ADDITIONAL OBSERVATIONS ABOUT *PHASEOLUS ROTUNDATUS* (FABACEAE), AN ENDEMIC BEAN SPECIES FROM WESTERN MEXICO

Jesús Salcedo C.
Bioversity International
Office for the Americas
c/o CIAT, COLOMBIA
j.m.salcedo@cgiar.org

Rogelio Lépiz I.
University of Guadalajara
Centro Universitario de Ciencias
Biológicas y Agropecuarias
Jalisco, MÉXICO
rlepiz@cucba.udg.mx

Nora Castañeda A.
Bioversity International
Office for the Americas
c/o CIAT, COLOMBIA

César Ocampo N. and Daniel G. Debouck
International Center for Tropical Agriculture (CIAT)
AA 6713
Cali, COLOMBIA
d.debouck@cgiar.org

ABSTRACT

Further information is presented about *Phaseolus rotundatus*, a new bean species for western Mexico, where it appears to be endemic and endangered, with very few populations reported to date, and all outside current protected areas. The differences between *P. rotundatus* and *P. marechalii* (both of *Phaseolus* section *Paniculati* Freytag), the closest taxon with which it can be confused, are highlighted to confirm the validity of the former taxon.

RESUMEN

Se presentan resultados que confirman la validez de *Phaseolus rotundatus*, como especie endémica y en peligro de extinción en el occidente de México, con muy pocas poblaciones conocidas a la fecha y ubicadas en su mayoría fuera de áreas protegidas. Se consignan las diferencias principales con *P. marechalii* (ambas de la sección *Paniculati* Freytag del género *Phaseolus*), especie cercana con la cual podría confundirse, para confirmar la validez de *P. rotundatus*.

INTRODUCTION

A new wild bean species, *Phaseolus rotundatus* Freytag & Debouck, was described for western Mexico (Freytag & Debouck 2002). It is a tall woody climbing vine with rounded rhombic, densely pubescent, trifoliolate leaves and stout panicles with lilac-purple flowers. The double racemic structure of its inflorescences with development of the secondary raceme axis (Debouck 1983) clearly places it in the section *Paniculati* Freytag of the genus. The species was first collected by Rogelio Lépiz in October 1978, and shown later in that year as a herbarium voucher to the senior author (DGD), who could not identify it, but confirmed it as a '*Phaseolus sensu stricto*' as the genus was understood by then (Maréchal et al. 1978). Although the voucher was slightly overburnt during drying, Robert Maréchal was able to obtain a living specimen in the glass-house in Gembloux, Belgium (as NI 1046, also G40693 at CIAT). George F. Freytag obtained later seed of that plant, and on the indication by the senior author (DGD) aptly described *P. rotundatus* as grown in a growth chamber at the Tropical Agriculture Research Station of USDA, Mayagüez, Puerto Rico (Freytag & Debouck 2002). Conditions were not ideal for the preparation of type specimens (currently the holotype is US3386751, and isotypes are kept at CS, F, and MICH, none with complete reproductive parts). Additional material was collected in the field by R. Lépiz and D. Debouck in recent years. These latest collections enabled additional observations on blastogeny and palynology, which are reported below. Because of a possible confusion with a closely related species, viz *Phaseolus marechalii* Delgado (Delgado 2000), attention is drawn to differences between these two taxa.

RESULTS

Morphological observations

The following complements the description given elsewhere (Freytag & Debouck 2002) on plants grown for several years in CIAT Palmira, Colombia, and seen in Río Verde, Jalisco, Mexico in November 2003. The small amount of variation observed for many morphological traits between plants grown artificially in Mayagüez (18°12'28" lat N, 67°08'18" long W !) and in the field in Palmira (3°30'06" lat N, 76°21'21"long W) is noteworthy.

Seedling 15–18 cm high, from hypogeal germination; epicotyl green, terete, 80–100 mm long, covered with white uncinate trichomes (Fig.1a, 2e left). Eophylls simple, deltoid, green (146B Yellow – green group; Anonymous 1966), opposite, with minute white uncinate trichomes on adaxial and abaxial surfaces, 30 × 25 mm, apex acute to acuminate, base slightly cordate; petioles green, 15 mm long, minute stipels, pulvini dark green, pubescent; stipules triangular, basifixed, 1–2 mm long, highly pubescent, 3- nerved, green. First true leaf trifoliolate, leaflets ovate to elliptic. **Root** diameter 8–12 cm or more, 50 cm long or more, pluriannual thick fleshy and woody, with 3–6 conical subdivisions 15–30 cm long of 1–4 cm diameter, with prominent whitish nodules and dark brown corky cortex. **Stems** terete stout erect in lower parts and climbing in upper parts, woody and enlarged at base, total length 2–4–8 m (Fig. 2b), diameter 2–5–8 mm, internodes 12–14 cm green (144A) densely covered with white short strigose pubescence. **Stipules** triangular acute 4 mm long 2 mm wide covered by whitish pubescence. **Leaves** trifoliolate 13–18 cm long, terminal leaflets rhombic rounded to orbicular (57 × 55 mm to 67 × 62 mm) greenish (147A) because of whitish dense pubescence, lateral leaflets similar but slightly inequilateral (53 × 45 mm to 65 × 64 mm); petioles 3–6–10 cm long, petiolules 9–20–30 mm long; lower pulvini 4–6 mm long, upper pulvini 2–3 mm long; stipels ligulate 2–3 mm long. **Inflorescence** a panicle with 20–30 or more secondary racemes, some of them developed at base, 35–75 cm long (Fig. 2a); the peduncle 12–22 cm long stout slightly curved and reddish at base densely covered with white short strigose pubescence and minute uncinate hairs; the rachis 18–51 cm long usually erect green with 15–20–30 secondary racemes irregularly spaced, often with development of axis beyond second flower, subtended by triangular aciculate primary bracts 2.5–3 × 1.2 mm strongly 3-nerved covered by whitish pubescence. Pedicels terete straight or slightly recurved 4–6 mm long covered with white short strigose pubescence and minute uncinate hairs. Pedicelar bracts linear 1 mm long 1-nerved densely covered by whitish pubescence. **Bracteoles** green triangular narrow hirsute 1mm long or less strongly 1-nerved densely covered by whitish pubescence (Fig. 1e). **Flowers** papilionaceous (Fig. 1c, 1d, 2d left) purple pink (72B red-purple) fading violet blue (85A violet), two for each secondary raceme (Fig. 1b); calyx round cupped green turning to tan at insertion of pedicel, hirsute, margin shortly ciliate, tube 3.5 mm long, two upper calyx lobes fused unconspicuous, three lower lobes triangular apiculate 1 × 1 mm long (Fig. 1e); standard outer face pale lilac glabrous with a few straight short hairs on top, inner face purple pink intense with auricles 4–5 veined, squarish with a deep central sinus, 11 × 8.5 mm, thickened at flexure, auricles rounded slightly reflexed, the right auricle more developed, claw green reddish 1.5 mm long with two parallel rounded green pinkish callosities (Fig. 1f); wings spreading horizontally, intense purple pink, obovate rounded subequal, the margins often revolute particularly on the left wing, the blade 8 × 6 mm glabrous, the squarish spur slightly adhering to the keel, claw linear 4 mm long (Fig. 1g); keel tubular in close asymmetrical spiral spreading to the left white greenish at base, pink purple in the ascending part, greenish at top, 1 ¾ counterclockwise closed coils, ca 12 mm long, two claws divided 2 mm long whitish with a few pink spots, a convex rounded pocket 1 mm long above each claw (Fig. 1h); stamens diadelphous (9+1): vexillary stamen free 11 mm long claw terete 2 mm long to cupped knob 1 mm diameter (Fig. 1j); staminal tube 11 mm long slightly veined with two small rounded callosities flanking the knob (Fig. 1i); anthers yellow dithecal oval dorsifixed. Ovary green glabrous 5 × 1 mm laterally compressed margins slightly pronounced inserted on a smooth basal disk 1 mm diameter, 4 ovules; style spiraled ca 11 mm long terete glabrous, a brush of straight 1 mm long hairs unilaterally extending below the stigma not beyond, stigma narrowly triangular white 1 mm long not extending beyond style tip (Fig. 1k). **Pods** falcate small 28–45

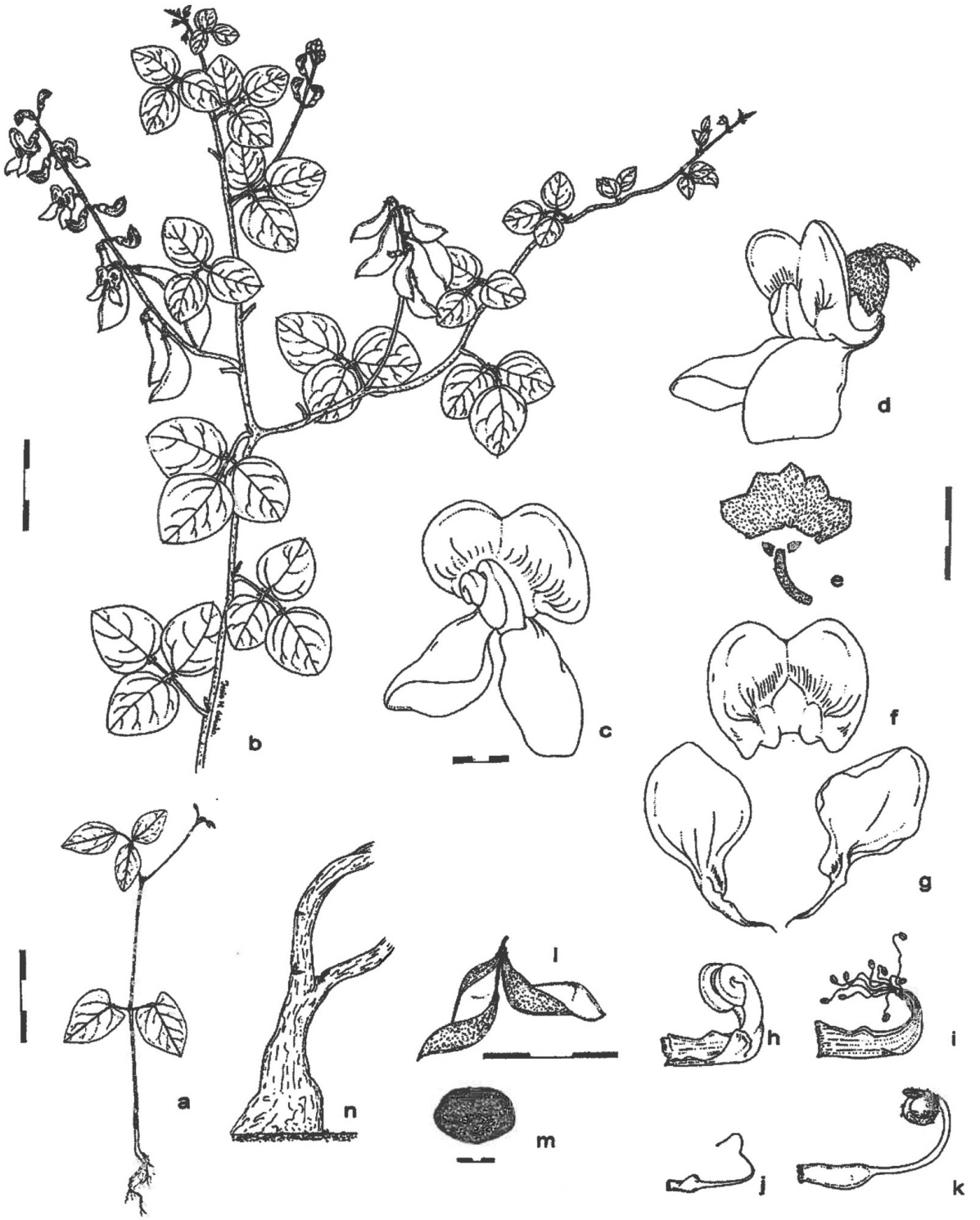

Fig. 1. *Phaseolus rotundatus* Freytag & Debouck. **a.** Seedling. **b.** Habit of young fertile stem. **c.** Flower (front view). **d.** Flower (lateral view). Floral parts (eh): **e.** Pedicel, bracteoles and calyx. **f.** Standard. **g.** Wings. **h.** Keel. **i.** Staminal tube. **j.** Vexillary stamen. **k.** Ovary and style. **l.** Pod. **m.** Seed.. **n.** Root system and lower part of oneyear plant. Scale: a–b, l, n in cm; d–m in mm. All drawings made from plants grown in Palmira, Colombia, of seed from the type collection (*Lépiz s.n.*) from near Río Verde, Tepatitlán, Jalisco, Mexico.

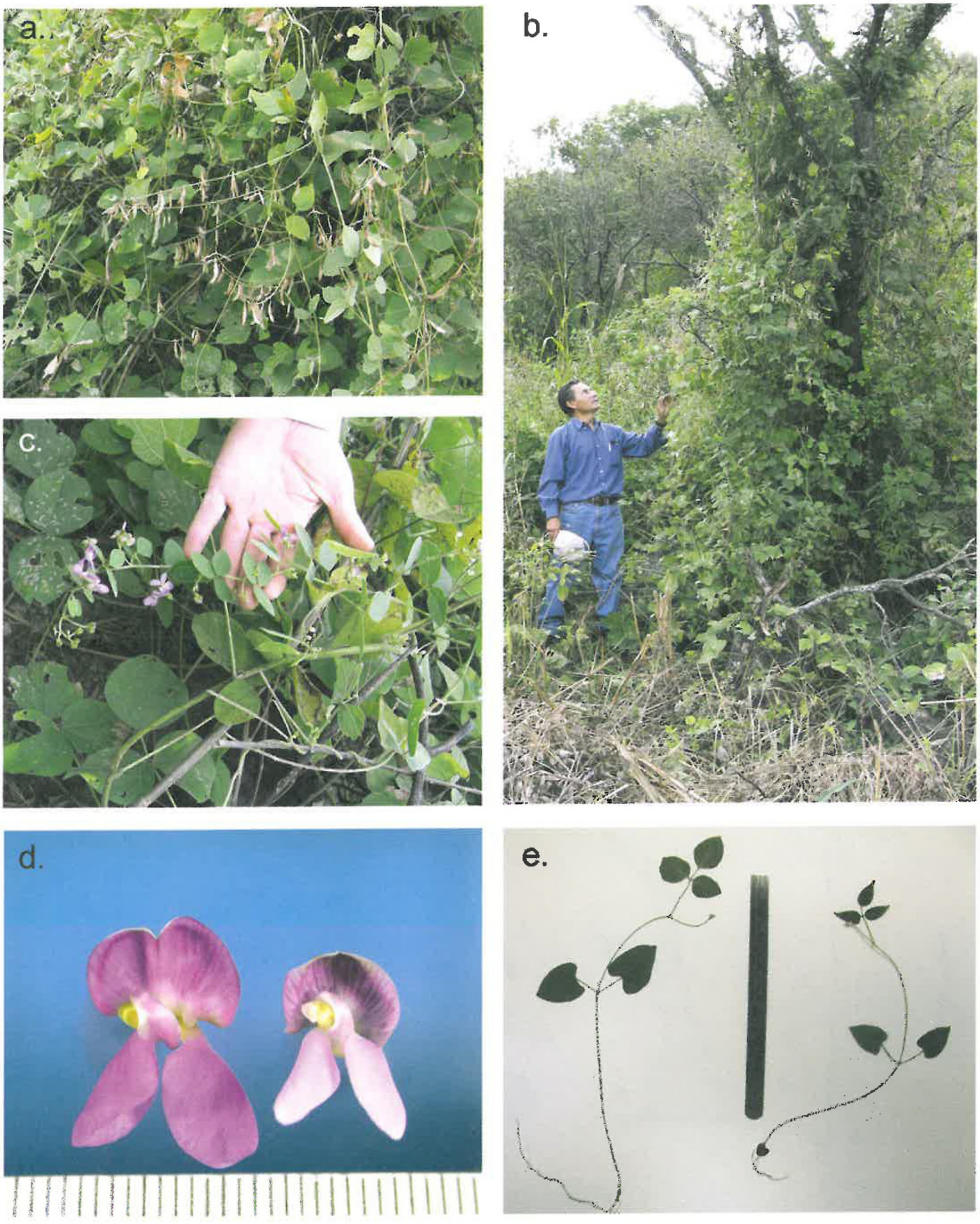

Fig. 2. **a, c.** Fruiting parts of *P. rotundatus*, fully mature and young, respectively. **b.** Fully developed plant at the type locality. **d.** Flowers of *P. rotundatus* (left) and *P. marechalii* (right; same materials as in Fig. 3a and 3b; each grade below is one mm). 2e. seedlings of *P. rotundatus* (left; G40693) and of *P. marechalii* (right; G40506). Steel rule at center: total length 15 cm.

mm long, 8–10 mm wide, 2–4 seeded, flattened, slightly constricted between the seeds; valves glaucous green (144B) drying tan (164B), twisting 1 ½ at dehiscence, the sutures finely thickened, the beak curved downwards 1–2 mm long. **Seed** round ovale oblong 6–8 mm long 5 mm wide 2–3 mm thick (Fig. 3a), 100-seed weight 7–9 g, cream tan background covered by a dense fine black speckle with a black ring around the hilum; hilum irregularly elliptic 1.2 mm long 0.6 mm wide; lens small and slightly raised. **Pollen** (Fig. 4a and 4d) round (polar view), subprolate, tricolporate with 6 pseudocolpi, medium-sized, diameter 25–27 µm, almost spherical; margins surrounding the colpi prominent and smooth 3 µm wide; endoaperture elliptic (longer axis 7 µm); endoaperture membrane smooth, ectoaperture membrane finely punctate; tectum finely punctuate.

Specimens examined: For *P. rotundatus*: [State of] **Jalisco:** [County of] Tepatitlán de Morelos: Río Verde, [Lat. 21°00'07"N. Long. 102°48' 10"W]. 1,200 m, 22 Oct 1978, *R Lépiz s.n.* (additional specimens from the type grown and bred true at CIAT Palmira station, and hereby distributed to BRIT, COL, CS, F, FHO, FI, GH, K, IBUG, IEB, MEXU, MICH, NA, NY, SI, TEX, UC; in addition, small amounts of seeds, accessioned as G40693, can be obtained from the Genetic Resources Program of CIAT).

For *P. marechalii*: **México:** Villa del Carbón, 12 km SE de Villa del Carbón, 19°41'N, 99°25'W, 2520 m, 6 Nov 1987, *DG Debouck & JS Muruaga Martínez 2377* (MICH1179985; US3168490). **Morelos:** Sierra Morelos, Cuernavaca, [19°01'N. 99°15'W], 2000 m, 7 Nov 1969, *Hinton 17462* (K; collected by James Hinton !?); Tepoztlán, 18°59'N, 99°06'W, 1900 m, *Leroi Mex-130* (COL, GH, K, IBUG); in pedregal barranca just below 62 Km marker, which is about 14 km north of Cuernavaca, [19°04'N. 99°15'W], 27 Oct 1947, *OW Norvell HM 215* (UC933928; isotype of *P. glaucocarpus* Norvell sp. nov. ined.); "No d'introduction 402. Faculté des Sciences Agronomiques de l'Etat Gembloux, Chaire de Phytotechnie des Régions Chaudes. Herbier no. 2386. *Phaseolus* sp. Provenance: gr[aines] reçues de M[r] *Schubert*, Morelos *623*, Mexique. [19°02'N. 99°17'W]. Rec: 10/2/1971 serre Gembloux" (K). **Puebla:** Acajete, cerro 4 km NE de Pueblo Acajete, 19°08'N, 97°54'W, 2400 m, 11 Nov 1987, *DG Debouck & JS Muruaga Martínez 2389* (BR; MICH1179986; US3168489).

On the basis of the revision of herbarium specimens mentioned above and the observation of plants grown out side-by-side in the experimental station of CIAT in Palmira, we summarize the main differences between *P. rotundatus* and *P. marechalii* in Table 1.

Ecology

From the two populations known so far (at Río Verde, with a difference in altitude of 200 m), *P. rotundatus* seems distributed in oak grasslands around the upper reaches of the valley of Río Grande de Santiago, while *P. marechalii* thrives in pine-oak forests of the Trans-Mexican Volcanic Belt (Fig. 6).

Electrophoretic evidence and species relationships

A quick survey of seed storage proteins in one-dimension SDS-PAGE electrophoresis, using 15% polyacrylamide slab gels as in Brown et al. (1981) modified by Gepts et al. (1986) (Fig. 5), indicates very similar patterns of banding for *P. rotundatus* (lane 3), *P. marechalii* (lane 4) and *P. jaliscanus* Piper (lane 5). *P. novoleonensis* Debouck (lane 6) of the *Coriacei* section (Salcedo et al. 2006) is then close, although with much less in globulins around 50–52 kD. *P. lunatus* L. (wild Mesoamerican form - lane 2) and *P. glabellus* Piper (lane 7) show almost no globulins in the range of 50–52 kD, but have significant amounts of storage proteins around 35 kD. The section *Phaseoli* is represented by *P. costaricensis* Freytag & Debouck (lane 9) and *P. vulgaris* L. (wild Mesoamerican - lane 10) with a significant amount of phaseolin (50–52 kD), a possible arcelin in wild *P. vulgaris* (35 kD) and a possible lectin-like protein in *P. costaricensis* (24–25 kD). *P. chiapasanus* Piper (lane 8) would have a significant amount of globulin too (50 kD).

DISCUSSION

The data above were collated to show the differences between *P. rotundatus* and *P. marechalii* and are additional to the ones reported elsewhere (Freytag & Debouck 2002). They elicit the following points for discussion. First, *P. rotundatus* is a taller, aggressively climbing vine as compared to *P. marechalii*; plants topping trees 5–6 m high (Fig. 2b) are frequent, thus with stems up to 8–10 m long. Racemes and flowers are larger as compared to those of *P. marechalii* (Fig. 2a, c, and d). Other differences exist in seedlings (Fig. 2e), seeds (Fig. 3a and 3b), and pollen (Fig. 4a,d and 4b,c). Terminal leaflets of fully developed leaves are 67 × 62 mm in *P. rotundatus*, while 50 × 32 mm in *P. marechalii*.

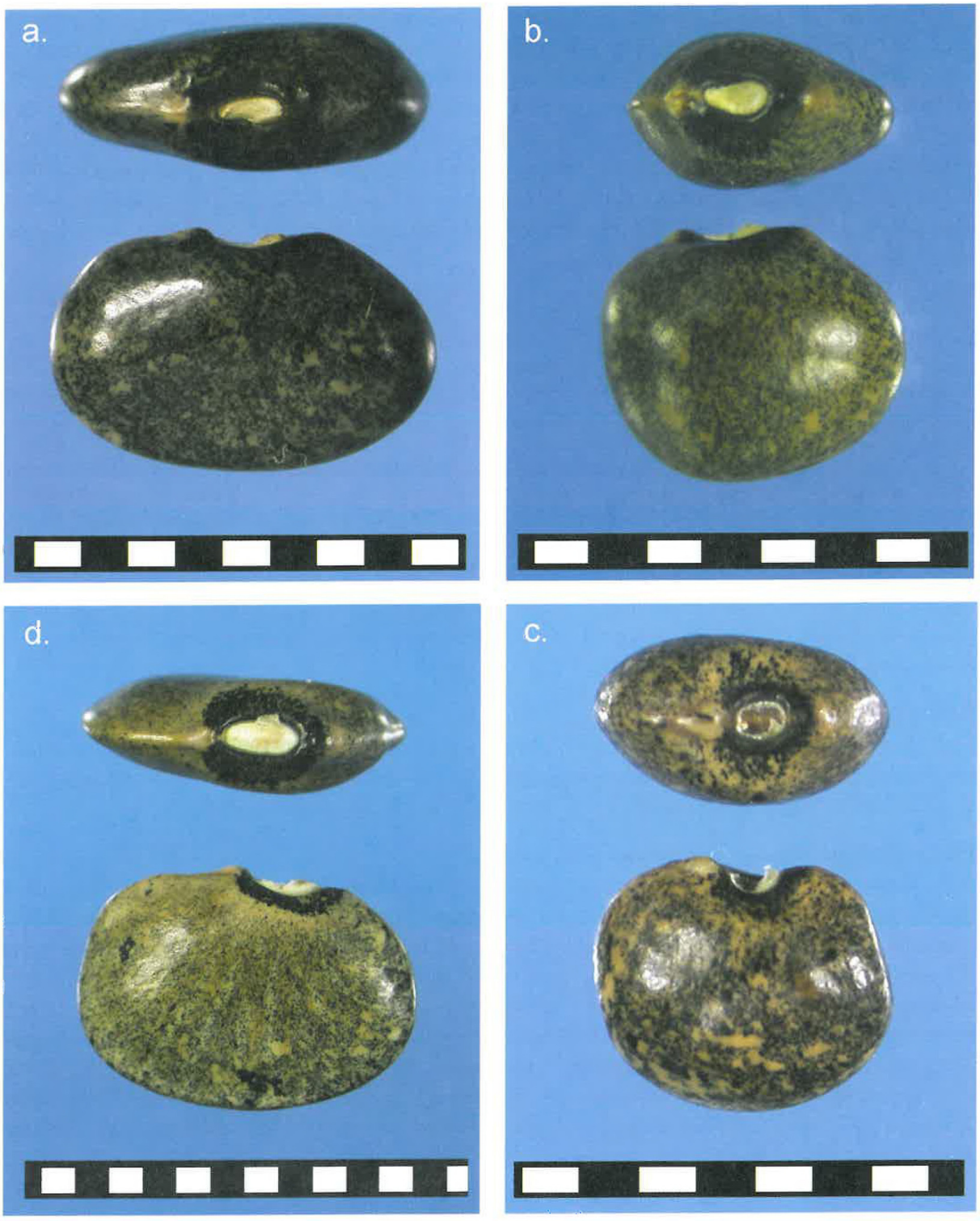

Fig. 3. Close-ups of seeds in lateral views and views from hilum (clockwise) of: **a.** *P. rotundatus* (*Lépiz s.n.*; G40693) from type collection site. **b.** *P. marechalii* (*Bernice Schubert 623*; G40506; NI 402) from surroundings of Huitzilac, Morelos, Mexico. **c.** *P. polystachyus* (*M Bassett s.n.*; G40783) from surroundings of Gainesville, Alachua County, Florida, USA. **d.** *P. lunatus* (*DGD-527*; G25741) from Chunhuas, Hecelchakan, Campeche, Mexico. The scale bar is one mm for each division, and may change slightly from one shooting to another.

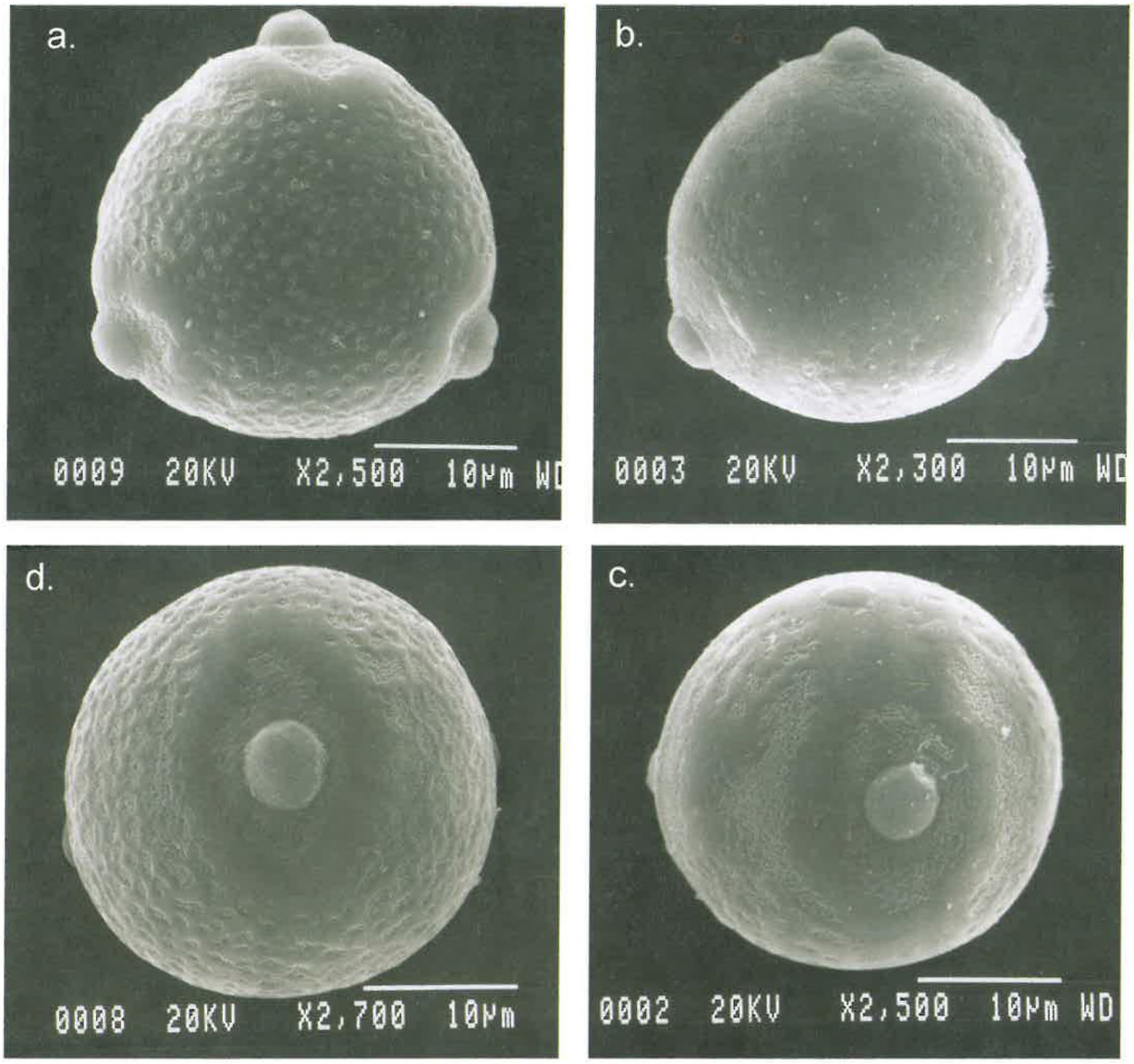

Fig. 4. Pollen types of *P. rotundatus* (left, 4a and 4d) and *P. marechalii* (right, 4b and 4c). Polar (4a, 4b) and equatorial (4c, 4d) views. Scale bar: 10 microns.

Table 1. Summary of the main differences between *P. rotundatus* and *P. marechalii*.

Trait	P. rotundatus	P. marechalii
Seedling	Larger eophylls (30 x 25 mm); leaflets of 1st true leaf bluntly acuminate	Smaller eophylls (22 x 15 mm); leaflets of 1st true leaf acuminate
Plant	Stout and robust climbing vine, usually more than 4 m high	Stout climbing vine, usually less than 3 m high
Leaves	Large 13–18 cm long, leaflets rhombic rounded	Small 7–11 cm long, leaflets ovate acuminate
Racemes	Large panicles, more than 20 cm long	Small panicles, less than 20 cm long
Inner standard	Veining diffuse	Clearly vertically veined
Seed	Ovale flattened	Round ovoid thicker
Habitat	Oak savannahs of N-NE Jalisco, Mexico	Pine-oak forests of Trans-Mexican Volcanic Belt, central Mexico

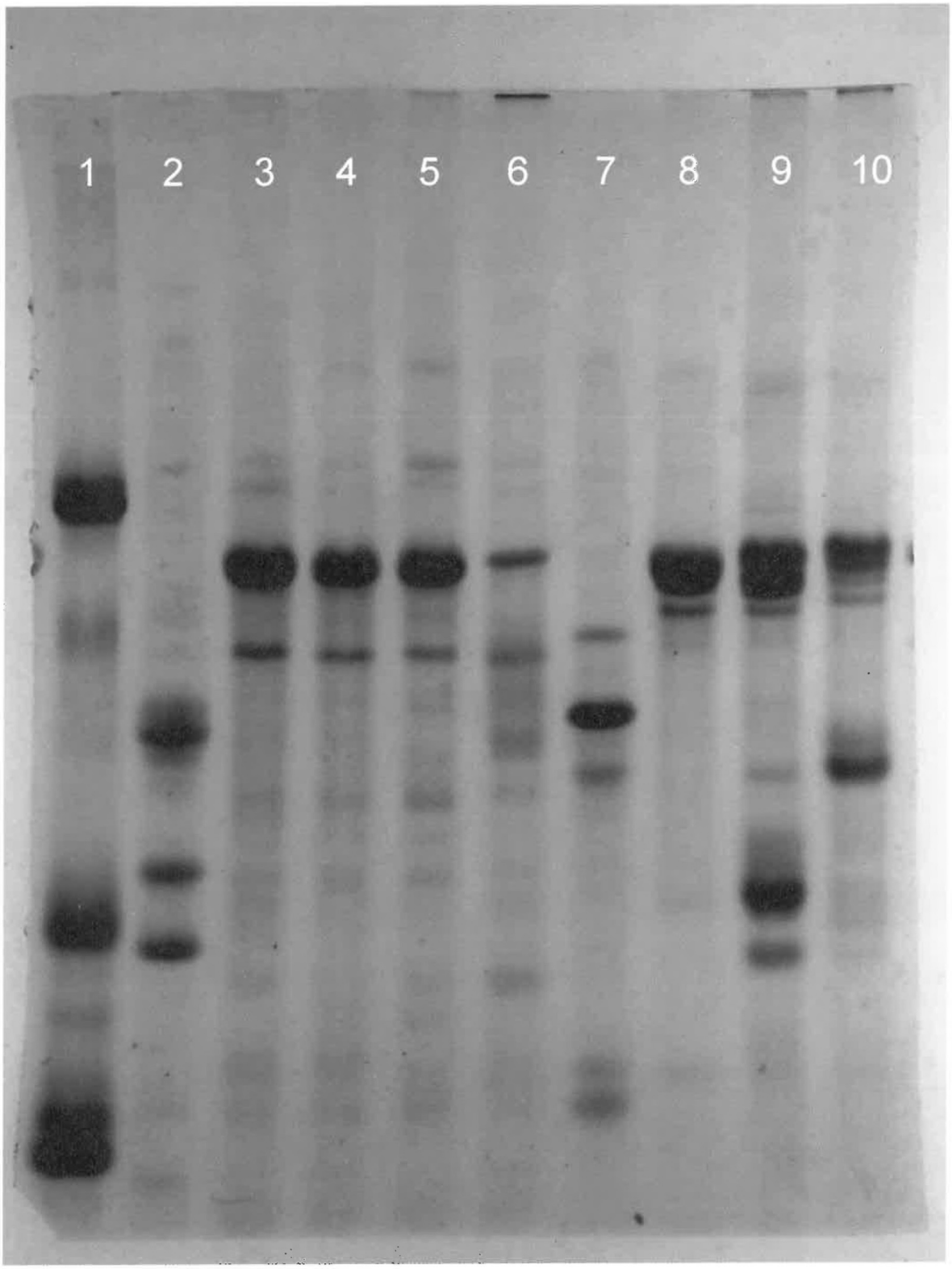

Fig. 5. One dimensional SDS-PAGE gel of *Phaseolus rotundatus* and selected taxa. **Lane 1:** molecular weights in kiloDaltons (range 14.3 lower band to 66 upper band). **Lane 2:** *P. lunatus* wild (*DGD-453* from Jalisco, Mexico; G25704). **Lane 3:** *P. rotundatus* (*Lépiz s.n.* from Jalisco, Mexico; G40728). **Lane 4:** *P. marechalii* (*B Schubert 623*; G40506). **Lane 5:** *P. jaliscanus* (*R Buhrow M21* from Jalisco, Mexico; PI 535313). **Lane 6:** *P. novoleonensis* (*DGD-2061* from Nuevo León, Mexico; G40590). **Lane 7:** *P. glabellus* (*DGD-2043* from San Luís Potosí, Mexico; G40585). **Lane 8:** *P. chiapasanus* (*J Muruaga Martínez 4005* from Oaxaca, Mexico; G40676). **Lane 9:** *P. costaricensis* (*DGD-2119* from Cartago, Costa Rica; G40604). **Lane 10:** *P. vulgaris* wild (*HSG-22202* from Jalisco, Mexico; G12866).

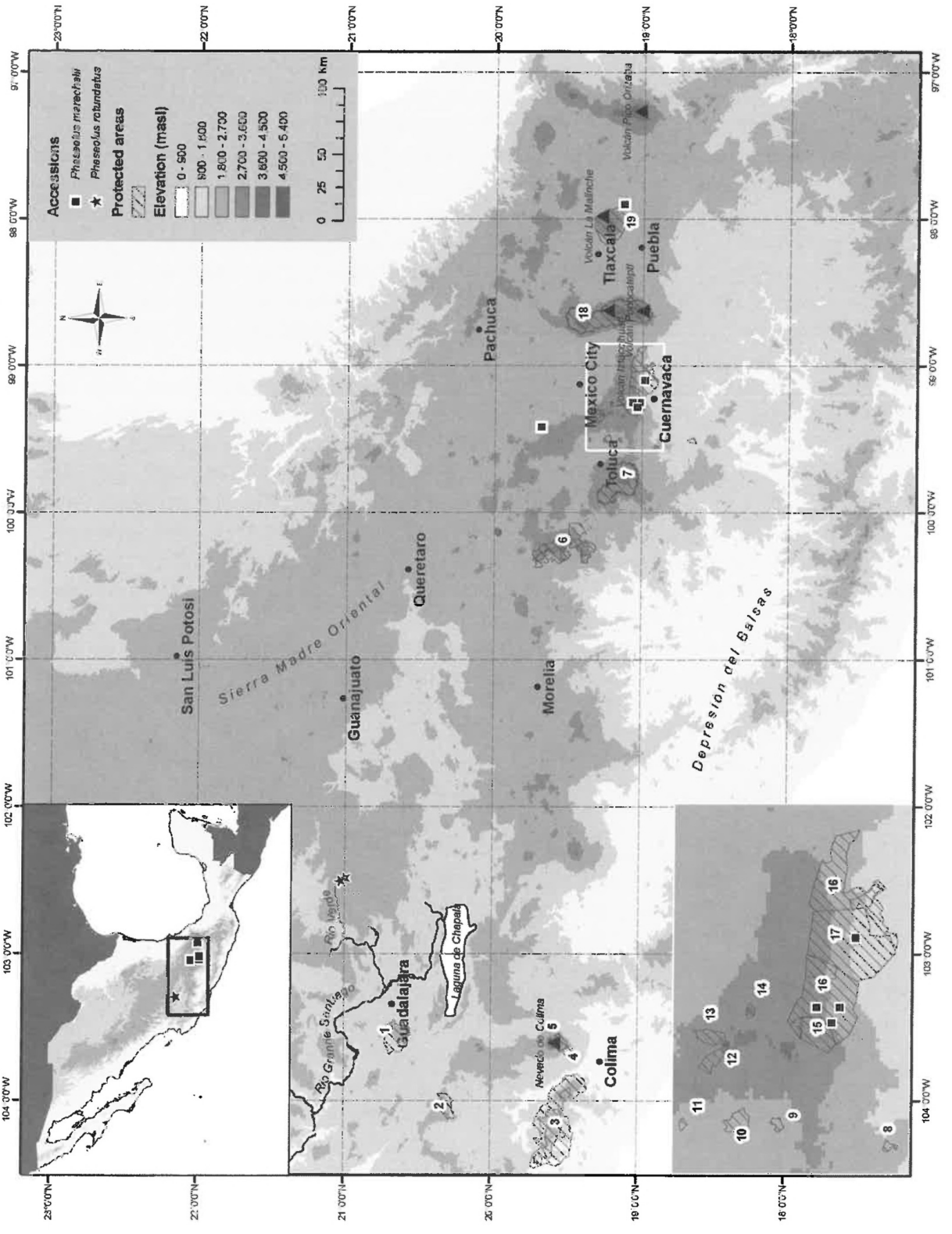

Fig. 6. Distribution map of populations of *Phaseolus rotundatus* (stars white outlined) and *P. marechalii* (solid squares white outlined) in western and central Mexico. 1 = Wildlife refuge "La Primavera"; 2 = Wildlife refuge "Sierra de Quila"; 3 = Biosphere reserve "Sierra de Manantlán"; 4 = Wildlife refuge "El Jabalí"; 5 = National park "Nevado de Colima"; 6 = Biosphere reserve "Mariposa Monarca"; 7 = National park "Nevado de Toluca"; 8 = National park "Desierto del Carmen"; 9, 10, 11 = Wildlife refuge "Cienagas de Lerma"; 12 = National park "Insurgente Manuel Hidalgo y Costilla"; 13 = National park "Desierto de Los Leones"; 14 = National park "Cumbres del Ajusco"; 15 = National park "Lagunas de Zempoala"; 16 = Wildlife refuge "Chichinautzin"; 17 = National park "El Tepozteco"; 18 = National park "Iztaccihuatl-Popocatepetl"; 19 = National park "La Malinche".

Second, *P. rotundatus* seems to be known from only one locality to date, distributed on the upper slopes of the high valley of Río Grande de Santiago and possibly surrounding mountains or volcanoes. Study of over fifty herbaria holding specimens of the section *Paniculati* (Debouck 2009) has not revealed additional populations. Delgado (2000) reported a distribution around the Mexican state of Morelos for *P. marechalii*; from the novel records it is still a rare species as he indicated, restricted to the Trans-Mexican Volcanic Belt. Both species were not reported in "Flora Novo-Galiciana" (McVaugh 1987), perhaps another indication of their scarcity in and around Jalisco. A hypothesis worth further testing is that *P. rotundatus* had a wider distribution in the past than at present, namely in the valley of Guadalajara, before encroachment by agriculture and urbanization. The putative reduction in its distribution could be attributed to its plant type: it is a perennial vine reaching considerable development, and unlikely to survive under intense grazing pressure, plowing and fire, all characteristic of post-Columbian land use practices in central Jalisco. Today it only survives where humans, cattle and goats have no access, although places with little deep soil like cliffs are not its primary habitat.

Currently, as it can be judged from few sources (Toledo & Ordoñez 1993; Castilleja et al. 1996; Toledo et al. 1997), few populations of *P. marechalii* and none of *P. rotundatus* are included in protected areas. However, it would still be timely to include some populations of these two species into protection schemes, by slightly expanding current protected areas (for example, to the east the National Park 'La Malinche', or to the north west the National Park 'El Tepozteco'), or creating an area S of Río Verde bridge for *P. rotundatus* (where the slopes of road sides of federal road Mex 25 are a wasteland anyway). An additional justification for further *in situ* conservation efforts stems from the fact that the upper Santiago watershed might be involved in the domestication of common bean (Chacón et al. 2005; Kwak et al. 2009), because of the presence of wild forms (our germplasm collections of 1978; Zizumbo et al. 2009).

On the other hand, the unicate specimen collected by Howard Scott Gentry (*HS Gentry 22509*) in Telixtlahuaca, Oaxaca, Mexico, and kept at the US National Arboretum (NA0027957) has been identified by GF Freytag on July 26, 1989, as *Phaseolus subrotundatus* Freytag & Debouck (ined.). We have seen this specimen on July 18, 2006, and can discard this identification because this specimen has two short racemes (12 and 9 cm) with 5–6 primary bracts and the leaflets are almost glabrous. This means that there would be no disjunct distribution for *P. rotundatus* between Jalisco and Oaxaca, of limited distribution in the upper valley of Río Grande de Santiago in Jalisco, and that *HS Gentry 22509* belongs to another taxon.

Third, on the basis of electrophoretic evidence of seed storage proteins, *P. rotundatus* seems to share phylogenetic affinities with species such as *P. marechalii, P. jaliscanus*, perhaps even with *P. novoleonensis*. Since Lima bean (lane 2) is the type species of the section *Paniculati* (Freytag & Debouck 2002), one would expect more similarities with other members of *Paniculati* (viz. *P. rotundatus, P. marechalii, P. jaliscanus*). This result confirms those of a study on an intergenic section of cpDNA using PCR-RFLP (Fofana et al. 1999), where *P. rotundatus* (= NI 1046) is shown to be close to *P. ritensis* Jones and *P. reticulatus* Freytag & Debouck (= NI 702), both of which are related to *P. marechalii*. Preliminary results of ITS sequencing (Gaitán et al. 2000) indicated a close proximity between *P. rotundatus* and *P. jaliscanus* and *P. acinaciformis* Freytag & Debouck. In a combined analysis of the nuclear ribosomal DNA ITS region and of the chloroplast DNA intron *trnK*, Delgado et al. (2006) have shown the close phylogenetic proximity between the *Paniculati* and the *Coriacei*.

As recognized by Freytag and Debouck (2002) and Delgado et al. (2006), the *Paniculati* seems to be the section of the genus with the largest number of species, and thus is of special interest to breeders of Lima bean given the possibilities for wide crossing (Baudoin 1990). The base for further progress lies first in the proper botanical identification of this biological asset and its conservation. From the review of the *Paniculati* carried out so far, clearly not all taxonomical problems are solved, but we hope to have herein advanced one step further for one of them, *P. rotundatus*.

ACKNOWLEDGMENTS

This work initiated in the fall of 1978 has been made possible thanks to generous grants from CIAT, INIA of Mexico, the University of Guadalajara (the latter for continuing field work in western Mexico), BMZ of Germany, and the World Bank for the visit of one of us to the U.S. National Arboretum. The continuing help of Orlando Toro for keeping track of all data and specimens over years has been immensely valuable to our research. The help of José Alejandro Arroyave and Camilo Oliveros for the scanning electron micrographs and the setting of the figures, respectively, is particularly appreciated. The authors desire to warmly thank Dr George Freytag for his continuing support and interest during all these years of additional observations on the poorly known bean species. The comments made by the Reviewers were particularly appreciated. One of us (DGD) would like to express his deepest gratitude to the Curators of the following herbaria (that keep specimens of section *Paniculati*; see Debouck 2009): A, AGUAT, AHUC, BAA, BAFC, BM, BR, BRIT, CAS, CHAPA, CICY, COL, CORD, CPUN, CR, CUZ, DAV, DES, DS, EBUM, ENCB, F, FI, G, GH, HAO, HNMN, HUT, IBUG, IEB, INB, K, L, LL, LIL, LPB, M, MA, MEXU, MICH, MO, MOL, MSC, NA, NEBC, NY, O, OXF, P, PH, PRG, QCA, SI, TEX, UC, US, USJ, USM, WIS, who allowed him to study their collections 'in situ'.

REFERENCES

Anonymous. 1966. Royal Horticultural Society Colour Chart. The Royal Horticultural Society, London. Fans 2, 3, and 4.

Baudoin, J.P. 1990. L'amélioration de *Phaseolus lunatus* L. en zones tropicales. 6. Réservoirs génétiques, travaux de sélection, conclusions et perspectives. Bull. Rech. Agron. Gembloux 25:395–442.

Brown, J.W.S., Y. Ma, F.A. Bliss, and T.C. Hall. 1981. Genetic variation in the subunits of globulin-1 storage protein of French bean. Theor. Appl. Genet. 59:83–88.

Castilleja, G., D. Evans, and S. Eggen-McIntosh. 1996. Mexico. In: C.S. Harcourt and J.A. Sayer, eds. The conservation atlas of tropical forests. The Americas. International Union for Conservation of Nature and Natural Resources, Simon & Schuster, New York, New York, USA. Pp. 193–205.

Chacón, M.I., B. Pickersgill, and D.G. Debouck. 2005. Domestication patterns in common bean (*Phaseolus vulgaris* L.) and the origin of the Mesoamerica and Andean cultivated races. Theor. Appl. Genet. 110:432–444.

Debouck, D.G. 1983. Observations sur les processus de floraison et de ramification chez quelques *Phaseolus*. Comp. Rend. Séances Acad. Sci., Sér. 3, Sci. Vie 296:425–428.

Debouck, D.G. 2009. Cahiers de phaséologie: section *Paniculati*. International Center for Tropical Agriculture (CIAT), Cali, Colombia. Accessed on line on 7 April 2009 at http://www.ciat.cgiar.org/urg. 261p.

Delgado Salinas, A.O. 2000. New Species of Mexican *Phaseolus* (Fabaceae). Syst. Bot. 25:414–436.

Delgado Salinas, A., R. Bibler, and M. Lavin. 2006. Phylogeny of the genus *Phaseolus* (Leguminosae): a recent diversification in an ancient landscape. Syst. Bot. 31:779–791.

Fofana B., JP Baudoin, X Vekemans, DG Debouck, and P. du Jardin. 1999. Molecular evidence for an Andean origin and a secondary gene pool for the Lima bean (*Phaseolus lunatus* L.) using chloroplast DNA. Theor. Appl. Genet. 98:202–212.

Freytag G.F. and D.G. Debouck. 2002. Taxonomy, distribution, and ecology of the genus *Phaseolus* (Leguminosae-Papilionoideae) in North America, Mexico and Central America. Sida Bot. Misc. 23:1–300.

Gaitán, E., O. Toro, J. Tohme, and D.G. Debouck. 2000. Molecular taxonomy of the genus *Phaseolus* through ITS sequencing. Annual report. Centro Internacional de Agricultura Tropical, Cali, Colombia. Pp. 56–60.

Gepts, P., T.C. Osborn, K. Rashka, and F.A. Bliss. 1986. Phaseolin protein variability in wild forms and landraces of the common bean (*Phaseolus vulgaris* L.): evidence for multiple centers of domestication. Econ. Bot. 40:451–468.

Kwak, M., J.A. Kami, and P. Gepts. 2009. The putative Mesoamerican domestication center of *Phaseolus vulgaris* is located in the Lerma-Santiago basin of Mexico. Crop Sci. 49:554–563.

Maréchal, R., J. Mascherpa, and F. Stainier. 1978. Etude taxonomique d'un groupe complexe d'espèces des genres

Phaseolus et *Vigna* (Papilionaceae) sur la base de données morphologiques et polliniques, traitées par l'analyse informatique. Boissiera 28:1–273.

McVaugh, R. 1987. Flora Novo-Galiciana—A descriptive account of the vascular plants of western Mexico—Volume 5 Leguminosae. The University of Michigan Press, Ann Arbor, Michigan, U.S.A.

Salcedo, J., J.A. Arroyave, O. Toro, and D.G. Debouck. 2006. *Phaseolus novoleonensis*, a new species (Leguminosae, Phaseolinae) from the Sierra Madre Oriental, Nuevo León, Mexico. Novon 16:105–111.

Toledo, V.M. and M.J. Ordoñez. 1993. The biodiversity scenario of Mexico: a review of terrestrial habitats. In: T.P. Ramamoorthy, R. Bye, A. Lot, and J. Fa, eds. Biological diversity of Mexico: origins and distribution. Oxford University Press, New York, New York, U.S.A. Pp. 757–777.

Toledo, V.M., J. Rzedowski, and J. Villa-Lobos. 1997. Regional overview: Middle America, Mexico. In: S.D. Davis, V.H. Heywood, O. Herrera-Macbryde, J. Villa-Lobos, and A.C. Hamilton, eds. Centres of plant diversity—A guide and strategy for their conservation, vol. 3 The Americas. World Wide Fund for Nature and International Union for Conservation of Nature and Natural Resources, Cambridge, United Kingdom. Pp. 97–107.

Zizumbo, D., R. Papa, M. Hufford, S. Repinski, and P. Gepts. 2009. Identification of new wild populations of *Phaseolus vulgaris* in western Jalisco, Mexico, near the Mesoamerican domestication center of common bean. Ann. Rept. Bean Improv. Coop. (U.S.A.) 52:24–25.