PAYPAYROLA ARENACEA (VIOLACEAE), A NEW SPECIES WITH AN UNUSUAL LIFE-FORM FROM A WHITE SAND SAVANNA IN THE AMAZON RIVER BASIN OF VENEZUELA

GERARDO AYMARD-C.,[1] LISA M. CAMPBELL,[2] AND GUSTAVO A. ROMERO-GONZÁLEZ[3,4]

Abstract. A new species of *Paypayrola* from a white sand savanna in the San Miguel river basin, a tributary of the lower Guainía river in Amazonas State, Venezuela, is described, illustrated, and its relationships with putatively allied species are discussed. This new species differs from all others in the genus in its small habit and aggregate life-form. The flowers are similar to those of *P. confertiflora* and *P. blanchetiana* but are intermediate in size and the petals are pink- or red-tinged. The phytogeography of white sand savannas is briefly discussed and a key and a synopsis of the known species of *Paypayrola* are presented in two appendices. Leaf structure and histology were studied using both light and scanning electron microscopy and a chemical test showed a positive reaction to aluminum accumulation in leaf tissues. However, it was not possible to ascertain if levels of aluminum accumulation exceeded what was present in the substrate.

Resumen. Se describe y se ilustra una nueva especie de *Paypayrola* de una sabana de arena blanca de la cuenca del río San Miguel, un afluente del bajo río Guainía, estado Amazonas, Venezuela, se discuten sus relaciones con las especies putativamente aliadas. Esta nueva especie es similar a *P. confertiflora* y *P. blanchetiana*, pero difiere en su pequeño hábito, los tallos agregados y las flores más pequeñas, con los pétalos rosados a rojo palidos. Se discute brevemente la fitogeografía de las sabanas de arena blanca y se presentan una clave y una sinopsis del género en dos apéndices. Se estudiaron la estructura y la histología de la hoja usando microscopía de luz y electrónica de barrido y un ensayo mostró una reacción positiva de acumulación de aluminio en los tejidos de las hojas. Sin embargo, no fue posible comprobar si los niveles de aluminio acumulado excedían a los que estaban presentes en el substrato.

Keywords: Aluminum, Guayana, leaf structure, upper Rio Negro basin, Violaceae, white sand habitats

Paypayrola Aubl. (Violaceae) is a neotropical genus comprising approximately eight to ten species of small trees or shrubs (Fernández del Valle, 2005; Wahlert et al., 2014; Ballard et al., 2014; see appendices I–II herein). The cosmopolitan Violaceae includes about 24 genera (Munzinger and Ballard, 2003; Ballard et al., 2014); *Paypayrola* has been treated as Violoideae, Rinoreeae, Paypayrolinae, based on the classification system proposed by Hekking (1988) and subsequently improved by other authors (e.g., Ballard et al., 2014). Some of this classification has not been supported by recent molecular phylogenies of Violaceae (Wahlert et al., 2014), and results are not congruent for Paypayrolinae (*Amphirrhox* Spreng., *Hekkingia* H. E. Ballard, and *Paypayrola*; Tokuoda, 2008; Wahlert et al., 2014). Tokuoda (2008) inferred that some morphological characters traditionally used to characterize taxonomic groups may be plesiomorphic or autapomorphic.

Paypayrola is characterized by a nearly actinomorphic corolla and staminal glands that are never elaborated into prolonged nectaries (characters that defined tribe Rinoreeae); one petal slightly to distinctly shaped from the others, a fused staminal tube (characters of Paypayrolinae); subsessile flowers, with pedicel bracts and bracteoles early deciduous, anthers with an obsolete dorsal connective appendage, and smooth capsules (Munzinger and Ballard, 2003; Ballard et al., 2014). Species of *Paypayrola* are restricted to South America, where they are common in lowland moist forest formations. Most species occur in the Amazon Basin and on the Guiana Shield. One species (*P. confertiflora* Tul.), however, has apparently has been collected in Panama (Tropicos, 2014).

Fernández del Valle (2005) reported three species of *Paypayrola* for the Venezuelan Guayana (*P. grandiflora* Tul., *P. guianensis* Aubl., and *P. longifolia* Tul.), later adding a fourth species (*P. confertiflora* Tul.; Fernández del Valle, 2008).

Several novelties to science (e.g., *Cleistes sp. nov.* and *Coryanthes sp. nov.*, Orchidaceae) and for the flora of Venezuela (e.g., *Caraipa valioi* Paula, Calophyllaceae; *Douradoa consimilis* Sleumer, Olacaceae; *Galeandra pubicentrum* C. Schweinf., Orchidaceae; *Mezilaurus caatingae* van der Werff, Lauraceae; and *Gleasonia uaupensis* Ducke, Rubiaceae) recently have been collected along the San Miguel river, a tributary of the Guainía river and therefore of the upper Río Negro in the Amazon river basin, including the new species of *Paypayrola* we describe herein. One of us (L.M.C.) also conducted a leaf structure and histology study, as well as Chenery's (1948) test to detect the presence of aluminum, using leaf samples from the type collection (*Romero et al. 3154*, GH).

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[1] UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Mesa de Cavacas, Estado Portuguesa 3350, Venezuela; gaymard@cantv.net

[2] The New York Botanical Garden, 2900 Southern Boulevard, Bronx, New York 10458, U.S.A.; lcampbell@nybg.org

[3] Oakes Ames Orchid Herbarium, Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A.; romero@oeb.harvard.edu

[4] Author for correspondence

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Materials and Methods

Specimens from the following herbaria were examined: GH, NY, PORT, TFAV, VEN, and from plants.jstor.org. in the JSTOR Portal (courtesy of JSTOR, 2014). The description of vegetative parts is based on herbarium material; that of the inflorescence and flowers based on alcohol-preserved material.

For scanning electron microscopy (SEM), samples from the type collection were coated with gold palladium in a Hummer 6.2 sputtering system (Anatech U.S.A., Union City, California). Observations were made at 10 kV using a JEOL JSM-5410LV SEM (JEOL, Tokyo, Japan).

For light microscopy observations, leaf tissue from the type collection was rehydrated using either a 5% aqueous solution of Aerosol® OT (Fisher Scientific Inc., USA; Ayensu, 1967) or Contrad® 70 (Decon Labs, Inc., PA; Schmid and Turner, 1977). A leaf was softened in a 5% NaOH solution, cleared with Stockwell's bleach (Johansen, 1940; Schmid,1977) and stained with safranin (50:50 water: ethyl alcohol solution). Medial and basal leaf sections were embedded using standard methods for Paraplast+ (McCormick Scientific,™ Leica Biosystems), trans sectioned (t.s.) at 12 μm thickness, and stained with safranin and astra blue (Roeser, 1972). For additional histochemical observations, sections were stained with Sudan IV for suberin and cutin (Johansen, 1940) and ruthenium red for mucilage (Gregory and Bass, 1989). Leaf architecture terminology follows Hickey (1979) and Wilkinson (1979). All images were edited using Photoshop CS4 (©Adobe Systems Inc.).

Chenery's (1948) aluminon test was employed to detect aluminum in leaves from the type collection. Several species of Rapateaceae (*Monotrema aemulans* Körn. *Campbell et al. 648* (NY), *Stegolepis humilis* Steyerm. (*Huber et al. 8080*, NY), *Stegolepis* sp. *Campbell et al. 797*, NY), from genera known to accumulate aluminum (Chenery, 1949), were also tested for comparison. Two hundred μl of the resulting solutions and control were dispensed onto bibulous paper for color comparisons. Color profiles were quantified in Photoshop CS4.

Taxonomy

Paypayrola arenacea Aymard & G. A. Romero *sp. nov.*, Fig. 1–2.

The new species differs from all others in the genus in its small habit and presence of a lignotuber; the flowers are intermediate in size between those of *Paypayrola confertiflora* Tul. and *P. blanchetiana* Tul., and the petals are pink- or red-tinged. *Paypayrola arenacea* resembles *P. longifolia* Tul., with which it shares lanceolate to elliptic-lanceolate leaves with a long-attenuate base, however, *P. arenacea* differs from the latter in its small habit and shorter petioles, leaves, and petals.

TYPE: VENEZUELA. Amazonas: Municipio Autónomo Maroa, riberas del río ("caño") San Miguel, transecto entre la orilla del río, caatinga y sabana amazónica, aguas abajo de Limoncito, detrás de un punto habitado pero abandonado recientemente, la sabana con vegetación típica y con pequeños arbustos; arbusto de hasta 0.75 m, flores blancas, localmente frecuente, aprox. 2°43'N, 67°33'O, 120 m, 22 enero 1998, *G. A. Romero, L. M. Campbell & C. Gómez 3154* (Holotype: VEN; Isotypes: GH, TFAV). Fig. 1–2.

Woody *shrubs*, to 0.75 [–1.7] m tall, *stems* glabrous throughout, gregariously resprouting from a lignotuber. Bark grey, rimous, partially warty. *Stipules* caducous, broadly lanceolate, ca. 0.2 mm long × 0.15 mm wide at the base, carinate, with a dark apiculum; *leaves* simple, alternate below, sub-opposite near the branch tips; petiole semi-rugose, 1–2 mm long × 1.0–1.5 mm wide, base grayish-black; leaf blade narrow-elliptic, 3.5–8.0 cm × 1.0–1.7 cm, chartaceous, dull, dark green to greenish-yellow above, brighter yellowish-green below *in vivo*, apex acute to slightly acuminate, margin entire. *Inflorescence* a cauline raceme, sessile, compact to somewhat lax at maturity, with 3–6 or more flowers; rachis robust, *in vivo* green, ca. 1.5–2.0 cm long × 2.0–2.5 mm wide; floral bracts lanceolate, 0.7 mm long × 0.5 mm wide, bracteole lanceolate, 1.0 mm long × 0.4 mm wide; pedicel ca. 0.2 mm long × 0.15 wide at the base, articulate. *Flower buds* in vivo reddish at the apex of the confluent petals, up to 9 mm long × 2 mm wide at the base of the petals. *Flowers*, at full anthesis, up to 6 mm long × 6.5 mm wide; sepals quincuncial, the margins slightly pilose at the apex, otherwise glabrous on both sides, broadly lanceolate, subcordate, equal, 1.8 mm long × 1.2 mm wide at the base, four of them with a dark, minute globular appendage that may be glandular in nature (one of the outer sepals consistently without this character); *corolla* bilaterally symmetrical; *petals* quincuncial, with one of the inner petals opposite the others, white with a red adaxial strip *in vivo*, narrowly pandurate, the apex rounded, shortly pilose, the margins denticulate, otherwise glabrous on both sides, four strongly recurved, convex in cross section, 7.6 mm long × 1.6 mm wide at their widest point, the opposite retuse, slightly recurved, v-shaped in cross section, with the margins entire; *stamens* 5, *filaments* fused into a 0.5 mm tall tube, tube glabrous, proliferated between the stamens, dorsal connective tissue proliferated, obscuring, but not exceeding the thecae, ventrally broadly deltoid, obscured distally, *thecae* gently curved and slightly slanting toward each other; *gynoecium* glabrous, cylindrical, ampulliform, 2.2 mm long × 0.5 mm wide at the base, stigma 3-lobed. *Fruit* not seen.

Etymology: From the Latin *arenaceus*, of sand, in reference to the sandy soils where the species was collected.

Distribution: Known from two separate collections made in the type locality. However, the new species most likely occurs in nearby white sand savannas elsewhere in the San Miguel river basin and perhaps in similar habitats in Brazil, Colombia, and Peru.

Additional specimen examined: VENEZUELA. Same locality as the type, arbusto de 30–50 cm de altura, en macollas, flores blancas, los pétalos en el envéz con una carina rosada hacia el ápice, frecuente en la parte oeste, más húmeda de Sabana Lisa, 2°41'13"N, 67°22'18"W, ca. 93 m, 25 julio 2013, *G. A. Romero & C. Gómez 4113* (GH, TFAV, VEN).

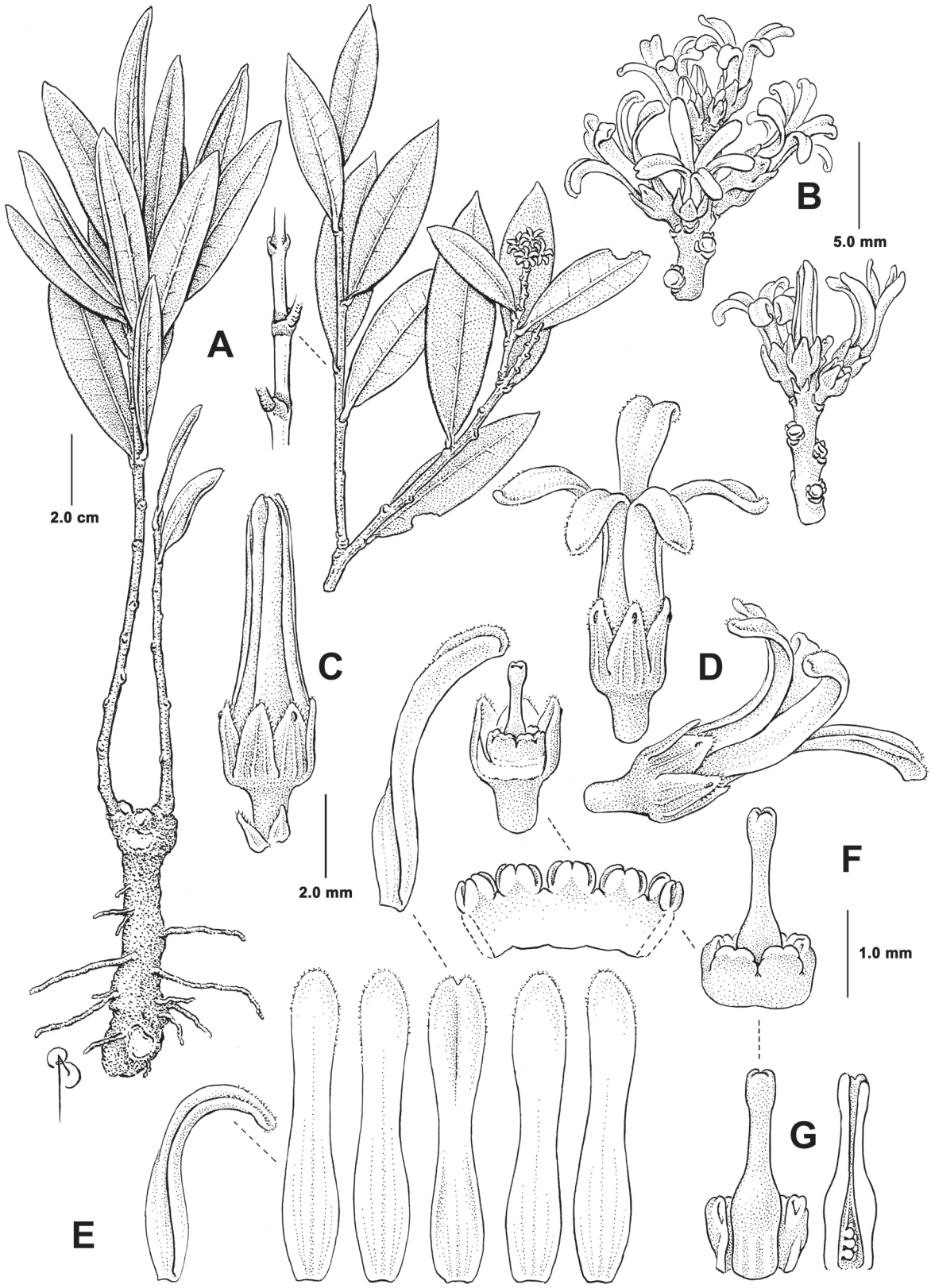

FIGURE 1. *Paypayrola arenacea* Aymard & G. A. Romero. **A**, views of a flowering stem showing a detail of the petiole insertion; **B**, inflorescences; **C**, flower bud; **D**, flower; **E**, petals; **F**, stamens, adaxial and abaxial views; **G**, gynoecium. Drawing by B. Angell based on the holotype and *Romero & Gómez 4113* (GH, K, TFAV, VEN).

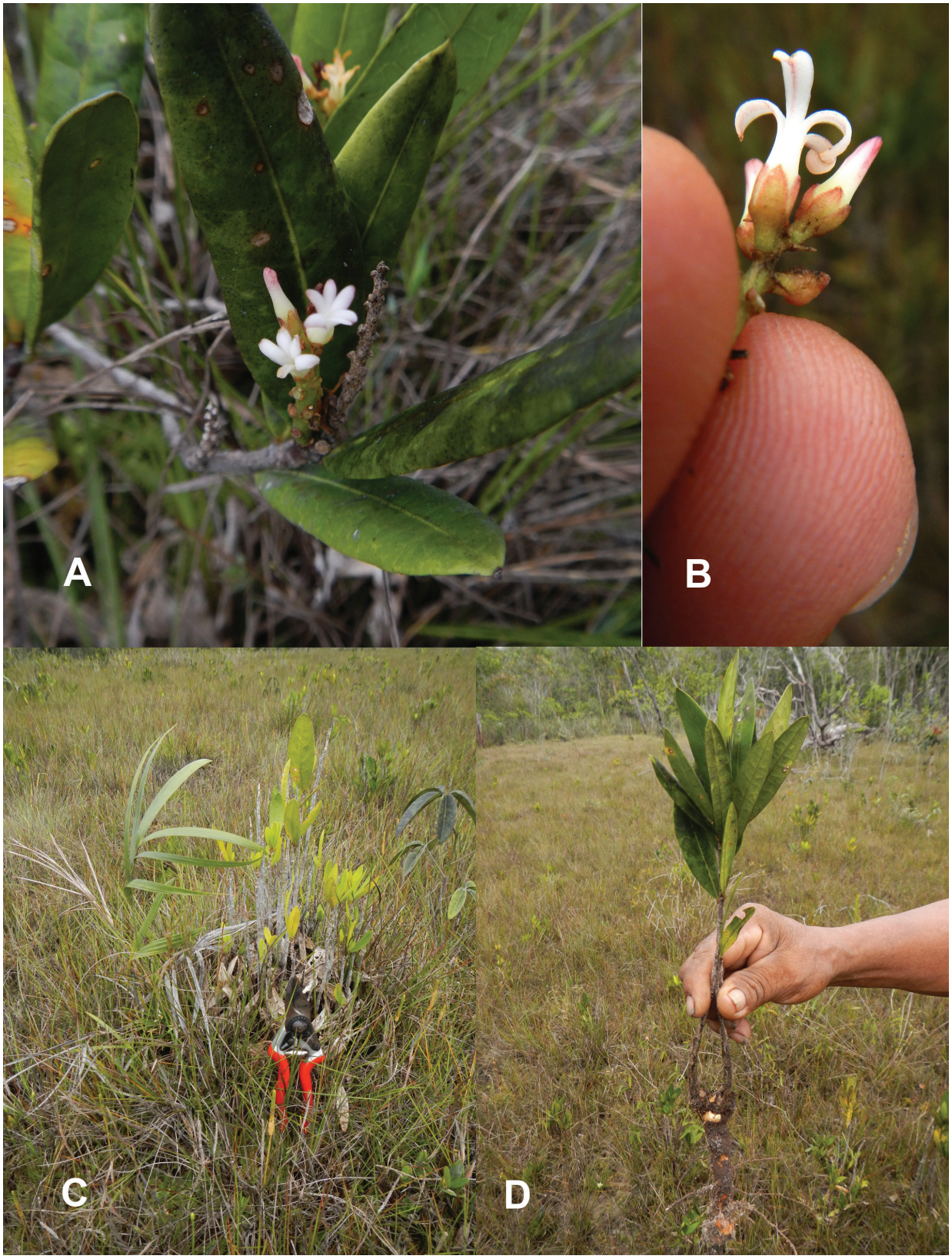

FIGURE 2. *Paypayrola arenacea* Aymard & G. A. Romero. **A**, flowering branch *in situ*; **B**, close-up of flowers, from below; **C**, a clump of *P. arenacea in situ*, note the stature of *Pachira amazonica* (A. Robyns) W. A. Alverson (Bombacaceae) at the right (the pruner shown is a Felco® model F-6); **D**, an individual "plantlet" from the clump shown in C. Photographs by G. A. Romero based on *Romero & Gómez 4113* (GH, K, TFAV, VEN).

Habitat*:* This new species was found growing in scrub-savanna locally called "*Sabanas de arena blanca*" (Spanish), further south "*campina de solo arenoso*" (Portuguese; Anderson, 1981; Lisbôa, 1975) or "*Campinarana graminea lenhosa*" (Portuguese; Pombo de Souza, 2012). This type of vegetation mainly occurs in the black water drainages of the Rio Negro and Guainía rivers in Venezuela (Amazonas state), Colombia (Guainía, Vaupes, and Vichada departments), Brazil (Amazonas, Pará, and Roraima states), and as far south as the Peruvian Amazon at the Jenaro Herrera district and the Allpahuayo-Mishana Reserve, near Iquitos, where apparently similar plant communities are known as "*Varillalles*" and "*Chamizales*" (Revilla, 1974; García-Villacorta et al. 2003). In addition, these communities go farther south in Brazil, in Acre and Rondônia ("Chapada de Parecis;" Prance, 2001). In Venezuela, white-sand savannas also are found, from north to south, in the Samariapo, Sipapo, Ucata, and Atabapo river basins, and most likely farther north in the states of Amazonas, Apure, and, Bolívar, as suggested by the presence of plant species found only in this particular habitat.

Leaf Structure and Histology

Leaf symmetric, narrow elliptic to narrow oblong in outline, apex acute, rarely obtuse, midvein often extended beyond the lamina and spine-like. Margin entire, revolute, most strongly so at the base. Venation brochidodromous, primary vein straight, secondary veins diverging at 60–70°, tertiary veins transverse ramified within the secondary veins, percurrent arches towards the margin, higher order venation random reticulate, veinlets multi-branched. Surface glabrous, cuticle slightly thicker adaxially. Cuticle and portion of anticlinal epidermal cell walls deeply stained with Sudan black B. Adaxial epidermal cells undulate in surface view (Fig. 3), columnar in t.s. (Fig. 4A), rounded to angular in outline, interior periclinal wall thicker than the others and deeply stained with Astra blue (Fig. 4A, B); abaxial epidermal cells wider than tall in t.s., irregularly oblate to pyriform in outline, interior periclinal wall thickened; hypostomatic, stoma irregularly distributed, not on the midvein, in t.s. guard cells shorter than or equal in height to the adjacent epidermal cells, cuticular ledges not seen, stoma laterocytic, subsidiary cells 2–4, unequal. Mesophyll well differentiated, palisade parenchyma bilayered (Fig. 4A), external layer dense, interrupted by a tapering band of 1–5 layers of collenchyma above and below the midvein, and a single layer at the margin, internal palisade layer loose, spongy parenchyma with some peg cells. Midvein slightly to prominently raised above the adaxial surface, more pronouncedly so abaxially, elliptic in t.s., bundle nearly concentric, amphicribal, external phloem interrupted by xylem, xylem with tracheary idioblasts (Fig. 4B), surrounded by a sheath of sclerenchyma, sheath to 4 cells wide. Smaller veins collateral, with or without some peripheral sclerenchyma.

Rehydration and subsequent treatment relaxed the enrolled margin of the sectioned leaves (Fig. 4A). Leaf sections stained with ruthenium red did not exhibit a positive result for polysaccharide mucilage.

The aluminum solution prepared with leaf tissue of *Paypayrola arenacea* exhibited a moderate color change compared to Rapateaceae, indicating the presence of this element.

Violaceae are reported to accumulate aluminum (Chenery, 1948), nickel (Peterson, 1983), heavy metal waste (Jędrzejczyk et al., 2002), as well as hyperaccumulate aluminum (Jansen et al., 2002) and nickel (Fernando et al., 2014). Plants are considered hyperaccumulators when the concentration of aluminum exceeds 1000 ppm in herbaceous tissue (Jansen et al., 2002). Species in the genera of Rapateaceae that we tested are reported to

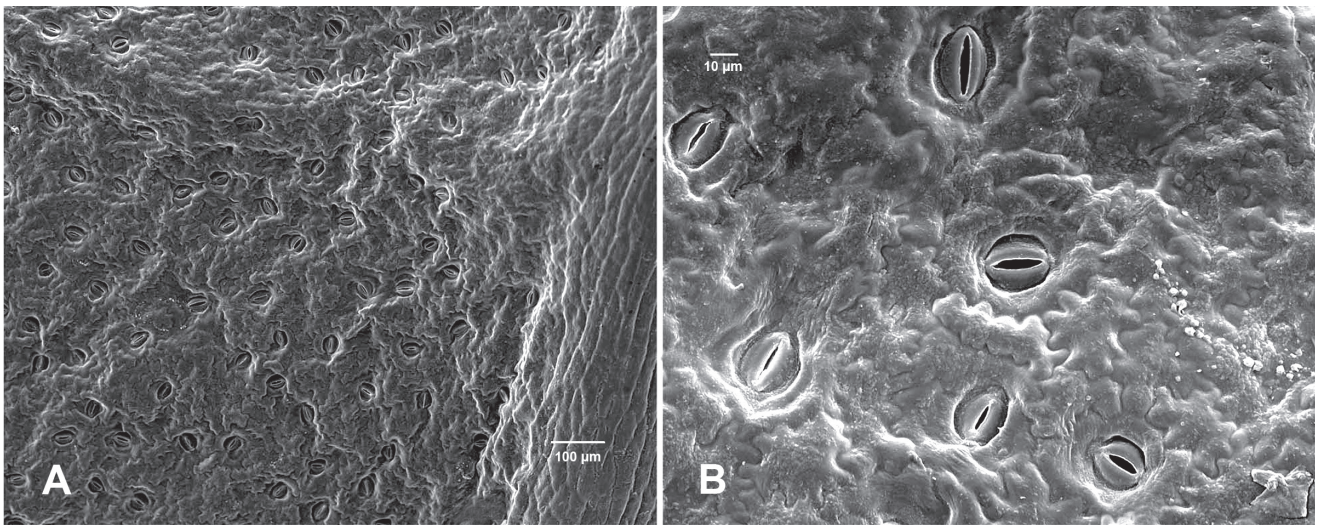

Figure 3. Abaxial leaf surface of *Paypayrola arenacea* Aymard & G. A. Romero. **A**, scattered distribution of stoma (note the presence of stoma on secondary veins but not on the midvien); **B**, detail of the stomata apparatus and undulate epidermal cells.

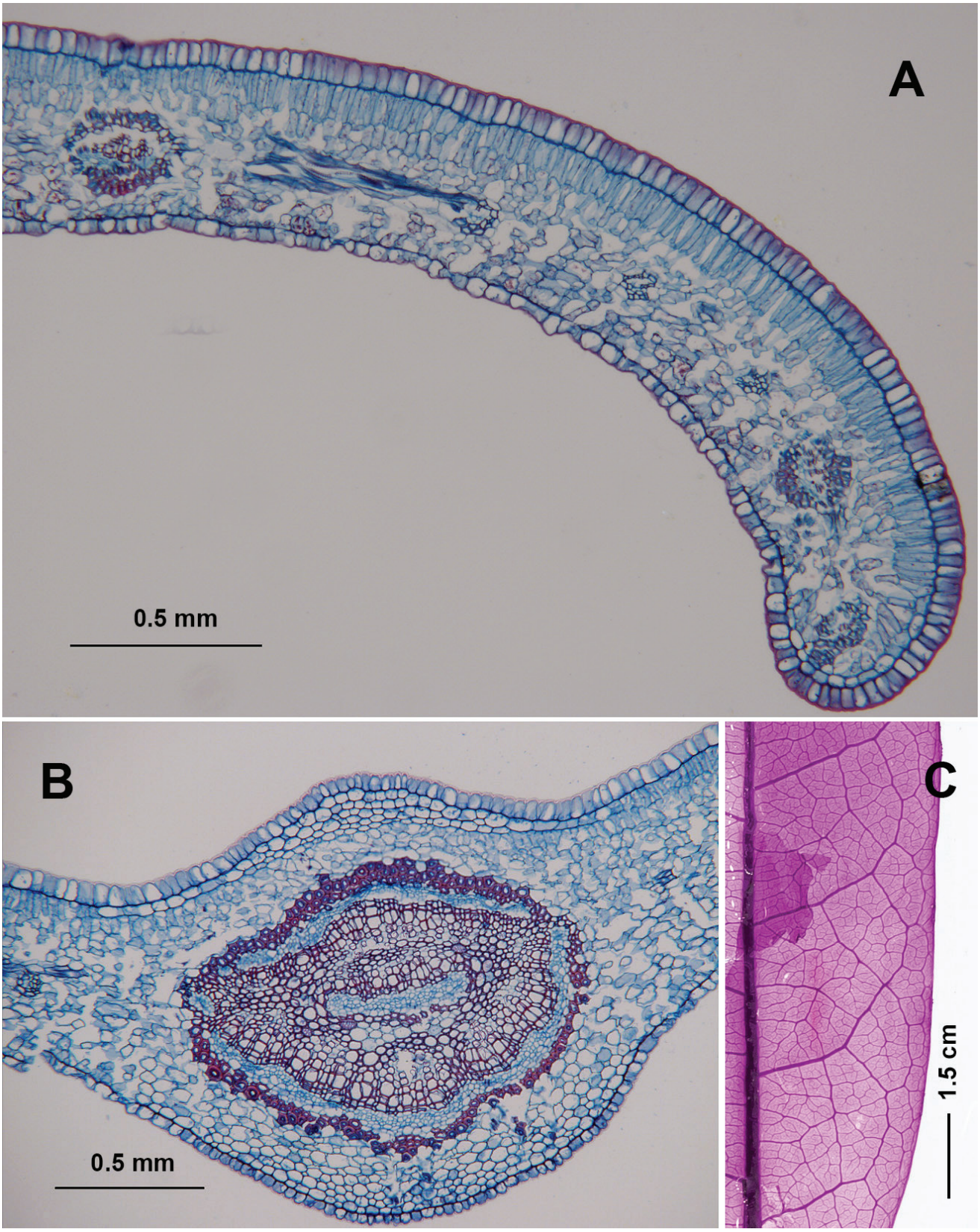

FIGURE 4. Leaves of *Paypayrola arenacea* Aymard & G. A. Romero. **A**, cross section showing the leaf margin; **B**, midvein; **C**, venation.

have 123–15000 ppm of aluminum (Chenery, 1949). The lamina in *Paypayrola arenacea* is a yellowy-green color that is associated with aluminum accumulation (Chenery, 1948). Our test for this mineral in leaves of *P. arenacea* was positive; however, without quantitative testing it isn't possible to ascertain if levels of aluminum accumulation exceed that of the soil (i.e., hyperaccumulation; see Jansen et al., 2002). It is of interest to note that Chenery (1949) found different levels of aluminum in samples of different maturity in the one species examined in replicate (*Rapatea paludosa* Aubl.); however, it was not indicated if these were from the same individual or even from the same soil.

Discussion

Paypayrola arenacea is remarkable in the genus for its small stature and smaller leaves. Fertile individuals seen in the type locality did not even reach 1.0 m in height, although sterile individuals found near the type locality, along a savanna-*caatinga* ecotone were up to 1.5–1.7 m tall. The reduced vegetative parts and the white flowers easily distinguish this new species from all others of *Paypayrola* (see appendices I and II). *Paypayrola arenacea* differs further in having brochidodromus vs. eucamptodromous venation sometimes with a few brochidodromus veins distally, and ramified tertiary venation vs. tertiary veins rarely branched.

This new species exhibits a steep angle of leaf insertion (Fig. 1A, 2A, C, D), a mechanism that is common in open-canopied vegetation in the region that minimizes exposure to intense insolation (Medina at al., 1990). Havran and Ballard (unpublished, cited in Ballard, 2014) suggest the number of palisade parenchyma layers in some *Viola* is correlated to light exposure.

Paypayrola arenacea leaves were covered by a thick cuticle, had slightly recessed guard cells, and increased palisade parenchyma, although other xeromorphic anatomical features (Esau, 1965: 429), such as mesophyll sclerenchyma not associated with the vascular bundles (Dickison, 2002: 312) were not present. In some Violaceae inner epidermal cell walls secrete mucilage, not detected here. Mucilage produced in quantity may function in water storage enabling plants to endure drought (Roth and Lindorf, 1991). Plants subjected to fluctuating inundation and dry periods may exhibit a structural combination of characters associated with both xerophytism and hydrophytism (e.g., *Equisetum*, see Foster and Gifford, 1988: 189; *Abolboda*, Campbell, 2004). We suggest that the leaf structure and stunted plant size (see Prance and Schubart, 1978; Klinge and Medina, 1979; Anderson, 1981), and presence of a lignotuber (see Fahn and Cutler, 1992; Fig. 1A, 2D) are adaptations to both limited water availability and oligotrophic soils (Seddon, 1974; Medina et al., 1990). Resprouting from lignotubers or xylopdia is a adaptation to fire-prone habitats in Australia (especially Myrtaceae; Burrows, 2013) and cerrado vegetation (Appessato da Gloria and Cury, 2011; Frisby et al. 2013; Many xerophytic characteristics can also result from insufficient nutrients, particularly N and P (Medina et al., 1990; Fahn and Cutler, 1992: 136). The leaf margin in some dried specimens of *Payparola* appears to be thickened, but not enrolled as in *P. arenacea*, where it is most prominent at the lamina base (see Wilkinson, 1979) and is underlain by a narrow layer of mechanical tissue. We did not observe any mites (Chevalier and Chesnais, 1941; Jacobs, 1966; Stace, 1965) or fungi inhabiting the leaf surface; however, further observations are warranted to determine if the enroll functions as a domatium. In Violaceae domatia are known in *Rinorea* (Ballard et al., 2014).

White sand savannas can be small to large (up to hundreds of hectares) patches of herbaceous vegetation, most often found near black water rivers, which can be partially or completely flooded during the peak of the rainy season (June–August in the northern hemisphere). These savannas are surrounded by Amazonian *caatinga*, *bana*, or sometimes by *terra firme* forest (Klinge et al. 1977; Prance 1996). The soils are deep sandy spodsols or quarzitaments, a very acidic parent material characterized by a subsurface accumulation of humus that is complexed with aluminium and iron (Herrera, 1979; Schargel et al., 2000). As in *banas*, this unique vegetation could be considered the ultimate seral state in reduction of biomass, caused by extreme levels of nutrient deficiency, periodic fires, and unfavorable soil-water conditions (Huber, 1995a, b; Klinge and Cuevas, 2000). The most profound climatic event in South America occurred during the Last Glacial Maximum (LGM), ca. 18000 years ago. There is evidence for a decline in precipitation and a decrease in temperature of up to 5 °C in some parts of this continent (Bush et al., 2004); climate was dry and cool, inducing a high degree of aridity in this region (van der Hammen and Hooghiemstra, 2000; Hooghiemstra et al., 2002). Some authors have used this evidence to suggest that large tracks of Amazonian forests were largely converted into savannas during the glacial periods. Pennington et al. (2000) proposed that much of the current extent of the Amazonian forest in the LGM was occupied by the now geographically restricted seasonally dry tropical forests and, in several areas of the Amazon basin, forest vegetation changed perhaps into present day savanna and others types of deciduous, scrubby vegetation (van der Hammen and Absy, 1994; Pessenda et al., 2004; Mayle et al., 2007). Nonetheless, others authors find no evidence for a widespread transition from forests to a woodland savanna system either in the paleoecological record (Colinvaux et al., 2000) or in modelling studies (Cowling et al., 2001). The pollen record suggests that glacial-age Amazonian forests, with their mix of currently Andean and lowland Amazonian taxa, have no modern analogues (Mayle et al., 2009).

Amazonian oligotrophic white sand savannas are characterized by many species only known from this particular habitat, but unlike others tropical savannas they harbor relatively few taxa of Poaceae (i.e., *Axonopus casiquiarensis* Davidse, *A. schultesii* G. A. Black, *Paspalum*

tillettii Davidse and Zuloaga, and *Steyermarkochloa angustifolia* (Spreng.) Judz.). Other remarkable examples of the unique white sand savanna flora are: *Gongylolepis martiana* (Baker) Steyerm. & Cuatrec. (Asteraceae), *Schefflera pimichinensis* Maguire, Steyerm. & Frodin, and *S. spruceana* (Seem.) Maguire, Steyerm. & Frodin (Araliaceae), *Pitcairnia juncoides* L. B. Sm. (Bromeliaceae), *Terminalia yapacana* Maguire (Combretaceae), *Blepharanda angustifolia* (Kunth) W. R. Anderson (Malpighiaceae), *Comolia prostrata* Wurdack (Melastomataceae), *Duckeella adolphii* Porto & Brade (Orchidaceae), *Cybianthus reticulatus* (Benth. ex Mez) G. Agostini (Primulaceae), and *Polygala sanariapoana* Steyerm. (Polygalaceae). Other families with species endemic to white sand savannas are Araceae, Cyperaceae, Eriocaulaceae, Euphorbiaceae, Gentianaceae, Haemodoraceae, Lentibulariaceae, Rapateaceae, and Xyridaceae.

Other cases of "dwarfism" are known in plant species that grow in white sand savannas, such as *Himatanthus semilunatus* Markgr. (Apocynaceae), *Lacmellea pygmaea* Monach. (Apocynaceae), *Macrolobium savannarum* R. S. Cowan (Fabaceae), *Pachira amazonica* (A. Robyns) W. A. Alverson (Malvaceae), *Parkia nana* D. A. Neill (Fabaceae), *Ouratea deminuta* Maguire & Steyerm., *O. yapacanae* Sastre and *O. huberi* Maguire & Steyerm. (Ochnaceae). Two particular cases of extreme vegetative reduction are *Pitcairnia juncoides* (authors' pers. obs.) and *Steyermarkochloa angustifolia* (Davidse & Ellis, 1984).

The unusual habit of *Paypayrola arenacea* is, to our knowledge, unique in woody Violaceae. What appear to be individual stems, as evidenced by a tap root, occur aggregated in isolated clumps, slightly elevated above the savanna (Fig. 2C). One of these clumps was excavated and it revealed a truncated stem without connection to other nearby clumps (Fig. 2D). The isolated plants form several woody stems branching near ground level from a nodular tuber atop a tap root. Plants inhabiting upper Rio Negro savannas are adapted to poor and acidic soils that can be periodically flooded; some species produce a greater below ground biomass relative to above ground (Campbell, 2004); however, the possible cause and selective advantage for the habit of *P. arenacea* warrant further study. Morphologically, *Paypayrola arenacea* does not appear to have close allies: its small vegetative size and its life-form easily distinguish it from all the other species in the genus. (see key to species in Appendix I.)

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Appendix I

Key to the species of *Paypayrola*

The authors could not locate the type of *Wibelia brasiliensis* Spreng., the base name of *Paypayrola brasiliensis* (Spreng.) Steud. (see Appendix II) and the original description of this species is quite succinct (*"W. pedunculis rameis unifloris aggregatis, foliis oblongis scabris, laciniis calycinic obtusis. Hab. Brasilia"*). Furthermore, we did not find any herbarium material referable to *Paypayrola brasiliensis*, which is lamentably excluded from the key. In writing the key, we struggled to find characters differentiating *Paypayrola blanchetiana* from *P. hulkiana*, which appear to the closely related.

1. Leaves lanceolate to elliptic-lanceolate, base long-attenuate 2
1. Leaves ovate, obovate, or oblong-lanceolate, base rounded, cuneate, or short-attenuate 4
2. Suffrutices, petiole <4 mm long; leaf blade 3.5–8.0 cm long . . . . . *P. arenacea*
2. Shrubs to small trees, petiole >5 mm long, leaf blade 16–30 cm long 3
3. Leaves obovate to obovate-lanceolate, petiole >12 mm; rachis elongate, inflorescence loose . . . . . *P. longifolia*
3. Leaves elliptic to obovate-elliptic, petiole 5–9 mm; rachis shortened, inflorescence congested . . . . . *P. confertifolia*
4(1). Flowers robust, 15–30 mm long, petals ovate . . . . . *P. grandiflora*
4. Flowers slender,10–15 mm long; petals linear 5
5. Leaves obovate-oblong; inflorescence 3–6 cm long, connective apex lacking . . . . . *P. guianensis*
5. Leaves lanceolate-oblong; inflorescence 1–3 cm long, connective apex present 6
6. Leaves 4–6 cm wide, apex long-acuminate; ovary conical . . . . . *P. hulkiana*
6. Leaves 6–10 wide, apex acute; ovary ovate-linear . . . . . *P. blanchetiana*

Appendix II

A synopsis of *Paypayrola*

Paypayrola Aubl., Hist. Pl. Guiane 1: 249, t. 99. 1775. TYPE SPECIES: *Paypayrola guianensis* Aubl. (see Farr and Zijlstra, 2014).

Paypayrola blanchetiana Tul., Ann. Sci. Nat., Bot. sér. 3, 7: 371. 1847. TYPE: BRAZIL. Bahia, 1836, *J. S. Blanchet 2312* (Holotype: P; Istoypes: F [1540468; 695196, fragment], G, K, P).

Paypayrola brasiliensis (Spreng.) Steud., Nomencl. Bot. [Steudel], ed. 2. ii. 280. 1841.

Basionym: *Wibelia brasiliensis* Spreng., Neue Entdeck. Pflanzenk. 3: 63. 1822. TYPE: BRAZIL. Without locality, date, or collector [type not located].

Homotypic synonym: *Paypayrola sprengelii* Tul., Ann. Sci. Nat., Bot. sér. 3, 7: 371. 1847.

Paypayrola confertiflora Tul., Ann. Sci. Nat., Bot. sér. 3, 7: 373. 1847. TYPE: FRENCH GUIANA. Rivière de la Compté, "Arbuste," September 1842, *E. M. Mélinon 150* (Holotype: P; Isotype: P).

Paypayrola grandiflora Tul., Ann. Sci. Nat., Bot. sér. 3, 7: 371. 1847. TYPE: BRAZIL. Pará, *ex Herb. Lusitanicum s.n.* (Holotype: P; Isotype: P).

Synonym: *Paypayrola ventricosa* Tul., Ann. Sci. Nat., Bot. sér. 3, 11: 153 [footnote]. 1849. TYPE: PERU. Maynas, *Arbor humilis*, *E. F. Poeppig 2327* (Syntype: P; Isosyntypes: G [not seen], P, W [not seen]), *E. F. Poepping 3077* (Syntype: P; Isosyntypes: G [not seen], P, W [not seen]).

Paypayrola glazioviana Taub., Bot. Jahrb. Syst. 15(2, Beibl. 34): 2. 1892 [5 Apr 1892]. TYPE: BRAZIL. Rio de Janeiro, entre Lagoa do Peixe et Rio Bonito, "Arbusto, flor amerellada," 22 September 1881, *A. F. M. Glaziou 12530* (Holotype: P; Isotype: C [ex herbario Eug. Warming], R).

In the original description, L. R. Tulasne compared *Paypayrola ventricosa* to *P. grandiflora*. Smith and Fernández-Pérez (1954) relegated the former to the synonymy of *P. grandiflora*. An examination of the syntypes and isosyntypes of *P. ventricosa* at P indeed show large, robust flowers. According to an annotation of W. H. A. Hekking attached to the holotype of *P. glazioviana* at P, dated 31 January 1996, this name is a taxonomic synonym of *P. grandiflora*.

Paypayrola guianensis Aubl., Hist. Pl. Guiane 1: 249, t. 99. 1775. TYPE: FRENCH GUIANA. Sin. loc., *F. J. B. C. F. Aublet s.n.* (Holotype: BM).

Paypayrola hulkiana Pulle, Recueil Trav. Bot. Néerl. 9: 155. 1912. TYPE: SURINAM. In forests in the upper Gran Rio ["In Wäldern am oberen Gran Rio"], 8 September 1910, ca. 200 m, *J. F. Hulk 248* [Syntype, not seen]; 25 September 1910, ca. 350 m, *J. F. Hulk 296* [syntype, not seen].

Paypayrola longifolia Tul., Ann. Sci. Nat., Bot. sér. 3, 7: 372. 1847. TYPE: GUYANA [Guiane Anglaise], 1844, *R. H. Schomburgk 826* (Holotype: P; Isotypes: G, K [*ex Herbarium Benthamianum*]).