A re-assessment of the beans of the last . . . and the future harvest

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Beans! Today to some of us the word evokes well cooked food of the pot in winter (Albala 2007), to others colorful salads of the summer (Dragonwagon 2011), to fewer who traveled deep into the central Andes an attractive toasted grain (National Research Council 1989). Beans have often been the food of last resort in impoverished suburbs, or on long journeys into the unknown during the 19th century, or on ships wandering in stormy seas, because in contrast to many food items they are a highly nutritive and well balanced food that stores well. These two key properties explain their worldwide adoption, well reflected by the numerous vernacular names (some reported by Davidson 2006), and being among food legumes only second to soybean and peanut (both being grown largely for their oil content). Today as dry bean they are the daily food of millions of people across Central America, Brazil and eastern and southern Africa (Broughton et al. 2003), and as snap bean a vegetable of worldwide importance (Silbernagel et al. 1991). But before Columbus landed in San Salvador of the Bahamas (Bergreen 2011), beans were one of the few staples on which relied thousands of Amerindians for their daily food intake (De la Vega 1609; Estrada-Lugo 1989; Parodi 1966; Soustelle 1955).

Being rightly acknowledged as 'the meat of the poor' (Heiser 1990, p. 117), these food plants of the legume family raise the following questions in their relationships with humans: which are these plants?, where and how did humans come into contact with them?, when did the relationships begin?, and why did they become established? Checking the naming of beans might be one way to start, because names might tell us something about aspects of the relationships such as geographical origin, purpose or history. Extended lists of vernacular names have been provided elsewhere for the tepary (Nabhan & Felger 1978), the scarlet runner (Bukasov 1930; Martínez 1979), the year-bean (Schmit & Debouck 1991; Hernández-Xolocotzi et al. 1959), the Lima bean (Chacón et al. 2012; Martínez 1979), and the common bean (Brown 2006; Martínez 1979; Voysest 1983) (some of them reported in Table 1 as examples). Although such lists were not available to him, De Candolle (1883) after studying the nature of names of food legumes available in the Old World, raised doubts about an origin of the later two beans in it. Going further along his argument, one notes the many derived words as the distance increases from the nuclear area of diversity where the bean crop seems present for centuries or millennia, and naturally the bean crop there has a specific name in the language locally spoken. One should note that all vernacular names in native languages in the Neotropics were given by the Amerindians of the first migration into the Americas after crossing Beringia some 20-15,000 years ago (Cavalli-Sforza 2000; Cavalli-Sforza et al. 1994). If linguists agree on durations of 6,000 years for the development of individual languages (Crystal 1997; Dixon 1997; Greenberg 1987; Nichols 1998), this would mean that some of the vernacular names in the aforementioned lists and in Table 1 have been assigned to the respective bean crop almost since the beginning of the relationship with humans. The Oto-Manguean languages (e.g. Mixtec, Zapotec) trace back through glottochronology to 5,200 years before present (b.P.) (Brown 2006); this author gave a date of 2,400 years b.P. for the Zapotec term for bean, while the archaeological record for beans at Monte Alban gave 2,000 years b.P. (Kaplan & Lynch 1999). Interestingly, native languages in northeastern America before 700 years b.P. lack names for common bean (Brown 2006), and this is compatible with a late introduction from Mesoamerica as shown by archaeological records (Kaplan & Lynch 1999).

Which are these plants?

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Beans include five species that have entered the human *domus* (Harlan 1992), that is, have become domesticated or dependent on humans for survival through the harvest of pods, conservation and planting of seeds at the right time in the right place. This result has been obtained originally through the alteration of pod dehiscence (Gepts & Debouck 1991) (Figure 1); conversely humans had the seed for their own consumption but were obliged to keep planting until now this induced artifact. The causative mutation responsible for the alteration of pod dehiscence is due to a major Quantitative Trait Locus being in linkage group 2 where the QTLs controlling pod length and reduced dormancy are also found (Papa et al. 2007), and is likely ancient (Meyer & Purugganan 2013). Authors (Harlan 1992; Heiser 1990; Pearman 2005; Sauer 1993) mentioned four domesticated species, but a fifth case has been established (Schmit & Debouck 1991), because of the identification of a distinct wild ancestor for all of them. The genus *Phaseolus* of about eighty species (Freytag & Debouck 2002; Porch et al. 2013) has contributed seven bean crops (Table 2), all from the same clade (Delgado-Salinas et al. 2006). Such a high number of cultigens is relatively uncommon in the plant kingdom (rather concentrated in few plant families: Meyer & Purugganan 2013), but has happened in other genera, namely *Capsicum*, *Cucurbita*, and *Solanum*, all in the Neotropics. One should note that the seven domestication events seem to be independent, in terms of botany, space and time.

Although more data are needed for confirmation, the genus *Phaseolus* might be 7-10 million years old (Delgado-Salinas et al. 2006; Serrano-Serrano et al. 2010); it split into two clades about five million years ago (Delgado-Salinas et al. 2006). This happened during the Pliocene in the southwestern corner of Laurasia (Sousa-Sánchez & Delgado-Salinas, 1993), while the closing of the Isthmus of Panama would be completed by 3.2 million years ago (Coates 1997; Graham 2011). About 4-3.5 million years ago a separation happened that would result in the currently identified sections *Paniculati* (including the Lima bean) and *Phaseoli* (including the common bean, the scarlet runner and the year-bean) (Delgado-Salinas et al. 2006; Serrano-Serrano et al. 2010). This would explain the genetic distance and impossibility to cross *P. vulgaris* with *P. lunatus* (reviewed by Debouck 1999). About 2.5 million years ago (Delgado-Salinas et al. 2006) another splitting happened that resulted in the separation of the section *Acutifolii* (including the tepary) from the section *Phaseoli*, explaining the difficulty to cross the former with *P. vulgaris* (Muñoz et al. 2004; Waines et al. 1988). In the *Phaseoli* the species would differentiate from one another about 2-1.3 million years ago (Chacón-Sánchez et al. 2007; Gepts et al. 2000). The major gene pools identified in wild *P. vulgaris* (Kwak & Gepts 2009; Tohme et al. 1996) would have separated about 500,000 years ago (Chacón-Sánchez et al. 2007), a duration over which minor morphological (Brücher 1988; Delgado-Salinas et al. 1988), physiological (González-Mejia et al. 1995) and genetic (Koinange & Gepts 1992) differences become established. When the would-be Amerindians walked through Beringia into the Americas some 20-15,000 years ago (Wells 2003; Zimmer 2005), they found some eighty wild species, two of them viz. *P. lunatus* and *P. vulgaris* being distributed north and south of Isthmus of Panama.

Where did Amerindians come in contact with beans?

The diversity of vernacular names given by Amerindians (Table 1, as an example) is a clear indication that these peoples knew many bean species for long in many parts of the respective ranges of distribution. So visual contact has been there for sure, but plant parts have been looked for too. Some use of wild *Phaseolus* species has been reported in the recent past: roots of *P. coccineus* (Hernández 1615) or *P. maculatus* (Nabhan et al. 1980), pods of *P. filiformis* (Nabhan 1985), seeds of *P. acutifolius* (Felger & Wilder 2012) or *P. vulgaris* (Brücher 1954), and it is likely that such uses go well back into the past. But as aforementioned, in seven cases the relationships went further, five bean species became domesticated, with an enormous stock of varieties fully depending on humans for survival.

Arguing about a place of domestication – because this is *the* major change - is uneasy for three reasons. First, it is not sure that the entire process extending over centuries can be completed in a small area. A good example in common bean is race 'Nueva Granada' that originated in the central Andes (Chacón-Sánchez et al. 2005) and acquired its final characteristics in the northern Andes (Singh et al. 1991). Another example is cassava, where the domestication process could have started in southwestern Amazonia (Léotard et al. 2009; Olsen & Schaal 2001), while this root crop was part of the classic Mayan agricultural system (Sheets et al. 2012). A third example is Flint corn, an early migrant to the northeast during the domestication of maize (Matsuoka et al. 2002), but key for the development of hybrid corn when crossed with southern Dents (Doebley et al. 1988; Galinat 1992). Second, it is not sure either that the geographic range of the wild progenitor has not experienced any change. Over short durations, for example a few centuries, oscillations in altitude are possible (in the Andes: Cardich 1985), but over millennia the wild bean progenitors have experienced major shifts in their ranges (Chacón-Sánchez et al. 2007; Rossi et al. 2009; Serrano-Serrano et al. 2010). One could think about climatic alterations as the driving forces behind (Buckler et al. 1998; Graham 2010), causing the highly structured gene pools in the wild, as evidenced by molecular marker studies (Andueza-Noh et al. 2013; Kwak & Gepts 2009; Tohme et al. 1996). However, it is possible to find and use markers that are neutral towards human selection, and with a low rate of mutation, mode of inheritance and such complexity so that a wild bean can be inferred as the progenitor of a cultigen. But the third call for caution may come from the gene flow between cultivated landraces and wild forms, and this has been shown to happen in Mesoamerica (Papa & Gepts 2003) and in the Andes (Beebe et al. 1997). So local putative wild ancestors may reflect the genetic makeup of beans transported by people from elsewhere, if the molecular marker is not selected carefully. One reason behind this is that early domesticators rarely select directly for modifications in mating systems of crop plants, but on phenotypic traits visually attractive such as size or color of fruits or seeds. Bearing these remarks in mind, a few places have been identified (Table 2); as we see below let us call them 'places of last harvest'. They are certainly unconspicuous in relation to bean production today, and just look as isolated spots in the entire geographic range of the wild forms. At this time a third domestication event in Lima bean, namely from wild forms distributed in Central America, cannot be discarded (Andueza-Noh et al. 2013). We simply (!) need a better sampling of wild forms and landraces from that area as well as from tropical South America. The marked founder effect associated with bean domestications (Table 3) would suggest that the founding populations were indeed not numerous, leaving untouched most of the genetic diversity in the wild.

When did the relationships initiate?

The relationships between beans as domesticates and humans started about 8,000 years ago (for the common bean, on the basis of genetic data: Mamidi et al. 2011). Archaeological records tell us a different story particularly in Mesoamerica (Table 4), but one can anticipate that with further findings genetic and archaeological data will eventually reconcile. Interestingly, the glottochronological data indicate a date of 3,400 years b.P. for the Quiché in western Guatemala (Brown 2006). A parallel can here be drawn with maize, where recent archaeological findings (Piperno et al. 2007, 2009) in contrast with the old records (Cohen 1978; Mangelsdorf et al. 1967) have become much in line with genetic data (Matsuoka et al. 2002; Smith 2001). They all point to a single domestication in the Balsas region of Guerrero, Mexico, from the *parviglumis* teosinte about 8,700 years ago (Piperno et al. 2009). This reconciliation for the beans pending, four considerations are however possible. First, particularly in Mesoamerica, five bean domestication events suggest that any of them could be equally ancient: early domesticators would hardly re-start the process for another species if they have in hand an already well domesticated bean. But if not equally ancient the domestication events look geographically independent (Table 2), perhaps along the same rationale. The hypothesis of relay domestication once discussed for common and tepary bean (Pratt & Nabhan 1988) is thus not certain, even if wild forms of both species can be found together at different sites (Debouck 2000a). Interestingly, the initial domestication events for the beans in Mesoamerica seem to be outside the Balsas region.

Second, domestication events involving common and Lima beans are ancient in the Central Andes, with - for the time being - earlier dates as compared to W Mexico (Table 4). Again such events seem geographically independent (Table 2). The reader may wonder why only Lima and common bean were domesticated in South America. The reason is that only these two species crossed the Isthmus of Panama as wild forms, first the Lima bean (Serrano-Serrano et al. 2010) and later the common bean (Chacón-Sánchez et al. 2007). As explained elsewhere (Schmit & Debouck 1991), *P. dumosus* (syn. *P. polyanthus*) exists in the northern Andes as a crop and as a weedy escape from cultivation. Because all maize races seem to come originally from Mexico and because Andean highland maize races seem to have a tropical origin (Matsuoka et al. 2002) – they migrated southeastward through Central American lowlands first! -, this would mean that there was a period of two thousand years when common and Lima beans were grown in the Central Andes in absence of maize. Absence of maize could also have been the context of tepary domestication in NW Mexico, but for ecological reasons (not sufficient rainfall to support the bean-corn association). As noted by Kaplan & Kaplan (1988), this association came after the separate domestication of its components. But the abundance of beans in archaeological deposits seems to be linked to the presence of maize (Kaplan & Lynch 1999). That said, it seems that archaeologists have focused their attention only on macrofossils, while microfossils (starch grains, mineralized hooked hairs) have not yet been exploited to the extent possible (Bozarth 1986; Piperno 2012). And microfossils should be exploited at archaeological sites close to the putative sites of last harvest. Third, in contrast with maize (Grobman & Bonavia 1978; Mangelsdorf et al. 1967), a transition in seed size from the wild state has not been found for any bean cultigen in archaeology so far (Kaplan 1967, 1981). Because of the complex inheritance of seed size (Koinange et al. 1996), one would thus expect earlier dates as compared to the few currently available. Fourth, although dating methods have altered some dates (Kaplan & Lynch 1999), archaeologists have often found early beans in absence of ceramics (pC for pre-ceramic horizon in Table 4). The repetition of such absence across sites for the oldest records can hardly be considered as an artifact, even if ceramics already existed elsewhere. [The earliest records of pottery in the Americas are of 7,000 years b.P. (Taperinha, Amazonia, Brazil; Roosevelt 1995) and 5,300 years b.P. (Monsú, Bolivar, Colombia; Reichel-Dolmatoff 1985), with a couple of more recent independent inventions (coastal Ecuador: 5,000 years b.P.; coastal Georgia: 4,800 years b.P.: Clark & Gosser 1995), but with no beans at these sites]. And this non-pottery context that some might think crucial for food processing (Wrangham & Conklin-Brittain 2003) leads us to the reason(s) for bean domestication.

Why have beans been domesticated?

The answer to this question will always be speculative because the possibility of interviewing the first domesticators has gone a long time ago as we have seen. In addition, the only two scripts known in all pre-Columbian America – Mixtec and Mayan - appeared in the last millennium before our era (Diamond 1997; Robinson 2007), quite late to record anything about the early domestication events. Further, it is not certain that there would have been a single reason for the seven cases (Table 2), nor that the original reason would have remained the same during the first millennia of the domestication process, namely as food processing technology developed. In this regard, one has to remind that seeds of wild beans are likely to be toxic to humans because of the presence of, among others, prussic acid precursor (Seigler et al. 1989), lectins (van der Poel 1990), antitrypsin factors (Lioi et al. 2010), α-amylase inhibitor (Pueyo & Delgado-Salinas 1997) and tannins (Espinosa-Alonso et al. 2006). The practice of soaking beans overnight and throwing the water away in the morning was not by chance, but a safe way to survive over a plate full of beans! The question thus might be tackled from different perspectives, such as: why beans at all? why *Phaseolus* beans and not species of another tropical legume such as *Mucuna*? why the beans for the purposes we know? why the populations at these locations (Table 2)? Bearing these points in mind, a couple of observations can be made.

First, the food value could well have been a driving force, if not directly at least indirectly (I mean, the natural selection and survival of those who did succeed in domesticating beans). Domestication of beans in the Americas appeared in a non livestock context, in contrast to pulses of the Old World (thus limiting our cross-comparisons). Absence of livestock may be the consequence of overhunting by the first Americans after crossing Beringia (Wilson 1992), or lack of appropriate behavior in the American fauna that survived extinction (Diamond 2012). During the first 10,000 years of hunting-gathering the Amerindians had time to know the extent of flora across the Americas. It has been repeatedly demonstrated (e.g. the Mixe in Oaxaca: Lipp 1998, or the Tzotzil in Chiapas: Breedlove & Laughlin 1993) that Amerindians had a profound knowledge of their local flora within each territory. Because of the climatic alteration 'Younger Dryas' (Wells 2010) and decreasing food resources (Buckler et al. 1998), some Amerindians changed behavior and started planting and harvesting some plants out of that vast repertoire. Abundant grasses and legumes were likely candidates if it was to fill a carbohydrate-protein equation after all. A kind of 'return on investment' may matter here: wild *P. microcarpus* Mart. (Fig. 2) and *P. vulgaris* (Fig. 1) might be equally widespread in some parts of central Mexico (Freytag & Debouck 2002), but the tiny one-seeded pods of the former did not help toward domestication, that eventually affected the latter. The big pod of *P. chiapasanus* Piper (Freytag & Debouck 2002) would surely confer a headstart (Fig. 2) but who knows it? Who has come across its few populations scattered in Chiapas, Oaxaca or Veracruz (Debouck 2013)? Perhaps with the exception of *P. dumosus*, one can note that all wild bean progenitors have a wide range of distribution; endemic species such as *P. macrolepis* Piper or *P. plagiocylix* Harms (Freytag & Debouck 2002) were not domesticated. That characteristic of the range helped *a priori* making these legumes more familiar to would-be domesticators, and *a posteriori* because planting – a fundamental act in domestication (Harlan 1992) – would be more successful with a wide range bean than with one of highly specialized ecology. In relation to the wide range, one should mention the hypothesis of the colonizing behavior of many of our crop wild relatives (Anderson 1952; de Wet & Harlan 1975; Hawkes 1969; Heiser 1969), that is, the capacity to reproduce and expand quickly in human made habitats. Notwithstanding the profound alteration of *Phaseolus* habitats over the last century, namely because of the expanding road network, it is likely to be the case for wild *P. coccineus, P. lunatus* and *P. vulgaris.* According to Sousa-Sánchez & Delgado-Salinas (1993), these three species have benefitted from human disturbance, but it might be the result of an intrinsic colonizing capacity. Back on the 'return on investment' for would-be domesticators, pods of legume species such as *Desmodium, Macroptilium* or *Mucuna* – although widely distributed in some parts of the Neotropics - would have had too many drawbacks (almost indehiscent loments, narrow width, itchy pubescence, respectively) to make them good candidates, while a few, relatively abundant *Phaseolus* species with high proteins and carbohydrates under low seed volume yet sizeable did. Paying further attention to pods – the first item catched by hand, one notes that *Canavalia, Inga* and *Phaseolus* with smooth pod epidermis in many widespread species contributed candidates for domestication.

Second, most legume species have defense mechanisms that protect their seeds, among them antinutritional factors to deter potential eaters, and *Phaseolus* species are no exception (Johns 1990; Lioi et al. 2010; Mirkov et al. 1994). Although this point has already been discussed elsewhere (Debouck 2000b), it might be worth updating. Eating young pods is an option, before antinutritional factors start accumulating in the seeds in the second fortnight close to maturity (for example, cyanide content in wild Lima bean: Frehner et al. 1990; or lectin in *P. lunatus*: Martin et al. 1964). In doing so, would-be domesticators are just following the example of birds (in spite of the differences in digestive tracks), as populations of wild beans show pod damages by birds (Debouck et al. 1993; also vouchers CR235450, US3168338 at these Herbaria). The use of green (immature to nearly mature) pods persists after ceramic was invented: the Mexicans today use the word '*ejote*' for it, an obvious modification of the word '*éxotl*' in nahuatl and early codices (Estrada-Lugo 1989; Vela 2010) for the same young pod. Given the very hard fruit cases of teosinte, Harlan (1995) after his own testing proposed that the ancestor of maize was first used as a vegetable. Another use – chewing the sugary stalks – although still seen in Mexico (Iltis 2000) seems not confirmed in early domestication steps (Piperno 2012). Of course cooking makes us essentially humans (Wrangham & Conklin-Brittain 2003; Wrangham & Carmody), but as seen in Table 4 domesticated beans existed before the appearance of ceramics at these sites, although apparently at low frequency in the archaeological layers (Kaplan & MacNeish 1960). But grains might be put close to a heat source, and dry roasting has been shown to reduce lectin haemagglutinating and trypsin inhibitor activities in common bean (van der Poel 1990). Interestingly, when dealing with grains, Amerindians first thought about toasting, that is, the direct exposure of grains to a heat source. This reaction is particularly relevant in altitude sites above 2,000 masl, where longer durations are required to cook the beans given the lower atmospheric pressure (National Research Council 1989). Amerindians did that for maize: across Latin America the most primitive races are popcorn (in Jalisco: 'Reventador', Anderson 1944, or 'Nal-Tel', Zizumbo-Villareal et al. 2014; in México: 'Palomero Toluqueño', Wellhausen et al. 1952; in Cundinamarca: 'Pira', Roberts et al. 1957; in Junín: 'Confite Morocho', Grobman et al. 1961; in Cuzco: 'Kculli', Grobman et al. 1961; in Potosí: 'Confite Puneño', Ramírez et al. 1960; in Cochabamba: 'Checchi', Freyre et al. 1996; in Jujuy: 'Pisingallo', Cámara-Hernández & Arancibia de Cabezas 2007). They did that for tepary and common bean in New Mexico (Kaplan 1956), for common bean in Jalisco and Oaxaca of Mexico (Zizumbo-Villareal et al. 2012; Kaplan 1965, respectively), for tepary in Puebla of Mexico (Kaplan 1967), or for common bean in the highlands of Peru and Bolivia (National Research Council 1989; Tohme et al. 1995), and confirmed in pre-Columbian times in Peru and Chile (Kaplan & Lynch 1999). They did that for amaranth too (National Research Council 1984; Sauer 1950). Some of these traditional uses of cooking without ceramics and the related germplasm have survived up to now, and are subject of renewed interest (National Research Council 1989). So there were good reasons to pick up seeds of wild beans and to plant them for food, at least to avoid walking for hours or days to get back to the original population. And one day the non dehiscent pod mutant appeared . . . There was no need to go back to the wild because a completely different evolutionary path was borne in a modified environment - the future cultivated field *milpa* or *chacra*; that mother wild population was the one of the last harvest!

Third, as aforementioned bean became abundant in the (Mesoamerican) record once maize agriculture intensified. As apparent in Table 5, maize (or Indian corn, a widely accepted vernacular name among English speaking immigrants into the New World) turned into the cornerstone of pre-Columbian agriculture, in Mesoamerica where it was domesticated and in South America where it was introduced (Matsuoka et al. 2002). The protein of maize was deficient in two essential amino acids, lysine and tryptophan (Heiser 1990); the former was complemented by beans, and the latter by some animal protein (and partly the potato in the Andes). That type of diet was unconsciously selected because it made people well fed (Ortiz de Montellano 1990), and secured the physical and intellectual development of childhood. As well noted by McNeill (1998, p. 212), "domesticated animals played a merely marginal part in human food patterns" in pre-Columbian America. With no buffering that is livestock in agricultural systems, many Amerindians were year after year pending on the success of their maize or bean crops. The beans being more tolerant to drought in drought-prone area such as Mesoamerica, Amerindians always looked after them. Having not found any grass alternative to Indian corn in terms of productivity per plant, they never gave up their maize varieties. This can perhaps explain much of the diffusion of maize from western Mexico northward up to Canada (Heiser 1990; Ott 2012) and southward down to Chile (Wilhelm de Mosbach 1992), almost matching that of beans (Kaplan & Kaplan 1992). At least for the five bean cultigens (just as it was for maize), the domestication process seems continuous, not abandoned, even though tepary could have suffered a (recent) regression because of the watering facilities provided in Aridoamerica since the 1900s (Nabhan & Felger 1978). Market forces since the 1950s – linked to urbanization? - have not helped either to integrating the other three cultigens (Debouck 1992). But beyond nutritional aspects the maize-bean association seems to have been a performant agronomic system, namely thanks to the addition of squash, in order to limit soil erosion (Summer 2004). Interestingly, this system was widely adopted with selections of the three crops much beyond their original places of domestication. And one should note that apart from the brilliant idea to domesticate beans, maize or squash where unconscious elements might have played a role, the other brilliant idea – and fully conscious – was to combine the three crops together into a relatively stable agricultural system. Metallurgy came late (aproxim. 3,000 years b.P., for limited bronze axes) in pre-Columbian history (Root 1963), and thus agricultural implements were limited. Interestingly, the illustrations by Guamán Poma (Poma de Ayala 1615) showed the Incas using the *chakitaqlla* or foot-plough, not a plow driven by a llama, although the animal was there for limited carrying of goods. So externalities such as lack of draught animals and only manpowered tools (the *macana* or planting stick!) pushed Amerindians' skills in plant breeding to the limits (Harlan 1992); their resourcefulness, acute sense of observation and selections came along with unique and superb results, because their crops responded. This was a brilliant anticipation of what plant breeding can achieve.

Concluding remarks

The relationships between beans and humans have been long and fruitful because they allow both species to expand. For the first five thousand (or more) years, that expansion took place in the Americas, allowing together with maize an improved diet, a sustainable agricultural system, and there onwards a sustained demographic growth and a social stratification. Have you seen the most prestigious pre-Columbian civilizations (of Mesoamerica) on another food basis than the corn-beans association? In this system beans brought sustainability from a nutritional perspective for humans and for the soil (nitrogen input and reduction of erosion). Over the last five hundred years a similar expansion took place in the Old World with similar benefits, particularly in Africa (Crosby 2003). Understanding these relationships in the Americas above all during the early steps of bean domestication can have very significant impact in the new territories of bean adoption, namely the Old World tropics and subtropics, where foreign crops (mostly American: maize, beans, peanut, cassava, sweet potato) have been and continue to be critical to food security. Under similar ecological conditions it is well known that crops perform better outside their centers of original diversity (Jennings & Cock 1977), being free from their ever lasting co-evolving pests. And farmers worldwide have been among the first to note this, thus the speed in adoption; for example, the 'patani' (*P. lunatus*) (Safford 1917) of the Philippines could have landed there together with the ‘chilli’ (*Capsicum annuum* L.) (Andrews 1995) with the galleons sailing from Acapulco to Manila as early as 1570 a.D. (Merrill 1954).

Beyond expansion, another question that can be asked is whether or not we have been equal to the domestication efforts by Amerindians and the bean biological heritage they left us. The use of race ‘Mesoamerica’ of common bean (Singh et al. 1991) has been wide (Singh 1999), less so the other races. And bean breeders have not always realized that there are four more bean crops to breed in addition to common bean. Obviously bean breeding nowadays will be in reply to demand; so is our society sufficiently aware of coming food challenges and of options provided by *Phaseolus* beans? We may finally put hunger out of the list of Millennium Challenges, to quickly turn into overnutrition and health problems because of excessive consumption of animal proteins at the expenses of plant proteins (Pollan 2006). Facing an emerging energy crisis in food production, transportation and processing (Diamond 2005), green shelled beans may be an option to recover. Equally, the popping beans that we know were present in Mesoamerica might turn into an example of a lost opportunity. As never before, understanding the early steps of crop domestication in the Neotropics has been so relevant.

Acknowledgments

The help by Mariano Mejía to get rare publications is deeply acknowledged.

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Table 1 – Bean crops and some ancient vernacular names (languages classified along Greenberg 1987).

Bean crops	vernacular names	language spoken (root); place (state)	sources
tepary			
	mare'k	Yuma (Yuman); SW Arizona	Nabhan & Felger 1978
	nókwina	Zuni (Penutian-Zuni); W New Mexico	Nabhan & Felger 1978
	tepari	Opata (Uto-Aztecan); NE Sonora	Nabhan & Felger 1978
	muní	Tarahumar (Uto-Aztecan); W Chihuahua	Nabhan & Felger 1978
scarlet runner			
	shaushana	Totonaco (Totonac); N Puebla	Delgado-Salinas 1988
	ayocote	Nahuatl (Uto-Aztecan); N Puebla	Hernández X. et al. 1959
	chomborote	Mam (Mayan); San Marcos	Schmit & Debouck 1991
	piloy	Kakchiquel (Mayan); Chimaltenango	Schmit & Debouck 1991
year-bean			
	xuyumel	Totonaco (Totonac); N Puebla	Delgado-Salinas 1988
	acaletl	Nahuatl (Uto-Aztecan); N Puebla	Hernández X. et al. 1959
	dzich	Mam (Mayan); San Marcos	Schmit & Debouck 1991
	piloya	Kakchiquel (Mayan); Chimaltenango	Schmit & Debouck 1991
Lima bean			
	ib	Yucatec (Mayan); S Yucatán	Martínez 1979
	ixpanqué	Quiché (Mayan); Suchitepéquez	McBryde 1947
	pallar	Mochica (Paezan-Chimu); Lambayeque	Yacovleff & Herrera 1934
	palatu	Cochabamba (Quechua); E Cochabamba	Cárdenas 1989
common bean			
	ju	Otomi (Oto-mangue); C Hidalgo	Martínez 1979
	etl	Nahuatl (Uto-Aztecan); C Mexico	Vela 2010
	tatzin	Tarascan (Chibchan); NW Michoacán	Martínez 1979
	pi-zaa	Zapotec (Oto-mangue); C Oaxaca	Martínez 1979
	purutu	Quechua (Andean Amerind); C Peru	Soukup 1986
	miculla	Aymara (Andean-Aymara); Puno-La Paz	Yacovleff & Herrera 1934

Table 2 – Domestication events in *Phaseolus* beans.

Bean species and vernacular name	Possible area(s) of last harvest	Sources
P. acutifolius A. Gray, tepary	NW of Neo-volcanic axis in Mexico	Garvin & Weeden 1994; Muñoz et al. 2006
P. coccineus L., scarlet runner	Central Mexico or Honduras	Debouck & Smartt 1995; Spataro et al. 2011
P. dumosus Macfady., year-bean	Volcanic mountains of SW Guatemala	Schmit & Debouck 1991
P. lunatus L. (small-seeded), Sieva bean	W of Tehuantepec in Mexico	Motta-Aldana et al. 2010; Serrano-Serrano et al. 2012; Andueza-Noh et al. 2013
P. lunatus L. (large-seeded), Lima bean	SW of Ecuador and/or NW of Peru	Motta-Aldana et al. 2010; Debouck et al. 1987; Chacón et al. 2012
P. vulgaris L. (small-seeded), common bean	W of Neo-volcanic axis in Mexico	Chacón et al. 2005; Kwak et al. 2009
P. vulgaris L. (large-seeded), common bean	Central Peru: Apurimac and around it	Chacón et al. 2005

Table 3 – Founder effects associated with the domestication of the different bean species.

Bean species	Sources
Tepary	Garvin & Weeden 1994; Muñoz et al. 2006; Schinkel & Gepts 1988; Blair et al. 2012
Year-bean	Schmit & Debouck 1991
Lima bean	Andueza-Noh et al. 2013; Gutiérrez-Salgado et al. 1995; Motta-Aldana et al. 2010; Chacón-Sánchez et al. 2012; Serrano-Serrano et al. 2012
Common bean	Beebe et al. 2001; Mamidi et al. 2011; Papa et al. 2005; Sonnante et al. 1994

Table 4 – Some archaeological records for different bean cultigens.

Sites (place, state, country)	Years before present	Sources
for *P. acutifolius*		
Durango, Colorado, USA	1,200	Kaplan 1967
Tehuacan, Puebla, Mexico	2,300	Kaplan & Lynch 1999
for *P. coccineus*		
Ocampo, Tamaulipas, Mexico	1,100	Kaplan & Lynch 1999; Kaplan & MacNeish 1960
Río Zape, Durango, Mexico	1,100	Kaplan & Lynch 1999
Tehuacan, Puebla, Mexico	500	Kaplan & Lynch 1999
Guilá Naquitz, Oaxaca, Mexico	1,100	Kaplan & Lynch 1999
for *P. lunatus*		
Verde Valley, Arizona, USA	700	Kaplan 1956, 1967
Río Zape, Durango, Mexico	500	Kaplan & Lynch 1999
Tehuacan, Puebla, Mexico	1,200	Kaplan 1967
Dzibichaltún, Yucatán, Mexico	1,200	Kaplan 1967
Huacaloma, Cajamarca, Peru	2,400	Kaplan & Lynch 1999
Guitarrero, Ancash, Peru	3,400 (pC)	Kaplan & Lynch 1999
Ñanchoc, Lambayeque, Peru	8,000 (pC)	Piperno & Dillehay 2008
Chilca, Lima, Peru	5,600 (pC)	Kaplan 1980; Kaplan & Lynch 1999
for *P. vulgaris*		
Tularosa, New Mexico, USA	2,200	Kaplan 1965; Smith 2001
Ocampo, Tamaulipas, Mexico	1,300	Kaplan & Lynch 1999
Tehuacan, Puebla, Mexico	2,300	Kaplan & Lynch 1999
San Andrés, Tabasco, Mexico	2,300	Pope et al. 2001
Huitzo, Oaxaca, Mexico	2,100	Kaplan & Lynch 1999
Soconusco, Chiapas, Mexico	3,000	Piperno & Pearsall 1998
Darién, Valle, Colombia	2,000	Kaplan & Smith 1985; Piperno & Pearsall 1998
Chorrera, Manabi, Ecuador	2,700	Piperno & Pearsall 1998
Huacaloma, Cajamarca, Peru	2,600	Kaplan & Lynch 1999
Guitarrero, Ancash, Peru	4,300 (pC)	Kaplan & Lynch 1999; Lynch et al. 1985
Pichasca, Coquimbo, Chile	1,400	Kaplan & Lynch 1999
Antofagasta, Catamarca, Argentina	5,000 (pC)	Pearsall 1992; Rodríguez & Aschero 2007

(pC): the beans were found in a preceramic horizon.

Table 5 – Some food systems often found in agricultural pre-Columbian Americas.

Region	Main food sources	Complement	Sources
NW Mexico, Tarahumar	maize, beans	deer, mice	Lumholtz 1902
Central Mexico	maize, beans, amaranth	dog, fish, frog, turkey	Schwartz 1997; Soustelle 1955
Costa Rica	maize, beans, squashes	tepesquintle	Harlan 1995
Colombia	maize, potato, bean, manioc	fish, game	Hernández de Alba 1963
Coastal Peru	maize, Lima bean	fish, llama, dog	Schwartz 1997
Central Andes	potato, maize, bean, tarwi	guinea pig, llama	Sauer 1950
Southern Andes	maize, potato, bean		Parodi 1966
Araucania Chile	mangu, potato, maize, beans	fish, llama	Montaldo 1988; Wilhelm de Mosbach 1992
Guarani area	cassava, maize, peanut, bean	fish, rodents	Arenas 1992

Figure Captions

Figure 1 – Pods of *Phaseolus vulgaris* L. (wild, above; and cultivated, below).

Figure 2 – Pods of *Phaseolus microcarpus* Mart. (above) and *P*. *chiapasanus* Piper (below).