columbian and rather recent introduction of that crop in these areas, in contrast to the situation prevailing in Mexico. The lower variability in the northern Andes (the presence of white seeded cultivars, Fig. 3g, in Colombia and Peru is a noteworthy exception, perhaps due to skewed sampling) as compared with Mesoamerica is compatible with that scheme and could be explained by either the presence of the wild-weed-crop complex in Mesoamerica or the presence of *P. coccineus* in that region. Both are absent from the Andes.

Of particular significance are these natural hybrids from the Putumayo displaying large variability in seed color and pattern in the *P. poly-*

anthus seed phenotype. Again, information from chloroplast DNA analysis might help here. We would thus have a single species and a single gene pool, but with a clinal genetic drift taking place between Mesoamerica and the northern Andes. The absence of any true wild *P. polyanthus* in the northern Andes but vigorous feral forms growing in secondary vegetations, together with very little morphological and biochemical variation prevents us putting forward the alternative hypothesis of a separate domestication of *P. polyanthus* in Mesoamerica and of *P. flavescens* in the northern Andes.

Finally, one could ask why the American Indians domesticated a fifth bean cultigen. Although we lack any archaeological records for that bean species (its ecological range is not conducive to the preservation of plant material over long periods of time), its larger seed size compared with the other bean cultigens tentatively suggests a more recent domestication. Of the three *Phaseolus* species present in the tropical montane rain forest and related plant communities (*P. macrolepis* Piper, *P. polyanthus* Greenm., *P. tuerckheimii* Donn. Smith) (Delgado Salinas 1985; and author's observations), the year-bean, because of its larger seeds, was perhaps the most attractive candidate to be grown in association with maize at intermediate altitudes in rainy habitats. As an indirect consequence of these origins, *P. polyanthus* may offer resistance to many fungal diseases such as *Ascochyta* (Schmit and Baudoin 1987), of particular interest for future bean breeding.

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