

The common bean has been part of the Great American Biotic Interchange: evidence from the study of cpDNA and implications for conservation and breeding*.





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Introduction

What do spectacled bears, deers, tree sloths, opossums, oaks, and common beans share in common? During the evolutionary history of their respective species in the Americas they have all crossed the Isthmus of Panama. North and South America are two land masses that became united only recently (by the late Pliocene, or 3.5 to 2 millions years ago; Coates et al. 2004), and their fauna and flora have had a long evolution in isolation before the Great American Biotic Interchange (Webb 1997).

The distribution of wild common bean (Phaseolus vulgaris L.) from northern Mexico to northwestern Argentina over 8,000 km is a discontinuous one (Freytag & Debouck 2002; Toro et al. 1990), probably resulting from local expansions and extinctions of natural populations, over thousands of years, long before humankind came into America through Bering (Crawford 1998). Molecular markers uniquely found in the wild as compared to the cultivated materials (Khairallah et al. 1992; Koenig et al. 1990; Tohme et al. 1996) allow concluding that the wild forms do not derive from the latter by regressive mutations. Such molecular markers, not only revealed the two major genepools in the wild (see also Becerra & Gepts 1994), but indicated evidence for considering a Pacific genepool (see also Kami et al. 1995), and a North-Andean one; in addition there would be reason for seeing the Guatemalan wild forms as distinct from the Mexican ones. Geological barriers for the distribution of wild common bean (the Isthmus of Tehuantepec, Lake Nicaragua, and the Darien Gap) - a species of the subhumid seasonal montane forests of the Neotropics (Freytag & Debouck 2002) - and this genetic heterogeneity naturally raise: how did this range of distribution over 8,000 km come into being?



Figure 1. Geographic distribution and frequency of 14 chloroplast haplotypes (graph pies).



Figure 2. Unrooted network of chloroplast haplotypes using ARLEQUIN 2000. Observed haplotypes with capital letter (in a dotted box when interior), with a black dot when missing (extinct?). One- (indicated 1-1 and 1-8) and two-step (2-1 and 2-3) clades are indicated by boxes, dotted and solid lines, respectively. Number of observed haplotypes are indicated by a figure within each box. The sister species link with the root of the network at haplotype 'A'.

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Results and Discussion

The chloroplast DNA supposedly invariant within a species (see discussion by Soltis et al. 1992) and here maternally inherited (Corriveau & Coleman 1988) when investigated on 106 wild and 20 weedy forms for seven non-coding regions reveals fourteen polymorphisms or haplotypes (Chacón et al. 2005, 2007). These haplotypes are not distributed at random, displaying some continuous ('L' in Mexico, Guatemala to Colombia), or localized ('E' in the Pacific range, 'H' in Costa Rica), or disjunct ('A' in Mexico and Bolivia) distribution (Fig. 1). The haplotypes can also be studied by means of Nested Clade Analysis (Templeton et al. 1995) and Mantel test as implemented in ARLEQUIN 2000 (Schneider et al. 2000). The haplotypes form a network (Fig.2) linked to the sister species of Phaseoli (Freytag & Debouck 2002), P. costaricensis and P. dumosus, through haplotype 'A' that can be considered as ancestral. The haplotypes can be grouped into one- and two-step nested clades along rules established by Templeton and co-workers (1987, 1993), resulting into three lineages of increased but differential speciation, and likely migration events. The first lineage differentiates little but is present in both subcontinents. The second lineage differentiates in the Pacific Andean range and from there into Central America. The third lineage differentiates in Mexico and then Central America up to Colombia.

Using ITS sequences retrieved from GenBank and divergence age estimates for legumes set by Lavin and co-workers (2005), Chacón et al. (2007) estimate that P. vulgaris separated from its sister species about 1.3 million years ago, and that the second lineage diverged by 0.6 million years ago. Gepts et al. (2000) estimated the separation of P. vulgaris from its sister species P. coccineus at 2 millions years ago, and the separation of the Mesoamerican and Andean genepools at 0.5 million years ago.

These results suggest the following points for discussion. First, P. vulgaris separates from a cluster of four sister species (= its secondary genepool), confirming early results (Debouck 1999; Delgado et al. 1999). Second, because of the current location of such sister species, it is likely that the separation took place in southern Mesoamerica, with an early migration into the Andes, once the Isthmus of Panama was established (as did Quercus, Alnus and Juglans; Gentry 1982). Third, another migration took place later from the Andean region into Mesoamerica (as did Gunnera, Podocarpus, and Weinmannia; Rzedowski 1993). Wild common bean continues thus its evolution between two continents, now under heavy pressure by humans, and breeders may find in its migrations during the early Pleistocene the reasons for their mishaps in breeding (e.g. Gepts & Bliss 1985).

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