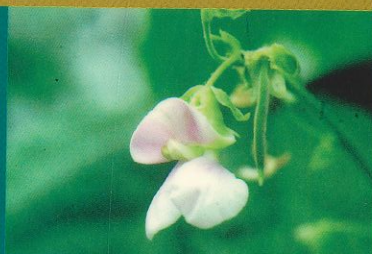


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Genetic resources of *Phaseolus* beans: patterns in time, space, and people

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1. INTRODUCTION

Phaseolus beans, although often a key source of proteins to poor people, are not renowned for high yields as compared to other tropical legumes such as soybean, groundnut or pigeon pea. Understanding limitations to yield and adaptation would be the logical starting point, and it is highly significant in author's view that three recent contributions about bean yield in different commercial classes (Beaver 1999; Brick & Grafton 1999; Singh 1999a) focus on analyses of constraints and sources of genetic diversity to solve these constraints. Many sources of useful traits have been already identified in beans (Singh 1992, 1999b). However, insufficient resistance has been reported in common bean for the following: ascochyta blight, common bacterial blight, bean fly, drought, leafhopper, low temperatures, root rot, web blight, and white mold. *P. acutifolius* has been found tolerant to drought (Markhart 1985), heat (Garver 1934), and resistant to common bacterial blight (Zapata et al. 1985). Resistance to root rots has been found mainly in *P. coccineus* (Dickson & Boettger 1977). *P. angustissimus* and *P. filiformis* have been found tolerant to low temperatures (Balasubra-

manian et al. 2000). *P. polyanthus* has been found resistant to ascochyta blight (Schmit & Baudoin 1992), bean fly (Schmit & Baudoin 1987) and white mold (Hunter et al. 1982). Resistance to leafhopper has been found in *P. lunatus* (Wolfenbarger & Slesman 1961). In reporting these sources of useful traits in alien germplasm, and in order to make full use of them, the breeder currently faces three questions: 1) is the searched trait totally lacking in any of the bean cultigens?, 2) in which other species has the trait its maximum expression?, and 3) can that (these) species be crossed with the target species?

Answering these questions forces us to examine the availability of *Phaseolus* genetic resources, the extent to which these genetic resources have been evaluated, and the information about genetic compatibility across different species. Debouck (1999) reported the number of accessions currently available from CIAT genebank: less than 2,000 accessions exist in the primary gene pool of common bean as wild forms, and less than 1,000 accessions exist in its secondary gene pool (Tables 1 and 2). Clearly, germplasm is still missing for many species, starting with wild forms of the primary gene pools. Several species are still to be evalua

Table 1—Gene pools of the different *Phaseolus* cultigens (after Debouck 1999)

Primary Gene Pool (GP1)	Secondary Gene Pool (GP2)			Tertiary Gene Pool (GP3)		
	Close	Intermediate	Distant	close	intermediate	distant
<i>P. vulgaris</i>	<i>P. costaricensis</i>	<i>P. polyanthus</i>	<i>P. coccineus</i>		<i>P. acutifolius</i>	<i>P. filiformis</i>
<i>P. polyanthus</i>	<i>P. coccineus</i>	<i>P. costaricensis</i>	<i>P. vulgaris</i>			
<i>P. coccineus</i>	<i>P. polyanthus</i>		<i>P. vulgaris</i>			
<i>P. acutifolius</i>		<i>P. parvifolius</i>			<i>P. vulgaris</i>	
<i>P. lunatus</i>	<i>P. pachyrrhizoides</i>		<i>P. maculatus</i>	<i>P. jaliscanus</i>	<i>P. salicifolius</i>	

Table 2.—List of *Phaseolus* species organized by possible phylums (adapted from Debouck 1999) and their geographic distribution

Taxa	Geographic distribution (state or province)
Section Chiapasana (sensu Delgado 1985) <i>chiapasanus</i> Piper	Oaxaca, Chiapas
Section Phaseolus Macrophylum of common bean and scarlet runner <u>Sub-phylum of common bean</u> <i>costaricensis</i> Freytag & Debouck <i>polyanthus</i> Greenman* <i>vulgaris</i> L.*	Alajuela, Cartago, San José; Boquete, Chiriquí Qzigo, Chintgo, Sololá, Sacatepéquez, Guatemala Chihuahua to San Luis through Central America and Andes
<u>Sub-phylum of scarlet runner</u> <i>coccineus</i> L.*	Chihuahua to Jalapa and El Paraíso
<u>Phylum of tepary bean</u> <i>acutifolius</i> Asa Gray* var. <i>acutifolius</i> var. <i>latifolius</i> var. <i>tenuifolius</i> <i>parvifolius</i> Freytag	Arizona, New Mexico; Sonora, Sinaloa Arizona, Sonora Arizona, New Mexico; Sonora, Sinaloa Durango, Nayarit; Jalapa
<u>Phylum of Lima bean</u> <i>jaliscanus</i> Piper <i>lunatus</i> L.* <i>maculatus</i> Scheele <i>marechalii</i> Delgado <i>mollis</i> Hook. & Arn. <i>pachyrrhizoides</i> Harms <i>polystachyus</i> Britt., Stern & Pogg <i>ritensis</i> Jones <i>salicifolius</i> Piper <i>xolocotzii</i> Delgado	Jalisco Sinaloa to Chaco; Imbabura to Cajamarca Ariz, New Mex, Tex; Chih, Dur, Zac, Pue México, Morelos, Puebla Galapagos Loja; Cajamarca, Junín, Cuzco; Cochabamba; Chuquisaca; Jujuy Québec; N York, Minn, Penn, Illi, Missou, Okla, Carol, Flor Ariz; Sonora, Chihuahua, Durango Sinaloa Oaxaca
<u>Phylum of wild beans with rugose testa</u> <i>angustissimus</i> Asa Gray <i>carteri</i> Freytag & Debouck <i>filiformis</i> Benthams	Arizona, New Mexico, Texas; Sonora Baja California Calif, Ariz, New Mex, Tex; Baja California, Sonora

<u>Phylum of <i>P. pedicellatus</i></u>	
<i>esperanzae</i> Seaton	México, Puebla
<i>grayanus</i> Woot. & Standl.	Arizona, New Mexico; Chihuahua, Durango
<i>laxiflorus</i> Piper	Hidalgo, Veracruz
<i>oaxacanus</i> Rose	Oaxaca
<i>pedicellatus</i> Benthham	Hidalgo, México, Nuevo León, Queretaro, San Luis Potosi
<i>polymorphus</i> S. Watson	San Luis Potosi, Guanajuato
<i>purpusii</i> Brandegee	San Luis Potosi
<u>Phylum of <i>P. neglectus</i></u>	
<i>altimontanus</i> Freytag & Debouck	Tamaulipas
<i>neglectus</i> Hermann	Nuevo León
<u>Phylum of <i>P. microcarpus</i></u>	
<i>microcarpus</i> Mart.	Durango, Guerrero, Puebla, Oaxaca
<i>minimiflorus</i> Norvell ex Freytag & Debouck	Sinaloa, Colima
<u>Phylum with $2n=2x=20$</u>	
<i>leptostachyus</i> Benthham	Nuevo León, Chihuahua through Guatemala to San José
<i>macvaughii</i> Delgado	Jalisco
<i>micranthus</i> Hook. & Arn.	Jalisco
<u>Isolated phylums</u>	
<i>glabellus</i> Piper	Tamaulipas, San Luis Potosi, Hidalgo, Oaxaca, Chiapas
<i>leptophyllus</i> G. Don	Guerrero
<i>macrolepis</i> Piper	Chimaltenango, Sololá, Sacatepéquez
<i>oligospermus</i> Piper	Chiapas; Guate, Sta Rosa; Fco Morazán; Cartago, Sn José
<i>sonorensis</i> Standley	Sonora
<i>talamancensis</i> Debouck & Torres	San José, Limón
<i>tuerckheimii</i> Donnell-Smith	Chiapas; Progreso, Sacatepéquez, Sololá; Fco Morazán; San José
Section <i>Minkelsersia</i> (sensu Lackey 1983; including <i>Alepidocalyx</i> M.M.S.)	
<i>amblyosepalus</i> (Piper) Morton	Durango
<i>nelsonii</i> Maréchal, Mascherpa & Stainier	Jalisco, México, Michoacán, Oaxaca
<i>parvulus</i> Greene	Arizona, Chihuahua, Durango
<i>pauciflorus</i> Sessé & Mociño	Chihuahua, DF, Durango, México, Michoacán
<i>perplexus</i> Delgado	México, Jalisco
<i>plagiocylis</i> Harms	Nuevo León
<i>pluriflorus</i> Maréchal, Mascherpa & Stainier	Jalisco, DF, México, Michoacán
<i>tenellus</i> Piper	Michoacán
Section <i>Xanthotricha</i> (sensu Delgado 1985)	
<i>esquicensis</i> Freytag	Chiapas
<i>gladiolatus</i> Freytag & Debouck	San Luis Potosi
<i>hintonii</i> Delgado	Jalisco, Mexico
<i>magnilobatus</i> Freytag & Debouck	Durango, Jalisco
<i>xanthotrichus</i> Piper	Chiapas; Chimtgo, Sac, Sta Rosa; Alajuela, Sn José
<i>zimapanensis</i> (Delgado) Jaaska	Hidalgo, Nvo León, Queretaro, San Luis Potosi

Note: * species with cultivated forms

ted for gene pool relationships; in Table 1, some squares might be left in blank or some species might be added. Possibilities for widecrossing in beans has been recently reviewed (Debouck 1999), and secondary gene pools of each cultivated species are wider than initially thought. For instance, *P. costaricensis* has been added to the gene pools of *P. vulgaris* and that of *P. polyanthus*. *P. parvifolius* has been added to the gene pool of *P. acutifolius*, and *P. pachyrhizoides* has been added to the gene pool of *P. lunatus*. On the other hand, agronomic evaluation has not been systematic nor complete, even though large sets of germplasm have been evaluated for reaction to anthracnose (Pastor-Corrales et al. 1995), angular leaf spot (Guzmán et al. 1995), and rust (Stavely & Pastor-Corrales 1989). In this context, it is useful to understand better mechanisms by which gene pools have come into being, and have been shaped by biological and anthropological forces.

2. THE BROAD PICTURE: A NATURAL GROUP OF NEW WORLD LEGUMES

The genus *Phaseolus* (subtribe Phaseolinae, tribe Phaseoleae, family Leguminosae) as currently accepted (Delgado Salinas 1985; Lackey 1983; Maréchal et al. 1978a,b) is of Neotropical origin, and has approximately 50 species, distributed into four sections (Table 2) (Debouck 2000).

Over the past two centuries, over 400 species have been named, often with poor description and/ or lacking good type specimens. Reviews by Piper (1926) and Urban (1928) have contributed to clarifications about generic delimitations, infrageneric grouping, and synonymy. The works by Burkart (1952), Wilczek (1954), Verdcourt

(1970), and Lewis & Delgado Salinas (1994) have helped to a progressively narrowing definition of *Phaseolus*, as separated from related legume genera such as *Macroptilium*, *Misanthus*, *Ramirezella*, and *Vigna*. The culmination of these taxonomical delimitations of *Phaseolus* was presented at the Legume Conference of Kew in 1978 (Lackey 1981; Maréchal et al. 1981). The infrageneric classification proposed by Delgado Salinas (1985), that is, the splitting of the genus into four sections, has been adopted here. *P. chiapasanus* with its very large flowers and all its parts turning black on drying, probably deserves a section on its own. Because of the additional coil of the keel, the *Xanthotricha* might be grouped together. With shorter pedicels as compared to the calyx and very short or absent bracteoles, the *Minkelersia* form another group.

So, we are now able to indicate if a legume is a *Phaseolus*; we are however much less certain how many *Phaseolus* species exist and which are they. Delgado Salinas (1985) has made an exhaustive review of *Phaseolus*, and has confirmed the existence of 36 species. Germplasm explorations carried out in Mexico, Central America and the Andes over the last two decades have brought new species to Science, such as *P. costaricensis* (Freitag & Debouck 1996). On the basis of hybridological evidence (reviewed by Debouck 1999) and several studies with help of molecular markers, namely those of Delgado Salinas et al. (1999), Fofana et al. (1999), Jaaska (1996), and Jacob et al. (1995), an updated tentative list of *Phaseolus* species can be proposed as well as their possible phylums (Table 2). That list is not a definitive one, and additional field work might likely reveal the presence of new taxa. The author considers significant the recent discovery of two new species of *Phaseolus* in Costa Rica, while the inventory was relatively well advanced

and established as early as 1937 (Standley 1937)! We will now comment on the phyla which we define here as infrageneric groups that share a common genetic evolutionary ancestry.

3. SPECIATION CAN'T STOP: THE FORMATION OF BEAN PHYLA, PATTERNS IN TIME

Molecular data, namely of cpDNA, analysis (Delgado Salinas et al. 1993, 1999) have shown that *Phaseolus* is monophyletic and that it has not come into being by convergence of separate legumes of the subtribe. The formation of the original branches of American Phaseolinae is likely to have occurred in northern "Central America" by early or mid Tertiary (Eocene-Oligocene) (Sousa Sánchez & Delgado Salinas 1993). By then, Central America did not exist as known today; it could have been a series of large volcanic islands still separated from South America (Coates 1997; Rich & Rich 1983). Authors (Coates 1997; Graham 1993, 1999a; Rich & Rich 1983) generally agree that the Isthmus of Panama was closed only about 3.5-2.5 million years ago in the late Pliocene. *Macroptilium* that can be considered as a sister group of *Phaseolus* (Delgado Salinas et al. 1999; Maréchal et al. 1978b), probably separated lately from *Phaseolus*, and migrated southwards into South America. *Macroptilium* has most of its diversity in the lowland savannas of South America (Barbosa Fevèreiro 1986-87), and has likely entered back into Mexico in the late Pliocene (Sousa Sánchez & Delgado Salinas 1993), once the continental bridge was closed. The original *Phaseolus*, once differentiated from *Macroptilium*, *Misanthus*, *Strophostyles*, and the American *Vigna* subgenus *Sigmoidotropis*, itself split into several subgroups or phyla. This evolu-

tion likely occurred in southern North America during the late Tertiary.

It is worth examining first whether recent molecular data confirm the subgeneric classification of *Phaseolus* proposed elsewhere (Delgado Salinas 1985; Lackey 1983; Maréchal et al. 1978a). ITS DNA sequence information (Delgado Salinas et al. 1999) separated the *Minkelersia* as a group, although within the large *Phaseolus* section. In the same study, *Chiapasana* and *Xanthotricha* were grouped together, also with other *Phaseolus* species such as *P. tuerckheimii* and *P. oligospermus*. The morphologically distinctive traits of *P. chiapasanus* and of the *Xanthotricha* could have been thus somewhat overemphasized. The sections initially defined by Delgado Salinas (1985), i.e. *Chiapasana*, *Phaseolus*, *Minkelersia*, and *Xanthotricha*, however make sense in author's view for the field taxonomist. In spite of the fact that the study by Delgado et al. (1999) revealed *P. microcarpus* as a completely isolated taxon (to which in author's view should be added *P. minimiflorus*), it would not make sense to elevate *P. microcarpus* as another section in the genus. This statement is also supported by the works of Fofana et al. (1999) and Jacob et al. (1995). These two taxa, in spite of the diminutive size of their reproductive parts, share the same taxonomical traits as the other taxa of the *Phaseolus* section. We shall now examine this section with greater detail.

Another clade separated by ITS DNA sequence information (Delgado Salinas et al. 1999) includes species such as *P. grayanus*, *P. pedicellatus*, *P. neglectus*, and *P. glabellus*. *P. glabellus* has been considered as a taxon close to (Maréchal et al. 1978b) or as a subspecies of *P. coccineus* (Delgado Salinas 1988). Other evidences (biochemical: Schmit & Debouck 1990; ecological: Schmit et al. 1996; molecular: Schmit et al.

1993, Llaca et al. 1994) strongly suggest it to be far away from the *P. coccineus* complex. Debouck (2000) considered it as relatively isolated in the section *Phaseolus*, while Delgado Salinas and co-workers (1999) see it as very close to *P. grayanus*. As indicated elsewhere (Debouck 1991, 1999), *P. esperanzae*, *P. grayanus*, *P. laxiflorus*, *P. pedicellatus*, *P. polymorphus*, *P. purpusii*, and *P. oaxacanus* should be considered as separate species, not as varieties or synonyms (Delgado Salinas 1985). This clade apparently differentiated only in Mexico, mostly around the Sierra Madre Oriental, with migrations to the south (Oaxaca: *P. oaxacanus*), the Eje Volcánico (*P. esperanzae*), and the dry Central Plateau (*P. purpusii*).

The study of ITS DNA sequences (Delgado Salinas et al. 1999) acknowledges *P. angustissimus* and *P. filiformis* as belonging to a separate group (to which *P. carteri* likely should be added: Debouck 1999). They share in common the rugose testa of their seeds, and thrive in dry habitats. While *P. filiformis* extends from around the Gulf of California into the Sonoran Desert of the USA, *P. carteri* is restricted to southern Baja California and *P. angustissimus* to Arizona, New Mexico, western Texas, and Chihuahua. This group has been shown to be quite distant from *P. vulgaris* and related taxa (hybridological data reviewed by Debouck 1999, 2000).

As expected, the study by Delgado Salinas et al. (1999) identifies a small group of wild beans with $2n = 2x = 20$ (while all other species have $2n = 2x = 22$), that includes *P. leptostachyus* and *P. micranthus*. This group would also include *P. macvaughii* with that chromosome number (Mercado Ruaro & Delgado Salinas 1998), a taxon unknown to the author. It is interesting to note in the former study that *P. micranthus* is indeed included within the *P. leptostach-*

us, and this result would confirm its varietal status (Delgado Salinas 1985).

Interestingly, the ITS DNA sequence analysis (Delgado et al. 1999) separated the group of Lima bean from that of *P. maculatus*, although they are closely related. After an extensive review of the hybridological information, Debouck (1999) has shown that the group of *P. maculatus* with species distributed today in the USA and Mexico would be the tertiary gene pool of *P. lunatus*. This conclusion is also supported by analysis of cpDNA polymorphisms (Fofana et al. 1999). The work by Delgado Salinas et al. (1999) supports the view presented elsewhere (Debouck 1996; Maquet et al. 1999) that *P. mollis* and *P. pachyrrhizoides* of western South America belong to the secondary gene pool of *P. lunatus*. There would thus be a strong justification to identify a clade with the Lima bean and nine wild species in the section *Phaseolus*. Its history could have been two-fold: this clade was formed in southern North America, and later a smaller phylum including the future Lima bean migrated into the Andean region. Speciation there led to the formation of *P. lunatus*, *P. mollis* and *P. pachyrrhizoides*, and with the closing of the Isthmus of Panama the wild form of Lima bean re-colonized several parts of the Neotropics, particularly the lowlands.

The last clade identified by Delgado et al. (1999) includes the subgroups of *P. acutifolius*, *P. polyanthus* and *P. coccineus*, and *P. vulgaris*. The hybridological evidence (reviewed by Debouck 1999) has long recognized the tepary bean as a remote gene pool of common bean. The ITS study (Delgado et al. 1999), using total genomic DNA, confirms the analysis done by Hervieu and co-workers (1994) on mtDNA that shows *P. coccineus*, *P. polyanthus* and *P. vulgaris* sharing a common ancestral stock. The former study fails however to reveal the

close relationship between *P. costaricensis*, *P. polyanthus* and *P. vulgaris*, as shown by cpDNA polymorphisms (Schmit et al. 1993). Interestingly, the former study shows a close relationship between *P. costaricensis* and *P. polyanthus*; field work (Debouck et al. 1989a) has indeed shown that these two species can hybridize when in contact. Gepts and co-workers (2000a) indicated that the time at which *P. coccineus* and *P. vulgaris* separated could be 2 millions years (transition from Pliocene to Pleistocene) and that the two major gene pools of common bean separated 500,000 years ago. On the other hand, Kami et al. (1995) and Gepts et al. (2000a) after sequencing genes coding for different seed storage proteins - phaseolin and α -amylase inhibitor, respectively - have shown that wild *P. vulgaris* existing in southern Ecuador and northern Peru (Debouck et al. 1993) could be close to the ancestral stock of this species as compared to the other two well known gene pools. Is it possible that the western slopes of the Andes of southern Ecuador and northern Peru is the cradle of wild common bean? One should note that the taxa of the *P. vulgaris* phylum on the basis of cpDNA polymorphisms are all distributed in Mesoamerica, from western Mexico (*P. albescens*: Ramírez Delgadillo & Delgado Salinas 2000) to western Panama (*P. costaricensis*: Freytag & Debouck 1996) through western Guatemala (*P. polyanthus*: Schmit & Debouck 1991). A conciliatory hypothesis would be that the formation of this phylum took place in eastern Mesoamerica, and that the third gene pool of *P. vulgaris* is a remnant of that early evolutionary process.

This last clade (Delgado et al. 1999) separates clearly from the other clades of the section *Phaseolus*, namely the one including the Lima bean, confirming previous studies (hybridological: Le Marchand & Maréchal 1977; molecular: Fofana et al. 1999, Jacob et

al. 1995; palynological: Maréchal et al. 1978b). The distance between the clade including the common bean and that of the Lima bean can be explained by reproductive isolation due to different evolutions in different land masses: the phylum of *P. vulgaris* likely evolved in southeastern Mesoamerica, while the phylum of *P. lunatus* evolved in the northern Andes. At the closing of the Isthmus of Panama, both species migrated in opposite directions. Some patterns in time have thus been established, that will reflect millennia afterwards in combining ability between gene pools and species. An unanswered question is the exact number of phyla within the genus: two could be seen as a minimum (Fofana et al. 1999), although this study did not include all available taxa, but likely could be 5-6. Is the number of taxa within each phylum indicative of the duration of speciation, or is it indicative of a more rapid and active speciation since the original splitting? Is the largest number of taxa within the *P. lunatus* phylum indicative of a longer evolution? According to Maréchal et al. (1978), pollen of *P. lunatus* could be seen as primitive. Baudet (1978) considered within the *Phaseoleae* species thriving in savannas as derived and more evolved as compared to species thriving in forest habitats. Few species of the genus (e.g. *P. acutifolius*, *filiformis*, *P. lunatus*, *P. microcarpus*, *P. vulgaris*) are typical colonizers of savannas, with a strong trend towards annualism, epigeal germination, fibrous roots, and a reproductive strategy oriented towards the sole production of seeds.

4. DISTRIBUTION OF WILD BEANS AS THE FIRST AMERINDIANS FOUND THEM, PATTERNS IN SPACE

Some authors (Lynch 1999; Zeitlin & Zeitlin 2000) mention the arrival of first

Amerindians about 15,000 years ago, perhaps even earlier (Schobinger 1994), at the moment of the last and ending ice period 'Wisconsin', from northeastern Siberia (Cavalli-Sforza et al. 1994; Crawford 1998). Over such a short period of time, it is unlikely that the distribution of wild beans was profoundly different from the one known today. In the USA, because of the late effects of the Laurentide Ice Sheet (Graham 1999b), the distribution of *P. polystachyus* was probably restricted to the southern and warmer parts of its range. The extension of this species into Minnesota (MacMillan 1892) and Québec (Rydberg 1965) is probably recent together with the warming up of this period of the Quaternary. For the same reasons, several species now entering the Southwest (i.e. *P. angustissimus*, *P. grayanus*, *P. ritensis*), were likely confined into northern Mexico. In Mesoamerica, species now occupying upper volcanic ridges (e.g. *P. macrolepis*, *P. tuerckheimii*) probably extended into valleys. With the warming, populations of *P. coccineus* were progressively confined to higher summits, and the resulting geographic isolation increased speciation processes and differences between populations. Given the extension in longitude of Mesoamerica, in the alternations of cooling-warming and dry-wet cycles, it was possible for species to extend through regions (i.e. Isthmus of Tehuantepec, central Nicaragua, Isthmus of Panama) otherwise not accessible. In the Andes, climatic changes drastically affected the altitudinal distribution of plant species (Cardich 1985), and the distribution of wild beans rather oscillated in altitude with little extension in longitude. To the west, the extension of wild beans topped against the Pacific, while to the east the increasingly wet and hot climate of the Amazon Basin prevented it. Distribution of wild *Phaseolus* species has been presented elsewhere (Debouck 1991,

1999, 2000; Delgado Salinas 1985); we shall hereafter concentrate on those giving cultivated forms.

Wild *P. vulgaris* extends from southern Chihuahua, Mexico to San Luis Argentina in mountains of mid elevations (800-2,800 masl); this represents a range of approximately 8,000 km (Toro Ch. et al. 1990). In Mexico, it is distributed along the Sierra Madre Occidental, the Eje Volcánico, and several mountainous ranges of Oaxaca and Chiapas. It is widely distributed throughout central Guatemala, and has been reported from Honduras, El Salvador, Nicaragua, and Costa Rica (Debouck et al. 1989a; Delgado Salinas et al. 1988). In the Andes, its range extends from western Venezuela through Colombia, Ecuador, Peru (Debouck et al. 1989b, 1993), Bolivia (Freyre et al. 1996), and northwestern Argentina (Burkart & Brücher 1953). Along that huge arc of distribution, slight morphological differences in seeds, racemes, and bracteoles have been observed (Burkart & Brücher 1953; Gentry 1969; Gepts & Debouck 1991). There are also physiological differences with respect to photoperiod and temperature requirements, but definite evidence about the organization of genetic diversity of wild *P. vulgaris* came from molecular markers, and first from polymorphisms in seed storage proteins (Gepts & Bliss 1986; Gepts et al. 1986; Koenig et al. 1990). Differences between wild populations of different geographic origins were shown with the help of isozymes (Debouck et al. 1993; Koenig & Gepts 1989), RAPDs (Freyre et al. 1996), RFLPs (Becerra Velásquez & Gepts 1994; Khairallah et al. 1992), and AFLPs (Tohme et al. 1996) markers. Two major gene pools - one located in Mesoamerica and another one in the Central Andes - were indeed confirmed with these markers, up to suggest a var. *mexicanus* and a var. *aborigineus*, respectively (Delgado Salinas et al. 1988). In

addition, unique genetic variability was also disclosed for Colombia (Chacón S. et al. 1996; Tohme et al. 1996), and for the region encompassing southern Ecuador and northern Peru (Chacón Sánchez et al. 1999; Khairallah et al. 1992; Tohme et al. 1996). Would have had wild common bean the opportunity to evolve without humans in both Mesoamerica and the Andes for another thousand of years, two more species would exist in the *P. vulgaris* phylum! Interestingly, the duration of evolution of the gene pools in the wild has been long enough (500,000 years according to Gepts et al. 2000a) as to favour a specialized evolution of diseases associated to these beans. A co-evolution has been indeed demonstrated for angular leaf spot (Guzmán et al. 1995), anthracnose (Geffroy et al. 1999), and perhaps rust (Sandlin et al. 1996), a wind borne highly versatile obligate pathogen.

The existence of two major gene pools already in the wild long before domestication raises the question of their origin. The two gene pools are distinct at morphological, biochemical and molecular level. However, the differences are small, and indicate that wild common bean is not an artificial assemblage of convergent legumes but a single species with starting differentiation along a huge distribution. An additional evidence of this differentiation (or speciation) is obtained when crossing wild forms between themselves: there are fertility and recombination problems (Koinange & Gepts 1992). Two scenarios are possible: either one gene pool is a direct derivative of the other one, or the two gene pools come both from an ancestral stock. Along the former scenario, the diversity found so far in both gene pools would suggest that the Andean gene pool is a derivative of the Mesoamerican one rather than the opposite. The former scenario is a plausible one,

given the fact that the highest diversity of species is found in Mesoamerica not in the Andes. In addition, the *P. vulgaris* phylum has several species distributed in Mexico and Central America (Debouck 1999, 2000). However, a group of wild common beans found in the western Andes of Ecuador and northern Peru displays unique genetic diversity. Its phaseolin 'I' is a simple one in comparison to other types (Koenig et al. 1990). Allozyme diversity has also shown its uniqueness (Koenig & Gepts 1989). Its mtDNA has been shown to be more and uniquely variable (Khairallah et al. 1992). There is thus evidence to consider this form as close to the ancestral branch of *P. vulgaris* (Gepts et al. 2000a; Kami et al. 1995; Tohme et al. 1996). The work by Geffroy et al. (1999) also identifies an ancestral resistance gene cluster to anthracnose that existed prior to the separation of the two major gene pools.

Wild *P. lunatus* - the wild form with small seeds - extends from Sinaloa, Mexico to Salta Argentina, through Central America, northern Colombia, and eastern Peru; this represents a range of approximately 7,000 Km (Gutiérrez Salgado et al. 1995; Maquet & Baudoin 1997). The wild form with slightly larger seeds seems restricted to the western Andes of Ecuador and northern Peru, from Imbabura to Cajamarca (Gutiérrez Salgado et al. 1995; Maquet & Baudoin 1997). Another wild form exists in the Andes of Boyacá, Colombia (Toro et al. 1993). There is morphological variation, namely in seed and flower, along the range of distribution of wild Lima bean (Debouck et al. 1987). Two major gene pools have been demonstrated, exploiting polymorphisms in lectins (Debouck et al. 1989c; Gutiérrez Salgado et al. 1995), isozymes (Lioi et al. 1998; Maquet et al. 1994), RAPDs (Fofana et al. 1997; Nienhuis et al. 1995), PCR-RFLPs (Fofana et al. 1999), and AFLPs (Caicedo et al. 1999). When

asking about the origin of such gene pools, a situation similar to the one of common bean may exist in wild Lima bean: both gene pools would not derive directly from each other but from an ancestral branch. Molecular evidence accumulated so far (Caicedo et al. 1999; Fofana et al. 1999) would favour the concept of a single species rather than two evolutionary legumes converging into a single morphotype. There would be thus an ancestral branch of wild Lima bean before the formation of two different gene pools (Debouck 1996), still to be found in the northern Andes. By judging the differences between wild forms of gene pools of each species, it is tempting to assume a longer separation of Lima bean gene pools as compared to common bean.

Wild *P. coccineus* extends from Chihuahua, Mexico to Jalapa, Guatemala, and El Paraíso, Honduras (Debouck 2000; Debouck & Smartt 1995). Because it frequently hybridizes with cultivated forms (Delgado Salinas 1988), true wild *P. coccineus* are uneasy to find. In addition, a lot of morphological variation is found in wild populations. Perhaps some variants deserve some recognition at taxonomic level (such as subsp. *griseus*: Delgado Salinas 1988), while for others it might be simply too early at this stage of their evolution to make such recognition.

Wild *P. acutifolius* extends from Arizona and New Mexico to Sinaloa, Mexico, through the Sierra Madre Occidental and the western part of the Central highlands (Chihuahua, Durango) (Debouck & Smartt 1995; Nabhan & Felger 1978).

Wild *P. polyanthus* seems restricted to the western volcanic range of Guatemala, from Guatemala to Quezaltenango (Schmit & Debouck 1991); its extension to the west needs further exploration. Particularly relevant here is the recently described species *P. albescens* (Ramírez Delgadillo & Delgado

Salinas 2000): is it a form of wild *P. polyanthus* distributed in western Mexico, or is it something else?

Wild *P. vulgaris* and *P. lunatus* are present in both Central and South America. *P. polyanthus* also exists in the Andes, but as an introduced - and successful - weed in secondary humid forests, likely in historic times (Schmit & Debouck 1991). Under reasonable disturbance, it is possible that the former two species - as wild forms - have experienced an expansion because of humans over the past 15,000 years. They are both however floristic elements of climax forests: subhumid montane forests in the case of wild common bean, and subhumid premontane and lower dry tropical forests in the case of wild Lima bean. Contrary to what has been claimed elsewhere (Delgado Salinas 1985), domestication does not seem responsible for the presence of these two species in South America. Their unique polymorphisms at DNA level between regions and as compared to the cultivated forms as we have seen above are an indication of their diversity and long presence before humans entered South America. Their ecological success and adaptation in disturbed habitats have been a positive factor towards domestication, but not the only one. One should note that species with an important range of distribution and broad ecological adaptation such as *P. leptostachyus* and *P. microcarpus* have not been domesticated, perhaps because of their very small seeds. Species with comparable range of distribution such as *P. acutifolius* and *P. coccineus* have indeed been domesticated, as was *P. polyanthus* with a smaller distribution. Obviously, wild endemic bean species such as *P. amblyosepalus*, *P. leptophyllus*, *P. mollis* or *P. plagiocylix* were not domesticated. So, some patterns in space were established at the moment the Amerindians progressively inhabited the Americas; an

immediate consequence of such patterns is the unequal domestication of *Phaseolus* species.

5. FIVE SPECIES MODIFIED BY DOMESTICATION, PATTERNS IN SELECTION PRESSURES

New World agriculture was developed independently in Mesoamerica and in South America by hunter-gatherers becoming agriculturists (Lynch 1999; MacNeish 1992). If all pre-Columbian peoples can be traced back to three or four major immigration movements (Cavalli-Sforza et al. 1994; Crawford 1998), thousands of years however separated the hunting phase from agriculture and settled life. At the beginning of agriculture, plants becoming domesticated were likely brought from the surroundings, not great distances. Five species of *Phaseolus* have been brought into the human domain and modified by domestication and are cultivated today: *P. acutifolius*, *P. coccineus*, *P. lunatus*, *P. polyanthus*, and *P. vulgaris*. Biologically, they are all coming from wild forms still present in different parts of the Neotropics. The differences between the cultivated forms and the wild ones are spectacular indeed, but are all - perhaps with the exception of the neutrality towards photoperiod - directly or indirectly related to the harvested part, and the genetical basis of these changes is rather narrow (Gepts & Debouck 1991; Koinange et al. 1996). This means that within each species cultivated and wild forms belong to the same gene pool (Debouck & Smartt 1995; Smartt 1980), and can continue to exchange genes. Complete genetic compatibility between both forms of each species has been shown through artificial crossing in common bean (Kornegay & Cardona 1991; Weiseth 1954), in Lima bean (Baudoin 1990), in tepary (O. Toro, personal

communication), and in year-bean (Schmit & Baudoin 1993). Useful traits present in the wild gene pool, such as the tolerance to bruchids (Osborn et al. 1988) or increased photosynthesis (Lynch et al. 1992), can thus be easily transferred to the cultivated forms. The fact that gene flow can happen between wild and cultivated forms (Beebe et al. 1997; Gepts et al. 2000b) will also contribute to the formation of races (Singh et al. 1991). Without a certain level of gene flow between these forms and within landraces, the formation of races and the maintenance of genetic diversity within landraces would be difficult to explain (Martin & Adams 1987; Singh et al. 1991).

The five bean species were not domesticated in the same place, although their wild forms are sometimes found sympatrically (Table 3), and probably were not domesticated at the same time. In contrast to cereals of the Fertile Crescent where barley, einkorn, and emmer could have been domesticated together (Zohary & Hopf 1993), antinutritional factors play against the simultaneous domestication of *Phaseolus* species. If early farmers find a mutant with less antinutritional factors, they are likely to keep it and favour it during the next generations, and the mutation is likely to occur once at a place, much less simultaneously in two different species. The same would apply to attractive mutations such as white seeded testa, that the author has observed once and in single individuals in wild *P. vulgaris* in Apurimac, Peru, and in wild *P. lunatus* in Campeche, Mexico. The "relay domestication" of tepary proposed by Pratt & Nabhan (1988) after that of common bean is an attractive hypothesis but still needs support. Garvin and Weeden (1994) have convincingly proposed Sinaloa as a place for its domestication, and evidence for the domestication of common bean in this part of Mexico is lacking. On the other hand, in

contrast to the Old World where cereals and pulses are sown and harvested in bulk, maize and beans are planted and harvested individually in the New World, with quick progress in selection for traits controlled by few genes. In a study of the domestication

syndrome in common bean, Koinange et al. (1996) indicate that the genes responsible for the syndrome could be located in three genomic regions, and because of their large phenotypic effect domestication could have proceeded rapidly.

Table 3.—Places where wild relatives of cultivated *Phaseolus* species have been found together.

Country, province, place	<i>Phaseolus</i> species and author's collection numbers
Mexico, Durango, Durango, Carlos Real	acutifolius (265), vulgaris (266)0
Mexico, Durango, Durango, Castillo Najera	acutifolius (268), vulgaris (267)
Mexico, Durango, Durango, Volc. La Breña	acutifolius (273), vulgaris (274)
Mexico, Durango, Fco. I. Madero, Cro. Ancho	acutifolius (302), coccineus (303), vulgaris (304)
Mexico, Durango, Fco. I. Madero, Jeronimo Hernández	acutifolius (308), vulgaris (306)
Mexico, Durango, Nombre de Dios, El Saltillo	coccineus (407), vulgaris (408)
Mexico, Jalisco, Pihuamo, Valle del Río del Naranjo	acutifolius (428), lunatus (429)
Mexico, Jalisco, Tepatitlán, Palmito, Río Verde	acutifolius (447), coccineus (448), vulgaris (445)
Mexico, Jalisco, Zapotan, San Isidro	acutifolius (455), lunatus (453), vulgaris (454)
Guatemala, Jalapa, San Luis Jilotepeque	lunatus (2429), vulgaris (2431)
Guatemala, Quezaltenango, Zunil, Estancia de la Cruz	coccineus (3084), vulgaris (3083)
Guatemala, Sacatepéquez, Alotenango	lunatus (1612), vulgaris (1611)
Guatemala, Sacatepéquez, San Miguel Dueñas	lunatus (1618), vulgaris (1616)
Guatemala, Santa Rosa, San Rafael de las Flores, Lag. Ayarza	lunatus (2441), vulgaris (2440)
Guatemala, Sololá, Panajachel	lunatus (1632), polyanthus (1631)
Guatemala, Guatemala, Mixco, Ciudad San Cristobal	lunatus (3058), vulgaris (3057)
Costa Rica, San José, Aserrí	lunatus (2113), vulgaris (2111)
Costa Rica, San José, Jérico	lunatus (3130), vulgaris (3131)
Ecuador, Chimborazo, Alausi, Sibambe	lunatus (2863), vulgaris (2769)
Peru, Cajamarca, San Pablo, Sangal	lunatus (1957), vulgaris (1956)
Peru, Cajamarca, Chota, Tocmoche	lunatus (2857), vulgaris (2855)

In the case of common bean, morphological (Evans 1976) and molecular (Becerra Velásquez & Gepts 1994; Gepts et al. 1986) evidences have shown that domestication took place independently in Middle and South America, leading to assume at least two separate domestication processes, and probably more (Bannerot & Debouck 1992). The precise location of the domestication in Mesoamerica is still unclear; it cannot be discarded that there would be more than one event, for instance in Jalisco and in Durango for each of the respective races (Singh et al. 1991). The race 'Durango' is typically adapted to the dry highlands of Zacatecas, Durango, and Chihuahua of northern

Mexico. The little and erratic rainfall prevents the mixed cropping system of maize, beans, and squashes. The sole growth habit surviving in this dry environment is type 3 that allows the maturity of a few pods. In contrast, this mixed cropping system is possible in the mountains of Jalisco, the Bajío, Puebla, most *sierras* of Veracruz, Oaxaca and Chiapas, and central America, mostly on the Pacific slope. Depending on the rainfall pattern, farmers may plant maize and beans together, or advance the planting of maize that will serve as sticks for the climbing beans. Given the variation in agronomic conditions and length of the growing season, farmers selected a very large num-

ber of landraces with growth habit 2, 3, and 4. Sometimes, bush determinate varieties were selected, mainly for kitchen-gardens, for earliness and convenience; even some sort of snap beans were known in pre-Columbian times (Estrada Lugo 1989). The exact number of common bean varieties selected in Mesoamerica will probably never be known; an estimate could be of 6,000 genotypes on the basis of what is already existing in gene banks (Acosta Gallegos et al. 1991). Some of them extended to the Caribbean and to the northern coast of Colombia (Gepts & Bliss 1986). The study of Gepts and Bliss (1986) has shown a lot of bean introductions in Colombia. In the northern coast and in the interandean valleys below 1,000 masl, small-seeded types from Central America were most common, while in the central and eastern *cordilleras* above 1,600 masl large-seeded types from the Central Andes were dominant (Debouck et al. 1993; Gepts & Bliss 1986). Nevertheless, the possibility exists for an additional domestication event in Colombia from wild forms distributed in this country (Chacón S. et al. 1996).

Molecular evidence points to the domestication of corn, *Zea mays* L., in Mexico from the annual teosinte of the Balsas region (Doebley 1990). Common bean in Mesoamerica is on the rise in archaeological records only once maize has been fully domesticated (Kaplan & Lynch 1999), and ceramics widely adopted (Clark & Gosser 1995). Before that, only few - fully domesticated - beans have been found (Kaplan & Lynch 1999). Oldest archaeological records for common bean are from Ancash, Peru (4,300 years before present (BP); revised) and 2,300 years BP (revised) for Puebla, Mexico (Kaplan & Lynch 1999), although much earlier dates have been repeatedly presented (Pearsall 1992). The transition from the wild is not known in beans, in contrast

with the situation of maize where progress in domestication from a very small cob has been documented (Mangelsdorf et al. 1967). Kaplan & Kaplan (1988) have indicated that from archaeological records maize and beans were not domesticated together but associated once domestication processes were well on their way. These facts for Mesoamerica can be interpreted as if the mixed cropping with maize has been the major driving force behind the domestication of beans, perhaps all species with the possible exception of *P. acutifolius*. The little rainfall in the original habitat of tepary (usually less than 400 mm/year) would prevent the association with maize. In addition, although there are few reports of toasted beans (Kaplan 1956), it seems that the dominant use of beans in Mesoamerica was soon as boiled beans, thus using ceramics. Initially, the idea to associate maize and beans could have come from simple observations, since wild teosinte and wild common beans frequently grow together in Mexico (Delgado Salinas et al. 1988; Miranda Colín 1967). The association however brought such agronomical and nutritional advantages so that the mixed cropping has been adopted by almost all pre-Columbian peoples of Mesoamerica. Conversely, the early association with maize imposed certain constraints on the bean crop, namely in terms of growth habit and length of growing period, at the expenses of a wider diversity. In contrast, in the Andes, maize came late and as an introduced crop (Lynch 1999), perhaps in the second half of the history of beans as domesticated plants (*P. vulgaris* and *P. lunatus* in this case). However, pre-Columbian peoples associated maize with their local varieties of common bean in Nueva Granada, Ecuador, Peru, Bolivia, and northwestern Argentina. They planted maize and beans together or at different dates, depending on the amount and

pattern of rainfall. In order to fit their diversity of soils and climates, they selected thousands of common bean varieties of growth habit 3 and 4, perhaps another 5,000 genotypes for the whole region, included in races Nueva Granada and Peru (Singh et al. 1991). In regions where rainfall did not allow the association with maize (central Chile and Pernambuco corner of northeastern Brazil), farmers selected landraces of growth habit 3. The importance of roots and tubers in so many pre-Columbian agricultures of South America as compared to Mesoamerica did not boost the trilogy maize-beans-squash to the same extent, also because of animal proteins (e.g. guinea pig, camelids, seafood) in the diet. But beans were fully domesticated by the time maize arrived, and it happened already in preceramic times. On the basis of currently available archaeological evidence (Kaplan & Lynch 1999), it seems that *P. lunatus* was domesticated before *P. vulgaris*, and in a preceramic context. This situation rightly raises the question about uses of beans if they cannot be regularly boiled. In folk traditions and folk names of beans, there is a lot of references about birds eating young pods, developing seeds, and germinating seedlings (Debouck et al. 1993; Tohme et al. 1995). Toasting seems to have been a common practice in preceramic periods in the Andes for any grain crop (cañihua: Gade 1970; common bean: Tohme et al. 1995; kiwicha: Sauer 1967; maize: Grobman et al. 1961; quinua: León 1964; tarwi: León 1964). The author considers highly relevant the fact that an introduced pulse from Spain, *Vicia faba* L., is consumed toasted in the highlands of Peru (Cabieses 1995). Another dimension to (early) bean domestication is the aesthetic selection, that is the selection of particularly attractive colours and colour patterns for non-food purposes (e.g. play, rituals), and would explain in part the great

diversity of grain colours and patterns of common and Lima beans unmatched in any other grain crop worldwide (Debouck 1989).

The small seeded wild Lima bean has long been reported from several parts of Central America (Standley & Steyermark 1946), and proposed as ancestor of the three cultigroups Sieva, Potato, and Big Lima (Mackie 1943). However, a couple of authors (Heiser 1965; Kaplan & Kaplan 1988; Vavilov 1949) have hypothesized two separate domestication histories, although on scarce biological basis. The discovery of another wild form with slightly larger seeds in northwestern Peru (Debouck et al. 1987) and southern Ecuador (Debouck et al. 1989b) has since changed the picture. Two separate domestication events have been demonstrated by biochemical (Debouck et al. 1989c; Gutiérrez Salgado et al. 1995) and molecular (Fofana et al. 1997; Nienhuis et al. 1995) evidence. The range of the 'Andean' wild form is restricted to southern Ecuador and northwestern Peru (Debouck et al. 1989b; Maquet & Baudoin 1997); this would lead to assume a domestication event within that range. In contrast, the range of the small-seeded wild Lima bean is huge, from Sinaloa in Mexico to Chaco in Argentina (Gutiérrez Salgado et al. 1995; Maquet & Baudoin 1997), and a precise location for the domestication of the small-seeded cultivated Lima beans is still to be determined. Earliest archaeological records (5,600 years BP; revised dates) are from the Coast of Peru and preceramic, slightly younger for the central Andes of Peru (3,500 years BP), and dates are much more recent in Mesoamerica (500 years BP: all by Kaplan & Lynch 1999).

The scarlet runner, *P. coccineus*, probably the third species in terms of economic importance, has a particularly variable gene pool of wild forms, distributed in Mexico, Guatemala and Honduras (Delgado Salinas

1988), and likely not all are ancestor of the cultivated form. Hybrid swarms between cultivated and wild forms have been mentioned in several parts of the original range, indicating interfertility between these forms. Which wild form is the precise ancestor of the scarlet runner is still unknown, as well as the place(s) where the domestication took place (Debouck & Smartt 1995). Revised dates for archaeological records indicate 1,100 years BP in Oaxaca and Durango, and 500 years BP in Puebla (Kaplan & Lynch 1999). Its reporting in several codices of different native languages of Mexico would let to assume an old domestication in pre-Columbian times (Estrada Lugo 1989). Worth mentioning is consumption of flowers and tuberous roots (Delgado Salinas 1988).

About the tepary bean, known first by its wild form (in contrast to the other cultivated species), the relationship with the cultivated form was established only last century (Freeman 1913; Pratt & Nabhan 1988). On the basis of currently available material, there is fair evidence to support a single domestication in western Mexico, around Sinaloa (Garvin & Weeden 1994). It migrated in prehistoric times to the southwestern USA and Central America (Guatemala, Nicaragua, and Costa Rica), where it has suffered an historic regression (Debouck 1992). The earliest archaeological record is 2,300 years BP in Puebla, Mexico (Kaplan & Lynch 1999). This site is outside the present range of distribution of wild teparies, so one may speculate about an introduction as a fully developed cultigen into this dry valley of central Mexico, and thus a wider diffusion. A couple of records (Kaplan 1956) report parched grains, so it is possible that its domestication is preceramic. In addition, the diversity of vernacular names in northwestern Mexico and southwestern USA (Nabhan & Felger 1978) strongly indicate where this crop has evolved.

P. polyanthus in cultivation was thought to be the result of a natural hybridization between cultivated forms of *P. coccineus* and *P. vulgaris* (Hernández Xolocotzi et al. 1959). According to other authors (Delgado Salinas 1988; Piñero & Eguiarte 1988), it would be only a particular variant of *P. coccineus*. A wild form has been discovered in central-western Guatemala, and since shown to be the ancestor of *P. polyanthus* (Schmit & Debouck 1991). *P. polyanthus* is not known in archaeology. It is not sure however that archaeologists are aware of the differences with *P. coccineus*, although morphological differences in seed hilum are clear-cut (Hernández Xolocotzi et al. 1959). Linguistic evidence indicates that 1) *P. polyanthus* has long been grown by Amerinds inhabiting in humid mountains of central and southern Mexico, and western Guatemala (Breedlove & Laughlin 1993; Schmit & Debouck 1991), and 2) Amerinds there separate *P. polyanthus* from *P. coccineus*. One could thus assume that *P. polyanthus* is pre-Columbian in Mexico and Guatemala. Its migration into Central America towards the northern Andes is probably historic, and its move in the Andes southwards from Cauca, Colombia, would have started last century (Schmit & Debouck 1991). Early uses of *P. polyanthus* include fresh seeds (shell beans), perhaps because of increased digestibility at higher altitudes.

Each cultivated species came from a couple of wild populations through the domestication process. This process affected mainly harvested parts (seeds, pods) and their nutritional quality. The presence of antinutritional factors played against 1) multiple (space), and 2) repetitive (time) domestications. So, just a few populations have been involved in the domestication process, with a marked founder effect, that is, a few individual plants being domestica-

ted contributed their genes to the next generations. Such a founder effect has been shown in common bean (Bannerot & Debouck 1992; Gepts et al. 1986; Sonnante et al. 1994). The same reduction of total genetic diversity has been shown - with the help of evolutionary neutral molecular markers - in Lima bean (Gutiérrez Salgado et al. 1995), the year-bean (Schmit & Debouck 1991), and the tepary (Garvin & Weeden 1994; Schinkel & Gepts 1988). As a consequence, much of the genetic diversity *per se* has been left out of the domesticated stocks, not because of highly negative traits in the wild, but simply because people were not there in time to domesticate all wild populations. Another explanation for the founder effect might be in the genetics - of highly heritable and searched for - traits such as variation in seed testa. Attractive mutations may occur at low frequency, but given its inheritance may easily be fixed and passed on to next generations. Farmers and rural inhabitants - as they do it today - separated these seeds from the bulk of the original population, and planted them in distant plots and/or at another time. A concrete case of useful trait left out of the gene pool of the cultivated common bean is provided by bruchid resistance, a trait that surely would have been retained by early agriculturists. Bruchid resistance is caused by antibiosis due to the presence of a special storage protein called arcelin (Osborn et al. 1988). This protein has not been found in any cultivated common bean variety but only in wild forms (Cardona et al. 1990), at low frequency in original wild populations (Osborn et al. 1986), specially in Guerrero of western Mexico (Acosta Gallegos et al. 1998), where bean domestication apparently did not take place. So, the true reserve of genetic diversity *per se* lies in the wild forms, less in the landraces, and much less in modern artificially bred cultivars, which

may show very little variation (Sonnante et al. 1994). The reduction of genetic diversity might be paralleled with the evolution of breeding systems in beans: while most wild species are outbreeders, there is a strong tendency towards autogamy in the cultivated forms of *P. acutifolius*, *P. lunatus*, and *P. vulgaris*. There might be variation among regions and/ or gene pools or genotypes (Ibarra Pérez et al. 2000), but a high outcrossing rate between wild forms and landraces if oriented towards to the crop is likely to mitigate the founder effect. In tepary, it is likely that all basic genetic variation for future crop improvement lies in fact in its wild forms, given its historic regression as a crop (Debouck 1992).

The end products of domestication are highly similar across the five cultivated species, an observation already made by Darwin (1868) and Vavilov (1922), as if the same results would have been selected for in different ecologies. There are thus similar patterns, and yet possibilities to be explored, in terms of unrealized potentials (Smartt 1990). A concrete example might be in the diversity of growth habits, yet to be obtained in *P. polyanthus*. This should be kept in mind when developing comparative gene mapping across *Phaseolus* species.

7. CONCLUDING REMARKS

Beans have had a long evolution in the Americas before domestication. *Phaseolus* while being one group in comparison to other New World legumes has progressively differentiated into possibly 5-6 phylums, surely two that include with a couple of wild species the common bean and the Lima bean, respectively. The closing of the Isthmus of Panama marks a second major exchange of *Phaseolus* materials between Central America and the Andes. The early

evolution in different areas separated by geographic distance (i.e. Central America and the northern Andes) explains the formation of gene pools and problems of compatibility in wide crossing as observed today. It also explains some aspects of co-evolution between wild forms and associated pathogens and symbionts. Would not have Man enter the Americas, the gene pools of common and Lima beans could have evolved into different species. With peoples coming in, domesticated species were however quickly moved around, while they were still open biological systems, exchanging genes with wild relatives. Some isolation of gene pools was frustrated, as observed today in Colombian common bean germplasm, or Central American Lima bean germplasm, and molecular complexity of both groups increased. Conversely, these germplasms may help to bypass fertility barriers that were building in. The early association of beans with maize in Mesoamerica oriented an evolution that would have been slightly different without it, namely in terms of selection pressures of growth habits. The association also helped towards the shaping of races in common bean. With the exception of tepary, most genotypes of the other cultigens were developed to be associated with maize. In the Andes, the early part of domestication was in a non-ceramic and non-maize environment. Selection for popping and for non-food purpose was once important, and some resulting diversity can still be seen. The mixed cropping with maize was exported or rebuilt in many parts with four of the five cultigens, given exceptional agronomic and nutritional advantages. This happened in pre-Columbian America, but also with common bean in post-Columbian times in Africa, parts of Spain, Italy, and the Balkans. The almost individual planting with maize has been conducive to strong selective pressures,

with increased phenotypical variation and frequent reduction of overall genetic diversity. Gene flow among landraces and with wild relatives has sometimes buffered that reduction, but with variable effects because of genotypes involved and environment conditions. Patterns established in time, space, and people, have shaped beans, and oriented their potentials.

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LITERATURE CITED

- ACOSTA GALLEGOS, J. A., C. QUINTERO, J. VARGAS, O. TORO, J. TOHME, C. CARDONA, 1998. A new variant of arcelin in wild common bean, *Phaseolus vulgaris* L., from southern Mexico. *Genet. Resources & Crop Evol.* **45**: 235-242.
- ACOSTA GALLEGOS, J. A., J. S. MURUAGA MARTÍNEZ, F. CÁRDENAS RAMOS, 1991. Utilización y disponibilidad de recursos genéticos de *Phaseolus* en México.

- In: R. Ortega Paczka, G. Palomino Hasbach, F. Castillo González, V.A. González Hernández, M. Livera Muñoz (eds.) Avances en los estudios de los recursos fitogenéticos de México. Sociedad Mexicana de Fitogenética, Chapingo, Mexico. pp. 187-196.
- BALASUBRAMANIAN, P. M., A. VANDENBERG, P. J. HUCL, L.V. GUSTA, 2000. Relative freezing resistance in the genus *Phaseolus*. Annu. Rept. Bean Improvement Coop. (USA) **43**: 66-67.
- BANNEROT, H., D. G. DEBOUCK, 1992. L'importance de la double domestication pour l'amélioration du haricot commun (*Phaseolus vulgaris*). In: J. C. Mounolou (ed.) Complexes d'espèces, flux de gènes et ressources génétiques des plantes. Colloque international en hommage à Jean Pernès. Publications du Bureau des Ressources Génétiques, Lavoisier - Technique et Documentation, Paris, France. pp. 495-506.
- BARBOSA FEVEREIRO, V. P., 1986-87. Macroptilium (Benth.) Urban do Brasil (Leguminosae-Faboideae-Phaseoleae-Phaseolinae). Arq. Jard. Bot. Rio de Janeiro **28**: 109-180.
- BAUDET, J. C., 1978. Prodrôme d'une classification générique des *Papilionaceae-Phaseoleae*. Bull. Jard. Bot. Nat. Belg. **48**: 183-220.
- BAUDOIN, J. P., 1990. L'amélioration de *Phaseolus lunatus* L. en zones tropicales. 5. Génétique, biologie florale et évolution des populations. Bull. Rech. Agron. Gembloux **25**: 281-312.
- BEAVER, J. S., 1999. Improvement of large-seeded race Nueva Granada cultivars. In: S. P. Singh (ed.) Common bean improvement in the twenty-first century. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 275-288.
- BECERRA VELÁSQUEZ, V. L., P. GEPTS, 1994. RFLP diversity of common bean (*Phaseolus vulgaris*) in its centres of origin. Genome **37**: 256-263.
- BEEBE, S., O. TORO, A. V. GONZÁLEZ, M. I. CHACÓN, D. G. DEBOUCK, 1997. Wild-weed-crop complexes of common bean (*Phaseolus vulgaris* L., Fabaceae) in the Andes of Peru and Colombia, and their implications for conservation and breeding. Genet. Resources & Crop Evol. **44**: 73-91.
- BREEDLOVE, D. E., R. M. LAUGHLIN, 1993. The flowering of man - A Tzotzil botany of Zinacantan. Vol. 1. Smithsonian Institution Press, Washington, D.C., USA, 285p.
- BRICK, M. A., K. F. GRAFTON 1999. Improvement of medium-seeded race Durango cultivars. In: S. P. Singh (ed.) Common bean improvement in the twenty-first century. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 223-253.
- BURKART, A., 1952. Las leguminosas argentinas silvestres y cultivadas. Second edition. Acme Agency, Buenos Aires, Argentina, 569p.
- BURKART, A., H. BRÜCHER, 1953. *Phaseolus aboriginus* Burkart, die mutmaßliche andine Stammform der Kulturbohne. Züchter **23**: 65-72.
- CABIESES, F., 1995. Cien siglos de pan. Consejo Nacional de Ciencia y Tecnología, Lima, Peru, 273p.
- CAICEDO, A. L., E. GAITAN, M. C. DUQUE, O. TORO, D. G. DEBOUCK, J. TOHME, 1999. Analyzing *Phaseolus lunatus* L. and related wild species of South America by AFLP fingerprinting. Crop Sci. **39**: 1497-1507.
- CARDONA, C., J. KORNEGAY, C. E. POSSO, F. MORALES, H. RAMÍREZ, 1990. Comparative value of four arcelin variants in the development of dry bean lines resistant to the Mexican bean weevil. Entomol. exp. appl. **56**: 197-206.
- CARDICH, A., 1985. The fluctuating upper limits of cultivation in the Central Andes and their impact on Peruvian prehistory. In: F. Wendorf & A.E. Close (eds.) Advances in world archaeology. Vol. 4. Academic Press Inc., Orlando, Florida, USA. pp. 293-333.
- CAVALLI-SFORZA, L. L., P. MENOZZI, A. PIAZZA, 1994. The history and geography of human genes. Princeton University Press, Princeton, New Jersey, USA, 1059p.
- CHACÓN S., M. I., A. V. GONZÁLEZ, J. P. GUTIÉRREZ, S. BEEBE, D. G. DEBOUCK, 1996. Increased evidence for common bean (*Phaseolus vulgaris* L.) domestication in Colombia. Annu. Rept. Bean Improvement Coop. (USA) **39**: 201-202.
- CHACÓN SÁNCHEZ, M. I., B. PICKERSGILL, D. G. DEBOUCK, 1999. Intraspecific chloroplast DNA diversity in common bean (*Phaseolus vulgaris*) for domestication studies. Annu. Rept. Bean Improvement Coop. (USA) **42**: 79-80.
- CLARK, J. E., D. GOSSER, 1995. Reinventing Mesoamerica's first pottery. In: W.K. Barnett & J.W. Hoopes (eds.), The emergence of pottery - Technology and innovation in ancient societies. Smithsonian Institution Press, Washington, DC, USA. pp. 209-221.
- COATES, A. G., 1997. The forging of Central America. In: A. G. Coates (ed.) Central America - A natural and cultural history. Yale University Press, New Haven, Connecticut, USA. pp. 1-37.
- CRAWFORD, M. H., 1998. The origins of Native Americans - Evidence from anthropological genetics. Cambridge University Press, Cambridge, UK, 308p.

- DARWIN, C., 1868. The variation of animals and plants under domestication. Reprint of 1998 by the John Hopkins University Press, Baltimore, Maryland, USA, 968p.
- DEBOUCK, D. G., 1989. Early beans (*Phaseolus vulgaris* L. and *P. lunatus* L.) domesticated for their aesthetic value? Annu. Rept. Bean Improvement Coop. (USA) **32**: 62-63.
- DEBOUCK, D. G., 1991. SYSTEMATICS AND MORPHOLOGY. In: A. VAN SCHOONHOVEN AND O. VOYSEST VOYSEST (EDS.), COMMON BEANS: research for crop improvement. Commonwealth Agricultural Bureaux International, Wallingford, United Kingdom. pp. 55-118.
- DEBOUCK, D. G., 1992. Frijoles, *Phaseolus* spp. In: E. Hernández Bermejo and J. León (eds.) Cultivos marginados: otra perspectiva de 1992. Food and Agriculture Organization of the United Nations, Rome, Italy. pp. 45-60.
- DEBOUCK, D. G., 1996 Colombian common and Lima beans: views on their origin and evolutionary significance. Revista CORPOICA **1**: 7-15.
- DEBOUCK, D. G., 1999. Diversity in *Phaseolus* species in relation to the common bean. In: S. P. Singh (ed.) Common bean improvement in the twenty-first century. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 25-52.
- DEBOUCK, D. G., 2000. Biodiversity, ecology and genetic resources of *Phaseolus* beans. - Seven answered and unanswered questions. In: K. Oono (ed.) Wild legumes. National Institute of Agrobiological Resources, Tsukuba, Japan. pp. 95-123.
- DEBOUCK, D. G., R. ARAYA VILLALOBOS, R. A. OCAMPO SÁNCHEZ, W.G. GONZALEZ UGALDE, 1989a. Collecting *Phaseolus* in Costa Rica. FAO/IBPGR Plant Genet. Resources Newsl. **78/79**: 44-46.
- DEBOUCK, D. G., R. CASTILLO, J. TOHME, 1989b. Observations on little-known *Phaseolus* germplasm of Ecuador. FAO/IBPGR Plant Genet. Resources Newsl. **80**: 15-21.
- DEBOUCK, D. G., J.H. LIÑAN JARA, A. CAMPANA SIERRA, J.H. DE LA CRUZ ROJAS, 1987. Observations on the domestication of *Phaseolus lunatus* L. FAO/IBPGR Plant Genetic Resources Newsl. **70**: 26-32.
- DEBOUCK, D. G., A. MAQUET, C. E. POSSO, 1989c. Biochemical evidence for two different gene pools in lima beans, *Phaseolus lunatus* L. Annu. Rept. Bean Improvement Coop. (USA) **32**: 58-59.
- DEBOUCK, D. G., J. SMARTT, 1995. BEANS, *Phaseolus* spp. (Leguminosae-Papilionoideae). In: J. Smartt and N. W. Simmonds (eds.) Evolution of crop plants. Second Edition. Longman Scientific & Technical, London, United Kingdom. pp. 287-294.
- DEBOUCK, D. G., O. TORO, O. M. PAREDES, W. C. JOHNSON, P. GEPTS, 1993. Genetic diversity and ecological distribution of *Phaseolus vulgaris* (Fabaceae) in northwestern South America. Econ. Bot. **47**: 408-423.
- DELGADO SALINAS, A., 1985. Systematics of the genus *Phaseolus* (Leguminosae) in North and Central America. PhD Thesis, University of Texas, Austin, Texas, USA, 363p.
- DELGADO SALINAS, A., 1988. Variation, taxonomy, domestication, and germplasm potentialities in *Phaseolus coccineus*. In: P. Gepts (ed.) Genetic resources of *Phaseolus* beans. Kluwer Academic Publishers, Dordrecht, Holland. pp. 441-463.
- DELGADO SALINAS, A., A. BONET, P. GEPTS, 1988. The wild relative of *Phaseolus vulgaris* in Middle America. In: P. Gepts (ed.) Genetic resources of *Phaseolus* beans. Kluwer Academic Publishers, Dordrecht, Holland. pp. 163-184.
- DELGADO SALINAS, A., A. BRUNEAU, J. J. DOYLE, 1993. Chloroplast DNA phylogenetic studies in New World Phaseolinae (Leguminosae: Papilionoideae: Phaseoleae). Syst. Bot. **18**: 6-17.
- DELGADO SALINAS, A., T. TURLEY, A. RICHMAN, M. LAVIN, 1999. Phylogenetic analysis of the cultivated and wild species of *Phaseolus* (Fabaceae). Syst. Bot. **24**: 438-460.
- DICKSON, M. H., M. A. BOETTGER, 1977. Screening plant introductions for *Pythium* and *Fusarium* resistance. Annu. Rept. Bean Improvement Coop. (USA) **20**: 80-81.
- DOEBLEY, J., 1990. Molecular evidence and the evolution of maize. Econ. Bot. **44S**: 6-27.
- ESTRADA LUGO, E. I. J., 1989. El Códice Florentino: su información etnobotánica. Colegio de Postgraduados, Chapingo, México, México, 399p.
- EVANS, A. M., 1976. Beans - *Phaseolus* spp. (Leguminosae - Papilionatae). In: N. W. Simmonds (ed.) Evolution of crop plants. Longman, London, United Kingdom. pp. 168-172.
- FOFANA, B., J. P. BAUDOUIN, X. VEKEMANS, D. G. DEBOUCK, P. DU JARDIN, 1999. Molecular evidence for an Andean origin and a secondary gene pool for the Lima bean (*Phaseolus lunatus* L.) using chloroplast DNA. Theor. Appl. Genet. **98**: 202-212.
- FOFANA, B., X. VEKEMANS, P. DU JARDIN, J. P. BAUDOUIN, 1997. Genetic diversity in Lima bean (*Phaseolus lunatus* L.) as revealed by RAPD markers. Euphytica **95**: 157-165.
- FREEMAN, G. F., 1913. The tepary, a new cultivated legume from the Southwest. Bot. Gaz. **56**: 395-417.
- FREYRE, R., R. RÍOS, L. GUZMÁN, D. G. DEBOUCK, P. GEPTS, 1996. Ecogeographic distribution of

- Phaseolus* spp. (Fabaceae) in Bolivia. *Econ. Bot.* **50**: 195-215.
- FREYTAG, G. F., D. G. DEBOUCK, 1996. *Phaseolus costaricensis*, a new wild bean species (Phaseolinae, Leguminosae) from Costa Rica and Panama, Central America. *NOVON* **6**: 157-163.
- GADE, D. W., 1970. Ethnobotany of cañihua (*Chenopodium pallidicaule*), rustic seed crop of the Altiplano. *Econ. Bot.* **24**: 55-61.
- GARVER, S., 1934. The Redfield tepary bean, an early maturing variety. *J. Amer. Soc. Agron.* **3**: 397-403.
- GARVIN, D. F., N. F. WEEDEN, 1994. Isozyme evidence supporting a single geographic origin for domesticated tepary bean. *Crop Sci.* **34**: 1390-1395.
- GEFFROY, V., SICCARD, D., J. C. F. DE OLIVEIRA, M. SÉVIGNAC, S. COHEN, P. GEPTS, C. NEEMA, T. LANGIN, M. DRON, 1969. Identification of an ancestral resistance gene cluster involved in the coevolution process between *Phaseolus vulgaris* and its fungal pathogen *Colletotrichum lindemuthianum*. *Molec. Plant-Microb. Inter.* **12**: 774-784.
- GENTRY, H. S., 1969. Origin of the common bean, *Phaseolus vulgaris*. *Econ. Bot.* **23**: 55-69.
- GEPTS, P., F. A. BLISS, 1986. Phaseolin variability among wild and cultivated common beans (*Phaseolus vulgaris*) from Colombia. *Econ. Bot.* **40**: 469-478.
- GEPTS, P., D. G. DEBOUCK, 1991. Origin, domestication, and evolution of the common bean (*Phaseolus vulgaris* L.). In: A. van Schoonhoven and O. Voysest (eds.) *Common beans: research for crop improvement*. Commonwealth Agricultural Bureaux International, Wallingford, United Kingdom. pp. 7-53.
- GEPTS, P., A. GONZÁLEZ, R. PAPA, J. ACOSTA, A. WONG, A. DELGADO SALINAS, 2000b. Outcrossing in Mexican wild and domesticated populations of common bean. *Annu. Rept. Bean Improvement Coop. (USA)* **43**: 25-26.
- GEPTS, P., T. C. OSBORN, K. RASHKA, F. A. BLISS, 1986. Phaseolin protein variability in wild forms and landraces of the common bean (*Phaseolus vulgaris* L.): evidence for multiple centers of domestication. *Econ. Bot.* **40**: 451-468.
- GEPTS, P., R. PAPA, S. COULIBALY, A. GONZÁLEZ MEJÍA, R. PASQUET, 2000a. Wild legume diversity and domestication - Insights from molecular methods. In: K. Oono (ed.) *Wild legumes*. National Institute of Agrobiological Resources, Tsukuba, Japan. pp. 19-31.
- GRAHAM, A., 1993. Historical factors and biological diversity in Mexico. In: T.P. Ramamoorthy, R. Bye, A. Lot and J. Fa (eds.), *Biological diversity of Mexico: origins and distribution*. Oxford University Press Inc., New York, USA. pp. 109-127.
- GRAHAM, A., 1999a. The Tertiary history of the northern temperate element in the northern Latin American biota. *Amer. J. Bot.* **86**: 32-38.
- GRAHAM, A., 1999b. Late Cretaceous and Cenozoic history of North American vegetation. Oxford University Press Inc., New York, New York, USA, 350p.
- GROBMAN, A., W. SALHUANA, R. SEVILLA, P. C. MANGELSDORF, 1961. Races of maize in Peru, their origins, evolution and classification. National Academy of Sciences, National Research Council, Washington, DC, USA, Publication **915**: 1-374.
- GUTIÉRREZ SALGADO, A., P. GEPTS, D. G. DEBOUCK, 1995. Evidence for two gene pools of the Lima bean, *Phaseolus lunatus*, in the Americas. *Genet. Resources & Crop Evol.* **42**: 15-28.
- GUZMÁN, P., R. L. GILBERTSON, R. NODARI, W. C. JOHNSON, S. R. TEMPLE, D. MANDALA, A. B. C. MKANDAWIRE, P. GEPTS, 1995. Characterization of variability in the fungus *Phaeoisariopsis griseola* suggests coevolution with the common bean (*Phaseolus vulgaris*). *Phytopathology* **85**: 600-607.
- HEISER, C. B., 1965. Cultivated plants and cultural diffusion in nuclear America. *Amer. Anthropol.* **67**: 930-949.
- HERNÁNDEZ XOLOCOTZI, E., S. MIRANDA COLÍN, C. PRYWER, 1959. El origen de *Phaseolus coccineus* L. *darwinianus* Hdz. X. & Miranda C., *subspecies nova*. *Rev. Soc. Mex. Hist. Nat.* **20**: 99-121.
- HERVIEU, F., H. BANNEROT, G. PELLETIER, 1994. A unique cytoplasmic male sterility (CMS) determinant is present in three *Phaseolus* species characterized by different mitochondrial genomes. *Theor. Appl. Genet.* **88**: 314-320.
- HUNTER, J. E., M. H. DICKSON, BOETTGER, M. A., J. A. CIGNA, 1982. Evaluation of plant introductions of *Phaseolus* spp. for resistance to white mold. *Plant Disease* **66**: 320-322.
- IBARRA PÉREZ, F. J., B. EDHAIE, J. G. WAINES, 2000. Re-thinking the population structure of common bean. *Annu. Rept. Bean Improvement Coop. (USA)* **43**: 23-24.
- JAASKA, V., 1996. Isoenzyme diversity and phylogenetic affinities among the *Phaseolus* beans (Fabaceae). *Pl. Syst. Evol.* **200**: 233-252.
- JACOB, M., D. ZINK, W. NAGL, 1995. RFLPs of the rRNA genes in the genus *Phaseolus*. *Genetic Resources & Crop Evolution* **42**: 97-106.
- KAMI, J., V. BECERRA VELÁSQUEZ, D. G. DEBOUCK, P. GEPTS, 1995. Identification of presumed ancestral DNA sequences of phaseolin in *Phaseolus vulgaris*. *Proc. Natl. Acad. Sci. USA* **92**: 1101-1104.

- KAPLAN, L., 1956. The cultivated beans of the prehistoric Southwest. *Ann. Mo. Bot. Gard.* **43**: 189-251.
- KAPLAN, L., L. N. KAPLAN, 1988 *Phaseolus* in archaeology. In: P. Gepts (ed.) Genetic resources of *Phaseolus* beans. Kluwer Academic Publishers, Dordrecht, Holland. pp. 125-142.
- KAPLAN, L., T. F. LYNCH, 1999. *Phaseolus* (Fabaceae) in archaeology: AMS radiocarbon dates and their significance for pre-Colombian agriculture. *Econ. Bot.* **53**: 261-272.
- KHAIRALLAH, M. M., B. B. SEARS, M. W. ADAMS, 1992. Mitochondrial restriction fragment length polymorphisms in wild *Phaseolus vulgaris* L.: insights on the domestication of the common bean. *Theor. Appl. Genet.* **84**: 915-922.
- KOENIG, R., P. GEPTS, 1989. Allozyme diversity in wild *Phaseolus vulgaris*: further evidence for two major centers of genetic diversity. *Theor. Appl. Genet.* **78**: 809-817.
- KOENIG, R. L., S. P. SINGH, P. GEPTS, 1990. Novel phaseolin types in wild and cultivated common bean (*Phaseolus vulgaris*, Fabaceae). *Econ. Bot.* **44**: 50-60.
- KOINANGE, E. M. K., P. GEPTS, 1992. Hybrid weakness in wild *Phaseolus vulgaris* L. *J. Hered.* **83**: 135-139.
- KOINANGE, E. M. K., S. P. SINGH, P. GEPTS, 1996. Genetic control of the domestication syndrome in common bean. *Crop Sci.* **36**: 1037-1045.
- KORNEGAY, J., C. CARDONA, 1991. Inheritance of resistance to *Acanthoscelides obtectus* in a wild common bean accession crossed to commercial bean cultivars. *Euphytica* **52**: 103-111.
- LACKEY, J. A., 1981. Phaseoleae DC. In: R. M. Polhill and P. H. Raven (eds.) Advances in legume systematics. Part 1. Royal Botanic Gardens, Kew, Richmond, United Kingdom. pp. 301-327.
- LACKEY, J. A., 1983. A review of generic concepts in American Phaseolinae (Fabaceae, Faboideae). *Iselya* **2**: 21-64.
- LE MARCHAND, G., R. MARÉCHAL, 1977. Chromosome pairing in interspecific hybrids reveals the value of pollen morphology for deducing phylogenetic affinities in the genus *Phaseolus*. Proceedings 8th Congress Eucarpia "Interspecific hybridization in plant breeding", Madrid, Spain, pp. 335-337.
- LEÓN, J., 1964. Plantas alimenticias andinas. Instituto Interamericano de Ciencias Agrícolas, Lima Perú, 112p.
- LEWIS, G. P., A. DELGADO SALINAS, 1994. *Mysanthus*, a new genus in tribe Phaseoleae (Leguminosae: Papilionoideae) from Brazil. *Kew Bull.* **49**: 343-351.
- LIOI, L., C. LOTTI, I. GALASSO, 1998. Isozyme diversity, RFLP of the rDNA and phylogenetic affinities among cultivated Lima beans, *Phaseolus lunatus* (Fabaceae). *Pl. Syst. Evol.* **213**: 153-164.
- LLACA, V., A. DELGADO SALINAS, P. GEPTS, 1994. Chloroplast DNA as an evolutionary marker in the *Phaseolus vulgaris* complex. *Theor. Appl. Genet.* **88**: 646-652.
- LYNCH, J., A. GONZÁLEZ, J. M. TOHME, J. GARCÍA, 1992. Variation in characters related to leaf photosynthesis in wild bean populations. *Crop Sci.* **32**: 633-640.
- LYNCH, T. F., 1999. The earliest South American lifeways. In: F. Salomon and S. B. Schwartz (eds.), The Cambridge history of the native peoples of the Americas. Vol 3 Part 1. Cambridge University Press, Cambridge, UK. pp. 188-263.
- MACKIE, W. W., 1943. Origin, dispersal, and variability of the lima bean, *Phaseolus lunatus*. *Hilgardia* **15**: 1-24.
- MACMILLAN, C., 1892. The Metaspermae of the Minnesota valley. Harrison & Smith, Minneapolis, Minnesota, USA, 826p.
- MACNEISH, R. S., 1992. The origins of agriculture and settled life. University of Oklahoma Press, Norman, Oklahoma, USA, 433p.
- MANGELSDORF, P. C., R. S. MACNEISH, W. C. GALINAT, 1967. Prehistoric wild and cultivated maize. In: D. S. Byers (ed.) The prehistory of the Tehuacan Valley. Vol 1. Environment and subsistence. University of Texas Press, Austin, USA. pp. 178-200.
- MAQUET, A., J. P. BAUDOIN, 1997. Aperçu de la distribution néotropical de *Phaseolus lunatus*. *Belg. J. Bot.* **130**: 93-116.
- MAQUET, A., X. VEKEMANS, J. BAUDOIN, 1999. Phylogenetic study on wild allies of Lima bean, *Phaseolus lunatus* (Fabaceae), and implications on its origin. *Plant Syst. Evol.* **218**: 43-54.
- MAQUET, A., B. WATHELET, J. BAUDOIN, 1994. Etude du réservoir génétique de la légumineuse alimentaire *Phaseolus lunatus* L. par l'analyse électrophorétique d'isozymes. *Bull. Rech. Agron. Gembloux* **29**: 369-381.
- MARÉCHAL, R., J. M. MASCHERPA, F. STAINIER, 1978a. Combinaisons et noms nouveaux dans les genres *Phaseolus*, *Minkelersia*, *Macroptilium*, *Ramirezella* et *Vigna*. *Taxon* **27**: 199-202.
- MARÉCHAL, R., J. M. MASCHERPA, F. STAINIER, 1978b. Etude taxonomique d'un groupe complexe d'espèces des genres *Phaseolus* et *Vigna* (Papilionaceae) sur la base de données morphologiques et polliniques, traitées par l'analyse informatique. *Boissiera* **28**: 1-273.
- MARÉCHAL, R., J. M. MASCHERPA, F. STAINIER, 1981. Taxonomic study of the *Phaseolus-Vigna* complex and related genera. In: R. M. Polhill and P. H.

- Raven (eds.) Advances in legume systematics. Part 1. Royal Botanic Gardens, Kew, Richmond, United Kingdom. pp. 329-335.
- MARKHART III, A. H. 1985. Comparative water relations of *Phaseolus vulgaris* L. and *Phaseolus acutifolius* Gray. *Plant Physiol.* **77**: 113-117.
- MARTIN, G. B., M. W. ADAMS, 1987. Landraces of *Phaseolus vulgaris* (Fabaceae) in northern Malawi. 2. Generation and maintenance of variability. *Econ. Bot.* **41**: 204-215.
- MERCADO RUARO, P., A. DELGADO SALINAS, 1998. Karyotypic studies on species of *Phaseolus* (Fabaceae: Phaseolinae). *Amer. J. Bot.* **85**: 1-9.
- MIRANDA COLÍN, S., 1967. Origen de *Phaseolus vulgaris* L. (frjol común). *Agrociencia (Mexico)* **1**: 99-109.
- NABHAN, G. P., R. S. FELGER, 1978. Teparies in south-western North America - A biogeographical and ethnohistorical study of *Phaseolus acutifolius*. *Econ. Bot.* **32**: 3-19.
- NIEHUIS, J., J. TIVANG, P. SKROCH, J. B. DOS SANTOS, 1995. Genetic relationships among cultivars and landraces of lima bean (*Phaseolus lunatus* L.) as measured by RAPD markers. *J. Amer. Soc. Hort. Sci.* **120**: 300-306.
- OSBORN, T. C., D. C. ALEXANDER, S. S. M. SUN, C. CARDONA, F. A. BLISS, 1988. Insecticidal activity and lectin homology of arcelin seed protein. *Science* **240**: 207-210.
- OSBORN, T. C., T. BLAKE, P. GEPTS, F. A. BLISS, 1986. Bean arcelin. 2. Genetic variation, inheritance and linkage relationships of a novel seed protein of *Phaseolus vulgaris* L.. *Theor. Appl. Genet.* **71**: 847-855.
- PASTOR-CORRALES, M. A., M. M. OTOYA, A. MOLINA, S. P. SINGH, 1995. Resistance to *Colletotrichum lindemuthianum* isolates from Middle America and Andean South America in different common bean races. *Plant Dis.* **79**: 63-67.
- PEARSALL, D. M., 1992. The origins of plant cultivation in South America. In: C. W. Cowan and P. J. Watson (eds.) The origins of agriculture - An international perspective. Smithsonian Institution Press, Washington, D.C. USA. pp. 173-205.
- PIÑERO, D., L. EGUIARTE, 1988. The origin and biosystematic status of *Phaseolus coccineus* subsp. *polyanthus*: electrophoretic evidence. *Euphytica* **37**: 199-203.
- PIPER, C. V., 1926. Studies in American Phaseolinae. *Contr. US Nat. Herb.* **22**: 663-701.
- PRATT, R. C., G. P. NABHAN, 1988. Evolution and diversity of *Phaseolus acutifolius* genetic resources. In: P. Gepts (ed.) Genetic Resources of *Phaseolus* Beans. Kluwer Academic Publishers, Dordrecht, Holland. pp. 409-440.
- RAMÍREZ DELGADILLO, R., A. DELGADO SALINAS, 2000. A new species of *Phaseolus* (Fabaceae) from west-central Mexico. *SIDA* **18**: 637-646.
- RICH, P. V., T. H. RICH, 1983. The Central American dispersal route: biotic history and paleogeography. In: D.H. Janzen (ed.) Costa Rican Natural History. The University of Chicago Press, Chicago, USA. pp. 12-34.
- RYDBERG, P. A., 1965. Flora of the prairies and plains of Central North America. Facsimile of 1932 edition. Hafner Publishing Co., New York, USA, 969p.
- SANDLIN, C. M., J. R. STEADMAN, C. M. ARAYA, D. P. COYNE, 1996. Bean rust pathogen isolates show specific virulence to Andean-origin bean landraces. *Annu. Rept. Bean Improvement Coop. (USA)* **39**: 80-81.
- SAUER, J. D., 1967. The grain amaranths and their relatives: a revised taxonomy and geographic survey. *Ann. Missouri Bot. Gard.* **54**: 103-137.
- SCHINKEL, C., P. GEPTS, 1988. Phaseolin diversity in the tepary bean, *Phaseolus acutifolius* A. Gray. *Plant Breeding* **101**: 292-301.
- SCHMIT, V., J. P. BAUDOIN, 1987. Multiplication et évaluation de *Phaseolus coccineus* L. et *Phaseolus polyanthus* Greenm., deux espèces intéressantes pour l'amélioration de la productivité des légumineuses vivrières. *Bull. Rech. Agron. Gembloux* **22**: 235-253.
- SCHMIT, V., J. P. BAUDOIN, 1992. Screening for resistance to *Ascochyta* blight in populations of *Phaseolus coccineus* L. and *P. polyanthus* Greenman. *Field Crops Res.* **30**: 155-165.
- SCHMIT, V., J. P. BAUDOIN, 1993. Intraspecific hybridizations in the food legume *Phaseolus polyanthus* Greenm. *Annu. Rept. Bean Improvement Coop. (USA)* **36**: 34-35.
- SCHMIT, V., D. G. DEBOUCK, 1990. *Phaseolus glabellus* Piper, a noteworthy variant of the *P. coccineus* complex? *Annu. Rept. Bean Improvement Coop. (USA)* **33**: 124-125.
- SCHMIT, V., D. G. DEBOUCK, 1991. Observations on the origin of *Phaseolus polyanthus* Greenman. *Econ. Bot.* **45**: 345-364.
- SCHMIT, V., D. G. DEBOUCK, J. P. BAUDOIN, 1996. Biogeographical and molecular observations on *Phaseolus glabellus* (Fabaceae, Phaseolinae) and its taxonomic status. *Taxon.* **45**: 493-501.
- SCHMIT, V., P. DU JARDIN, J. P. BAUDOIN, D. G. DEBOUCK, 1993. Use of chloroplast DNA polymorphisms for the phylogenetic study of seven *Phaseolus* taxa including *P. vulgaris* and *P. coccineus*. *Theor. Appl. Genet.* **87**: 506-516.

- SCHOBINGER, J., 1994. The first Americans. William B. Eerdmans Publishing Company, Grand Rapids, Michigan, USA, 195p.
- SINGH, S. P., 1992. Common bean improvement in the tropics. *Plant Breeding Reviews* **10**: 199-269.
- SINGH, S. P., 1999a. Improvement of small-seeded race Mesoamerica cultivars. In: S. P. Singh (ed.) Common bean improvement in the twenty-first century. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 255-274.
- SINGH, S. P., 1999b. Integrated genetic improvement. In: S. P. Singh (ed.) Common bean improvement in the twenty-first century. Kluwer Academic Publishers, Dordrecht, The Netherlands. pp. 133-165.
- SINGH, S. P., P. L. GEPTS, D. G. DEBOUCK, 1991. Races of common bean (*Phaseolus vulgaris*, Fabaceae). *Econ. Bot.* **45**: 379-396.
- SMARTT, J., 1980. Evolution and evolutionary problems in food legumes. *Econ. Bot.* **34**: 219-235.
- SMARTT, J., 1990. Vavilov's Law of Homologous Series and *de novo* crop plant domestication. *Biol. J. Linnean Soc.* **39**: 27-38.
- SONNANTE, G., T. STOCKTON, R. O. NODARI, V. L. BECERRA VELÁSQUEZ, P. GEPTS, 1994. Evolution of genetic diversity during the domestication of common bean (*Phaseolus vulgaris* L.). *Theor. Appl. Genet.* **89**: 629-635.
- SOUSA SÁNCHEZ, M., A. DELGADO SALINAS, 1993. Mexican Leguminosae: phytogeography, endemism, and origins. In: T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa (eds.), Biological diversity of Mexico: origins and distribution. Oxford University Press Inc., New York, USA. pp. 459-511.
- STANDLEY, P. C., 1937. Flora of Costa Rica. *Field Mus. Nat. Hist. Bot.* **18**: 1-1616.
- STANDLEY, P. C., J. A. STEYERMARK, 1946. Flora of Guatemala - Part V. *Fieldiana, Botany* **24**: 1-502.
- STAVELY, J. R., M. A. PASTOR-CORRALES, 1989. Rust. In: H. F. Schwartz & M. A. Pastor-Corrales (eds.), Bean production problems in the tropics. 2nd edition. Centro Internacional de Agricultura Tropical, Cali, Colombia. pp. 159-194.
- TOHME, J., D. O. GONZÁLEZ, S. BEEBE, M. C. DUQUE, 1996. AFLP analysis of gene pools of a wild bean core collection. *Crop Sci.* **36**: 1375-1384.
- TOHME, J., O. TORO, J. VARGAS, D. G. DEBOUCK, 1995. Variability studies in Andean *nuña* common beans (*Phaseolus vulgaris*, Fabaceae). *Econ. Bot.* **49**: 78-95.
- TORO, O., L. LAREO, D. G. DEBOUCK, 1993. Observations on a noteworthy wild Lima bean, *Phaseolus lunatus* L., from Colombia. *Annu. Rept. Bean Improvement Coop. (USA)* **36**: 53-54.
- TORO CH., O., J. TOHME, D. G. DEBOUCK, 1990. Wild bean (*Phaseolus vulgaris* L.): description and distribution. Centro Internacional de Agricultura Tropical, Cali, Colombia, 106p.
- URBAN, I., 1928. Plantae cubenses novae vel rariores a clo. Er. L. Ekman lectae. IV. Symbolae Antillanae **9**: 433-568.
- VAVILOV, N. I., 1922. The law of homologous series in variation. *J. Genet.* **12**: 47-89.
- VAVILOV, N. I., 1949. Phyto-geographical basis of plant breeding. (initially published in 1935 in *Teoreticheskie osnovy selektsii*, 1). *Chron. Bot.* **13**: 13-54.
- VERDCOURT, B., 1970. Studies in the Leguminosae-Papilionoideae for the Flora of Tropical East Africa. IV. *Kew Bull.* **24**: 507-569.
- WEISETH, G., 1954. Una variedad silvestre del poroto común (*Phaseolus vulgaris* L.), autóctona del noroeste argentino y su relación genética con variedades cultivadas. *Rev. Agron. Noroeste Arg.* **1**: 71-81.
- WILCZEK, R., 1954. Phaseolinae. Flore du Congo Belge et du Rwanda-Burundi. Bruxelles, Belgium, pp. 260-409.
- WOLFENBARGER, D., J. P. SLEESMAN, 1961. Resistance to the potato leafhopper in Lima bean lines, interspecific *Phaseolus* crosses, *Phaseolus* spp., the cowpea, and the Bonavist bean. *J. Econ. Entomol.* **54**: 1077-1079.
- ZAPATA, M., G. F. FREYTAG, R. E. WILKINSON, 1985. Evaluation for bacterial blight resistance in beans. *Phytopathology* **75**: 1032-1039.
- ZEITLIN, R. N., J. F. ZEITLIN, 2000. The paleoindian and archaic cultures of Mesoamerica. In: R. E. W. Adams and M. J. Macleod (eds.), The Cambridge history of the native peoples of the Americas. Vol 2 Part 1. Cambridge University Press, Cambridge, UK. pp. 45-121.
- ZOHARY, D., M. HOPF, 1993. Domestication of plants in the Old World. 2nd edition. Clarendon Press, Oxford, United Kingdom, 278p.