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Historical Review

Although many explorers and naturalists have visited Bolivia in the past, only the most important will be treated in the following account. Those included have each contributed in some significant way to our scientific knowledge of Bolivian potatoes, either directly through the collection and study of various wild and cultivated species, or indirectly through the general sampling of the flora.

Many new species of tuber-bearing *Solanum* have been discovered in Bolivia since the beginning of the last century. With some exceptions, as will be pointed out again later under the individual treatments of species, neither the holotypes nor the isotypes of the Bolivian plants have remained within the country of their origin, all having been deposited instead in the larger herbaria of Europe and the United States.

Our story of potato collecting in Bolivia begins with the celebrated French explorer, Alcides D'Orbigny. From his travelogues to South America, covering the years 1830-1833, we have learned a great deal about the geography and natural history of this country during an era when it was first being organized as a republic. His monumental travelogue, *Voyage dan's la Amerique Meridionale*, remains as an important general reference today not only for Bolivia, but also for Argentina, Brazil, Chile, Uruguay, and Peru (D'Orbigny, 1945).

Although not trained originally as a botanist, D'Orbigny collected an enormous quantity of material of all classes during his three years of explorations in Bolivia. Among his collections were more than 3000 herbarium specimens that have been deposited today in the Natural History Museum of Paris. The great majority of these plants turned out to be new species. This explorer made the first collection ever of a wild potato species for Bolivia, *S. boliviense*, which was described by Michel-Felix Dunal in 1852. Although neither the exact place nor the date of this collection are known, it is probable that this plant was collected in the vicinity of Chuquisaca, or Sucre as it is known today, during

D'Orbigny's two-month visit to this historic locality from December 1832 to March 1833 (D'Orbigny, 1945, Vol. IV, pp. 1477-1486).

Gilbert Mandon, a French traveler and collector of plants in Bolivia, as well as in Madeira and the Canary Islands, lived during the second half of the nineteenth century in Sorata, Bolivia, where he was the business director of a gold mine from 1855 to 1861. During this period, he collected numerous botanical novelties in the vicinities of Sorata and Mapiri. According to Hugh Weddell (1867), Mandon collected more than 1800 herbarium specimens, which are now deposited in the Museum of National History of Paris. Among the many new species discovered for the flora of Bolivia by this dedicated collector were *S. candolleanum* Berthault (1911), *S. circaeifolium* Bitter (1912), *S. alticolum* Bitter (1913), and *S. boliviense* subsp. *virgultorum* Bitter (1913).

Toward the end of the nineteenth century, Miguel Bang, a Danish gardener and botanical collector, who had been trained at Kew Gardens, London, was sent to Bolivia by Kew to collect living orchids. Later, when he was already a resident of Bolivia, he came in contact with one of the greatest botanical explorers of this country, the American physician, Henry H. Rusby. Rusby's first expedition to Bolivia was in 1885-1886, by which time Bang had already made a substantial start on the classification of the flora of Bolivia. In 1889, Rusby and Bang agreed to collaborate in a joint effort to continue their floristic collections of Bolivia. Bang's collections were eventually sent to Rusby, and the largest of these sets is now housed permanently in herbaria of the New York Botanical Garden and the Smithsonian Institution in Washington, D.C. The results were published in four parts, mainly in the *Memories of the Torrey Botanical Club* (Rusby, 1893).

Of the 50 new Bolivian species of plants discovered by Bang, perhaps the most notable is *S. brevicaule*. This wild potato species, known from the vicinity of Cochabamba, was collected by him in 1891 under the No. *1100*. It was described as new by the German solanologist, Georg Bitter, in 1912.

Among the German collectors of the early twentieth century, Karl Fiebrig and Otto Buchtien both hold a prominent place. In 1903, Fiebrig undertook an expedition to the Andean region of southern Bolivia and northwestern Argentina for the purpose of making phytogeographic studies. The results of his expedition, which was sponsored by the Botanical Museum of Berlin, were later published in Leipzig (Fiebrig, 1910). To this explorer and phytogeographer we owe the discovery of two other important tuber-bearing species, *S. acaule* and *S. megistacrolobum*, both of which were collected by him in the Punas of Patanca, Department of Tarija, Bolivia. He also collected two species, *S. bijugum* and *S. microdontum*, at Toldos, in the vicinity of Bermejo, Bolivia (located today in the Province of Jujuy in the northwest territory of Argentina). These four species were described by Bitter in 1912.

Buchtien collected actively in both Bolivia and Chile. During his long

residence in Bolivia, covering almost three decades, he made extensive field trips throughout the country and completed his botanical studies in the mid-1930s. Between 1911 and 1915, he issued a series identified as *Herbarium bolivianum*. Buchtien's contributions to the flora of Bolivia list 45 new species of various genera and families (Buchtien, 1910). These plants were originally described by specialists from the University of Breslau, Germany, in the botanical journal *Fedde Repertorium*, between 1908 and 1909. Buchtien had probably collected more abundant and diverse material from Bolivia than any other botanist. His valuable herbarium, consisting of more than 45,600 specimens, was acquired in 1922 by the Smithsonian Institution. Duplicates also exist in the University of Breslau Herbarium and in other German herbaria.

Among the type collections of Buchtien are *S. violaceimarmoratum*, a species from Unduavi, Province of Nor Yungas, and *S. acaule* var. *subexinterruptum* from the Bolivian altiplano, both of which were described by Bitter in 1912. Buchtien also discovered *S. leptophyes* and *S. tuberosum* subsp. *sparsipilum* in the vicinity of La Paz; these latter two were described by Bitter in 1913. Buchtien also collected the type specimen of *S. yungasense*, near Milluhuaya, Province of Nor Yungas, in 1917. This species was described by Hawkes (1954) almost 40 years later. Also to Bitter (1913), we owe the description of *S. acaule* var. *caulescens*. The latter plant was grown in Grenoble, France, from tubers that were collected originally at Viacha, near La Paz, by Claude Verne in 1913.

In 1914, the Bolivian agronomist, Walter Cevallos Tovar, published a work on the classification of Bolivian cultivated potatoes, which was the first work of this type for South America. These investigations are based largely on tuber shape, in which he presents a total of 184 perfectly distinct clones grouped in round, long, flat, and irregular shapes, and he also indicates for each tuber the flesh and skin color, eye characteristics, and other attributes. Moreover, he gives the native name for each sample, mostly in the Aymara language. Although Cevallos Tovar does not indicate the exact locality from whence the material came, the majority was probably collected from the Bolivian altiplano (Cevallos Tovar, 1914).

Among other travelers to Bolivia between 1913 and 1920 were the American plant and seed collector, William F. Wight (1916), and the Swedish botanist, Eric Asplund (1926). These two explorers made general collections of the Bolivian flora, and a few of their herbarium specimens of potato can be found today in European and American museums. In addition, Wight, in 1913, collected nearly 50 samples of cultivated potatoes in La Paz and Oruro for the United States Department of Agriculture (Washington, D.C.).

The first expedition to collect living material in South America for inclusion in potato improvement programs was probably made by the Soviet Union in 1925. This work, which evolved under the leadership of Nicolai I. Vavilov, included Sergei M. Bukasov, who made collections in Mexico, Guatemala,

and Colombia between 1925 and 1926, and Sergei W. Juzepczuk, who did the same for Peru, Bolivia, and Chile between 1927 and 1928. Vavilov, in addition to making extensive trips in 1932 to North and Central America, collected in Ecuador with the assistance of E. Kesselbrenner (Bukasov and Lechnovitch, 1935). Many new wild and cultivated potato species resulted from these explorations (Juzepczuk and Bukasov, 1929; Bukasov, 1933, 1934, 1971b).

After nearly eight months of work in Peru, Juzepczuk arrived in La Paz, Bolivia, by mid-August of 1927, via the Puno-Guaqui route. In Bolivia, he worked mainly in the vicinities of Lake Titicaca, Viacha, La Paz, and Sorata. Given the season of his visit and the briefness of his stay in Bolivia, Juzepczuk dedicated himself exclusively to the collection of native cultivated potatoes.

Juzepczuk, in collaboration with Bukasov (1929), described for Bolivia the following new species: *S. ajanhuiri*, *S. andigenum*, *S. curtilobum*, *S. chaucha*, *S. juzepczukii*, *S. phureja*, and *S. tenuifilamentum*. In 1937, they also elevated *S. tuberosum* subsp. *sparsipilum* to the rank of *S. sparsipilum*, the name by which it is known today (Bukasov, 1937). In conection with their cultivated collections, later cytological studies by the Russians revealed the presence of a polyploid series in which the chromosome number varied from 2n=2x=24 to 2n=3x=36, 2n=4x=48, and 2n=5x=60 (Rybin, 1929, 1933).

A more complete classification of the South American cultivated potatoes, mostly based on the Juzepczuk and Bukasov collections, was carried out many years later by V. S. Lechnovitch (1971), also from Vavilov's Institute.

Shortly after the Soviet efforts in 1929, expeditions were undertaken by other countries with the purpose of collecting potatoes in the South American Andes. In 1930, the German Institute of Erwin Bauer sent Rudolph Schick to Bolivia and Peru (Schick, 1931). In 1932, an American expedition was made by H. G. MacMillan and C. O. Erlanson (Anonymous, 1934). In 1933, the Swedish Svalof Institute sent Karl Hammarlund to the same countries (Hammarlund, 1943). These expeditions collected primarily in the region of the Bolivian altiplano and southern Peru.

Hammarlund worked in Bolivia during 1933 and part of 1934. While in the altiplano, he worked principally in Lucurmata, Tiahuanacu, and Viacha. Later, he traveled to Oruro via Eucaliptus and Huancaroma. Afterward, he traveled from Rio Mulatos to Potosi, visiting along the way, Laja, Tambo, and Otavi in the Province of Linares. Later, he went from San Lucas to Irukasa, Tambillo, Sivingamayo, Tacaquira, and Camargo (Province of Nor Cinti, Department of Chuquisaca), to San Pedro and Culpina. Little is known about the results of this Swedish expedition; however, ten years later, Hammarlund reported a total of 800 general collections of the flora, which included many wild and cultivated potato species. He did not indicate the native names of the cultivated varieties or the precise localities where these were collected, nor did he undertake the taxonomic classification of this material.

In 1939, an English expedition was undertaken by the horticulturalist, Edward K. Balls, the physician William Balfour Gourlay, and the botanist Jack G. Hawkes. Their goal was to collect cultivated potatoes and their wild relatives, as well as other native cultivated species. The results of these explorations, which covered essentially the area from Colombia to northwest Argentina, are given in detail by Hawkes (1944). The expedition entered Bolivia in late January 1939 by the Guaqui-La Paz route and then traveled to the Argentine Provinces of Salta and Jujuy. From there they returned to Bolivia by the Villazon-Tarija route, and from Tarija they later traveled to Potosi and Sucre. Afterward, they visited Oruro and Cochabamba, where they visited with the Bolivian botanist, Martín Cárdenas. Later, they traveled from Colomi to the eastern side of the Cordillera of Tunari. Of the original group, only Balls returned to the altiplano from Cochabamba. After making short trips to the Lake Titicaca region, he completed his travels in Bolivia by late April 1939 and then proceeded to Peru, Ecuador, and Colombia.

The material collected by this two-month British expedition to Bolivia enabled Hawkes (1944) to describe the following wild species: *S. anomalocalyx*, *S. berthaultii*, *S. brevimucronatum*, *S. lapazense*, *S. oplocense*, *S. pachytrichum*, *S. platypterum*, *S. subandigena*, *S. sucrense* and its variety *brevifoliolum*, *S. tarijense*, and *S. violaceimarmoratum* var. *papillosum*. For the cultivated group, he described *S. cardenasii* and two new varieties, *S. phureja* var. *pujeri* and *S. chaucha* var. *roseum*. Also, Hawkes (1954) proposed the new Bolivian series Circaeifolia, under which were placed *S. circaeifolium* and *S. capsicibaccatum*.

Martín Cárdenas, the well-known Bolivian botanist (Argandoña, 1971), began floristic studies of his country in July of 1921, when he was assigned by the Bolivian government to assist Rusby on his record year-long 'Mulford Biological Exploration of the Amazon Basin.' It was during this expedition that Cárdenas learned, in particular, how to identify the complex flora of the Amazon Basin. At a later date, he also accompanied Asplund on plant collecting trips in Bolivia. Cárdenas was also in contact with many other foreign botanists, including Buchtien, the German botanist who resided in Bolivia for more than 30 years. The contributions that Cárdenas made to the flora of Bolivia were principally in the families Amaryllidaceae and Cactaceae, plus he also did important studies on the wild and cultivated potato species of this country.

In 1944, Cárdenas described his first two new Bolivian species of wild potatoes, *S. capsicibaccatum* and *S. pinnatifidum* (Cárdenas, 1944), both names based on type collections made by Humberto Gandarillas. In 1945, Cárdenas also published a work in collaboration with Hawkes concerning new or little known potato species from Bolivia and Peru (Cárdenas and Hawkes, 1945). In this work, they described for the first time, *S. decurrentilobum*, *S. toralapanum* and its variety *subintegrifolium*, and *S. ellipsifolium*, all of the series Megistacroloba. In

addition, they proposed the following Bolivian species for series Tuberosa: *S. mollepujroense*, *S. liriunianum*, and three subtaxa of *S. anomalocalyx*, vars. *llallaguanianum*, *brachystila*, and *muralis*. Also proposed was the species *S. virgultorum*, which was based on *S. boliviense* subsp. *virgultorum* Bitter. Moreover, there also appeared under the sole authorship of Hawkes, the species *S. xerophyllum*, which he placed in the series Cuneoalata Hawkes.

Ten years after the appearance of this joint paper by Cárdenas and Hawkes, the most extensive work published by Cárdenas on the Bolivian wild species of potato was published in the 1956 *Bulletin of the Peruvian Society of Botany*. In this publication, the author (Cárdenas, 1956), based on his own type collections, described the following new species: *S. achacachense*, *S. alandiae*, *S. arnezii*, *S. caipipendense*, *S. candelarianum*, *S. cevallos-tovari*, *S. colominense*, *S. cuevoanum*, *S. gandarillasii*, *S. higueranum*, *S. subandigena* var. *camarguense*, *S. torrecillasense*, *S. trigalense*, *S. ureyi*, *S. uyunense*, *S. vallegrandense* and its var. *pojoense*, *S. vidaurrei*, and *S. zudanense*. With the description of *S. ruiz-zeballosii* in 1968 (Cárdenas, 1968), he ended his contributions to the taxonomy of the Bolivian potatoes.

Also worthy of mention here are two Bolivian agronomists, Humberto Gandarillas and Segundo Alandia. These two scientists assisted, for many years, in the field collections of Cárdenas, as well as in those of other botanists, and their names have been cited frequently in works by Donovan Correll and Hans Ross. Individually, both have contributed to the production and improvement of Bolivian potato varieties (Gandarillas, 1961). Moises Zavaleta, another Bolivian agronomist, is known to have made a collection of cultivated potatoes which he maintained for a long time at Caquiaviri, a locality southeast of Lake Titicaca (Zavaleta, 1968). Unfortunately, these collections have been lost and are no longer available.

It is also important to mention here that a large cultivated germplasm collection was gathered by the Bolivian Ministry of Agriculture at the Experimental Station of Toralapa, near Cochabamba (Cárdenas, 1963).

In 1955, under the sponsorship of the Plant Improvement Institute of Wageningen, Holland, the author of the present work made a two-month trip to Bolivia to collect native cultivated potatoes. A year later, this work on the potatoes of the border region of Lake Titicaca, Department of Puno, Peru, was completed (Ochoa, 1958), in which were given the descriptions and chromosomal determinations of more than 500 collections of potato. The living materials collected in connection with this study were accessioned by the Dutch Potato Improvement Program. In 1956, the author published a single illustration and complete description of the little-known wild diploid species, *S. candolleanum*, which was collected in 1955 during a visit to Tacacoma, north of Sorata (Ochoa, 1956).

In February of 1959, a German expedition, headed by Hans Ross and

including the scientists R. Rimpau and Ludwig Diers, entered southern Bolivia (Ross and Rimpau, 1959; Ross, 1960a, b). They were sent to South America by the Max-Planck-Institute for the sole purpose of collecting germplasm of Bolivian potatoes for inclusion in a plant improvement program. They entered Bolivia from La Quiaca, Argentina, and collected initially in the Bolivian localities of Tarija, Potosi, and Sucre. Later, they continued on to Cochabamba via Aiquile-Totora. After making collections in the above localities, including the tributaries of the Tunari River, they headed to La Paz via the Oruro-Belen route, visiting Sorata and Los Yungas along the way. Finally, they crossed from Tiahuanacu to Desaguadero and arrived in Puno, Peru, on the first of April 1959, where they worked for several months collecting material. The living collections made during these travels were deposited in the Max-Planck-Institute, near Cologne, West Germany.

In 1960, the American botanist, Donovan S. Correll, undertook an expedition to collect the potatoes of Argentina, Bolivia, and Peru under the auspices of the Texas Research Foundation, the National Science Foundation, and the U.S. Department of Agriculture (Correll, 1962). Besides Correll, the expedition included Kenneth S. Dodds, Graham J. Paxman, and Heinz H. Brücher. Even though this expedition was in Bolivia for barely two weeks in February, they covered an enormous stretch of mountainous territory, traveling from Lake Titicaca and Los Yungas to La Paz, Oruro, Cochabamba, Sucre, Potosi, Tarija, and Villazon, and entering Argentina through La Quiaca. One result of this expedition was a new wild potato species for Bolivia that was described by Correll in 1961 under the name of *S. doddsii* (Correll, 1961).

In addition to the Andean trips already mentioned, Dodds and Paxman also spent several months collecting samples of the cultivated potatoes, 'chaucha' and 'phureja.' Dodds' expedition led ultimately to a revision of the cultivated potatoes based upon their inferred evolution. His work is explained and illustrated in a chapter in Correll (Dodds, 1962) entitled, 'Classification of Cultivated Potatoes.'

In 1962, the American botanist, Donald Ugent, organized a year-long expedition to collect the potatoes of Mexico, Ecuador, Peru, and Bolivia. This expedition was sponsored by the University of Wisconsin and the National Science Foundation. After five months in Peru, Ugent traveled to Bolivia via the Puno-Desaguadero route, arriving at La Paz in February of 1963. In Bolivia, Ugent collected principally in the mountainous zone from the vicinity of La Paz to Santa Cruz in the southeast. Some collections were made in collaboration with the Bolivian botanist, Martín Cárdenas, and the biology teacher, Arturo Vidaurre.

Although new species of potato were not collected during Ugent's expedition to Bolivia, the results of his work contributed valuable information on the distribution and ecology of many species. Tuber and seed collections from this

expedition are maintained by the U.S.D.A. Potato Introduction Station at Sturgeon Bay, Wisconsin.

In 1971, a potato collecting expedition to Peru and Bolivia was organized by J. G. Hawkes and Philip J. Cribb of the University of Birmingham, United Kingdom. This expedition, which was supported in part by the International Potato Center (CIP) in Lima, Peru, also included Jean P. Hjerting of the Copenhagen Botanical Garden and Zósimo Huamán of CIP. The expedition began in La Paz, Bolivia, in January of 1971, and followed a route that took them as far south as Entre Rios, Argentina, concluding several months later in April. Summarized results of the potato collecting expeditions in Bolivia, Chile, and Peru were also published by the author (Ochoa, 1975b).

Hawkes also organized other trips to Bolivia between the years 1978 and 1981. Participating at various times in these expeditions were Dave Astley (England), W. Hondelman and Jean P. Hjerting (Denmark), A. M. van Harten and J. M. Soest (Holland), Zósimo Huamán and Juan Landeo (Peru), Israel Aviles, Carlos Alarcón, Arturo Moreira, and Gerardo Caero (Bolivia), and Armando Okada (Argentina). Complete information on these expeditions has been given in recent publications by Soest et al. (1980, 1983).

Hundreds of samples of Bolivian wild and cultivated potato species resulted from the scientific expeditions of Hawkes and his various collaborators. Many of these collections were accessioned by the Germplasm Station of the University of Birmingham, and by the more recently organized Potato Bank of Germany and Holland, located in Braunsweig, West Germany. Some of the above collections were also received by the Potato Introduction Station at Wisconsin in the United States and by CIP in Peru. From the above-mentioned explorations came the following new species, all of which were described by Hawkes and Hjerting (1983, 1985a, b): *S. astleyi*, *S. avilesii*, *S. circaeifolium* subsp. *quimense*, *S. hondelmannii*, *S. neocardenasii*, *S. okadae*, and *S. soestii*.

In conclusion, it should be noted that the number of potato collecting expeditions to Peru and Bolivia increased substantially between 1971 and 1981. In this respect, credit must be given here to the valuable role played by the International Potato Center (CIP) (1973, 1976, 1979a, b). Thus, a major potato collecting expedition to Bolivia was organized by the author of this work in 1978 under the sponsorship of the International Potato Center. The expedition route included every major potato collecting locality from the border of northern Peru to Tarija in southeastern Bolivia. A detailed account was later published in the journal *Biota* (Ochoa, 1979d).

In 1983-1984, with the assistance of Alberto Salas of CIP, the explorations of the author were expanded to include areas never before collected. Moreover, the goals of these explorations were broadened to include the collection of topotypes of rare or little-known species. Tuber and seed collections made in

connection with these studies were incorporated into the CIP germplasm bank in Peru, and duplicate collections were sent to the Potato Introduction Station in Wisconsin. Included among the many species collected in Bolivia by the author are the following new taxa: *S. bombycinum*, *S. flavoviridens*, *S. litusinum*, *S. neovavilovii*, *S. venatoris*, *S. capsicibaccatum* var. *latifoliolatum*, *S. infundibuliforme* var. *albiflorum*, and *S. microdontum* var. *montepuncoense* (Ochoa, 1980a, b, 1981, 1982, 1983b, c, 1984a, b).

From D'Orbigny to the present time, more than 60 wild species of tuber-bearing *Solanum* have been described for Bolivia. In the following revision, this number has been reduced to approximately one half of the original proposals.

2

Geography and Climate

GEOGRAPHY

Bolivia, a land of diversified habitats and climates, is situated between latitude 9°38′ and 22°53′ S and longitude 57°26′ and 69°38′ W. It borders Brazil on the north and east, Peru and Chile on the west, and Argentina and Paraguay on the south (Map 1), with a total land area of 1,098,521 km^2 (Muñoz Reyes, 1977).

According to the last census made in 1983, the population of Bolivia was 5,966,000, with the majority of the country's population living in the highland areas. Even though more than half of Bolivia is either uninhabited or isolated from the main centers of production and economic importance and the country lacks a seaport and access to the coast, its railroads, highways, rivers, and airlines facilitate communication with neighboring countries. Traditionally, there has been free and open boat traffic on Lake Titicaca between Bolivia and southeastern Peru.

According to the Bolivian geographer, Jorge Muñoz Reyes (1977), this country is divided into several physiographic regions (Map 2), in which he refers to the high, cold tableland, or altiplano of Bolivia, as the 'Bloque Andino.' This great plateau, which is situated at an elevation between 3200 and 4400 m, dominates approximately one-third of the country. To the west of the altiplano is the Cordillera Occidental de los Andes, which is also known locally as either the 'Cordillera Occidental' or the 'Cordillera Volcanica,' while to the east of this vast plain is the Cordillera Real de los Andes (Map 2). These two major mountain chains converge in the north toward the Nudo de Vilcanota in La Raya, south of Cusco, Peru (14°31′ S), and in the south toward the Nudo de Licancabur in Chile (23° S), where the two ranges then trend south to the Punas de Atacama.

At still higher elevations in Bolivia, according to Cabrera and Willink