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Systematics of *Vigna* subgenus *Lasiospron* (Leguminosae: Papilionoideae: Phaseolinae)

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Abstract—A taxonomic treatment is herein provided for the six primarily Neotropical species of *Vigna* subg. *Lasiospron*. This subgenus is distinguished, in part, by its close relationship with Old World *Vigna* species, but rather than having an Old World *Vigna* floral asymmetry where distal floral parts can have a right-hand curvature (from a face-view perspective), distal parts of *Vigna* subg. *Lasiospron* flowers, like those of American Phaseolinae, curve to the left. Our proposed taxonomy reflects published phylogenetic analyses that resolve the *Vigna* subg. *Lasiospron* species in a subclade of the primarily Old World clade of species of *Vigna* sensu stricto. *Vigna* subg. *Lasiospron* is therefore distinctive in having a primarily neotropical distribution. Three of the six *Vigna* subg. *Lasiospron* species have an amphi-Atlantic distribution, which we suggest was achieved naturally by the ability of these species to disperse and colonize coastal habitats. Nomenclatural and taxonomic synonyms are reported, along with species descriptions and the biogeographical, genetic, and morphological evidence that argues for each of the six *Vigna* subg. *Lasiospron* species fitting a unified species concept.

Keywords—Biogeography, Fabaceae, legumes, Madagascar, Neotropics, Paleotropical Africa, phylogenetic taxonomy, riparian, wetlands.

Previous taxonomic studies and recent phylogenetic analyses of molecular and non-molecular data suggest that the economically important genus *Vigna* Savi now comprises approximately 80 mostly Paleotropical species nested within the Phaseolinae clade (Delgado-Salinas et al. 2011). This clade of mostly Paleotropical species of *Vigna*, plus the genus *Physostigma* Balf., is sister to a clade of New World Phaseolinae genera, which includes genera recently segregated from *Vigna* sensu stricto: *Ancistrotropis* A.Delgado, *Cochliasanthus* Trew, *Condylostylis* Piper, *Helicotropis* A.Delgado, *Leptospron* (Benth.) A.Delgado, and *Sigmoidotropis* (Piper) A.Delgado (Delgado-Salinas et al. 2011). The mostly Old World *Vigna* clade includes species of *Vigna* subgenera *Ceratrotropis* (Piper) Verdc., *Haydonia* (R.Wilczek) Verdc., and *Plectrotropis* (Schumach.) Bak., as well as the mostly New World species of *V.* subg. *Lasiospron* (Benth.) Maréchal, Mascherpa & Stainier, the latter resolved as a well-supported early branching clade (Thulin et al. 2004; Delgado-Salinas et al. 2011).

We herein present a taxonomic treatment on the species of *Vigna* subg. *Lasiospron*, which are morphologically distinct from all other *Vigna* species, as well as from species of New World *Phaseolinae* genera, in sharing deeply emarginate standards, wing petals embracing the keel all with an left-hand curvature (as viewed face-on), and fruits becoming resupinate by the torsion of the pedicels. According to Delgado-Salinas et al. (2011), *V.* subg. *Lasiospron* is monophyletic and comprises six species that form the basis of our taxonomic account. These six are *Vigna diffusa* (Scott Elliott) A. Delgado & Verdc., *V. juruana* (Harms) Verdc., *V. lasiocarpa* (Mart. ex Benth.) Verdc., *V. longifolia* (Benth.) Verdc., *V. schottii* (Benth.) A.Delgado & Verdc., and *V. trichocarpa* (C.Wright) A.Delgado.

MATERIALS AND METHODS

Taxonomic Study Group—Delgado-Salinas et al. (2011) report the materials and methods from which stems this taxonomic account of *Vigna* subg. *Lasiospron*. These include visits to and loans of herbarium specimens from BH, BM, BR, CAS, CHAPA, F, FLAS, G, GH, K, LJ, M, MEXU, MONT, NY, OXF, P, PHILA, RB, RBGE, SI, TEX-LL, US, VEN, and WU (herbarium acronyms follow Thiers 2020). The bibliographic citations in the original publications and databases such as IPNI (The International Plant Names Index; http://ipni.org/), TROPICOS (http://www.tropicos.org/), and The Plant List (http://www.theplantlist.org/) were consulted. Flowers in the microscope slide collection of Bernard Verdcourt at Kew were consulted and, when appropriate, measurements of corolla structures were usually made on rehydrated flowers under a dissecting microscope. Some other structures, including pollen, were examined using scanning electron microscopy (SEM), with the assistance of the Micromorphology Group of the Jodrell Laboratory, Royal Botanic Gardens, Kew.

Our taxonomic focus derives from the phylogenetic results of Delgado-Salinas et al. (2011), which resolved the six species of *V.* subg. *Lasiospron* as an early branching subclade of the Old World *Vigna* clade (*Vigna* sensu stricto in Delgado-Salinas et al. 2011). In contrast to the more comprehensive study of Delgado-Salinas et al. (2011), the focus here is primarily on the species of *V.* subg. *Lasiospron* species and the coalescence of conspecific samples of this clade. We reanalyzed only the ITS sequence data because these data are sampled for multiple conspecific accessions of *V.* subg. *Lasiospron* species and because we have corrected some misidentifications since Delgado-Salinas et al. (2011). Ultimately, we wanted to demonstrate how genetic data covary with geographical and morphological variation to bolster our species delimitations in *V.* subg. *Lasiospron*. All data have been submitted to Dryad (Delgado-Salinas et al. 2022) and updated in GenBank.

Taxon Sampling—We reanalyzed 160 ITS accessions representing the 67 species of the *Vigna* sensu lato clade resolved by Delgado-Salinas et al. (2011). This clade comprises the African genus *Physostigma* and the mostly African and Asian species of *Vigna* sensu stricto. The latter includes the focal subclade of this analysis, *Vigna* subg. *Lasiospron*, the American *Vigna*. The *Vigna* sensu stricto clade and *Physostigma* form the sister clade to the American Phaseolinae (*Ancistrotropis, Cochliasanthus, Condylostylis, Dolichopsis, Helicotropis, Leptospron, Macroptilium, Mysanthus, Phaseolus, Oxyrhynchus, Ramirezella, Sigmoidotropis,* and *Strophostyles*; Delgado-Salinas et al. 2011). We included conspecific samples of species from these genera to test the delimitation of species of *Vigna* subg. *Lasiospron* and compare patterns of coalescing conspecific genetic samples within *V.* subg. *Lasiospron* with such patterns in other subclades of *Vigna* sensu lato.

Phylogenetic Analysis—We conducted a Bayesian phylogenetic analysis of an ITS sequence data set from Delgado-Salinas et al. (2011) using BEAST 2.6.2 (Bouckaert et al. 2019). We did not redo the analysis of the chloroplast locus *trnK/matK* because those data do not include multiple conspecific accessions of *Vigna* subg. *Lasiospron* species (Delgado-Salinas

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et al. 2011) and because such studies as Raveenadar et al. (2018) find ITS sequence data to be significantly more informative at the species level in the genus *Vigna* than any of the commonly used cpDNA loci. The Bayesian analysis included partitioning the ITS region into three subregions (i.e. the internal transcribed spacer 1, the 5.8S locus, and the internal transcribed spacer). The nucleotide substitution model involved model averaging using bModelTest (Bouckaert and Drummond 2017) or using the general time reversible nucleotide substitution model, as in Delgado-Salinas et al. (2011).

Multiple MCMC chains each included 100 M generations sampled every 90 K generations such that a 10% burn-in yielded 1000 sample points at likelihood stationarity. Using Tracer (Rambaut et al. 2018), we inspected likelihood scores simultaneously from multiple Bayesian runs, which invoked the same or differing combinations of settings (e.g. one versus three ITS data partitions, bModelTest versus general time reversible site models, and birth-death versus Yule tree models). In this manner we verified that all Bayesian runs achieved likelihood stationarity and determined the effect on the results of invoking different combinations of site and tree models.

The main tree prior included the root of *Vigna* sensu lato (the entire data set) with an age constraint set as a normally distributed density calibration of 8.0 ± 0.8 Ma (Lavin et al. 2005) rather than 9.1 ± 1.0 Ma (Delgado-Salinas et al. 2011). This is because we wanted to bias ages toward conservative (minimum) estimates. With the root age so constrained, we made age estimates for the stem clades of *Vigna* sensu stricto plus *Physostigma*, the American Phaseolinae, all genera of the American Phaseolinae, and all the main subclades of *Vigna* sensu stricto including *V.* subg. *Lasiospron*.

Abiotic Variables—We wanted to climatically circumscribe the lowland wet tropical environments of *Vigna* subg. *Lasiospron* species, so we georeferenced a total of 427 herbarium collections of *V.* subg. *Lasiospron* (Supplemental Information, Delgado-Salinas et al. 2022). From the latitude and longitude of each collection, monthly precipitation, and minimum and maximum temperatures were extracted from the WorldClim v. 2.0 model layers (WGS84 projection; Fick and Hijmans 2017) using the R library raster (Hijmans et al. 2020). Bioclimatic variables (O'Donnell and Ignizio 2012) were derived from these climate models using the biovars function in the raster library. We extracted elevation data from STRM altitude models (Jarvis et al. 2008) using resampled data with spatial resolution of approximately 250 m on the line of the equator. A principal components analysis and generation of biplots were performed on all climate data in order to detect the orthogonal climate variables that showed the greatest amount of variation among the *V.* subg. *Lasiospron* sample sites.

Results

Phylogenetic Analysis—Likelihood stationarity was readily achieved with MCMC chains run for 100 M generations, including when such runs involved different combinations of site and tree models (Fig. S1, Delgado-Salinas et al. 2022). *Vigna* subg. *Lasiospron* and multiple conspecific accessions of five of the six constituent species were each resolved as monophyletic (Fig. 1). Samples of *V. diffusa* did not yield amplifiable DNA. *Vigna* subg. *Lasiospron* was resolved as sister to the rest of the *Vigna* sensu stricto (Fig. 1). The *Vigna* sensu stricto plus *Physostigma* clade was resolved as sister to the American Phaseolinae clade (Figs. 1–2). Mean age estimates of the stem clades representing genera and subgenera range from about 4–5 Ma for *Vigna* subgenera *Ceratotropis* and *Lasiospron* (Fig. 1) to about 2–3 Ma for many of the American Phaseolinae genera (Fig. 2).

Each of the five *Vigna* subg. *Lasiospron* species represented by multiple conspecific accessions resolved as well-supported coalescent clades with stem clade age estimates ranging from about 1.7 Ma for *V. trichocarpa* to about 1.0 Ma for *Vigna juruana* and *V. schottii* (Fig. 1). Coalescing conspecific ITS samples with similar to slightly older stem clade age estimates occur elsewhere in the *Vigna* sensu lato clade; for example, *Vigna aconitifolia* and *V. umbellata* of *Vigna* subg. *Ceratotropis*, *Vigna luteola*, and *Vigna unguiculata* (Fig. 1). Stem age estimates of American Phaseolinae species represented by coalescing

conspecific samples tend to average less than 1 Ma in age (Fig. 2). Regardless, coalescing conspecific samples may not be the rule in Phaseolinae. The American Phaseolinae genera *Ancistrotropis*, *Helicotropis*, *Leptospron*, *Macroptilium*, and *Sigmoidotropis* are sufficiently sampled to resolve conspecific ITS samples as paraphyletic (Fig. 2). Age estimates did not differ significantly with respect to site and tree model combinations, except that invoking the Yule tree model resulted in older age estimates (Fig. S2, Delgado-Salinas et al. 2022).

Age estimates derive from nucleotide substitution models sampled at likelihood stationarity, which using bModelTest included mostly variants of the Tamura-Nei 93 (TN93) model with four substitution parameters. These models account for the difference between transitions and transversions, two kinds of transitions ($C \leftrightarrow T$ more frequent than $A \leftrightarrow G$), and two kinds of transversions (purine $\leftrightarrow$ pyrimidine). Mean estimates for the gamma shape parameter for among site rate heterogeneity were lowest for the 5.8S regions (< 0.30), highest for ITS1 (> 2.0), and intermediate for ITS 2 (1.0–2.0). Overall mean estimates of nucleotide substitution rates were about 5.5×10^{-8} substitutions per site per year with the bModelTest site model, the birth-death tree model, and three ITS partitions. Substituting in either the general time reversible site model, the Yule tree model, or not partitioning the ITS region resulted in slower substitution rate estimates (and thus generally older age estimates). For example, using either the general time reversible site model or the Yule tree model resulted in mean substitution rate estimates around 4.2×10^{-8} substitutions per site per year (Fig. S1).

Biogeography—*Vigna* subg. *Lasiospron* species are distributed latitudinally as three pairs. One member of each pair is strictly neotropical and the other neotropical and tropical African or Madagascan. *Vigna lasiocarpa* and *V. trichocarpa* average the most northern latitude of the three pairs and center on Mesoamerica, the Greater Antilles, and northern South America with *V. trichocarpa* extending across the Atlantic to coastal tropical West Africa (Fig. 3, top panel). *Vigna juruana* and *V. longifolia* center on northern tropical South America with *V. juruana* extending across the Atlantic to west Central Africa (Fig. 3, middle panel). *Vigna schottii* and *V. diffusa* average the most southern latitude with most collections coming from southern Brazil, Uruguay, Paraguay, and northern Argentina, and with *V. diffusa* extending across the Atlantic to Madagascar (Fig. 3, bottom panel). Notably, none of these pairs represent sister species (Fig. 1). Generally, interspecific relationships are not well supported among the *V.* subg. *Lasiospron* species with the exception of *Vigna juruana* and *V. schottii* (Fig. 1). The most northerly species, *V. trichocarpa* (Fig. 3), possibly represents the sister clade to the rest of *V.* subg. *Lasiospron* species (Fig. 1), but this relationship is tentative given that it is weakly supported (Fig. 1) and that *Vigna diffusa* has yet to be sampled for ITS sequence variation.

The ecological predilection of all *Vigna* subg. *Lasiospron* species to the edges of tropical wet forests along riparian corridors or to coastal environments suggests the evolution of the Lasiospron clade has been phylogenetically niche conserved to such lowland tropical wet settings. The early branching *V. trichocarpa* samples (Fig. 1) come from the Amazon River basin, northern and southern Restinga Atlantic Forest, and Paraguay-Paraná fluvial system. The similarly early branching clade of *V. longifolia* accessions come from the Amazon River basin, northern Restinga Atlantic Forest in Brazil, and the Paraguay-Paraná fluvial system. The clade
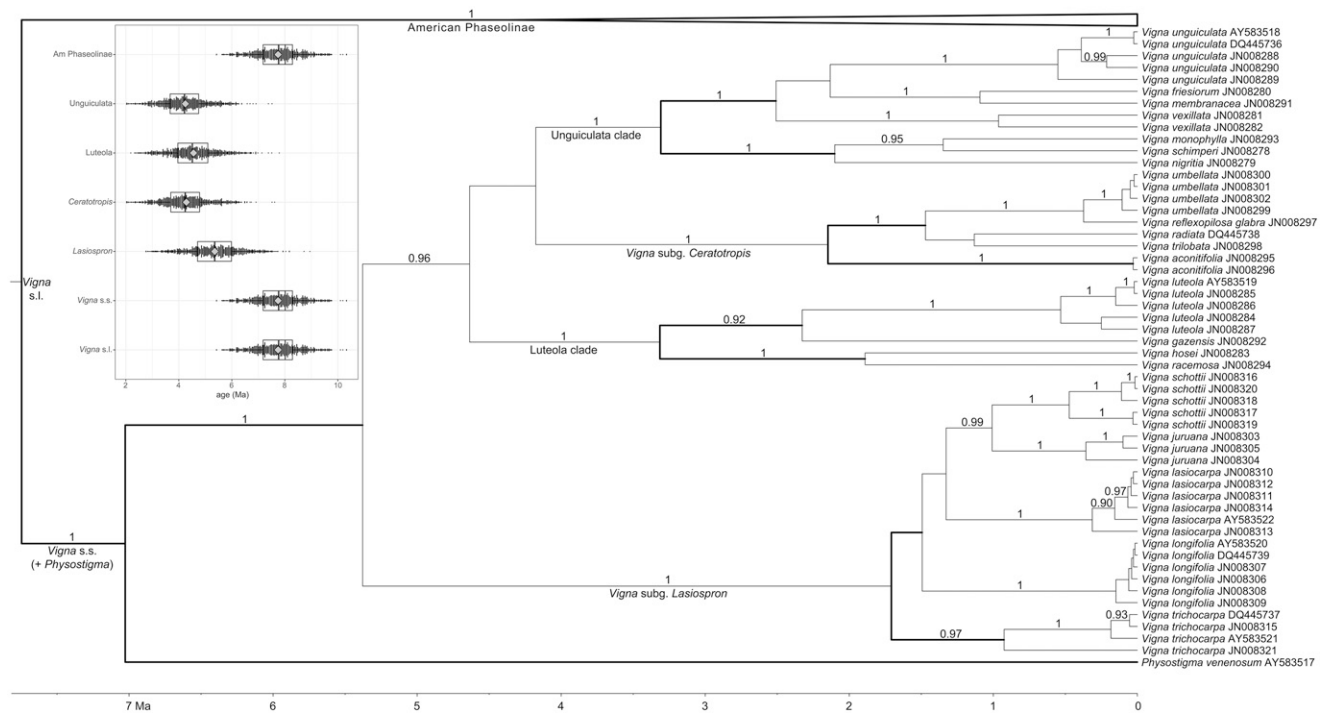
Fig. 1. ITS phylogeny derived from a BEAST2 analysis of *Vigna* sensu lato (s. l.) featuring the subclade with *Physostigma* and *Vigna* sensu stricto (s. s.). Branches with high support values report posterior probabilities adjacent to the corresponding branch. Inset: Age distributions, estimated for stem clades with labels (the crowns of which are delimited by thick branches), come from 1000 samples at likelihood stationarity.

that includes accessions of *V. lasiocarpa* mostly come from the Amazon River basin and Paraguay-Paraná fluvial system. Accessions of *Vigna schottii*, all from the Paraguay-Paraná fluvial system of southern Brazil and adjacent countries and the southern Restinga Atlantic Forest in southeastern Brazil, resolve as sister to the clade of *V. juruana* accessions (Fig. 1), all from the Amazon River basin and eastern Restinga Atlantic Forest. The one species unsampled for ITS sequence variation, *V. diffusa*, is represented by accessions that come from the southern Restinga Atlantic Forest. Sympatry is common among the species of *V.* subg. *Lasiospron*. The long stem branches of each species of *Vigna* subg. *Lasiospron* resolve with strong clade support (Fig. 1), which suggests that sympatry has likely resulted from secondary contact over the long evolutionary history of each of these species.

The six species of *Vigna* subg. *Lasiospron* inhabit a broad latitudinal range of tropical wetlands from western Cuba and southern Mexico (ca. 23.2°N) to northern Argentina and southern Uruguay (34.9°S) at altitudes mostly well below 500 m (Fig. 4, top panel). The average elevation of the three amphi-Atlantic species is 112 m, whereas the average elevation of the three species confined to the New World is 151 m (the 95% CI of the difference in these means, 0.5–77 m, does not encompass 0).

For the 427 collection sites of the six species of *V.* subg. *Lasiospron* for which longitudes and latitudes could be assigned, climate variables that varied most included annual mean temperature, annual mean precipitation, and precipitation seasonality (Fig. 4). The collection sites of the six *V.* subg. *Lasiospron* species tend to come from low elevations where the annual mean temperature is around 26°C and the annual mean precipitation measures about 2000 mm with low precipitation seasonality (Fig. 4). *Vigna schottii* and *V. diffusa* occur at more southern latitudes with annual mean temperatures

closer to 20°C and with more uniform monthly precipitation (Fig. 4, right hand columns of each panel).

TAXONOMIC TREATMENT

VIGNA SUBG. LASIOSPRON (Benth.) Maréchal, Mascherpa & Stainier, Taxon 27: 201 (1978). TYPE: *Vigna lasiocarpa* (Benth.) Verdc., designated by Verdcourt (1970: 539).

Phaseolus section *Strophostyles sensu* Bentham, pro parte, Comm. Leg. Gen.: 74 (1837); Hassler in Candollea 1: 462 (1923), non Elliot; Piper in Contr. U.S. Natl. Herb. 22: 677 (1926).

Phaseolus section *Strophostyles* emend. Benth., in Martius, Flora Brasiliensis 15(1): 187 (1859).

Vigna section *Lasiospron* (Benth.) Verdc., Kew Bulletin 24: 539 (1970).

Perennials or occasionally annuals, scrambling or climbing (sinistrorsely) vines up to 5 m or more long, with foliage and reproductive parts covered with yellow hairs, these often over 1 mm long, some individuals also conspicuously invested with minute glandular hairs. **Stems** herbaceous, hollow, angulate (sturdy), older ones lignescent, frequently developing adventitious roots, stems and roots reported to have nodules. **Leaves** entire or seldom lobed, rarely with sinuous margins, membranaceous to chartaceous, oblong to ovate or widely ovate, sometimes rhombic or linear-lanceolate, usually obtuse or acute or even acuminate at apex, with 3 basal or supra-basal nerves (one prominent and central, and one to either side), lateral leaflets asymmetrical, lateral vein on the broader side diverging ca. 30°, venation brochidodromus; stipules extended at the base or point of insertion, scarcely to distinctly and unequally bilobed or very

distinctly spurred (sometimes adnate to the stem), membranaceous to chartaceous, triangular to lanceolate, 6–10-veined, not reflexed, persistent; stipels oblong to triangular, often trapezoidal, shorter than petiolules, glanduliferous due to glandular hairs; petioles mostly shorter than terminal leaflets, petioles and rachis bifacial, adaxially canaliculate, drying angled. **Inflorescences** few-flowered pseudoracemes, the flowers clustered at the apex, 2 flowers per node, the nodes adhering laterally to the rachis, swollen, with few to ca. 10 vestured glanduliferous orifices, these sparsely scattered or distributed in rows; primary and secondary bracts caducous, bracteoles mostly persistent at anthesis, as long or twice as long as the calyx tube, bracts and bracteoles lanceolate and at base geniculate, often spurred; pedicels shorter than calyx tube, longer and twisting in fruit, covered with straight, retrorse hairs; calyx campanulate, calyx-teeth generally short and subequal or forming two lips, the upper lobe broad and emarginate or the sinus as deep as the other three lower lobes, the lower lobe (two laterals and one central tooth) mostly equalling the tube length. **Flowers** predominately orange yellow or greenish yellow, glabrous; standard petal asymmetric, deeply emarginate or bilobed at apex, two parallel callosities on the centre of lamina at the point of folding, with two thick, fleshy auricles at the margins above the claw, the portion of the lamina immediately above the claw covered with micro-papillae; wing petals longer than keel, right wing (flower's right-side seen from the front) positioned clearly as a landing platform for visiting insects, the left wing (flower's left side) distally clasping around the left-side wall of the keel; keel distinctly beaked, loosely coiled to ca. 270° or through ca. 360°, twisted to the right side of the flower, the keel wider at region of connation with wings; stamens 10, diadelphous, the single free stamen with a broad or cup-shaped appendage on the basal portion; pollen grains triporate, with coarsely reticulate exine, interstitium granular; ovary with a basal nectary disc less than 1 mm long, lobed distally; ovules few to many, style tenuous to variously thickened, with a short, curled or spreading pollen brush, twisted at the apex, thus placing the stigma sideways and mostly extended beyond the stigma and projected into a horn-like or hook-like appendage, stigma small, elliptic or transversely ovate, introrse [= opening inwards and a term usually referring to anthers] or terminal, sparsely ciliate. **Fruit** inverted by a post-pollination twisting of the pedicel, patent (diverging from the axis at ca. 90°), or held erect (parallel to rachis), often placed on one side of the rachis (secund), straight to slightly falcate, subcylindrical or flattened, valves membranaceous or coriaceous, turning dark brown or black at maturity, covered with bristly, yellow, straight hairs, elastically dehiscent. **Seeds** asymmetrical, broader than long (D-shaped), compressed to subglobose (surrounded in fruit by a membranaceous whitish layer), hilum oblong, as long as seed width, covered by an epihilum and this often by a short epi-groove, with a distinctly raised rim-aril, and often with a conspicuous white membranaceous aril towards the lens. **Seedlings** with hypogeal germination. Chromosome number: $2n = 20$ or 22.

Etymology—Bentham (1837) possibly named this group of plants *Lasiospron* to emphasize the hairiness of their pods: *Lasio* (hairy); *spron* (beak).

Taxonomic History—The taxonomy of this group of plants began with Bentham (1837), who published five new species in his taxonomic treatment of the genus *Phaseolus*. In *Phaseolus* section *Strophostyles* (Elliott) Benth., Bentham described *Phaseolus schottii*, *P. longifolius*, and *P. ovatus*, and an unnamed variety under the last. In addition, *P. hirsutus* and *P. lasiocarpus* were described under a newly proposed *Phaseolus* section *Lasiospron* Benth. Bentham classified *P. pilosus* Kunth (1823) under *Phaseolus* section *Leptospron* Benth. In his treatment of the genus in *Flora Brasiliensis*, Bentham (1859) synonymized *P. schottii* under *P. longifolius*, *P. hirsutus* under *P. lasiocarpus*, and recircumscribed *P. campestris* Benth. (1837). All these were included within *P.* section *Strophostyles* and not within Bentham's *P.* section *Lasiospron*. Chodat and Hassler (1904) and later Hassler (1923), in his treatment of the genus for South America, reduced all published taxa classified under *P.* section *Strophostyles* to two species, *Phaseolus schottii* with four varieties (and six formas) and *P. pilosus* with two varieties. Piper (1926) recognized only four species in this group, *P. hirsutus*, *P. campestris*, *P. schottii*, and *P. pilosus*. Verdcourt (1970), as part of a taxonomic study of subtribe Phaseolinae for the Flora of Tropical East Africa, which involved delimiting the genus *Phaseolus*, transferred this group of species into the reinstated section under *Vigna* Savi and recognized only three species, *V. lasiocarpa*, *V. juruana*, and *V. longifolia*. Maréchal et al. (1978) raised *V.* section *Lasiospron* to the subgenus rank under *Vigna* and followed Verdcourt's species classification. Lackey (1983) preferred the placement of *V.* subg. *Lasiospron* under *V.* subg. *Vigna* and followed again Verdcourt in recognizing only three species.

In sum, taxonomic misconception and uncertainties likely result, in part, from the similar morphologies of the six *V.* subg. *Lasiospron* species, which are all adapted to thrive in riparian and wetland habitats. In addition, ambiguities occur in original species descriptions, such as Hassler's (1923) description of *P. schottii* var. *campestris*, which combines diagnostic traits of more than one species (see Notes under *Vigna juruana*). Imprecise label information of critical herbarium specimens causing taxonomic uncertainty is exemplified by *Vigna trichocarpa* (see Notes under this species). Original and type specimens have been lost, as in the case of the holotype of *V. juruana*. We thereby provide a modern taxonomic synthesis of *Vigna* subg. *Lasiospron*, a group that has puzzled taxonomists for almost 200 yr.

Morphological, Ecological, and Karyological Traits (Figs. 5–6)—**Habit.** All species of *Vigna* subg. *Lasiospron* are vines, mostly herbaceous and rarely woody and then mostly with age and at the base of the stem, which climb mainly on trees at forest edges particularly along riparian corridors. **Stems.** Mainly herbaceous, hollow or with a spongy pith, angulate (sturdy), becoming lignescent with age. Floating stems of *Vigna lasiocarpa* have been reported carrying nitrogen fixing nodules on adventitious roots and on stems, but vascularly attached to the bases of adventitious roots (James et al. 2001). Vegetative multiplication by stems occurs in plants of *Vigna lasiocarpa* (Pott and Pott 2000). Climbing direction in *Vigna longifolia* has been noted in the field label of the herbarium specimen *Ahumada et al. 3373* (K), which records the direction of twining from left to right (sinistrorsum), when in other species it is from right to left. **Leaves.** The leaflets display a wide variation in size and shape even within the same species. They range in form from narrowly linear to broadly ovate, sometimes even with lobes at the base. In addition to showing different shapes, *Vigna lasiocarpa* leaflets have undulate margins. Due to this variation, leaflet shape and size are not reliable characters for species separation. **Stipules and stipels**. The stipules are moderately
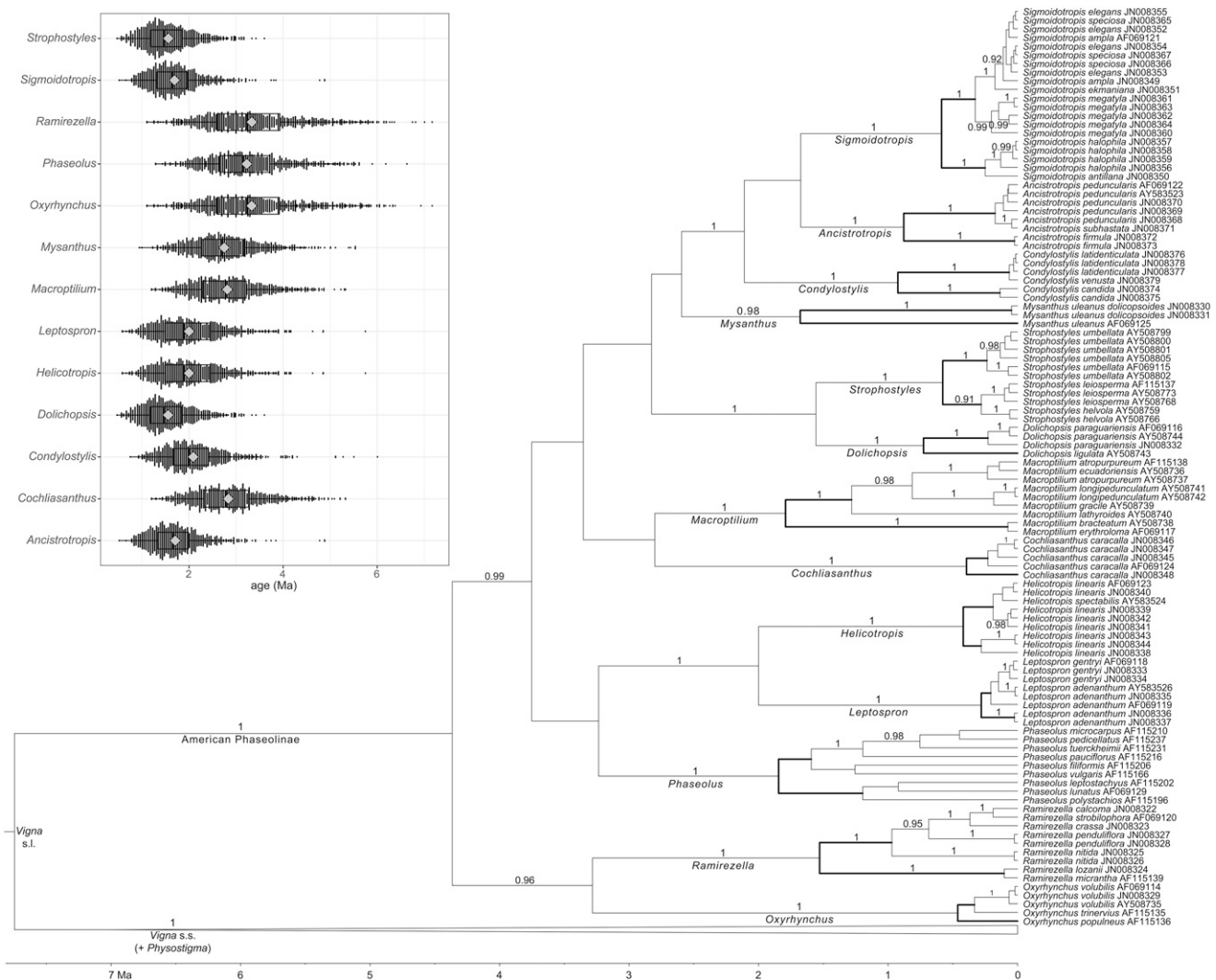
Fig. 2. ITS phylogeny derived from a BEAST2 analysis of *Vigna* sensu lato (s. l.) featuring the subclade American Phaseolinae. Branches with high support values report posterior probabilities adjacent to the corresponding branch. Inset: Age distributions, estimated for stem clades with labels and included in the American Phaseolinae (the crowns of which are delimited by thick branches), come from 1000 samples at likelihood stationarity.

appendaged or distinctly produced below their point of insertion. The upper portion is generally lanceolate or widely triangular, and always conspicuously veined. The lower portion or appendage can be a single spur or bilobed (Fig. 5A–B). The texture varies from membranaceous to somewhat chartaceous and brittle. Stipules tend to be loosely fixed to stems, although often, as in *V. lasiocarpa*, they are closely adnate to the stem. Stipels are mostly ovate, although trapezoidal forms also occur. They tend to be covered with minute glandular hairs forming a nectariferous area. **Inflorescence and node's extrafloral nectary**. The inflorescences of *Vigna* subg. *Lasiospron* are pseudoracemes, where all secondary branches have been completely reduced and transformed into cushion-like glanduliferous nodes that generally carry two flowers each. These nodes are attached laterally to the inflorescence rachis and have few to ca. 10 vestured secretory orifices or extrafloral nectaries (Marazzi et al. 2019). These orifices are distributed sparsely or in close rows (Fig. 5C–F). In *Vigna* subg. *Lasiospron* species the shape of these nodes varies, as does the placement of the secretory orifices. The nodes in *Vigna juruana* are spatuliform, and the orifices are distributed in a scalariform pattern, with transverse separations, whereas in

Vigna lasiocarpa, the nodes are elliptical and voluminous, and the orifices are displayed in two rows. In other species of the subgenus, they are subspherical or obpyriform, with the orifices distributed in a sparse-alternate pattern, and no transverse separations are visible.

Although notably different in shape and orifice distribution, the nectaries present in *Vigna* subg. *Lasiospron* may have a similar vascular supply to that found in *Vigna unguiculata* (L.) Walp. (Kuo and Pate 1985). These extrafloral nectaries in *V. lasiocarpa* have been reported to be active during the day even when the plants are fruiting (Lewis and Owen 1989) and are often visited by bees of the genus *Trigona* (da Silva et al. 2384) and by other Hymenoptera (Hoc et al. 1993). In Argentina, Hoc et al. (1993) registered wasps and ants actively sucking nectar from the inflorescence nodes. Ants were observed patrolling the plant displaying deterrent behaviour against other visitors to the plant. **Flower**. Flower colour varies from yellow to greenish yellow (Fig. 5D). The standard petal is deeply emarginate or bilobed at its apex and is sometimes not fully extended because the standard bends backwards in anthesis, leaving a portion of the margins joined to form a hood. On the internal face of the standard petal, two parallel
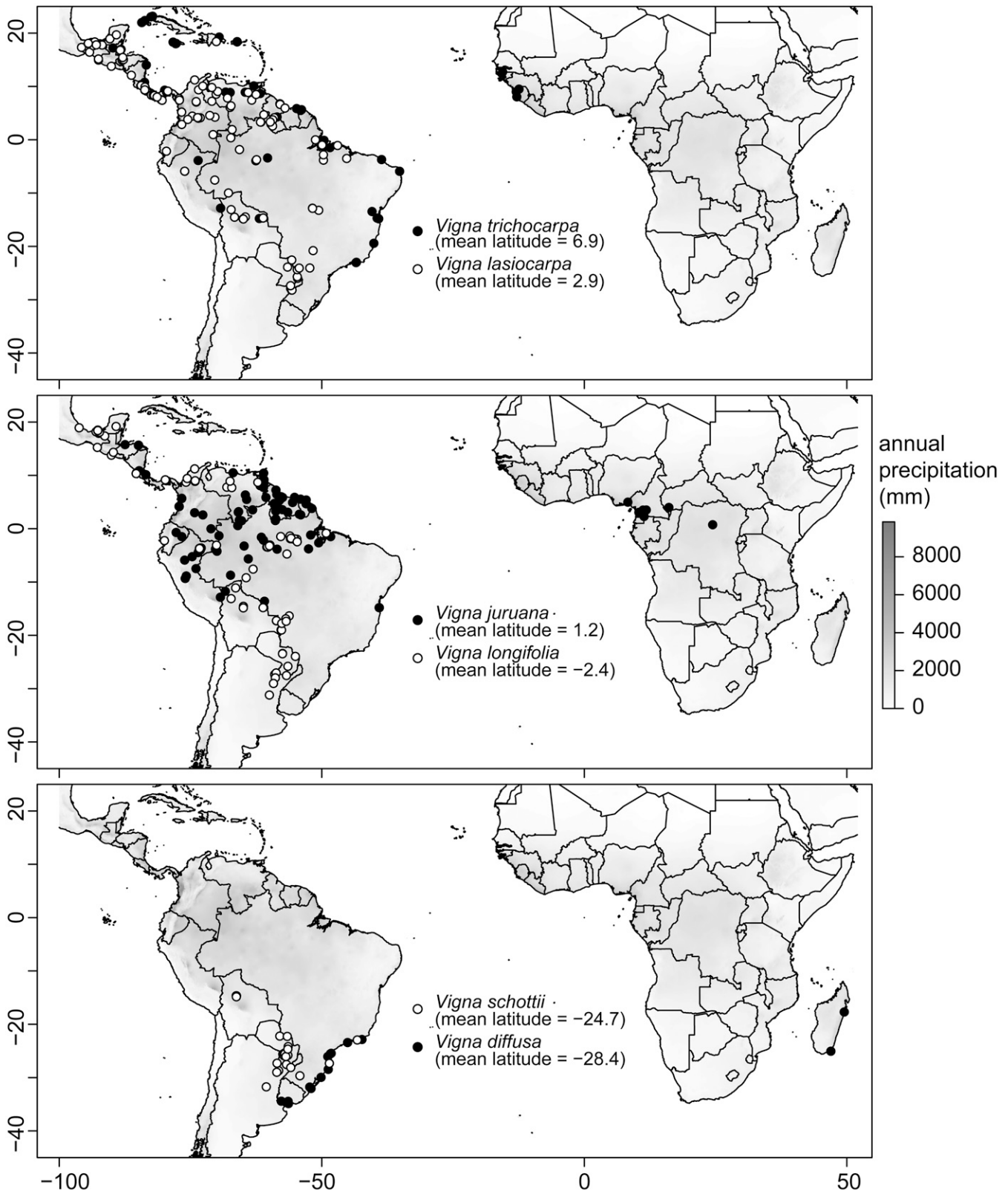
F~IG~. 3. Geographic distributions of the six species of *Vigna* subg. *Lasiospron*, which are ordered, top to bottom, by mean latitude. Filled circles indicate species with amphi-Atlantic distributions.

thickenings or appendages, and two prominent, thick fleshy auricles, are located above a short petal claw. The concavity or furrow produced by the backward bending of the standard at anthesis, enclosed by the parallel thickenings and auricles, is papillate. This protected region directs the bee's mouth parts to the nectary, which is located at the base of the gynoecium.

Wing petals are adnate to the keel by their claws, and by their positioning upon the keel lateral pocket. Wing

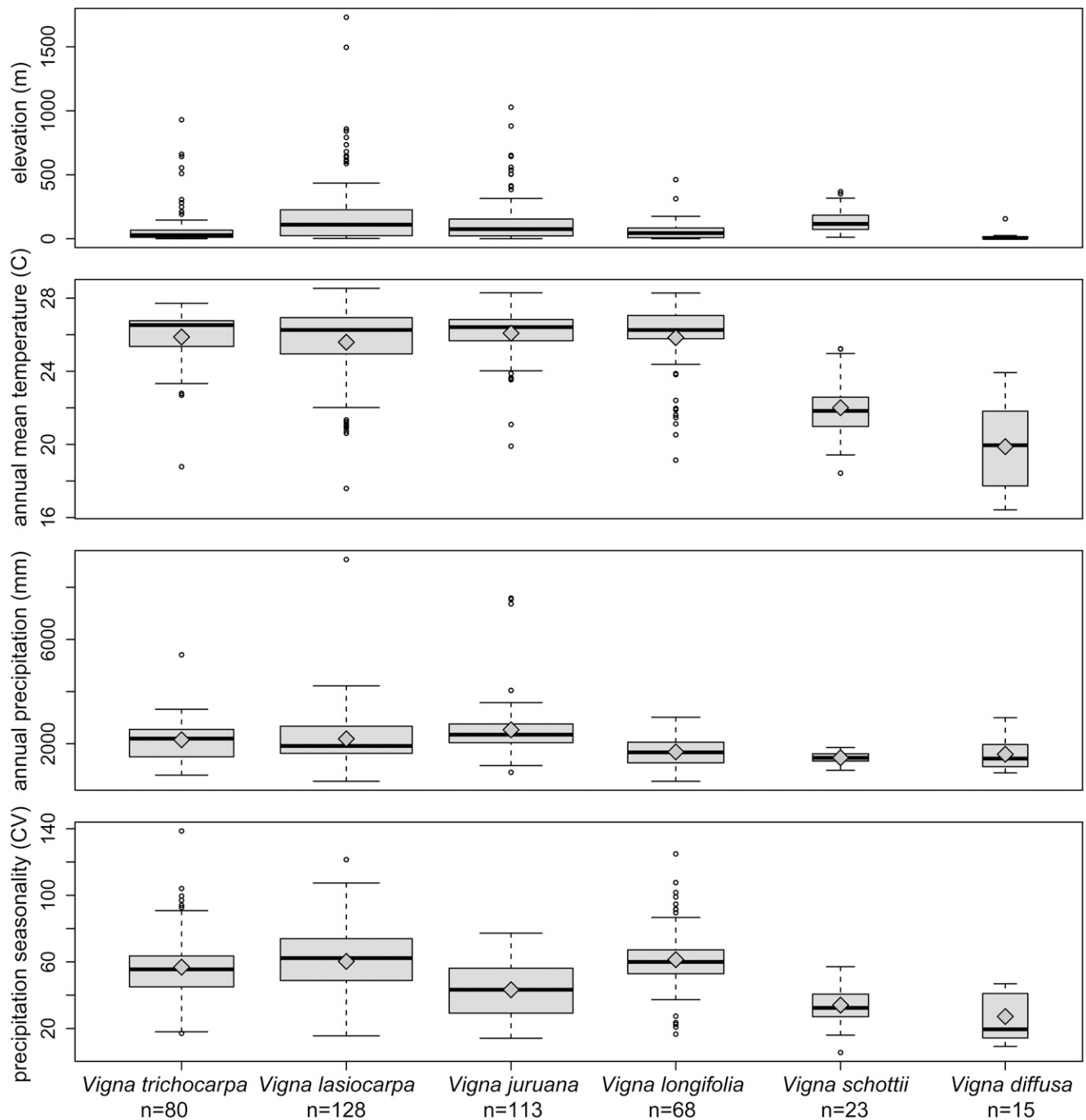Fig. 4. Elevation and climate variables, the latter of which varied most among 427 georeferenced collection sites of *Vigna* subg. *Lasiospron* species. From the top panel, elevation (m), annual mean temperature (C), annual precipitation (mm), and precipitation seasonality, which is the coefficient of variation (CV) of mean monthly precipitation (i.e. values close to 100% indicate highly seasonal climates, whereas values less than 60% indicate more uniform monthly precipitation regimes throughout the year). Species are ordered, left to right, by average north to south latitude (corresponding to Fig. 3). For each boxplot, the horizontal bar indicates the median, the box encompasses 50% of the data points, the whiskers approximately 99% of the data, and individual points represent outliers. Filled diamonds indicate mean values.

sculpturing occurs mainly on the right-side wing (as observed from the front of the flower). The sculpturing is in a lamellate pattern in the upper basal and upper central regions of the petal, and the upper basal margins of the petal are incurved. The auricles in the upper basal region are thick and fleshy, and in *V. juruana* a line of four to five hairs or cilia are present. These interlock with the basal auricles of the standard. The right-side wing petal extends distally and rotates to form a landing platform, whereas the left-side wing is held

vertically and distally embraces the keel, thus blocking entry to the nectary by unwanted flower visitors.

Keel petals are united to each other for almost their whole length and form a tubular structure that encloses the androecium and gynoecium. The keel is curved at its mid-length position and there held erect between the wings; distally it is curved and rotated towards the right side of the flower. The two keel petal claws are strongly adnate to the staminal tube, whereas their lateral basal walls have a concave pocket
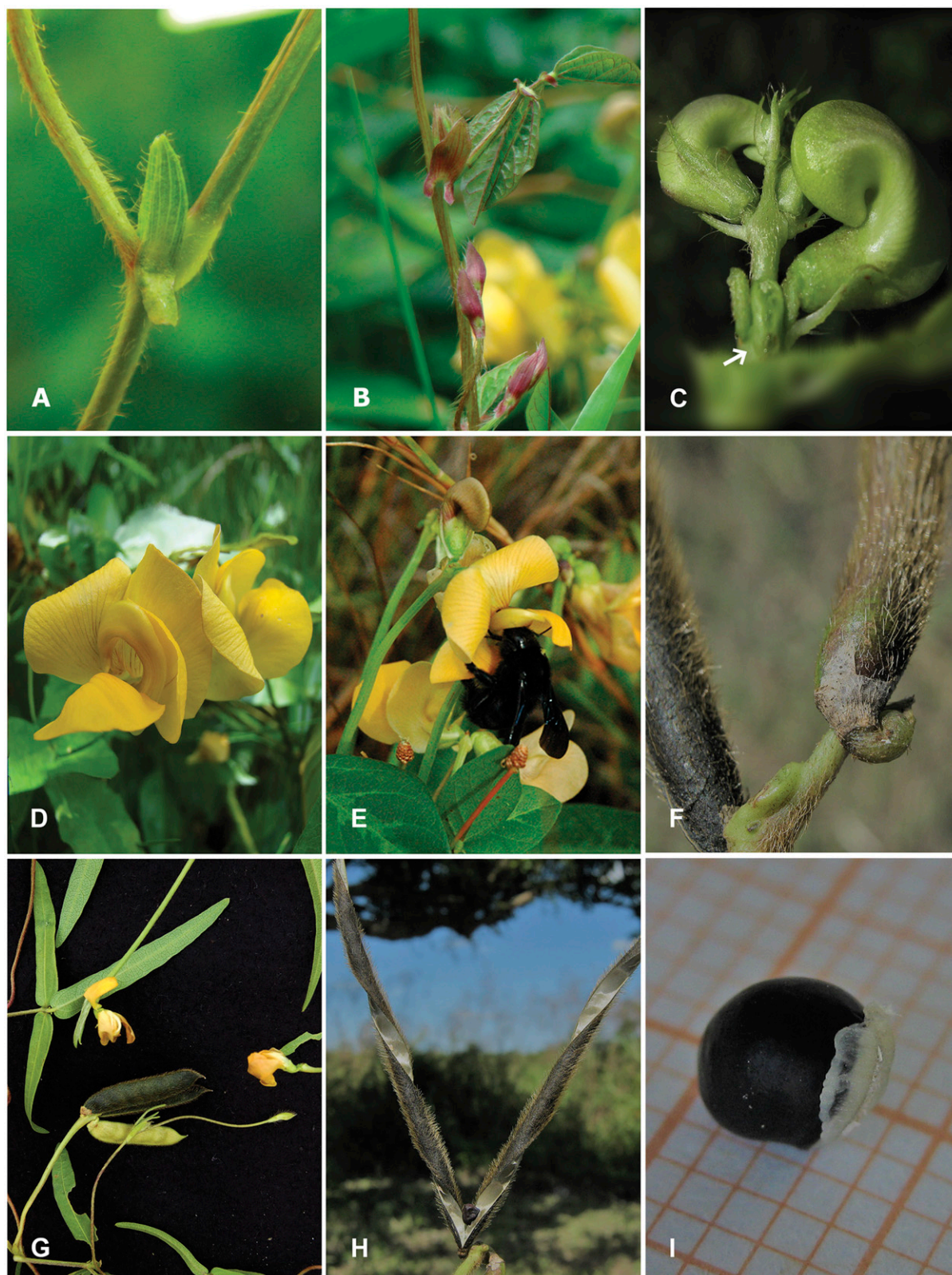
FIG. 5.   Photographic images of reproductive structures of *Vigna* subg. *Lasiospron*. A. Stipules peltate or medifixed of *Vigna trichocarpa* (*Snak 1066*). B. Stipules with a bilobed spur of *Vigna diffusa* (*Snak 269*). C. *Vigna lasiocarpa* floral buds, notice the long bracts and bracteoles and the arrow pointing to extrafloral nectaries (*Vibrans 8246*). D. *Vigna diffusa* flower (*Snak 269*). E. *Xylocopa brasilianorum* pollinating *V. diffusa* (*Snak 501*). F. Pods of *Vigna lasiocarpa*, with rotated pedicels (*Vibrans 8246*). G. Flattened pods of *Vigna trichocarpa* (*São-Mateus s.n.*). H. Nearly cylindrical, dehiscent pods of *Vigna lasiocarpa* (*Vibrans 8246*). I. Seed aril of *Vigna lasiocarpa* (*Vibrans 8246*). Photographs taken by Wallace M. B. São-Mateus, Cristiane Snak, and Heike Vibrans.
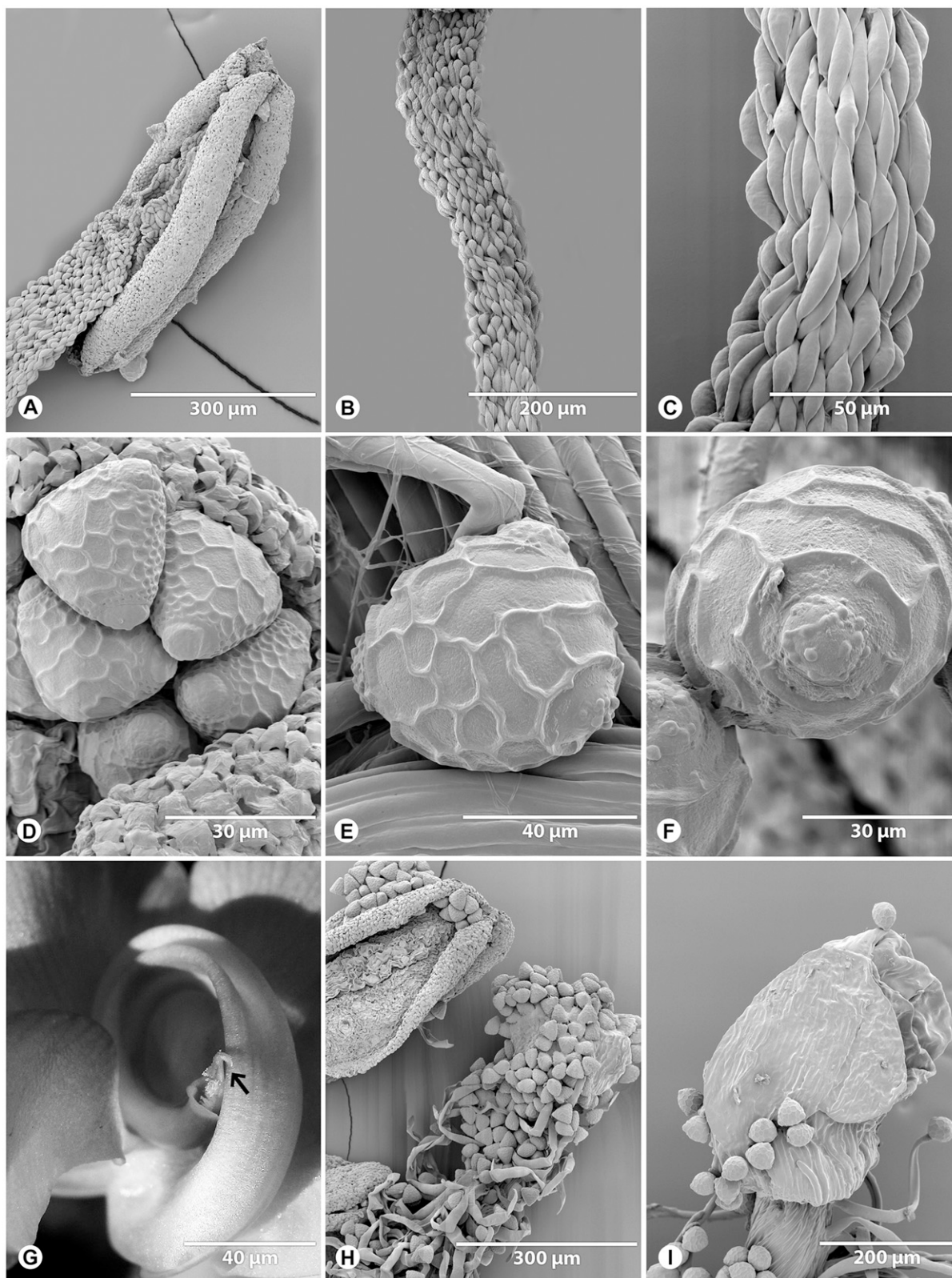
FIG. 6.   SEM images of reproductive structures of *Vigna* subg. *Lasiospron*. A. *Vigna diffusa*, dorsifixed anther with pollen grains. B. detail of filament showing helically orientated, intertwining arrays of cell walls. C. *Vigna schottii*, detail of filament showing cell walls helically orientated. D. *Vigna diffusa*, triporate pollen grains, equatorial and polar view. E. *Vigna lasiocarpa*, pollen grain, equatorial view. F. *Vigna lasiocarpa*, pollen grain, polar view. G. *Vigna longifolia*, stigma with wet stigmatic membrane and hooked style-tip (arrow). H. *Vigna juruana*, pollen brush of style comprising curly hairs. I. *Vigna schottii*, truncate stigma with fringed hairs and secretion containing pollen grains. Specimens: (A, B, D) *Vigna diffusa* (*Cordeiro 616*); (H) *Vigna juruana* (*Henkel 5321*); (E) *Vigna lasiocarpa* (*Jansen-Jacobs 5019*); (G) *Vigna longifolia* (*Vibrans 8246*); (F) *Vigna longifolia* (*Kew Slide Collection 279*); (C, I) *Vigna schottii* (*Zardini 8650*). Scale bars on images A–I. SEM photos by Hannah Banks. Image G, by H. Vibrans.

TABLE 1. Comparison of morphological traits of *Vigna* subg. *Lasiospron* species.

Character	Vigna. lasiocarpa	Vigna longifolia	Vigna juruana	Vigna diffusa	Vigna trichocarpa	Vigna schottii
Stipules	Biauriculate	Biauriculate	Biauriculate	Biauriculate	Peltate	Peltate
Inflorescence: Number of floral nodes	5–7	2–3(–4)	up to 7	1–2	1–3(–5)	up to 8
Keel length	ca. 3.0 cm	ca. 2.5 cm	ca. 7.0 mm	ca. 1.5 cm	ca. 7.0 mm	ca. 1.5 cm
Keel petal beak	Loosely coiled, with a complete coil	Loosely coiled, almost with a complete coil	Hook-like	Loosely coiled, almost with a complete coil	Hook-like	Hook-like
Corolla length range	ca. 2.0 cm or more	ca. 2.0 cm	8.0 mm	ca. 2.0 cm	8.0–12 mm	ca. 1.5 cm
Style pollen brush	Long	Long	Short	Long	Short	Long
Style extension shape	Short hook	Not developed	Not developed	Conical	Conical	Short hook
Ovule number per ovary	12–18	11–13	8–9	7–10	7–8	7–8
Fruit length and width	8.0–9.0 cm × 7.0–10.0 mm	8.5 cm × 5.0 mm	4.5–5.2 cm× 5.0–7.0 mm	4.0–5.5 cm × 5.0 mm	3.5–4.0 cm × 6.0–8.0 mm	5.0–6.0 cm × 5.0 mm
Fruit position on the infructescence	Patent or rarely ascending	Patent	Patent	Patent	Ascending	Patent or rarely ascending
Seed shape	Oblong	D-shaped	D-shaped	D-shaped	Oblong	—
Seed length and width	3.0–4.0 × 3.0 mm	4.0 × 3.0 mm	4.5 × 3.5 mm	3.0 × 4.0 mm	2.0–3.0 × 3.0–4.0 mm	—
Seed aril	Developed	Developed	Not developed	Not developed	Not developed	Variably developed

and fold which attaches them to the wing petals, thus forming a lever mechanism of the four united petals when a pollinator lands on them. A semi-circular opening of the keel apex exposes the protruding stigma which is adjusted for nototribic or pleurotribic pollination.

The androecium is diadelphous and comprises nine stamens partially united to form a staminal sheath or tube, and one free vexillary stamen. The vexillary stamen filament has a conspicuous appendage just above its base. The appendage upper surface is verrucate. Verrucate surfaces are also present on adjacent margins of the staminal tube, constituting a shield that protects the ovary, as a visiting insect's proboscis searches for the basal fenestrae that lead to the nectary cavity. Stamen filaments are cylindrical with vascular traces running internally. The walls of the filaments have spirally coiled, free, elongate epidermal cells (Fig. 6A–B). These stretchy interweaved walls may provide the filament with some degree of elasticity that may play a role in promoting pollen transfer to the stylar pollen brush. Anthers are uniform, oblong in shape, basifixed to almost dorsifixed, and of longitudinal dehiscence.

Pollen grains are characterized by being triporate and with a wide reticulum, as seen in other species of *Vigna* (Maréchal et al. 1978). Their shape is suboblate to oblate, with a semi-angular to angular outline as viewed from the polar region (Fig. 6D–F). Pores comprise a globular to granulate operculum membrane. Pollen studies have described the interstitium as granular (non-orientated to orientated, and without a foot layer; Horvat and Stainier 1980; Ferguson and Skvarla 1983). However, the interstitium has been reported for *Vigna lasiocarpa* as columellar (Di Stilio 1994).

The gynoecium comprises a sessile, non-stipitate, straight ovary, with a lobed basal nectary disc confined within the base of the staminal tube. The length of the style is highly variable and ranges from around 1.5 cm in *V. juruana* to 5–6 mm in *V. lasiocarpa*. The style is thread-like or tenuous for about one-third of its length, then thickened uniformly for the next third, and narrows once again for the final third. A pollen brush is confined to the upper part of the style and is made up of curly (Fig. 6H) or straight hairs (Fig. 6I). The style-tip may be curved inwards to very different degrees, placing the stigma in a subterminal position (Fig. 6G), except in *V. juruana* where it is in an apical position (Fig. 6I). The stigma bears a whorl of non-receptive, short hairs (Drewes and Gamba 2011). In mature flowers of *Vigna lasiocarpa* the stigma surface produces a copious exudate and is located at the opening of the keel.

Pollination Studies—Flowers of *Vigna longifolia* and *V. diffusa* are effectively pollinated by bees of the genus *Megachile*, and *V. diffusa* by *Apis mellifera*, *Bombus morio*, and *Xylocopa brasilianorum* (Hoc et al. 1993; Souza et al. 2017, initially reported as *V. longifolia* but later determined to be *V. diffusa*). Pollen transference is nototribic, placing the pollen in an area between the head and thorax of the bee, or pleurotribic and sternotribic, in the case of the deposition of the pollen of *V. diffusa* in the entire metasoma, where the pollen brush slides from the dorsal to the ventral region in *Megachile* spp. (Hoc et al. 1993; Souza et al. 2017). Label data of *da Silva et al. 2384* (in herb.) mentioned that large bees (Fig. 6E) are struck by the stigma on the side of their bodies (pleurotribic) while visiting the flowers of *V. lasiocarpa*.

Fruit and Seeds—The pods in *Vigna* subg. *Lasiospron* are usually laterally flattened, with chartaceous, thin valves (Fig. 5G). However, in *Vigna lasiocarpa* and *V. longifolia* the pods are nearly cylindrical, with their valve walls thicker than those of the rest of the species in the subgenus. Pod valves are covered with golden-yellow appressed hairs which turn black on drying. Pods are usually elastically dehiscent (Fig. 5H) along both sutures and the pedicels rotate and twist as the fruit matures, presenting it in either an ascending or pendent position. In an ascending position the abaxial suture faces the inflorescence axis, whereas in the pendent position the abaxial suture faces upwards. Seed orientation in the pod is mostly with its long axis parallel to the suture, although in *V. lasiocarpa* it tends to be somewhat oblique. Funicles in nearly all species are short, except in *V. trichocarpa* where they are approximately 1 mm.

Seeds vary in size and shape and are sometimes almost isodiametric to oblong-elliptic. Although more generally flattened to some extent, in *V. lasiocarpa* and *V. longifolia* seeds tend to be subglobose. In these two species, a white hippocrepiform aril develops at the edge of the hilum (Fig. 5I); the

other four species have variable or no aril development (Table 1). Arils are found also in some species of Old World *Vigna* such as in wild plants of *Vigna aconitifolia* (Jacq.) Maréchal (Takahashi et al. 2016). A comparison of some morphological characters of the species of *V.* subg. *Lasiospron* is presented in Table 1.

Seed Dispersal—Marsh deer, waterfowl, and cattle have been seen eating the foliage and seeds of *Vigna* species in the Brazilian Pantanal (Pott and Pott 1994, 2000). Waterfowl species that breed in North America and winter in Central and South America and the Antilles, which migrate across the Atlantic to Africa, are potentially able to disperse seeds over long distances (Somenzari et al. 2018). Species with a seed aril could be dispersed by birds and vertebrates. The widest ranging New World species, *Vigna lasiocarpa* and *V. longifolia*, have seed arils that are consistently well developed. In contrast, the least widely ranging species, *Vigna schottii*, has seed arils that are variably developed. However, the three amphi-Atlantic species, *Vigna trichocarpa*, *V. juruana*, and *V. diffusa*, have seed with little or no aril development (Table 1), suggesting the development of cartilaginous arils is not required for long distance trans-oceanic dispersal.

Chromosome Numbers—Chromosome counts of three *Vigna* subg. *Lasiospron* species have been reported (Maréchal 1969; Senff et al. 1992, 1995; Mercado-Ruaro and Delgado-Salinas 1996; Schifino-Wittmann 2000). *Vigna diffusa* (as *V. longifolia*) and *V. longifolia* have 22 somatic chromosomes, with counts of $2n = 22$, whereas *V. lasiocarpa* is a dysploidy species, with a chromosome count of $2n = 20$. These counts conform with the overall pattern found in *Vigna* (Goldblatt and Johnson 1979; Costa et al. 2019), which is a base chromosome number of $n = 11$ being most common, and base number of $n = 10, 12$, and others uncommon.

Synapomorphies of Vigna Subg. Lasiospron—In a mature flower, the distal portion of the keel twists to the right-hand side of the corolla, often into a complete coil. Pedicels, which are shorter than the calyx tube, twist following pollination to render the adaxial suture of the fruit upside down (resupinate). Fruits are pendent or ascending and their valves turn brown or black at maturity.

KEY TO THE SPECIES OF VIGNA SUBG. LASIOSPRON

1. Stipules scarcely to distinctly bilobed, below the point of insertion 2
    2. Upper extension of stipules 3 mm long; calyx 2–2.5 mm long; flowers pale greenish yellow, 8–10 mm long; style not extended beyond stigma, stigma apically placed; pollen brush 1 mm long, with hairs curled; fruit flattened . . . . 1. *Vigna juruana*
    2. Upper extension of stipules 3–12 mm long; calyx 3–10 mm long; flowers orange to golden yellow, 12–35 mm long; style extended beyond stigma, stigma laterally placed, pollen brush 3–6 mm long, hairs spreading; fruit flattened or cylindrical 3
        3. Upper extension of stipules 2–4 mm wide, membranaceous to chartaceous, up to 10-veined; calyx 3–3.5 mm long; inflorescence rachis with 2–3 nodes; style extension projecting into a small crustaceous horn-like appendage; ovules 8–10 per ovary; pods oblong, flattened, thin-valved; seed without rim-aril . . . . 2. *Vigna diffusa*
        3. Upper extension of stipules 1–2 mm wide, chartaceous, up to 6-veined; calyx 4–10 mm long; inflorescence rachis with 3–8 nodes; style-extension projecting into a horny, hook-like appendage; ovules 10–18 per ovary; pods linear to slightly falcate, cylindrical, thick-valved; seed with rim-aril 4
            4. Inflorescence rachis with 2–4 nodes; calyx $4–5 \times 2–3$ mm, sparsely hirsute to strigose at base, upper teeth slightly divided, narrow and acute, not forming a lip; keel-beak not quite completing one coil; pods linear to slightly falcate, $4–8 \times 0.5$ cm, tapering to the apex, rostrum ca. 5 mm long . . . . 3. *Vigna longifolia*
            4. Inflorescence rachis with (3–)5–8(–9) nodes; calyx $5.5–10 \times 3.5–8$ mm, densely hirsute-strigose, upper teeth deeply divided and broadly rounded at apex to form a lip; keel beak fully completing one coil; pods linear-oblong, $6–9 \times 0.7–1.1$ cm, abruptly truncate at the tip, rostrum 2–3 mm long . . . . 4. *Vigna lasiocarpa*
1. Stipules distinctly spurred, below the point of insertion 5
    5. Inflorescence rachis with 4–6 nodes, nodes oblong, spatuliform, orifice distribution scalariform, with transverse separations; calyx 1.5–2 mm long, teeth 0.5 mm long; flower 8–12 mm long; pollen brush 2–3 mm long; pod oblong, flattened, (3–)3.5–4 cm long, 7–8 mm wide, ascending. . . . . 5. *Vigna trichocarpa*
    5. Inflorescence rachis with 3–5(–8) nodes, nodes subspherical, obpyriform, orifice distribution sparse-alternate, without transverse separations; calyx 3–4 mm long, teeth 1 mm long; flower 12–14 mm long; pollen-brush 3.5–4 mm long; pod linear, subcylindrical, 4–6 cm long, ca. 6 mm wide, patent or ascending . . . . 6. *Vigna schottii*

1. VIGNA JURUANA (Harms) Verdc., Kew Bulletin 24: 540 (1970). *Phaseolus juruanus* Harms, Notizbl. Bot. Gart. Berl. 7: 506 (1921). TYPE: BRAZIL. Amazonas, Jurua miry, Jul 1901, *E. Ule* 5533 (holotype: B, presumably destroyed; isotypes: K!, U!). Figure 7.

Phaseolus campestris sensu Benth., in Mart., Flora Brazil. 15(1): 188 (1859). TYPE: BRAZIL. "in Braziliae septentrionalis campis et pascuis ad Pará." *Martius* s.n. (lectotype M!, designated here), *nom. illeg.*, non *P. campestris* Benth., *Comm. Legum. Gen.*: 77 (1837), non *Vigna campestris* (Mart. ex Benth.) R.Wilczek, in Fl. Congo Belge 6: 391 (1954). See nomenclatural notes below.

Phaseolus schottii var. *campestris* forma *brasiliensis* Hassl., Candollea 1: 464. 1923. TYPE: BRAZIL. "Alto Amazonas: ad ostium fluminis Saliman [sic]", *Spruce* 1641 (lectotype: K, herb. Benth., designated here; isolectotypes: G, K!, M!), synon. nov., non *P. schottii* var. *campestris* forma *guyanensis* Hassl., Candollea 1: 464. 1923. TYPE: FRENCH GUIANA. *Poiteau* s. n. (holotype: G), synon. nov., non *P. schottii* var. *campestris* forma *transiens* Hassl., Candollea 1: 464. 1923. TYPE: BRAZIL. Bahia in pratis humidis, *Salzmann* s.n. (holotype: G; isotypes: K!, MO!). See nomenclatural notes below.

Phaseolus schottii Benth. var. *tucumanensis* Hassl., Candollea 1: 464 (1923). Type: Argentina. Tucumán, cumbre de Anfama, alt. 2500 m, *Schreiter* 866 (holotype: Herb. Osten, not seen). See nomenclatural notes below.

Perennials or annuals (?), procumbent or climbing vines up to 3 m, with foliage and reproductive parts covered with minute glandular hairs, and sparse or dense pubescence. **Stems** hollow, slightly woody at base, often with adventitious roots, sparsely to densely strigose, with yellow to reddish, retrorse hairs. **Leaves** with stipules ovate to narrowly-lanceolate, unequally bilobed, upper portion ca. 3 mm long, 1–2 mm wide, 5–6-veined, not reflexed, persistent; lower portion ca. 2 mm long, sparsely pilose; stipels oblong
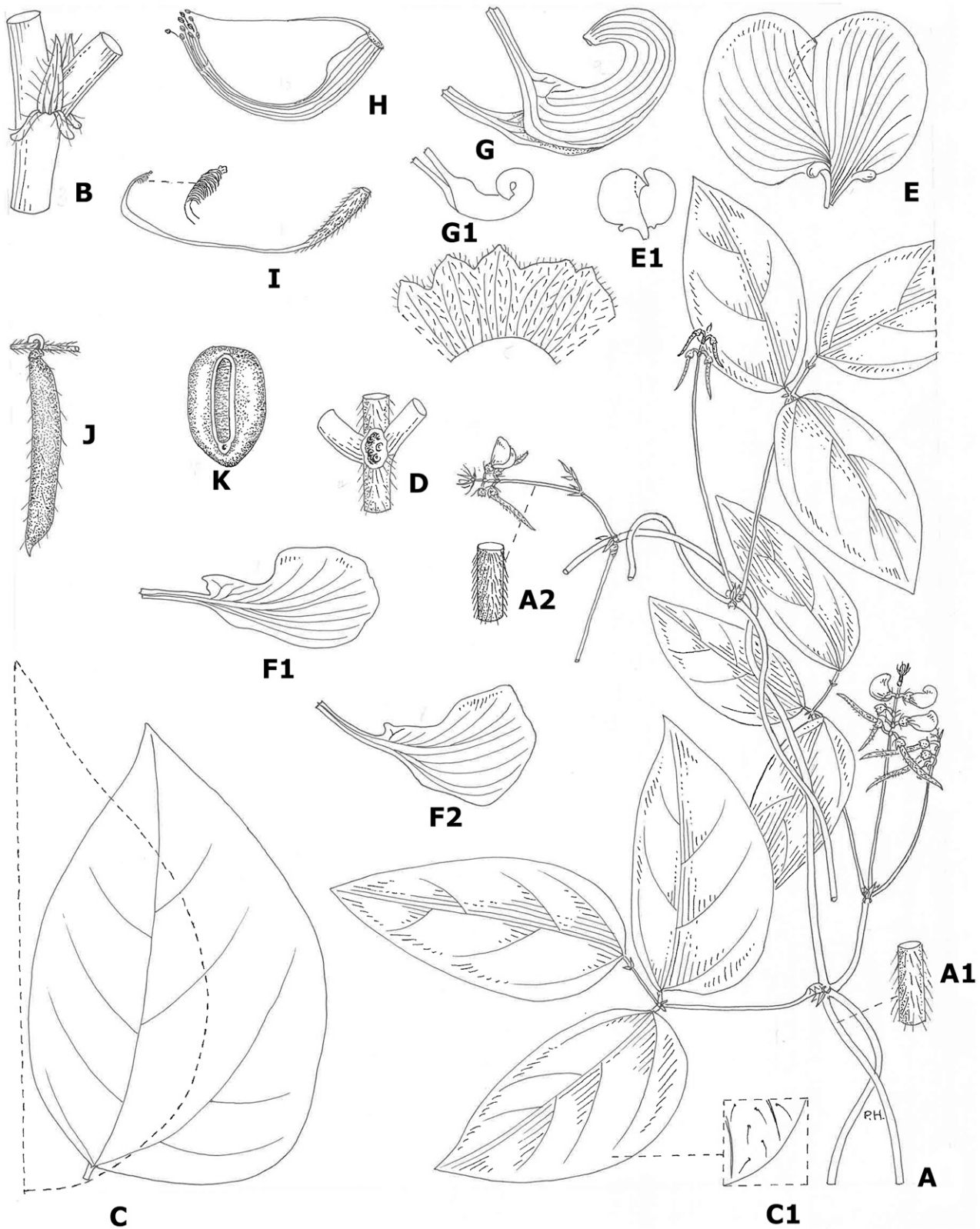
FIG. 7.   Illustration of *Vigna juruana*. A. Habit, natural size. A1. Portion of stem. A2. Portion of peduncle. B. Stipules, some indumentum omitted for clarity (× 6). C. Leaflet outlines to show variation. C-1. Close-up of trichomes on upper leaflet surface. D. Extrafloral nectaries on inflorescence node (× 6). E, E1. Standard petal, ventral (× 6) and dorsal view. F1, F2. Wing petals (× 6). G, G1. Keel petals (× 6), taken from floral buds and flower. H. Staminal tube and vexillary stamen free (× 6). I. Gynoecium (× 5) and stigma enlarged. J. Fruit, natural size. K. Seed, hilar view (× 9). Drawn from *Plowman, Schultes & Tovar 6387* (habit and dissection); *Henkel et al. 3153* (stipules); *Steyermark 87773* (fruit); *Hill 13046* (seed). Illustration by Pat Halliday.

or triangular, ca. 1 mm long, subequal in length to petiolules, glabrous except for minute glandular trichomes; petioles 3.5–11 cm long, covered with retrorse hairs, rachis considerably shorter, ca. 0.5–2.5 cm long, with some antrorsely appressed hairs on the adaxial side, canaliculate; leaflets entire, ovate to narrowly ovate, or lanceolate, acute at apex, with raised veins below, membranaceous, sparsely to densely strigose, terminal leaflet 4–12 × 1.5–9 cm, lateral leaflets 4.5–10.5 × 2–7 cm. **Inflorescences** up to 15 cm long, peduncles ca. 13.5 cm long, covered with short retrorse hairs, densely strigose distally; rachis 1.5–2 cm long, with 5–8(–10) swollen, oblong, 2–3 mm long nodes, 5–8 orifices alternately distributed, flowers clustered distally; primary bracts caducous, secondary bracts ca. 6 mm long, caducous; bracteoles mostly persistent at anthesis, ca. 4.5 mm long, longer than calyx tube; pedicels shorter than calyx tube, 1–1.5 mm long, longer and twisting in fruit, covered distally with straight, retrorse hairs; calyx campanulate, sparsely strigose at the base, glabrous distally, ca. 2 × ca. 1.5 mm, upper teeth slightly divided, narrow and acute, not forming a lip, teeth triangular, subequal, 0.5 mm long, lower tooth slightly longer than lateral teeth. **Flowers** pale greenish yellow, 8–10 mm long; standard petal asymmetric, broadly ovate, ca. 8 × ca. 8 mm, bilobed at apex, two parallel callosities on the lamina above the point of folding, two fleshy auricles above a short claw; wing-petals longer than keel, with an obovate lamina, ca. 1 cm long, 5–6 mm wide, with an auricle at base, claw ca. 3 mm long; keel distinctly beaked, twisted through ca. 270°, the apex hook-like; ca. 7 mm above wing petals, with transverse pockets above the claws, claws ca. 2 mm long, fused to staminal tube; androecium ca. 1 cm long, vexillary stamen with a basal appendage; anthers oblong-ovate, ca. 1 mm long, basifixed to sub-basifixed to filaments; pollen grains triporate, with a coarsely reticulate exine; ovary straight, with a basal nectary disc ca. 0.5 mm long, ovules 8–9 per ovary, style with a tenuous lower part, upper portion thickened, cylindrical, curved, pollen-brush ca. 1 mm long, with curled hairs; stigma globose, apical. **Fruit** patent, linear-oblong to slightly falcate, flattened, valves thin-walled, not constricted between the seeds, turning dark brown or black at maturity, 4–7 cm long, 4–7 mm wide, elastically dehiscent, sparsely strigose, with yellow, straight hairs, beak 1 mm long, straight. **Seeds** D-shaped, 3.5–6.5 × 3–4 mm, surface smooth, testa dark brown, mottled lighter brown, hilum oblong, as long as seed width, rim-aril distinctly raised, covered by an epihilum, without aril. Figure 7.

Illustrations—Wilczek (1954) as *Vigna campestris* (Fig. 7).

Distribution and Habitat—Southern Mexico (Tabasco), Central America (Costa Rica, Honduras, Panamá), and South America (Bolivia, Brazil, Colombia, Ecuador, Guyana, French Guiana, Suriname); also including Trinidad (Republic of Trinidad and Tobago). Likely native in west and central Africa (Cameroon, Democratic Republic of Congo, Central Africa Republic, and Nigeria; Fig. 3). Seasonal or permanently flooded plains or in riverine forests; in South America, in the Solimões River and Amazon River basin and eastern Restinga Atlantic Forest. Sometimes reported growing on the floodplains of Amazonian black water and clear water rivers (i.e. Igapó, common name "feijão do Igapó"), sprawling in floating plant islands or growing in old rice fields; altitudinal range mostly 0–700 m (collected at 1400–1600 m in the Peruvian Ucayalli Department). This species grows in habitats similar to *V. trichocarpa* and *V. longifolia* with which it is sometimes sympatric (e.g. Iquitos, Perú). Flowering and fruiting have been registered all year except for June.

Etymology—Named after the River Juruá in Brazil.

Vernacular Names—"Soematalan" (Amshoff 1939); "feijão do Igapó" (*Fróes 21065*); "frijolillo" (Colombia); "namiatá" (French Guiana, Wayapi); "porotillo" (Perú); "kwakwa" (Wilczek 1954).

Representative Specimens Examined—See Appendix 1 for complete list. **Bolivia.** —PANDO: Manuripi, a lo largo del arroyo Bay, entre el campamento Bay y La Poza, 17 Oct 1989, *St. G. Beck 19433* (MEXU). **Brazil.** —AMAPA: Rio Araguari, vicinity Camp 12, 1°10'60"S, 52°7'60"W, 30 Sep 1961, *J. Murca Pires 51366* (MICH, US). **Colombia.** —AMAZONAS: Leticia, Río Amazonas, Isla de Mocagua, frente del Vergel, Lago Resaca, 3°51'0"S, 70°15'0"W, 110–120 m, 3 Oct 1991, *A. Prieto 92* (MO). **Costa Rica.** —ALAJUELA PROVINCE: Los Chiles, R. V. S. Caño Negro, cuenca del Río Frío, 10°53'18"N, 84°46'37"W, 60 m, 27 Sep 2000, *L. Acosta et al. 2772* (G). **French Guiana.** Cayenne, Saut Nacibo, 4°41'0"N, 52°59'0"W, 20 m, 25 Mar 1994, *B. Bordenave 892* (K). **Guyana.** Essequibo Isl.-W Demerara, lower 7 km of Tiger Creek; 6°30'0"N, 58°39'0"E, 15 m, 11 Dec 1992, *T. W. Henkel 403* (US). **Honduras.** —ATLANTIDA DEPARTMENT: Tela River near Puerto Sierra, 3 May 1903, *P. Wilson 669* (NY). **México.** —TABASCO: a 300 m de la desviación del Río González, hacia Boca Grande, 14 Feb 1990, *M. A. Magaña A 2255* (MEXU). **Panamá.** —PANAMÁ PROVINCE: Fort Clayton, Canal Zone, 14 Jul 1966, *J. D. Dwyer 4584* (MEXU, MO). **PERÚ.** —HUÁNUCO DEPARTMENT: Estación Experimental Agrícola, 701 m, 4 Dec 1945, *R. J. Seibert 2268* (F, US). **Suriname.** Lucie Rivier, 2–10 km below confluence of Cost Rivier, 225 m, 9 Sep 1963, *H. S. Irwin 55541* (NY). **Trinidad.** Nariva Swamp, E of Sand Hill, 5 Apr 1977, *C. D. Adams 14246* (K). **Venezuela.** —AMAZONAS: Departamento Río Negro, Río Siapa, near base of Cerro Aracamuni, 1°39'0"N, 65°40'0"W, 4 Nov 1987, 250 m, *R. Liesner 22785* (MO). **Cameroon.** Bipinde, Urwaldgebeit, Dec. 1912, *G. Zenker 4300* (M). **Central African Republic.** Left bank of Mambére R., near Bania, 26 Nov 1965, *A. J. M. Leeuwenberg 7040* (K). **Democratic Republic Of The Congo.** Jangauellei, ile Esali II, 12 Jul 1988, *J. Louis 10294* (K). **Nigeria.** River Old Calabar, 1863, *G. Mann 2319* (K).

Notes—In Martius Flora Brasiliensis, Bentham (1859) described *Phaseolus campestris*, a name already used (Bentham 1837) and thus a later homonym and illegitimate under Article 53 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018) and unavailable for use (Verdcourt 1970). Hassler (1923), while possibly considering that Bentham (1837) listed *Phaseolus schottii* before *V. longifolia*, published four varieties, *P. schottii* var. *genuinus*, *P. schottii* var. *campestris*, *P. schottii* var. *longifolia*, and *P. schottii* var. *tucumanensis*. Under *P. schottii* var. *campestris*, Hassler combined characters diagnostic of different taxa and, in consequence, listed specimens of different taxa under his new combinations. Under *P. schotti* var. *campestris* forma *brasiliensis* he cited three collections from Brazil: Minas, in silvis ad Salgado [sic], *Martius 1680* (M!), since identified as *V. luteola* (refer to Verdcourt 1970: 540); Alto Amazonas: ad ostium fluminis Saliman [sic], *Spruce 1641* (G), identified here as *V. juruana*; and a collection from Bahia by *Salzmann 182* (G), here identified as *V. trichocarpa*. The exact locality of Spruce's specimen has been established by consulting the expedition notes in Spruce (1851–1855). He recorded his collection numbered 1641, collected in Solimões and Manaquirý, on June 1851, as a *Phaseolus* close to *P. ovatus* (*P. ovatus* aff.). Such information only appears on one of the two sheets of *Spruce 1641* at K (herb. Benth.), and we have designated this specimen as the lectotype of *P. schottii* var. *campestris*. Amshoff (1939) considered *P. schottii* var. *campestris* f. *guyanensis* Hassl. as a synonym of *Phaseolus trichocarpus*. Unfortunately, original material could not be found at P, and the description does not give enough information to elucidate its identity; therefore, we accept Amshoff's judgment here. Concerning the type of *Phaseolus schottii* var. *campestris* f. *transiens* Hassl., see statements under *Vigna trichocarpa* in this treatment.

Vigna juruana has the smallest flowers of all *Vigna* subg. *Lasiospron* species and has a very distinctive style on its gynoecium. The style has a tenuous lower part, with a thicker, cylindrical, and curved upper portion, which becomes rather slender again towards the stigma. Its pollen brush is short and with unique curled short hairs. In addition, the style has no extension beyond the stigma, a characteristic seen in all other species of *V.* subg. *Lasiospron*.

We have not seen the type of *Phaseolus schottii* var. *tucumanensis*, and despite Hassler's lengthy description in the taxon protologue it is not obvious where it belongs taxonomically. Lackey (1983) placed this variety as a synonym of *Macroptilium fraternum* (Piper) Lackey. We tentatively place var. *tucumanensis* as a nomenclatural synonym under *Vigna juruana*. This is because the original description includes floral dimensions that best fit *Vigna juruana* (e.g. a small calyx ca. 2.5 cm long). However, the original description describes the fruits as ca. 2.5 cm long and 3 mm wide, and the fruit length is too small for *V. juruana*. Regarding the type locality, no herbarium specimen has been found with a collection locality in the Tucumán province that matches the protologue of *Phaseolus schottii* var. *tucumanensis*. Moreover, no *V.* subg. *Lasiospron* species, including *V. juruana*, is reported from such a high elevation. *Vigna juruana* and *V. lasiocarpa* are the two *V.* subg. *Lasiospron* species with the widest elevational ranges (Fig. 4) with *V. juruana* occurring up to 1028 m and *V. lasiocarpa* up to 1731 m. The Tucumán collection locality and the reported altitude of 2500 m for var. *tucumanensis* are both exceptional for the subgenus (Figs. 3–4).

2. Vigna diffusa (Scott Elliot) A. Delgado & Verdc., American Journal of Botany 98(10): 1711 (2011). *Phaseolus diffusus* Scott Elliot, J. Linn. Soc. 29: 12 (1891). TYPE: MADAGASCAR. sandy dunes near Fort Dauphin, Sep 1890, *G.F. Scott Elliot 2366* (lectotype: K!, designated by Du Puy et al. 2002; isolectotypes: BM!, P!).

Phaseolus ovatus sensu Benth. *Comm. Legum. Gen.*: 77 (1837) in Brazil, pro parte.

Vigna longifolia sensu Du Puy et al. (2002), non (Benth.) Verdc.

Perennial prostrate or climbing vines, foliage and reproductive parts covered with long yellow hairs, with minute glandular hairs intermingled, sparsely or densely pilose. **Stems** herbaceous, fibrous, often with adventitious roots, sparsely to densely pilose with yellow, straight hairs. **Leaves** trifoliolate, stipules lanceolate to sagittate, upper extension 4–12 mm long, 2–4 mm wide, membranaceous to chartaceous, 8- to 10-veined, lower portion biauriculate, 1–2 mm long, stipels ovate-lanceolate, shorter than petiolules, ca. 2 mm long, covered with long straight and minute glandular hairs; petioles 2–6 cm long, covered with hirsute, retrorse hairs, rachis considerably shorter, 5–10 mm long, with antrorsely appressed hairs, canaliculate; leaflets entire, ovate, elliptic-ovate, or oblong, usually obtuse or acute at apex, often with raised veins below and the veins outlined in light green relative to the darker green lamina, chartaceous, densely strigose to softly pilose on both surfaces; terminal leaflet 4–6.5 × 2–2.5 cm, lateral leaflets 3–6 × 2–3 cm. **Inflorescences** 7–13.5 cm long, peduncles up to 13 cm long, covered with straight, retrorse hairs, densely strigose distally, rachis ca. 5 mm long, with 2–3 swollen, ampulliform nodes, ca. 1.5 mm long, with 3–5 vestured orifices, alternately distributed, flowers clustered distally; primary bracts caducous, secondary bracts lanceolate, ca. 10 mm long, caducous; bracteoles mostly persistent at anthesis, lanceolate, 6–10 mm long; pedicels shorter than calyx tube, 3–5 mm long, longer and twisting in fruit, covered with retrorse, straight hairs, antrorse at base of calyx; calyx campanulate, sparsely pilose at base, tube longer than teeth, ca. 3 × ca. 3 mm, upper teeth emarginate, rounded at apex, not forming a lip, lateral teeth and lower tooth oblong and rounded, ca. 1 mm long. **Flowers** golden yellow, 1.5–2 cm long, standard petal asymmetric, broadly ovate, ca. 1.5 × ca. 1.5 cm, bilobed at apex, two parallel, thick callosities on the lamina above the point of folding, two fleshy auricles, 1 mm wide, above a short claw; wing petals longer than keel, with an obovate lamina, 1.5–1.7 × ca. 1.5 cm, with a prominent auricle at base, claw ca. 3 mm long; keel distinctly beaked, curved through 270°, almost forming a complete coil, ca. 1.5 cm above the wing, with transverse pockets above the petal claws, claws ca. 4 mm long, fused to staminal tube; androecium 2 cm long, vexillary stamen with a basal appendage; anthers oblong-ovate, ca. 1 mm long, basifixed to sub-basifixed to their filaments; pollen grains triporate, with a coarsely reticulate exine, interstitium granular; ovary straight, with a basal nectary disc ca. 1 mm long, ovules 10–11 per ovary, style with a tenuous lower part, upper part thickened, cylindrical, curved, pollen brush 4–5 mm long, with long spreading hairs produced beyond the stigma to form a short conical appendage; stigma transversally-ovate, laterally placed. **Fruit** patent, linear-oblong, flattened, truncate at the apex, valves thin-walled, turning dark brown or black at maturity, densely pilose with yellow hairs, 4.5–6 cm long, ca. 7 mm wide, beak 1 mm long, elastically dehiscent. **Seeds** (immature) D-shaped, ca. 3 × ca. 4 mm, surface smooth, testa brown, hilum oblong, ca. 2 mm long, covered by an epihilum, rim-aril raised, aril when present poorly developed, membranaceous and whitish. Chromosome number: $2n = 22$ (Senff et al. 1992, 1995; Schifino-Wittmann 2000).

Illustrations—Herter (1952) as *Phaseolus ovatus*; Isaguirre and Beyhaut (1997) as *Vigna longifolia*; Cordazzo and Seeliger (1995) as *Vigna luteola*; Snak, Miotto and Goldenberg (2011) as *Vigna longifolia*.

Distribution and Habitat—*Vigna diffusa* occurs in southern Brazilian restinga, a coastal low forest or scrub vegetation on sand, along the coast of Rio Grande do Sul, Santa Catarina, and São Paulo, south to Uruguay (Fig. 3). According to herbarium labels, *Vigna diffusa* was first collected in the nineteenth century on the eastern coast of Madagascar. Three specimens of this species from Madagascar have been found in herbaria, and 1964 was the last time the species was collected on the island. The occurrence in Madagascar is just as likely the result of natural trans-Atlantic dispersal as human introduction because *Vigna diffusa* occurs on coastal sand dunes, flooded or moist environments, and in grasslands and Restinga communities all at sea level. Flowering and fruiting have been registered in most months except June, and August to November.

Etymology—The species name refers to the spreading habit of the species (*diffusus,* spreading).

Vernacular Name—"Feijão-da-praia" (Cordazzo and Seeliger 1995).

Representative Specimens Examined—See Appendix 1 for complete list. **Brazil.** —PARANÁ: Paranaguá, Ilha do Mel, 30 Dec 2009, *C. Snak et al. 269* (UPCB). **Uruguay.** —CANELONES: bords de Santa Lucía, Mar 1867, *E. Gilbert 311* (K, W). **Madagascar.** Sandy dunes near Fort Dauphin, Sep 1890, *G. F. Scott Elliot 3023* (BM, K).

Notes—A new combination is here proposed for the name *Phaseolus diffusus*. Specimens of this species collected by *Tweedie* s.n. (K) and *St. Hilaire* s.n. (P) in southern Brazil were listed by Bentham (1859) under *P. ovatus*. With reference to nomenclatural and taxonomic decisions about the latter see under *V. schottii*.

Vigna diffusa is morphologically similar to *V. schottii* but differs from it by its biauriculate stipules and mainly ovate leaflets. The diagnostic sagittate upper portion of the stipule has a wide base and scarious texture. The ovate to elliptic-ovate (sometime oblong) leaflets are often bicolored, where the main veins are lighter green compared to the darker green leaflet lamina. In addition, although originally described as *Phaseolus diffusus* from Madagascar, *V. diffusa* has the most southerly and easterly distribution of any of the six species of *V.* subg. *Lasiospron* in South America; it is most frequently encountered in coastal habitats of southern Brazil and Uruguay (Fig. 3).

3. VIGNA LONGIFOLIA (Benth.) Verdc., in Kew Bulletin 24: 541 (1970). *Phaseolus longifolius* Benth., Comm. Legum. Gen.: 75 (1837). TYPE: BRAZIL. "ad Brasilia", *Schott* s.n. (holotype: W!). Figure 8.

Phaseolus schottii var. *longifolius* f. *intermedius* Hassl., Candollea 1: 463. 1923. TYPE: PARAGUAY. Chaco. *Hassler* 2769 (G, not seen); *Jörgensen* 2959 (lectotype: G!, designated here; MO!, US! = *V. longifolia*) synon. nov. Syntypes *Rojas* 2917 (SI! = *V. longifolia*). ARGENTINA. *Jörgensen* 2951 (SI! = *V. longifolia*).

Phaseolus schottii var. *longifolius* f. *grandiflorus* Hassl., Candollea 1: 464. 1923. TYPE: PARAGUAY. "in Paraguaria septentrionales", 1901–1902, *E. Hassler* 7320 (lectotype: G!, designated here; isolectotypes: BM!, F!, G!, GH!, MO!, NY!), synon. nov.

Perennial or annual (?), scrambling or climbing vines up to 3 m, with foliage and reproductive parts covered with minute glandular hairs, and a sparse or dense pubescence. **Stems** rhizomatous, hollow, slightly woody at base, often with adventitious roots, sparsely strigose, with yellow, retrorse hairs less than 1 mm long. **Leaves** with stipules narrowly-lanceolate, unequally bilobed, upper portion 4–6 × 1–2 mm, 5–6-veined, not reflexed, persistent; lower portion ca. 2 mm long, sparsely pilose; stipels oblong or triangular, 1.5–2 mm long, subequal in length to petiolules, glabrous except for minute glandular trichomes; petioles 4–10 cm long, covered with retrorse hairs, rachis considerably shorter, 5–20 mm long, with some antrorsely appressed hairs on the adaxial side, canaliculate; leaflets entire, ovate to narrowly ovate or lanceolate, acute or acuminate at apex, often with raised veins below, membranaceous to chartaceous, sparsely to densely strigose, terminal leaflet 9–15 × 1.3–5.5 cm, lateral leaflets 7–11 × 2–5.5 cm. **Inflorescences** up to 35 cm long, peduncles 14–32 cm long, covered with short retrorse hairs, densely strigose distally; rachis 1.5–3 cm long, with 2–4 swollen ovoid nodes, these 2–4 mm long, with 4–6 alternate orifices, flowers clustered distally; primary bracts, caducous, secondary bracts ca. 6 mm long, caducous; bracteoles mostly persistent at anthesis, 6–10 mm long, longer than calyx tube; pedicels shorter than calyx tube, longer and twisting in fruit, covered distally with retrorse, straight hairs; calyx campanulate, sparsely strigose at the base, glabrous distally, 4–5 × 2–3 mm, upper teeth slightly divided, narrow and acute, not forming a lip, other teeth triangular, subequal, 1.5–2 mm long, lower tooth slightly longer than lateral teeth. **Flowers** golden yellow, ca. 2.5 cm long, standard petal asymmetric, broadly ovate, ca. 2 × ca. 2.5 cm, bilobed at apex, with two parallel, thick callosities on the lamina above the point of folding, and two fleshy auricles above a short claw; wing petals longer than keel, with an obovate lamina, ca. 2.5 × ca. 1.5 cm, with an auricle at base, claw ca. 3 mm long; keel distinctly beaked, coiled ca. 360°, almost forming a complete circle, ca. 1.5 cm above the wing, with transverse pockets above the claws, claws ca. 4 mm long, fused to staminal tube; androecium ca. 3.5 cm long, staminal tube ca. 2.5 cm long, vexillary stamen with a basal appendage; anthers oblong-ovate, ca. 1 mm long, basifixed to sub-basifixed to filaments; pollen grains triporate, with a coarsely reticulate exine; ovary straight, with a basal nectary disc ca. 1 mm long, ovules 12–14, style with a tenuous lower part, upper part thickened and cylindrical, curved, pollen brush ca. 8 mm long, with long spreading hairs, produced beyond the stigma to form a short hook; stigma transversally-ovate, laterally placed, surrounded by short cilia. **Fruit** patent, oblong to slightly falcate, sub-cylindrical, valves thick-walled, not constricted between the seeds, turning dark brown or black at maturity, (4–)6–8 cm long, 5–6 mm wide, elastically dehiscent, densely strigose, with yellow and white, straight hairs, beak straight, 5–7 mm long. **Seeds** globose to D-shaped, ca. 3 × ca. 4 mm, surface smooth, testa light brown, mottled darker brown, hilum oblong, as long as seed width, rim-aril prominent, covered by an epihilum, aril consistently present, hippocrepiform, cartilaginous with white-banded crenate margins, mostly surrounding the hilum. Chromosome number: $2n = 22$ (Mercado-Ruaro and Delgado-Salinas 1996). Figure 8.

Distribution and Habitat—Southern Mexico (Campeche, Chiapas, Tabasco, Veracruz), Central America (Guatemala, El Salvador, Costa Rica, Panamá) and in South America, Amazon River basin, and Amazonian savannas, Restinga Atlantic Forest and in the Paraguay-Paraná fluvial system (Argentina, Bolivia, Brazil, Colombia, Ecuador, Paraguay, Perú, Venezuela). Although widely distributed, this species has not to our knowledge been collected in Guyana, French Guiana, and Suriname. *Vigna longifolia*, as well as *V. lasiocarpa*, have been collected in the Pacific lowlands of Ecuador (Guayas Province), the most western location for species of *V.* subg. *Lasiospron* in South America. This species also has one of the most southern occurrences of a *V.* subg. *Lasiospron* species in northeastern Argentina (Fig. 3). *Vigna longifolia* generally inhabits seasonal or permanently flooded plains or savannah-type grasslands, and is sometimes reported sprawling on floating vegetation. It also grows in old rice fields; altitudinal range from 0–600 m. Flowering and fruiting throughout the year.

Etymology—The species epithet *longifolia* refers to the long, narrow leaflets.

Vernacular Names—"Baul ch'ó" (*E. Ucan* 1607); "feijão bravo" (*Melo* 3352); "Siratro de Agua" (*Lock* 83/66).

Uses—The species is relished by livestock, and its seeds are eaten by birds (Pott and Pott 1994).

Representative Specimens Examined—See Appendix 1 for complete list. **Argentina.** —CHACO PROVINCE: Colonia Benítez, without date, *A. G. Schulz* 10328 (G). **Bolivia.** —EL BENI: Trinidad, Jan 1965, *O. Braun* 11 (US). **Brazil.** —AMAZONAS: Alenquer, Margem do Rio Amazonas, 30 May 2014, *C. Snak et al. 1216* (HUEFS). **Colombia.** —AMAZONAS: Río Lontoyacu, 2 Oct 1946, *R. E. Schultes* 46–173 (US). **Costa Rica.** Guanacaste Province, Cantón Bagaces P.N. Palo Verde, valle de Tempique, Sector Catalina, La Espuela y el área administrativa de Palo Verde, 10°21'0''N, 85°21'0''W, 10 m, 22
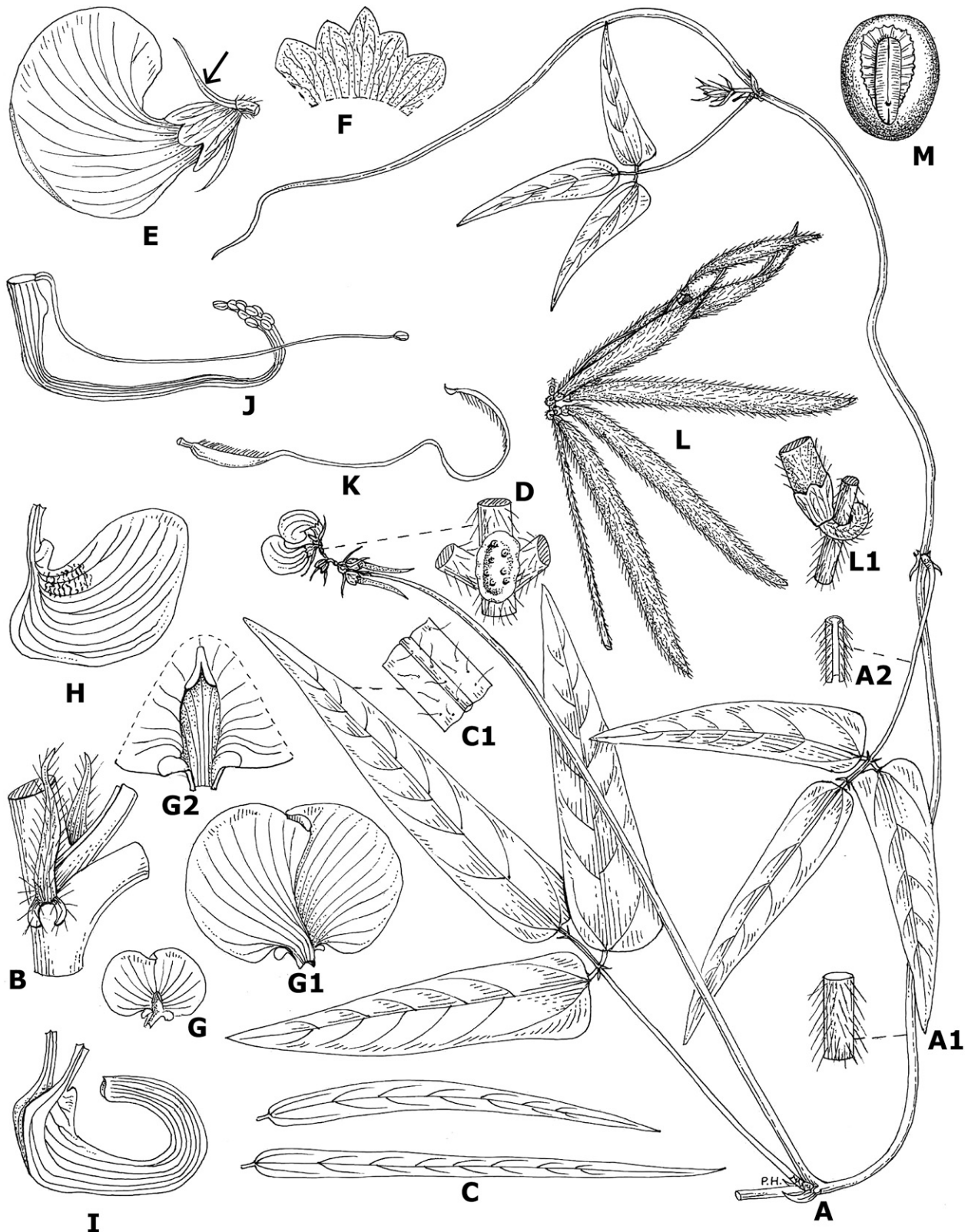
FIG. 8. Illustration of *Vigna longifolia*. A. Habit, natural size. A1. Portion of stem. A2. Portion of petiole. B. Stipules, only a portion of indumentum shown for clarity (× 6). C. Leaflets showing variation in shape (natural size). C1. Detail of vein. D. Extrafloral nectaries on inflorescence node (× 6). E. Flower bud (pre-anthesis), including bracteoles, indicated by arrow (× 3). F. Calyx opened out, external surface (× 3). G. Standard petal, ventral surface (× 0.5). G1. Standard petal, external surface (× 1). G2. Standard petal inner surface showing thickenings and auricles (× 6). H. Wing petal (× 3). I. Keel petals, drawn from young flower (× 3). J. Staminal tube with free vexillary stamen (× 3). K. Gynoecium (× 3). L. Fruits, natural size. L1. Twisted pedicel at base of fruit. M. Seed (× 6). Drawn from *Barbosa & Silva 1927* (habit and flower dissection); *Herbarium Lehmannianum 8757* (fruit and seed). Illustration by Pat Halliday.

Sep 1994, *U. Chavarría 1047* (K). **Ecuador.** —Guayas: Estación Psicícola Santa Priscila, Est. 3, 2°23′0″N, 79°46′W, 5 m, 20 May 2000, *X. Cornejo and C. Bonifaz 7049* K). **El Salvador.** —Ahuachapán: A.P. Santa Rita, ruta 7, La Laguna, 13°48′0″N, 90°4′0″W, 20 m, 12 Apr 2004, *J. M. Rosales 2365* (MEXU). **Guatemala.** Depto. Jutiapa, potreros between Trapiche Vargas and Asunción Mita, 500–600 m, 15 Nov 1939, *J. A. Steyermark 31881* (F). **México.** —Campeche: Hopelchén District, a 2.2 km al ENE de Chun-Ek, 19°11′42″N, 89°10′25″W, 90 m, 26 Aug 2005, *D. Álvarez 11670* (MEXU). **Panamá.** —Canal Zone: vicinity of Frijoles, 3 Mar 1923, *C. V. Piper 5164* (US). **Paraguay.** —Chaco: campos bajos estero Estancia Loma Pará, Apr 1917, *T. Rojas 2917* (SI). **Perú.** —Loreto: Lower Río Nanay, May-Jun 1929, *Ll. Williams 555* (US). **Venezuela.** —Apure: Payarita, entre San Fernando y Achaguas, Bajo Apure, 12 Aug 1972, *M. Ramia 4852* (VEN).

Notes—Bentham (1859) considered *Phaseolus longifolius* and *P. schottii* as conspecific, placing the latter as a synonym of the former. As mentioned above, Hassler (1923) recognised *P. schottii* published earlier in Bentham's (1837) treatment, and he published four varieties, *P. schottii* var *genuinus*, *P. schottii* var. *campestris*, *P. schottii* var. *longifolia*, and *P. schottii* var. *tucumanensis*. In our treatment, the typical variety is discussed under *Vigna schottii*, and varieties *campestris* and *tucumanensis* under *V. juruana*.

In more recent classifications (Verdcourt 1970; Maréchal et al. 1978), *Vigna longifolia* included three of the six species here considered as part of *V.* subg. *Lasiospron*. The species *V. diffusa*, *V. schottii* and for some time even *V. trichocarpa* were considered as synonyms of this distinctive species. *Vigna longifolia* is distinguished from the other *V.* subg. *Lasiospron* species by a combination of features, including its bi-auriculate stipules with a long, narrowly triangular upper portion, up to 6 mm long, and lanceolate leaflets, up to 15 cm long. Its flowers are approximately 2 cm long, with a conspicuous hooked style tip. The long-tapering pods with thick-walled valves have seeds each with a conspicuous white aril. Seeds with cartilaginous white arils are also consistently present in *V. lasiocarpa*.

4. Vigna lasiocarpa (Mart. ex Benth.) Verdc., in Kew Bulletin 24: 539 (1970).

Phaseolus lasiocarpus Mart. ex Benth., Comm. Legum. Gen.: 76 (1837). TYPE: BRAZIL. "ad Ega Amazonum", *Martius s.n.* (lectotype: M!, designated here; isolectotype: M!). *P. pilosus* Kunth var. *lasiocarpus* (Mart. ex Benth.) Hassl., Candollea 1: 465 (1923). See nomenclatural notes below.

Phaseolus pilosus Kunth, Nov. Gen. Sp. 6: 453 (1823). TYPE: [COLOMBIA]. "crescit in arenosis fluminis Magdalenae, prope Morales", *Humboldt & Bonpland 1542* (holotype: P!; isotype: B–W!, annotated as *P. hirtus*).

P. pilosus Kunth var. *genuinus* Hassl., Candollea 1: 465 (1923).

Phaseolus hirsutus Mart. ex Benth., Comm. Legum. Gen.: 76 (1837). TYPE: BRAZIL. "in campis provinciae Rio Negro", *Martius s. n. [2729]* (lectotype: M!, designated here).

Phaseolus balansae Micheli, Mem. Soc. Phys. Hist. Nat. Genéve 28(7): 29, Contr. Flor. Paraguay 1:29. Figure 8 (1883). TYPE: PARAGUAY. "cosme inter Villa Rica et Caaguazu, in pratis, Mart.", *M. Balansa 1549* (holotype: G; isotypes: P-2!).

P. lasiocarpus var. *balansae* (M. Micheli) Chod. & Hassl., in Bull. Herb. Boiss. 2: 909 (1904).

Phaseolus lasiocarpus var. *igatimianus* Chod. & Hassl., in Bull. Herb. Boiss. 2: 909 (1904). TYPE: PARAGUAY. [Canindeyú Department], "iter ad Yerbales montimun Sierra de Maracayú, in regione vicini Igatimí", Nov 1885, *E. Hassler 5535* (holotype: G, not seen; isotypes: BM!, F!, MO!, NY!, P!, W!).

Phaseolus diversifolius Pittier, Bol. Tecn. Minist. Agric. 5: 56 (1944). TYPE: VENEZUELA. Anzoátegui, sabanas de Guaraguara, cerca de Santamé, *H. Pittier 14302* (holotype: not traced), non *P. diversifolius* Pers., Syn. Pl. 2(2): 296 (1807).

Perennial scrambling or climbing vine up to 5 m or more, foliage and reproductive parts covered with long yellow (rarely brown) hairs, and minute glandular hairs intermingled, pubescent or glabrescent. **Stems** herbaceous, fibrous (sturdy), older stems woody, with nitrogen fixing nodules, often with adventitious roots with nodules, sparsely to densely pilose with yellowish-fulvous, straight hairs. **Leaves** with stipules ovate-lanceolate, often apiculate, unequally bilobed, upper portion 4–7 × 1–2 mm wide, obscurely veined; lower portion ca. 2 mm long, sometimes adnate to the stem, densely strigose; stipels oblong to triangular, 1–2 mm long, shorter than petiolules, 2-veined, covered with minute glandular trichomes; petioles 4–6 cm long, covered with hirsute, retrorse hairs, rachis considerably shorter, 5–10 mm long, with antrorsely appressed hairs, canaliculate; leaflets entire or lobed, with sinuous margins, oblong to ovate or widely ovate, sometimes rhombic or linear-lanceolate, usually obtuse or acute or even acuminate at apex, often with raised veins below, chartaceous, densely strigose to softly pilose on both surfaces, usually more densely so beneath; terminal leaflet 4–11.5 × 2.5–5 cm, lateral leaflets 3–9.5 × 2–4.5 cm. **Inflorescences** 10–50 cm long, peduncles up to 45 cm long, covered with straight, retrorse hairs, densely strigose distally; rachis 3–5 cm long, with (3–)5–8(–9) swollen nodes, these oblong, 2–4 mm long, with ca. 10 secretory orifices in two parallel rows, flowers clustered distally; primary bracts caducous, secondary bracts lanceolate, 8–10 mm long, caducous; bracteoles mostly persistent at anthesis, lanceolate, 6–15 mm long; pedicels shorter than calyx tube, 3–5 mm long, longer and twisting in fruit, covered with retrorse, straight hairs, antrorse at base of calyx; calyx campanulate, densely hirsute-strigose, tube longer than teeth, 5.5–10 × 3.5–8 mm, upper teeth deeply divided and broadly rounded at apex forming a lip; 5–6 × 5–6 mm, sinuses 3 mm, lower lip with lateral teeth oblong and rounded, 5–6 × 2–3 mm, and with the middle lower tooth 4–5 × 2 mm. **Flowers** golden yellow, (1.8–)2.5–3.5 cm long, standard petal asymmetric, broadly ovate, 2.5–3 × 2.7–3 cm, bilobed at apex, two parallel, thick callosities on the lamina above the point of folding, and two fleshy auricles above a short claw; wing petals longer than keel, with an obovate lamina, 2.5–3.5 × ca. 1.5 cm, with a prominent auricle at base, ca. 2 mm long, claw ca. 4 mm long; keel distinctly beaked, curved through 360°, forming a complete coil, ca. 3 cm above the wing, with transverse pockets above the claws, claws 4–5 mm long, fused to staminal tube; androecium 3.5–4 cm long, staminal tube ca. 3 cm long, vexillary stamen with a basal appendage; anthers oblong-ovate, ca. 1 mm long, basifixed to sub-basifixed to filaments; pollen grains triporate, with a coarsely reticulate exine, interstitium granular; ovary straight, with a basal nectary disk ca. 1 mm long, ovules 16–18, style with a tenuous lower part, upper portion thickened, cylindrical, curved, pollen brush 7–10 mm long, with long spreading hairs, produced beyond the stigma to form a short hook; stigma transversally-ovate, laterally placed. **Fruit** patent or rarely ascending, linear-oblong, cylindrical, truncate at the apex, valves coriaceous to woody, turning dark brown or black at maturity, densely pilose with a

mixture of white and yellow hairs becoming more brownish at the sutures and base, 6–9 cm long, 7–11 mm wide, elastically dehiscent, beak 2–3 mm long, seeds arranged obliquely. **Seeds** oblong, subglobose, 3–4 × 3–4 mm, surface smooth, testa brown, hilum oblong, ca. 2 mm long, covered by an epihilum, rim-aril raised, with a white, excentric hippocrepiform aril consistently present towards the lens. Chromosome number: $2n = 20$ (Maréchal 1969, as *P. pilosus* Kunth; Mercado-Ruaro and Delgado-Salinas 1996).

Illustrations and Photographs—Bentham (1859) as *Phaseolus lasiocarpus,* or in http://floraBrasiliensis.cria.org.br; Micheli (1883) as *Phaseolus balansae*; Pittier (1944) as *Phaseolus lasiocarpus*; Lackey and D'Arcy (1980) as *Vigna lasiocarpa*; Lewis and Owen (1989) photographs of flower and fruit, as *V. lasiocarpa*; Pott and Pott (2000) photograph of *V. lasiocarpa*.

Distribution and Habitat—The species occurs in southern Mexico (Campeche, Chiapas, Oaxaca, Tabasco, Veracruz, and Yucatán); Central America (Belize, Costa Rica, El Salvador, Honduras, Nicaragua, and Panamá); South America (Colombia, Venezuela, Guyana, French Guiana, Suriname, Bolivia, Brazil, Ecuador, Perú, Paraguay, and Argentina) and in the Dominican Republic (Fig. 3). Mainly in seasonal or permanently flooded plains or savannas or swampy grasslands, reported growing in sugar plantation ditches and on bank edges of rice fields; mostly from sea level to ca. 600 m, but ascending in México and Colombia to 1200 m. In South America, in the Solimões and Amazon River basins, and in the Paraguay-Paraná fluvial system. An ecological study of aquatic macrophyte diversity in the Pantanal Matogrossense National Park found *Vigna lasiocarpa* to be one of the most frequent species and distributed among ca. 60% of the 17 sampling sites (Pott et al. 2011). Flowering and fruiting occur throughout the year.

Vernacular Names—"Frijolillo" (*H. Vibrans* 8246), "Feijãozinho-do-brejo" (Pott and Pott 2000).

Etymology—The species epithet alludes to the hairiness of the fruits (*Lasio* woolly or hairy and *Carpus* fruit).

Uses—The species is relished by livestock, and its seeds are eaten by birds (Pott and Pott 2000).

Representative Specimens Examined—See Appendix 1 for complete list. **Argentina.** —Corrientes: Depto. Santo Tomé, Estancia Garruchos, 14 Feb 1960, *T. M. Pedersen* 5446 (RBGE, US). **Belize.** —Stann Creek District: Carib Switch, Stann Creek-Middlesex Road, 13 Jan 1953, *P. H. Gentle* 7839 (MEXU). **Bolivia.** —El Beni: Trinidad, 236 m, *O. Braun* 75 (US). **Brazil.** —Acre: Rio Branco, Amazonia, Baixo Rio Branco, 1 Jan 1948, *R. de Lemos Fróes* 23013 (NY). **Colombia.** —Cauca: east of Aganche, 1200–1500 m, 14 Jul 1922, *F. W. Pennell* 8328 (NY). **Costa Rica.** —Alajuela: Alfaro Ruiz, entre Tapezco de Arriba y Tapezco de Abajo, 1900 m, 12 Nov 1964, *A. Jiménez M.* 1145 (NY). **Dominican Republic.** —San Cristóbal: Station Hatillo, 1 Nov 1977, *A. H. Liogier* 9073 (NY). **Ecuador.** —Guayas: Milagro, 50 m, 30 Jun 1923, A. S. Hitchcock 20275 (NY US). **El Salvador.** —Ahuachapán: A.P. Santa Rita, ruta 7, La Laguna, 13°48′0′′N, 90°4′0′′W, 20 m, 12 Apr 2004, J. M. Rosales 2355 (MEXU). **Guyana.** Demerara-Mahaica Region, east coast Demerara, Cane Grove Conservancy, Flagstaff, 6°37′60″N, 57°55′60′′E, 19 Feb 1989, L. J. Gillespie 706 (US). **Honduras.** —Cortés: en bananales de La Lima, 60 m, Jun 1977, *R. H. Stover* 4 (MEXU). **México.** —Campeche: Municipio Champotón, Aguada Paraíso, 18°55′60′′N, 90°21′0′′W, 12 m, 15 Oct 1981, *C. Chan* 887 (XAL). **Nicaragua.** —Managua: Banco de Germoplasma, Hacienda Experimental de la Universidad Centroamericana, 15 Nov 1984, *D. Soza* 247 (MO). **Panamá.** —Chiriquí: vicinity of San Félix, eastern Chiriquí, 1 Jan 1912, *H. Pittier* 5225 (US). **Paraguay.** —Alto Paraná: in regione fluminis Alto Paraná, 1 Oct 1909, *K. Fiebrig* 6177 (BM, SI, US). **Perú.** —Loreto: Mishuyacu, near Iquitos, 100 m, 1 Feb 1930, *C. Klug* 1022 (NY, US). **Suriname.** —District Nickerie: Nickerie, 28 Jun 1951, *A. T. Semple* 358 (US). **Venezuela.** —Amazonas: at Cerro Yavita, Río Atabapo, Río Orinoco; 19 Oct 1950, *B. Maguire* 29294A (NY).

Notes—Verdcourt (1970) designated *Vigna lasiocarpa* as the type species of *V.* sect. *Lasiospron* and, in addition, gave reasons for selecting the species *Phaseolus lasiocarpus* opposed to *P. pilosus* or *P. hirsutus*. Unfortunately, no lectotype was designated at that time between the two cited syntypes under *P. lasiocarpus*. Both syntypes were studied by us, and the Martius collection at M has been designated as lectotype. Regarding the original material of *P. hirsutus* at M, all syntypes were found except the one of Poeppig. The lectotype here designated is the Martius specimen from Rio Negro, which bears a description of this species in Martius' handwriting. Recently, Cremers and Hoft (1998), following Grisebach (1860), listed *Dolichos jacquinii* DC. (De Candolle 1825) in synonymy under *V. lasiocarpa*; however, no new combination was proposed by those authors. De Candolle published *Dolichos jacquinii* for a plant described by Jacquin (1788) from the Caribbean jungles under the epithet *D. lignosus* L. (Linnaeus 1753). No type specimen of the binomial has been found at G-DC or at BM-Banks herbarium, and only the species description can be used to interpret the name. Jacquin described a plant with white flowers on peduncles shorter than the leaves, and long straight pods with 18 seeds. Although *Vigna lasiocarpa* sometimes has pods containing 18 seeds, its inflorescences always exceed the length of the leaves and the species never has been reported to have white flowers. Thus, from its description *Dolichos jacquinii* is not identifiable as *V. lasiocarpa*, and the decision here is to exclude this name.

Phaseolus diversifolius Pittier was proposed as a synonym of *V. lasiocarpa* by Aymard (1999). We have not seen Pittier's plant and, thus, cannot comment upon its identity. The protologue of *Phaseolus diversifolius* is not in Latin and the name has been shown to be a later homonym of *P. diversifolius* Pers. (Persoon 1807). Therefore, in accordance with Article 53 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018), this species was not validly published, and the name is unavailable for use.

Vigna lasiocarpa is the most vigorous and conspicuous of all the species of *V.* subg. *Lasiospron*. It is most similar in overall morphology to its sister species *V. longifolia*. *Vigna lasiocarpa* differs from *V. longifolia* in being more often pubescent (especially on the leaves), having longer and wider calyces with the upper teeth more deeply divided and broadly rounded at the apex to form a lip, and having longer and thicker fruits. Both species have distinctive arillate seeds. *Vigna lasiocarpa* is the only species in the subgenus, up to now, that has been reported as a dysploid.

5. **Vigna trichocarpa** (C. Wright) A. Delgado, Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1254 (1993). *Phaseolus trichocarpus* C. Wright, in F. A. Sauvalle, An. Acad. Ci. Habana, Rev. Ci. 5: 337 (1869) and in Fl. Cuba: 30 (1873). TYPE: CUBA. [Pinar del Río Province], "en la orilla de las lagunas dentro del agua. Vuelta Abajo", no date, *C. Wright* s.n. (holotype: GH!; isotypes: BM!, G-2!, K-3!, MO!, NY-3!, P!, US!, WU!). (See notes). Figure 9.

Phaseolus ovatus Benth. var. *glabratus* Benth., in Mart. Flora Brazil. 15(1): 188 (1859). TYPE: BRAZIL. "prope Bahiam, in humidis cum forma pilosa", *W. D. Salzmann* s.n. (holotype: M, not seen; isotypes: K!, MO!, RBGE!). non sensu Chodat & Hassler, Bull. Herb. Boiss. Ser. 2, 4: 909. (1904).

Phaseolus schottii var. *campestris* forma *transiens* Hassl., Candollea 1: 464. 1923. TYPE: BRAZIL. Bahia in pratis humedis, *W. D. Salzmann* s.n. (holotype: G-DEL, not seen; isotypes: K!, MO!, RBGE!), **synon. nov.** (See notes).

Phaseolus lanceolatus Bello, Anales Soc. Esp. Hist. Nat. 10: 262 (1881). TYPE: PUERTO RICO. Without locality, *Bello* s.n. (holotype: B, destroyed). Neotype designated by Santiago-Valentín et al. Taxon 64: 333, 2015: Puerto Rico, Pueblo Viejo, 19 July 1914, *J.A. Stevenson* 2097 [NY, barcode 01007063].

Phaseolus schottii var. *campestris* forma *guyanensis* Hassl., Candollea 1: 464. 1923. TYPE: FRENCH GUIANA. Without locality, *Poiteau* s.n. (G, not seen) **synon. nov.** (See notes).

Phaseolus productus Ducke, Arch. Jard. Bot. Río de Janeiro 4: 99 (1925). TYPE: [BRAZIL. Pará State], "in campis inundatis Jutahy inter Almeirim et Prainha inter frutices ad ripam fluminis", 16 Apr 1923, *Ducke* s.n. (lectotype: RB!, No. 17.285, designated here).

Vigna paludosa Milne-Redh., Kew Bulletin 2: 27 (1947). TYPE: SIERRA LEONE. Rokupr, common among grass in swamps, 29 Jan 1935, *Deighton* 2953 (holotype: K!).

Perennials or annuals (?), scrambling or climbing vines up to 3 m, with foliage and reproductive parts covered with minute glandular hairs, and sparse or dense pubescence. **Stems** hollow, slightly woody at base, often with adventitious roots, sparsely to densely strigose, with yellow, retrorse hairs. **Leaves** with stipules ovate to narrowly-lanceolate, spurred, upper portion 8–12 × 1–2 mm, 5–6-veined, not reflexed, persistent; lower portion 3–4 mm long, sparsely pilose; stipels oblong or triangular, ca. 1.5 mm long, subequal in length to petiolules, glabrous except for minute glandular trichomes; petioles 3.5–8 cm long, covered with retrorse hairs, rachis considerably shorter, ca. 1 cm long, with some antrorsely appressed hairs on the adaxial side, canaliculate; leaflets entire, ovate, narrowly ovate, to lanceolate, acute or acuminate at apex, with raised veins below, membranaceous; sparsely to densely strigose, terminal leaflet 3.5–11 × 1.5–3 cm, lateral leaflets 7–9 × 2–3.5 cm. **Inflorescences** up to 22 cm long, peduncles 16–20 cm long, covered with short retrorse hairs, densely strigose distally; rachis 1.5–2 cm long, with 1–4(–5) nodes, the nodes oblong, spatuliform, 2–3 mm long, orifice distribution scalariform, with transverse separations, flowers clustered distally; primary bracts, caducous, secondary bracts ca. 6 mm long, caducous; bracteoles mostly persistent at anthesis, 5–8 mm long, longer than calyx tube; pedicels shorter than calyx tube, 1–2 mm long, longer and twisting in fruit, covered distally with retrorse, straight hairs; calyx campanulate, sparsely strigose at the base, glabrous distally, 1.5–2 × ca. 2 mm, upper teeth slightly divided, narrow and acute, not forming a lip, teeth triangular, subequal, 0.5 mm long, lower tooth slightly longer than lateral teeth. **Flowers** golden yellow, 8–12 mm long, standard petal asymmetric, broadly ovate, ca. 10 × ca. 10 mm, bilobed at apex, with two parallel callosities on the lamina above the point of folding, and two fleshy auricles above a short claw; wing petals longer than keel, with an obovate lamina, ca. 1.2 cm long, 5–6 mm wide, with an auricle at base, claw ca. 1.5 mm long; keel distinctly beaked, coiled through ca. 360°, almost forming a complete circle; ca. 7 mm above the wing, with transverse pockets above claws, the claws ca. 2 mm long, fused to the staminal tube; androecium ca. 1.5 cm long, vexillary stamen with a basal appendage; anthers oblong-ovate, ca. 1 mm long, basifixed to sub-basifixed to filaments; pollen grains triporate, with a coarsely reticulate exine; ovary straight, with a basal nectary disc ca. 0.5 mm long, ovules 7–8 per ovary, style with a tenuous lower part, upper portion thickened, cylindrical, curved, pollen brush 2–3 mm long, with long spreading hairs, produced beyond the stigma to form a conical appendage; stigma transversely-ovate, sub-apically placed. **Fruit** ascending, oblong, flattened, valves thin-walled, not constricted between the seeds, turning dark brown or black at maturity, sparsely strigose, with yellow, straight hairs, (3–)3.5–4 cm long, 6–7(–8) mm wide, beak 2 mm long, straight, elastically dehiscent. **Seeds** D-shaped, 2–3.5 × 3–4 mm, surface smooth, testa light to dark brown, hilum oblong, as long as seed width, rim-aril distinctly raised, covered by an epihilum, lacking a cartilaginous aril. Seedlings with hypogeal germination, eophylls without stipules. Figure 9.

Illustrations—Berhaut (1976) as *Vigna paludosa* Milne-Redh. Maxted et al. (2004) and Acevedo-Rodríguez (2003) as *Vigna longifolia*.

Distribution and Habitat—Southern Mexico to Brazil, including the Greater Antilles, and likely native in west Africa (Fig. 3). In general, in seasonal or permanently flooded plains or marshy environments, sometimes reported in coastal vegetation and sprawling in floating plant islands in rivers and lakes of South America, or growing in old rice fields; altitude 0 to 300 m. Flowering and fruiting have been recorded throughout the year, except in June. In South America, in the Solimões and Amazon River basins and northern Restinga Atlantic Forest and in the Paraguay-Paraná fluvial system and the southern Restinga Atlantic Forest.

Etymology—The specific epithet refers to the plant's hairy fruits (*Trichos* hairs and *Carpos* fruit).

Vernacular Names—"Feijãozinho amarelo" (Brazil). "Habichuela cimarrona" (Puerto Rico).

Representative Specimens Examined—See Appendix 1 for complete list. **Belize.** —Stann Creek District: ca. one mile, WSW of Hopkins, 17 Apr 1976, *G. R. Proctor 35795* (IJ, MO). **Bolivia.** —Santa Cruz: Velasco Province, Reserva Ecológica El Refugio, 14°45′47″S, 61°52′51″W, 100 m, 15 Oct 1994, *T. J. Killeen 6839* (MEXU). **Brazil.** —Amazonas: District Careiro, Lago Redondo, 3 Jan 1964, *G. Marlier 14375* (US). **Colombia.** —Chocó: Río Atrato, 2–5 hr below Río Sucio, above Loma Teguerre, 16 May 1967, *J. A. Duke 10988* (MO, NY). **Costa Rica.** —Cartago: Instituto Interamericano de Ciencias Agrícolas, 609 m, 1 Feb 1959, *A. T. Semple 1* (US). **Dominican Republic.** —Samaná: Sánchez District, sección La Majagua, Yaqueson (Jackson), entre caño La Bestia y caño Punta Arena, 19°16′0″N, 69°31′60″W, 30 Mar 1996, *B. Peguero 134* (MEXU). **French Guiana.** 10 km west of Mana, Savane de Criques Jacques, near St. Laurent, 19 Dec 1954, *R. S. Cowan 38884* (NY, US); St. Laurent do Maroni, 24 Feb 1914, *R. Benoist 75* (P). **Guatemala.** —Petén: Lake Zotz, 18 May 1933, *C. L. Lundell 3299* (MICH). **Guyana.** Siparuni-Potaro Region, Essequibo R., near Iwokrama Rainforest Reserve, 4°16′60″N, 58°30′0″W, 65 m, 20 Mar 1996, *D. Clarke 1356* (NY). **Honduras.** —Cortés: Agua Azul tract No. B. North shore of Lake Yojoa near the canyon, 16 Aug 1951, *P. Kamb 2092* (BM). **Jamaica.** —Slipe District: without locality, 22 Jul 1973, *G. R. Proctor 33461* (IJ). **México.** —Tabasco: ejido San Ramón, campo petrolero San Ramón, 17 Jun 1996, *G. Ortíz 2051* (MEXU). **Nicaragua.** —Río San Juan: delta of Río San Juan, 23 Mar 1961, *G. S. Bunting 829* (F, US). **Panamá.** —Canal Zone: bridge over inlet of Limón Bay, S of Ft. Sherman, 22 Aug 1960, *J. E. Ebinger 975* (MO). **Perú.** —Loreto: Province Maynas, Urco-Cocha, comunidad de Várgea, 10 Aug 1998, *A. Zamora U. 11* (HUT). **Puerto Rico.** Guaynabo, 3 Jul 1924, *H. H. Whetzel 1* (BH); Pueblo Viejo, no date, *J. A. Stevenson 2097* (NY). **Suriname.** —Commewijne District: Charlottenburg, no date *Wullschlaegel* s.n. (W). **Senegal.** —Regione de Sédhiou: Ile du Diable, Silinki, Sorange, Forest de Bondié, 2 Mar 1964, *R. P. Berhaut 7165* (M-2). **Sierra Leone.** Madina (Buya-Romende), 11 Aug 1953 *H. D. Jordan 907* (K).

Notes—Howard (1988), using the sparse information available for Wright's collections in Cuba, listed among nine collections of *Phaseolus*, two collections named as *P. trichocarpus*: *C. Wright* s.n., and *C. Wright 2341*. The latter was collected in San Mateo (Pinar del Río), whereas the former lacking a collection number was given no exact collection locality. Furthermore, Howard considered as the holotype the specimen
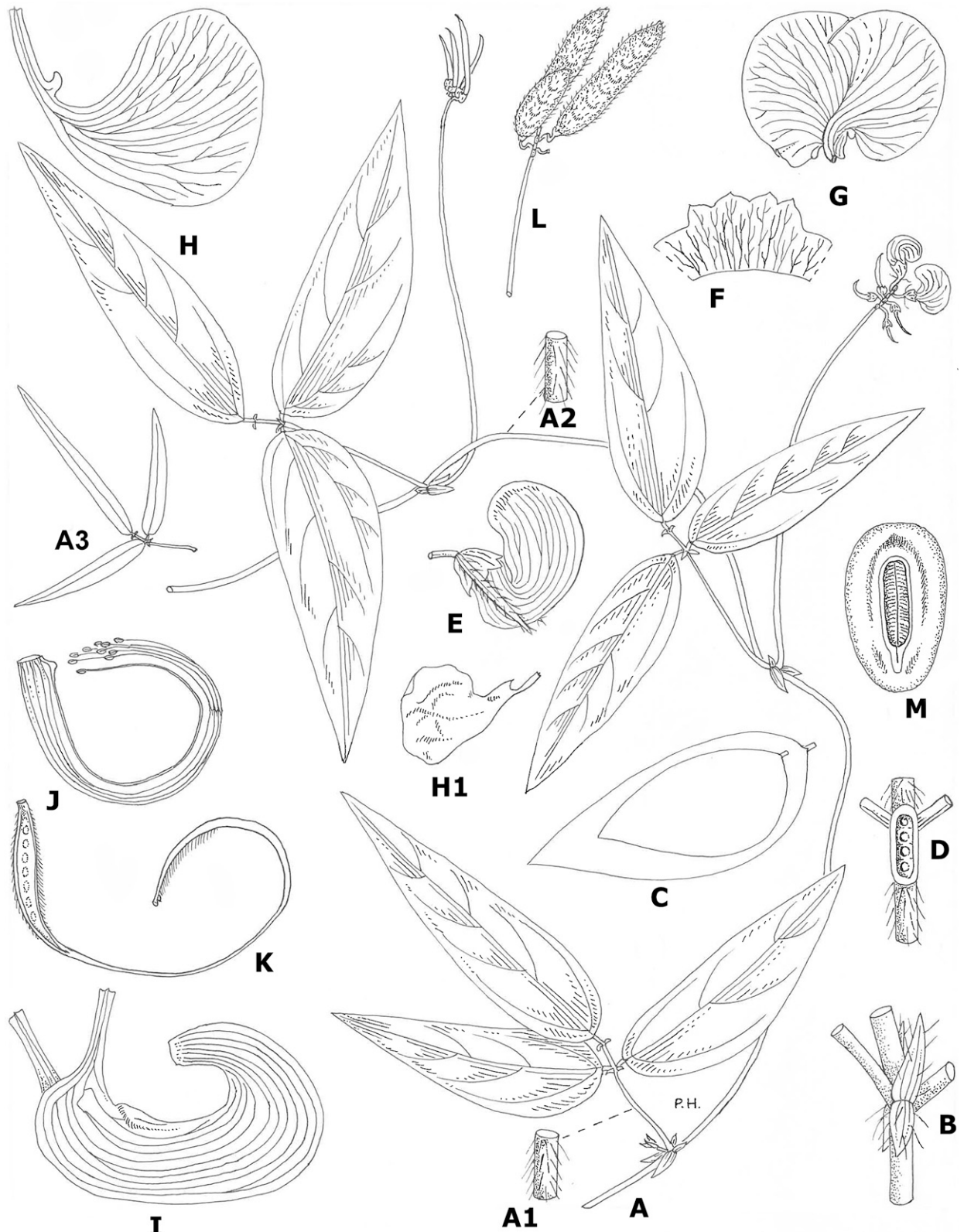
FIG. 9. Illustration of *Vigna trichocarpa*. A. Habit, natural size. A1. Portion of petiole. A2. Portion of stem. A3. Leaf showing narrow leaflets. B. Stipules (× 3). C. Variation in leaflet shape outlines (× 1). D. Extrafloral nectaries on inflorescence node (× 6). E. Flower bud, including bracteoles (× 3). F. Calyx opened out, external surface (× 6). G. Standard petal outer surface (× 3). H. Wing petal (× 6). H1. Wing petal from bud (× 3). I. Keel petals (× 6). J. Staminal tube with free stamen (× 6). K. Gynoecium (× 6). L. Fruits, natural size. M. Seed, hilar view (× 9). Drawn from *Jansen Jacobs 4681* (habit and flower); *Berg et al. 19796* (fruit and seed); *Prance et al. 8048*; *Berg et al. 19796*; *Glaziou 9392* (leaflet outlines). Illustration by Pat Halliday.

at GH of *Wright 2341*, although Wright's protologue mentions a plant listed by Grisebach as *P. ovatus* non Benth., "growing in the water, next to the shore of the lagoons in Vuelta Abajo." Vuelta Abajo is also located in the Cuban province of Pinar del Río, and was several times visited by Wright in 1862 (21, 22 July, 4 August, 4 November). Delgado-Salinas (1993) transferred *Phaseolus trichocarpus* C. Wright to *Vigna*, and designated as lectotype the same collection *C. Wright 2341*, pointing out that the holotype might possibly be found in HAB. Numerous duplicates of *C. Wright 2341* as well of *C. Wright* s.n. were distributed to different herbaria (BM, G-2, K-3, MO, NY-3, P, US, WU). In some herbaria (e.g. MO), both collections were mounted on the same sheet. The specimen at US even has a different collection locality: La Habana, Playa Santa Ana, with the collection year given as 1860, whereas duplicates at NY, US, and WU show 1865 as the year of collection.

Bello's type material of *Phaseolus lanceolatus* is no longer extant at B. With no original material, Bello's description, particularly of the stipules and the collecting locality (Puerto Rico), leaves little doubt as to the plant's identity. A neotype was designated by Santiago-Valentín et al. (2015).

As mentioned earlier, we did not locate the type specimen of *P. schottii* var. *campestris* forma *guyanensis* and, therefore, we have accepted Amshoff's (1939) taxonomic decision in placing it under *Phaseolus trichocarpus* (= *Vigna trichocarpa*). Regarding the forma *transiens* of Hassler, Salzmann's collection from Bahia, Brazil "in humidis" with Bentham's handwriting on the specimen was designated as lectotype. It is important to mention that different collections of *Phaseolus* were made by Salzmann in Bahia and those have been considered in different publications under different names: Bahia in humidis "*Phaseolus luteus*," 1831, *Salzmann* s.n. (RBGE); Bahia, in collibus humidis, *Phaseolus luteus*, *Salzmann* s.n. (MO), and also Bahia in humidis, 1830, *Salzmann 181* (G); a mixed collection at G of *Salzmann 182 / Salzmann 183* (MO), are all here identified as *Vigna trichocarpa*. In addition, Bahia "hirsutis," *Salzmann* s.n. (P), and Bahia "*Phaseolus luteus*" Salzm., foliis hirsutis, *Salzmann* s.n. (P) are also assignable to *Vigna trichocarpa*, and it is possible that at least some of these specimens (especially those without a number) are from the same gathering.

Vigna trichocarpa is by far the most widely distributed and morphologically distinctive species of the subgenus, especially in fruit. The ascending fruits that parallel the inflorescence axis characterize *V. trichocarpa*. In addition, the seeds of *V. trichocarpa* hang from longer funicles relative to the shorter funicles of other species of *V.* subg. *Lasiospron*. The stipules of *Vigna trichocarpa* are distinctive in having the lower portion forming a spur with entire margins. Such a stipule is found otherwise among *V.* subg. *Lasiospron* species in *V. schottii*.

6. VIGNA SCHOTTII (Benth.) A. Delgado & Verdc., in American Journal of Botany 98(10): 1711 (2011). *Phaseolus schottii* Benth., Comm. Legum. Gen.: 75 (1837). TYPE: BRAZIL. ad Tejuco. *Schott* s.n. (holotype: W!; isotype: NY!). non *P. schottii* Benth. *sensu* Hassler *in part*, Candollea 1: 463. 1923; non *P. schottii* var. *longifolius* (Benth.) Hassler, Candollea 1: 463. 1923; non *P. schottii* var. *longifolius* forma *intermedius* Hassler, Candollea 1: 463. 1923; non *P. schottii* var. *longifolius* forma *grandiflorus* Hassler, Candollea 1: 464. 1923; non *P. schottii* var. *campestris* Hassler, Candollea 1: 464. 1923; non *P. schottii* var. *campestris* forma *braziliensis*

Hassl., Candollea 1: 464. 1923; non *P. schottii* var. *campestris* forma guyanensis Hassl., Candollea 1: 464. 1923; non *P. schottii* var. *campestris* forma *transiens* Hassl., Candollea 1: 464. 1923; non *P. schottii* var. *tucumanensis* Hassl., Candollea 1: 464. 1923. (See notes).

Phaseolus ovatus Benth., Comm. Legum. Gen.: 75 (1837). Syntypes. BRAZIL. "In campis et pascuis ad Pará" *Martius* s.n. (not traced). "Ad Tejuco", *Schott* s.n. (NY!), **synon. nov.** (See notes).

Phaseolus ovatus Benth. var. *glabratus* Benth., sensu Chodat & Hassler, Bull. Herb. Boiss. Ser. 2, 4: 909. (1904).

Phaseolus schottii var. *genuinus* Hassl., Candollea 1: 463. 1923. Syntypes. BRAZIL. *Blanchet 58* (G!, P! = *V. trichocarpa*); *Salzmann 181* (G! = *V. trichocarpa*); PARAGUAY. *Hassler 1818* (G, not seen); *Hassler 5892 [5982]* (NY!, US! = *V. schottii*); *Hassler 6465* (not seen); *Hassler 6743* (G!; NY!; P!; US! = *V. schottii*); *Rojas 477* (G, not seen). *Phaseolus schottii* var. *genuinus* forma *ovatus* Hassl., Candollea 1: 463. 1923. Syntypes. BRAZIL. *Salzmann 183* (G! *pro parte*; P-3! = *V. trichocarpa*); *Blanchet 1159* (G, not seen); URUGUAY. *Berro 843* (G, not seen); *Osten 4671* (G, not seen); PARAGUAY. *Balansa 1548* (G-3!, P-3! = *V. longifolia*); *Hassler 1818a* (G, not seen); *Hassler 6465a* (G, not seen); *Hassler 8470* (G-3!; K!; NY!; US!; W! = *V. schottii*); *Hassler 9352* (G, not seen). Specimens reported to be at G were not found in the collection. This varietal name *genuinus* was found to comprise more than one taxon.

Perennial (?), trailing and climbing herbaceous vine, up to 1.5 m, with fibrous roots ca. 50 cm long, foliage and reproductive parts covered with minute glandular hairs, and yellowish-white, straight hairs. **Stems** slender, fibrous, often with adventitious roots, sparsely to densely pilose or often hirsute, with yellowish or white hairs, ca. 2 mm long. **Leaves** with stipules lanceolate, distinctly spurred, upper portion 5–10 × ca. 1 mm, 6-veined; lower portion ca. 2 mm long, pilose to densely strigose; stipels ovate-lanceolate, 1.5–2 mm long, subequal in length to petiolules, covered with minute glandular trichomes; petioles 2.4–6 cm long, hirsute with retrorse hairs, rachis considerably shorter, 5–10 mm long, with some antrorsely appressed hairs, canaliculate; leaflets ovate to ovate-lanceolate, usually acute at apex, with raised veins below, chartaceous and sparsely to densely sericeous, terminal leaflet 4.2–10 × 2–4 cm, lateral leaflets 4–7.8 × 1.8–4.2 cm. **Inflorescences** up to 11 cm long, peduncles 5–9 cm long, almost entirely covered with short retrorse hairs, densely strigose distally; rachis 1.5–2 cm long, with 3–5(–8) swollen, obpyriform nodes, 2.5–3 mm long, each with 4–6 alternate orifices, flowers clustered distally; primary bracts caducous, secondary bracts ca. 6 mm long, caducous; bracteoles mostly persistent at anthesis, ca. 6 mm long, longer than calyx-tube, bracts and bracteoles lanceolate and at base geniculate; pedicels shorter than calyx tube, longer and twisting in fruit, covered with retrorse, straight hairs; calyx campanulate, sparsely strigose at the base, glabrescent distally, tube longer than teeth, ca. 4 mm long, teeth triangular, subequal, 1–2 mm long, the adaxial pair broad and emarginate, lateral teeth slightly longer than lower tooth. **Flowers** described as golden yellow, ca. 1.5 cm long; standard broadly ovate, 1.2–1.4 × 1.4–1.6 cm, bilobed at apex, with two parallel callosities on the lamina above the point of folding, the left one more prominently developed, and two fleshy auricles above the claw, claw ca. 3 mm long; wing petals longer than keel,

with an obovate lamina, ca. 1.5 cm long, 8–10 mm wide, with an auricle at base, claw ca. 2 mm long; keel beaked, curved through ca. 270°, 1.2–1.4 cm above the wing, with a transverse pocket above the petal claws, the claws ca. 3 mm long, fused to staminal tube, androecium with staminal tube ca. 2 cm long, vexillary stamen with a basal appendage; anthers ovate, ca. 0.5 mm long, basifixed to sub-basifixed to filaments; pollen grains triporate, with a coarsely reticulate exine; ovary straight, with a basal nectary disc less than 1 mm long, ovules 9 per ovary, style with a tenuous lower part, upper portion thickened, cylindrical, curved, pollen brush 3–4 mm long, with long-spreading hairs, produced beyond the stigma to form a short hook; stigma transversally-ovate, laterally placed. **Fruit** patent or rarely ascending, oblong, subcylindrical, valves thin-walled, not constricted between the seeds, turning dark brown or black at maturity, densely strigose, with golden yellow, straight hairs, 4–6 cm long, ca. 6 mm wide, elastically dehiscent, beak straight, 3 mm long. **Seeds** (immature) D-shaped, surface smooth, testa brown, hilum oblong, as long as seed width, covered by an epihilum, and with variable aril development.

Illustrations—Burkart (1987), as *Vigna longifolia*; Hoc et al. (1993) as *Vigna longifolia*; Ferrucci et al. (2002) as *Vigna longifolia*.

Distribution and Habitat—This species ranges across the provinces of Corrientes, Entre Ríos, and Misiones in Argentina. In Paraguay it occurs mainly in the River Paraguay basin, and it is disjunct in El Beni, Bolivia and in the states of Espírito Santo, Rio de Janeiro, and possibly ranges south to Rio Grande do Sul, in Brazil (Fig. 3). The species occurs in woodland margins, along the shores of lakes or temporary ponds and riverbanks, and low swampy grasslands or "pajonal," below 200 m. Flowering and fruiting throughout the year.

Etymology—Named in honour of H. W. Schott, who collected in Brazil.

Vernacular Name—"Feijão biriba."

Representative Specimens Examined—See Appendix 1 for complete list. **Argentina.** —CORRIENTES: Depto. Ituzaingó, Isla Apipé Grande, Puerto San Antonio, 8 Dec 1973, *A. Krapovickas 23806* (MO). **Bolivia.** —EL BENI: Yacuma Province, unos 60 km al E de San Borja, 22 Jul 1989, *St. G. Beck 16929* (LPB, MEXU). **Paraguay.** —ALTO PARAGUAY: swamp bordering Río Tapiracuai, 11 Sep 1957, *A. L. Woolston 872* (K, NY).

Notes—Bentham's (1837) original description of *Phaseolus ovatus* was based on two specimens: *in campis et pascuis* ad Pará collected by *Martius s.n.* and *ad Tejuco* [Tijuca, Río de Janeiro] collected by *Schott* s.n., neither of which has been found in any of the herbaria visited or consulted by Bentham. However, there is a specimen at K which has long been considered the type of *P. ovatus*. The herbarium sheet has a label that reads Pohl (not Schott) as the collector of this plant in Tejuco, Brazil. In addition, there are two comments in pencil, one in Bentham's handwriting, in the left bottom corner identifying it as *P. ovatus*, and the other by Piper annotating it as, "possibly the type of *P. ovatus*". Regarding the confusing information about Pohl and Schott's collections, Urban (1899) in Flora Brasiliensis pointed out that, "It is a matter for grieving because which specimens Pohl [and] which specimens Schott might have collected cannot always be settled from the sheets of the Vienna herbarium". Nonetheless, the specimen has spurred stipules, as mentioned in the description of *Phaseolus schottii*. Concurrently, Bentham (1837) distinguished an unnamed variety of *P. ovatus*, the type of which, at M, was identified as *Vigna luteola* (Jacq.) Benth. by Verdcourt (1970). This leaves the description as the only extant original

material. In addition, Bentham (1859), in Flora Brasiliensis, listed under *P. ovatus* seven specimens, including another variety: var. *glabratus*, the type of which at M is conspecific with what is currently known as *V. trichocarpa*. Of the other six, two are the Martius and Schott collections cited in the original protologue, as well as the taxon mentioned above as an unnamed variety. Of the remaining three Brazilian specimens cited under *P. ovatus*, two: in humidis Banda Oriental frequens, *Tweedie* s.n. (K), and in Brasilia meridional, *A. de St. Hilaire* s.n. (P), are plants like *Phaseolus diffusus* (= *Vigna diffusa* of this treatment) and the third, collected in Río Grande do Sul, *Herb. Imp. Br. 1536* (P), is here treated as *Vigna schottii*. Without extant syntypes, and the material cited in Flora Brasiliensis under *P. ovatus* being heterogeneous, different taxonomic interpretations have been given by authors dealing with this species name. We suggest that the name should be abandoned as it seems impossible to establish its identity.

Accordingly, the range of *Vigna schottii* extends to southern Brazil, which is a possibility. In the absence of any other collections from that area, we suspect there may have been a mistake in specimen labelling.

Hassler (1923) included a number of diverse elements within his concept of *Phaseolus schottii*, held together by their straight-beaked pods and sparsely hirsute-pilose to glabrescent calyces, characteristics common in *V.* subg. *Lasiospron*. Most of the infraspecific taxa described under *P. schottii* by Hassler are morphologically heterogeneous and difficult to interpret.

As discussed previously, *Vigna schottii* and *V. diffusa* share some morphological characters although *V. schottii* is much more robust, and its leaves are commonly ovate-lanceolate, and its stipules are spurred (while those of *V. diffusa* are bi-auriculate). *Vigna schottii* also shares some characteristics with *V. trichocarpa* as well; some forms of *V. schottii* in central eastern Brazil have narrower leaflets similar those of *V. trichocarpa*. The fruits of *V. schottii*, however, are narrower and longer than those of *V. trichocarpa*, in addition to being held pendent on the infructescence.

Excluded Taxa—*Dolichos jacquini* DC., in A. DC. Prodr. 2: 397 (1825), nom. nov. for *D. lignosus* Jacq., Select. Stirp. Amer. Hist.: 263 (1788), nom. illeg., non *D. lignosus* L. (1753).

DISCUSSION

The six species of *Vigna* subg. *Lasiospron* grow mostly in seasonal or permanently flooded plains or marshy environments, such as gallery forests, swamp forests and grasslands. Herbarium labels report that they sprawl in floating plant islands in rivers and lakes or grow along ditches in sugar cane plantations and along banks at the edges of rice fields. Two or sometimes three species of the subgenus grow sympatrically within the same fluvial system. For example, *Vigna juruana* and *V. lasiocarpa* co-occur along the black-water courses of the Rio Negro basin. Regardless of sympatry, no hybrids have been reported. Regarding likely adaptations to these aquatic and wetland environments, nitrogen-fixing nodules are borne on stems and adventitious roots in *V. trichocarpa* growing in flooded areas of Puerto Rico (Dubey et al. 1972). Similarly, plants of *V. lasiocarpa* in the Brazilian Pantanal with nodules on their floating stems and on adventitious roots (James et al. 2001) have been reported as frequent (Pott et al. 2011).

The phylogenetic position of *Vigna* subg. *Lasiospron*, nested within the *Physostigma* + *Vigna* sensu stricto clade (Figs. 1–2) concurs with the results of Delgado-Salinas et al. (2011). We do not propose here to rank *V.* subg. *Lasiospron* at the genus level because the more comprehensive analysis of Delgado-Salinas et al. (2011) did not resolve the *V.* subg. *Lasiospron* clade as sister to the rest of the *Vigna* (cf. Figure 1). The results of Delgado-Salinas et al. (2011) suggest that ranking *V.* subg. *Lasiospron* at the genus level would require doing the same for all the infrageneric taxa of *Vigna* (e.g. *V.* subg. *Ceratotropis*), which are not as distinct apomorphically as are the newly ranked genera of the American Phaseolinae (Fig. 2; Delgado-Salinas et al. 2011). We therefore maintain *Vigna* subg. *Lasiospron* as it has been traditionally ranked and circumscribed.

Species Concept—Coalescing conspecific ITS sequence samples of *V.* subg. *Lasiospron* species are resolved with high branch support values (Fig. 1), as found by Delgado-Salinas et al. (2011). These results concur with those of Raveenadar et al. (2018), a study that found ITS barcodes to more accurately identify *Vigna* species compared to cpDNA barcodes. We analyzed the *V.* subg. *Lasiospron* ITS accessions in Raveenadar et al. (2018), which come from *Vigna lasiocarpa* and *V. longifolia*. Raveenadar et al.'s ITS accessions of *Vigna lasiocarpa* were resolved with our accessions of *V. lasiocarpa* in a well-supported coalesced clade (1.0 posterior probability; data not shown). Their ITS accessions of *Vigna longifolia* were resolved with our accessions of *V. trichocarpa* in a well-supported coalesced clade (1.0 posterior probability). From our perspective, the three *Vigna longifolia* ITS accessions in Raveenadar et al. (2018) likely derived from specimens of *V. trichocarpa*. Regardless of this discrepancy, well-supported coalescing conspecific ITS samples of *Vigna* subg. *Lasiospron* suggest the ITS region is a potentially highly informative barcode for identifying *V.* subg. *Lasiospron* species.

Coalescing conspecific genetic samples, especially from nuclear loci and especially when sampled in a geographically comprehensive manner, are not common in plant species (Fazekas et al. 2009; Hollingsworth et al. 2011). This is explained by one or a combination of factors (Naciri and Linder 2015). These factors include persistence in low effective population sizes due to either population or genomic attributes (e.g. low ploidy levels), adaptation to dispersal limited habitats (Pennington and Lavin 2016), or long evolutionary persistence of populations (antiquity of species ages).

The coalescing conspecific ITS sequence samples of the species of *V.* subg. *Lasiospron* may reflect the relatively older age of this clade and its constituent species (Figs. 1–2) and perhaps other factors such as low ploidy level, or that species of *V.* subg. *Lasiospron* somehow persist in low effective population sizes in dispersal limited environments. However, the wet forest and riparian habitat, especially for clades of tropical vines, is not predicted to promote genetic coalescence of conspecific samples. Lowland tropical wet habitats are prone to regular or profound disturbances (e.g. drought, wind, mudslides), which promote continuous cycles of local mortality and recolonization (Pennington and Lavin 2016). Indeed, *Vigna* species commonly have widespread distributions indicative of high levels of dispersal ability (e.g. via hydrochory; Tomooka et al. 2002) or adaptation to dispersal prone wet tropical environments.

Regardless, the finding of coalescing conspecific ITS sequence samples bolsters species delimitation in this clade because genetic evidence covaries with the diagnostic species traits enumerated in the taxonomy section (Table 1). Thus, the species of *V.* subg. *Lasiospron* fit the universal species concept (e.g. De Queiroz 2007), which requires a combination of ecological, genetic, geographical, and phenotypic evidence for separately evolving metapopulations.

Trans-Atlantic Dispersal—Of the three amphi-Atlantic species of *V.* subg. *Lasiospron*, *Vigna trichocarpa* and *V. juruana* presumably dispersed across the Atlantic from Meso-America to West Africa and from South American to Central Africa, respectively (Fig. 3). *Vigna diffusa* likely dispersed from southern tropical South America (e.g. present day coastal Brazil) across the Atlantic to Madagascar. These three amphi-Atlantic species have been considered as not native to Africa or Madagascar (Verdcourt 1970; Maréchal et al. 1978; Maxted et al. 2004). These three species could have attained an amphi-Atlantic distribution because of indirect human-mediated dispersal, either via slave-trade migration (e.g. by Portuguese sailors as part of ship ballast) or as seed contaminants among New World crops brought to Africa and Madagascar (Voeks 2009). However, the three amphi-Atlantic species of *V.* subg. *Lasiospron* are abundant in coastal and riparian environments (cf. Figure 3), including sand dunes in the case of *Vigna diffusa*. These three amphi-Atlantic species are well adapted to coastal habitats and thus most amenable to trans-oceanic dispersal. Natural transoceanic dispersal is possible given reports of floating *Vigna* seeds, as in *V. marina* (Burm.) Merr. (Lawn and Cottrell 2016).

The two most northern amphi-Atlantic species, *Vigna trichocarpa* and *Vigna juruana*, also have neotropical distributions in Amazonia and the Atlantic wet forests (Fig. 3). Such neotropical disjunctions between the Amazon and Atlantic forests could result from historical connections (e.g. Batalha-Filho et al. 2013). However, for *Vigna trichocarpa* and *V. juruana*, such disjunctions could be due to ongoing coastal migration routes or long-distance dispersal by birds, which often explains widely disjunct aquatic plant species distributions (e.g. Les et al. 2003).

The amphi-Atlantic distributions of *Vigna* subg. *Lasiospron* species are therefore likely a result of long-distance over-water dispersal associated with species having a predilection to colonizing coastal environments. Notably, *Vigna lasiocarpa* and *V. longifolia*, two of the widest ranging species confined to the Americas (Fig. 3), rarely inhabit coastal settings in contrast to the three amphi-Atlantic species. Indeed, a predilection to coastal environments covaries with a lower average elevation of the three amphi-Atlantic species compared to the three species confined to the Americas (Fig. 4; Results section).

Trans-oceanic, including amphi-Atlantic, geographical distributions are common among tropical legume clades (Lavin et al. 2004) and species. Examples of this include *Aeschynomene sensitiva* Sw., *Canavalia. bonariensis* Lindl. (which has a geographical distribution similar to *Vigna diffusa*), *C. rosea* (SW.) DC, *Machaerium lunatum* (L.) Duke, *Macropsychanthus comosus* (G.Mey.) L.P. Queiroz & Snak, *Rhynchosia caribaea* Benth., *R. minima* (L.) DC., *Tephrosia purpurea* (L.) Pers., *Vigna luteola* (Jacq.) Benth., *V. marina* (Burm.) Merr., and *V. vexillata* (L.) A.Rich (e.g. Snak et al. 2016; Yamamoto et al. 2019; Queiroz and Snak 2020). It is therefore likely that *Vigna* subg. *Lasiospron* species also have this natural trans-Atlantic dispersal ability independent of human-mediated dispersal.

AUTHOR CONTRIBUTIONS

ADS conceived of the idea, generated and analyzed the data, and wrote the paper. ML generated and analyzed the data and assisted in writing and revising the paper. CS and GPL assisted in writing and revising the paper.

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APPENDIX 1   Index to numbered collections examined. Numbers in parentheses refer to the order of species in the taxonomic section (1 = *Vigna jurana*, 2 = *V. diffusa*, 3 = *V. longifolia*, 4 = *V. lasiocarpa*, 5 = *V. trichocarpa*, 6 = *V. schottii*).

Abraham, A. 200 (1).
Acosta, L. 2772 (1).
Adams, C. D. 14246 (1).
Adams, P. 162 (5).
Aguilar Zepeda, J. A. 55 (3).
Ahumada, O. 3373 (3).
Allen, C. 345 (4).
Allen, P. H. 1059 (4).
Alston, A. H. G. 7627 (4).
Álvarez, D. 11670 (3).
Anderson, B. 1853 (3).
Araque M., J. 19044 (1).
Arbo, M. M. 6894 (6).
Archer, W. A. 2041 (1); 2690 (1); 2803 (1).
Arias, L. A. 113 (4).
Aristeguieta, L. 4133 (4); 6172 (5).
Austin, D. F. 7012 (4).
Aviles, S. 56 (5).
Aymard C., G. 2595 (4).
Balcazar, J. 1123 (3); 1237 (3).
Baldwin, J. T. 3571 (4); 4716 (1).
Barbour, P. J. 5173 (1).
Bartlett, H. H. 1647C (5); 16497 (5); 16524 (5); 21185 (2).
Basurto Peña, F. s.n. (4).
Beck, St. G. 10122 (3); 16929 (6); 18854 (6); 19433 (1); 24295 (6); 27577 (3).
Belém, R. P. 686 (1).
Bell, D. 88–157 (5).
Benoist, R. 75 (5).
Berg, C. C. 19786 (5).
Berhaut, R. P. 7165 (5).
Betancurt, J. 1990 (3).
Black, G. A. 52-14427 (3).
Blanchet, J. S. 58 (5).
Bordenave, B. 892 (1).
Braun, O. 11 (3); 75 (4).
Breteler, F. J. 1637 (1); 3851 (1).
Bunting, G. S. 829 (5).
Burchell, W. J. 9258 (4).
Burt, R. L. 162 (4).
Cavalcante, P. 676 (1).
Chan, C. 887 (4).
Chavarría, U. 1047 (3).
Cid, C. A. 2422 (3); 3489c (4).
Clarke, D. 1356 (5); 344 (1); 3871 (1).
Clewell, A. 4010 (1).
Colonnello, G. 1525 (5); 1594 (1); 1783 (1).
Cordeiro, J. 616 (2).
Cornejo, X. 7049 (3).
Cowan, R. S. 38884 (5).
Croat, T. B. 13238 (5); 8250 (5).
Croizat, L. 147 (4).
Cuatrecasas, J. 21411 (1); 7451 (1).
Curran, H. M. 119 (4); M. 337 (1); 47 (4); 546 (5); SN1 (1).
da Costa Sacco, J. 288 (2).
Dahlgren, B. E. 407 (5).
Daniels, A. G. H. 1337 (1).
D'Arcy, W. G. 13431 (4); 9651 (4).
Davidse, G. 18127 (4).
Davidson, C. 10242 (3).
de Alba, J. 8 (4); 83 (4).

de Almeida, C. 1034 (3).
de la Cruz, J. S. 3283 (1); 4130 (1).
de Lemos Fróes, R. 20249 (4); 23013 (4).
de St. Hilaire, A. s.n. (2).
de Wilde, W. J. J. O. 2752 (1).
Debouck, D. G. 2946 (4).
Delascio Chitty, F. 17125 (5).
Delgado Salinas, A. 791 (4); 995 (4).
Díaz, C. 308 (1).
Drouet, F. 1989 (4); 2666 (5).
Ducke, A. 11873 (3); 11874 (3); 16649 (1); 24325 (1).
Duke, J. A. 10988 (5).
Dupré, M. 1842 (5).
Dwyer, J. D. 2882 (4); 4583 (5); 4584 (1).
Ebinger, J. E. 975 (5).
Eiten, G. 9062 (4).
Ekman, E. L. 1610 (4); 18095 (5); 18259 (5).
Encarnación, F. 25123 (1); 26338b (1).
Fernández Casas, J. 5833 (4).
Fiebrig, K. 501 (6); 6177 (4).
Flores, A. 317 (6).
Folli, D. A. 2427 (5).
Forero, E. 4009 (1).
Fosberg, F. R. 29259 (4).
Freitas, M. 18 (2).
Frey, R. 514 (3).
García Barriga, H. 14188 (4).
Garvizu, M. 151 (1); 275 (1).
Gentle, P. H. 3076 (4); 7839 (4).
Gentry, A. 7511 (1); 9277 (4); 18428 (1); 21252 (1); 25798 (1); 64320 (1).
Gerrard, W. J. 168 (2).
Gilbert, E. 311 (2).
Gillespie, L. J. 706 (4).
Gines, L. A. 109 (1).
Gleason, H. A. 869 (1).
Goodland, R. 524 (4); 770 (4).
Granville, J. J. 10041 (1).
Grayum, M. 6071 (4).
Guaglianone, E. R. 1031 (4).
Guareco, I. 391 (4).
Guedes, M. 11876 (5).
Gutiérrez B., C. 6299 (4).
Hahn, W. 2080 (4).
Hamilton, C. 3135 (5).
Hanan Alipi, A. 1001 (3).
Hariusa, S. G. 533 (5).
Hariusa, S. G. 904 (5).
Harley, R. M. 10432 (4).
Hassler, E. 1880 (4); 5982 (3); 5982 (6); 6743 (3); 6743 (6); E. 6828 (4); 7320 (3); 8470 (3); 8470 (6).
Hatschbach, G. 29389 (2); 8869 (4).
Haught, O. 1535 (4).
Henkel, T. W. 403 (1); 3675 (4); 5321 (1).
Hepper, F. N. 2626 (5).
Herb. Imp. Br. 1536 (6).
Heringervet, E. P. 841 (3).
Hermann, F. J. 10948 (4).
Herter, G. 675 (2).
Hill, S. R. 13046 (1).
Hitchcock, A. S. 20275 (4).
Hoff, M. 6357 (1).
Holt, E. G. 457 (1).
Hopkins, M. J. G. 784 (4).
Horner, C. 267 (1).
Humbert, H. 27508 (4).
Hunter, A. A. 470 (4).
Ibarrola, T. 2844 (6).
Ijjasz, E. H. 655 (5).
Irwin, H. S. 55541 (1); 57688 (1).
Jangoux, J. 1579 (3).
Jansen Jacobs, M. J. 4681 (5); 1770 (1).
Janssen, A. 513 (3).
Jaramillo, R. 336 (4).
Jenman, G. S. 2111 (5); 5230 (5).
Jenman, J. S. 1855 (1).

Jiménez M., A. 1145 (4).
Jones, J. 9715 (1).
Jordan, H. D. 402 (5); 907 (5).
Jörgensen, P. 2929 (3); 2951 (3); 2959 (3); 4559 (3); 4559 (6); 4625 (4).
Junk, W. 13 (3).
Kamb, P. 2092 (5).
Killeen, T. J. 6839 (5); 6894 (4).
Killip, E. P. 34360 (4).
King, R. M. 1096 (4); 944 (4).
Klein, R. M. 9961 (6).
Klug, C. 1022 (4).
Klug, G. 931 (1); 1251 (5).
Kortught, P. 8894 (1).
Koster, H. W. 113 (4).
Krapovickas, A. 16987 (6); 21638 (4); 23806 (6); 2520 (3); 41113 (6).
Krukoff, B. A. 1242 (3).
Kuhlmann, J. G. 1789 (3).
Lanjouw, J. 1118 (5); 1480 (1); 1539 (5); 2050 (1); 3207 (5).
Leeuwenberg, A. J. M. 7040 (1).
Lehmannian, F. C. 8454 (3); 8757 (3).
León, B. 7197 (5).
León, H. 666 (4).
Letouzey, R. 10023 (1); 11500 (1).
Lewis, G. P. 1427 (4).
Lewis, W. H. 769 (4).
Liesner, R. 22785 (1).
Liogier, A. H. 9073 (4).
Lisboa, P. 1444 (4).
Lock, J. M. 83/66 (3).
López, M. G. 326 (4).
Louis, J. 10294 (1).
Lundell, C. L. 3299 (5).
Maas, P. J. M. 4088 (4); 5555 (1); 7298 (4).
MacDougal, J. M. 3094a (5).
Magalhães, G. M. 19506 (5).
Magaña A., M. A. 1237 (3); 1867 (5); 2255 (1).
Maguire, B. 23773 (1); 23849 (1); 29294A (4); 32059 (4); 35830 (4).
Mann, G. 2319 (1).
Marlier, G. 14375 (5).
Martínez S., E. 37259 (4).
Mattos, J. 8952 (2).
Matuda, E. 3594 (3).
McDowell, T. 1981 (4).
McKee, G. S. 11123 (4).
Melo, F. 3352 (3).
Milliken, W. 266 (1).
Molina R., A. 32000 (4).
Montes, R. A. 1363 (3).
Moreira, A. S. 86 (5).
Mori, S. 21308 (1); 21309 (1); 21716 (1).
Murca Pires, J. 51366 (1).
Mutchnick, P. 418 (1).
Mutis, J. C. 2344 (4).
Nelson, C. 5731 (4); 5732 (4).
Nelson, E. W. 2848 (4).
Novelo Retana, A. 3298 (3).
Oldeman, R. A. A. 3233b (1).
Oldenburger, F. H. F. 202 (5).
Oliver, R. L. 3538 (4).
Orellana, M. R. 655 (4).
Orozco S., A. 19 (3); 86 (5); 105 (5).
Ortega, R. V. 905 (3).
Ortíz, G. 2051 (5).
Pabst, G. 9078 (2).
Palacios, W. 650 (1).
Pasand, R. 1581 (5).
Paulo H., E. 901 (4).
Pedersen, T. M. 4826 (3); 5446 (4); 8318 (3); 9605 (6); 12992 (2).
Peguero, B. 134 (5).
Peltier, J. 4641 (2).
Pennell, F. W. 1654 (4); 8328 (4).
Philcox, D. 4189 (4).
Piper Vibrans, C. V. 5164 (3).
Pittier, H. 2247 (4); 5225 (4); 10640 (4); 14590 (4); 15132 (4).
Plowman, T. 6387 (1).

Pohl, J. E. s.n. (6).
Poole, J. M. 1628 (1).
Prance, G. T. 1319 (1); 2566 (1); 5264 (3); 10328 (1); 10791 (1); 13403 (1).
Prévost, M. F. 1011 (1).
Prieto, A. 92 (1).
Proctor, G. R. 21926 (5); 33106 (5); 33461 (5); 35795 (5).
Pueyrredon, E. 17924 (3).
Ramia, M. 4851 (4); 4852 (3); 5379 (3).
Ramírez A., J. G. 4589 (3).
Ramírez, I. 300 (1).
Rentería A., E. 1902 (4).
Revilla, J. 1767 (1); 1946 (1); 2014 (1).
Riedel, L. 246 (1).
Rimachi Y., M. 10566 (1).
Rodrigues, W. 2724 (1); 9267 (1).
Rodríguez,? . 1913 (4).
Rojas, T. 2917 (3).
Rombouts, H. E. 714 (1).
Rosales, J. M. 1257 (1); 2302 (3); 2355 (4); 2365 (3).
Rosengurtt, B. 3039b (2).
Rovirosa, J. N. 442 (4).
Rudas, A. 4282 (1).
Salzmann, Ph. 182 (5); 183 (5); s.n. (5); s.n. (5).
Sanjines, A. 175 (3).
São-Mateus, W. M. B. 58 (5).
Schaller, G. 165 (3); 278 (3).
Schinini, A. 21809 (4).
Schipp, W. A. 620 (4).
Schott, A. C. V. s.n. (6).
Schultes, R. E. 46-173 (3); 46-189 (1); 929 (4); 5858 (1); 12595 (1); 17973A (4).
Schulz, A. G. 10328 (3); 11036 (3).
Schunke Vigo, J. 9228 (1).
Schwarz, G. J. 11894 (4).
Scott Elliot, G. F. 3023 (2).
Segadas-Vianna, F. 3590 (5).
Seibert, R. J. 2268 (1); 632 (5).
Semple, A. T. 1 (5); 7 (4); 10 (4); 19 (4); 23 (5); 39 (4); 130 (5); 358 (4).
Shattuck, O. 245 (5); 909 (5).
Sieber, F. W. s.n. (4).
Silva, M. G. 1256 (3); 35285 (4).
Silva, N. T. 4848 (4).
Skutch, A. F. 3006 (4); 3086 (4).
Smith, A. C. 2242 (5).
Smith, D. 103 (3).
Smith, L. B. 7102 (2).
Smith, S. F. 778 (5).
Snak, C. 269 (2); 1066 (5); 1216 (3).
Sobel, G. L. 4874 (4).
Solomon, J. C. 16823 (3).
Sousa Sánchez, M. 8788 (4); 11711 (4).
Soza, D. 247 (4).
Sprague, R. A. 100 (4).
Spruce, R. 467 (3); 1641 (1); 1641 (1).
Stahl, A. 97 (1).
Standley, P. C. 26690 (4); 48407 (1).
Starry, D. E. 257 (5).
Stergios, B. 6186 (1).
Stevenson, J. A. 2097 (5).
Stevenson, P. 1355 (1).
Steyermark, J. A. 31881 (3); 87773 (1); 114844 (1).
Stover, R. H. 4 (4).
Tamayo, F. 2912 (4).
Tenorio Lezama, P. 19602 (3).
Traill, J. W. H. 153 (3).
Tweedie, J. 343 (2); s.n. (2).
Tyson, E. L. 4583 (5).
Ucan, E. 1607 (4).
Ule, E. 8171 (4).
Usteri, P. A. 956 (2).
Van der Sluys,? . 781 (5).
Vanni, R. 1272 (3).
Vásquez, R. 6417 (1); 10593 (1).
Ventura V., E. 785 (4).
Vibrans, H. 8246 (3).

Vogel, S. 100 (4); 103 (1).
von Luetzelburg, P. 21465 (1).
Werdermann, E. 2326 (4).
Wetmore, R. H. 190 (5).
Whetzel, H. H. 1 (5).
Williams, L. 555 (3); 1038 (1); 15210 (1); 15267 (1).
Wilson, P. 669 (1).
Wood, J. R. I. 20751 (3).
Woodson, R. E. 1217 (4).

Woodworth, R. H. 473 (5); 564 (5).
Woolston, A. L. 872 (6).
Wright, C. 2341 (5).
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