

PHASEOLUS BEANS (LEGUMINOSAE: PHASEOLEAE): A CHECKLIST AND NOTES ON THEIR TAXONOMY AND ECOLOGY

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ABSTRACT

This work presents an updated list of the species belonging to the genus *Phaseolus* following its definition of 1978; it is the outcome of the study of eighty-six herbaria and forty-one explorations in the field in the period 1978–2019. There are currently eighty-one species, all of them native to the Americas, most of them distributed north of Panama (the genus is a migrant into South America), and half of them being known by very few records. They thrive in warm to mild temperate, seasonally dry, open forest, with rains under favorable temperature, from sea level up to 3,000 m. The recent increase in the number of recognized species is due to the endemic ones; this in combination with few unclassified specimens may indicate that the total number of species is not final yet, and that field work will be rewarding.

RESUMEN

Este trabajo presenta una lista actualizada de las especies que pertenecen al género *Phaseolus* según la definición de 1978. Es el resultado del estudio de ochenta y seis Herbarios y de cuarenta y una bioprospecciones en el campo durante el periodo 1978–2019. Hay ochenta y una especies hasta la fecha, siendo todas parte de la flora americana, la mayoría distribuida al norte de Panamá (el género es un migrante en Suramérica), y más de la mitad conocida por sólo muy pocas poblaciones. Crecen en climas cálidos a templados moderados, con estación seca y con las lluvias durante el periodo de temperaturas favorables, en bosques abiertos desde el nivel del mar hasta los 3,000 m. El crecimiento reciente en el número de especies se debe al descubrimiento de especies endémicas. Esta situación combinada con la presencia de algunos especímenes aún por identificar puede indicar que el número total de especies no sea definitivo, y que el trabajo de campo aún puede ser muy gratificante.

RÉSUMÉ

Ce travail présente une liste actualisée des espèces appartenant au genre *Phaseolus* suivant la définition adoptée en 1978. C'est le résultat de l'étude de quatre-vingt-six Herbiers et de quarante et une prospections. Quatre-vingt-une espèces sont actuellement recensées, elles font toutes partie de la flore américaine. La majeure quantité des espèces ont leur distribution au nord du Panama (le genre est un migrant en Amérique du Sud), y plus de la moitié des espèces sont connues seulement par quelques populations. Elles se trouvent dans des climats chauds à modérément tempérés, avec une saison sèche et les pluies distribuées pendant la période de températures favorables. Elles font partie de forêts ouvertes, depuis le niveau de la mer jusqu'à 3,000 m. L'accroissement récent du nombre d'espèces est dû à la découverte d'espèces endémiques. Cette situation combinée à la présence de quelques spécimens encore non identifiés peut indiquer que le nombre total d'espèces n'est pas définitif, et que le travail de terrain peut encore être très positif.

KEY WORDS: Crop Wild Relatives, endemism, Neotropics, phytogeography

INTRODUCTION

The question about the number and identity of bean species is often raised by botanists and agronomists, but also by the authorities in charge of conserving such plant resources. The purpose of this note is to present an updated list of species according to the current definition of the genus. The reader will note the general agreement with the list of accepted *Phaseolus* species developed independently for the ongoing project on “Vascular Plants of the Americas” (Ulloa Ulloa et al. 2017; Tropicós 2020), with comments hereafter on discrepancies and on synonymy at the end of the note. This update confirms or increases the information provided elsewhere (Freytag & Debouck 2002; Porch et al. 2013). It was felt important to also report a few vouchers for readers to check about species identity and distribution, once all specimens held in Herbaria worldwide are available online (LaSalle et al. 2016; Rogers 2016). This note also updates other regional or country checklists (Miranda-Colin

1966; Janzen & Liesner 1980; Breedlove 1986; Dávila-Aranda et al. 1993; Zarucchi et al. 1993; Espinosa-Garduño & Rodríguez-Jimenez 1996; Hoc 1999; Neill et al. 1999; Correa et al. 2004; Zamora 2010).

While the genus *Phaseolus* was defined by Linnaeus (1753, p. 723), a revised definition came at the international legume conference held in Kew, England, in August 1978, set forth by independent researchers (Maréchal et al. 1978a, 1981; Lackey 1981, 1983). Different authors have since used and validated this definition of the genus (Delgado-Salinas 1985; Freytag & Debouck 2002; Schrire 2005; Delgado-Salinas et al. 2011). The genus is monophyletic (Delgado-Salinas et al. 1993) and naturally distributed in mild temperate to warm regions (mostly frost-free during the growing period) of the New World. There is thus a natural group of over eighty wild legumes sharing ten diagnostic traits (Table 1), variously distributed in open oak, pine, alder and hackberry seasonally dry woodlands of the New World from sea level up to 3,000 m (the tree limit) (Table 2), with genotypes under cultivation for five species (*P. acutifolius*, *P. coccineus*, *P. dumosus*, *P. lunatus*, and *P. vulgaris*). When dealing with these five species, the data provided hereafter are for the wild forms.

The genus is distributed in the Americas from the eastern to southern United States south to Argentina. Lackey (1983) indicated it to be naturally absent in Alaska, Canada, NW USA, California and Chile. While absence from Alaska and NW USA can be confirmed, the presence in Canada is debatable, because citation of unquestioned specimens is lacking: some authors claimed it to be present for Québec and Ontario (Torrey & Gray 1838; Small 1903; Rydberg 1965; Sousa-Sánchez & Delgado-Salinas 1993; Mercado-Ruaro et al. 2009), while others reported absence (MacMillan 1892; Voss 1985; Oldham & Brinker 2009). California (as a whole with Mediterranean climate, with winter rains) is an interesting case because its southeastern end occupied by vegetation of the Sonoran Desert (Shreve & Wiggins 1964) (climate with summer rains) holds a population of *P. filiformis* (Isely 1993). Field work has confirmed absence as wild in Chile (Becerra-Velásquez et al. 2011). The genus is present in two oceanic archipelagoes (to note: these are somehow connected to the mainland Americas by sea currents): the Bermudas and the Galapagos, each with one endemic species: *P. lignosus* and *P. mollis*, respectively (Debouck 2015 and Wiggins & Porter 1971, respectively). In the Revillagigedo Islands and in the Antilles (Greater and Lesser), the only true wild bean seems to be *P. lunatus* (Debouck 2019a). *Phaseolus polystachyus* has been claimed to be present in Puerto Rico (Liogier 1988, p. 194) but not evidenced by a specimen. From Jamaica *P. dumosus* has been described (Macfadyen 1837) but as feral, as it is in several secondary forests of Central America and the northern Andes at mid elevation (Berglund-Brücher & Brücher 1974; Schmit & Debouck 1991).

In addition to the taxonomic criteria presented elsewhere (Freytag & Debouck 2002), the author has relied on habitat and ecological information (herbarium labels and field notes), and data generated by molecular genetics. All these data must be convergent and back up each other. There is no *a priori* hierarchy between the different fields of evidence, but if contradictory evidence is found, then there is need to go back to the plant, field, or lab. The example of *P. glabellus* well made this point: while it was found morphologically close to wild *P. coccineus* (Piper 1926; Maréchal et al. 1978a; Delgado-Salinas 1988), the ecology (Schmit et al. 1996) and the genetic data (Schmit et al. 1993; Llaca et al. 1994; Delgado-Salinas et al. 1999) told another story, and it is now considered as unrelated to wild *P. coccineus*.

About the range shown in Table 2, species are considered as endemic (along a classic understanding: Avise 2002) once the area where they grow (area of occupancy) is less than 50 km² and with a total number of populations equal or less than 30, and as widespread when that area is more than 100 km² (often split into several subareas) and with a total number of populations equal or more than 100 (these figures are conservative estimates but in line with those used for a subsequent threat assessment: Khoury et al. 2020). A population is considered as a group of wild bean plants freely growing and reproducing over years without the intervention of humans; it usually occupies one hectare or less. It can be shown as distinct from other neighboring populations by molecular markers (Freyre et al. 1996; González-Torres et al. 2004). A population can be evidenced by an herbarium specimen kept in a museum of natural history and/or by a seed sample kept in a seed repository or germplasm bank. A few vouchers are mentioned (in geographical N-S or W-E gradient) by first collector's name and number ("s.n." if no collecting number is reported on the label). Herbaria where the

TABLE 1. Traits helping to distinguish *Phaseolus* species from other New World Phaseoleae.

Plant part	Diagnostic feature
1 all aerial plant parts, vegetative or reproductive	presence of minute uncinata hairs
2 leaves	usually 3-foliolate, stipules and stipels present
3 stipules of leaves excluding eophylls	basifixed attachment
4 primary bracts on peduncle and rachis	persistent till anthesis often beyond
5 nectariferous glands at pedicel insertion	absent; could be present on stipels or bracteoles
6 length of pedicel as compared to calyx tube	equal or longer
7 terminal part of the keel	1.5–2 closed coils and laterally projected
8 terminal part of the style	caducous after anthesis
9 pod with two valves, of longitudinal dehiscence	no internal septa separating the seeds
10 hilum of the seed	epihilum present, aril absent

Sources: Maréchal et al. 1978a, Lackey 1981, Delgado-Salinas et al. 2011.

specimens have been studied (Appendix 1), are indicated by acronyms along *Index Herbariorum* (Thiers 2020), with the number of the voucher in the herbarium if such numbering exists (with preference to a bar code numbering if present). Care has been taken to present for distribution and as far as possible new records as compared to those presented previously (Freytag & Debouck 2002). Specimens not seen are indicated as “n.v.” (*non visus*: Stearn 1993). Range data with emphasis on extremes are provided above all to encourage readers to document further both the distribution and the conservation status. Photographs have been taken by the author unless indicated otherwise.

RESULTS

The organization of the genus into two clades A and B (Delgado-Salinas et al. 2006) and sections as proposed by Delgado-Salinas (1985) and Freytag & Debouck (2002) has here been followed. Clade A only with wild species has eight sections (viz. *Bracteati*, *Brevilegumeni*, *Chiapasana*, *Digitati*, *Minkelsia*, *Pedicellati*, *Revoluti*, and *Xanthotricha*), and clade B with wild species (that include cultivated forms) has six sections (viz. *Acutifolii*, *Coriacei*, *Falcati*, *Paniculati*, *Phaseoli*, and *Rugosi*) (Porch et al. 2013). The total number of species is currently eighty-one, with forty-two species in clade A (with three species *P. glabellus*, *P. microcarpus*, and *P. oaxacanus* not being assigned to any section), and thirty-nine in clade B (Table 2).

Phaseolus acutifolius A. Gray (1852: 43) [clade B; sect. *Acutifolii* Freytag]. TYPE: C Wright 1311 (LECTOTYPE: GH-64068).

In the original description (p. 44) there is no mention of a specimen. However, through the work of George Freeman (1912, p. 20 and following) and his interactions with the staff of the Gray Herbarium, it was possible to locate and identify the type. Although the contribution by Asa Gray has been accepted for publication in March 1850, it has been published in March 1852. Two wild forms are often recognized, var. *acutifolius* and var. *tenuifolius* (Delgado-Salinas 1985) (Fig. 1). There might be ecological characteristics that separate these two forms (Pratt & Nabhan 1988), with var. *tenuifolius* being a colonizer of open sunny, slightly more xeric habitats. This variety often displays narrow leaflets (width 4–10 mm), the lateral ones often sublobate at base, with heteroblastic development being more expressed as the stem gets exposed to direct sun light. But studies using molecular markers (Muñoz et al. 2006; Blair et al. 2012) are less affirmative about the differences between the two forms, giving support to the synonymy proposed by Russ Buhrow (1983). Considered a member of the *Vulgaris* group (Delgado-Salinas et al. 2006), it is here maintained apart as the phylogenetic distance to common bean is not the same as for the other members of this group (Debouck 1999).

Specimens: U.S.A. **Arizona**: FS Coburn 1490 (ASU-292151). **New Mexico**: JT Columbus 1588 (NMCRC). **Texas**: P Manning 4080 (K). MEXICO. **Baja California Sur**: R Moran 18725 (ARIZ-185218). **Sonora**: P Jenkins 88-329 (ARIZ-322133). **Chihuahua**: HS Gentry 2465 (ARIZ-300374). **Coahuila**: E Palmer 261 (PH). **Sinaloa**: J González-Ortega 870 (ENCB). **Durango**: P Tenorio-Lezama 9850 (TEX-272994). **Nayarit**: G Flores-Franco 1249 (MO-3851303). **Jalisco**: R Lépiz-Ildefonso 125 (IBUG-208586). **Guanajuato**: LI Aguilera G. 293 (CHAPA). **Michoacán**: JN Labat 1279 (P).

TABLE 2. List of currently valid *Phaseolus* species (only as native wild plants) and general indication about clade and geographic distribution and qualification of their range R (E= endemic, I= intermediate, W= widespread).

Bean species	Area of geographic distribution	Clade	R
1. <i>acutifolius</i>	SW USA, NW Mexico down to Neo-volcanic axis	B	W
2. <i>albescens</i>	W of Neo-volcanic axis of Mexico	B	I
3. <i>albicarminus</i>	Fila Bustamante in central Costa Rica	A?	E
4. <i>albiflorus</i>	N of Sierra Madre Oriental in Mexico	A	E
5. <i>albinervus</i>	W Chihuahua of Mexico	B	E
6. <i>albiolaceus</i>	N of Sierra Madre Oriental in Mexico	A	E
7. <i>altimontanus</i>	N of Sierra Madre Oriental in Mexico	A	E
8. <i>amabilis</i>	N Sierra Madre Occidental in Mexico	A	E
9. <i>amblyosepalus</i>	Durango and Sinaloa border in Mexico	A	E
10. <i>angucianae</i>	Fila Cruces SE of Costa Rica	A?	E
11. <i>angustissimus</i>	SW USA and NW Mexico	B	W
12. <i>anisophyllus</i>	SW Chihuahua and S Durango of Mexico	A	E
13. <i>augusti</i>	Andes, from S Ecuador to NW Argentina	B	W
14. <i>campanulatus</i>	W end of Neo-volcanic axis of Mexico	A	E
15. <i>carterae</i>	S end of Baja California of Mexico	B	E
16. <i>chiapasanus</i>	parts of Veracruz, Oaxaca and Chiapas in Mexico	A	I
17. <i>coccineus</i>	from Chihuahua, Mexico, down to Fco. Morazán, Honduras	B	W
18. <i>costaricensis</i>	Central and E Costa Rica to W Panama	B	I
19. <i>dasycarpus</i>	S end of Sierra Madre Oriental in Mexico	A	E
20. <i>debouckii</i>	Pacific slope of Andes in SW Ecuador and NW Peru	B	I
21. <i>dumosus</i>	Volcanic mountains of SW Guatemala	B	E
22. <i>esperanzae</i>	Central and E of Neo-volcanic axis of Mexico	A	I
23. <i>esquincensis</i>	Central Chiapas of Mexico	A	E
24. <i>filiformis</i>	Gulf of California to NW Mexico to Texas	B	W
25. <i>glabellus</i>	Gulf of Mexico, from Tamaulipas to Chiapas	A	W
26. <i>gladiolatus</i>	Central Mexico	A	I
27. <i>grayanus</i>	N Mexico to Arizona, New Mexico and Texas down to Jalisco	A	W
28. <i>hintonii</i>	Central W Mexico	A	E
29. <i>hygrophilus</i>	Central S Costa Rica	A?	E
30. <i>jaliscanus</i>	C and S Sierra Madre Occidental of Mexico	B	I
31. <i>juquilensis</i>	NW and Central Oaxaca of Mexico	B	E
32. <i>laxiflorus</i>	E of Neo-volcanic axis of Mexico	A	E
33. <i>leptophyllus</i>	Central Guerrero of Mexico	A	E
34. <i>leptostachyus</i>	N Mexico to SE Costa Rica	B	W
35. <i>lignosus</i>	Bermuda	B	E
36. <i>lunatus</i>	Central and South America, Caribbean	B	W
37. <i>macrolepis</i>	Central and SW Guatemala	A	E
38. <i>maculatifolius</i>	N of Sierra Madre Oriental in Mexico	B	E
39. <i>maculatus</i>	Arizona through Texas to Puebla of Mexico	B	W
40. <i>macvaughii</i>	Coastal W Mexico from Sinaloa to Guerrero	B	W
41. <i>magnilobatus</i>	Central W Mexico	A	E
42. <i>marechalii</i>	Central and E of Neo-volcanic axis of Mexico	B	I
43. <i>micranthus</i>	W of Neo-volcanic axis and all Pacific coastal Mexico	B	W
44. <i>microcarpus</i>	from Durango, Mexico to NW Costa Rica	A	W
45. <i>mollis</i>	Galapagos Islands	B	E
46. <i>montanus</i>	Arizona down to E Guatemala	B	W
47. <i>neglectus</i>	N of Sierra Madre Oriental, Mexico	A	E
48. <i>nelsonii</i>	S Mexico down to Chiapas	A	I
49. <i>nodosus</i>	W of Neo-volcanic axis of Mexico	B	E

TABLE 2. continued

Bean species	Area of geographic distribution	Clade	R
50. <i>novoleonensis</i>	N of Sierra Madre Oriental, Mexico	B	E
51. <i>oaxacanus</i>	Central Oaxaca of Mexico	A	E
52. <i>oligospermus</i>	Chiapas of Mexico to central Costa Rica	A	W
53. <i>parvulus</i>	SW USA to end of Sierra Madre Occidental of Mexico	A	W
54. <i>pauciflorus</i>	Chihuahua to Oaxaca, Mexico	A	W
55. <i>pedicellatus</i>	Neo-volcanic axis, Sierra Madre Oriental and Occidental of Mexico	A	W
56. <i>perplexus</i>	W Neo-volcanic axis of Mexico	A	I
57. <i>persistens</i>	Central volcanoes of Guatemala	B	E
58. <i>plagioclyx</i>	Eastern central Nuevo León of Mexico	A	E
59. <i>pluriflorus</i>	Western and central Mexico	A	I
60. <i>polymorphus</i>	Northern and eastern central Mexico	A	I
61. <i>polystachyus</i>	Eastern USA from New York to Florida to E Texas	B	W
62. <i>purpusii</i>	Western San Luis Potosí of Mexico	A	E
63. <i>reticulatus</i>	SW of Durango in Mexico	B	E
64. <i>ritensis</i>	SW of USA and NW of Mexico	B	W
65. <i>rotundatus</i>	Central Jalisco and Michoacán of Mexico	B	I
66. <i>salicifolius</i>	W Durango and E Sinaloa of Mexico	B	E
67. <i>scrobiculatifolius</i>	N Michoacán of Mexico	B	E
68. <i>sinuatus</i>	SE of USA from North Carolina to Florida	B	I
69. <i>smilacifolius</i>	Central Florida of USA	B	E
70. <i>sonorensis</i>	SE Sonora and SW Chihuahua of Mexico	B	E
71. <i>talamancensis</i>	Central S and SE of Costa Rica	A	E
72. <i>tenellus</i>	Central Neovolcanic axis of Mexico	A	E
73. <i>texensis</i>	SW Texas of USA	A	E
74. <i>trifidus</i>	SE Nuevo León of Mexico	A	E
75. <i>tuerckheimii</i>	from Chiapas of Mexico to western Panamá	A	W
76. <i>venosus</i>	Aguascalientes and surroundings of Central Mexico	B	E
77. <i>viridis</i>	Veracruz, Mexico to Alta Verapaz, Guatemala	B	W
78. <i>vulgaris</i>	SW Chihuahua in Mexico down to W Córdoba in Argentina	B	W
79. <i>xanthotrichus</i>	Chiapas of Mexico to central Costa Rica	A	W
80. <i>xolocotzii</i>	Sierra Madre del Sur of Mexico	B	E
81. <i>zimapanensis</i>	SW Sierra Madre Oriental of Mexico	A	I

N.B.: in the list above, the species *P. coccineus*, *P. lunatus* and *P. vulgaris*, although originally described on cultivated forms, are considered as wild.

Phaseolus albescens McVaugh ex R. Ramírez & A. Delgado (1999: 638) [clade B; sect. *Phaseoli* DC. emend. Freytag]. TYPE: *A. Delgado-Salinas et al. 1705* (HOLOTYPE: MEXU n.v.; ISOTYPES: GH-423041, K-651820, NY-1104834).

It is a pluriannual vine in montane pine, fir, oak, ash forests on a few mountainous ridges of western Mexico (Ramírez-Delgadillo & Delgado-Salinas 1999) at 1300–2300 m. Apparently, it was Rogers McVaugh who first realized that this plant was not a *P. coccineus* nor a *P. dumosus* (McVaugh 1987, p. 654). Primary bracts and bracteoles are smaller as compared to those of *P. dumosus*, corolla pale lavender to old rose contrasting with purple in *P. dumosus* (Fig. 2), and 4–5 seeds per pod (one less on average in wild *P. dumosus*). It is possibly at risk because of the logging in these old-growth forests, namely in the area of El Fresnito (county of Zapotiltic in Jalisco) as noted by the author in November 2003.

Specimens: MEXICO. **Jalisco:** *T. Kajita 95120310* (MEXU-1235511). **Colima:** *L. Rico 926* (IBUG-133696). **Michoacán:** *C. Medina G. 3601* (IEB-148134). **Guerrero:** *E. Velázquez 479* (K).

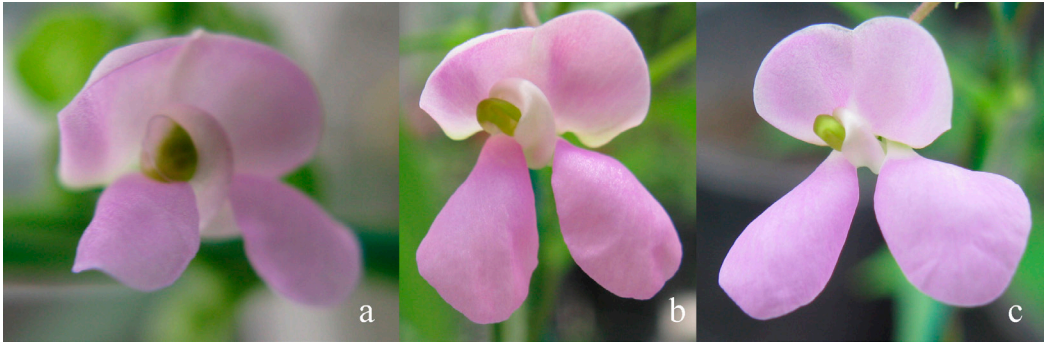


Fig. 1. Close-ups of flowers of: **a.** *P. acutifolius* var. *acutifolius* (DG Debouck 455), **b.** var. *tenuifolius* (DG Debouck 388), and **c.** *P. montanus* (DG Debouck 413).

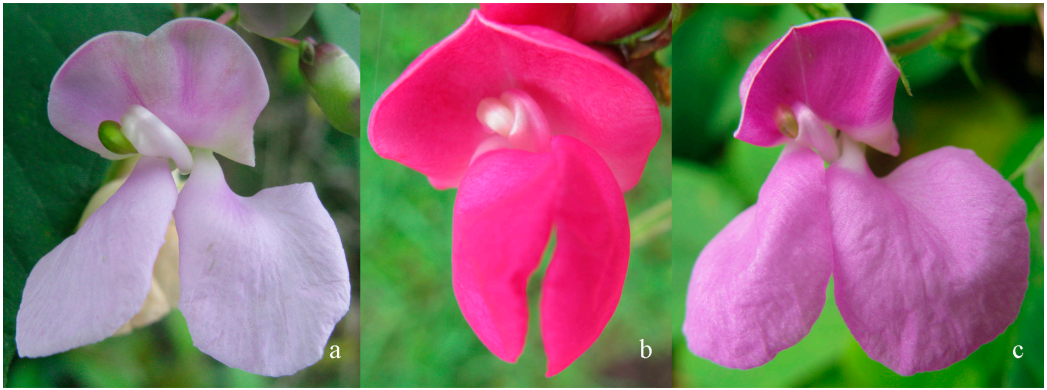


Fig. 2. Close-ups of flowers of: **a.** *P. albescens* (R Lépiz 141), **b.** *P. costaricensis* (DG Debouck 2116), and **c.** *P. dumosus* (DG Debouck 1631).

Phaseolus albicarminus Debouck & N. Chaves (2020: 3) [possibly in clade A and sect. *Brevilegumeni* Freytag]. TYPE: DG Debouck et al. 3347 (HOLOTYPE: USJ-111997; ISOTYPES: BRIT, CR-282240, F, GH, K, MICH, MO, P, UC).

It is a recent addition to the flora of Costa Rica (Fig. 3), growing in premontane wet forest at 1600–2000 m, and known from three populations so far, from a small area south of mount Caraigres at the western end of the Talamanca mountain range (Debouck et al. 2020). The area is affected by the expansion of coffee plantations and pastures.

Specimens: COSTA RICA. **San José:** DG Debouck 3242 (CR-281568), DG Debouck 3342 (USJ-111444).

Phaseolus albiflorus Freytag & Debouck (2002: 177) [clade A; sect. *Digitati* Freytag]. TYPE: DG Debouck et al. 1510 (HOLOTYPE: US-3168862 and 3168864; ISOTYPES: COL-58795, G, K, M, MICH-1179903, SI, UNL n.v., UC, WIS).

It is a tall (more than 3 m) climbing plant, growing in oak and pine-oak forest at 1000–2200 m, with white flowers (fading dull ochre yellow after anthesis) (Fig. 4) and floral buds like fingertips, thus belonging to the *Digitati* section. The stems display heteroblastic development, with leaflets usually much lobed in the upper flowering parts. The keel is much deflected towards the left wing, the last coil being almost horizontal (Fig. 4). Recent collections have been done in northeastern Mexico (Acosta-Díaz et al. 2019).

Specimens: MEXICO. **Coahuila:** JA Encina 591 (ANSM-74394). **Nuevo León:** DG Debouck 1507 (US-3168358). **Tamaulipas:** FO Zuloaga 9700 (ANSM-89228).



FIG. 3. Close-ups of flowers of: **a.** *P. albicarminus* (DG Debouck 3242), **b.** *P. anguciana* (DG Debouck 3243), **c.** *P. hygrophilus* (DG Debouck 3172), **d.** *P. oligospermus* (DG Debouck 3333), and **e.** *P. tuerckheimii* (DG Debouck 2134).



FIG. 4. Close-up of flowers of: **a.** *P. albiflorus* (DG Debouck 1528), **b.** *P. albiviolaecus* (DG Debouck 2063) (photograph by J. Gereda, CIAT), and **c.** *P. altimontanus* (DG Debouck 1523).

Phaseolus albinervus Freytag & Debouck (2002: 127) [clade B; sect. *Paniculati* Freytag]. TYPE: *M Lavin et al.* 5426 (HOLOTYPE: TEX-371372; ISOTYPES: CAS-817320, F-2060227, MO-3412308, NY, UCR-46735).

This scandent pluriannual shrub seems to be known only from the type locality in W Chihuahua, Mexico. This species has been validated as a member of the *Paniculati* (Delgado-Salinas et al. 2006); it seems to share with *P. salicifolius* and *P. sonorensis* the trait of blooming in spring.

Phaseolus albiviolaecus Freytag & Debouck (2002: 179) [clade A; sect. *Digitati* Freytag]. TYPE: *DG Debouck et al.* 2063 (HOLOTYPE: US-3168863; ISOTYPES: BR, COL-235996, G, K, M, MICH-1179904, UNL n.v., WIS).

This species (Fig. 4) has been considered a synonym of *P. neglectus* (Delgado-Salinas et al. 2006); in the latter, on the type, the primary bracts are bigger (4–7 vs 2–2.5 mm), and the rachis of inflorescence is much shorter (2–4 vs 5–8 cm) as compared to the peduncle. Pending more material for study, this synonymy is kept on hold.

Specimen: MEXICO. **Nuevo León:** *DG Debouck* 2059 (BR, K, US-3168519).

Phaseolus altimontanus Freytag & Debouck (2002: 183) [clade A; sect. *Digitati* Freytag]. TYPE: *DG Debouck et al.* 1525 (HOLOTYPE: US-3168865; ISOTYPES: BR, G, K, M, SI, UNL n.v., UC-1716192).

This reclining vine with light purple standard and white wings (Fig. 4) is considered as endemic because only a few populations are known to date, from pine-oak forests of Santiago and Cola de Caballo south of Monterrey in Nuevo León and neighboring Tamaulipas, Mexico, at 1500–1900 m (also noted by Acosta-Díaz et al. 2015). The species is considered threatened (Acosta-Díaz et al. 2019).

Specimens: MEXICO. **Nuevo León:** *S Rodríguez-Tijerina* 138 (ANSM-63277). **Tamaulipas:** *J Hinton* 24657 (ANSM-71567).

Phaseolus amabilis Standley (1940a: 28) [clade A; sect. *Minklersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE: *HS Gentry* 2471 (HOLOTYPE: F n.v.; ISOTYPES: DES, GH-64083, K-478471, MO-1163243, UC-581881).

It has larger flowers as compared to other species of the section (*P. pauciflorus* being another case in this section but with a different floral morphology). It seems to be rare, but possibly not a hybrid as suggested elsewhere (Fishbein et al. 1998) because of the following collection found at different time and place.

Specimen: MEXICO. **Chihuahua:** *T Lebgue* 2481 (NMC-70649).

Phaseolus amblyosepalus (Piper) Morton (1944: 85) [clade A; sect. *Minkelpersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE: *P Ibaña-García* 456 (HOLOTYPE: US-1013387).

The voucher 1013387 kept at US consists of two plants; the plant to the right is the type of *P. amblyosepalus*. This member of the *Minkelpersia* can be easily identified by its large, rounded stipules. Its distribution seems to be the contact zone between Sinaloa and Durango in the Sierra Madre Occidental of Mexico, in pine forest at 2000–2700 m.

Specimens: MEXICO. **Durango:** *Y Herrera* 215 (ENCB), *AC Sanders* 21466 (UCR-105163), *P Tenorio-Lezama* 9685 (TEX-272982).

Phaseolus angucianae Debouck & Araya (2018: 508) [possibly in clade A and sect. *Brevilegumeni* Freytag]. TYPE: *DG Debouck et al.* 3369 (HOLOTYPE: USJ-111488; ISOTYPES: BRIT-476561, CR-286418, GH, K, MICH, MO, NY, P).

This is an endemic species from SE Costa Rica (Fig. 3), the distribution of which seems to be restricted to the “Fila Costeña Sur” in lower montane rain forest at 1400–1600 m. Because of deforestation its habitat seems shrinking (Debouck et al. 2018).

Specimens: COSTA RICA. **Puntarenas:** *N Chaves-Barrantes* 6 (USJ-111737), *M Grayum* 10618 (MO-6103483).

Phaseolus angustissimus A. Gray (1853: 33) [clade B; sect. *Rugosi* Freytag]. TYPE: *C Wright* 68 (distributed as 951) (SYNTYPES: GH-64073; ISOSYNTYPES: BM, K-H922/76-1, GH-64074, MO-1731218).

The original material (no. 951 in Gray’s herbarium, with “n. sp.” handwritten on the label, possibly by Asa Gray himself; Padovani & Cucuini 2006 reported a series of handwritings) seems to refer to two gatherings, one made in New Mexico in July 1851 and another one made in Sonora in September 1851 (the plant to the left in GH-64073), thus the use of syntypes along Art. 9.5. of the Melbourne Code (2012). As noted by James Lackey (1983) this taxon has a tuberculate seed coat (Fig. 5), different from the raised lines radiating from the hilum which can be seen in wild *P. lunatus* or *P. microcarpus*. It is a widespread species, growing in pine, oak, ash or plane forest or chaparral at 800–2400 m, with distribution well documented in S Arizona, S New Mexico and the W end of Texas, but with few records from N Mexico (although claimed to be present: Hermann 1966; Correll & Johnston 1970; Estrada & Martínez 2000). In the original description of *P. angustissimus*, Asa Gray (1853, p. 33) wrote “between San Pedro and Santa Cruz, Sonora, Sept.”. Two specimens of collection 951 have been found in PH and TCD with the indication of Sonora.

Specimens: U.S.A. **Arizona:** *D Atwood* 18881 (NY). **New Mexico:** *ND Atwood* 30820 (DAV-175765). **Texas:** *TL Steiger* 927 (NY).

Phaseolus anisophyllus (Piper) Freytag & Debouck (2002: 155) [clade A; sect. *Minkelpersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE: *EW Nelson* 4911 (HOLOTYPE: US-332953).

It seems to be a too tall and vigorous plant to be considered merely as a variant of *P. parvulus* (see discussion by George Freytag, 2002, p. 155), and it has been validated as a separate species of this section (Delgado-Salinas et al. 2006). It has been found above 2,000 m in oak woodland in the Sierra Madre Occidental from SW Chihuahua to S Durango.

Specimens: MEXICO. **Chihuahua:** *A McDonald* 2513 (ARIZ-340049). **Durango:** *R Spellenberg* 12747 (NMC-85870).

Phaseolus augusti Harms (1921: 503) [clade B; sect. *Paniculati* Freytag]. TYPE: *A Weberbauer* 6439 (HOLOTYPE: B n.v.; ISOTYPES: G, GH-64117, MOL, US-1496218).

The type was probably lost in Berlin during WWII; while the isotype at G consists only of fragments, the other three are complete blooming specimens. If there is any need (see Turland 2013, p. 64 and following), on the basis of the number of flowering racemes, the author wishes to indicate: “Neotype designated here: A

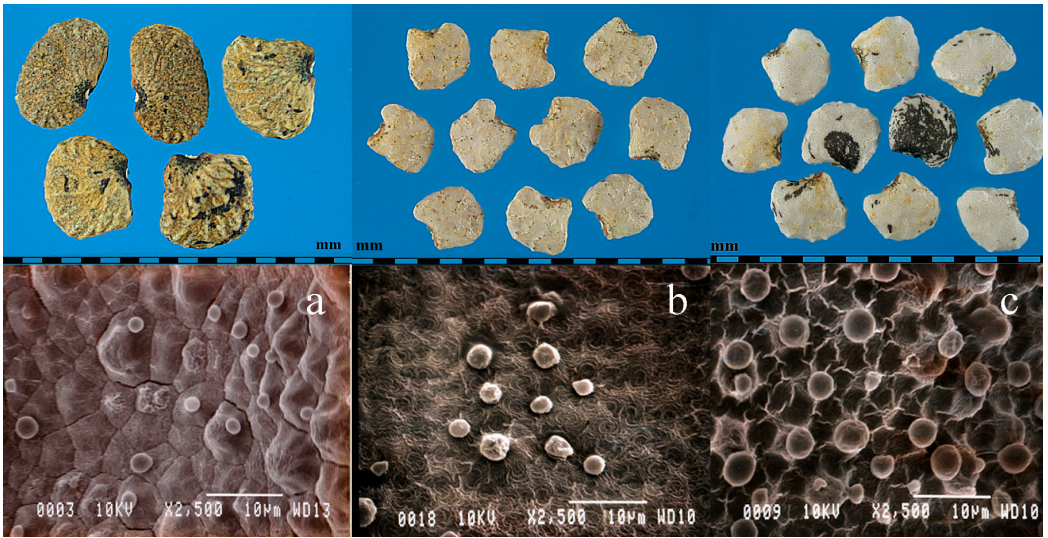


Fig. 5. Seed coat of the *Rugosi* (top row: macrophotos of seed, scale in mm, by O. Toro, CIAT; lower row: scanning electronic microscope photographs (x 2,500, scale bar 10 microns, by J.A. Arroyave, CIAT) of: a. *P. angustissimus* (G40669, R Buhrow 85-1), b. *P. carterae* (G40675, León de la Luz 3751), and c. *P. filiformis* (G40510, VE Rudd 3396).

Weberbauer 6439 (GH-64117)". Using this specimen and the specimen US-1058964 (= the type of *Phaseolus bolivianus* Piper), the author fully endorses the synonymy of the latter with *P. augusti* proposed by James Zarucchi and Alfonso Delgado-Salinas (1993, p. 508). Incidentally, it is quite strange that Charles Vancouver Piper (1926) did not mention *P. augusti* (thus creating a need for *P. bolivianus*) while he mentioned *P. pachyrrhizoides* (with one "r," p. 700). The original population of *P. bolivianus* is probably gone by now due to the expanding city of Cochabamba; an alternative could be the population found NW of Quillacollo DG Debouck 3000 (DAV-167638, MO-5613159, NY) (Freyre et al. 1996). Along recommendation 60C.2 of the Code (McNeill et al. 2012, p. 134), the spelling of the current termination of the epithet can be used.

Phaseolus augusti is a species well distributed in the Andes in alder seasonal forest at 1400–3200 m, related to the Andean form of wild *P. lunatus* (Delgado-Salinas et al. 2006; Serrano-Serrano et al. 2010), and thus included into the *Paniculati* where the Lima bean is the reference species (Fig. 10).

Specimens: ECUADOR. **Azuay:** DG Debouck 2764 (QCA). **Loja:** L Ellemann 91733 (K). PERU. **Piura:** DG Debouck 2816 (COL-332611). **Cajamarca:** N Angulo 1609 (F-1746428). **La Libertad:** S Leiva 453 (HAO-3037). **Huánuco:** C Ochoa 1085 (MOL). **Junín:** DG Debouck 2146 (UC-1571124). **Apurímac:** C Vargas 8858 (CUZ-7418). **Huancavelica:** O Tovar 1919 (US-2490509). **Cuzco:** E Petersen 1535 (LIL-410643). **Puno:** J Soukup 726 (CUZ-7417). BOLIVIA. **La Paz:** SG Beck 8659 (BAB). **Cochabamba:** DG Debouck 2483 (UC-1716208). **Norcinti:** DG Debouck 2504 (LPB). **Chuquisaca:** DG Debouck 2490 (LPB). **Tarija:** JRI Wood 9539 (K). ARGENTINA. **Jujuy:** A Burkart 11591 (SI). **Salta:** DG Debouck 1774 (BAA). **Tucumán:** R Fortunato 3565 (BAB). **Catamarca:** M Cerana 318 (CORD).

Another species is often reported from the Central Andes and the author may report the following:

Phaseolus pachyrrhizoides Harms (1921: 504) [clade B; sect. *Paniculati* Freytag]. TYPE: A Weberbauer 1769 (HOLOTYPE: B.n.v.).

The type was probably lost in the fire of B in 1943; it is survived as a black-and-white photograph with number 2440 (seen by the author at G and US). It was probably a unicate because the author has not seen any other specimen with that field collection number during this study. August Weberbauer (1945) mentioned this taxon only once (and without any number) from the surroundings of Huacapistana, Junín, while Francis McBride (1943) mentioned a few collections from Junín and Huánuco. Zarucchi and co-workers (1993)

reported it to be present also in Ayacucho and Huancavelica. Material that matches well the description given by Hermann Harms, namely in raceme size and size and shape of primary bracts and bracteoles, is *DG Debouck* 2149 (BR, COL-236000, MICH, UC-1571119, US-3168424, USM n.v.) found not far from Huacapistana in Junín, Peru. The following specimens give indication about the range of this taxon (note it is within the range of *P. augusti* reported here and by Zarucchi et al. 1993).

Specimens: PERU. **Amazonas:** *R Ferreyra* 15552 (USM-26770). **Cajamarca:** *DG Debouck* 2011 (MO-2828586). **Huánuco:** *PG Smith* s.n. (USM-26765). **Junin:** *TB Croat* 57694 (USM-56590). **Apurimac:** *DG Debouck* 2294 (UC-1716200).

While *P. augusti* and *P. pachyrrhizoides* share the same pollen type (Maréchal et al. 1978a), differences between populations of both taxa revealed by biochemical (Maquet et al. 1999) and molecular studies (Caicedo et al. 1999; Delgado-Salinas et al. 1999; Fofana et al. 1999) seem to be of the same magnitude as those between gene pools within wild Lima or common bean. Having studied in the field 36 populations of *P. augusti* and 24 of *P. pachyrrhizoides*, respectively, and in herbaria 112 and 40 specimens, respectively, the following synonymy can be proposed:

Phaseolus pachyrrhizoides Harms, based on *A Weberbauer* 1769 (B, as holotype, lost; photographed by Chicago Natural History Museum, formerly Field Museum of Natural History, through the Rockefeller Foundation Fund for Photographing Type Specimens, Types of the Berlin Herbarium, b/w photograph nr. 2440, in G and US), and originally published in: Notizbl. Bot. Gart. Mus. Berlin-Dahlem 7:504. 1921.

= *Phaseolus augusti* Harms, based on *A Weberbauer* 6439 (GH-64117) as isotype (see above), and originally published in: Notizbl. Bot. Gart. Mus. Berlin-Dahlem 7:503. 1921.

Phaseolus campanulatus Freytag & Debouck (2002: 224) [clade A; sect. *Brevilegumeni* Freytag]. TYPE: *R McVaugh* 16341 (HOLOTYPE: MICH-1210016).

This species known by only a few collections from western Mexico is close to *P. oligospermus*, but with differences such as leaf shape and number of seeds (five) per pod (Lépiz-Ildefonso & Ramírez-Delgadillo 2010). It grows in mixed broadleaf oak forest at 1300–1400 m.

Specimens: MEXICO. **Jalisco:** *JA Solis-Magallanes* 1961 (MEXU-330005). **Nayarit:** *O Téllez-Valdés* 9346 (IBUG-169372).

Phaseolus carterae Freytag & Debouck (2002: 194) [clade B; sect. *Rugosi* Freytag]. TYPE: *FW Gould* 12181 (HOLOTYPE: MICH-1210182).

According to Recommendation 60C of the Melbourne Code (2012) and information provided by Turland (2013, p. 91–92), the termination of the epithet has been corrected. This species shows an infrequent first trifoliate lobed leaf and rugose seed testa (Fig. 5); it needs additional collecting across the Peninsula of Baja California to confirm its status as endemic of southern Baja California Sur (Freytag & Debouck 2002).

Specimens: MEXICO. **Baja California Sur:** *TS Brandege* sn (UC-137617), *JL León de la Luz* 3751 (K).

Phaseolus chiapasanus Piper (1921: 41) [clade A; sect. *Chiapasana* A. Delgado]. TYPE: *CA Purpus* 6881 (HOLOTYPE: US-567182; ISOTYPES: F-415699, GH-64086, NY-26707, UC-172989).

This species stands alone in the genus because the large size of flowers, pods and seeds, and the black color of all plant parts upon drying. Its range at 700–1700 m goes beyond Chiapas, raising the question whether it enters into western Guatemala. Its lower montane deciduous forest habitat is shrinking because of the progress of coffee plantations (Rzedowski 1978).

Specimens: MEXICO. **Chiapas:** *M Sousa-Sánchez* 11410 (CAS-676163). **Oaxaca:** *A Flores-Martínez* 1685 (IEB-79142). **Veracruz:** *S Avendano* 554 (F-1974958).

Phaseolus coccineus L. (1753: 724) [clade B; sect. *Phaseoli* DC emend. Freytag]. TYPE (LECTOTYPE): according to Westphal (1974) and Delgado-Salinas (1985) the lectotype is the specimen 899.2 in LINN, a plant cultivated in the garden of Uppsala, behaving there as an annual and of unknown origin (McVaugh 1987).

The wild form of the scarlet runner is rather polymorphic (Delgado-Salinas 1988), namely in pubescence (McVaugh 1987), also at molecular level (Mina-Vargas et al. 2016); not surprisingly it has received many names



FIG. 6. Close-ups of flowers of: **a.** *P. coccineus* (GF Freytag 81-7) and **b.** *P. glabellus* (DG Debouck 2041).

(Freytag & Debouck 2002). Some populations are clearly distinct, but possibly because of outcrossed pollination interbreeding is frequent and many intermediate forms between taxonomic entities are found. The treatment of McVaugh (1987) for “*P. coccineus* and its allies” (Piper 1926, p. 683) is followed here, excepting *P. glabellus* (Fig. 6). While wild *P. coccineus* extends from Chihuahua in Mexico down to Francisco Morazán in Honduras in very diverse but open habitats at 800–3000 m, feral forms exist in El Salvador (e.g., Chalatenango: *D Rodríguez 1316* (LAGU)), Costa Rica (e.g., Alajuela: *A Jiménez M. 2550* (CR-118121)), Colombia (e.g., Cundinamarca: *H García-Barriga 12582* (COL-30058)) and Ecuador (e.g., Pichincha: *JL Luteyn 8770* (QCA)). *Phaseolus multiflorus* Willdenow mentioned in the list of “Vascular Plants of the Americas” (Tropicos 2020) is a synonym. Many populations of the Central Valley of Mexico sampled by Eugène Bourgeau in 1865–1866 seem to be extinct.

Specimens: MEXICO. **Chihuahua:** *RL Oliver 612* (DUKE-215258). **Coahuila:** *JS Marroquín s.n.* (ANSM-11433). **Nuevo León:** *FG Meyer 2742* (BR). **Tamaulipas:** *R Díaz 512* (RB-372771). **Sinaloa:** *L McGill 9574* (ASU-47963). **Durango:** *S Acevedo 312* (NY). **Zacatecas:** *JN Rose 2725* (K). **San Luis Potosí:** *J Rzedowski 5107* (ENCB). **Guanajuato:** *A Rubio-Chacón 118* (EBUM-10582). **Querétaro:** *E Carranza 2731* (CHAPA). **Hidalgo:** *R Hernández-Magaña 6788* (MO-3851282). **Nayarit:** *B Bartholomew 2614* (NY). **Jalisco:** *A Delgado-Salinas 1505* (BM). **Michoacán:** *Ch Feddema 197* (NY). **México:** *H Bravo H. 2006* (MA-263923). **Distrito Federal:** *E Bourgeau 334* (G). **Morelos:** *HS Gentry 22490* (NA). **Tlaxcala:** *MA Martínez A. 1714* (NCU-501422). **Puebla:** *IK Langman 2081* (PH-802749). **Veracruz:** *E Bourgeau 3351* (P). **Guerrero:** *DG Debouck 2359* (UC-1716201). **Oaxaca:** *WR Anderson 13109* (DUKE-327868). **Chiapas:** *DE Breedlove 6900* (ENCB). GUATEMALA. **San Marcos:** *DG Debouck 1637* (M). **Huehuetenango:** *GF Freytag 78-Guat-109* (K). **Quezaltenango:** *DG Debouck 1675* (COL-324592). **Sololá:** *M Nee 47366* (NY). **Chimaltenango:** *DG Debouck 1625* (COL-324586). **Sacatepéquez:** *WC Shannon 3683* (G). **Alta Verapaz:** *WE Harmon 4290* (ENCB). **Guatemala:** *A Molina R. 27546* (ENCB). **El Progreso:** *DG Debouck 2419* (AGUAT). **Santa Rosa:** *ET Heyde 4167* (K). **Jalapa:** *DG Debouck 2437* (SI). HONDURAS. **Ocatepeque:** *A Molina R. 22149* (G). **Intibucá:** *D Dey 202* (MO-3626750). **Francisco Morazán:** *J Gómez 94* (BM).

Phaseolus costaricensis Freytag & Debouck (1996: 157) [clade B; sect. *Phaseoli* DC emend. Freytag]. TYPE: *DG Debouck et al. 2135* (HOLOTYPE: US-3168869; ISOTYPES: BR, CR-125599, K, UC-1571112, USJ-30270).

This taxon was confused with *P. coccineus* in previous floras of Costa Rica and Panama (Standley 1937 and Lackey & D'Arcy 1980, respectively), although several collectors noted the “bright crimson” or “brilliant fuschia” color of the corolla (Fig. 2). It thrives in alder or oak humid montane forest at 1400–2200 m. Some populations seem already extinct because of the expansion of urban areas and coffee plantations: the one at Ochomogo found in 1896 by *A Tonduz 10914* (US-472031) or the one of San Isidro de Coronado found in 1937 by *PH Allen 555* (F-920349). Urbanization and the raising of vegetable crops of temperate climate also affect some populations in the Chiriquí province of Panama (Debouck & Rodríguez-Quiel 2020).

Specimens: COSTA RICA. **Alajuela:** *N Chaves-Barrantes 11* (CR-296552). **San José:** *JF Morales 10156* (K). **Cartago:** *DG Debouck 3365* (USJ-111614). PANAMA. **Chiriquí:** *DG Debouck 3372* (UCH).

Phaseolus dasycarpus Freytag & Debouck (2002: 120) [clade A; sect. *Pedicellati* (Benth.) Freytag]. TYPE: *R Hernández-Magaña 872* (HOLOTYPE: F-1845525; ISOTYPE: MEXU n.v.).

This member of the *Pedicellati* (Mercado-Ruaro et al. 2009) seems to thrive only in the region of contact between the Sierra Madre Oriental and the Trans-Mexican Volcanic Belt in eastern central Mexico. It grows in pine-oak and montane forests with frequent mist at 1900–2200 m. The current number of populations—less than ten (Mercado-Ruaro et al. 2009; Debouck 2019b)—suggests considering this species as endemic.

Specimens: MEXICO. **Hidalgo:** *O Alcántara-Ayala 2721* (MEXU-794839). **Veracruz:** *M Nee 25183* (F-1916163).

Phaseolus debouckii A. Delgado (2017: 260) [clade B; sect. *Phaseoli* DC emend. Freytag]. TYPE: *DG Debouck et al. 2889* (HOLOTYPE: MEXU n.v.; ISOTYPE: P).

This is the interesting case of a species demonstrated to exist as such because of the progress in genomics (Rendón-Anaya et al. 2017a, b), while it was originally collected as “wild *P. vulgaris*” (Fig. 7). Found by “accident” (the author was looking for the wild form of the large-seeded Lima bean), this species is distributed on the Pacific slope of the Andes in the Amotape-Huacabamba depression. When the author was consulted about this wild bean, the reply was “ancient and different”, and not less than 29 publications in the period 1992–2017 have precisely demonstrated that. The montane chaparral where it thrives at 1000–2000 m is at risk in many parts according to Michael Dillon (1994).

Specimens: ECUADOR. **Chimborazo:** *JN Rose 23838* (US-1023151). **Azuay:** *DG Debouck 2762* (QCA). PERU. **Cajamarca:** *A Sagastegui 15887* (HAO-5155).

Phaseolus dumosus Macfadyen (1837: 279) [clade B; sect. *Phaseoli* DC emend. Freytag]. TYPE: not found so far (and no indication about it in the original publication), but a description without illustration. Therefore, George Freytag designated a neotype (*GF Freytag 78-Guat-47*: US-3168877; ISONEOTYPES: BR, MO) using a wild form that he collected with Nader Vakili in Sololá in October 1978.

It is perhaps the only species of hybrid origin (Mina-Vargas et al. 2016). The wild form with lilac flowers (Fig. 2) has a restricted distribution mainly along the volcanic rim of Guatemala and SE Chiapas at 1400–1900 m. This is in contrast with the white-flowered feral form distributed from Veracruz (*M Rosas 722* (P)) down to Cuzco (*L Valenzuela 2760* (K)) (Debouck 2019c). *Phaseolus harmsianus* Diels (1937) from Ecuador (type: *L Diels 1028*: B n.v.; syntype: *E Heinrichs 191*: SI-2418) and *P. polyanthus* Greenman (1907) from Veracruz (type: *CR Barnes 20*: F-194750) mentioned in the list of “Vascular Plants of the Americas” (Tropicos 2020) are synonyms as indicated elsewhere (Freytag & Debouck 2002, p. 45).

Specimens: MEXICO. **Chiapas:** *E Ventura 2517* (MEXU-877627). GUATEMALA. **San Marcos:** *JA Steyermark 37495* (F-1058746). **Sololá:** *A Gentry 6516* (MO-2161807).

Phaseolus esperanzae Seaton (1893: 118) [clade A; sect. *Pedicellati* (Benth.) Freytag]. TYPE: *HE Seaton 371* (HOLOTYPE: GH-64087; ISOTYPE: F-266758).

A species of the *Pedicellati* distinguishable by torulose pods with thick sutures, spherical seeds and slightly coriaceous lobed leaflets. It seems to be distributed along the Mexican Trans-Volcanic Belt of central Mexico in oak or pine-oak woodland at 2000–2600 m.



FIG. 7. Close-ups of flowers of: **a.** *P. debouckii* (DG Debouck 1956) and **b.** *P. vulgaris* (DG Debouck 3222).

Specimens: MEXICO. **México:** *A Pineda* R. 570 (ARIZ-178735). **Distrito Federal:** *J Espinosa* 1043 (ENCB). **Hidalgo:** *A Ventura* A. 318 (ITIC). **Puebla:** *M Jiménez-Chimil* 30220 (K).

Phaseolus esquinensis Freytag (2002: 170) [clade A; sect. *Xanthotricha* A. Delgado]. TYPE: *GF Freytag 78-Mex-75* (HOLOTYPE: US-3168870; ISOTYPES: BR, F-2107873, GH, K-262842, MICH-1210017, NA-27952).

Apparently known only from the type material, this member of the *Xanthotricha* has been validated elsewhere (Delgado-Salinas et al. 2006). While the other members of this section have variously shaped tuberous tap-roots, this species seems to have a fibrous root; the terminal leaflets are hastately lobed, markedly towards the base (infrequent trait).

Phaseolus filiformis Bentham (1844: 13) [clade B; sect. *Rugosi* Freytag]. TYPE: *Hinds s.n.* (LECTOTYPE: K- 478487; ISOLECTOTYPE: K).

There is no reference to a specimen in the original description. There is however in Kew Herbarium a specimen collected by Richard Brinsley Hinds in 1841, stamped “Herbarium Benthamianum 1854” and with a handwritten note “Bot. Sulph. p. 13. Bay of Magdalena” that the author considers as the lectotype. The second collection of 1841 by Hinds kept at Kew and stamped “Herbarium Hookerianum 1867” is considered as isolectotype. It is the reference species of the section *Rugosi* (Fig. 5) with a huge distribution (from southern Arizona and New Mexico to trans-Pecos Texas to Baja California, including several islands of the Gulf of California, to coastal Sonora with a few spots in Chihuahua, Coahuila and Durango (Debouck 2019d). It is a component of the flora of the Sonoran Desert (Shreve & Wiggins 1964) at 3–1900 m.

Specimens: U.S.A. **Arizona:** *R Buhrow* 30 (ARIZ-209019). **New Mexico:** *EM Jercinovic* 1415 (NMC-84700). **Texas:** *WR Carr* 10951 (TEX-18035). MEXICO. **Chihuahua:** *B Barlow sn* (F-409658). **Coahuila:** *JA Villareal-Quintanilla* 5326 (ANSM-53105). **Durango:** *A Garcia* 2786 (ANSM-79586). **(northern) Baja California:** *B Ertter* 8062 (UC-1563744). **Baja California Sur:** *P Tenorio-Lezama* 12914 (MO-3599672). **Sonora:** *GA Levin* 2188 (UCR-84152).

Phaseolus glabellus Piper (1926: 683) [clade A; not assigned to a sect.]. TYPE: *CJW Schiede* 229 (LECTOTYPE: HAL-54634; ISOLECTOTYPES: G, P-36703).

This taxon was published in 1926 as a new name within “*Phaseolus coccineus* and its allies”. Charles Vancouver Piper faced the situation of two names: *Phaseolus glaber* Schlecht. and *Phaseolus glaber* Roxb., but on two different biological entities within the same genus! The former name was published in *Linnaea* (1838: 327) on two bean plants (n. 649 et n. 651) collected “in dumetis Jalapae et pr. S. Andres” by Christian Julius Wilhelm Schiede. The latter name was published in *Flora Indica* (1832: 291) on a legume from Mauritius (now *Vigna glabrescens* Maréchal, Mascherpa & Stainier, 1978a, p. 212). The way out for Piper studying bean plants from the same region of Mexico was to rename the taxon. Because the plant is almost glabrous, but with the minute uncinat hairs namely at the nodes, a logical choice for the name was *glabellus* (a shorter synonym of *glabriusculus*, itself a diminutive of *glaber* or glabrous).

Piper (1926, p. 683) indicated that the type is in Paris, while Delgado-Salinas (1985, p. 207) indicated it is in Halle. When comparing the labels and handwritten notes on the herbarium sheets, it seems clear that the materials in G and P are specimens sent from elsewhere (Halle?). In HAL there are three specimens collected by C.J.W. Schiede. Bearing in mind Article 8.2. of the Code and applying some anteriority rule in the type description of *P. glaber* by Diederich Franz Leonhard von Schlechtendal (1838, p. 327–328), it seems that the lectotype is HAL-54634 (lectotype because there is none unequivocally indicated in the original publication; Art. 9.2. of the Code). It is a collection made in August 1828 near Jalapa (with number 229 becoming 649 in the herbarium, the latter being mentioned in the original publication), while specimen HAL-54633 is of May 1829 also “in dumetis Jalapae”. The third specimen HAL-54632 is collection 229 (too! but becoming 651 in the original publication) by C.J.W. Schiede made near (= *prope*) San Andres in August 1828, a syntype.

It is a taxon mimicking *P. coccineus* (note in Fig. 6 the hooded standard and shorter wings, brick red or dark orange rather than true scarlet) but quite isolated in the genus (Delgado-Salinas et al. 2006), with an intermediate distribution around the Gulf of Mexico in alder, oak, sweet gum montane forest at 700–1800 m (Schmit et al. 1996).

Specimens: MEXICO. **Tamaulipas:** *S Rodríguez* 83 (CICY-21373). **San Luis Potosí:** *DG Debouck* 2046 (BR). **Hidalgo:** *L González-Quintero* 1570 (ENCB). **Querétaro:** *R Fernández* 3115 (ENCB). **Puebla:** *A Delgado-Salinas* 1582 (K). **Veracruz:** *E Bourgeau* 2919 (G). **Oaxaca:** *M Sousa-Sánchez* 8886 (CR-91424). **Chiapas:** *M Linden* s.n. (P).

Phaseolus gladiolatus Freytag & Debouck (2002: 167) [clade A; sect. *Xanthotricha* A. Delgado]. TYPE: *DG Debouck* 2057 (HOLOTYPE: US-3168871; ISOTYPE: CHAPA n.v.).

A member of the section *Xanthotricha* with fusiform pluriannual tuberous root, terminal leaflets like spades and lateral leaflets with a round external lobe, growing in oak-pine forests of central Mexico at 1500–1800 m, and validated by Delgado-Salinas and co-workers (2006).

Specimens: MEXICO. **Jalisco:** *A Castro* 4001 (IBUG-205436). **Michoacán:** *VW Steinmann* 4751 (NY).

Phaseolus grayanus Wootton & Standley (1913: 139) [clade A; sect. *Pedicellati* (Bentham) Freytag]. TYPE: *EA Mearns* 2124 (HOLOTYPE: US-232982; no isotype indicated in the original publication nor seen during this study).

A widely distributed member of the *Pedicellati* in the oak-pine forest of the Chihuahuan Desert at 1400–2800 m. Once considered as variety of *P. pedicellatus*, it deserves the specific rank because of stronger trailing and then climbing stems, slightly coriaceous leaflets with squarish lobes, strong peduncles with 6–14 primary bracts. *Phaseolus pyramidalis* Freytag and *P. teulensis* Freytag mentioned in the list of “Vascular Plants of the Americas” (Tropicos 2020) seem to be synonyms of *P. grayanus*.

Specimens: U.S.A. **Arizona:** *JC Blumer* 1347 (MIN-141973). **New Mexico:** *R Spellenberg* 12579 (NMC-69787). **Texas:** *AC Sanders* 3152 (UCR-37304). MEXICO. **Sonora:** *SS White* 3419 (GH). **Chihuahua:** *E Estrada-Castillón* 2806 (BRIT). **Coahuila:** *DH Riskind* 2245 (TEX-273493). **Nuevo León:** *JA Villareal-Quintanilla* 9083 (ANSM-73611). **Durango:** *HS Gentry* 8376 (ARIZ-300362). **Zacatecas:** *DG Debouck* 331 (K). **San Luis Potosí:** *CL Lundell* 5521 (WIS). **Jalisco:** *R Ramírez-Delgadillo* 1708 (IBUG-107601).

Phaseolus hintonii A. Delgado (2000: 431) [clade A; sect. *Xanthotricha* A. Delgado]. TYPE: *GB Hinton 6728* (HOLOTYPE: K-118675; ISOTYPES: GH, POM-348563).

A climbing vine resembling *P. xanthotrichus* from an almost cylindrical pluriannual tuberous root, differing in subcylindrical pods with more than ten seeds, thriving in oak woodlands of central western Mexico at 1200–1900 m.

Specimens: MEXICO. **Jalisco:** *EA Suárez-Muro 628* (IBUG-197086). **México:** *A Delgado-Salinas 1567* (IBUG-198458). **Michoacán:** *JC Soto-Núñez 4554* (IBUG-198014). **Oaxaca:** *A Delgado-Salinas 1346* (IBUG-197386).

Phaseolus hygrophilus Debouck (2011: 54) [possibly in clade A and sect. *Brevilegumeni* Freytag]. TYPE: *DG Debouck & R Araya Villalobos 3172* (HOLOTYPE: INB-4026793; ISOTYPES: BRIT, CR, F, FI, G, GH-351974, INB, K-780075, MEXU, MICH-1229077, NY-1365122, P, UC, USJ).

As indicated in the original publication (Salcedo-Castaño et al. 2011, p. 53), the series of herbarium specimens on which the holo- and isotypes were made from a cutting grown in the Popayán station of CIAT in Colombia (Fig. 3). It seems to be an endemic species of the premontane rain forests of Costa Rica at 1300–1600 m (Debouck et al. 2020). It is not mentioned in “Vascular Plants of the Americas” (2020).

Specimens: COSTA RICA. **San José:** *DG Debouck 3173* (USJ-88816), *DG Debouck 3370* (USJ-111489), *DG Debouck 3371* (USJ-111736).

Phaseolus jaliscanus Piper (1926: 697) [clade B; sect. *Paniculati* Freytag]. TYPE: *EW Nelson 4030* (HOLOTYPE: US-763708; no isotypes seen nor mentioned in the original publication).

A species of the *Paniculati* found in pine or oak forest (with palms at lower altitude) at 500–2700 m, with a clear heteroblastic development, variegated leaflets and an internally striped banner (Fig. 8).

Specimens: MEXICO. **Sinaloa:** *IL Wiggins 13184* (US-2365635). **Nayarit:** *O Téllez-Valdés 9512* (IBUG-198882). **Jalisco:** *J1 Calzada 9488* (ENCB). **Michoacán:** *A Delgado-Salinas 1137* (CAS-855044).

Phaseolus juquilensis A. Delgado (2000: 421) [clade B; sect. *Paniculati* Freytag]. TYPE: *M Sousa-Sánchez et al. 6353* (HOLOTYPE: MEXU n.v.; ISOTYPES: BM-898068 and 898069, CHAPA, ENCB).

A member of the *Paniculati* found in pine-oak forest with little disturbance, the distribution of which seems restricted to Oaxaca (in the Mixteca Alta and on the inner slope of Sierra de Miahuatlán), at 1800–2000 m. The few populations known to date invite to still consider it as endemic for the time being. The synonymy proposed by Delgado-Salinas and co-workers (2006) for *P. acinaciformis* Freytag & Debouck makes sense to this author.

Specimen: MEXICO. **Oaxaca:** *R. Hernández-Magaña 5143* (IBUG-197641).

Phaseolus laxiflorus Piper (1926: 692) [clade A; sect. *Pedicellati* (Bentham) Freytag]. TYPE: *CG Pringle 13690* (HOLOTYPE: US-462384; ISOTYPES: GH-64092, MICH-1104260).

It is not mentioned in “Vascular Plants of the Americas” (2020); it seems, however, to be a valid species distributed in the eastern part of the Mexican Trans-Volcanic Belt at 2100 m.

Specimen: MEXICO. **Veracruz:** *GF Freytag 78-Mex-29* (CS-77522).

Phaseolus leptophyllus G. Don (1832: 350) [clade A; sect. *Revoluti* Freytag]. TYPE: *Sessé & Mocino s.n.* (LECTOTYPE: OXF; ISOLECTOTYPES: F-846796, FI-4903 (in Herbarium Webbium no. 51912), MA-601675, OXF, P-36706).

Its unique foliar morphology suggests we consider it as in a separate section (Freytag & Debouck 2002). Considering it close to *P. acutifolius* (Delgado-Salinas 1985) and next as a member of the *Minkeliersia* (Delgado-Salinas et al. 2006) is a clear indication of the need for additional (and living) material. Some authors (Delgado-Salinas & Gama-López 2015; Acosta-Díaz et al. 2019) have considered it as extinct. It is known only from the type collected in Guerrero in 1789. It is not mentioned in the list of “Vascular Plants of the Americas” (Tropicos 2020).

Phaseolus leptostachyus Bentham (1837: 72) [clade B; sect. *Falcati* Freytag]. TYPE: *WF Karwinski s.n.* (LECTOTYPE: M; ISOLECTOTYPE: SI).

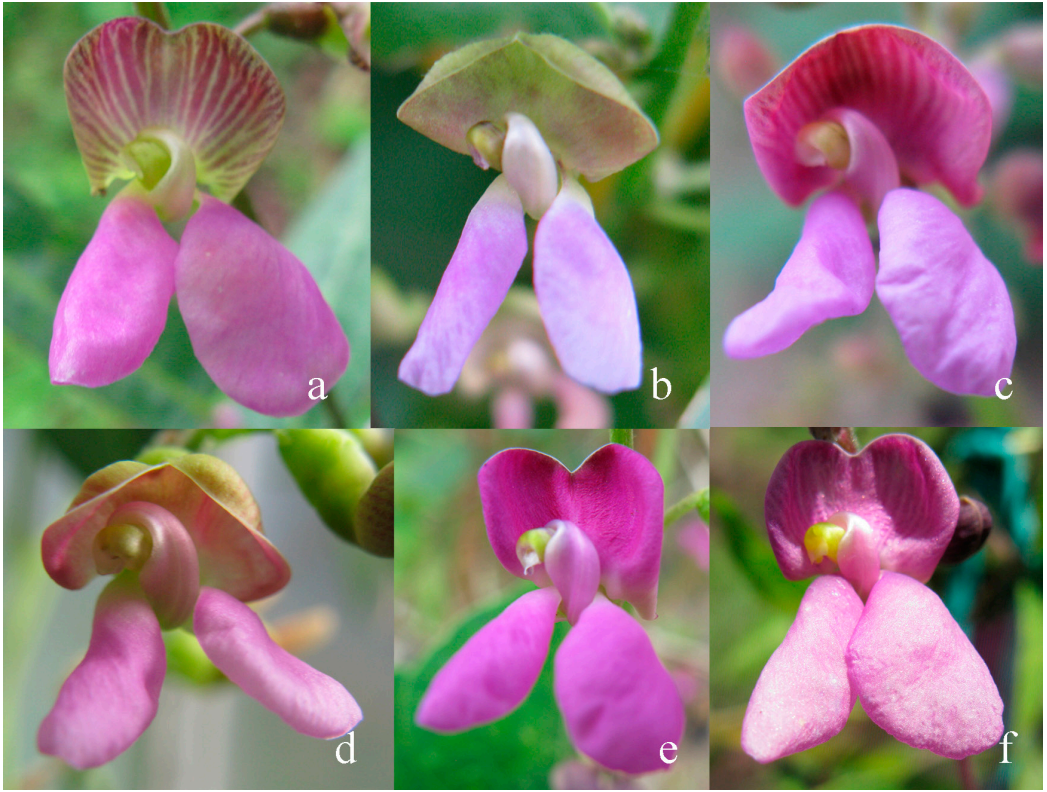


FIG. 8. Close-ups of flowers of some members of the *Paniculati*: **a.** *P. jaliscanus* (R Buhrow M21), **b.** *P. lunatus* (DG Debouck 2103), **c.** *P. marechalii* (B Schubert 623), **d.** *P. nodosus* (R Lépiz 148), **e.** *P. rotundatus* (R Lépiz 171) and **f.** *P. salicifolius* (R Buhrow M2).

The original publication about *P. anisotrichos* is of 1838 (von Schlechtendal 1838), therefore this name falls into synonymy. There would thus be no reason to maintain the latter as a separate species in the list of “Vascular Plants of the Americas” (Tropicos 2020). Note the specimen at the Darwinion is a small fragment of the original of M (from a loan?). It is a common species in openings of oak, pine-oak and tropical deciduous forests, from almost sea level to 2,500 m (Fig. 9). The synonymy proposed elsewhere (Delgado-Salinas 1985) for *P. opacus* Piper (1926) with *P. leptostachyus* makes sense. Five botanical varieties were recognized in this species (Freytag & Debouck 2002), while in author’s view they represent the natural variation of this widespread species.

Specimens: MEXICO. **Sonora:** IL Wiggins 6995 (DS-264709). **Tamaulipas:** E Estrada-Castillón 2726 (CAS-794254). **Chiapas:** A Delgado-Salinas 823 (DS-719855). GUATEMALA. **Huehuetenango:** DG Debouck 3073 (AGUAT). **Jalapa:** PC Standley 76999 (F-1202124). HONDURAS. **Francisco Morazán:** LO Williams 17292 (MO-1737913). EL SALVADOR. **Santa Ana:** JL Linares 1070 (LAGU). **La Libertad:** AC del Cid 1681 (ITIC). NICARAGUA. **Nueva Segovia:** DG Debouck 3198 (O-V2147547). **Granada:** P Levy 1096 (P). COSTA RICA. **Guanacaste:** DG Debouck 3288 (USJ-111503). **Puntarenas:** F Oviedo-Brenes 2776 (USJ-111843).

Phaseolus lignosus Britton (1918: 183) [clade B; sect. *Paniculati* Freytag]. TYPE (LECTOTYPE): Fig. 205 in “Flora of Bermuda” (from C Watlington 3: EPITYPE K-556376 and K-556377; ISOEPITYPES: BRIT, CAS, COL, F, FHO, FI, G, GH, MEXU, MICH, MO, NCU, NY, P; see Debouck 2015).

Reasons were presented elsewhere (Debouck 2015) for choosing an epitype (and several duplicates from a single gathering), since the original type was an illustration. So, the “Bermuda bean” was confused with wild *P. lunatus* as indicated on some labels (Debouck 2019a); the differences on living plants however are striking



Fig. 9. Close-ups of flowers of: **a.** *P. leptostachyus* (DG Debouck 3165), **b.** *P. macvaughii* (J Acosta 211), and **c.** *P. micranthus* (R Buhrow M28), the three species currently recognized in the section *Falcati*.

(Debouck 2015) (Fig. 10). It is not mentioned in the list of “Vascular Plants of the Americas” (Tropicos 2020), although in author’s view it is a valid species of the section *Paniculati* (also validated by Delgado-Salinas et al. 1999). This species is endemic to the Bermuda archipelago where 29 mature individuals thrive, explaining its status of critically endangered (Copeland et al. 2014).

Specimens: BERMUDA. **Long Island:** *E Manuel* 637 (A), *C Watlington* 3 (K-650154).

Phaseolus lunatus L. (1753: 724) [clade B; sect. *Paniculati* Freytag]. TYPE: *E Westphal* 8622 (NEOTYPE, here designated: BR-18325706; isoneotypes K n.v., P n.v.).

Given the absence of a type in LINN and of indication about one in the catalogue produced by Carl August von Bergen in 1744 (p. 99, and referred to by both Carl von Linné, 1753, p. 724 and Bernard Verdcourt, 1971, p. 615), Egbert Westphal (1974, p. 146) used the cultivar “Didessa Mosaic” that he collected in Ethiopia and raised in a glasshouse in Wageningen, Holland, to select a neotype (the specimens claimed to be deposited in K and P have not been seen during this study). A variety var. *silvester* of possible Mexican origin (*Le Marchand* 2499, BR-839814) has been named (Baudet 1977).

It is perhaps the wild species of the genus with the widest range in (sub-)tropical America: from the Revillagigedo Islands off the Mexican Pacific coast, up to S Sonora and S Tamaulipas, through Central America, the Greater and Lesser Antilles down to the Chaco region of Argentina at 10–1900 m. The former distribution is that of the two lowland genepools (Motta-Aldana et al. 2010), which may have come from the northern Andes (Serrano-Serrano et al. 2010).

The Andean wild form is distinct (Serrano-Serrano et al. 2010), with a possible subcenter in the Colombian Andes (Chacón-Sánchez & Martínez-Castillo 2017). The distribution of the Andean wild form, on the western slope of the Andes at 400–2000 m, is from SW Ecuador to NW Peru (down to the Jequetepeque Valley). This form is *P. rosei* Piper mentioned in the “Vascular Plants of the Americas” (Tropicos 2020) and can be considered as a synonym of *P. lunatus* (Freytag & Debouck 2002, p. 103). The following specimens are to indicate the extremes of ranges of the two wild forms.

Specimens: MEXICO. **Revillagigedo Islands:** *FE Barkelew* 211 (UC-137615). **Sonora:** *JF Wiens* 94-053 (ARIZ-324638). **Tamaulipas:** *E Martínez-Ojeda* 345 (ARIZ-207605). **Quintana Roo:** *F May* 2075 (CICY-54083). **Chiapas:** *CP Cowan* 5023 (CAS-834700). BELIZE. **Orange Walk:** *C Whiteford* 2675 (BM). GUATEMALA. **Quezaltenango:** *L Rodríguez* 1621 (P). HONDURAS. **Francisco Morazán:** *JL Linares* 2271 (MEXU-798503). EL SALVADOR. **Ahuachapán:** *JM Rosales* 2131 (LAGU). NICARAGUA. **Esteli:** *DG Debouck* 3209 (O-V2147454). COSTA RICA. **Guanacaste:** *M Grayum* 11508 (INB-3746751). PANAMA. **Panamá:** *C Guerra* 539 (PMA-88343). CUBA. **Villa Clara:** *JG Jack* 6725 (A). HAITI. **Dept. du Nord:** *EC Leonard* 8484 (US-1149957). TRINIDAD-AND-TOBAGO. **Trinidad:** *RE Baker* 14822 (K). COLOMBIA. **Sucre:** *G Moreno* 16 (COL-256468). VENEZUELA. **Aragua:** *C Vogl* 592 (DAV-59372). PERU. **Cuzco:** *DG Debouck* 2316 (US-3168369). BOLIVIA. **El Beni:** *E Werdermann* 2349 (MO-1000136). PARAGUAY. **Alto Paraná (?):** *MS Bertoni* 3649 (G). ARGENTINA. **Chaco:** *AG Schulz* 17027 (BAB). And for the Andean wild form: ECUADOR. **Chimborazo:** *DG Debouck* 2863 (QCA). PERU. **Cajamarca:** *A Sagastegui* 16062 (HAO).



FIG. 10. Close-ups of pods of: **a.** *P. augusti* (DG Debouck 2571), **b.** *P. pachyrrhizoides* (DG Debouck 2155), **c.** *P. lignosus* (C Watlington 3), **d.** *P. lunatus* (DG Debouck 3236), and **e.** *P. viridis* (G Juárez 1086).

Phaseolus macrolepis Piper (1926: 698) [clade A; sect. *Bracteati* Freytag]. TYPE: *O Salvin* s.n. (HOLOTYPE: K-478468; no isotypes seen so far, nor mentioned in the original publication).

This species, reference of the *Bracteati*, grows in the now much logged old-growth pine forests, endemic of the volcanic axis of SW Guatemala at 2200–3000 m. It is not reported in the list of “Vascular Plants of the Americas” (Tropicos 2020).

Specimens: GUATEMALA. **Chimaltenango:** JC Montero-Castro 245 (NY). **Sololá:** DG Debouck 3095 (K).

Phaseolus maculatifolius Freytag & Debouck (2002: 119) [clade B; sect. *Paniculati* Freytag]. TYPE: DG Debouck *et al.* 1509 (HOLOTYPE: US-3168873 and US-3168873A; ISOTYPES: BR, K-642355, M, UNL n.v., UC-1571140).

In addition to the type, five other populations have been reported recently, lowering the risk of extinction in the immediate future (Acosta-Díaz *et al.* 2015, 2019).

Phaseolus maculatus Scheele (1848: 465) [clade B; sect. *Coriacei* Freytag]. TYPE: *F Lindheimer* 263 (NEOTYPE: MO-1731163; ISONEOTYPES: BM, BRIT, CAN n.v., FI (in Herbarium Webbianum, no. 51931), G, GH-274635, K, MO-1731164, NA, NY, OXF, PH, TCD, UC-248307).

In the large series of “Flora Texana exsiccata. 367. Fasc. III” (Gillett & Shchepanek 1977), the specimen with more information (i.e., “Cibolo, 15 miles west of New Braunfels, Texas.”) is the one out of three kept at Missouri Botanical Garden, and A. Delgado-Salinas (1985) was right in selecting it as neotype, since according to his interpretation the holotype was lost in Berlin during WWII. This sprawling legume component of the grasslands of the Chihuahuan Desert from Texas down to Puebla (Gentry 1957) at 1500–2800 m has often been confused with *P. ritensis*, a closely related species of the same section; apart from the seedlings (Fig. 11) the differences between them have reported elsewhere (Buhrow 1983; Delgado-Salinas 1985; Freytag & Debouck 2002).

Specimens: U.S.A. **Arizona:** LA McGill 5683 (ASU-187971). **New Mexico:** JT Columbus 432 (NMCR). **Texas:** P Manning 4082 (K). MEXICO. **Chihuahua:** HS Gentry 8252 (RSA-411984). **Coahuila:** DH Riskind 2099 (ANSM-51545). **Sonora:** EA Mearns 1637 (DS-35348). **Durango:** S González 3195 (IEB-145721). **Zacatecas:** DG Debouck 346 (K-1041740). **San Luis Potosí:** JG Schaffner 252 (PH). **Aguascalientes:** JN Rose 6197 (US-396010). **Guanajuato:** MC Johnston 2625B (TEX-273258). **Jalisco:** R Ramírez-Delgadillo 1285 (IBUG-99837). **Querétaro:** R Hernández-Magaña 12035 (IEB-173103). **Hidalgo:** JN Rose 8318 (US-451812). **Tlaxcala:** H Vibrans 2267 (TEX-273253). **Puebla:** A Delgado-Salinas 1400 (TEX-273252).

Phaseolus macvaughii A. Delgado (2000: 414) [clade B; sect. *Falcati* Freytag]. TYPE: A Delgado *et al.* 129 (HOLOTYPE: MEXU-200563; ISOTYPES: ANSM-8396, ARIZ-218681, CHAPA, ENCB, IBUG-52725, MICH-1180016, MO-2575900).



FIG. 11. Seedlings of: **a.** *P. ritensis* (left) (GP Nabhan 8478) and **b.** *P. maculatus* (right) (DG Debouck 269). Note the sessile eophylls and the unifoliate first true leaf in the former, and the petiolate eophylls and trifoliate first true leaf in the latter (steel ruler 15 cm).

The “var. no. 1” of *P. micranthus* (McVaugh 1987, p. 660) eventually resulted in a new species of the *Falcati*, with chromosome number $2n = 20$ (Mercado-Ruaro & Delgado-Salinas 1998). This annual vine can be recognized by its fibrous narrow taproot, the unique dimorphism in pods and perhaps the smallest flower in the genus (Fig. 9). It grows in tropical dry forest and coastal dry scrub often close to the beach, from sea level up to 300 m. The author found it in 1978 in the dry bed of Río Salado in Colima, anticipating some salinity tolerance that was evidenced afterwards (Bayuelo-Jiménez et al. 2002).

Specimens: MEXICO. (northern) **Baja California:** *P Tenorio-Lezama* 10857 (ASU-179342). **Sinaloa:** *RS Ferris* 5199 (CAS-DS-149866). **Jalisco:** *R Lépez-Ildelfonso* 385 (IBUG-208597). **Colima:** *DG Debouck* 427 (US-3168522). **Michoacán:** *E Martínez S.* 4610 (IBUG-197388). **Guerrero:** *J Acosta-Gallegos* 211 (K).

Phaseolus magnilobatus Freytag & Debouck (2002: 167) [clade A; sect. *Xanthotricha* A. Delgado]. TYPE: *GF Freytag 81-Mex-22* (HOLOTYPE: US-3386752).

The type is material grown in screenhouse in Mayagüez from seed originally collected in SE Jalisco, Mexico; several isotypes not seen during this study were made from the same gathering. A couple of collections from S Durango complete the current range, thus suggest it as endemic. It has been proposed as a synonym of *P. hintoni*, a move that is not done here (because of the leaflet and seed traits) pending on additional collections and cross comparisons based on living materials.

Specimens: MEXICO. **Durango:** *DG Debouck* 402 (K), *HS Gentry* 22086 (NA).

Phaseolus marechalii A. Delgado (2000: 427) [clade B; sect. *Paniculati* Freytag]. TYPE: *A Delgado-Salinas 115* (HOLOTYPE: MEXU n.v.; ISOTYPES: GH-423042, K-651819).

Some differences with *P. rotundatus* and other related species have been presented elsewhere (Salcedo-Castaño et al. 2009) (note the striped standard in Fig. 8). Its range is mainly along the Mexican Trans-Volcanic Belt, at 2400–2500 m, in oak, pine-oak and pine forest.

Specimens: MEXICO. **México:** *DG Debouck* 2377 (MICH-1179985). **Morelos:** *OW Norvell HM215* (UC-933928). **Puebla:** *DG Debouck* 2389 (IBUG-182551).

Phaseolus micranthus Hooker & Arnott (1841: 287) [clade B; sect. *Falcati* Freytag]. TYPE: *Lay & Collie s.n.* (LECTOTYPE: K-478473).

In the book about Captain Beechey’s voyage (1841), there is no reference to a specimen. However, there is a specimen kept in the Kew Herbarium stamped “Herbarium Hookerianum 1867” and with a handwritten note directly on the sheet “Phaseolus micranthus Hook. Mexico Beechey,” that the author considers as the

nomenclatural type. It seems to be an annual plant with distribution in tropical deciduous forest and oak forest on the Pacific slopes of Sierra Madre Occidental and Sierra Madre del Sur from 20 up to 2,000 m (Fig. 9).

Specimens: MEXICO. **Sonora:** *AC Sanders 14340* (UCR-113614). **Sinaloa:** *JA Beltrán M. 418* (IBUG-97924). **Nayarit:** *RS Ferris 5957* (US-1587247). **Jalisco:** *TS Cochrane 12169* (WIS). **Michoacán:** *LM Villareal de Puga 10263* (IBUG-99743). **Oaxaca:** *SH Salas M. 4070* (IEB-161096). **Chiapas:** *G Flores-Franco 5097* (MEXU-1232886).

Phaseolus microcarpus Martius (1829: 18) [clade A; not assigned to a sect.]. TYPE (lectotype): Plate 12 (the illustration of a plant raised from seed in a greenhouse at München, Germany).

It seems that the original seed, obtained from Mr. FW Keerl, was collected near Tlalpujahua [Michoacán], Mexico. It is an annual vine from dry (warm) (sub-) and tropical deciduous forests, with a wide distribution from Durango, Mexico down to NW Costa Rica (Debouck et al. 2019), in the range 0–2000 m. It is an isolated species in the genus, with no clear link with any current section (Delgado-Salinas et al. 1999).

Specimens: MEXICO. **Durango:** *S González 2185* (ENCB). **Guanajuato:** *LI Aguilera 279* (CHAPA). **Nayarit:** *O Téllez-Valdés 9344* (RSA-482469). **Jalisco:** *R Ramírez-Delgadillo 2270* (IBUG-109694). **Morelos:** *G Flores-Franco 305* (BM). **Puebla:** *F Miranda 2312* (MEXU-74655). **Michoacán:** *JN Labat 1201* (P). **Guerrero:** *JC Soto-Núñez 5966* (MO-3851263). **Oaxaca:** *E Domínguez-Licona 1897* (K). **Chiapas:** *DE Breedlove 46145* (CAS-651680). HONDURAS. **Francisco Morazán:** *JL Linares 6995* (MEXU-1161332). EL SALVADOR. **La Unión:** *G Cerén 972* (LAGU-6096). NICARAGUA. **Carazo:** *A Grijalva 4131* (MO-5149166). COSTA RICA. **Guanacaste:** *B Hammel 24516* (INB-4136116).

Phaseolus mollis Hooker f. (1847: 228) [clade B; sect. *Paniculati* Freytag]. TYPE: *C Darwin s.n.* (LECTOTYPE: K).

Among the plants collected by Charles Darwin during the voyage of H.M. Ship “Beagle,” Joseph Dalton Hooker described this bean plant; the specimen apparently unicate without collection number and stamped “Herbarium Hookerianum 1867” was found in Kew Herbarium. This is an endemic species of the Galapagos Islands (at 40–1200 m), possibly related to the Andean wild form of *P. lunatus* (Delgado-Salinas et al. 1999). Similar relationships between biota of the Galapagos and the Pacific coast of South America have been noted for wild species of cotton and tomato (Wendel & Percy 1990 and Alvarez et al. 2001, respectively).

Specimens: GALAPAGOS ISLANDS (ECUADOR). **I. Isabela** (= Albarmar I.): *Ch Huttel 578* (QCA). **I. Santa Cruz** (= Indefatigable I.): *A Adersen 1599* (QCA). **I. Santiago** (= I. San Salvador = James I.): *C Darwin s.n.* (K).

Phaseolus montanus Brandegee (1893: 130) [possibly clade B; sect. *Acutifolii* Freytag]. TYPE: *TS Brandegee 162* (LECTOTYPE: UC-82396).

When Townshend Stith Brandegee reported about the flora of the Cape region of Baja California in 1893, he included his collection numbers, namely a “162. *Phaseolus montanus*,” but he did not make explicit that it was a new species nor that it was the type. That plant in the Brandegee Herbarium now at Berkeley, although labelled as type, was considered as synonym of *P. acutifolius* var. *tenuifolius* A. Gray (Delgado-Salinas 1985 p. 178), a treatment endorsed by George Freytag who did not see it. Comparing this plant with the holotype of *P. parvifolius* (US-3168875), the following synonymy can be indicated:

Phaseolus montanus Brandegee (based on *TS Brandegee 162* as lectotype UC-82396 and published in: Proc. Calif. Acad. Sci. ser. 2, 3:130. 1893)

= *Phaseolus parvifolius* Freytag (based on *GF Freytag & J Sullivan 81-13* as holotype US-3168875; ISOTYPES: BR, EAP n.v., MEXU n.v., MO, and published in: Sida Bot. Misc. 23:32. 2002).

This taxon has consistently been evidenced as closely related to *P. acutifolius* (Fig. 1), but with differences that warrant the species status (Florez-Ramos et al. 2003; Muñoz et al. 2006; Gujaria-Verma et al. 2016).

Specimens: U.S.A. **Arizona:** *RA Darrow 2261* (ARIZ-15237). MEXICO. **Sonora:** *P Tenorio-Lezama 10254* (TEX-272992). **Chihuahua:** *CH Muller 3443* (LL-273004). **Baja California Sur:** *R Domínguez 313* (MEXU-431892). **Sinaloa:** *A Delgado-Salinas 1042* (BM). **Nayarit:** *O Téllez-Valdés 12306* (MEXU-490786). **Jalisco:** *M Lavin 5072* (CHAPA). **Colima:** *AC Sanders 11455* (RSA-554182). **Michoacán:** *VW Steinmann 3860* (IEB-169341). **Guerrero:** *DG Debouck 2354* (MICH-1180063). **Oaxaca:** *M Sousa-Sánchez 9420* (NCU-531247). **Chiapas:** *GF Freytag 78-Mex-77* (F-2107874). GUATEMALA. **Jalapa:** *DG Debouck 2434* (MICH-1180058).

Phaseolus neglectus F.J. Hermann (1948: 238) [clade A; sect. *Digitati* Freytag]. TYPE: *CH Muller 2881* (HOLOTYPE: NA-227795, now US-2216220 since transfer in 1953).

In the original publication Frederick Joseph Hermann noted the “corolla . . . pale salmon to light blue”. Alfonso Delgado-Salinas (1985, p. 198) defined two races, interestingly “not been found growing intermixed”. With the specimens available, field work and the cultivation of several materials of this section, the author now considers race A corresponding to the species described by Hermann, and race B to *P. albiflorus*. A couple of populations have been sampled recently (Acosta-Díaz et al. 2015).

Specimens: MEXICO. **Nuevo León:** *R Rodríguez 377* (ANSM-5423). **Tamaulipas:** *OL Briones s.n.* (ANSM-31020).

Phaseolus nelsonii Maréchal, Mascherpa, & Stainier (1978b: 199) [clade A; sect. *Minkellersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE: *EW Nelson 1362* (LECTOTYPE: US-764858, as *Minkellersia pauciflora* Rose (1897: 142)).

Specimens: MEXICO. **Oaxaca:** *M Sousa-Sánchez 8540* (RSA-272960). **Chiapas:** *DE Breedlove 46259* (CAS-651595).

Phaseolus nodosus Freytag & Debouck (2002: 127) [clade B; sect. *Paniculati* Freytag]. TYPE: *R McVaugh 13433* (HOLOTYPE: MICH-1210018).

A member of the *Paniculati* with distribution in pine-oak forest of the western part of the Trans-Mexican Volcanic Belt (at 1900–2500 m), also with a striped standard (Fig. 8).

Specimens: MEXICO. **Jalisco:** *A Delgado-Salinas 1181* (IBUG-198016). **Colima:** *R Lépiz-Ildelfonso 148* (IBUG-208602).

Phaseolus novoleonensis Debouck (2006: 105) [clade B; sect. *Coriacei* Freytag]. TYPE: *DG Debouck 2061* (HOLOTYPE: IBUG; ISOTYPES: ANSM, BR, CHAPA, COL, ENCB, F, G, K-478467, MEXU, MICH-1287074, MO, P, SI, UC, US).

A member of the *Coriacei* with rounded leaflets. One more population could have been found recently (Acosta-Díaz et al. 2015); the species is however considered as endangered because of its extremely small range (Acosta-Díaz et al. 2019).

Specimen: MEXICO. **Nuevo León:** *AE Estrada-Castillón 633* (ANSM-33436).

Phaseolus oaxacanus Rose (1903: 48) [tentatively in clade A; sect. *Pedicellati* (Benth.) Freytag]. TYPE: *CG Pringle 5814a* (LECTOTYPE: US-372011; ISOLECTOTYPES: ENCB, MEXU, MO-1731120).

This endemic species distributed in pine forests in the mountains surrounding the valley of Cd. Oaxaca at 2200–2700 m has been recently questioned as member of the section *Pedicellati* (Delgado-Salinas et al. 2006). In a previous study (Delgado-Salinas et al. 1999) it was considered as related to this section, and also distinct enough to be seen as a valid species as compared to *P. pedicellatus* (a move from his varietal treatment of 1985). New data are needed to reassess the position of this taxon in the genus.

Specimens: MEXICO. **Oaxaca:** *R Acevedo-Rodríguez 130* (ENCB), *CG Pringle 5661* (GH), *M Sousa-Sánchez 7816* (MEXU-209055).

Phaseolus oligospermus Piper (1926: 698) [clade A; sect. *Brevilegumeni* Freytag]. TYPE: *AS Oersted 30* (HOLOTYPE: K-478466; no isotypes seen so far nor mentioned in the original publication).

It is the reference species for the section. Sometimes confused with *P. tuerckheimii* (Fig. 3), it is known by scattered populations from Mexico east of the Isthmus of Tehuantepec down to central Costa Rica in premontane moist mixed (oak, pine, alder, sweet gum) forest at 450–2100 m.

Specimens: MEXICO. **Oaxaca:** *R Torres-Colin 10589* (IBUG-169373). **Chiapas:** *J Acosta-Gallegos 194* (K-1041773). HONDURAS. **Francisco Morazán:** *JL Linares 6520* (MO-6132749). EL SALVADOR. **Ahuachapán:** *JL Linares 3303* (LAGU). NICARAGUA. **Esteli:** *CA Padilla-Gómez 40* (MO-6244283). **Madrid:** *WD Stevens 16119* (MO-5149147). COSTA RICA. **San José:** *DG Debouck 3333* (USJ-111445).

Phaseolus parvulus Greene (1881: 217) [clade A; sect. *Minkellersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE: *EL Greene s.n.* (LECTOTYPE: NDG-27852; ISOLECTOTYPES: F-133379, G, K, MO-1731190, NA-27001, NY).

Edward Lee Greene presented the descriptions of “New plants of New Mexico and Arizona” based on specimens kept in his herbarium. For *Phaseolus parvulus* no specimen is mentioned, and there is no illustration in the paper. However, in the Greene Herbarium currently kept at the university of Notre Dame in Indiana, there is a specimen with three small plants stamped “Herbarium Greeneanum 32412” and labelled *Phaseolus parvulus* Greene n.sp. (handwritten by EL Greene?), that the author considers as the nomenclatural type. Because

the original population had many plants (not uncommon in rainy years, from author's field experience in 1978) from the same gathering Greene was able to distribute duplicates to several Herbaria. A small plant (up to 30–40 cm) from an almost spherical tuberous root (diam. 10–20 mm) of the section *Minkelsersia* growing in altitude (1900–2900 m) pine-oak forests from New Mexico down the Sierra Madre Occidental as far south as the states of Jalisco and México!

Specimens: U.S.A. **Arizona**: *D Atwood 17171* (NY). **New Mexico**: *EH Roalson 1111* (NMCR). MEXICO. **Sonora**: *AL Reina G. 99-546* (NMC-71768). **Chihuahua**: *A Bénéitez 2066* (ANSM-59059). **Durango**: *S Acevedo 296* (IEB-79531). **Zacatecas**: *JN Rose 2723* (US-301650). **Sinaloa**: *AC Sanders 21202* (UCR-168974). **Nayarit**: *JN Rose 3425* (US-302402). **Jalisco**: *Luquín 160* (IBUG-32344). **México**: *GB Hinton 4708* (GH).

Phaseolus pauciflorus Sessé & Mociño ex G. Don (1832: 356) [clade A; sect. *Minkelsersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE: *Sessé & Mociño s.n.* (LECTOTYPE: OXF).

This taxon was briefly described by Martín de Sessé y Lacasta and José Mariano Mociño in 1791 (date of the unpublished manuscript, according to McVaugh (1977), but eventually published in 1887) on a specimen that ended up in the Lambert Herbarium (now in Oxford, England). As explained by Sousa-Sánchez and Delgado-Salinas (1981), George Don published the description in 1832, while he wanted to give credit to these botanists. On page 117 of “Plantas de Nueva España” by Sessé and Mociño (1887) and on page 356 of “A general system of gardening and botany” by Don (1832), no specimen is mentioned, but as aptly explained by Drs. Sousa and Delgado (1981) the type is the one-raceme specimen with the handwritten note “*Phaseolus linearis*” and stamped “Fielding Oxford Herbarium.” A sprawling vine usually less than 1 m long in pine or oak grassland (at 1300–2700 m), with clover-like leaves and erect often twin pods, from a pluriannual tuberous root.

Specimens: MEXICO. **Sonora**: *M Fishbein 2471* (NY). **Chihuahua**: *R Corral-Díaz 3964* (NMC-65116). **Sinaloa**: *FW Pennell 20114* (PH-773300). **Durango**: *S Acevedo 306* (ANSM-57382). **Zacatecas**: *J Rzedowski 1022* (MO-2209626). **Nayarit**: *G Flores-Franco 1169* (ENCB). **Jalisco**: *P Carrillo-Reyes 4324* (IBUG-169374). **México**: *A Delgado-Salinas 1004* (CHAPA). **Distrito Federal**: *E Matuda 21400* (K). **Morelos**: *LH MacDaniels 269* (F-838137). **Michoacán**: *CP Cowan 5668* (UCR-63757). **Guerrero**: *I Wagenbreth 282* (MO-5043672). **Oaxaca**: *H Galeotti 3175* (G). GUATEMALA. **Quiché**: *JJ Aguilar 1472* (F-1121845).

Phaseolus pedicellatus Bentham (1837: 73) [clade A; sect. *Pedicellati* (Benth.) Freytag]. TYPE: *WF von Karwinski s.n.* (LECTOTYPE: M; ISOLECTOTYPE: US-1326445).

In the original description, George Bentham did not indicate any specimen. There is however a specimen kept in Munich that along the written indications on the sheet has been object of correspondence between Charles Vancouver Piper (at US) and Herman Ross (at M) in November 1924; it can be considered as the nomenclatural type, the specimen at US being a fragment obtained on loan. In spite of lack of data, it might be that the type material (a unicate) was collected in September 1827 near Mexico City during the first trip of Wilhelm Friedrich von Karwinski (McVaugh 1980). While it is abundant in Sierra Madre Oriental from Pico de Orizaba northwards and the Mexican Trans-Volcanic Belt, it is also known by a couple of collections from Sierra Madre Occidental (Nabhan 1990; Lépiz-Ildefonso & Ramírez-Delgadillo 2010). It thrives in pine-oak, oak, mixed (oak, laurel, alder), cedar and fir forest at 1500–2800 m.

Specimens: MEXICO. **Coahuila**: *E Palmer 2022* (K). **Tamaulipas**: *OL Briones V s.n.* (ENCB). **Nuevo León**: *J Hinton 23424* (ANSM-61416). **Guanajuato**: *R Santillán I 496* (ENCB). **Querretaro**: *E Carranza 2729* (IEB-79444). **Hidalgo**: *O Alcantará-Ayala 2354* (BM). **Veracruz**: *J Ventura A 14780* (ENCB). **Puebla**: *P Tenorio-Lezama 17126* (MEXU-522602). **Distrito Federal**: *A Ventura A. 3566* (IEB-79463). **Morelos**: *J García C. 180* (ENCB). **México**: *H Bravo H. 2375* (MA-263930). **Jalisco**: *JA Machuca-Núñez 6392* (IBUG-109697). **Colima**: *R Lépiz-Ildefonso 147* (IBUG-208605). **Michoacán**: *H Díaz-Barriga 1693* (IEB-79446). **Guerrero**: *GB Hinton 11142* (RSA-411988).

Phaseolus perplexus A. Delgado (2000: 418) [clade A; sect. *Minkelsersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE: *JA Solis-Magallanes 1965* (HOLOTYPE: MEXU n.v.; ISOTYPE: WIS-255906).

Specimens: MEXICO. **Sinaloa**: *AC Sanders 21145* (UCR-105133). **Jalisco**: *R Ramirez-Delgadillo 4571* (IBUG-198783). **México**: *B Bartholomew 2951* (TEX-273390). **Michoacán**: *JN Labat 406* (P).

Phaseolus persistentus Freytag & Debouck (2002: 217) [clade B; sect. *Phaseoli* DC emend. Freytag]. TYPE: *DG Debouck 1621* (HOLOTYPE: US-3168876; ISOTYPES: BR, K-478465, USCG n.v.).

It is known only from the type locality in the area of the volcanoes W of Guatemala City. This taxon has been moved from the section *Falcati* into the section *Phaseoli* by Delgado-Salinas and co-workers (2006). It is not reported in the list of “Vascular Plants of the Americas” (Tropicos 2020).

Phaseolus plagiocylix Harms (1921: 508) [clade A; sect. *Minklersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE: *E Selser 1042* (HOLOTYPE: B n.v.; ISOTYPE: GH-64098).

The type was probably lost at Berlin during WWII, and in the original publication (p. 508) there is no mention about isotypes. There is however a specimen labelled “Ex Museo botanico Berolinensi” kept in the Gray Herbarium (GH-64098) and annotated by Hermann Harms “1042 *Phaseolus plagiocylix* Harms n.sp.” that can be considered as the nomenclatural type. Known by few collections from Nuevo León, it has been reported from southern Coahuila (Carranza-P. & Villareal-Quintanilla 1997), but no specimens are indicated (nor seen by the author during his visit at ANSM in 2011). Some authors (Acosta-Díaz et al. 2019) consider it as extinct.

Phaseolus pluriflorus Maréchal, Mascherpa, & Stainier (1978b: 199) [clade A; sect. *Minklersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE (as *Minklersia multiflora* Rose (1897: 142): *CG Pringle 6471* (LECTOTYPE: US-304095; ISOLECTOTYPES: BM, G, ISC-41284, K, MO-3379357, UC-83969).

A 1–2 m climbing plant from a pluriannual tuberous root, often found among grasses and thickets on lava beds at 1400–2900 m in variously mixed pine-oak woodland.

Specimens: MEXICO. **Sinaloa:** *HS Gentry 6307* (ARIZ-115055). **Durango:** *S González 1803* (ANSM-59324). **Nayarit:** *R Ramírez 944* (MEXU-541169). **Jalisco:** *A Rodríguez-Contreras 28* (IBUG-42761). **Guanajuato:** *A Rivas-Hernández 245* (EBUM-10619). **Michoacán:** *J Espinosa-Garduño 1831* (ENCB). **México:** *A Ventura A. 3289* (MO-3593725). **Distrito Federal:** *E Bourgeau 576* (G). **Tlaxcala:** *M Provance 2947* (UCR-151311). **Morelos:** *JN Rose 7228* (US-450811).

Phaseolus polymorphus Sereno Watson (1882: 346) [clade A; sect. *Pedicellati* (Benth.) Freytag]. TYPE: *JG Schaffner 811* (SYNTYPES: GH-64100, *CC Parry & E Palmer 188* (MO-1731110)).

Just above the original publication of this species, the specimen *JG Schaffner 811* is also considered as *Phaseolus heterophyllus* Willd., that is, *Macroptilium gibbosifolium* (Ortega) A. Delgado! As aptly noted by Alfonso Delgado-Salinas (1985, p. 281), the specimen GH-64100 is a mix including *P. grayanus*. The specimen *JG Schaffner 811* kept in Kew (K-478482) consists of (mainly) *P. grayanus*, possibly a small stem of *P. polymorphus* and a small blooming stem of *P. purpusii* to the lower right. The specimen *CC Parry & E Palmer 186* kept in Harvard (GH-64101) and in Kew, and also cited as syntype, is *P. grayanus*, and thus not considered to represent this species. The specimen *CC Parry & E Palmer 188* kept in Saint-Louis (MO-1731110) is not a mixture and makes sense for *P. polymorphus* (different from *P. filiformis* Benth. and *P. wrightii* A. Gray sensu 1853) along the brief description provided by Watson. It is a climbing vine displaying heteroblastic development growing in pine-oak mixed forest and oak grassland at 900–2500 m.

Specimens: MEXICO. **Chihuahua:** *J Passini 6654* (ENCB). **Coahuila:** *Henrickson 22501* (ANSM-73568). **Nuevo León:** *J Hinton 23421* (TEX-273397). **Tamaulipas:** *JA Encina 1743* (ANSM-85810). **Zacatecas:** *LA García-R. 758* (IBUG-167893). **San Luis Potosí:** *DG Debouck 2056* (UC-1716191). **Guanajuato:** *DG Debouck 2398* (US-3168517). **Querétaro:** *L Paray 2480* (ENCB). **Hidalgo:** *CA Purpus 1365* (POM-17092). **Jalisco:** *LA García-R. 650* (IBUG-163783).

It might be appropriate to finish here with a note about *P. scabrellus* Benth. ex S. Watson that is described in the same publication (1882: 346–347) just after *P. polymorphus* (and mentioned in the list of “Vascular Plants of the Americas” (Tropicos 2020)). Sereno Watson referred to two specimens (thus syntypes): *Ed Palmer 2122* (GH-64106) and *Th Coulter s.n.* (GH-64105, K-478484). The author concurs with A. Delgado-Salinas (1985, p. 277) in considering this taxon as synonym of *P. pedicellatus*. Interestingly, Piper (1926, p. 691) wrote “*Palmer 2122*, which really is *P. pedicellatus* Benth.”.

Phaseolus polystachyus (L.) Britton, Sterns, & Poggenburg (1888: 15) [clade B; sect. *Paniculati* Freytag]. TYPE: *J Clayton 568* (LECTOTYPE: BM-51643).

In the “Preliminary Catalogue of Anthophyta . . . New York City” (1888, p. 15), Justus Ferdinand Poggenburg and his co-authors spelled the species as *Phaseolus polystachyus*; in line with the “golden rule” presented by

Nicholas Turland (2013, p. 88) it is thus unclear to this author why this taxon is often changed into “*Phaseolus polystachios*.” The “*Flora Virginica*” by Jan Fredrik Gronovius (1762, p. 106) was key to consider the collection 568 by John Clayton as the lectotype.

The “thicket bean” is a species with a huge distribution at 30–700 m in oak grassland and mixed deciduous woods of the eastern USA where its habitat is shrinking (Dohle et al. 2019). It has been reported from E Texas (Turner et al. 2003), goes as far north as New York and Connecticut (Hollick & Britton 1895), and down to southern Florida (Small 1933). The following specimens just indicate the approximate extremes of the range.

Specimens: U.S.A. **Connecticut**: *EB Harger 4148* (NEBC-643445). **Florida**: *RP Wunderlin 5667* (POM-348542). **Oklahoma**: *J Taylor 26884* (BRIT). **Texas**: *WR Carr 18597* (TEX-201584).

Phaseolus purpusii Brandegee (1912: 271) [clade A; sect. *Pedicellati* (Benth.) Freytag]. TYPE: *CA Purpus 5196* (HOLOTYPE: UC-149841; ISOTYPES: BM, G, GH-64102, L-501280, MO-1731111, P).

Its deeply lobed narrow leaflets (with main nerves almost perpendicular) incite to maintain it separate from *P. pedicellatus*, while keeping it in the section *Pedicellati*. Few collections are known from W San Luís Potosí, Mexico. It is not mentioned in the “*Vascular Plants of the Americas*,” while *P. pyramidalis* Freytag belonging to the same section is cited. The author would agree on considering the latter as a synonym of *P. grayanus* (Delgado-Salinas et al. 2006).

Specimen: MEXICO. **San Luis Potosí**: *R Grether 782* (MEXU-274666).

Phaseolus reticulatus Freytag & Debouck (2002: 262) [clade B; sect. *Coriacei* Freytag]. TYPE: *DG Debouck 409* (HOLOTYPE: US-3168878; ISOTYPES: CHAPA n.v., K-642353 and K-642354, M, MICH-1180182).

It is a member of the *Coriacei* with heteroblastic development, lobed leaflets with recurved nervation and variegation, that seems to be endemic of the SW Durango-Sinaloa border. Found in pine-oak grassland at 2000–2500 m.

Specimens: MEXICO. **Durango**: *M Lavin 5022* (GH), *P Tenorio-Lezama 4282* (IEB-79482), *P. Tenorio-Lezama 4310* (RSA-506258).

Phaseolus ritensis M.E. Jones (1908: 14) [clade B; sect. *Coriacei* Freytag]. TYPE: *ME Jones s.n.* (LECTOTYPE: POM-28786; ISOLECTOTYPES: DS-145645, GH-64079, NY-312364, POM-28788).

In 1908 Marcus Eugene Jones made the description of a bean plant from the Santa Rita mountains of Arizona; although no specimen is indicated, the botanist wrote (p. 12) that “the types of all species described are in my herbarium”. The ME Jones Herbarium was purchased in 1923 by the Pomona College, and now kept at the Rancho Santa Ana Botanic Garden, where the author saw the specimen (with barcode RSA3602) in November 2010 (here considered as lectotype). *P. ovatifolius* reported in the list of “*Vascular Plants of the Americas*” (Tropicos 2020) is a synonym of this species (as also reported by Delgado-Salinas 1985). *Phaseolus ritensis* is a tall plant of the *Coriacei* with upper stems twining, often confused with *P. maculatus* (Fig. 11). It thrives on slopes in pine-oak forests from S Arizona down to Jalisco, mostly along the eastern slope of Sierra Madre Occidental, at 1200–2600 m. The presence in New Mexico and Texas is still to be documented, as the author has not seen specimens from these two states (neither reported by Wootton & Standley 1915, nor by Turner et al. 2003, respectively), in contrast with *P. maculatus*.

Specimens: U.S.A. **Arizona**: *JC Blumer 3360* (UC-153734). MEXICO. **Chihuahua**: *R Corral-Díaz 2190* (NMC-2904). **Durango**: *ME Maury 138* (IEB-79536). **Jalisco**: *A Rodríguez-Contreras 1454* (IBUG-94444).

Phaseolus rotundatus Freytag & Debouck (2002: 132) [clade B; sect. *Paniculati* Freytag]. TYPE: *R Lépiz 410511.1* (HOLOTYPE: US-3386751; ISOTYPES: ARIZ-347215, CS-77509, F, MICH-1180113).

Because the planting of original seed resulted in a big flowering (Fig. 8) and fruiting plant in Palmira, Colombia, additional observations were made, as well as a good series of reference specimens (Salcedo-Castaño et al. 2009). It is a tall plant with scattered populations in W Mexico, the habitat of which is shrinking because of the recent expansion of agave planting. The author has doubts that the specimen *HS Gentry 22509* (ARIZ-321197, NA-27957) belongs to *P. rotundatus* (see Freytag & Debouck 2002, p. 134).

Specimens: MEXICO. **Jalisco:** *MC de Anda Virgen 24* (IBUG-134932), *HS Gentry 22188* (ARIZ-300442). **Michoacán:** *R Lépiz-Ildefonso 496* (IBUG-208608).

Phaseolus salicifolius Piper (1926: 692) [clade B; sect. *Paniculati* Freytag]. TYPE: *J González-Ortega 4065* (HOLOTYPE: US-1083789; isotype: MEXU n.v.).

A species still considered as endemic (its range seems to be the Sierra Madre Occidental along the border of the state of Sinaloa in pine-oak woodlands at 1300–2500 m, pending on more data (Fig. 8). The author has doubts that the specimen *Ed Palmer 142* (K, US-571163) belongs to *P. salicifolius* (see Delgado-Salinas 1985, p. 215).

Specimens: MEXICO. **Durango:** *DG Debouck 411* (K-1041820). **Sinaloa:** *DE Breedlove 1689* (DUKE-157400).

Phaseolus scrobiculatifolius Freytag (2002: 126) [clade B; sect. *Paniculati* Freytag]. TYPE: *CP Cowan 4902* (HOLOTYPE: TEX-371373; isotype MEXU n.v.).

This taxon has been put in synonymy of *P. jaliscanus* (Delgado-Salinas et al. 2006), a move that the author is not ready to make at this time, because it lacks the heteroblastic development, so common in *P. jaliscanus*.

Specimens: MEXICO. **Michoacán:** *AE Estrada C. 2354* (MEXU-1109087), *R Lépiz-Ildefonso 502* (IBUG-208610).

Phaseolus sinuatus Nuttall ex Torrey & A. Gray (1838: 279) [clade B; sect. *Paniculati* Freytag]. TYPE: *N Ware s.n.* (SYNTYPE: PH-28331).

John Torrey and Asa Gray mentioned two specimens for *P. sinuatus* (a name they have seen in a manuscript by Nathaniel Nuttall): one collected by Mr. Ware (studied at the Academy of Natural Sciences of Philadelphia and afore-mentioned) and another one by Dr. Burrows (not seen during this study). No strong arguments have been found to consider it as a variety or subspecies of *P. polystachyus*. It is worth remembering the footnote by Asa Gray (1852, p. 43): “*P. sinuatus* Nutt., of which I have five specimens from Ruge’s Florida collection, No. 132, is widely different from *P. perennis* (since a synonym of *P. polystachyus*)”. The leaflets are distinctly (small round) lobed, the stems trailing instead of climbing and with heteroblastic development, and the perennial root system is much more globose. Further, it occupies a specific ecological niche of the SE United States: the longleaf and loblolly pine forests on sandy soils (Radford et al. 1968) at 100–140 m.

Specimens: U.S.A. **North Carolina:** *JA Duke 1768* (NCU-126435). **South Carolina:** *CR Bell 11063* (NCU-174816). **Georgia:** *LC Anderson 15917* (BRIT). **Florida:** *EA Bessey sn* (MSC), *F Rugel 132* (NA).

The specimen collected by *Charles Louis Pollard 1017* (F-48720, GH, NY) from Jackson Co. in Mississippi belongs to *Rhynchosia cinerea* Nash. While *P. sinuatus* has been claimed to be present in Alabama and Mississippi (Small 1903; Radford et al. 1968), no specimens from these states have been seen during this study (thus the indication of intermediate range in Table 2).

Phaseolus smilacifolius Pollard (1896: 233) [clade B; sect. *Paniculati* Freytag]. TYPE: *GV Nash 2505* (HOLOTYPE: US-252673; ISOTYPES: F-48642, G, GH-64080, K, MICH-1104263, MSC, P, PH).

The fact that this species has been found in another county of Florida 101 years after the type collection lessens seriously the hypothesis of this species being a natural hybrid between *P. polystachyus* and *P. sinuatus* (Isely 1990, p. 156). Further, the planting of seeds with a progeny identical to the parents confirmed *P. smilacifolius* as a distinct species (Abbott & Judd 2000, p. 497). With few collections from central Florida, it should be considered an endemic; from these few collections it is reported growing on hammock land in oak-juniper-palmetto association. According to Dohle and co-workers (2019), it seems that no accessions are currently kept in genebanks.

Specimens: U.S.A. **Florida:** *JR Abbott 9557* (WIS), *AS Hitchcock 483* (F-232856).

Phaseolus sonorensis Standley (1940a: 31) [clade B; sect. *Paniculati* Freytag]. TYPE: *HS Gentry 1396* (HOLOTYPE: F-770502; ISOTYPES: BM, DES, GH-64109, K, MICH-1104264, MO-1089160, UC-646354, WIS-3983).

A tall plant growing in pine-oak forest at 1100–1800 m with large showy magenta flowers. It blooms in spring as often does *P. salicifolius* and *P. albinervus* too. Pending additional field work, it is still considered as endemic (an opinion shared by Fishbein et al. 1998), but it might have a larger range in the Sierra Madre Occidental.

Specimens: MEXICO. **Chihuahua:** *R Spellenberg 8081* (NMC-14198). **Sinaloa:** *RA González 236* (MEXU-800335). **Sonora:** *M Fishbein 1015* (ARIZ-304231).

Phaseolus talamancensis Debouck & Torres-González (2001: 280) [clade A; sect. *Bracteati* Freytag]. TYPE: *Debouck et al. 2130* (HOLOTYPE: CR-224324; ISOTYPES: K-478463, MO-5260537).

An exploration carried out in 2003 in Costa Rica informed us that this species although uncommon can be found outside the Talamanca range *sensu stricto*: population #3182 was found in the county of Santa María de Dota. During the cultivation of population #3182 for seed conservation, the species eventually produced tuberous roots (Fig. 12). This taxon grows in openings of the lower montane oak forest at 1500–2000 m.

Specimens: COSTA RICA. **Puntarenas:** *E Alfaro 2508* (CR-247762). **San José:** *DG Debouck 3182* (CR-238742), *JF Morales 8861* (K).

Phaseolus tenellus Piper (1926: 696) [clade A; sect. *Minklersia* (Martens & Galeotti) Maréchal, Mascherpa, & Stainier]. TYPE: *G Arsène 8310* (HOLOTYPE: US-1003657 n.v.; ISOTYPES: BM, F-48495, GH-64112, MO-541731, SI).

A member of the *Minklersia* found in openings of pine-oak forest at 2100–2900 m.

Specimens: MEXICO. **Zacatecas:** *CL Díaz-Luna 2352* (MICH-1180118). **Michoacán:** *A Delgado-Salinas 1775* (K-1041785). **México:** *GB Hinton 6528* (GH).

Phaseolus texensis A. Delgado & W.R. Carr (2007: 13) [clade A; sect. *Pedicellati* (Bentham) Freytag]. TYPE: *WR Carr 24232* (HOLOTYPE: TEX; ISOTYPE: MEXU n.v.).

This species seems to be endemic from the Edwards Plateau of SW Texas—an area noteworthy for its plant endemism (Johnston 1997)—and is included into the *Pedicellati* (Delgado-Salinas & Carr 2007). It thrives in mixed woodland with oak, elm, ash, sycamore and black cherry at 170–580 m.

Specimens: U.S.A. **Texas. Kerr Co.:** *VL Cory 52444* (BRIT), *GF Freytag 90-1* (CS-77512). **Travis Co.:** *T Wendt 7379* (TEX).

Phaseolus trifidus Freytag (2002: 181) [clade A; sect. *Digitati* Freytag]. TYPE: *FG Meyer & DJ Rogers 2899* (HOLOTYPE: MO-1597351; ISOTYPES: BM, G).

This species only known from the type specimens has been put in synonymy of *P. neglectus* (Delgado-Salinas et al. 2006), a move that is kept on hold, because the terminal leaflets are differently lobed, and the ratio peduncle/ floral rachis is different as compared to the former (in addition to the different morphology of primary bracts).

Phaseolus tuerckheimii Donnell-Smith (1913: 54) [clade A; sect. *Brevilegumeni* Freytag]. TYPE: *H von Tuerckheim II-1536* (LECTOTYPE: US-942247; ISOLECTOTYPES: BR, US-860832, US-942248). SYNTYPE: *H Pittier 10539* (US-942246).

John Donnell Smith referred to two collections, the one by Hans von Tuerckheim (no. II-1536) and the one by Henri Pittier (no. 10539) in that order, without indicating the holotype. As there were several duplicates of no. II-1536 at the US National Herbarium, the selection of the voucher US-942247 by George Freytag as nomenclatural type seemed appropriate: it would have been impossible for JD Smith to write down a description of the floral parts of *P. tuerckheimii* without dissecting its flower! This species is a tall (6–10 m) vine growing in the moist montane forests of Central America at 1500–2600 m (Araya-Villalobos et al. 2001) (Fig. 3).

Specimens: MEXICO. **Chiapas:** *U Bachem 398* (CHAPA). GUATEMALA. **Huehuetenango:** *LO Williams 22323* (F-1656438). **El Quiché:** *AJ Sharp 45191* (MEXU-136531). **Quezaltenango:** *DG Debouck 3085* (AGUAT). **Sololá:** *DG Debouck 3097* (AGUAT). **Chimaltenango:** *DG Debouck 1624* (MICH-1180126). **Sacatepéquez:** *M Véliz 14771* (MO-5871374). **Guatemala:** *DG Debouck 2473* (US-3168469). **Jalapa:** *JA Steyermark 32551* (F-1035022). **El Progreso:** *DG Debouck 2418* (COL-324860). **Zacapa:** *JA Steyermark 42471* (F-1202181). COSTA RICA. **San José:** *JL Luteyn 4541* (DUKE-242717). PANAMA. **Chiriquí:** *R Villareal 494* (PMA-108353).

Phaseolus venosus Piper (1926: 687) [clade B; sect. *Coriacei* Freytag]. TYPE: *JN Rose 2688* (HOLOTYPE: US-301614; no isotype found during this study).

This species has been put in synonymy of *P. maculatus* (Delgado-Salinas et al. 2006) but differences in size of plant, leaflet nervation and acumen, shape, nervation and size of primary bracts as compared to the ones found in the “Metcalf bean” prevent to make this move till more living material allows cross comparisons. It has



FIG. 12. Root of *P. talamancensis* (DG Debouck 3182) grown in CIAT Popayán experimental station in Cauca, Colombia (as G40814) (steel ruler 15 cm).

been seen in pine-oak woodland at 2000–2200 m. This taxon is not reported in the list of “Vascular Plants of the Americas” (Tropicos 2020).

Specimens: MEXICO. **Zacatecas:** G Starr 672 (UCR-32721). **Aguascalientes:** S Gallegos G. 12 (IBUG-52731). **Jalisco:** R Ramírez-Delgadillo 1447 (IBUG-99829).

Phaseolus viridis Piper (1926: 693) [clade B; sect. *Paniculati* Freytag]. TYPE: *H von Tuerckheim II-897* (= *John Donnell-Smith 8510*) (HOLOTYPE: US-576636 n.v.; ISOTYPES: F-185839, GH-64113, O, US-942171).

This species seems to be valid, namely because of flower, pod (Fig. 10) and seed number traits, in spite of previous transfers into synonymy of *P. lunatus* (Delgado-Salinas 1985, Freytag & Debouck 2002). It is known by scattered populations across tropical Mexico and Guatemala and found in semi-evergreen seasonal forest at 10–730 m. Studies with molecular markers on ITS/5.8S DNA and *trnK* cpDNA (Delgado-Salinas et al. 1999, 2006) have indicated a clear difference with *P. lunatus*. *Phaseolus longiplacentifer* Freytag would be a synonym of this species (Delgado-Salinas et al. 2006). *Phaseolus longiplacentifer* is reported in the list of “Vascular Plants of the Americas” (Tropicos 2020), while *P. viridis* is not.

Specimens: MEXICO. **Veracruz:** M Botteri 680 (P). **Oaxaca:** G Juárez-García 1086 (ARIZ-389122). **Chiapas:** E Palacios-Espinosa 1757 (CAS-852127).

Phaseolus vulgaris L. (1753: 723) [clade B; sect. *Phaseoli* DC emend. Freytag]. TYPE: *C. Linnaeus s.n.* (LECTOTYPE: LINN-899.1).

The type of the reference species of the section and of the genus is a plant cultivated at Uppsala, Sweden (Verdcourt 1971). Ironically, the most common (Linnaeus was right in naming it *vulgaris*!) species of the genus has its wild ancestor disclosed quite late: Arturo Burkart in Salta, NW Argentina in 1941 (Burkart 1941, 1952), and Felix Webster McBryde in W Guatemala in 1947, and not referring to each other's finding! Keeping *P. aborigineus* Burkart as a separate species (as suggested in the List of Tropicos 2020) might result in hiding the biological link with the Andean cultivated form and its three races (Singh et al. 1991). The double independent domestication of the wild form of common bean distributed from Chihuahua (Nabhan 1985) down to Córdoba (Drewes 2008) is now widely agreed upon (Chacón-Sánchez et al. 2005; Kwak & Gepts 2009; Bitocchi et al. 2013). There would be enough evidence (Tohme et al. 1996; Chacón-Sánchez et al. 2007; Ariani et al. 2017) to recognize five wild genetic pools: one W of Isthmus of Tehuantepec (Chihuahua down to Oaxaca), one including Chiapas, Guatemala, Honduras, El Salvador and NW Nicaragua, one including Costa Rica, one including the NE Andes of Colombia and W Andes of Venezuela, and one including the central and southeastern Andes of Peru (Huánuco down to Cuzco), eastern Andes of Bolivia (Cochabamba down to Tarija), and NW Andes of Argentina (Jujuy down to Córdoba; although Salinas Grandes might be another break). The significance of a formal treatment of botanical varieties, i.e., a var. *mexicanus* for the Mexican and Central American wild forms and a var. *aborigineus* for the Andean one (Delgado-Salinas et al. 1988), is pending on what the wild forms from Venezuela will reveal (Beebe & Debouck 2019), while the recognition of a var. *vulgaris* for all cultivated forms (Baudet 1977) may blur their complex origins. The following specimens (different from the ones reported previously in Freytag & Debouck 2002 p. 38–39) are wild forms and give an indication about the range.

Specimens: MEXICO. **Durango:** DG Debouck 276 (COL-324695). **Zacatecas:** JM González-Corraea 30 (IBUG-29683). **Nayarit:** RS Ferris 5946 (DS-214469). **Jalisco:** JS Peñaflores-Cortés 9 (IBUG-36127). **Colima:** HS Gentry 22189 (ARIZ-300349). **México:** A Delgado-S. 1006 (CHAPA). **Morelos:** E Bourgeau 1375 (FI). **Puebla:** R Torres-C. 7544 (RSA-537099). **Michoacán:** DG Debouck 439 (COL-324743). **Guerrero:** GB Hinton 11551 (POM-348560). **Oaxaca:** B Bartholomew 3033 (CAS-747013). **Chiapas:** E Cabrera 5930 (CAS-819944). GUATEMALA. **Sacatepéquez:** DG Debouck 1610 (K). **Santa Rosa:** E Martínez-S. 19230 (MEXU-526662). **Jalapa:** DG Debouck 2432 (COL-324875). HONDURAS. **El Paraíso:** JG Hawkes 2053 (K). **Morazán:** A Molina R. 731 (F-1262709). EL SALVADOR. **Sonsonate:** DG Debouck 3226 (LAGU). **La Libertad:** DG Debouck 3221 (LAGU). NICARAGUA. **Madriz:** DG Debouck 3202 (O-V2147425). **Esteli:** DG Debouck 3216 (O-V2147423). COSTA RICA. **Alajuela:** DG Debouck 3133 (CR-235446). **Cartago:** DG Debouck 3126 (CR-247283). **San José:** CO Morales 621 (USJ-48426). VENEZUELA. **Mérida:** O Berglund 26667 (SI). **Lara:** G Davidse 21172 (NY). COLOMBIA. **Cundinamarca:** JO Toro-Chica 498 (COL-520043). PERU. **Huánuco:** JF Macbride 3947 (G). **Junin:** R Ferreyra 14964 (USM-71284). **Huancavelica:** O Tovar 3910 (US-2490506). **Apurímac:** C Ochoa 2420 (MOL). **Cuzco:** OF Cook 1073 (US-604244). BOLIVIA. **Cochabamba:** R Caballero-Pardo s.n. (NY). **Chuquisaca:** DG Debouck 3007 (DAV-128327). **Tarija:** DG Debouck 3020 (MO-5613149). ARGENTINA. **Jujuy:** O Ahumada 4173 (SI). **Salta:** R Fortunato 3576 (BAB). **Tucumán:** M Lillo 1626 (LIL-62049). **Catamarca:** DG Debouck 645 (COL-324753). **San Luis:** R Batallanez s.n. (SI). **Córdoba:** T Stuckert 12831 (SI).

Phaseolus xanthotrichus Piper (1926: 698) [clade A; sect. *Xanthotricha* A. Delgado]. TYPE: *ET Heyde & E Lux 4171* (HOLOTYPE: US-247544 n.v.; ISOTYPES: GH-64114, M, US-942184).

While its habitat (lower montane moist forest with alder, oak, pine, cedar, at 1400–2400 m) has been invaded by *Coffea arabica* mostly over the last two centuries, it has been able to survive under the fences of coffee plantations where herbicide sprays are less frequent.

Specimens: MEXICO. **Chiapas:** DE Breedlove 53235 (CAS-668979). GUATEMALA. **Sacatepéquez:** M Veliz 7362 (MEXU-999506). **Santa Rosa:** DG Debouck 2438 (US-3168340). EL SALVADOR. **Ahuachapán:** EA Montalvo 4596 (ITIC). **Santa Ana:** DG Debouck 3229 (LAGU). **Sonsonate:** EA Montalvo 4926 (ITIC). COSTA RICA. **San José:** DG Debouck 3176 (CR-247291), DG Debouck 3358 (USJ-111605), B Hammel 23864 (INB-3974385). **Cartago:** DG Debouck 3125 (USJ-88822).

Phaseolus xolocotzii A. Delgado (2000: 429) [clade B; sect. *Paniculati* Freytag]. TYPE: *R Torres-Colin 7700* (HOLOTYPE: MEXU n.v.).

A member of the *Paniculati* known by scattered populations along the internal slope of W Sierra Madre del Sur up to the S slope of the Trans-Mexican Volcanic Belt, in dry pine-oak forest at 1200–1900 m. The author has

doubts that the specimen *DG Debouck* 2346 (BR, COL-58966, M, SI, US-3168881) belongs to *P. xolocotzii* (see Freytag & Debouck 2002, p. 137).

Specimen: MEXICO. **México:** *GB Hinton* 2484 (K-118678).

Phaseolus zimapanensis A. Delgado (2000: 432) [clade A; sect. *Xanthotricha* A. Delgado]. TYPE: A Delgado-Salinas 1113 (HOLOTYPE: MEXU n.v.; ISOTYPES: K-651818, NY-1104835).

A member of the section *Xanthotricha* with distribution in the central dry highlands of Mexico along the western slope of Sierra Madre Oriental, in oak, pine, pine-oak, cedar forest and mesquite scrub at 900–2400 m.

Specimens: MEXICO. **Coahuila:** *JA Villareal-Quintanilla* 3961 (ANSM-37738). **Tamaulipas:** *TF Daniel* 307 (MICH-1180184). **Nuevo León:** *DG Debouck* 1513 (UC-1716197). **San Luis Potosí:** *OS Fearing* 2042 (TEX-273467). **Querretaro:** *UT Waterfall* 14114 (IA-111313). **Hidalgo:** *A Frias-Castro* 701 (IBUG-182428).

Additional observations in relation to the list of “Vascular Plants of the Americas”

About some species out of the eighty-nine mentioned in that list (Tropicos 2020), one could mention: *P. pachycarpus* Standley (1940a: 29; type F-910041) from Chihuahua, Mexico, is a synonym of *Ramirezella strobilophora* (Robinson) Rose (1903: 44). *Phaseolus pilosus* Kunth (1823: 453; lectotype P-660144) from the department of Bolívar, Colombia, is a synonym of *Vigna lasiocarpa* (Mart. ex Benth.) Verdc. (1970: 539). *Phaseolus reptans* Ducke (1925: 98; syntype: US-1442068) from the state of Pará, Brazil, is a synonym of *Ancistrotropis peduncularis* (Fawcett & Rendle) A. Delgado (2011: 1704). *Phaseolus rimbachii* Standley (1940b: 81; holotype F-766421) from the highlands of Ecuador, is a synonym of *Dipogon lignosus* (L.) Verdc. (1968: 537). *Phaseolus unilobatus* Pittier (1944: 55; lectotype: US-1800757) from Monagas, Venezuela, is a synonym of *Macroptilium gracile* (Poepp.) Urban (1928: 457).

DISCUSSION

The checklist suggests the following points for discussion. **First**, before dealing with numbers, it might be worth reflecting back on criteria defining bean species. At the genus level (Table 1), it seems that the criteria are becoming robust as shared by all species listed in Table 2. In some species primary bracts (e.g., *P. salicifolius*) or bracteoles (e.g., *P. amblyosepalus*) may seem wanting, they are however fully formed but early caducous during floral ontogenesis. And there is an increasing number of Neotropical legume species matching these criteria. Such an increase is a bit against expectations, as several *Phaseolus* basionyms of the Old World were moved to other genera (Verdcourt 1970; Maréchal et al. 1978a). Similarly, for the New World, other *Phaseolus* basionyms were moved into newly defined genera, for example *Helicotropis* A. Delgado, *Misanthus* G.P. Lewis & A. Delgado or *Sigmoidotropis* (Piper) A. Delgado (Delgado-Salinas et al. 2011). So, through a couple of genus reviews, the number of *Phaseolus sensu stricto* species rose from 31 (Maréchal et al. 1978a), to 36 (Delgado-Salinas 1985), 75 (Freytag & Debouck 2002), 71 (Delgado-Salinas et al. 2006), and 81 (present results). How has this increase been possible? The coverage of the study of herbarium collections likely holding New World legumes (30 by Delgado-Salinas 1985, 50 by Freytag & Debouck 2002, 86 by the author to date; Appendix 1) and numbers of specimens examined has become significant. But the increase is also due to field work over the last decades. This brings a **second** point, related to the kind of materials disclosed in recent times. While there is little doubt that the botanical survey of the Neotropics has been shaped by access conditions (there were outstanding exceptions, for example George Boole Hinton: Hinton & Rzedowski 1972), it falls within all probabilities that the common and widespread species (23 in Table 2) have been found at least once over the last 250 years. At the beginning of any survey however, in herbaria or in the field, the number of populations is low because botanists do not know the full range from the first materials seen. But an in-depth study soon teaches about distribution (widespread versus local) and frequency (common versus rare). As an example, for Costa Rica, there were early on a couple of records of both *P. leptostachyus* and *P. xanthotrichus* (Standley 1937) because these species are widespread and common (Freytag & Debouck 2002), but the last third of *Phaseolus* species described for that country seem to be endemic species (Debouck et al. 2020). It is thus quite possible that from now onwards the number of species will continue to increase, because of the endemic ones (43 in

Table 2), with an area of occupancy of just a few square miles. **Thirdly**, a consensus of three independent research works (Delgado-Salinas et al. 2006; Tropicos 2020, and present results) seems emerging about the validity of some 65 species, meaning the tacit sharing of species concepts and criteria. Apart the recently described species, discrepancies are mainly on species known by one or few specimens, highlighting the need for additional field work. Besides, additional field work will also solve the “highly problematic” specimens (e.g., *DG Debouck 2346*, *HS Gentry 22509*, *Ed Palmer 142*) that happen to be found in large scale taxonomic studies. Rather than changing the concept of “good” species to accommodate these puzzling collections, it might be worth going back to the original site. A similar situation was experienced with the specimen *M Grayum 10618* (MO-6103483) and eventually resulted into a new species (Debouck et al. 2018). And this is doubly positive towards the countries (if extinction can be checked they are richer than they assume) and the younger generation of botanists (there are still new species to be disclosed and described). Concluding, an expected question from the readership would be: is this list final? With the risk of losing all credibility towards a patient reader, the author may have to answer evasively “possibly not”. Citing Jack Rodney Harlan (1992, p. xiii), “there would be little fascination in science if it were static”. This no doubt applies to the taxonomy of our beans.

APPENDIX 1

List of Museums of Natural History and Herbaria studied, and dates of visit.
(acronyms after *Index Herbariorum*, Thiers 2020; month and year)

1. A: Arnold Herbarium; it is together with the herbaria ECON and GH at Harvard University, Cambridge, Massachusetts, USA (Jul-2006; Sep-2016).
2. AGUAT: herbarium of the Universidad de San Carlos, Guatemala City, Guatemala (Nov-1987; Aug-2007; Apr-2011).
3. AHUC: herbarium of the Department of Agronomy of the University of California; it is together with the herbarium DAV of the University of California-Davis, Davis, USA (Sep-2008).
4. ANSM: herbarium of the Agricultural University “Antonio Narro,” Saltillo, Coahuila, Mexico (Dec-2011).
5. ARIZ: herbarium of the University of Arizona, Tucson, USA (Feb-1979; Sep-2012).
6. ASU: herbarium of the Arizona State University, Tempe, USA (Sep-2015).
7. BA: herbarium of the Museo Argentino de Historial Natural, Buenos Aires, Argentina (Aug-2010).
8. BAA: herbarium of the Facultad de Agronomía, Universidad de Buenos Aires, Argentina (Mar-1985; Oct-2006).
9. BAB: herbario del Instituto Nacional de Tecnología Agropecuaria, Castelar, Argentina (Aug-2010).
10. BAFC: herbarium of the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina (Mar-1985).
11. BACP: herbarium of the Centro de Estudios Farmacológicos y de Principios Naturales; it is in the Argentinean Museum of Natural History, Buenos Aires, Argentina (Aug-2010).
12. BM: herbarium of the British Museum, London, England (Aug-1985; Dec-2006).
13. BR: herbarium of the National Botanical Garden, Meise, Belgium (Jun-2005; Oct-2005; Oct-2007).
14. BRIT: herbarium of the Botanical Research Institute of Texas, Fort Worth, USA (Feb-2002; Jun-2002).
15. CAS: herbarium of the California Academy of Sciences, San Francisco, USA (Sep-2008).
16. CHAPA: Herbario-hortorio of the Colegio de Postgraduados, Montecillo, México (Jul-2004; Sep-2005).
17. CICY: herbarium of the Centro de Investigaciones Científicas de Yucatán, Mérida, México (Apr-2005; Jan-2011).
18. COL: Herbario Nacional Colombiano, Instituto de Ciencias Naturales, Bogotá, Colombia (May-1985; Jul-1990; Jul-2002; Feb-2009; Jun-2010).
19. CORD: Museo Botánico, Universidad Nacional de Córdoba, Córdoba, Argentina (Oct-2009).
20. CPUN: herbarium of the Universidad Nacional de Cajamarca, Cajamarca, Perú (Jun-1985; Jul-1986).
21. CR: herbarium of the Museo Nacional, San José, Costa Rica (Jan-1987; Jun-1991; Jun-2004; Aug-2005; Oct-2017; May-2019).
22. CS: herbarium of Colorado State University, Fort Collins, USA (Aug-2008).
23. CUZ: herbarium of the Universidad San Antonio Abad, Cuzco, Perú (Feb-2001; Nov-2019).
24. DAV: herbarium of the University of California-Davis, Davis, USA (Sep-2008; Nov-2010).
25. DES: herbarium of the Desert Botanical Garden, Phoenix, Arizona, USA (Feb-1979).
26. DS: Dudley herbarium of Stanford University, USA (now in CAS) (Sep-2008).
27. DUKE: herbarium of Duke University, Durham, USA (Aug-2011).
28. EBUM: herbarium of the Escuela de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, México (Feb-2003).
29. ECON: Oak Ames herbarium, Harvard University, Cambridge, USA (Jul-2006; Sep-2016).
30. ENCB: herbarium of the Escuela Nacional de Ciencias Biológicas, Ciudad de México, México (Jul/Aug-1978; Sep-2004; Apr-2005).
31. F: Field Museum of Natural History, Chicago, USA (Jul/Aug-2004).
32. FI: herbarium of the Museo di Storia Naturale dell’Università, Firenze, Italy (Jul-2008).
33. FHO: herbarium of the School of Forestry of the University of Oxford, Oxford, England (Feb-2007).
34. G: herbarium of the Conservatoire et Jardin Botaniques, Genève, Switzerland (Feb-2002).
35. GH: Gray Herbarium; it is together with the A and ECON herbaria at Harvard University, Cambridge, Massachusetts, USA (Jul-2006; Sep-2016).

36. HAO: herbarium of the Universidad Antenor Orrego, Trujillo, Perú (Oct-2000).
37. HNMN: national herbarium of Nicaragua, Universidad Centroamericana, Managua, Nicaragua (Apr-2006).
38. HUT: Herbario Truxillense, Universidad Nacional de Trujillo, Perú (Oct-2000).
39. IA: herbarium of the University of Iowa, Ames, USA (Apr-2010).
40. IBUG: herbarium of the Instituto de Botánica de la Universidad de Guadalajara, Guadalajara, México (Oct-2003; May-2008; Jan-2011; Nov-2018; June-2019).
41. IEB: herbarium of the Instituto Ecológico del Bajío, Patzcuaro, México (May-2008).
42. INB: herbarium of the Instituto Nacional de Biodiversidad, Santo Domingo, Costa Rica (Aug-2003; Jul-2004; Aug-2005; Sep-2010; March 2013).
43. ISC: herbarium of Iowa State University (formerly Iowa State College), Ames, USA (Apr-2010).
44. ITIC: herbarium of the university of El Salvador, Escuela de Biología, San Salvador, C.A. (Apr-2011).
45. K: herbarium of Royal Botanic Gardens, Kew, England (Aug-1985; Mar-1986; Mar-2005; Oct-2005; Jun-2006; Jun-2011; Mar-2018).
46. L: herbarium of the University of Leiden, Netherlands (Oct-2007).
47. LAGU: herbarium of the botanic garden "La Laguna," Antiguo Cuscatlán, El Salvador, C.A. (Nov-2012).
48. LL: Lundell herbarium; it is together with TEX at the university of Texas, Austin, USA (Sep-2008).
49. LIL: Miguel Lillo herbarium, Tucumán, Argentina (March-1985).
50. LPB: Herbario Nacional de Bolivia, La Paz, Bolivia (April-1988).
51. M: herbarium of the Botanische Staatssammlung, München, Germany (Oct-2005).
52. MA: herbarium of Jardín Botánico Real, Madrid, Spain (Sep-2000; June-2006).
53. MEXU: Herbario Nacional de México, Instituto de Biología, UNAM, Mexico (July-1978; Aug-1994; Nov-2007; Jan-2011; March-2012; April-2013).
54. MICH: herbarium of the University of Michigan, Ann Arbor, USA (June-1988; Sep-2007).
55. MIN: herbarium of the University of Minnesota, St. Paul, USA (Apr-2010).
56. MO: herbarium of the Missouri Botanical Garden, St. Louis, USA (May/June 2002; June 2013).
57. MOL: herbarium of the Universidad Nacional Agraria, La Molina, Peru (March-1985; Oct-2000).
58. MSC: herbarium of Michigan State University, East Lansing, USA (June-1988).
59. NA: herbarium of the National Arboretum, Washington D.C., USA (July-2006).
60. NCU: herbarium of the University of North Carolina at Chapel Hill, USA (Aug-2011).
61. NEBC: herbarium of the New England Botanical Club, Harvard University, Cambridge, USA (July-2006).
62. NMC: herbarium of New Mexico State University at Las Cruces, USA (Aug-2017).
63. NMCR: herbarium of Range Science of New Mexico State University at Las Cruces, USA (Aug-2017).
64. NY: herbarium of the New York Botanical Garden, New York, USA (June 1993; June 2003; Feb-2014).
65. O: herbarium of the University of Oslo, Norway (Feb-2008).
66. OXF: herbarium of the University of Oxford, Oxford, England (Jan-2007).
67. P: herbarium of the Musée National d'Histoire Naturelle, Paris, France (Feb-2004).
68. PH: herbarium of the Academy of Natural Sciences, Philadelphia, USA (Sep-2007).
69. PMA: herbarium of the University of Panama, Panama (Apr-2018).
70. POM: herbarium of the Pomona College, CA; it had been received by the Rancho Santa Ana Botanic Garden, Claremont, CA, USA (Nov-2010).
71. PRG: herbarium of the national university Pedro Ruíz Gallo of Lambayeque, Peru (Oct-2000).
72. QCA: herbarium of the Pontificia Universidad Católica del Ecuador, Quito, Ecuador (July-2003).
73. RB: herbarium of the Jardim Botânico de Rio de Janeiro, Rio de Janeiro, Brazil (Oct-2011).
74. RSA: herbarium of Rancho Santa Ana Botanic Garden, Claremont, CA, USA (Nov-2010).
75. SGO: herbarium of the Museo Nacional de Historia Natural, Santiago, Chile (March-1999).
76. SI: herbarium of the Instituto Darwinion, San Isidro, Argentina (March-1985; Oct-1985; April-1988; Nov-2005).
77. TCD: herbarium of the Trinity College, Dublin, Ireland (June-2011).
78. TEX: herbarium of the University of Texas, Austin, USA (Sep-2008).
79. UC: Herbarium of the University of California, Berkeley, USA (Oct-2003).
80. UCR: Herbarium of the University of California, Riverside, USA (Aug-2014).
81. UFG: herbarium of the Universidade Federal de Goiás, Goiânia, Goiás, Brazil (Oct-2011).
82. US: National Herbarium, Smithsonian Institute, Washington, D.C., USA (Aug-1994; May-1997; Aug-2003; Sep-2009).
83. USJ: herbarium of the University of Costa Rica, San José, Costa Rica (Jan-1987; June 1991; Aug-2005; Dec-2018; May-2019).
84. USM: herbarium of the Universidad Nacional Mayor de San Marcos, Lima, Peru (March-1985; Oct-1997; Oct-2000).
85. UVAL: herbarium of the Universidad del Valle de Guatemala, Guatemala, C.A. (April-2011).
86. WIS: Herbarium of the University of Wisconsin, Madison, USA (Nov-2007).

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