



A new *Paypayrola* (Violaceae) from Panama, with notes about the species complexes for the genus

HARVEY E. BALLARD, JR.¹

Department of Environmental and Plant Biology, Ohio University, Athens, OH 45701, USA

¹ [✉ ballard@ohio.edu](mailto:ballard@ohio.edu); <https://orcid.org/0000-0003-2396-784X>

Abstract

A new species of *Paypayrola* is described from multiple exsiccatae from west-central and east-central Panama. *Paypayrola panamensis* sp. nov. is represented by dozens of herbarium specimens from 26 putatively distinct populations located at lower elevations on the northern slope, in wet evergreen tropical forest on slopes and ridgetops, as well as along streams and rivers. By its moderately short-petiolate leaves and yellow corollas, the new species resembles northern South American *P. guianensis* and *P. hulkiana*. It differs from *P. guianensis* in its proportionally longer leaf blades, subsessile to short-pedunculate, short inflorescences, and puberulent sepals longer than broad. It differs from *P. hulkiana* in its proportionally broader leaf blades, and proportionally broader elliptical to suborbicular sepals, commonly with two (rarely four) distinct lateral nerves besides the medial nerve, and a broadly rounded to frequently truncate or retuse apex. The new species also differs from both in its larger leaf blades with more lateral nerves, tapering to a narrowly rounded or weakly subattenuate apex, and a more densely flowered inflorescence. A key differentiating it from other species of *Paypayrola* is provided. In discussing the genus, three species complexes are well separated based on corolla color and inflorescence features.

Resumen

Se describe una nueva especie de *Paypayrola* de numerosas exsiccatas del centro-oreste y centro-este de Panamá. *Paypayrola panamensis* sp. nov. está representada por docenas de especímenes de herbario de 26 poblaciones supuestamente distintas, ubicadas en elevaciones bajas en la ladera norte, en bosques húmedos siempreverdes localizados en laderas y crestas, así como a lo largo de arroyos y ríos. Por sus pecíolos moderadamente cortos y las corolas amarillas, la nueva especie se parece a *P. guianensis* y *P. hulkiana* del norte de América del Sur. Sin embargo, se diferencia de *P. guianensis* en sus láminas foliares proporcionalmente más largas, subsésiles a cortamente pedunculadas, las inflorescencias pequeñas y los sépalos puberulentos más largos que anchos. Se diferencia de *P. hulkiana* en sus láminas foliares proporcionalmente más anchas, y los sépalos proporcionalmente más anchos, de elípticos a suborbiculares comúnmente con dos (rara vez cuatro) nervios laterales diferentes del nervio medio, y un ápice ampliamente redondeado a frecuentemente truncado o retuso. Igualmente, difiere de ambas especies en sus láminas foliares más grandes, con nervios laterales más numerosos, con un ápice estrechamente redondeado o débilmente subattenuado, y las inflorescencias con numerosas flores. Se presenta una clave para diferenciar las especies de *Paypayrola*. Al discutir el género, se distinguen tres complejos de especies según el color de la corola y las características de la inflorescencia.

Introduction

The Violet family (Violaceae) is a moderate-sized monophyletic lineage of 27 currently recognized genera and five additional genera awaiting description or resurrection, that collectively include 1,000–1,100 species worldwide (Ballard Jr. *et al.*, 2014; Wahlert *et al.*, 2014). The greatest generic diversity is found in the Neotropics, the family's "center of origin". The family has received increasing scrutiny in recent decades at both the genus and species levels

following active phylogenetic studies, which have driven narrowed recircumscription of the formerly polyphyletic genera *Hybanthus* Jacquin (1760: pl. 2) and *Rinorea* Aublet (1775: 235, pl. 93) and recognition of several disparate lineages as smaller monophyletic, oligotypic or monotypic genera.

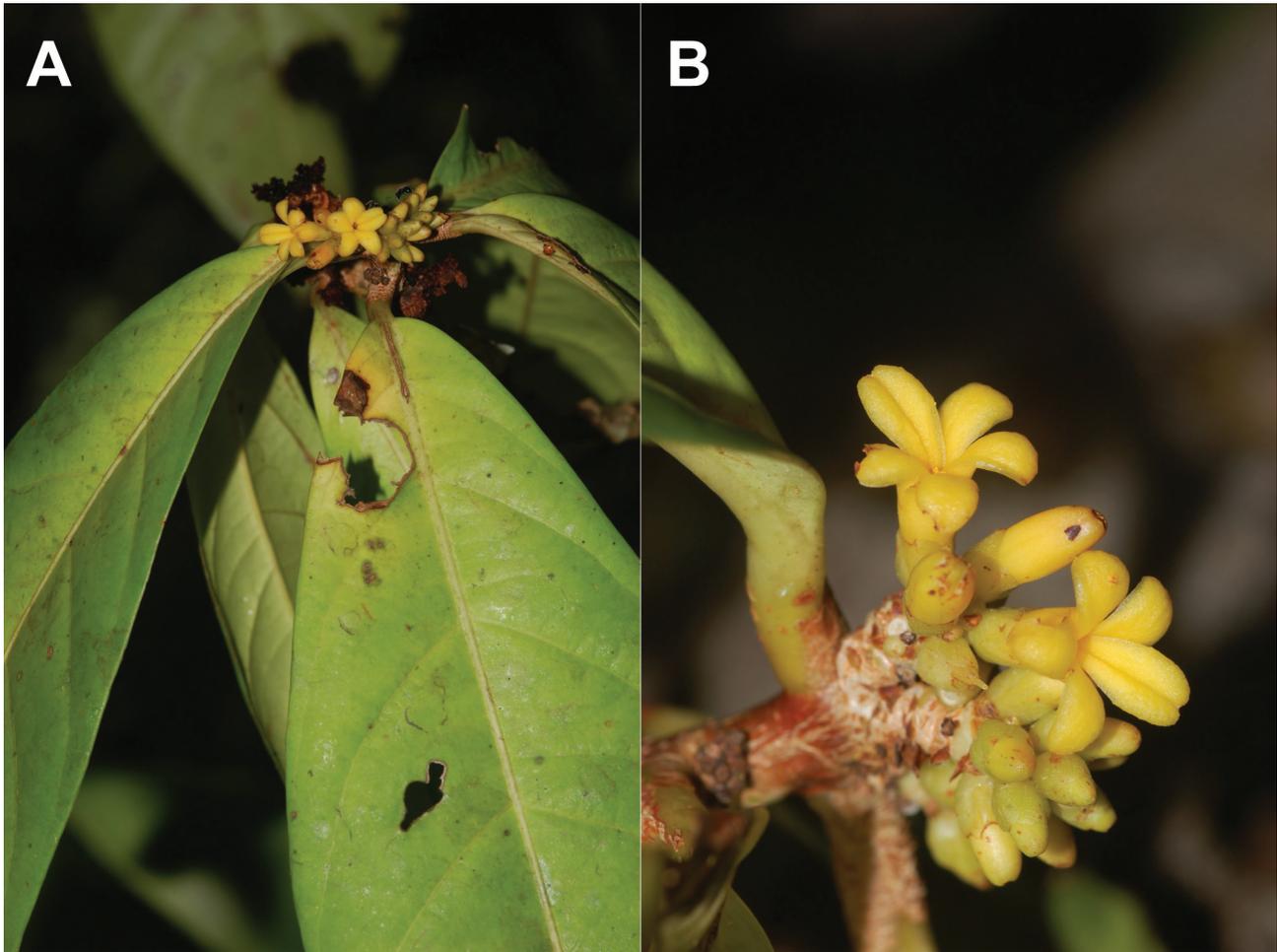


FIGURE 1. Features in life of flowering *Paypayrola panamensis*. A. Branch with leaves and inflorescences. B. Closeup of flowers. Photos by Barry Hammel.

The genus *Paypayrola* Aublet (1775: 249, pl. 99) is one of several smaller genera in the family. As a neotropical lineage, it is distributed broadly at lower elevations in northern South America, and it is disjunct in central Panama. Its main center of diversity is the Guianan Shield from eastern Venezuela to French Guiana and southward into northern Amazonian Brazil.

Regarding early intrafamilial classifications including *Paypayrola* in the Violaceae, Bentham and Hooker recognized three tribes in the family, the *Violeae* DC. (1824: 288) with distinctly zygomorphic flowers, the *Paypayroleae* Bentham & Hooker (1862, vol. 1, part 1: 115) with weakly zygomorphic flowers and lower portion of the petals claw-like coherent into an elongate tube, and the *Alsodeieae* Bentham & Hooker (1862, vol. 1, part 1: 116) with essentially actinomorphic flowers and petals more or less lacking a distinct claw. The *Paypayroleae* tribe *Amphirrhox* Sprengel (1827, 4(2): 51), *Isodendrion* A.Gray (1852, 2: 324), and *Paypayrola*. Reiche and Taubert followed this classification but replaced the name *Alsodeieae* with *Rinoreeae* Reiche & Taubert (1895, III, 6: 327). Melchior later subordinated the *Paypayroleae* to a subtribe, the *Paypayrolinae* Melchior (1925, ed. 2, 21: 356) under tribe *Rinoreeae* and removed *Isodendrion* to its own subtribe, leaving only *Amphirrhox* and *Paypayrola* in subtribe *Paypayrolinae*. Hekking (1988) continued this last treatment of the *Paypayrolinae*. In this context, *Amphirrhox* and *Paypayrola* share a mostly arborescent habit, a well developed staminal tube, and weakly zygomorphic flowers with one petal broader and slightly differentiated in shape relative to the others, all petals with elongate slender claw-like base coherent into a pronounced tube (Ballard Jr. *et al.*, 2014). A comprehensive family-level molecular phylogenetic study (Wahlert *et al.*, 2014), however, has revealed that the actinomorphic-zygomorphic distinction prevalent in previous classifications is evolutionarily labile, and has provided moderate support for removing *Amphirrhox* to a separate clade with other genera possessing simple to compound cymose or dichasial inflorescences (these reduced to solitary flowers in some

Australian members of the *Hybanthus caledonicus* group). The clade containing the relatively recently described monotypic genus *Hekkingia* H.E. Ballard & Munzinger (Munzinger and Ballard 2003: 345) and *Paypayrola* is well supported but part of an unresolved grade of lineages. The two genera share a close but equivocal relationship, presumably based on low sampling and low genetic divergence of the few plastid loci utilized; the basal polytomy involving *Hekkingia* and *Paypayrola grandiflora* provides equal support for a sister relationship between the two genera on one hand and inclusion of *Hekkingia* in *Paypayrola* on the other.

The clade demands closer phylogenetic scrutiny with comprehensive sampling of species diversity and populations over the range of widely distributed species, ideally employing a multi-locus marker system. The very recent practice of sinking multiple genera in the Violaceae into larger and phenotypically heterogeneous genera without consistency and without reference to cumulative published knowledge about the genera involved, as done by Byng and Christenhusz (2018), is regrettable. Abundant evidence supports the distinctness and maintenance of all genera in the family recognized prior to the publication mentioned above; published combinations by Byng and Christenhusz are rejected by the author. Given the equivocal evidence regarding the relationship of *Hekkingia* and *Paypayrola* and their equally probable sister relationship, the action to synonymize them is premature and must await further compelling phylogenetic evidence with comprehensive taxon sampling. Therefore, the author does not accept the proposed merger.

Since Jean Baptiste Christophe Fusée Aublet described *Paypayrola* in 1775, the genera *Lignonia* Scopoli (1777: 292), *Payrola* Jussieu (1789: 427), *Periclistia* Benthams (1842: 108), and *Wibelia* Persoon (1804, 1: 210) have been described, and several new species and combinations made under them. During the last century, as herbarium collections and knowledge of the taxa increased and access to type specimens became available, taxonomists eventually synonymized the other genera under *Paypayrola*. By the close of the last century, the consensus taxonomic view recognized six species of *Paypayrola*: *P. blanchetiana* Tulasne (1847: 371), *P. confertiflora* Tulasne (1847: 373), *P. grandiflora* Tulasne (1847: 371), *P. guianensis* Aublet (1775, 1: 249, pl. 99), *P. hulkiana* Pulle (1912: 155) and *P. longifolia* Tulasne (1847: 372).

While generally considered a South American genus, *Paypayrola* has also been reported from Costa Rica and Panama. Robyns (1967) did not mention *Paypayrola* in the treatment of Violaceae for the “Flora of Panama” series. Nevertheless, many collections have subsequently been taken in central Panama from the 1970s to well into the current century. These specimens have been attributed to *P. confertiflora*, *P. grandiflora*, *P. guianensis* and *P. longifolia*. Some authors have recently reported the genus from Costa Rica. Such reports appear to be based on a Tropicos record from MO. Research in preparation for the 2015 Violaceae treatment in the “Manual de Plantas de Costa Rica” (Ballard Jr., 2015) found no specimens at CR and MO to substantiate the existence of *Paypayrola* in Costa Rica. Absence of supporting specimens has been reconfirmed for this manuscript, and the basis of the record has been determined to be a collection number transcription error that confused species determination and locality (Mike Grayum, Barry Hammel and Jim Solomon, pers. comm.).

Intensified taxonomic interest in Violaceae since the beginning of the present century has prompted the description of five genera and 130 new species worldwide, as well as numerous new combinations raising infraspecific taxa to species, and many interspecific hybrids. Concerning Latin American genera, four genera, *Bribria* Wahlert & H.E. Ballard (Wahlert *et al.* 2018: 146), *Hekkingia* H.E. Ballard & Munzinger (Munzinger and Ballard 2003: 345), *Hybanthopsis* Paula-Souza (de Paula-Souza and Souza 2003: 210) and *Ixchelia* H.E. Ballard & Wahlert (Wahlert *et al.* 2015: 275), and 35 new species, were described. Nine of the new species were described from lowland rainforests, and attracted attention due to their peculiar morphology, disjunct distribution, or occupation of unusual and regionally restricted habitats. As the first new *Paypayrola* described in more than a century, *P. arenacea* Aymard & G.A. Romero (Aymard-C. *et al.* 2014: 176, figs. 1–2) was published in 2014 for its novel short stature, suffruticose habit and propagation from tubers, as well as its unusual white sand shrubby savanna habitat in upper Rio Negro basin, Amazonian Venezuela. *Paypayrola arenacea* is similar to *Paypayrola longifolia* in leaf shape but with shorter petioles and smaller reproductive structures, and white corolla (often pink-tinged). Comparison with other species in the genus also demonstrates that it has exceedingly short petioles relative to other species.

Close scrutiny of herbarium specimens and images of living plants from Panama, and comparisons to specimens of other known *Paypayrola* taxa in South America, has led the author to conclude that the Panamanian specimens represent one distinct morphologically coherent new species. This new species has close morphological similarities to *P. guianensis* and *P. hulkiana* (especially the latter) while expressing multiple quantitative and qualitative differences in foliage and reproductive structures. Additionally, studies of type specimens and protologues, and reexamination of numerous herbarium specimens, have revealed a substantial number of misidentifications of specimens in South American *Paypayrola* by violet specialists and lay taxonomists alike. These misidentifications have obscured species-

level diagnostic differences in inflorescence morphology, sepal shape and indument, corolla color and petal indument, as well as leaf blade shape and number of nerves. Moreover, corrected identifications of specimens have prompted the author to distinguish three informal species complexes in *Paypayrola* based on corolla color, inflorescence and sepal traits, discussed below, that may prove upon further analysis to represent natural evolutionary sublineages.

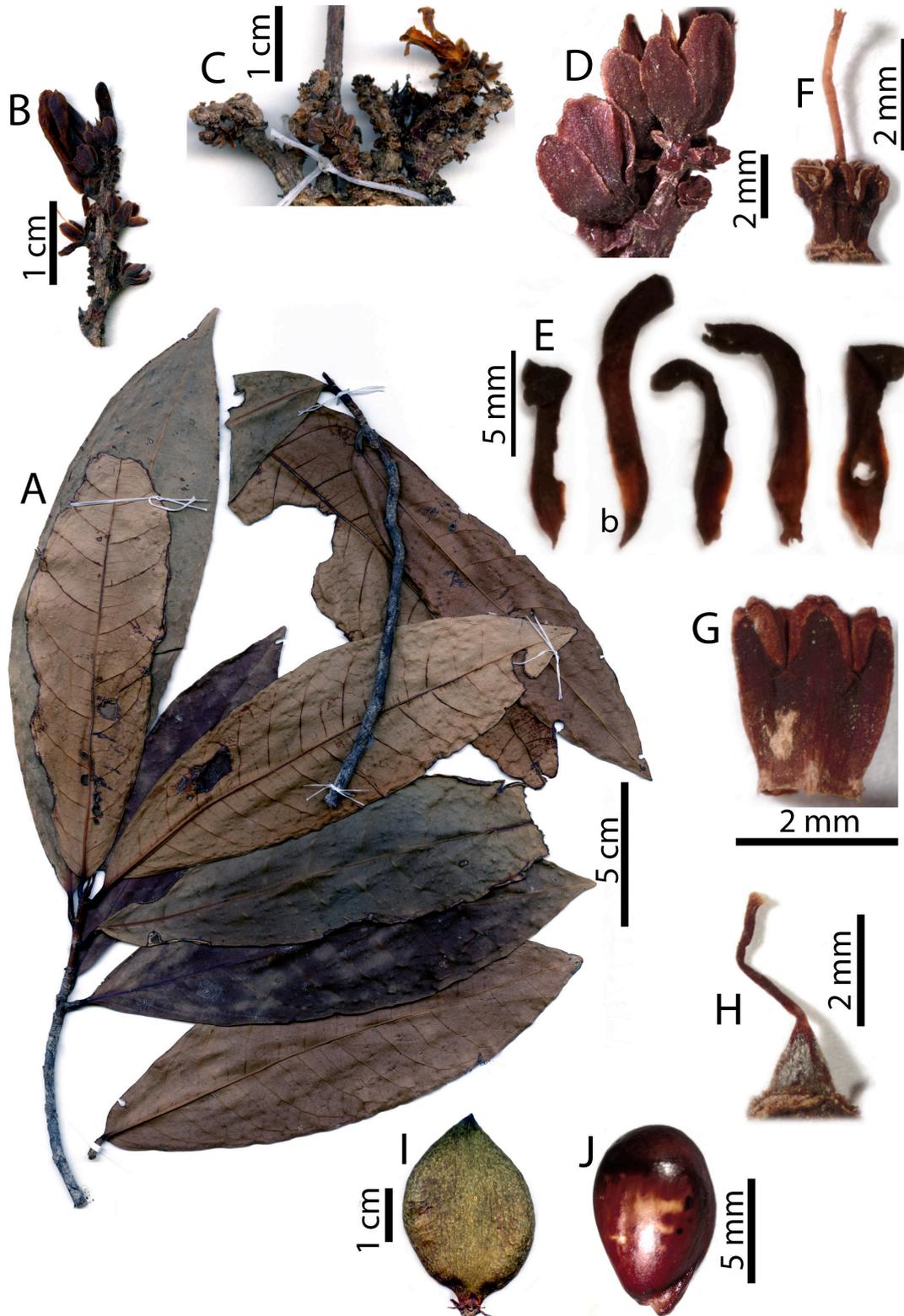


FIGURE 2. Features of *Paypayrola panamensis*. A. Branches and leaves (*de Nevers et al.* 5363, holotype, MO4998611). B. Inflorescence, unbranched botryoid (*de Nevers et al.* 5363, isotype, WIS). C. Inflorescence, branched botryoid (*McPherson* 20241, MO6284427). D. Sepals (*de Nevers et al.* 5363, isotype, WIS). E. Petals; broadest (b) is conduplicate and folded in half (*Maas et al.* 2794, MO2639559). F. Intact reproductive structures (*McPherson* 7586, MO3311495). G. Androecium (*de Nevers et al.* 5363, isotype, WIS). H. Gynoecium (*Maas et al.* 2794, MO2639559). I. Capsule (*McPherson* 20241, MO6284427). J. Seed (*McPherson* 20241, MO6284427).

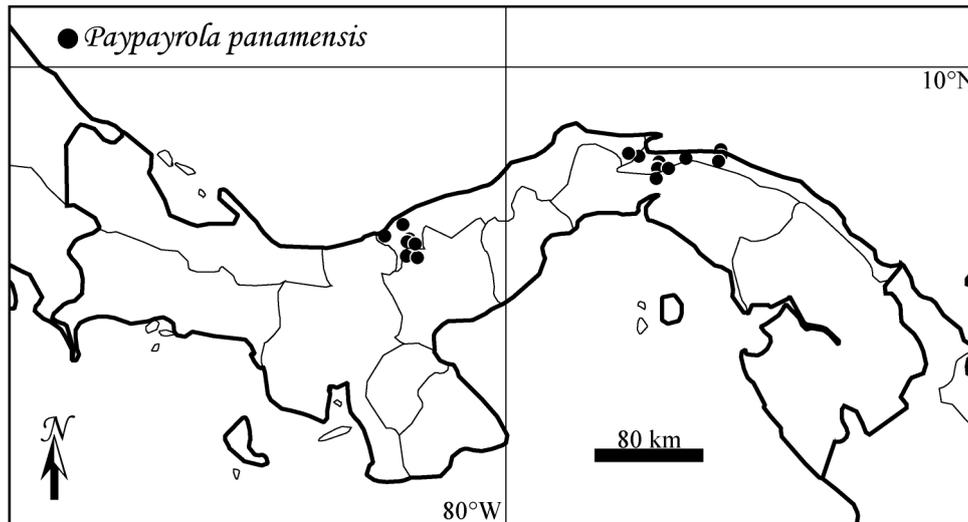


FIGURE 3. Map of the distribution of *Paypayrola panamensis*.

A dichotomous key differentiating the new species from others in the genus, a diagnosis and complete description, ecological and other notes, images of living plants and illustrations, and a geographic distribution map are presented.

Materials and methods

An explicit morphological species concept was used in this study, applying the International Code of Nomenclature (Turland *et al.*, 2018) to nomenclature and typifications. The new species was delineated on the basis of 46 herbarium specimens and two images of living plants. Delineation and characterization of other members of *Paypayrola*, including types, were based on examinations of herbarium specimens or images. Herbarium specimens are cited with the herbarium acronym (Thiers, 2019) followed by the accession or barcode number (which are differentiated by the latter preceded by the term “barcode”). For this study, comprehensive herbarium specimens or their online images were examined from HBG, L, LPB, MO, P, U, US, WAG, and WIS; additional selected specimens were examined from B, BR, C, CUZ, F, G, K, M, NY, S, and W.

Where a specimen label lacked latitude-longitude coordinates but provided a relatively specific location, a location was georeferenced manually using Google Earth Pro; decimal degree coordinates in such cases are in brackets after the location. Conservation assessment of *Paypayrola panamensis* according to IUCN categories and criteria (IUCN, 2017), the extent of occurrence (EOO) and area of occupancy analysis cell width set to 2 km (AOO) were calculated for all georeferenced collections using the GeoCAT Geospatial Conservation Assessment Tool (Bachman and Moat, 2012), constantly updated through the <https://www.kew.org/science/our-science/projects/geocat-geospatialconservation-assessment-tool>.

After careful examination and redefinition of species as needed, specimens were confirmed or reidentified. In order to aid in precise comparisons of species, the detailed description for *Paypayrola arenacea* was atomized into numerous individual traits in an Excel spreadsheet, to which a number of other potentially species-diagnostic features were added, totaling 92 quantitative and qualitative features. Features of spread petals and reproductive structures were observed after soaking mature flowers from multiple specimens in a dilute soapy water solution in microfuge tubes, followed by dissection, pressing, drying and gluing of parts onto acid-free paper. Dissections were subsequently wrapped in tissue and returned to packets on the specimens. Traits were initially recorded for individual specimens of each recognized species, then traits were summarized across specimens. Measurements on structures were performed on images of herbarium specimens or floral dissections using ImageJ software (Rasband, 2019). Imaging of larger structures or whole herbarium specimen sheets utilized an Epson Expression 10000 XL large-format flatbed scanner set at 300 dpi, while imaging of smaller structures, including floral dissections, employed video capture from an Olympus SZ61 boom binocular dissecting microscope equipped with an Olympus SC30 videocamera, using the prepackaged Olympus Cells and Imaging software, under illumination by a VOLPI V-Lux 1000 dual fiberoptic light source. All

traits represent character states on dried specimens except where indicated (i.e., designated “in life”), with these latter *in vivo* states extracted from herbarium specimen labels or from the two images of living plants.

Taxonomy

Paypayrola panamensis H. E. Ballard, *sp. nov.* (Figs. 1–3)

Type:—PANAMA. **Panamá**: El Llano-Cartí Road, Km 26.5, 9°19'N, 78°55'W, 200 m, Tree 8 m, petals yellow, 14 April 1985, *de Nevers, Herrera & Charnley 5363* (holotype, here designated: MO4998611!; isotypes: U1757190!, US3556948!, WIS!).

Paypayrola panamensis differs most obviously from *P. guianensis* in its proportionally longer leaf blades, subsessile to short-pedunculate, short inflorescences, and puberulent sepals that are commonly slightly to distinctly longer than broad; from *P. hulkiana* in its proportionally broader leaf blades, proportionally broader elliptical to suborbicular sepals commonly with two (rarely four) distinct lateral nerves in addition to the medial nerve and a frequently truncate or retuse apex; and from both in its larger leaf blades with more lateral nerves, blade apex weakly subattenuate to narrowly rounded, and a densely flowered inflorescence.

Small trees, (1.5)3–10 m tall. **Stem** glabrous throughout, bark gray to brownish-gray, branches often minutely longitudinally ridged. **Stipules** promptly caducous, narrowly attenuate-triangular to lance-attenuate, 6–8 mm long × 2 mm wide at the base, sometimes carinate, apex acuminate to attenuate. **Leaves** simple, alternate below, sub-opposite or clustered near the branch tips; petiole slightly swollen, on young leaves blackish and smooth, on older becoming woody, grayish-brown and transversely rugose or furrowed, (4)6–21 × 1.6–3.9 (medial) mm; leaf blade oblanceolate to broadly oblanceolate, 18.4–29.3 × (4.1)5.9–9.8, 2.6–3.9(4.6), subcoriaceous, drying dull gray-green above, distinctly paler below, base narrowly cuneate to cuneate or weakly convexly tapering, 26–74(83)°, apex tapering or subattenuate to a narrowly rounded tip, rarely convexly rounded to an obtuse or broadly rounded tip, 39–78(149)°, complete veins 8–12 on each side, margins entire. **Inflorescences** cauliflorous and ramiflorous, 1–4 unbranched and/or branched botryoids per node, inflorescence bracts caducous, rachis 7–20 × 1.0–1.6 mm, subsessile to short-pedunculate, peduncle 0.6–3.8 mm, rachis densely flowered, at least distally. Mature **flowers** 6–15 per botryoid, the proximal commonly aborted; pedicel 0.6–1.9 × 0.8–1.2 mm, articulate, pedicel bracteoles ovate-lanceolate to broadly deltate-triangular, 0.9–1.3 × 0.5–1.3 mm; flower buds yellow in life, oblanceoloid, flowers, at full anthesis, 7–18 mm long. **Sepals** 5, quincuncial, subequal, outer shorter than inner, fleshy basally, narrowly to broadly oblong-elliptical or suborbicular, as long as to distinctly longer than broad, 1.6–3.9 × 1.4–2.7 mm, length: width ratio 1.0–1.7(2.0), base abruptly rounded to subtruncate, apex broadly rounded or frequently truncate to retuse, minutely puberulent adaxially, margins ciliolate, (1)3 or 5 nerves, frequently raised and prominent, small black subapical subconical to cylindrical appendage frequently terminating medial nerve. **Corolla** weakly bilaterally symmetrical, petals 5, quincuncial, bright yellow, fleshy, strongly recurved in life, one petal ca. 2 × broader in distal half than others, all petals with five obscure nerves visible upon hydration, glabrous or sparsely to moderately minutely puberulent adaxially in basal half, sometimes sparsely minutely hirtellous along costa, margins eciliate or minutely ciliolate, narrow petals weakly pandurate, convex in cross-section, apex narrowly rounded, 7–11 mm long × 1.4–2.2 mm wide in their distal half, broadest petal pandurate, v-shaped in cross-section, apex retuse, 10–17 mm long × 3.2–3.4 mm wide in its distal half. **Androecium** 1.6–2.6 mm tall, stamens 5, filaments fused into a 0.8–1.6 mm tall tube (measured to highest point between the stamens), tube glabrous or sparsely pilosulous, dorsal connective slightly exceeded by the thecae, connective appendage small, 0.14–0.27 mm tall, conical to narrowly triangular proximally and attenuate distally, projecting slightly beyond thecae, thecae slanting diagonally to connective appendage. **Gynoecium** 3.8–4.0 mm tall, pistil tricarpellate, compound, placentation parietal, ovary densely appressed-pilosulous, style glabrous, filiform, often bent in the middle, 2.7–2.9 mm long, stigma trilobate. **Fruit** a 3-valved capsule, ovoid to rhombic-ovoid, immature whitish to pale green in life, at maturity pale green or green in life, dried often with small irregular reddish streaks or blotches, smooth, glabrous or sparsely and minutely puberulent in basal one-third, 22–40 × 16–20 mm. **Seeds** 2–3 per carpel, oblong-ellipsoid to obovoid with broadly rounded apex, medium to dark reddish-brown, smooth and shiny, 8.7–9.5 × 5.1–5.8 mm including basal appendage.

Etymology:—Being the sole *Paypayrola* in Mesoamerica and well represented by many collections in a bimodal distribution of west-central and east-central Panama, the species is named for the country of Panama to which it is endemic.

Distribution and habitat:—*Paypayrola panamensis* is presently confirmed from 48 herbarium specimens representing 26 separate localities inferred as distinct populations in central Panama (Fig. 3). The species grows in moist to wet evergreen forest on low slopes and low local ridgetops often near or along streams and rivers but rarely in riparian forest, on the Atlantic slope, to the west and east of the Canal Zone but not near it, at 30–500 m in elevation.

Phenology:—The species is in flower throughout the year. Fruits apparently mature within a month or two of flowering. Flower buds, mature open flowers, young fruits, and ripening or mature fruits are apparently produced on the same tree at all times of the year.

Proposed Conservation Status:—Conservation assessment using GeoCAT provided a “VU” (Vulnerable) designation based on Extent of Occurrence (5,852.847 km²), and a “EN” (Endangered) designation based on Area of Occupancy (84.000 km²). Endangered status is proposed as the most conservative conservation status for this rather narrow endemic.

Discussion:—Comparisons of herbarium specimens from Panama with those of South America, and studies of types and protologues for known species, have revealed many misidentifications. Correctly assigned specimens demonstrate that inflorescence morphology, corolla color, sepal shape, and to a lesser degree, leaf morphology, are fixed in individual species. Importantly, species are readily placed into three species complexes based on corolla color, with supporting traits of inflorescence and sepal morphology. Thus, the genus consists currently of eight species divided in three morphological groups. The Blanchetiana species complex possesses white, commonly pink-tinged, corollas, sepals much longer than broad, and inflorescences subsessile or short-pedunculate and densely flowered. This group consists of *P. arenacea*, narrowly endemic to Amazonian Venezuela; *P. blanchetiana*, endemic to eastern and southeastern near-coastal Brazil; and *P. confertiflora*, with a bimodal distribution in northern French Guiana and northern Brazil. The Guianensis species complex possesses yellow to orange corollas, sepals glabrous and scarcely longer than broad to broader than long (distinctly longer than broad in *P. longifolia*), inflorescences short- to long-pedunculate, elongate, and laxly flowered, with deep yellow, yellow-orange or orange corollas (*P. grandiflora*, *P. longifolia*, and some *P. guianensis*). The Guianensis group comprises *P. grandiflora*, ranging over the Amazonian basin; *P. guianensis*, widely distributed over much of northern South America; and *P. longifolia*, in Venezuela, Guyana, and Surinam. Some specimens of *Paypayrola guianensis* have a shorter, moderately densely flowered inflorescence with the axis still visible, and corollas bright yellow rather than yellow-orange or orange, suggesting that it may itself represent a species complex with multiple undescribed taxa. The Hulkiana species complex possesses bright yellow corollas in a subsessile to short-pedunculate, moderately laxly to densely flowered inflorescence, and sepals puberulent and as long as to distinctly longer than broad. This last species complex consists of *P. hulkiana*, with a distribution in southeastern Venezuela east to French Guiana and south into northern Brazil, and *P. panamensis*, endemic to central Panama.

Comments:—*Paypayrola panamensis* is as distinct in features of its foliage, inflorescence, and floral characteristics as any other previously described species in the genus. The new species is similar to *P. guianensis* and *P. hulkiana* in certain traits but differs consistently in several non-overlapping qualitative and quantitative features as well as additional divergent tendencies. It is recognized here as a distinct and geographically disjunct *Paypayrola* species endemic to Panama. It is one of two species belonging to the Hulkiana species complex, and is the first described from Mesoamerica.

OTHER SPECIMENS EXAMINED: PANAMA. Coclé: La Pintada, Parque Nacional G.D. [General de Division] Omar Torrijos H. Rio San Juan [8°43'33" N, 80°39'57" W], 198 m, 22 July 2013, *Martínez, Arcia, Rodríguez & Espinosa 1338* (MO6468115!). La Pintada, Parque Nacional General de Division Omar Torrijos Herrera, La Rica [8°42'59" N, 80°35'30" W], 240 m, 23 July 2013, *Ortiz, Zapata, Flores & Mora 1475* (MO6614119!, PMA). **Colón:** Donoso Distrito, [Campamento de] Botija, Carretera pionera, 08°50'06"N 080°39'17"W, 11 September 2012, *van der Werff, Gray, Martínez & Sanchez 24441* (MO6450909!, NY02714036 image!, US3667240!). Distrito de Donoso, [Campamento de] Botija, antigua cantera, sección 35, Cordenadas: N 8°50'00.8" W 80°38'59.8", 181 m. altura, 16 January 2016, *Batista 1512, González & Lester* (NY04080735 image!). MPSA Concession, Botija Camp, Along Quebrada Botija, 08°50'10"N 080°39'00"W, 22 May 2012, *Hammel, De Gracia, Flores, Martínez, Merello & Quiel 26313* (MO6450910!). Teck Cominco Petaquilla mining concession, along exploration road, 08°50'22"N 080°38'51"W, 184 m, 15 September 2007, *McPherson 19558* (MO6284425!). Teck Cominco Petaquilla mining concession, near transect C002 [8°50'22" N, 80°38'51" W], 205 m, 18 September 2007, *McPherson 19679* (MO6284424!). Teck Cominco Petaquilla mining concession, along road [8°49'29" N, 80°40'12" W], 323 m, 1 December 2007, *McPherson & van der Werff 19910* (MO6284426!). Teck Cominco Petaquilla mining concession, along ridge road [8°49'22" N, 80°39'32" W], 300 m, 25 February 2008, *McPherson & Merello 20241* (MO6284427!). Site of proposed copper mine (MPSA) [8°48'27" N, 80°36'20" W], 100 m, 13 December 2009, *McPherson & Merello 21283* (MO6208597!).

del Norte, area del helipad BL02, tomando hacia el norte [8°51'47" N, 80°48'29" W], 20 July 2012, *Aranda B. 4265* (PMA). Cocolé del Norte, area del helipad CR10, tomando hacia el sur [8°56'18" N, 80°41'19" W], 18 July 2012, *Aranda B. 4233* (PMA). Río Taindi (Taimdi of maps) 6 km above confluence with Río Mandinga, 9°25'N, 79°11'W, 30–100 m, 5 April 1986, *de Nevers & Herrera 7665* (U1757196!, WIS!). **Guna Yala.** Between Río Diablo & Río Acuati near Nargana [mapped to 9°26'24"N, 78°34'12"W, same as other Duke collections in the area], 3 November 1967, *Duke 14895* (MO2191599!). 9°24'N, 78°34'W, 65 m, [no date], *Galdames, Montenegro, Chung & Herrera 1587* (MO5557973!). Trail to Cerro Óbu (Habu of maps) from Río Urgandi (Río Sidra), 9°23'N, 78°48'W, 100–300 m, 24 June 1986, *de Nevers, Herrera & Gernado 7974* (MO04633270!, U1757193!). Vicinidad de Río Diablo, desde el campamento Duque Sui hasta Ispere Yala, 9°22'N, 78°35'W, 70–100 m, 3 July 1992, *Herrera, B. Obaldía, R. Obaldía & Blanco 1210* (MO5770374!, WIS!). 12 mi on Carti Road from Inter-American Highway then 3 hr walk along road down Atlantic side [mapped at 33 km from Delta Llano Carti at Pan-American Highway, 9°21'27" N, 78°58'40" W], 304 m, 15 February 1980, *Antonio 3782* (MO2936115!). Río Cangandí, hills W of river S of confluence with Río Titamibe, 9°24'N, 79°8'W, 50–150 m, 27 January 1985, *de Nevers, Herrera, Charnley & Paredes 4669* (MO3244722!). Río Cangandí at confluence of Quebrada Titamibe, 9°24'N, 79°7'W, 60 m, 8 February 1986, *de Nevers & Herrera 7025* (MO04633271!, U1757198!). 16 km above Pan-Am Highway on road from El Llano to Carti-Tupile, Near campsite [9°19'08" N, 78°59'49" W], 350–400 m, 21 February 1973, *Kennedy 2542a* (MO2906175!, U1757199!). North of El Llano [9°19'05" N, 78°59'35" W], 13 February 1973, *Dressler 4270* (MO2153862!). Road from El Llano to Carti, 14.8 km north of the Panamerican Highway [9°19'03" N, 78°59'17" W], 300–500 m, 3 September 1977, *Folsom & Maas 5221* (MO2936070!). El Llano-Carthi Road, km 15 [9°19'05" N, 78°59'23" W], 300–400 m, 3 September 1977, *Maas, Berg & Foulson 2794* (MO2639559!, NY01340902 image!, U1757192!). **Panamá:** Along Llano-Carti road, c. 9°15'N, 79°00'W, 400 m, 24 November 1985, *McPherson 7586* (MO3311495!). Along Llano-Carti road, c. 9°15'N, 79°00'W, 400 m, 24 November 1985, *McPherson 7588* (MO3311494!). On El Llano-Carti road, near Nusigandí, along trail to waterfall, 9°15'N, 79°00'W, 250 m, 1 November 1992, *McPherson & Richardson 16007* (MO4251239!). El Llano-Cartí Road, Km 26.5, 9°19'N, 78°55'W, 200 m, 17 June 1986, *de Nevers, Herrera, McPherson, D'Arcy & Allen 7828* (MO04633269!, U1757194!). El Llano-Cartí road, Km 22, 9°19'N, 78°55'W, 350 m, 17 June 1986, *de Nevers & Herrera 7853* (U1757195!). El Llano-Cartí Road, Km. 26.5, Trail NE from road, 9°19'N, 78°55'W, 175 m, 9 March 1985, *de Nevers, Herrera & Charnley 5078* (MO3244726!). El Llano-Cartí Road, Km. 26.5, trail to Río Carti Chico and up ridge on E side, 9°19'N, 78°55'W, 200 m, 7 April 1985, *de Nevers, Schatz, Herrera & Charnley 5236* (MO3474324!). Nusagandí, Sede de Campo de PEMASKY, Approx. 20 km on El Llano-Carti Road, Trails near station, Aprox. 78°59'W, 9°18'N, 350 m, 29 March 1992, *Paredes, Foster, Peña & Welton 657* (F!). El Llano-Cartí highway, 14–17 km. [mapped at 15.5 km along road, 9°19'5"N, 78°59'35"W] ca. 1/2 [way] between the Continental Divide and Atlantic coast opposite Carti, Near Atlantic base camp, 23 February 1973, *Kennedy 2616* (MO2985556!).

Taxonomic key to flowering *Paypayrola*

Note: all traits refer to those observed on dried herbarium specimens unless otherwise noted; corolla color was interpreted from label data.

1. Inflorescence long-pedunculate, rachis somewhat short to elongate (commonly much longer than 2 cm), laxly flowered (sometimes moderately densely flowered but with rachis visible in *P. guianensis*); sepals as broad as long or broader than long (much longer than broad in *P. longifolia*); corolla deep yellow or yellow-orange to orange in life (Guianensis complex) 2
- Inflorescence sessile or subsessile to short-pedunculate, rachis relatively short (usually to 2 cm long), densely flowered with rachis not visible; sepals much longer than broad; corolla white often tinged with pink or red, or bright yellow in life 4
2. Leaves long-petiolate, blades oblanceolate to linear-oblanceolate, base and apex attenuate; sepals distinctly longer than broad, elliptical *P. longifolia*
- Leaves relatively short-petiolate, blades broadly oblanceolate to obovate, base cuneate to narrowly rounded, apex abruptly attenuate or subattenuate to narrowly rounded; sepals about as broad as long or broader than long, broadly ovate to deltate 3
3. Leaf blades broadly lance-obovate to obovate, apex tapering or convexly rounded to a narrowly rounded tip, full-length lateral nerves per side 9–12; inflorescence elongate, laxly flowered; mature flower buds and unopened corollas long-conic *P. grandiflora*
- Leaf blades obovate, apex abruptly short- to long-attenuate to a sharply narrowly acute tip, full-length lateral nerves per side 5–8(–9); inflorescence shorter to elongate, laxly to moderately densely flowered; mature flower buds and unopened corollas cylindrical *P. guianensis*
4. Sepals puberulent abaxially; corolla bright yellow in life (Hulkiana complex) 5
- Sepals glabrous abaxially; corolla white often tinged with pink or red in life (Blanchetiana complex) 6
5. Leaf blades 11.7–18.0 × 4.7–5.3 cm, apex abruptly subattenuate to long-attenuate; complete lateral nerves per side (5)6–10; inflorescence laxly to moderately densely flowered with up to 7 mature flowers at anthesis; sepals 1.8–2.4 × as long as broad, narrowly linear-oblong to narrowly oblong-triangular, apex narrowly rounded, the 1 medial nerve often raised and prominent *P. hulkiana*

5. Leaf blades 18.4–29.3 × (4.1)5.9–9.8, cm, apex weakly subattenuate to narrowly rounded, rarely convexly rounded to an obtuse or broadly rounded tip; complete lateral nerves per side 8–12; inflorescence densely flowered with 6–15 mature flowers at anthesis; sepals 1.0–1.7(2.0) × as long as broad, narrowly to broadly oblong-elliptical or uncommonly suborbicular, apex broadly rounded to truncate or retuse, the (1)3 or 5 nerves frequently raised and prominent *P. panamensis*
6. Short shrub to 2 m; petioles < 2 mm long; sepals acute at apex *P. arenacea*
6. Shrub or treelet to 12 m (rarely as short as 1–2 m); petioles > 4 mm long; sepals broadly rounded to truncate at apex 7
7. Leaf blades linear-oblong to oblong-oblong, base truncate to convexly rounded (rarely subcuneate), apex weakly subattenuate, tapering or convexly rounded to a narrowly rounded or sharply acute tip; full-length lateral nerves per side 10–12; sepals 1.1–1.4 × as long as broad, broadly elliptical or oblong-ovate to suborbicular *P. blanchetiana*
7. Leaf blades oblanceolate to narrowly obovate, base cuneate, apex abruptly short- to long-attenuate to a sharply narrowly acute tip; full-length lateral nerves per side 7–8(11); sepals > 1.5 × as long as broad, narrowly elliptical or ovate-lanceolate to narrowly oblong-ovate *P. confertiflora*

Acknowledgements

The author is indebted to the curators of the cited herbaria for providing work space during visits or for administering loans of specimens. He also thanks Barry Hammel for use of the color images in Figure 1, Missouri Botanical Garden for permission to use an image of the holotype, and Barry Hammel, Mike Grayum, and Jim Solomon for resolving the erroneous *Paypayrola* report from Costa Rica. The author thanks anonymous reviewers for improvements to the manuscript.

References

- Aublet, J.B.C.F. (1775) *Histoire des plantes de la Guiane Française : rangées suivant la méthode sexuelle, avec plusieurs mémoires sur différents objets intéressans, relatifs à la culture & au commerce de la Guiane Française, & une notice des plantes de l'Isle-de-France*. P.F. Didot jeune, Londres.
<https://doi.org/10.5962/bhl.title.64646>
- Aymard-C., G., Campbell, L.M. & Romero-González, G.A. (2014) *Paypayrola arenacea* (Violaceae), a new species with an unusual life-form from a white sand Savanna in the Amazon River Basin of Venezuela. *Harvard Papers in Botany* 19: 175–184.
<https://doi.org/10.3100/hpib.v19iss2.2014.n2>
- Bachman, S. & Moat, J. (2012) GeoCAT—an open source tool for rapid Red List assessments. *BGCI* 9: No. 1. Available from: <https://www.kew.org/science/our-science/projects/geocat-geospatial-conservation-assessment-tool> (accessed 1 May 2021)
- Ballard Jr., H.E. (2015) Violaceae. In: Hammel, B., Grayum, M., Herrera, C. & Zamora, N. (Eds.) *Manual de Plantas de Costa Rica, Dicotyledoneas (Sabiaceae-Zygophyllaceae)*. Missouri Botanical Garden, St. Louis, MO, pp. 593–611.
- Ballard Jr., H.E., Paula Souza, J. & Wählert G.A. (2014) Violaceae. In: Kubitzki, K. (Ed.) *The families and genera of vascular plants*. Springer-Verlag, Berlin, Germany. pp. 303–322.
https://doi.org/10.1007/978-3-642-39417-1_25
- Bentham, G. (1842) Schomburg's Guiana plants [Capparidaceae to Tiliaceae]. *Journal of botany :being a second series of the Botanical miscellany* 4: 99–133.
- Bentham, G. & Hooker, J.D. (1862) *Genera plantarum*. A. Black, London, England.
- de Candolle, A.P. (1824) *Prodromus systematis naturalis regni vegetabilis*. Treuttel et Würtz, Paris, France.
- Christenhusz, M.J.M., Fay, M.F. & Byng J.W. (2018) *Plant Gateway's the Global Flora: A practical flora to vascular plant species of the world*. Bradford, United Kingdom.
- Gray, A. (1852) *Isodendrion*, Three hundred sixty-first meeting. *Proceedings of the American Academy of Arts and Sciences* 2: 324–325.
- Hekking, W.H.A. (1988) Violaceae part 1—*Rinorea* and *Rinoreocarpus*. *Flora Neotropica* 46: 1–207.
- Jacquin, N.J. (1760) *Enumeratio systematica plantarum*. Theodor Haak, Lugduni Batavorum [Leiden, The Netherlands].
- de Jussieu, A.L. (1789) *Genera plantarum : secundum ordines naturales disposita, juxta methodum in Horto regio parisiensi exaratum*. Herissant et Theophilum Barrois, Paris, France.
<https://doi.org/10.5962/bhl.title.284>
- Melchior, H. (1925) Violaceae. In: Engler, H.G.A. & Prantl, K.A.E. (Eds.) *Die natürlichen Pflanzenfamilien*. Duncker and Humblot, Berlin, Germany. pp. 329–363.
- Munzinger, J.K. & Ballard, H.E. (2003) *Hekkingia* (Violaceae), a new arborescent violet genus from French Guiana, with a key to genera in the family. *Systematic Botany* 28: 345–351.

- de Paula-Souza, J. & Souza, A.C. (2003) *Hybanthopsis*, a new genus of Violaceae from Eastern Brazil. *Brittonia* 55: 209–213.
[https://doi.org/10.1663/0007-196X\(2003\)055\[0209:HANGOV\]2.0.CO;2](https://doi.org/10.1663/0007-196X(2003)055[0209:HANGOV]2.0.CO;2)
- Persoon, C.H. (1805) *Synopsis plantarum, seu Enchiridium botanicum, complectens enumerationem systematicam specierum hucusque cognitarum*. C.F. Cramer, Paris, France.
<https://doi.org/10.5962/bhl.title.638>
- Pulle, A.A. (1912) Neue Beiträge zur Flora Surinams III. *Recueil des travaux botaniques néerlandais* 9: 125–168.
- Rasband, W.S. (2019) *ImageJ*. Available from: <https://imagej.nih.gov/ij/> (accessed 1 February 2021)
- Reiche, K. & Taubert, P. (1895) Violaceae. In: Engler, A. & Prantl, K. (Ed.) *Die natürlichen Pflanzenfamilien*, W. Engelmann, Leipzig, Germany, pp. 322–336.
- Robyns, A. (1967) Flora of Panama Part VI. Family 127. Violaceae. *Annals of the Missouri Botanical Garden* 54: 65–84.
<https://doi.org/10.2307/2394894>
- Scopoli, J.A. (1777) *Introductio ad historiam naturalem sistens genera lapidum, plantarum, et animalium :hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae*. Wolfgang Gerle, Pragae [Praha, Czech Republic]
<https://doi.org/10.5962/bhl.title.10827>
- Sprengel, C.[K.]. (1827) *Caroli Linnaei,....Systema vegetabilium*. Librariae Dieterichianae, Gottingae [Göttingen, Germany].
- Thiers, B. (continuously updated) *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from: <http://sweetgum.nybg.org/science/ih/> (accessed 1 May 2021)
- Tulasne, L.-R. (1847) Flore de la Colombie-Plantes nouvelles [Samydeae to Violarieae]. *Annales des Sciences Naturelles; Botanique, Série III* 7: 360–373.
- Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (2018) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Koeltz Botanical Books, Glashütten, Germany.
- Wahlert, G.A., Ballard Jr., H.E. & de Paula-Souza, J. (2015) *Ixchelia*, a new genus of Violaceae from Mexico and Mesoamerica. *Brittonia* 67: 273–283.
<https://doi.org/10.1007/s12228-015-9375-3>
- Wahlert, G.A., Hoyos-Gómez, S.E. & Ballard Jr., H.E. (2018) Systematic studies in Neotropical Rinorea (Violaceae): Two new sections and a new generic segregate. *Brittonia* 70: 140–147.
<https://doi.org/10.1007/s12228-017-9507-z>
- Wahlert, G.A., Marcussen, T., de Paula-Souza, J., Feng, M. & Ballard, H.E. (2014) A Phylogeny of the Violaceae (Malpighiales) Inferred from Plastid DNA Sequences: Implications for Generic Diversity and Intrafamilial Classification. *Systematic Botany* 39: 239–252.
<https://doi.org/10.1600/036364414X678008>