

The South American Wild Bean (*Phaseolus aborigineus* Burk.) as Ancestor of the Common Bean

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DEDICATION

Professor Ing. Agr. Arturo Burkart (1906–1975), the well known Leguminosae specialist and Professor of Botany at the University of Buenos Aires, died recently. We dedicate this article to his Memory.

INTRODUCTION

Two recent publications on wild and primitive beans in the Americas lead us to review earlier reports of South American authors covering the last twenty years which seem to have been neglected. Gentry (13) restricts the origin of the common bean to Mexico where he found *Phaseolus vulgaris* growing wild. But he rejects a South American origin for archeological reasons, “. . . cultivation was much earlier in Mexico, 7,000 BP. . . .” He believes that cultivated beans may have been carried further south by migrant tribes crossing the Equator. Gentry regards our South American wild bean (*Phaseolus aborigineus*) as an escape from early cultivation “as their seeds suggest.”

This point of view hardly stands up against our chemotaxonomic and phytogeographic arguments (2, 3, 6, 8, 11, 12, 20) which, at the time they were made, lacked archeological support, as the earliest findings of South American beans were considered to be only 2500 years old. With a recent publication describing very early

preceramic remains of primitive beans from Peru (probably 7,000–10,000 BP), the situation has changed. We refer to Kaplan, Lynch and Smith (23), who report a sensational find of early cultivated beans (*Ph. vulgaris*) from an intermontane Peruvian valley in the deposits of the Guitarrero Cave near Huaylas (Depto. Ancash). This discovery sheds new light on the evolutionary history of the common American bean, and confirms what we have maintained for twenty years: that kidney beans have been domesticated and selected from the wild-growing South American *Ph. aborigineus* in the meridional part of the continent. It does not exclude the possibility of other sub-regions of domestication, e.g., the mountain valleys of Honduras or Mexico, because we have been aware of the existence of the variety *hondurensis* of our wild bean since 1953.

Phylogenetic relationships in the neotropical wild bean *Ph. aborigineus* Burk. as the ancestor of our cultivated garden bean, *Ph. vulgaris* L., were established by Burkhardt and Brücher (5). This publication was the result of several years' herbarium and field work in Argentina, combined with experiments on photoperiodical and flowering behavior, artificial crossings, chromosome studies (*Ph. aborigineus* has $2n = 22$), and

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field tests for resistance against *Uromyces*, *Fusarium* and *Colletotrichum*. The high genetic resistance of Argentine wild beans to leaf diseases was later confirmed in glass-house tests by several European plant breeders (15, 27, 36).

The South American wild bean received its first taxonomic-systematic treatment by Arturo Burkhart, the well-known specialist in Leguminosae and Professor of Botany at the University of Buenos Aires. As early as 1941 he mentioned the existence of a "raza silvestre de *Phaseolus vulgaris*" (Resoluciones de la I. Reun. Argent. Agron., Buenos Aires, p. 52). In 1943 he repeated his statement of "absolutely spontaneously growing beans" from the Tucuman-Bolivian forests of northern Argentina. But due to the limited distribution of his publications outside of Latin America, these reports of true wild beans in the meridional part of America received little notice.

For this reason, having come from Sweden to explore the Anconquiya mountains in December of 1948, we too were unaware of Burkhart's findings. We rediscovered huge populations of wild-growing beans in the high, intermountain valleys of the provinces of Tucuman and Catamarca, and sent seeds of them to various institutes of Europe and America, labeling them "die argentinische Wild-Bohne." Burkhart received these bean seeds with the remark that this species must be the wild ancestor of the garden bean, and after informing us of his previous studies, we arranged a collaboration.

Other recipients of seed of our Argentine wild bean included: The Max-Planck Institute for Plant Breeding at Voldagsen, where our wild bean was used extensively in hybridization schemes for improving European garden bean cultivars; the United States Department of Agriculture Experiment Station at Beltsville where Dr. Rodenheiser acknowledged (August, 1953) earlier receipts of samples of *Ph. aborigineus*, resistant to *Colletotrichum*, sent by the authors; the Dutch Plant Breeding Institute at Wageningen, which was most successful in resistance breeding using our wild bean. Hubbeling (15) reported the source of his breeding material in the fol-

lowing statement (among others): "It was a biotype from Tucuman which excelled in resistance to the four known races of *Colletotrichum lindemuthianum*, the well-known cause of bean anthracnosis." The Academy of Sciences of Czechoslovakia received samples of our Argentine wild bean and with it a team of biochemists [Klotz, Turkova, Klozova *et al.* (24) (25)] completed successful research on serological tests which elucidated the phylogenetic relationships between different *Phaseolus* species. The Venezuelan Nutrition Institute and the Biochemistry Department of the University at Caracas also received samples of our collections. Jaffe and his co-workers approached the chemotaxonomy of the genus *Phaseolus* by means of haemagglutinin reactions and discovered significant differences between cultivars and their wild forms (20). Finally, the Department for Tropical Plant Genetics at the Faculty of Agronomy in Gembloux, Belgium, investigated the cytology of our wild beans and included them in their breeding program (31).

All of the above-mentioned scientists and institutions used only our Argentine wild bean for their experiments and showed successfully, in their hybridization work with *Ph. vulgaris*, the outstanding breeding value of *Ph. aborigineus*. Therefore we were astonished that these facts did not seem to deserve mention in Gentry's essay on wild beans. Furthermore, it seems an inexcusable omission in the "Bibliographia de Frijol" (No. 4, 300 pp.) published recently in Turrialba (1972) that neither Burkhart's book on Leguminosae, in Spanish, and with many chapters on *Phaseolus*, nor his publications on the wild bean of South America were cited.

The formal Latin diagnostic description of the new species *Ph. aborigineus* was published by Burkhart (4). For the Central American biotype of this wild bean he created the variety *hondurensis*. The description of this variety was based on Herbarium No. 3897 of the Estacion Experimental Panamericana, Depto. Morazan, Honduras, and on material sent by Standley to Buenos Aires. The seeds were described as brownish-grey, mottled, with a

dark ring around the hilum, kidney-shaped, smaller in size than the Argentine wild bean being 5 mm long, 4 mm wide and 2.2 mm thick. The pods were 5 cm long and 7 mm wide. An illustration of this variety *hondurensis* was published on page 70 of our 1953 paper (5). A comparison of this sample with the pictures on pp. 57-59 of Gentry's publication shows clearly the striking similarity of the two findings. It seems that Gentry was not aware of this taxon, otherwise surely he would have mentioned it, perhaps either classifying his meso-American wild bean as *Ph. aborigineus*, or rejecting the taxon.

In 1954 we published (6, 7) details³ of the fact that even today primitive inhabitants of the northern Argentine mountains make regular use of the wild bean as food. By chance we came upon an indigenous family in the valley of Chabarilla (Province of Catamarca) at the moment they were preparing a meal of beans which they had collected from wild stands shortly before. We consider this casual discovery a fortunate circumstance since, generally, natives are reluctant to disclose to foreigners ancient customs involving primitive food plants. Once we had won their confidence, the natives of Chabarilla revealed to us that each autumn they organize collecting trips to other valleys for harvesting wild beans. During threshing of the ripe pods, the seeds are scattered around their huts where they sometimes germinate and grow by accident. They are not sown on purpose, as there are no fenced gardens and cattle graze all over the valleys. Obviously we are confronted here with one of the few examples of a transition stage between wild and domesticated food plants. As we stated in 1954: "Es handelt sich hier offensichtlich um eine Wildart, die für Primitivmenschen bereits so viele erwünschte Nutzeigenschaften vereinigt, daß sie sich zur Domestikation geradezu anbietet."

During the International Gene Center Expedition to South America in 1958, we dedicated special attention to such casual

³ It seems unfortunate to us that these and other communications (1, 4, 5, 6, 7, 8, 9, 24) on South American wild beans which appeared prior to Gentry's publication on Mexican wild *Ph. vulgaris* received no notice.

use of wild beans by native peoples for food. In northern Argentina in the remote high valleys of the Province of Salta, some 100 km from Chabarilla, we found similar cases. In the Ussuri Valley of Salta where *Ph. aborigineus* is abundant in the *Alnus-Juglans* forest, indigenous mestizos regularly collect dry beans from wild stands and store them as emergency food. In 1966, in the mountains of the Province of Merida, Venezuela, we noted the casual use of wild beans by poor families; in 1968 we observed a similar custom in the Pampalona district of Colombia.

Having been on the trail of *Ph. aborigineus* throughout the whole South American continent during several expeditions, we established a "distribution arc" (1, 10, 11) which extends for 5,000 km and has an altitude range of 1,000-2,800 m above sea level. This region coincides with the *Alnus-Sambucus-Juglans-Celtis* association of the eastern slopes of the Andes. We have no doubt that South America has played a paramount role in the evolution and domestication of the common bean.

HISTORICAL DATA

The strange fact that the phylogeny of such a useful American plant as the common bean was so long neglected has its reason in the very circumstances of the discovery of the New World and the contempt shown by the Iberian invaders, from the beginning, for the indigenous populations, their nutrition and living habits. After having subjugated the Central and South American highlands (1532), the Spanish showed astonishing little interest in the preservation of agriculture and the useful plants of the destroyed Aztec and Inca empires. Up to this time, beans must have been a prominent protein source for pre-Columbian America, and even today the black bean (the primitive "caraota negra") is a basic food in Venezuela, Colombia and Brazil. The fact that the ruler of Mexico received each year a contribution of 28,000 bushels of maize and 23,000 bushels of bean seed (cited from Frederick Peterson, "Codex Matricula de Tributos," 1962) confirms the high esteem in which pulses, and especially *Phaseolus* beans were held in pre-Columbian nutrition.

In the Inca empire—what is now actually Peru and Bolivia—the indigenous Aimara and Kechua tribes without doubt had reached a high level in their selection of different leguminous crops. For example, in the altiplano they had selected edible “Tawri” from wild-growing *Lupinus* species for climatic reasons; *Phaseolus* does not grow at this high altitude. The use of “purutus”, *Phaseolus* beans, was restricted to the intermountain valleys below 2,500 m. Recently, in such a valley samples of 7,000-year-old bean seeds were discovered in the Guitarrero Cave. It is situated between the “Cordillera Blanca” and the “Cordillera Negra” in the Callejon de Huylas (Depto. Ancash) of Central Peru. For 10,000 years this fertile area must have been the scene of Indian cultural activities. The discovery of Kaplan, Lynch and Smith is a most fortunate event and it appears that their dates, obtained by ¹⁴C-dating and ranging from 7680 (± 280) to 10,000 (± 300) years, are correct. As the authors say, their discoveries lend further support to the proposition that the people of the Guitarrero Cave practiced the cultivation of common and lima beans between 5500 and 8,500 B.C. This finding throws much light on the plant-breeding abilities of early South American Indians who, as is well-known, also created numerous tuberous crops such as Oka (*Oxalis*), Ulluko (*Ullucus*), Mashua (*Tropaeolum*), Achira (*Canna*), Rachaca (*Arracacia*), Mauka (*Mirabilis*), Ajipa (*Pachyrrhizus*) and, finally, an impressive quantity of indigenous potatoes of the genus *Solanum* (9, 10, 12, 37, 38, 43) on different ploidy levels.

In addition to Guitarrero we have only a few well preserved archaeological sites south of the Equator, all of later date such as Nazca, Ancon, Pachacamac and Huaca Prieta. Soukup (40) mentioned that in pre-Columbian graves of the Peruvian coast, bean pods and seeds had been stored in small cotton sacks, perhaps for religious purposes, another proof that the bean plant played an important role in the life of ancient Indian tribes.

An authentic statement on Indian beans comes from a descendant of the Incas, Garcilaso de la Vega (1539–1616), who de-

clares in “Comentarios Reales” that three different types of beans existed in ancient Peru. The non-edible ones (lima beans) were used for “playing”; they had different names and colors. Such “chuy” beans are still in use today in some rare mountain places much as “playing chips” are used in other countries. He mentioned that the edible “purutus” were small and rather round. Oviedo y Valdez (“Historia de Las Indias”, 1535) is the first Spanish author to mention beans from the newly discovered continent. However, he reports only that he saw Indian fields planted with this crop in different localities. Cieza de Leon describes in his “Cronica del Peru” (1538) the high productivity of beans planted around Popayan, now in Colombia. We found another citation in the book “Historia Natural y Moral de las Indias” by Jose de Acosta (1590), who says that the aborigines had the custom of sowing different bean varieties in large plots and that there were two different types: “pallares” (*Ph. lunatus*) and “frijoles” (*Ph. vulgaris*). Padre Cobo (1653) explains in a rather peculiar way why beans did not form part of the diet of the Spanish in the early days of the Conquest. “Los purutos son tenidos por los mas groseros y de ordinario (because of their ability to produce flatulence). No los comen, sino los indios y gente de servicio.” As he states, the people of the higher social classes did not eat *Ph. vulgaris*. On the other hand, he reports that “pallares” had a pleasant taste and were well received by the ruling castes.

But none of the Spanish authors was able to describe what he really saw in acceptable botanical terms. We can only conclude from their casual remarks that *Phaseolus vulgaris* must have been the traditional food of the lower classes for a long time and was not an “imported one” (e.g., from Mexico). Parodi supports this view in his “Agricultura Prehispanica” (34) and points to the very long-standing use of beans in the indigenous agriculture of South America.

The scientific knowledge that *Ph. vulgaris* had its origin in the New World is not even 100 years old. The first unmistakable proof for this was presented by

Wittmack (47) in 1879. Performing studies on prehistoric seeds excavated from the remains of graves near Ancon (10 miles north of Lima, Peru), he recovered well-preserved *Phaseolus* seeds. According to Martens' nomenclature, he described them as "purpureus, oblongus"; others with black seeds were classified as "atrofusca, ellipticus." During a recent visit to the "Museo Nacional de Antropología y Arqueología" in Pueblo Libre (Peru), we had the occasion to review some of the bean samples from Pachacamac and Ancon. We got the impression that e.g., No. 5-266 of Pachacamac could be seeds of *Ph. aborigineus* judging from their angular form and small size, whilst the later samples from Ancon more closely resemble the well-known "caraota negra" type.

It seems that Wittmack himself was rather surprised by his discoveries because he believed, as did nearly all of the botanists of his epoch, in an Asiatic origin of the garden bean. He said: "Wie soll man sich den Fund der gewöhnlichen Gartenbohne (*Ph. vulgaris*) in den Peruanischen Gräbern erklären? . . . wenn man nicht die kühne Behauptung aufstellen will daß die Gartenbohnen nicht allein in der Alten Welt sondern auch in der Neuen Welt heimisch seien." Finally he accepted, however reluctantly, the idea of the American origin of the common bean in the following negative way: "So erscheint die Annahme daß Asien das Vaterland von *Ph. vulgaris* sei mindestens als noch nicht erwiesen."

De Candolle (1858), in the beginning of his work on plant geography, was no less skeptical when he declared: "Les botanistes on crut pendant long temps que l'haricot comun était originaire de l'Inde. Personne ne l'avait trouvé sauvage ce qui est encore le cas actuellement." But in the last edition of his "Origine des Plantes Cultivées" (1884) he had already changed his mind and accepted *Ph. vulgaris* as a New World crop.

It seems rather strange that botanists with a great deal of field experience, living for decades in Latin America, such as Cardenas, Fiebrig, Hassler, Lillo, Pittier, Vargas and Weberbauer, did not discover

true wild beans of the *Ph. vulgaris* group during collecting trips in the countries where they were doing their research. Weberbauer (1911) mentions superficially in his "Flora of the Peruvian Andes" the "plantas trepadoras" of *Ph. vulgaris* growing in a natural habitat between 2,000 and 2,600 m together with *Passiflora*, *Dioscorea* and *Lathyrus*, but he did not recognize them as wild. Hassler, in Paraguay, published a revision of the australo-American species of the genus *Phaseolus* in 1923 without even indicating possible wild ancestors of the kidney bean in the meridional part of America. Pittier (1857-1950) dedicated much research to the Venezuelan species which, unfortunately, was not completed for publication. However, he did note on an herbarium sheet of *Ph. lunatus* that he had found this "en estado silvestre." But with respect to *Ph. vulgaris* he mentioned: "el origen de esta especie es incierto; hemisfero oriental?" It seems astonishing that this experienced botanist and traveler did not observe the abundant wild bean stands during his field explorations in the Province of Merida; *Ph. aborigineus* grows, for example, right on the access road to the town of Merida under some large *Erythrina* trees! This wild bean has its natural habitat along the Santo Domingo River between Barinitas, Mitisus and Pueblo Llano, and is well-known to the natives there under the local name "mitoño".

Piper (35), to whom we owe an outstanding revision of the American Phaseolinae, side-stepped the phylogenetic aspects of cultivated beans. He mentions only his own species, *Ph. macrolepis*, from a high mountain region of Guatemala (2,500 m) as "perhaps the nearest related species to *Ph. vulgaris*." Obviously he was not aware of much more closely related wild beans of South America.

Russian botanists, under the direction of Vavilov (1887-1943) organized several collecting expeditions to Central and South America between 1926 and 1933. Busakov, Ivanov, Juzepzuk and Vavilov himself were searching eagerly for ancestral forms of cultivated beans, and especially for the wild garden bean, but could not find them. Recently Ivanov confirmed for us, during a

visit to the Soviet Institute for Plant Industry in Leningrad (VIR), that before our *Ph. aborigineus* material reached that Institute, the Russian botanists did not possess a true wild bean. Admittedly there must have been some rather primitive *Phaseolus* populations in the VIR collections as we might conclude from the following statement in Ivanov's book: "The dominant characters clearly manifest themselves in the generative and vegetative parts of the plant: small seeds, dark color, variegated color of the flowers and seeds, purple anthocyanin pigmentation in the stem. . . . The twining varieties grown under the relatively long day of Sukhum (43°N) were conspicuous by their vigorous development. They are distinguished by an extremely large vegetative mass and by a very long vegetative period."

MacBride (30) mentions two findings of spontaneously growing beans in Peru without going into further detail or classifying them either as true wild beans or as ancestral forms of *Ph. vulgaris*. Bailey (1954) in his "Manual of Cultivated Plants" (p. 574) makes only a short statement about kidney beans as "probably of American origin."

For Merrill (33) "the ancestors of the common garden bean are yet unknown as wild species," and in his typical apodictic way he declares further: "In only a few cases in the plant kingdom are the ancestors of our cultivated crops plants as yet unknown as wild species. Perhaps the two most striking cases are both plants of American origin: maize and the garden bean." It seems that Merrill's authoritative but erroneous opinion is still to be found in some ethnographical and socioecological circles.

In the last decades, some European bean breeders were skeptical with respect to the phylogenetic background of their crops, and denied living, wild ancestors. Kooiman (26) declared in his monographic work on the genetics of *Phaseolus* that "*Ph. vulgaris* is not known in a wild state. Moreover, as it belongs to the oldest cultivated plants, which in prehistoric times must have been distributed all over the world, we cannot be absolutely sure of its native country."

The very experienced bean geneticist

Lamprecht never accepted the existence of a systematically separated wild bean and maintained his negative statement of 1939: "Mit einem natürlichen Vorkommen von *Ph. vulgaris* kann nicht gerechnet werden".

This was the general opinion about the non-existence of a wild bean in South America until the appearance of the work of Burkhart and Brücher in 1953 (5).

GEOGRAPHICAL DISTRIBUTION

The species generally prefers the mesophytic mountain climate of the subtropical zone with elevated day temperatures and cool nights. In Argentina *Ph. aborigineus* is a rather abundant species in the Andean provinces of Jujuy, Salta and Tucuman, and it occurs with minor frequency in the provinces of Catamarca, Cordoba and San Luis.

The first herbarium collection from Argentina (No. 12,831) is about 70 years old. Our wild bean was found in 1903 by Stuckert during his exploration of the Sierras de Cordoba (Depto. Punilla). The Miguel Lillo herbarium of the University of Tucuman possesses various exsiccata of *Ph. aborigineus*. They were collected more than fifty years ago by Schreiter (No. 860, 1919), Venturi (1924) and Meyer (1942) but without indication that they were wild beans. Burkhart first observed the species in 1933 in the cloud forest of Tafi del Valle (Tucuman Province) and later on in the Cerros de Yala (No. 11,256, 1940) and in the Valle Rio Grande (Jujuy Province).

The southernmost habitat of *Ph. aborigineus* on the whole American continent is in Merlo (San Luis Province) at latitude 32°20'S where Batallanez collected it. This extreme meridional area could be interesting for future photoperiodical studies of wild beans. Brücher has studied the distribution of the Argentine wild bean in the Provinces of Tucuman, and Catamarca since 1948 and noted its abundance in the intermountain valleys of the eastern slopes of the Aconquija massif (5,500 m). Later on we collected samples from the northern province of Salta (Rio Ussuri, Valle de Lerma, Chicoana). The border region between Salta and Bolivia (Rio Bermejo, Toldos) is also rich in wild beans. In Jujuy

Province it occurs in all the valleys which communicate with the main river, Rio Grande. An easily accessible habitat there is the "Estancia Alvarado" on the main road from the town of Jujuy to León.

The existence of *Ph. aborigineus* in Bolivia was not reported prior to our explorations in the provinces of Tarija and Cochabamba in the fifties (Berglund-Brücher, 1958). We found the wild bean growing along the rivers which flow eastward. In the company of Prof. Cardenas we found it near Liriuni; it is rather common near "Aguas Calientes" and in the vicinity of Quillacollo. An easy place to collect it is in the area surrounding the German brewery outside the town of Cochabamba where it abounds in the shrubs nearby.

In Peru (1967) we found the wild bean in the valley of the Urubamba approximately 30 km from the Machupicchu railway station, and also near Ocos in the Department of Apurimac. This is the first record of the presence of *Ph. aborigineus* in Peru. In the herbarium of Dr. Vargas we observed dried specimens (No. 7,110) of a wild bean which we determined as *Ph. aborigineus*. It was collected between Rio Blanco and Rio Vilacanota. Paul Smith-Davis confirmed to us (verbal communication, 1973) that he had found wild growing beans, probably *Ph. aborigineus*, near Tarma and Huanaco. MacBride mentions in his "Flora of Peru" several places for wild growing beans, e.g., in the shrubwoods near Muna (No. 3,947), but he does not state that these could represent the wild ancestors of the cultivated Peruvian "purutus." Wild beans have been collected by Weberbauer on several occasions during his botanical exploration of Peru. He gives a detailed account of his finding from "Ceja de Marcapata" (46). This wild bean (No. 7,847) was growing in a natural environment between 2,000–2,600 m in the valley of the Urubamba river, together with *Pasiflora cuzcoensis*, *Lathyrus longipes* and *Dioscorea*, i.e., in a plant association which indicates a spontaneous habitat. He describes his finding as a "planta trepadora" and a wild bean, but he did not specifically decide that he considered it the indigenous

ancestor of the common puruto bean, which is cultivated in many "land races" and local varieties by natives of the Urubamba valley according to our own observations there in the summer of 1967.

We are still missing reliable data on wild-bean collections in Ecuador. Due to heavy erosion and deplorable overgrazing in the mountain valleys that are appropriate for agriculture, it must now be difficult to find *Ph. aborigineus* in its natural habitat. Some decades ago Diels (1937) reported the existence of a wild bean which he considered the progenitor of *Ph. vulgaris* describing his material as *Ph. harmsianus*.

It seems the species was not observed in Colombia before our own collections during the years 1966 and 1967. We found it in abundance in the valley of Pampalona, 30 km distant from the town, near the "Estancia Topon," where people call it "frijol de matica." But the wild bean occurs also in the mountain district of the Tachira river and near Bochalema. We are convinced that a good field survey of Colombian mountain districts would yield many more details concerning the distribution of *Ph. aborigineus* in these areas.

We first discovered the wild bean in Venezuela in 1965 during an Andean botanical excursion with Dr. Foldats. In the following years we performed a phytogeographical survey in the provinces of Lara, Trujillo, Merida, and Tachira, and found not only a wide extension of *Ph. aborigineus* in these provinces, but also proof of the fact that the native people are using the wild bean (mitoño) regularly for food especially, they told us, in bad years when the ordinary bean harvest is poor.

Reviewing these decade-long observations from South America, we are definitely convinced that phytological and ecological circumstances exclude the possibility that such wild beans are escapes from indigenous bean fields. We did search for possible spontaneous hybrids in remote regions where the natives still plant their beans in forest clearings where *Ph. aborigineus* has its natural habitat, but we could not find them. Outcrossing in the *Ph. vulgaris* group is practically inhibited for floral-biological reasons. We did not observe "introgressed

populations" of wild and primitive cultivated beans along the distribution arc, which extends for several thousand miles through South America. It is evident that the evolution of the garden bean from the South American wild bean is one of the few good models where the separation between domesticated and ancestral forms is quite perfect and not disturbed by spontaneous hybrids.

Whilst Nature favored hard-shelled strains with a long generative phase, the native planters selected biotypes with soft seed integuments, shorter ripening period and quick cooking abilities, as well as many other characters that are quite opposite to the demands of the natural environment with respect to procreation and seed dissemination. This domestication process began perhaps 8000 years ago, but was still going on when the Spaniards entered the New World and became acquainted with the *Phaseolus* bean. It is obvious from the first reports of early bean introductions from Latin America to Europe that they had poor cooking quality, sometimes hard-shelled seeds, and pods that shattered when ripe. The first beans reaching the Old World must have been similar to native bean varieties we found occasionally in remote parts of Bolivia. It seems to us that one of the first illustrations of *Phaseolus* beans (Oellinger, 1553) depicted just such primitive beans with dark seeds and shattering pods. During the same period, there appeared also the "Cruydebook" of Dodoenus (1565) where a rather stylized picture of a "garden bean" plant was published.⁴ Concerning the place of origin of the first Spanish bean introductions, we suppose that they came most probably from the southern andine group, mainly for climatic and photoperiodic reasons. *Phaseolus* beans from the equinoctial regions hardly could have produced a reasonable yield under the long day conditions of Central Europe. From an old remark that we found in the book of Dierbach (1836) about bean cultivation in Germany, we may conclude that

⁴ According to Kooistra (27), the earliest report of bean cultivation in Europe goes back to 1542. From this we may guess that the first seeds may have reached the European continent between 1530 and 1540.

originally the garden bean was used more as a garden flower than as a field crop because of its reported low yield.

CHARACTERISTICS OF THE WILD BEAN

Linnaeus created two binomes (1753), *Phaseolus nanus* and *Phaseolus vulgaris*, probably under the assumption that these exotic bean species would have some real existence in their respective homelands. His diagnosis was based on some casual seed samples which were adapted to the long day conditions of his botanical garden. He did not even try to link these "agrotypes" with presumable wild forms, nor did he discuss the geographical origin of his cultivars. Even if his taxon "*Ph. nanus*" (for bush beans) could have some practical application for the design of dwarf mutants in actual bean breeding, it lacks systematic value and its use in taxonomy should be abolished. The rather short original description of *Ph. vulgaris* contains an unfortunate erroneous detail: "Bracteis calyce minoribus." Were this diagnostic detail to be applied rigorously to bean cultivars, a considerable portion of actual bean varieties would have to be excluded because only some southern bean biotypes from Chile and wild beans from northern Argentina have, in fact, smaller bracteoles. A critical evaluation of the individual diagnosis of *Ph. vulgaris* and *Ph. aborigineus* inevitably leads to the conclusion that only the latter gives an accurate description of the realities.

Shortly after Burkhart introduced the epithet "aborigineus" in 1952, some taxonomists questioned the appropriateness of separating the wild ancestors from their domesticated offspring. We are definitely in favor of maintaining the two taxa as separate species. We consider *Ph. aborigineus* Burk., together with its northern form, var. *hondurensis*, a really "good species." Strengthening the nomenclatural separation could only benefit understanding of the evolutionary process. There can be no doubt that before *Ph. vulgaris* existed on the American continent, its wild fore-runner, *Ph. aborigineus*, with its different local varieties (like *hondurensis* in Central America) formed an essential element of

the climax vegetation of the mountain forest along the eastern slopes of the Andes. We refer especially to the "montano-district" which, according to Cabrera, contains in its lower parts (1,000–1,500 m) *Phoebe porphyria*, *Schinus molle*, *Celtis spinosa*, *Fagana coco*, and certain Myrtaceae. In the higher regions (1,600–2,500 m) however, we find particularly *Sambucus peruviana*, *Juglans australis*, *Alnus jorullensis* and *Datura insignis*. It is in this cool, temperature mountain region with mostly deciduous trees that the wild bean thrives as a climber on shrubs.

After twelve years of field work through the whole South American Andean region, we established a dispersion arc that extends more than 5,000 km along the eastern slopes of the cordillera. This rather narrow band of mesothermic forest is the natural habitat of the wild bean *Ph. aborigineus*. It seems superfluous to underline the fact that such an extended arc of several thousand miles is quite incompatible with Vavilov's postulate of geographically restricted gene centers as the places of origin of cultivated plants. [See criticism of the gene center theory by Brücher (11) and Harlan (14).]

Gentry expounded upon the idea that our South American *Ph. aborigineus* may be a bean escaped from ancient cultivation. The above-mentioned phytogeographical fact contradicts this. Furthermore, we never observed that *Ph. vulgaris* ever produced "escape biotypes" or "weed beans" as happens with other cultivated plants such as potato, batata or papaya. A domesticated bean would not survive free in nature. If, by chance, some seed were to drop among the dense vegetation of a temperate mountain forest, it would have no chance for survival; seeds of cultivated beans may germinate on indigenous garbage heaps and produce a casual plant, but they would not propagate. We must therefore reject the opinion of Gentry that the South American wild beans (*Ph. aborigineus*) "are rather escapes from early cultivars." Likewise we discard the possibility that they are the result of a continuous intercrossing between wild and cultivated beans. The floral-biological circumstances and wide-spread self-

pollination in the genus *Phaseolus* inhibits outcrossing and favors autogamy. We have cultivated hundreds of local bean varieties over the last several years and we consider spontaneous hybridization to be negligible. Obviously the genetic barrier between *Ph. vulgaris* and *Ph. aborigineus* in their natural habitats is definitely established even if we can produce artificial hybrids between the two species rather easily.

It should be mentioned that the size and number of chromosomes in these two species are similar. The first author to determine the chromosome number of *Ph. aborigineus* was F. E. Saez in Uruguay (1946). In the mitosis of root tips he found twenty-two chromosomes of 3 μ length, mainly with metacentric insertions [see Burkhart and Brücher (5)]. More recently, Maréchal (31) included the Argentine wild bean in his investigations of the caryology of American and African species of the subtribe Phaseolineae. He confirmed $2n = 22$ and found the largest to be 2.5 μ , the smallest 1.4 μ in length, two of them with satellites. In this respect, the wild bean does not differ essentially from other American bean species such as *Ph. acutifolius*, *coccineus* or *lunatus*. Unfortunately cytogenetics does not offer fair possibilities for species differentiation in the genus *Phaseolus*.

The morphological and final phylogenetic differentiation between *Ph. aborigineus* and *Ph. vulgaris* was recognized by Schwanitz (37). He examined the affluence of typical domestic factors in *Ph. vulgaris* after the garden bean had dissociated from its wild progenitor and came to the following conclusion: "Nehmen wir als Beispiel einmal unsere Gartenbohne (*Ph. vulgaris* L.) und ihre vermutliche wilde Ausgangsform (*Ph. aborigineus* Burk.), so können wir ohne Schwierigkeit feststellen, daß Wildart und Kulturform sich in einer ganzen Reihe von Eigenschaften unterscheiden, die wir als typische Merkmale von Wildpflanzen, bzw. Kulturpflanzen, kennengelernt haben." As relevant morphological differences, Schwanitz points to several gigas factors acquired by the cultivars: their loss of sclerenchymous tissues in the fruits, the changes in the permeability of

seed membranes, and their different phasein content. This toxic substance serves as protection for the wild growing bean plant. In Schwanitz's opinion, once man took over the care of beans in cultivation this hereditary factor was no longer essential for survival, and its content diminished in the modern bean cultivars.

Stem, roots and growing habit. Gentry mentions perennial wild beans from Mexico, sometimes with corky stems, and says: "Perennialism is frequent in the wild bean populations of Nayarit, Jalisco and Michoacan." But in South America we did not observe *Ph. aborigineus* with a persisting root or stem system that would have indicated that it resprouts each year from a surviving rootstock, a characteristic well known in the runner bean, *Ph. coccineus*, and many other related Central American species. Besides, we suppose that 90% of all wild Phaseolineae have such perennial rootstocks which enable them to withstand long periods of drought. Therefore we consider it a remarkable fact that our South American wild bean was an annual herb from the very beginning. As in the garden bean, which likewise exists only as an annual crop, in this special case annualism was not acquired after domestication, as is the case with many other crops. In our collections all the entries from Argentina, Bolivia, Colombia and Venezuela are recorded as annuals with a rather weak superficial root system, long twining stems and deciduous foliage. The vines are often 3-6 m in length, covering rocks, trees and shrubs in search of sunlight. The slender stems need support by associated bush vegetation. *Ph. aborigineus* twines always from left to right;⁵ its long internodes are covered with dense bristly hairs which adhere readily to other herbs, lianas and shrubs, forming dense thickets.

In *Phaseolus* taxonomy, beginning with Linnaeus, there had been a tendency to use the anatomy and growing habit of the bean stem as a decisive characteristic for diagnosis. Linnaeus himself differentiated his two bean species, as we mentioned above, primarily on the growth of the stem and

⁵ Surely it would be interesting if mutations with an opposite winding system should occur.

the distances between internodes. Notwithstanding the fact that "*Ph. nanus*" has to be abolished taxonomically, certain bean cultivars with an extremely short stem and terminate growing habit do exist, whilst the bulk of the primitive "land races" and, above all, the wild bean, have indeterminate growth, long internodes with stems reaching several meters in length.⁶ For horticultural purposes these two extreme biotypes are called "pole beans" and "bush beans" respectively.

The original habit of long, twining bean stems is the dominant factor in most native bean selections in South and Central America, favored by the agricultural customs of the indigenous farmers who are wont to plant beans together with maize so as to make use of ripening corn stalks as natural support for the climbing bean stems. These "pole beans" have a prolonged vegetative period and produce an astonishing quantity of inflorescences on the upper stem nodes. On the contrary, natives had scarcely a use for "bush beans" with a rather short vegetative cycle and considerably lower yield.

If one crosses certain strains of pole beans with bush beans, the F₂ descendants show a simple 3:1 segregation in stem length. This indicates that a supposed basic systematic character for differentiating species is but a monohybrid segregating gene.

It is interesting that Kaplan and MacNeish (22) and Gentry (13) refer to the early existence of bush beans dating to some 1800 years ago as evidenced by bean remains in the Palmilla phase of Tamaulipas. These had a bushy habit and yellow seeds similar to the present small-seeded "frijol bolito" in the Central Plateau. In modern bean breeding, the occurrence of bushy biotypes (dwarf mutants) is considered a valuable improvement in bean domestication. It appeared quite independently in Asiatic and American beans and represents a further example of the so-called "parallel variation" (Vavilov's Law of Homologous Series).

In spite of the extremely wide distribu-

⁶ Even if actual bean breeding is directed toward rapid ripening dwarf forms and bush beans, we must mention that there still exist some high-yielding runner forms of *Ph. vulgaris* such as the local strain "Balin de Albenga."

tion of *Ph. aborigineus*, one cannot report spectacular morphological differences between wild beans from such distant locations as San Luis in Argentina and Merida in Venezuela. Yet there are remarkable differences in their photoperiodical and physiological behavior.

Leaves. Nearly all the Phaseolineae have an astonishingly similar leaf morphology. Therefore leaf shape is a difficult diagnostic feature. Each leaf has six small stipulate leaflets, two on the insertion of the main petioles, two on the base of the terminal leaflets and only one on each lateral leaflet. The lamina is always thin, acuminate, and covered with multicellular hairs. Even if there are certain differences in leaf formation between cultivated and wild beans, it is rather difficult to use this as a differential characteristic. Within the *Ph. aborigineus* populations themselves however, there exist certain hereditary variations in leaf shape (1). For example, if one compares the Argentine with the Venezuelan collections, the Argentine wild type has terminal leaflets with rather long (4 cm) petioles, a basic angle of 96° and dimensions of 6×3.5 cm; the wild bean from Venezuela has larger terminal leaflets with a short petiole and a basic angle of 116° .

Inflorescences. The flowers of *Ph. vulgaris* are characterized by large bracts that cover the whole calyx and persist on the ripening fruit. This is especially remarkable because neither *Ph. lunatus* nor *Ph. acutifolius* have bracts. A further striking morphological feature is its spiral keel with a pistil that is pubescent on its distal side and surrounded by united stamens. These features, and the size of the bracts, are considered by *Phaseolus* taxonomists very important and genuine characters for species differentiation (35); Ivanov (17). We examined a large series of flower samples of both *Ph. vulgaris* and *Ph. aborigineus* collected in South America and found certain differences. Those of *Ph. aborigineus* are considerably narrower.⁷ Comparing bean

⁷ This was also observed by Gentry (p. 60) when he stated that his *Ph. aborigineus* (we suppose an introduction from Tucuman) is readily separable by its bractlets, only half as wide as the other species.

cultivars, it seems a rule that the northern biotypes have big bracts sometimes covering the flower buds completely until the petals develop their color. However, the southern cultivars, as well as the wild beans from Argentina, possess rather small sometimes inconspicuous bractlets. We found also typical differences in the nervation of certain *Ph. aborigineus* samples. In general, the Venezuelan collections had ten nerves, those of Argentina only three. The anatomy of the flower of *Ph. aborigineus* prevents outcrossing. Its anthers open even before the flowers are visited by insects. As a rule its pollen sheds on its own stigma at an early stage with the slightest mechanical irritation of the spirally wound keel. The flowering epoch is very extended, and as a consequence of the intermediate cycle of growth, flowers will still appear when the pods are ripening until frost kills them all. With respect to size and color, we did not observe very much variation in *Ph. aborigineus* samples from the two extreme localities. We got the impression that the wing petals are looser in the Venezuelan samples and therefore the flowers appear larger than those in Argentina. Different shades of color occur, from lilac to pink and light lavender, but no white flowers were seen. Usually the plants with dark (anthocyanin) spots on the pods and stems have darker flowers.

Fruits. *Ph. aborigineus* produces a considerably higher number of pods than any commercial bean variety. In autumn, hundreds of fruits of wild beans hang in dense clusters from the numerous nodes of the elongated stems. The pods themselves are rather small, 7–10 cm long and 1 cm wide, with a sharp apex. In general their color is dark green in Argentine material whilst those of Venezuela are sometimes dark purple or with a violet brindle. An important difference between wild and cultivated beans lies in the anatomy of the pod walls and the structure of the dorsal and ventral suture fibers. The well-known stringless beans of today no longer have the fibers and the heavy inner parchment layers that are so characteristic of wild and primitive bean legumes. For this reason the latter do not make good vegetable dishes.

Ph. aborigineus possesses hard suture strings and fibers which induce a twisting of the ripe pod valves in opposite directions to release the seeds. The actual tender pods of modern commercial bean cultivars represent, in our view, "loss mutations" of a formerly important anatomical feature for spontaneous seed propagation. It seems that this recently selected domestic property follows a rather simple hereditary scheme. By the way, it should be mentioned that we found the stringless factor in autochthonous (!) native beans of northern Argentina. Pod dehiscence in *Ph. aborigineus* takes place only during really dry weather. We must indicate here that the valves do not curl tightly as is the case with other wild Leguminosae, e.g., *Lupinus*, *Lathyrus* or *Vicia*, catapulting the seeds away often with a perceptible crack. It is a remarkable fact that the dehiscence mechanism in our South American wild beans is less developed than in other wild growing Phaseolineae having fruits which really "explode" when they are ripe. As stated before, in the natural habitat of *Ph. aborigineus* it is common to see considerable quantities of closed pods hanging on dry wild bean plants. This peculiarity was undoubtedly attractive for domestication and indigenous people may have used it when they harvested wild beans, collecting the ripe pods during damp weather and threshing them out on a sunny day in the wintertime.

Seeds. The characteristics of the seeds must have played a paramount role in the early days of domestication because primitive prehistoric man used the edible ripe seeds of the bean and not the pods as a cooked vegetable as we do with modern snap beans. Therefore selection from wild beans to early cultivars was mainly directed to change their seed properties. *Ph. aborigineus* can be recognized easily by its seeds which are flat and sometimes angular. Their size varies according to ecological conditions, but on the average they measure 5–10 mm long, 3.5–7 mm wide and 3–4.5 mm thick. Soaked, they reach a considerable size: 12 × 8 mm. In form they resemble the primitive land race "subcompressus" (Alefeld) or "nigerrimus" (Zuc-

cagni). The "thousand-kernel-weight" is 116 gm. We performed various cooking tests with wild beans and found that they have an agreeable taste, are not bitter, and are without phaseolunatin effects. Our South American wild bean kernels remain below the size and volume of indigenous cultivars from Venezuela, Colombia and Ecuador. Once in a Bolivian market (Tarija), however, an indigenous agriculturist offered us a bean sample which was almost the size of the wild beans.

Ph. aborigineus has hard seed coats which prevent rapid soaking thus delaying quick germination. In repeated germination trials published previously (1) we realized the following: 60% of the ripe seeds began to germinate two days after soaking in Petri dishes; the rest were delayed. After a few weeks, even this group gradually lost its impermeability and began to sprout. However, after four weeks in water some 10% still remained hard. We cannot share the view of Kaplan (21), who referred to the dormancy of wild beans, including seeds of *Ph. aborigineus*, by saying they are "100% impermeable and remain so for periods of more than one year." If the seed coat is not disturbed or scratched, the most probable entrance for water is the micropyle or the hilum. This slow and retarded mechanism of saturation is an advantageous characteristic of great importance for survival of the species. In view of the tropical habitat of the wild bean on the eastern ranges of the Andes, with their established seasons of wet and dry epochs, the right timing for germination is essential. No bean plant would survive there should it germinate and grow during the "wrong" dry season by some accidental stimulation of casual slight rainfall. Therefore, a long dormancy, regulated by a "physiological clock," which prevents untimely germination of the seed is a great advantage. This hereditary dormancy was eliminated when man began to domesticate the wild bean. Retarded germination was absolutely unfavorable and was soon abolished, especially under conditions of irrigation. Therefore we consider that one of the first steps the Indians took to adapt *Ph. aborigineus* as a useful crop was the selection of evenly sprouting bean

plants. The peculiar germination behavior of the wild bean is based not only on a few anatomical features like seed tegument and permeability, but also on a series of physiological mechanisms which are most probably directed by an intricate genetic mechanism and not by a simple pair of alleles. From this we conclude that the two species have been separated for genuine reasons. Heredity of seed color constitutes another genetic complex separating *Ph. aborigineus* from *Ph. vulgaris*, each with distinctly manifest color series. What seemed to be a color puzzle of infinite combinations during the last century has been clarified by Kooiman (26). He established two main series for bean coat colors: a yellow-brown-black group and a red-purplish-blue series. Furthermore there exists a colorless (white) seed group. Anatomically all the dark pigments (anthocyanins and flavanols) are situated as granules in the lumina of the palisade cells. When we assume that the *Phaseolus* genome has four different chromogenous factors plus a ground factor for color expression, even the most striking color combinations find their genetic explanation. The yellow-brownish-buff seed coats are the phenotypical results of interaction of at least three recessive genes. On the contrary, the dark red-purple-violet or black bean seeds are caused by three or four dominant alleles. The "mottled pattern" which is often found on *Ph. aborigineus* seeds derives from another gene series. The grey-brown mottle on this wild bean is rather similar to those of other *Phaseolus* species such as *Ph. ovalatus* or *Ph. formosus* and even appears in the kernel of other genera such as *Clitoria* and *Vigna*.

We consider this mottled pattern a very old phylogenetic acquisition. It must have provided a positive selection advantage. Mottled seeds are nearly invisible when they fall on a debris-covered soil. We suppose that neither man nor animals like rats and birds could easily discover such seeds between rotted leaves on the ground. That our South American wild bean races have different seed colors (black, brown or mottled greyish brown) has been overlooked occasionally by other botanists. On the other hand, we were unable to find the

yellow wild bean seeds described by Gentry from Mexico. This must have been a local mutation in Central America which gave rise to certain North American bean land races. This recessive gene seems abundant even today in the local varieties of the northwestern region of Mexico (Sinaloa, Durango, Copala) with pale yellow or buff-colored seed coats.

Even if we do not believe that one could differentiate certain Indian tribes by their preferences for distinct bean colors, we find it interesting to read Gentry's statement that the northwestern tribes selected yellow and "pinto" seeds whilst the indigenous populations of southeastern Mexico created black, red and brown beans. He believes that these cultivars developed from different colored wild ancestors. From what we know, the preferred seed color south of Guatemala is, in general, red while the natives of Colombia and Venezuela plant their traditional "caraotas negras" (black beans). In this respect a rather remarkably conservative trend persists in several Latin American countries.

On other continents, progressive agriculture considers dark colored seeds undesirable. In the whole world, dark seeds are in retrogress—primitive black soya, black-hulled oats and barley, etc. Therefore it is astonishing that black beans are still produced in America annually in hundreds of thousands of tons. It seems that dark pigmentation is linked to certain advantageous resistance factors. The bean weevil (*Bruchus*) attacks stored black beans to a lesser extent. We observed that the dark-coated strains had a better germination and a higher juvenile resistance than white beans grown in the fungus-infected tropical soils of Trinidad.

Biochemical characters. Recent experiments using electrophoresis with wild and cultivated beans proved very helpful in elucidating interspecific and interracial relationships in the genus *Phaseolus*. For example, *Ph. coccineus* differs markedly in its albumin fractions from *Ph. vulgaris* (cultivar "Saxa") according to Klozova (25). On the other hand, the serological examination of *Ph. aborigineus* and *Ph. vulgaris* indicates that their biochemical background is

nearly the same. According to Kloz and Turkova (24) "our results are in agreement with the morphological and genetic data of Burkhart and Brücher on the close relationship . . . both contain a character designated as '*Ph. vulgaris* Protein No. I' which is lacking in the others. Both contain an identical phaseoline and exhibit only negligible differences in protein specificity."

After this attempt by the Czechoslovakian team to differentiate closely related *Phaseolus* species, Jaffe and his Venezuelan collaborators (Palozzo, Levy, Wecksler) elucidated the phylogenetic relationships between wild and cultivated beans from quite another point of view. They used the agglutinin activity of bean extracts with the aim of tracing the evolution of different cultivars back to certain populations of *Ph. aborigineus*.

The phytohemagglutinin (PHA) reaction seems a rather objective method for such a purpose because it is independent of human interference. The content of "Lectin" (PHA) in beans (28, 41) is not affected by human domestication, nor has it played any role as a natural selection factor. It seems to be a rather casual peculiarity, lacking any selective importance as Liener (29) has stated: "At this point, we may ask ourselves the inescapable question—what function, if any, does this hemagglutinin have in the plant? Quite obviously the hemagglutinin was not elaborated by the plant for the express purpose of agglutinating the red blood cells of animals."

Since 1908, when Landsteiner and Raubitschek discovered the agglutinating effect of beanflour extracts, human medicine has been using it for blood-group specific reactions. Many other Leguminosae contain PHA. This bean agglutinin is of further interest because it induces mitosis in cultured human lymphocytes. But we discovered recently (2) that there are remarkable exceptions: *not all the South American Phaseolus biotypes possess PHA activity.*

The existence of bean cultivars and wild populations of *Ph. aborigineus* with and without hemagglutinating properties may have vast phylogenetic consequences that could be helpful in elucidating the steps in the evolutionary history of the American

common bean. We analyzed several hundred indigenous bean introductions from our collections in Argentina, Chile, Colombia, Ecuador, Peru and Venezuela together with samples of tropical beans from Brazil and Central America. We discovered a striking absence of hemagglutinin activity in about 10% of the bean flour extracts. This lack of PHA in certain bean varieties may be the explanation of the occasional failure of PHA tests reported by various authors especially in clinical medicine. More information about the biochemical reasons for the apparent lack of hemagglutinating and mitogenic activity in certain *Phaseolus* strains may be of importance for the chemical definition of lectins (42).

According to the blood agglutinating reaction, the bean varieties can be divided into four groups: extracts of those which give no agglutination with any kind of erythrocytes used (0 + 0); those which agglutinate rabbit blood cells strongly, but act only slightly on trypsinated cow blood (A + 0); those which agglutinate trypsinated cow blood strongly but show no activity with rabbit blood (B + 0); finally, those which possess the most common type of reaction, agglutination of both types of red blood cells strongly (A + B). The A + 0 and the A + B extracts are likewise active on human blood cells.

With certain restrictions, the agglutinin reaction and the difference of the PHA effect shown by certain wild bean populations and cultivars can be useful for phylogenetic interpretations. We found, for example, that northern Argentine *Ph. aborigineus* strains have a weak PHA reaction or are lacking it completely. The same weak agglutinin effect has been observed in primitive local varieties of Chile and Argentina such as "Hallado," "Bolita saltena," "Alubia" and "Trigito." On the contrary, many central Andean and meso-American Indian beans often showed a strong PHA reaction similar to our Venezuelan wild bean. Therefore it is not impossible that differences in agglutinin behavior may offer the key to understanding bean evolution, and allow us to trace back certain cultivars of *Ph. vulgaris* to different ecological races

of *Ph. aborigineus* along its wide distribution arc in the South American continent.

CONCLUSIONS

If we agree that plant domestication is at once a natural evolution and a man-directed event, we can establish the following steps which were essential for the evolution of *Ph. aborigineus* into *Ph. vulgaris*:

- a. increase in seed size
- b. elimination of shattering pods
- c. elimination of hard coated seeds.
- d. selection of big, fleshy fruits
- e. selection of stringless pods
- f. improvement in taste and elimination of toxic substances
- g. creation of bushy types
- h. selection of day-neutral forms
- i. combination of genetic resistance against diseases and pests with high yield.

We have learned recently through archeological discoveries in the Guitarrero Cave in Peru that this improvement process can be traced back at least 7,000 and perhaps 10,000 years. But it must still be older than 10,000 plant generations. It began at the moment a semi-nomadic Indian food gatherer collected wild growing beans and sowed them around the dwelling places of his tribe. This event may have been repeated in different places and in different generations along the 5,000 km distribution arc of *Ph. aborigineus* in America. The Indians deserve our admiration for their impressive achievements in the diversification of bean seed factors with extremely limited means. As a result, the American bean became the most important staple food and source of protein in Indian America.

Plant geneticists and bean breeders of the present time are now faced with the challenge of still greater improvement of this valuable legume, e.g., by mutation breeding, to introduce more resistance genes by interspecific crossings, and finally by eliminating the remaining toxic principles of *Ph. vulgaris*.

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