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Understanding *Paloué* (Leguminosae: Detarioideae)

Revision of a Predominantly Guiana
Shield Endemic

*Karen M. Redden,
Patrick S. Herendeen, and
Gwilym P. Lewis*

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ABSTRACT

Redden, Karen M., Patrick S. Herendeen, and Gwilym P. Lewis. Understanding *Paloue* (Leguminosae: Detarioideae): Revision of a Predominantly Guiana Shield Endemic. *Smithsonian Contributions to Botany*, number 109, viii + 44 pages, frontispiece + 30 figures, 2 appendices, 2018. — On the basis of morphological and molecular phylogenetic analyses, the genus *Paloue* is revised to include the genera *Elizabetha* and *Paloveopsis*. As newly circumscribed, *Paloue* comprises 17 species, 2 subspecies, and 2 varieties. The following 11 new combinations in *Paloue* are made: *P. bicolor* (Ducke) Redden, *P. coccinea* (Schomb. ex Benth.) Redden, *P. duckei* (Huber) Redden, *P. durissima* (Ducke) Redden, *P. emarginata* (R. S. Cowan) Redden, *P. fanshawei* (R. S. Cowan) Redden, *P. leiogyne* (R. S. Cowan) Redden, *P. macrostachya* (Benth.) Redden, *P. paraensis* (Ducke) Redden, *P. princeps* (M. R. Schomb. ex Benth.) Redden, *P. speciosa* (Ducke) Redden; and one new hybrid: *P. × grahamiae* (R. S. Cowan) Redden. Based on a total evidence phylogeny, the two varieties of *Paloue coccinea* are no longer recognized, and a lectotype has been designated for *Paloue guianensis* Aubl. The species of *Paloue* are small to large woody trees that are distributed in northern South America; most are endemics in the Guiana Shield. All species are taxonomically evaluated and revised based on examination of herbarium specimens, alcohol-preserved floral material, rehydrated reproductive material, laboratory studies, label information, and field observations. All type material was examined either directly or remotely as scanned specimens. All georeferenced material was used to construct the distribution maps; localities without these data were estimated by label locality information, and all were found to occur within the range of the georeferenced species distribution. A key to the species is provided as well as detailed descriptions of all species, subspecies, and varieties. Illustrations are included. A list of all specimens examined is provided for each species, and a list of numbered exsiccatae is also given.

Cover images, from left to right: *Paloue sandwithii* inflorescence (detail from Figure 29F); field illustration of *Paloue × grahamiae* (detail from Figure 14); and *Paloue riparia* inflorescences and developing fruit (detail from Figure 30B).

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Dedication

We dedicate this manuscript to the memory of Claudius Paul Perry (17 November 1977–14 June 2011), Guyanese guide and best friend of author Karen Redden.

Claudius worked with numerous scientists from many different disciplines and was an extremely talented parataxonomist. Claudius and Karen worked together for more than a decade, and he spotted and collected her first sample of *Paloue* in 2003. Without his hard work and dedication, this manuscript would not have been possible.



Claudius Paul Perry (17 November 1977–14 June 2011).
Photograph by K. Redden.

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Understanding *Paloue* (Leguminosae: Detarioideae): Revision of a Predominantly Guiana Shield Endemic

Karen M. Redden,¹ Patrick S. Herendeen,^{2*}
and Gwilym P. Lewis³

INTRODUCTION

Paloue Aubl. belongs to the *Brownea* clade within subfamily Detarioideae Burmeister (LPWG, 2017; tribe Detarieae of Cowan and Polhill, 1981, and Mackinder, 2005). This clade also includes *Elizabetha* Schomb. ex Benth., *Paloveopsis* R. S. Cowan, and *Heterostemon* Desf., genera that are morphologically and geographically similar to *Paloue* (Figure 1). Each genus shares a number of morphological characters with at least one of the other genera, making generic delimitation and identification problematic. Richard Cowan (1957:253) noted this problem and went on to say that “it may be necessary to combine some or all of these genera into one.” The results from a recent phylogenetic analysis of morphological and molecular data show that *Heterostemon* is monophyletic and sister to a clade in which *Paloue* and *Paloveopsis* are nested within *Elizabetha* (Figure 2; Redden et al., 2010). *Paloue* was first described by Jean Baptiste Christophe Fusée Aublet in 1775, and the name has priority over the two other generic names. It is therefore necessary to combine *Elizabetha* and *Paloveopsis* into *Paloue*. The members of *Paloue* sensu lato are found in northern South America, and many are endemic to the Guiana Shield. These plants are medium-sized trees that occur along riverbanks and in lowland rainforests. Although the habit and habitat of these plants should facilitate their collection, many of the species are represented by only one or a few herbarium sheets. Other attributes and life history information of these taxa are also insufficiently studied, including animal interactions, pollination biology, and economic importance. The purpose of this investigation is to evaluate the morphological variation among the species of *Paloue* and related genera and produce a revised taxonomic treatment for the group based on extensive field observations, herbarium study, and phylogenetic analyses that utilize data from morphology and DNA sequences.

¹ Formerly with Smithsonian Institution, Department of Botany, National Museum of Natural History, MRC 166, Post Office Box 37012, Washington, D.C. 20013-7012, USA.

² Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, Illinois 60022, USA.

³ Comparative Plant and Fungal Biology Department, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK.

* Correspondence: pherenden@chicagobotanic.org

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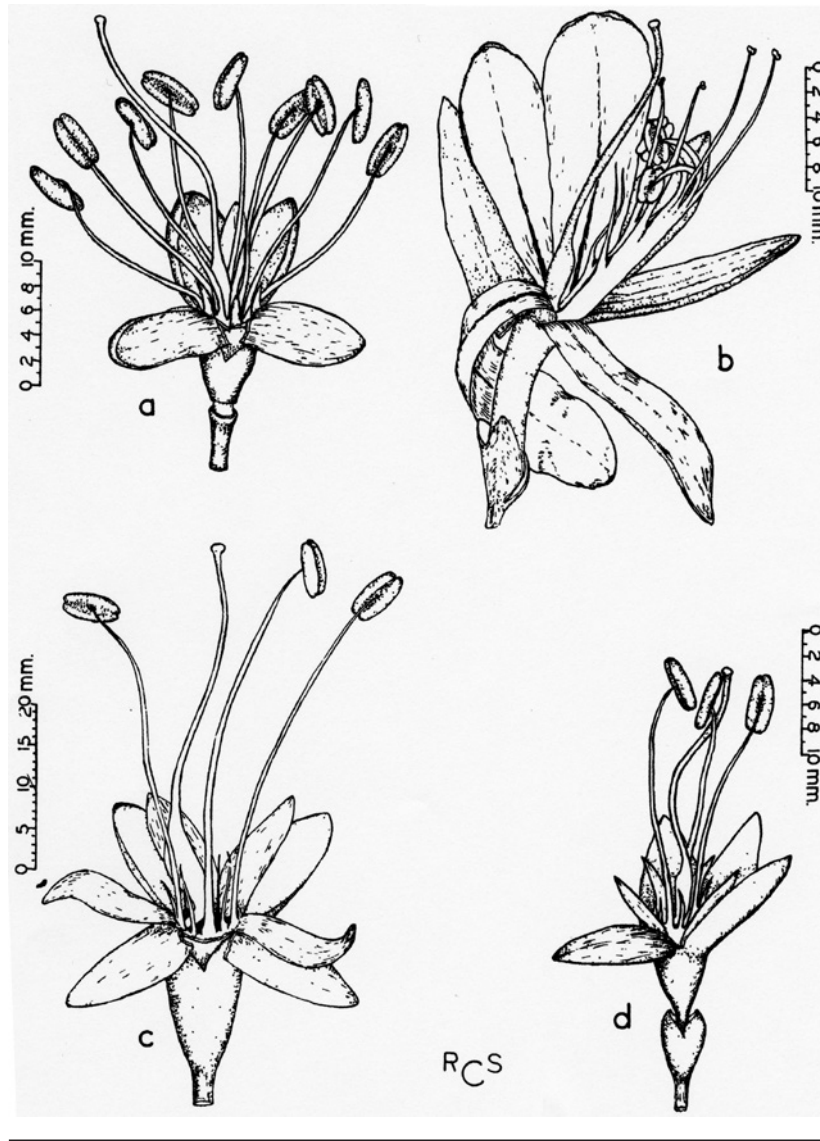


FIGURE 1. Flowers of *Palouea* (a), *Heterostemon* (b), *Elizabetha* (c), and *Paloveopsis* (d). Reproduced from Cowan (1957) with permission from New York Botanical Garden.

TAXONOMIC HISTORY

Aublet (1775) described and named the genus *Palouea*. He learned of the name from the indigenous people of French Guiana (Aublet, 1775). According to Jussieu (1789), Aublet's spelling of *Palouea* was not correct and he renamed the genus *Palovea* (orthographical variant, orth. var.). *Palovea* was widely accepted and numerous publications cited Jussieu's interpretation of the spelling of the genus name. In 1906 Pulle described a new species of *Palovea* and named it *P. riparia* Pulle based on the specimen he collected on the banks of the Saramacca River, near Janbasigado in what was then called British Guiana (Pulle

1906), now Guyana. Ducke (1915) described *Palovea brasiliensis* from the forest near the Cachoeira do Apuhy on the Tapajoz River in Brazil. He also used Jussieu's name, *Palovea*. Sandwith (1937) described the most recently published species, *Palouea induta* Sandwith, with the genus name reverting back to Aublet's original spelling. Scopoli (1777) used the same specimen as Aublet (1775) to describe his new genus, *Ginannia* Scop. This name was quickly recognized as a synonym of *Palouea* and was subsequently used in the literature only four times. Necker (1790) cited Scopoli but spelled the genus name *Ginnania*, which resulted in further confusion. All recent publications that recognize *Palouea* use this spelling and attribute the authorship to Aublet.

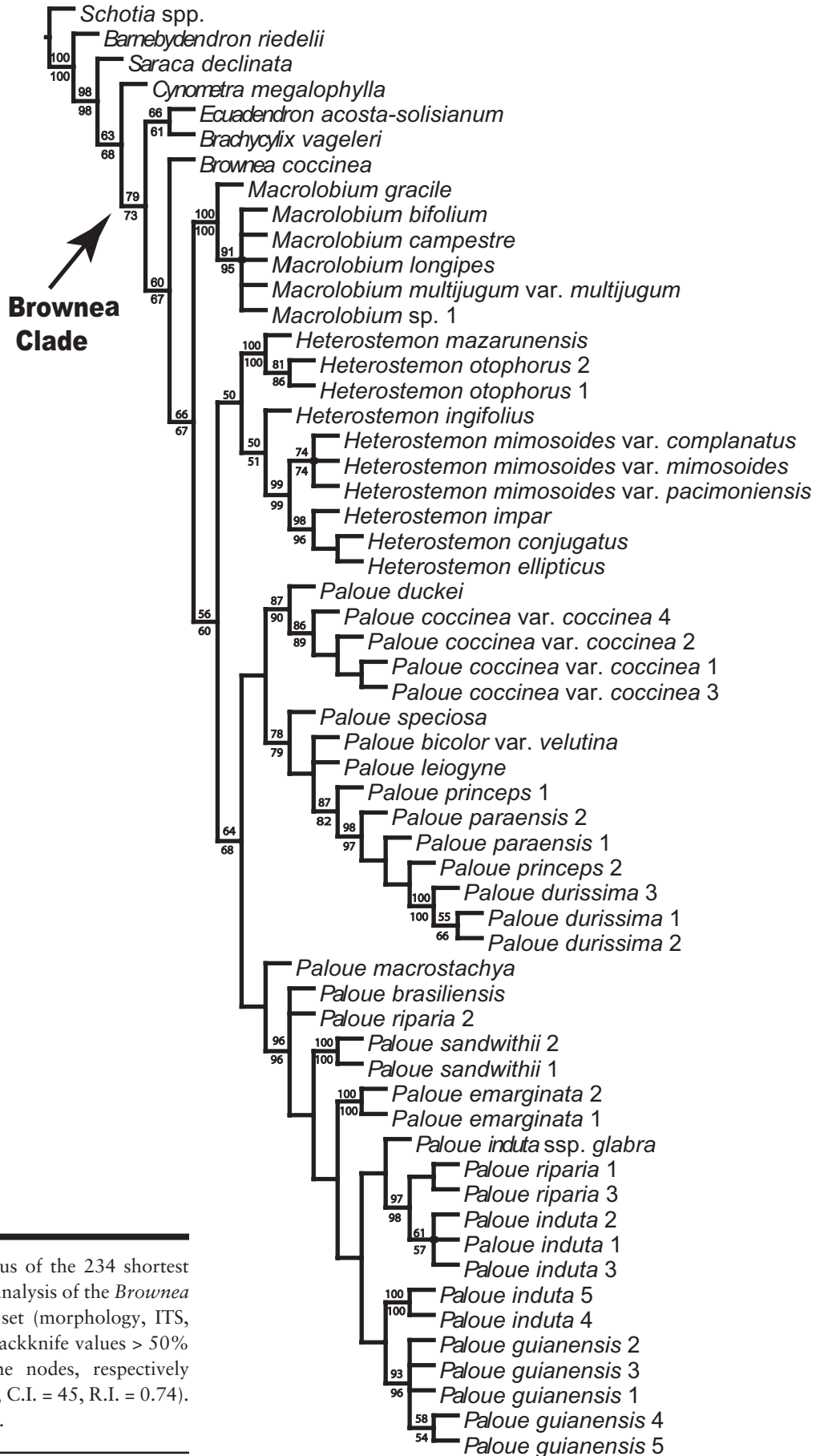


FIGURE 2. Strict consensus of the 234 shortest trees based on parsimony analysis of the *Brownea* clade total evidence data set (morphology, ITS, and *trnL*). Bootstrap and jackknife values > 50% are above and below the nodes, respectively (1,476 characters, L = 986, C.I. = 45, R.I. = 0.74). From Redden et al. (2010).

The genera *Elizabetha* and *Paloveopsis* have straightforward nomenclatural histories. *Elizabetha* was described by Bentham (1840) and *Paloveopsis* by Cowan (1957). Cowan's (1976) revision of *Elizabetha* included all recognized species, and since its publication no new species have been described.

MATERIALS AND METHODS

All species were directly observed from herbarium sheets (BM, BRG, F, K, L, MO, NY, P, U, US, WAG; Thiers, continuously updated) from the following institutions:

BM	Herbarium, Algae, Fungi and Plants Division, The Natural History Museum, London, UK
BRG	Guyana National Herbarium, Biology Department, University of Guyana, Georgetown, Guyana
F	Herbarium, Botany Department, Field Museum of Natural History, Chicago, Illinois, USA
K	Herbarium, Royal Botanic Gardens, Kew, Richmond, Surrey, UK
L	National Herbarium Nederland, Botany Section, Naturalis Biodiversity Center, Leiden, Netherlands
MO	Herbarium, Missouri Botanical Garden, Saint Louis, Missouri, USA
NY	William and Lynda Steere Herbarium, The New York Botanical Garden, Bronx, New York, USA
P	Herbier National, Muséum National d'Histoire Naturelle, Paris, France
U	National Herbarium Nederland, Botany Section, Naturalis Biodiversity Center, Leiden, Netherlands
US	United States National Herbarium, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA
WAG	National Herbarium Nederland, Botany Section, Naturalis Biodiversity Center, Leiden, Netherlands

Other abbreviations used in synonymies and specimens examined sections or elsewhere in text are defined as follows:

comb. nov.	new combination
fl.	flower
fr.	fruit
imm. fr.	immature fruit
s.n.	sine numero (unnumbered collection)

In addition, field observations, measurements, and notes were integrated into the descriptions. In general, vegetative measurements were made from dried herbarium material, whereas reproductive structures were measured directly from field specimens, alcohol-preserved specimens, and rehydrated herbarium specimens. Length of leaf and leaflet is given from the apex of the leaf or leaflet lamina to the basalmost insertion point of the blade on the petiole or petiolule. The petiole length is also measured from this point. Colors of corollas, fruits, and other organs are described from herbarium label data, field observations, and original descriptions. Conventions used in measuring and

describing various organs follow Cowan's revision of *Elizabetha* (Cowan, 1976). In his revision, Cowan refers to the supporting stalk of the hypanthium as the "stipec," which is measured from the insertion of the bracteoles to the base of the hypanthium. Collection locality details in the specimens examined sections are taken directly from herbarium labels and given verbatim without translation.

Cowan's (1976) revision of *Elizabetha* was complete and comprehensive, and this monograph follows his convention for all taxa now included in *Paloue*. Much of the taxonomy for *Elizabetha* and *Paloveopsis* was taken directly from his revision with minor modifications to measurements, additional information about structures not previously seen, new locality information, and addition of recent collections.

GENERIC DELIMITATIONS AND AFFINITIES

Paloue historically has been placed in the *Brownea* group of the tribe Detarieae within the subfamily Caesalpinioideae (Cowan and Polhill, 1981). Other members of this group have included *Barnebydendron* J. H. Kirkbr. (synonym: *Phyllocarpus* Riedel ex Tul.), *Eperua* Aubl., *Ecuadendron* D. A. Neill, *Paloveopsis*, *Elizabetha*, *Brachycylix* (Harms) R. S. Cowan, *Heterostemon*, *Brownea* Jacq., and *Browneopsis* Huber. The *Brownea* group is now part of the recently reinstated subfamily Detarioideae (LPWG, 2017), but the genera traditionally placed in the *Brownea* group are considered to belong to three different tribes (de la Estrella et al., 2018), with *Eperua* and *Barnebydendron* not grouping with the other genera retained within it. The group also now includes the diverse neotropical genus *Macrobium* (de la Estrella et al., 2018; Murphy et al., 2018; Schley et al., 2018). In Cowan's (1957) description of *Paloveopsis*, he compared the morphological attributes of many of these genera and noted that each shares a number of common characters with the other genera, leading to a blurring of generic boundaries (Cowan, 1957; Figure 1). A phylogenetic analysis of the tribes Detarieae and Amherstieae using chloroplast *trnL* intron sequences has shown that these two tribes together form a monophyletic group but that neither tribe individually is monophyletic (Bruneau et al., 2000). An analysis of the *Brownea* clade using 125 morphological, anatomical, and reproductive characters grouped *Paloue*, *Paloveopsis*, *Elizabetha*, and *Heterostemon* into a monophyletic group (Redden and Herendeen, 2006). However, support for nodes along the backbone of the tree was low. In a recent phylogenetic study using combined morphological and molecular data [chloroplast *trnL* spacer and nuclear internal transcribed spacer (ITS)], it was shown that *Elizabetha*, *Paloveopsis*, and *Paloue* together form a monophyletic group that is sister to a monophyletic *Heterostemon* (Redden et al., 2010; Figure 2). These results have been corroborated by Murphy et al. (2018) and Schley et al. (2018). Nevertheless, it is apparent that there is a distinct difference between the white-flowered *Paloue* (formerly *Elizabetha*, in part) and the red-flowered *Paloue*. The size of the flowers, leaf structure, size of the leaflets, and pollen type differ. A few of

the red-flowered species are known to hybridize, something not observed in the white-flowered species. These differences should be investigated further in future studies. The monographic revision presented here is based on the total evidence phylogeny obtained in the study of Redden and Herendeen (2006).

Within the *Brownea* clade, *Paloue* s.l. can be distinguished from other members by a unique combination of morphological characters. The leaves range from simple to multijugate. In a number of specimens of *P. guianensis* a pair of lateral, vestigial leaflets has been noted at the base of the “leaf,” suggesting that the “simple” leaves are actually unifoliolate and a reduction from a compound leaf. These vestigial leaflets are caducous and have only been seen in specimens that included very young leaves. The androecium of *Paloue* consists of either nine fertile stamens, or three fertile stamens and six staminodes with vestigial anthers

(as in *P. grahamiae*), or three fertile stamens plus six staminodes without vestigial anthers. The fruit is a flattened pod, usually with a lip or a flange along the placental margin, a character not found in its closest relative, *Heterostemon*. The pollen exine is gemmate to verrucate, unlike the striate pollen in *Heterostemon*.

DISTRIBUTION AND HABITAT

Species of *Paloue* are predominately found in riparian and lowland rainforests of Brazil, Venezuela, Suriname, French Guiana, and Guyana and are almost exclusively concentrated in the Guiana Shield (Figure 3). One species, *Paloue duckei* (Huber) Redden, is found in Colombia. Many of these species are represented by only a handful of specimens, and as collection efforts

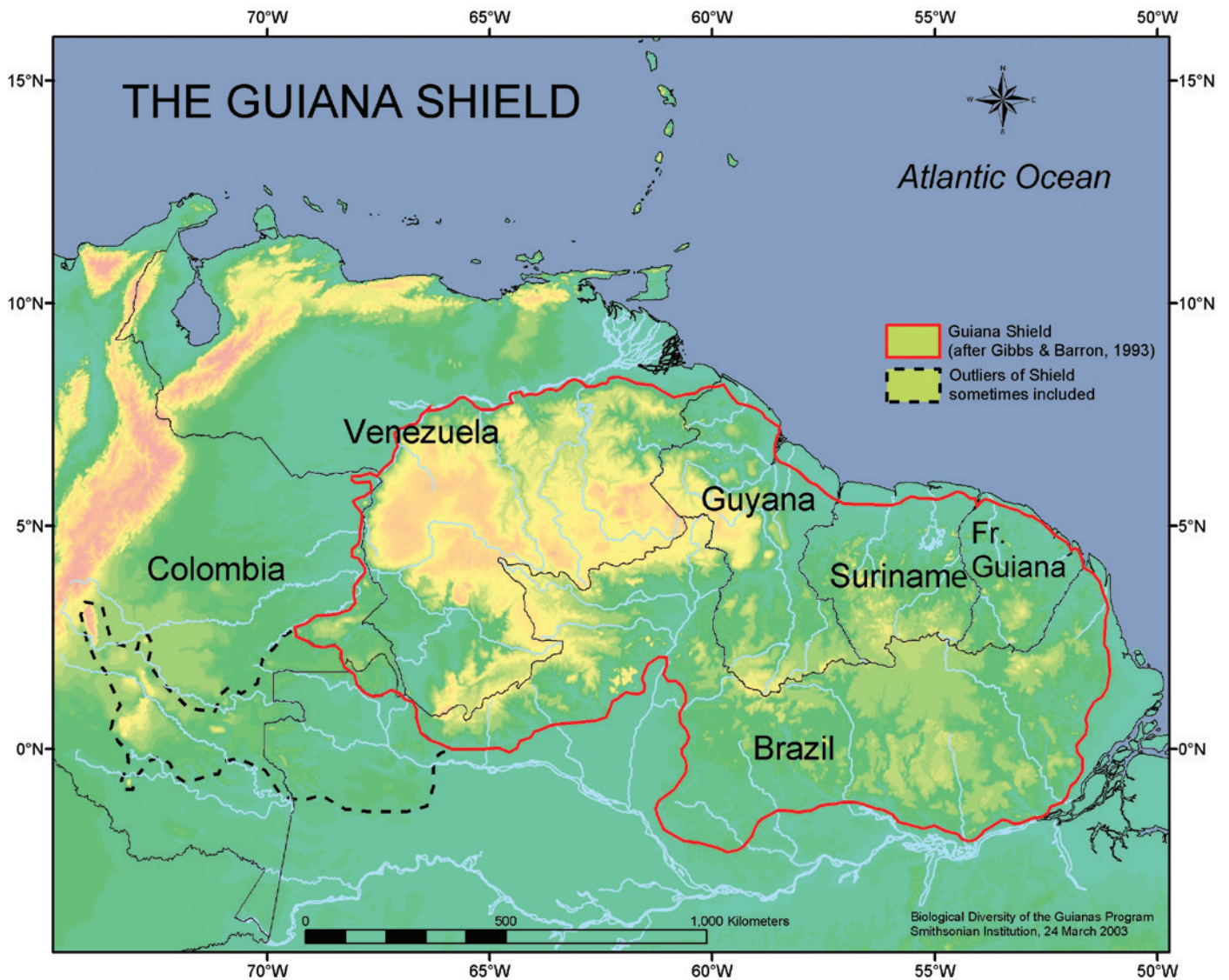


FIGURE 3. Map of the Guiana Shield area of South America. Map by Thomas H. Hollowell, Smithsonian Institution.

increase, knowledge of distributional patterns may change and geographic ranges increase. Most species are found at elevations below 500 m, but a few occur predominantly in the foothills of mountain ranges and in the tepui regions of Venezuela and Guyana. Most species are found on poor soils or white sands in seasonally flooded forests. There exist few data on nodulation or mycorrhizal fungi association for these species. Five species of *Paloue* (as *Elizabetha*) have been reported as non-nodulating and one (*E. coccinea*) as nodulating (Souza et al., 1994), although the positive report needs to be checked (Sprent, 2001). There are no reports on nodulation for *Paloue* sensu stricto and *Paloveopsis* (Sprent, 2001).

TAXONOMIC TREATMENT

Paloue Aubl., Historie Des Plantes de La Guiane Francoise. Paris, Ches Pierre-Francoise Didot. 1775. Type: *P. guianensis* Aubl.

Elizabetha Schomb. ex Benth., J. Bot. (Hooker) 2: 92. Mar 1840. Lectotype: *E. princeps* Schomb. ex Benth. (R. S. Cowan, Taxon 8: 59. 1959).

Paloveopsis R. S. Cowan, Brittonia 8: 251. 9 Jan 1957. Type: *Paloveopsis emarginata* R. S. Cowan.

Small to large trees, 7–50 m tall, branchlets brown to gray, glabrous to pubescent. Stipules intra-petiolar, persistent to caducous, lanceolate to oblanceolate–obovate, linear to foliaceous, thin to membranous, joined on inner margin throughout or

shortly above the base, sometimes bifid. Leaves simple to multijugate, usually paripinnate but imparipinnate in one species (*P. grabamiae*), alternate; petioles 0.5–5 mm long; when leaves simple (unifoliolate), blade margin entire, oblong to lanceolate to ovate, coriaceous, pinnately nerved, glabrous, apex obtuse to long-acuminate, base rounded to acute to auriculate; when multijugate, 2–57 leaflet pairs, the leaflets narrowly oblong to elliptic; rachis usually narrowly alate, the wing interrupted at insertion of leaflet pairs, often with short distal extension of the wing at junction of leaflet pairs. Inflorescences dense or open, spike-like, terminal or axillary racemes, bracts orbiculate, caducous or persistent, bracteoles connate into a bilobed tube enclosing the flower bud, or shorter than the calyx, rounded, persistent beyond anthesis; pedicels 2–22 mm long, hypanthium 10–29 mm deep including the stipe, glabrous to pubescent. Sepals 4, usually unequal in shape with the dorsal sepal broader, reflexed, glabrous to pubescent. Petals 5, subequal or of different sizes. Fertile stamens 3 or 9, filaments of fertile stamens 2–6 cm long, connate with staminodes basally to form a tube or connate except at dorsal petal, glabrous to pilose, anther oblong, uniform (except in *P. grabamiae*), glabrous to densely pilose. Stigma capitate, style elongate, filiform, the ovary narrowly oblong, velutinous to glabrous, the stipe shorter than the ovary, adnate to the upper surface of the hypanthium tube, ovules numerous. Fruit a legume, straight to curved, oblong to scimitar-shaped, two-valved, compressed, woody, the upper sutures thickened with a ridge or lip perpendicular to the valve face or parallel to the pod surface (*P. coccinea*); seeds ovate, compressed.

Key to the Species of *Paloue*

1. Leaves simple, usually with a pair of crater-like glands at the base of the lamina, one on either side of the main vein. . . . 2
Leaves compound, crater-like glands present but usually scattered on lamina. 9
2. Ovary glabrous. 3
Ovary pubescent. 7
3. Staminodes present. 6. *P. emarginata*
Staminodes absent 4
4. Stamen filaments less than 2.5 cm. 2. *P. brasiliensis*
Stamen filaments greater than 2.5 cm 5
5. Petals approximately equal. 16. *P. sandwithii*
Petals not equal. 6
6. Petals: 3 large (2–3 cm long) plus 2 small (2–3 mm long) 9. *P. guianensis*
Petals: 1 large (5–7 mm long) plus 4 small (1–3 mm long) 15. *P. riparia*
7. Petals: 3 large (2–3 cm long) plus 2 small (2–3 mm long) 9. *P. guianensis*
Petals: 1 large (1.3–1.4 cm long) plus 4 small (1.8–3.5 mm long) 8
8. Inflorescence covered with golden brown trichomes; densely tomentose. 10a. *P. induta* subsp. *induta*
Inflorescence sparsely tomentose to glabrous 10b. *P. induta* subsp. *glabra*
9. Leaves 2–12 jugate; pedicels mostly 1 cm long or longer, the hypanthium glabrous 10
Leaves 18–57 jugate; pedicels always less than 1 cm long, usually much less, the hypanthium glabrous or pubescent . . . 13
10. Leaves imparipinnate, the terminal leaflet larger than lateral leaflets, with paired glands at base of lamina . . . 8. *P. × grabamiae*
Leaves paripinnate 11
11. Inflorescences 10–100 cm long; petals red or white. 12
Inflorescence to 8 cm long; petals white, the dorsal one well developed and the other 4 reduced to petaloidia about 2 mm long 7. *P. fanshawei*

12. Leaflet base equal, acute; 3 fully developed petals and 2 reduced, usually white; staminodes absent; fruit with woody lip perpendicular to face of legume **12. *P. macrostachya***
 Leaflet base unequal, obtuse; 5 fully developed petals, usually red; staminodes present; fruit with woody lip parallel to face of legume **3. *P. coccinea***
13. Leaf rachis wing with apical extensions at each pair of leaflets [see Figure 10C]. 14
 Leaf rachis wing without apical extensions at each pair of leaflets 18
14. Flowers white; hypanthium pubescent; petals dimorphic, the dorsal usually larger and broader than laterals. 15
 Flowers red; hypanthium glabrous; petals about equal in size and shape 17
15. Inflorescence dense, spike-like; hypanthium tube shorter than its stipe; ovary velutinous; leaflet apex obtuse or truncate. 16
 Inflorescence elongate, not dense, nor spike-like; hypanthium tube longer than its stipe; ovary glabrous; leaflet apex acute. **5. *P. durissima***
16. Leaflets about 6 or 7 times as long as wide, tapering to a rounded tip; bracts mostly 28–38 mm long and 24–35 mm wide, the bracteoles 20–23 mm long **14. *P. princeps***
 Leaflets broader, apex usually truncate or rounded, often retuse, rarely tapering apically; bracts 15–27 mm long and 8–15 mm wide, the bracteoles 14–19 mm long **13. *P. paraensis***
17. Fertile stamens 37–63 mm long; bracteoles united for a greater length on one side; ovary glabrous; leaflets rounded apically. **4. *P. duckei***
 Fertile stamens 19–22 mm long; bracteoles equally united; ovary velutinous; leaflets truncate apically. **17. *P. speciosa***
18. Leaves mostly 37–50 jugate, leaflets 19–28 mm long, the undersides with a tuft of long hairs on one side of the main vein at its base; inflorescence 50–70 mm long; hypanthium glabrous. **11. *P. leiogyne***
 Leaves 23–34 jugate, leaflets 11–16 mm long; hypanthium strigulose. 19
19. Ovary pubescent. **1b. *P. bicolor* var. *velutina***
 Ovary glabrous. **1a. *P. bicolor* var. *bicolor***

1. *Paloue bicolor* (Ducke) Redden comb. nov.

Elizabetha bicolor Ducke, Trop. Woods 1934. No. 37: 22. 1 Mar 1934.

Type. Brazil. Pará: Rio Itapacura, affluent Rio Tapajoz, Cachoeira do Americano, 25 Jan 1933 (fl., fr.). A. Ducke 23726 (RB # 34-961) (holotype: RB; isotypes: G, K!, P!, U!, US!).

FIGURE 4

Small tree 6–15 m tall, the trunk 10–20 cm in diameter, branchlets brown to gray, pilose or pilosulose, hairs dark and shiny. **Stipules** caducous, membranous, narrowly oblong–oblanceolate, apex slightly bifid, pilosulose externally at the base but otherwise glabrous. **Leaves** compound, alternate, paripinnate; petioles 1–2.5 mm long, pilosulose; rachis 6–11 cm long, the rachis wing narrow and spreading without apical projections, contracted at each leaflet insertion, the axis pilosulose; **leaflets** 11–16 × 2–3 mm, 23–34(–38)-jugate, sessile, narrowly oblong to lanceolate–oblong, the base obtuse, inequilateral, apex rounded and minutely apiculate, glabrous, the lower surface microscopically red-dotted. **Inflorescences** 2.5–7 cm long, dense racemes, axillary, or terminal and axillary, at tips of branchlets, usually densely strigulose to strigose; bracts 10–17 × 14–21 mm, caducous, oblate to sub-rotund, red, strigulose both inside and out, margins ciliolate; pedicels 2–6 mm long, puberulous or strigulose; bracteoles 9–17 × 8–9 mm, caducous, connate, united marginally in a tube enclosing the flower bud, rounded, more or less carinate dorsally, red, strigulose inside and out, or glabrous on inner surfaces. **Flowers:** hypanthium red or white, strigulose; stipe 2.5–4(–9) mm long; tube 7.5–12 × 5–7.5 mm, cylindrical;

sepals 11–15 × 5–9 mm, oval–oblong, the dorsal one larger, red or white, strigulose externally but glabrous on inner surfaces, the margins ciliolate; the dorsal petal 10–18 × 8–10 mm, ovate, cordate–auriculate basally, emarginate apically, the other four petals 12–14 × 5–7 mm, obovate–oblanceolate, red or white, ciliate; androecium monadelphous forming a sheath, 2.5–3 mm deep, open at insertion of dorsal petal; fertile stamens 3, white; filaments 18–23 mm long, villose on lower parts; anthers 5–6.5 × 1.5–2 mm, narrowly oblong, glabrous; staminodia 6, 4.5–6 mm long; gynoeceum dark red; ovary 7.5–12 × 2–2.5 mm, narrowly elliptic to elliptic–oblong, velutinous or glabrous; gynophore 2–8 mm long, adnate to upper surface of the hypanthium tube near its rim, geniculate–arcuate, glabrous or puberulous near the apex, style 12–23 mm long, glabrous, stigma capitellate. **Immature fruit** 12–22 × 3–4.5 cm, the dorsal suture bi-marginate, velvety or glabrous, ca. 6–8-seeded.

1a. *P. bicolor* (Ducke) Redden var. *bicolor*

Ovary glabrous.

DISTRIBUTION. Brazil: Amazonas and Pará.

PHENOLOGY. Known to flower and fruit in January.

1b. *P. bicolor* (Ducke) Redden var. *velutina* (R. S. Cowan) Redden, comb. nov.

Elizabetha bicolor Ducke var. *velutina* R. S. Cowan, Proc. Kon. Ned. Akad. Wetensch. Ser. C. 79: 334. 1976. Type. Brazil. Amazonas: Parintins, above Lake Jose-Assu, 29 Dec 1935 (fl.), A. Ducke 113 (holotype: RB; isotypes: F!, G, K!, NY!, P!, R, RB, U!, US!).

Ovary velutinous.

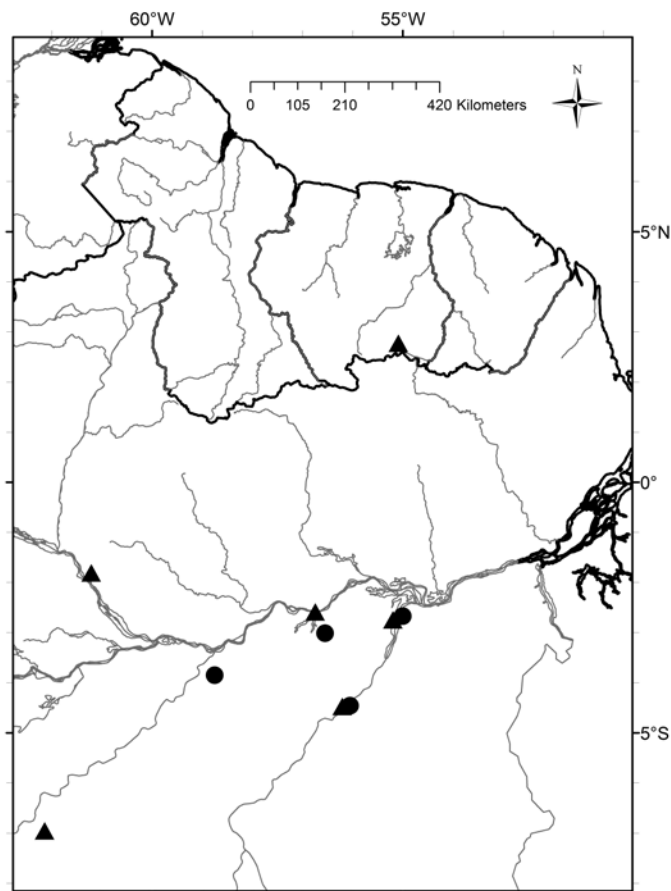


FIGURE 4. Geographic distribution of *Paloue bicolor* (Ducke) Redden subsp. *bicolor* (dots) and *P. bicolor* subsp. *velutina* (R. S. Cowan) Redden (triangles) in Suriname and Brazil.

DISTRIBUTION. Brazil: Amazonas and Pará.

PHENOLOGY. Flowering from November to February and fruiting from December to March.

ADDITIONAL SPECIMENS EXAMINED. **BRAZIL.** AMAZONAS: Borba, Rio Madeira inferior near Amazonas, 16 Jan 1930 (imm. fr.), *Ducke s.n.* (RB 23287, K!, US!); Rio Itapeçerica affluent Tapajoz near Pará, 25 Jan 1953 (fl.), *Ducke s.n.* (RB 23727, K!, US!); Borba, Rio Madeira (near Amazonas), 8 Nov 1935 (fl.), *Ducke s.n.* (RB 34-959, K!, US!); Parintins (Amazonas), 29 Dec 1935 (fl.), *Ducke s.n.* (RB 34-960, K!, U!, US!); 29 Dec 1935 (fl.), *Ducke s.n.* (RB 34-961, K!); Mt. Dourado, Gleba Pacanari, 0°40'S, 52°35'W, 20 Jan 1988 (fl.), *Pires & Silva 1954* (K!, NY!); Monte Dourado, Estação Ecol. do Jari (SEMA), 0°27'S, 52°51'W, 4 Feb 1988 (fl.), *Pires & Silva 1984* (K!, NY!). Manaus–Caracarai km 60, Reserva INPA-SUFRAMA, 9 Dec 1976 (fl.), *Prance & Ramos 24350* (A, C, COL!, F!, INPA, K!, M, MG, MICH, MO!, NY!, P, R, S, U!, UFMG, US!, VEN!); Estrada Manaus–Itacoatiara, km 68, 29 Feb 1968 (fr.), *Rodrigues et al. 8461* (US!); Estrada Manaus–Itacoatiara, km 68,

5 Mar 1970 (fr.), *Rodrigues 8730* (US!). PARÁ: Rio Tapajoz colines des environs des cataractes du Mangabal, 10 Feb 1917 (fl., fr.), *Ducke 16751* (US!); 10 Dec 1919 (fr.), *Ducke s.n.* (RB 10984, K, 2 sheets!).

2. *Paloue brasiliensis* Ducke, Arch. Jard. Bot. Rio de Janeiro 1: 27. 1915. Type. Brazil. Pará: Habitat ad fluvium Tapajoz in silvis ad Cachoeira do Apuhy 1, 28 Dec 1908 (fl., fr.), *E. Sneathlage s.n.*, H.A.M.P. 10.117 (holotype MG; isotype: F!).

FIGURES 5, 29C

Small to medium-sized tree 12–25 m tall, branchlets gray/brown, glabrate. **Stipules** caducous, not seen. **Leaves** simple, alternate, entire, 8.5–16 × 3–7 cm, the blade oblong-lanceolate, glabrous, coriaceous; petiole 3.5 mm long, base rounded to truncate, usually with paired crater-like glands at the base of the lamina, apex long-acuminate. **Inflorescences** 11–14 cm long, elongated terminal racemes; pedicels 6–10 mm long; bracts 10 mm long, caducous, orbiculate; bracteoles persistent beyond anthesis, connate, bilobed, carinate, rounded, glabrous. **Flowers:** hypanthium 29 mm long, glabrous, tubular, red; sepals 4, 1.1–1.5 × 0.7 cm, reflexed, rounded at the apex, dark red; petals 5, largest petal 20–22 × 6 mm, clawed, second petal 6–18 × 4 mm, third petal 8 × 8 mm, the remaining two petals are minute, red, margins of all petals pilose; stamens 9, red; filaments 2–2.5 cm long, connate to form a tube, sparsely long-pilose; anthers 5–7 mm long, oblong, sparsely pilose; ovary 10 mm long, narrowly elliptic to elliptic-oblong, glabrous, stipe adnate to upper surface of the hypanthium tube near its rim; style 2 cm long; stigma capitate. **Fruits** 11 × 3 cm, oblong, margin slender, stipitate, transversely veined, acuminate, glabrous, ca. 4–8-seeded.

DISTRIBUTION. French Guiana; Brazil: Pará.

PHENOLOGY. Flowering from August to December; fruiting from February to May and in October.

ADDITIONAL SPECIMENS EXAMINED. **BRAZIL.** PARÁ: Rio Tapajoz, cachoeiras inferiores, lugar Pimentel, 28 Aug 1916 (fl., fr.), *Ducke s.n.* (MG-16416, RB 10882, K!, U!, US!); Parque Nacional do Tapajoz, km 60 da estrada Itaituba–Jacarecanga; ilha em frente a Pimentel, 26 Sep 1978 (fr.), *Silva & Rosario 3967* (MG, INPA, K!, US!); Rio Tapajoz (near Pará) loco Bella Vista, 6 Dec 1919 (fl.), *Ducke s.n.* (RB 10883, BM!, INPA, K!, U!, US!).

FRENCH GUIANA. CAYENNE: Rives de l'Oyapock à la hauteur des Itets Yacaescin, 10 Dec 1965 (fl.), *Oldeman 1734* (P!, U!, US!). CAMPOI: Rivière Yaroupi, rive gauche, environ 9 km en amont du Saut Mouroucioutou, 18 Apr 1970 (fr.), *Oldeman 3030* (CAY!, K!); Rives du bas de la crique Inipi (affluent de la rivière Camopi), 3 km de son embouchure, 7 Feb 1968 (fr.), *Oldeman & Sastre 77* (P!, U!, US!); Rives du Camopi (affluent de l'Oyapock) entre les sauts Petit Impossible et Grand Impossible, 10 Feb 1968 (fl.), *Oldeman & Sastre 163* (U!, US!).

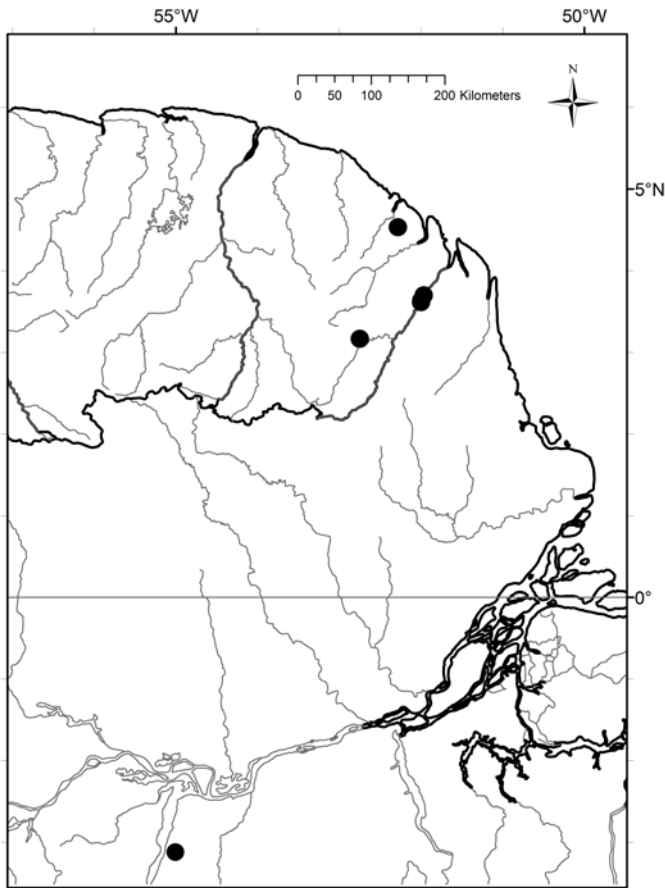


FIGURE 5. Geographic distribution of *Paloue brasiliensis* Ducke (dots) in French Guiana and Brazil.

ROURA: Bas-Camopi, 21 May 1965 (fr.), *Cremers 1328* (CAY!); Rivière Counana, 5 km en aval de Dégrad Lalanne, 4°32'N, 52°17'W, 6 Oct 2000 (fr.), *Sabatier & Prévost 4674* (CAY!, US!). ST. GEORGES: Fleuve Oyapock, entre St. Georges et Camopi, 3°38'25"N, 51°59'42"W, 25 Feb 2000 (fr.), *Fleury & Pignal 1691* (CAY!, US!). SAINT-LAURENT DU MARONI: Marouini River, Ile d'Antecume Pata, confluent de l'Itany (Haut Maroni) et du Marouini, 17 Nov 1977 (fl.), *Cremers 5063* (CAY!, P!, U!, US!).

3. *Paloue coccinea* (M. R. Schomb. ex Benth.) Redden comb. nov.

Elizabetha coccinea M. R. Schomb. ex Benth., Hook. Jour. Bot. 292. 1840. Type. Guyana: without locality but probably Upper Essequibo River (Cowan, 1976), *R. Schomburgk s.n.* (holotype: K!).

Elizabetha coccinea var. *oxyphylla* (Harms) R. S. Cowan, Proc. Kon. Ned. Akad. Wetensch. 79: 340. 1976. Type. Brazil. Rio Branco, Gebiet des Surumu, Ufer des Yalburg, Nov 1909 (fl., fr.), *E. Ule 8146* (holotype: B, destroyed; isotypes: F!, G, K!, L!, RB).

FIGURES 6, 30C

Tree 6–20 m tall, trunk 10–20 cm in diameter, branchlets puberulous to tomentulose, glabrescent. **Stipules** caducous, not seen. **Leaves** compound, alternate, paripinnate; petioles (1–) 3–5(–9) mm long, puberulous; rachis (6.5–)9–14(–18) cm long, rachis wing narrow and erect without apical projections, contracted at each leaflet insertion, puberulous to tomentulose, rarely glabrous; **leaflets** (3–)6–9(–10.5) × (1–)2–3(–4) cm, (4–)6–8(–12) jugate, sessile, elliptic to oblong–elliptic or obovate to oblanceolate–oblong, thinly coriaceous to coriaceous, the base inequilateral, the upper side shorter and attenuate, the lower rounded–obtusate, the apex acute or rounded to truncate and usually retuse to emarginate, usually puberulous on the salient midvein or at the blade base, more or less ciliolate along the margins, the lower surface micro-punctate. **Inflorescences** (5.5–)10–20(–30) cm long, terminal racemes, elongating in fruit, the axis glabrous to pilosulose; pedicels (3–)5–9(–11) mm long, glabrous; bracts 23–30(–40) × 18–25 mm, oval to obovate, rounded apically, glabrous; bracteoles 15–30 × 8–15 mm, caducous, elliptic to obovate, united marginally in a tube enclosing the flower bud, acute apically, more or less carinate dorsally, joined marginally for $\frac{1}{2}$ – $\frac{3}{4}$ their length, glabrous. **Flowers**: hypanthium glabrous; stipe (2–)7–10 mm long; tube (11–)15–22 mm long and 5–7.5 mm in diameter, cupular, green to red; sepals 4, (1.3–)1.8–2.6 × 0.4–0.8(–1.1) cm, the adaxial one largest, narrowly elliptic to oblong, obtuse, red or greenish white, glabrous; petals 5, 12–20 × 6–15 mm, the adaxial one ovate to triangular–ovate, the base auriculate to cordate, the apex acute, the other four petals 12–20 × 6–9.5 mm, narrowly elliptic, acute to caudate-acuminate, usually bright red but sometimes white with red streaks, glabrous except apically ciliolate; stamens 3, red; filaments 4–7.5 cm long, more or less pilose; anthers 8–10.5 × 1.5–3 mm, linear to narrowly oblong, glabrous; staminodia 6, 10–20 mm long; tube 0.8–1.5(–3) mm, basally united, except at the base of adaxial petal, more or less villose; gynoeceum dark red with green margins, stigma capitate, style (1.2–)2–4(–6.8) cm long, glabrous except basally velutinous; ovary (5–)8–12(–15) × (1–)2–3 mm, narrowly elliptic to elliptic–oblong, velutinous, gynophore (1.5–)3–7.5 mm long, adnate to upper surface of the hypanthium tube near its rim, glabrous except velutinous apically. **Fruit** 12–21 × 4–6 cm, oblong–oblanceolate, bright red, velvety, transversely venose, a woody vertical flange parallel to legume valves along the placental suture, the flange 4–5 mm wide, ca. 6–10-seeded.

DISTRIBUTION. Guyana; Suriname; Brazil: Amazonas, Roraima.

PHENOLOGY. Flowering and fruiting throughout the year (flowering specimens collected in all months except May and August, fruiting specimens lacking only for August and October).

NOTES. This species is abundant in Guyana and is found in rainforest as well as savannah vegetation. On the 2004 expedition of author K.R., multiple individuals of the species were observed along the rivers and streams in the Rupununi region.

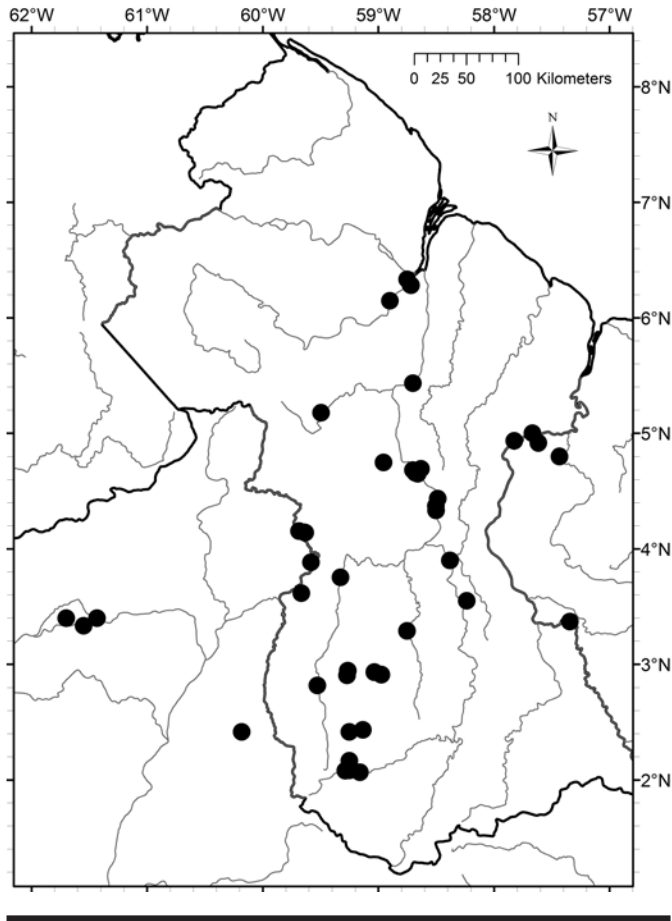


FIGURE 6. Geographic distribution of *Paloue coccinea* (M. R. Schomb. ex Benth.) Redden (dots) in Guyana and adjacent regions.

On the return trip, the rainy season had begun and many of the trees were entirely submerged in water.

ADDITIONAL SPECIMENS EXAMINED. BRAZIL. AMAZONAS: Territory of Roraima, Serra da Lua, Dormida, foothills of Serra da Lua, 2°25'–29'N, 60°11'–14'W, 15 Jan 1969 (fl., fr.), *Prance et al.* 9287 (A, C, COL!, F!, G, INPA, K!, MG, MICH, MO!, NY!, P, R, S, U!, US!, VEN!); **RORAIMA:** Ilha de Maracá, Mun. Alto Alegre, 3°24'N, 61°26'W, 14 Jul 1986 (fl.), *Henderson & de Lima* 604 (K!, US!); Mun. Alto Alegre, SEMA Estação, 3°24'N, 61°26'W, 14 Jun 1986 (fl.), *Hopkins et al.* 741 (K!); Mun. Boa Vista, Reserva Ecológica de Maracá, 14 Oct 1987 (fl., fr.), *Lewis* 1673 (K, 2 sheets!); SEMA Ecological Reserve, Ilha de Maracá, 3°20'N, 61°33'W, 3 Jul 1988 (st.), *Milliken & Bowles* 389 (K!).

GUYANA. CUYUNI-MAZARUNI: Essequibo River, 6–8 km downstream of Omai, 5°26'N, 58°42'W, 10–15 m, 1 Jun 1989 (fl., fr.), *Gillespie* 1579 (BRG!, K!, MO!, NY!, US!); Mazaruni River, Marshall Falls to several kilometers downstream, 6°20'0"N, 58°45'0"W, 5 m, 26 Apr 1993 (fr.), *Henkel* 1969 (BRG!, K!,

MO!, NY!, US!); Mazaruni River, small islands throughout river, 3.14 mi N of base camp, 6°8'51.2"N, 58°53'59.7"W, 31 m, 13 Oct 2004 (fr.), *Redden* 3297 (BRG!, K!, MO!, NY!, US!); Mazaruni River, Marshall Falls, 6°16'54.4"N, 58°42'58.4"W, 4 m, 17 Oct 2004 (fr.), *Redden* 3312 (BRG!, K!, NY!, US!). **EAST BERBICE-CORENTYNE:** Along banks of Corentyne River, above Baba Grant sawmill, above Cow Falls, 5°00'N, 57°40'W, 10–20 m, 17 Apr 1990 (fl., fr.), *McDowell* 2305 (BRG!, K!, MO!, NY!, US!); Corentyne River, between Cow Falls and Baba Grant sawmill, 5°00'N, 57°42'W, 10–25 m, 21 Apr 1990 (fl.), *McDowell* 2374 (BRG!, K!, MO!, NY!, US!); Corentyne River, Marabunta Creek, 4°56'N, 57°49'W, 10 m, 24 Mar 1995 (fl., fr.) *Mutchnick* 987 (BRG!, NY!, US!). **POTARO-SIPARUNI:** Iwokrama Forest Reserve, along Essequibo River between Turtle Mountain trail and Kurupukari Field Station, 4°41'N, 58°42'W, 160 m, 18 Sep 1995 (fl.), *Clarke* 168 (BRG!, NY!, MO!, U!, US!); Essequibo River at Kurupukari crossing, small island 0.25 km SE of W bank landing, 4°40'N, 58°41'W, 55 m, 18 Apr 1992 (fr.), *Hoffman* 1317 (BRG!, K!, MO!, NY!, US!); Iwokrama Forest Reserve, Kurupukari Village, base camp 2 km N on Essequibo River, 04°41'N, 58°37'W, 60 m, 16 Mar 1997 (fr.), *Mori* 24362 (BRG!, US!); Essequibo River, Kurupukari Falls, 4°40'N, 58°40'W, 100 m, 7 Dec 1994 (fl.), *Mutchnick* 563 (BRG!, MO!, NY!, US!); Essequibo River, Kurupukari Falls and 2 km upstream, 4°39'N, 58°39'W, 100 m, 12 Dec 1994 (fl.), *Mutchnick* 672 (BRG!, MO!, NY!, US!); Iwokrama Forest Reserve, Essequibo River, Akramukra Falls, 4°22'N, 58°30'W, 50 m, 16 Feb 1995 (fl.), *Mutchnick* 758 (BRG!, K!, MO!, NY!, US!); Iwokrama Forest Reserve main field station, 4°40'17.7"N, 58°41'7.1"W, 64 m, 27 Oct 2002 (fr.), *Redden* 1094 (BRG!, K!, NY!, U!, US!); Iwokrama Forest Reserve, Siparuni River heading toward the Burro-Burro River, between Pakatau Falls base camp and junction with Burro-Burro River, 4°44'57.8"N, 58°57'14.2"W, 56 m, 1 Nov 2002 (fl. & fr.), *Redden* 1117 (BRG!, K!, US!); Iwokrama Forest Reserve main field station, on trail leading to Fairview Village, 4°40'17.7"N, 58°41'7.1"W, 64 m, 10 Nov 2002 (fl.), *Redden* 1179 (BRG!, K!, NY!, US!); 10 Nov 2002 (fl.), *Redden* 1180 (BRG!, K!, NY!, U!, US!); 10 Nov 2002 (fl.), *Redden* 1181 (BRG!, K!, NY!, U!, US!). **UPPER TAKUTU-UPPER ESSEQUIBO:** Rupununi area, Karanambo, 3°53'0"N, 59°35'0"W, 110 m, 17 Feb 1990 (fl.), *Acevedo-Rodríguez* 3266 (BRG!, K!, MO!, NY!, US!); Iwokrama Rainforest Reserve, Akromukru Transect at Akromukru Falls, Essequibo River, 4°29'N, 58°30'W, 70–90 m, 18 Mar 1996 (fl.), *Clarke* 1327 (BRG!, K!, MO!, NY!, US!); Kuyuwini River, area near camp, 2°05'N, 59°17'W, 240 m, 19 Jul 1996 (fl., fr.), *Clarke* 2314 (BRG!, K!, MO!, NY!, US!); Kwitaro River, landing at terminus of trail from Shea Village, 2°54'N, 58°58'W, 135 m, 7 Feb 1997 (fl.) *Clarke* 3408 (BRG!, K!, NY!, MO!, U!, US!); Rewa River, 0–5 km S of confluence with Kwitaro River, 3°17'N, 58°45'W, 90 m, 25 Feb 1997 (fl., fr.), *Clarke* 3916 (BRG!, K!, MO!, NY!, US!); Kuyuwini River, 0–5 km W of landing at terminus of trail from Karaudar-nau and Parabara Savanna, 2°5'N, 59°14'W, 240 m, 31 May

1997 (fr.), *Clarke 5068* (BRG!, K!, MO!, NY!, US!); N. Rupununi, Apr 1968 (fr.), *Davis 815* (K!); Iteballi Falls, Essequibo River, 1 Feb 1944 (fl.), *Fanshawe F1667* (K!); South Rupununi savanna, Ikirap Creek along Marudi Road, 2°25'N, 59°15'W, 250 m, 23 Dec 1993 (fl.), *Henkel & James 3566* (BRG!, K!, MO!, NY!, U!, US!); South Rupununi savanna, Katambar Mtn. SE of Aishalton, 2°26'N, 59°08'W, 200 m, 17 Jan 1994 (fr.), *Henkel 3662* (BRG!, K!, MO!, NY!, US!); Northern Rupununi savannas, Karanambo Ranch, trail SW of compound, 3°45'12"N, 59°19'36"W, 90–120 m, 17 Feb 1992 (fl.), *Hoffman 979* (BRG!, K!, MO!, NY!, US!); Kuyuwini Landing, Kuyuwini River, 02°10'N, 59°15'W, 200 m, 1 Feb 1991 (fl., imm. fr.), *Jansen-Jacobs et al. 2273* (K!, U!, US!); 2°05'N, 59°15'W, 150–250 m, 12 Oct 1992 (fl., imm. fr.), *Jansen-Jacobs et al. 2890* (BRG!, K!, U!, US!); Rupununi district, Kumukowau River, Camp 3, 2°56'N, 59°2'W, 160 m, 13 Feb 1994 (fl., fr.), *Jansen-Jacobs et al. 3731* (BRG!, K!, U!, US!); Ireng River base camp, 4°08'38.9"N, 59°38'28.3"W, 136 m, 24 Mar 2004 (fl., imm. fr.), *Redden 3018* (BRG!, K!, MO!, NY!, US!); *Redden 3019* (BRG!, K!, MO!, NY!, US!); Ireng River near Ireng River base camp, 4°08'25.8"N, 59°37'57.9"W, 113 m, 25 Mar 2004 (fl., imm. fr.), *Redden 3031* (BRG!, K!, MO!, NY!, US!); Achimar Wau (Haimara creek), 2°54'21.1"N, 59°16'14.6"W, 155 m, 2 Apr 2004 (fl., fr.), *Redden 3045* (BRG!, K!, MO!, NY!, US!); Rupununi River, 2°49'5.5"N, 59°31'41.6"W, 113 m, 31 Mar 2004 (fl., imm. fr.), *Redden 3038* (BRG!, K!, MO!, NY!, US!); Rupununi savanna, 2°56'42.6"N, 59°15'48.7"W, 165 m, *Redden 3056*, (fr.) *Redden 3057* (BRG!, K!, MO!, NY!, US!); Kuyuwini River, 02°05'41.4"N, 59°14'50.8"W, 124 m, 14 Apr 2004 (fl., fr.), *Redden 3082* (BRG!, K!, MO!, NY!, US!); Kuyuwini River, 02°05'41.4"N, 59°14'50.8"W, 124 m, 14 Apr 2004 (fl.), *Redden 3088* (BRG!, K!, MO!, NY!, US!); Kuyuwini River, 2°5'41.4"N, 59°14'50.8"W, 124 m, 14 Apr 2004 (fl., fr.), *Redden 3089* (BRG!, K!, MO!, NY!, US!); Conservation International Concession on the Essequibo River, 3°53'58.1"N, 58°22'50.2"W, 97 m, 19 Jan 2007 (fl.), *Redden 5081* (BRG!, K!, MO!, NY!, US!); Basin of Kuyuwini River (Essequibo tributary), about 150 mi from mouth, 21–26 Nov 1937 (fl.), *Smith 2521* (F!, K!, MAD, NY!, P, U!, US!); Pirara, 1841–1842 (fl.), *Schomburgk 251* (K!, US!); Basin of Kuyuwini River (Essequibo tributary), about 150 mi from mouth, 12 Feb 1938 (fl., fr.), *Smith 3031* (K!, US!); Rupununi River, Sep 1948 (fl., fr.), *Wilson Browne WB 136* (K!); Oronoque, New River, 25 Dec 1935 (fl.), *Myers 3906* (K!); Kanuku foothills, 2 Feb 1952 (fl.), *Guppy G172* (K!); without exact locality, without date (fl.), *Appun 857* (K!).

SURINAME. NICKERIE: Area of Kabalebo Dam project, 4–5°N, 57°30'–58°W, 30–130 m, 6 Sep 1980 (fr.), *Lindeman et al. 172* (K!, US!). SIPALIWINI: South side of Kuruni Island, riverbank E of trail from camp to canoe landing on S branch of Kuruni River around island, ca. 30 airline km E of confluence on Corantijn River, 3°22'12"N, 57°20'36"W, 180 m, 25 Nov 1994 (fl., imm. fr.), *Evans et al. 1998* (MO!, U!, US!); Wonotobo, Corantyn, 13 Oct 1916 (fr.), *Stabel & Goggryp 2861* (U!).

4. *Paloue duckei* (Huber) Redden comb. nov.

Elizabetha duckei Huber, Bol. Mus Goeldi 7: 291. 1913. Type. Colombia. Amazonas: Puerto Cordoba, Rio Japura (Caqueta) near the Cupati Rapids, 14 Nov 1912 (fl.), *A. Ducke 12245* (holotype: MG; isotypes: BM!, G, P!, RB, US!).

FIGURES 7, 8

Small tree to 10 m tall, branchlets pilose or pilosulose. **Stipules** ca. 6 cm long, caducous, thin, oblanceolate, the apex reflexed, puberulous externally and ciliolate on margins. **Leaves** compound, alternate, paripinnate, lanceolate; petioles 1.5–3.5 mm long, terete, pilosulose, rachis 9–14.5 cm long, rachis wing narrow, apical projections at each leaflet insertion, glabrous; **leaflets** 17–25 × 3–5 mm, 18–30-jugate, sessile, lanceolate to narrowly oblong, base inequilaterally truncate, the apex rounded, slightly retuse, micro-mucronulate, the mucro caducous, micro-punctate beneath, glabrous; venation sub-obscure. **Inflorescences** 5–7 cm long, open, axillary, sessile racemes, the axis puberulous but soon glabrescent; bracts ca. 6 × 4 mm, caducous, obovate, glabrous; bracteoles 10–11.5 × 4–4.5 mm, caducous, acute, slightly carinate dorsally, united unequally, the union more complete on the adaxial side of the flower, red, glabrous; pedicels 3–6 mm long, often puberulous but glabrescent. **Flowers:** hypanthium 13–17 mm long, 5.5–8.5 mm wide, usually glabrous but occasionally a pilose patch present on tube; stipe 3–9 mm long; tube (12–)20–21 mm long, 4–7 mm in diameter at the apex, gradually tapering to the stipe, red; sepals 4, 1.3–1.7 × 0.5–0.9 cm, oblong, glabrous; petals 5, (12–)14–17 × (3.5–) 5–8.5 mm, about equal in size and shape, elliptic, glabrous except ciliate apically; stamens 3, red, “very long erect” (fide Ducke, 1934), filaments 3.7–6.3 cm long, sparingly villose; anthers 5.5–8.5 × 2.5–3 mm, more or less elliptic; staminodia 6, 0.5–1 mm long, highly reduced; tube united for 0.5–1 mm; gynoeceium glabrous; glabrous; ovary 8–10 × 1.5–2.5 mm, narrowly oblong; gynophore 2–4 mm long, style 3–4.5 cm long, stigma capitellate. **Immature fruit** 12–13 × 3–3.5 cm, flat, oblong, narrowly alate, glabrous, 4–8-seeded.

DISTRIBUTION. Brazil: Amazonas, Belém; Colombia: Amazonas.

PHENOLOGY. Collected in flower in March, August, and November, and in fruit in August and September.

ADDITIONAL SPECIMENS EXAMINED. **BRAZIL:** AMAZONAS: Igarape Jacitari, 01°23.197'N, 68°10.377'W, 19 Aug 2008 (fl., fr.), *Acevedo-Rodríguez 14648* (K!, US!); Belém, in horto Musei e Rio Caquetá, Puerto Córdoba, anno 1912 introducta, *Ducke 767* (F, K!, MO!, NY!, R, US!); culta in Horto Musei Paraensis (e regione cataractarum inferiorum fluminis Caquetá, Colombia), 4 Mar 1926 (fl.), *Ducke s.n.* (RB-20311, K!, NY!, P, R, U!, US!); Rio Icana, Tunui, 28 Mar 1952 (fl.), *Fróes 28100* (NY!, US!). **BELÉM:** Jardim Botânico do Museu Goeldi, 3 Sep 1942 (fr.), *Archer 7626* (US!).

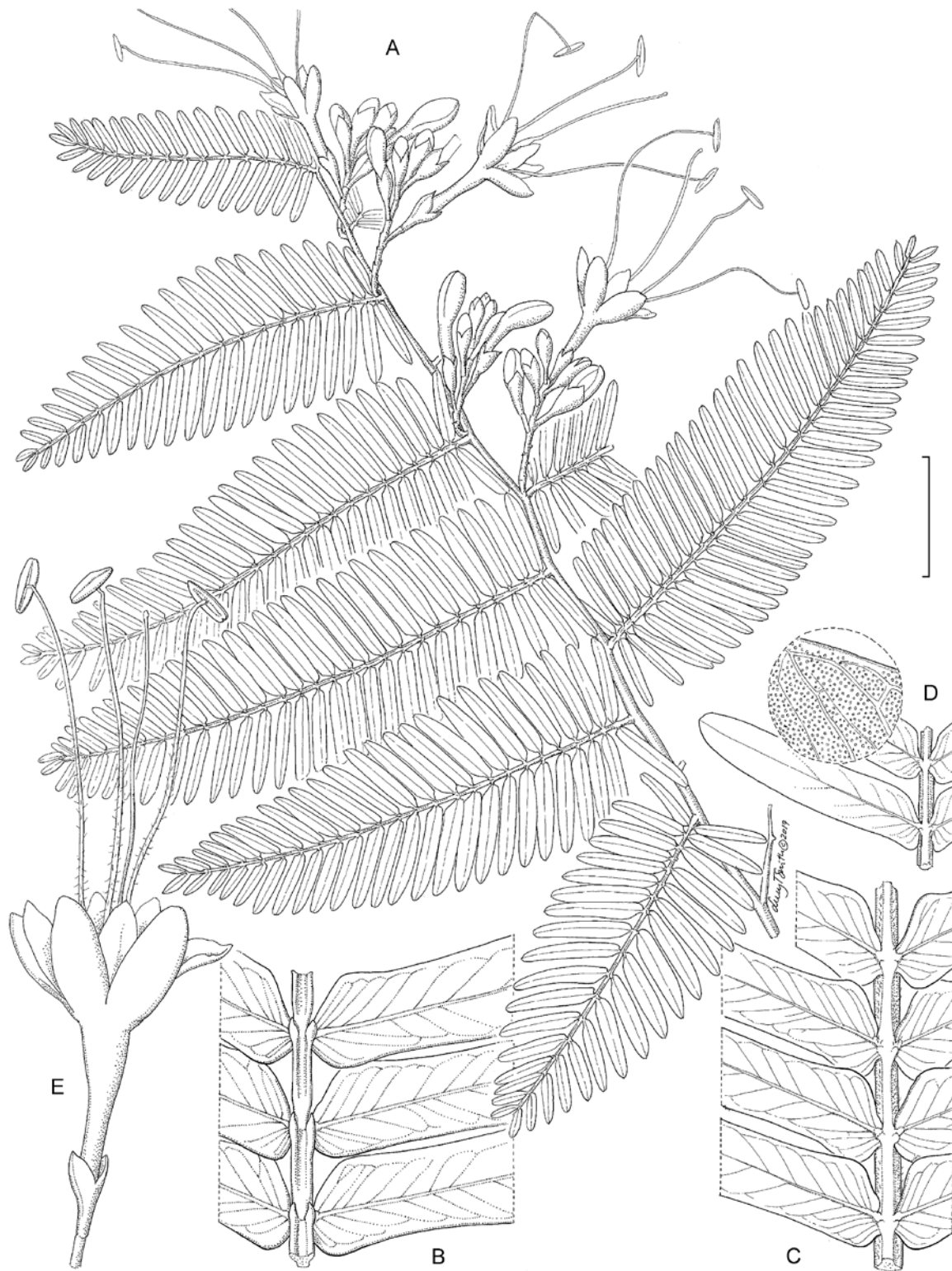


FIGURE 7. *Paloue duckei* (Huber) Redden: A, flowering branch; B, detail of upper surface of leaflets; C, detail of lower surface of leaflets; D, glands on lower surface of leaflets; E, flower. Scale bar length for each: A = 3 cm; B, C = 7 mm; D = 1.6 mm; E = 1.5 cm. Drawn from *Ducke 20311* (K) by Lucy Smith. Copyright © The Board of Trustees of the Royal Botanic Gardens, Kew.

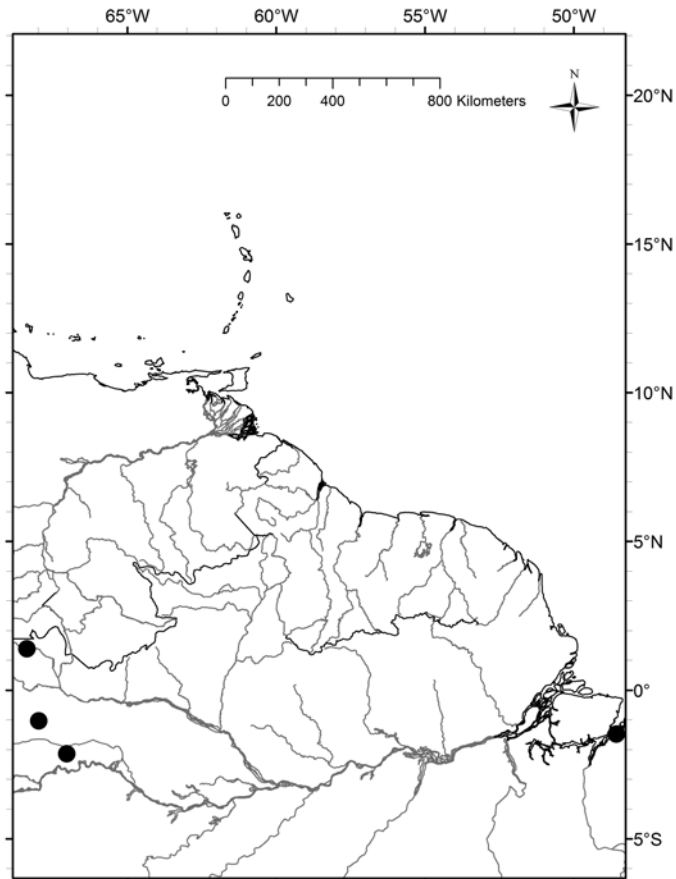


FIGURE 8. Geographic distribution of *Paloue duckei* (Huber) Redden (dots) in Brazil.

5. *Paloue durissima* (Ducke) Redden comb. nov.

Elizabetha durissima Ducke, Trop. Woods 37: 26. 1 Mar 1934. Type. Brazil. Amazonas: Parintins, Lago Jose-Assu, 16 Sep 1932 (fl.), A. Ducke 23729 (holotype: RB; isotypes: FI, G, IAN, K!, MAD, NY!, PI, R, U!, US!).

FIGURES 9, 10, 29A

Tree ca. 25 m tall, the branchlets pale brown to black, pilosulose. **Stipules** ca. 25 × 5 mm, caducous, membranous, acute, narrowly oblanceolate, strigulose externally, ciliolate on the apical half. **Leaves** compound, alternate, paripinnate, oblong to lanceolate; petiole 1.5–2 mm long, pilosulose; rachis 7.5–11.5 cm long, rachis wing narrow, puberulous with apical projections at each leaflet pair insertion, the axis pilosulose; **leaflets** 1.6–1.8 × 0.2–0.3 mm, 34–41-jugate, sessile, narrowly lanceolate-oblong, slightly arcuate, the base inequilaterally obtuse, the apex acute, ciliolate, the venation sub-obscure. **Inflorescences** 2–4 cm long, short axillary racemes, the axis densely tomentose; pedicels 2–3 mm long; bracts 7–9 × 5–10 mm, caducous,

rounded, obtuse, white, strigulose externally and ciliolate on margins; bracteoles 5–8.5 mm long, united almost to their apex, thin, acute, externally sparingly tomentulose, pilosulose, or tomentose. **Flowers:** hypanthium, pilosulose to tomentulose; stipe 3.5 mm long; tube ca. 4 mm long and 4.5 mm in diameter, cupular, white; sepals 8–10 × 3–6 mm, narrowly ovate to lanceolate, white, glabrous except ciliolate near apex; petals ca. 8 × 6.5 mm, the dorsal one triangular-ovate, acute, the other four narrower, sublinear-oblong, 9–9.5 × 1.5–2 mm, acuminate, white, glabrous; stamens 3, white; filaments 2.3–2.5 cm long, sparingly villose; anthers ca. 3 × 1.5 mm, elliptic, glabrous; staminodia 6; gynoecium red; ovary ca. 5 × 1.5 mm, oblong-elliptic, glabrous; gynophore 2 mm long, style 1.8–2.5 cm long, stigma capitate. **Fruits** 10–15 × 4–4.5 cm, glabrous, ca. 3–6-seeded.

DISTRIBUTION. Guyana; Brazil: Amazonas and Pará.

PHENOLOGY. Collected in flower in September, November, and January, and in fruit in April.

NOTE. A specimen was collected by Ducke (81000) in the Rio de Janeiro Botanical Garden in October 1952 (Cowan, 1976).

ADDITIONAL SPECIMENS EXAMINED. GUYANA. UPPER DEMERARA-BERBICE: Mabura Hill, 30 km S on Mabura Hill-Kurupukari Road, 5°05'N, 58°44'W, 75–85 m, 2 Jan 1996 (fl.), Clarke 753 (BRG!, MO!, NY!, US!). **POTARO-SIPARUNI:** Iwokrama Forest Reserve, base of Turtle Mountain in gap clearing, 4°43'56.2"N, 58°44'1.6"W, 20–25 m, 9 Nov 2002 (fl.), Redden 1171 (BRG!, K!, MO!, NY!, US!), Redden 1178 (BRG!, MO!, NY!, US!); Upper Takutu, just below Pakatau Falls, 4°45'10.00"N, 59°01'25"W, 26 Apr 1992 (fr.), Pennington et al. 400 (K!).

BRAZIL: PARÁ: Estação Ecologia do Jari, Projeta Reserva Genetica, SEMA, 00°75'S, 52°30'W, 17 Oct 1997 (fl.), Beck et al. 139 (K!, US!).

6. *Paloue emarginata* (R. S. Cowan) Redden comb. nov.

Paloveopsis emarginata R. S. Cowan, Brittonia 8: 4. 1957. Type. Guyana. Side of Bunawau Creek, 31 Oct 1952 (fl.). N. Guppy 513 (holotype: NY!; isotypes: FI, K!, US!).

FIGURES 11, 29D

Medium-sized tree 11 m tall, 20 cm in diameter, branchlets and petiole pilose, later becoming glabrous. **Stipules** 9 mm long, caducous, glabrous. **Leaves** simple (unifoliate), alternate; petiole 3–4 mm long, glabrous, leaf blade 5.5–7.5 × 2.5–3.5 cm, elliptic, base acute, apex acute and emarginate, pubescent on the midvein on upper surface of leaf blade, upper surface glabrous and minutely punctuate, midvein salient, venules conspicuous. **Inflorescences** axillary or terminal racemes, 3–5 cm long, bracts 2 × 1.5 mm, caducous, sessile, glabrous, minutely ciliolate on margins; bracteoles connate, 5 × 2.5 mm, obovate, apex ciliolate on margins; pedicels 5.5–6 mm long, glabrous. **Flowers:** hypanthium glabrous, 5 mm long, 4 mm in diameter, funnel-shaped,

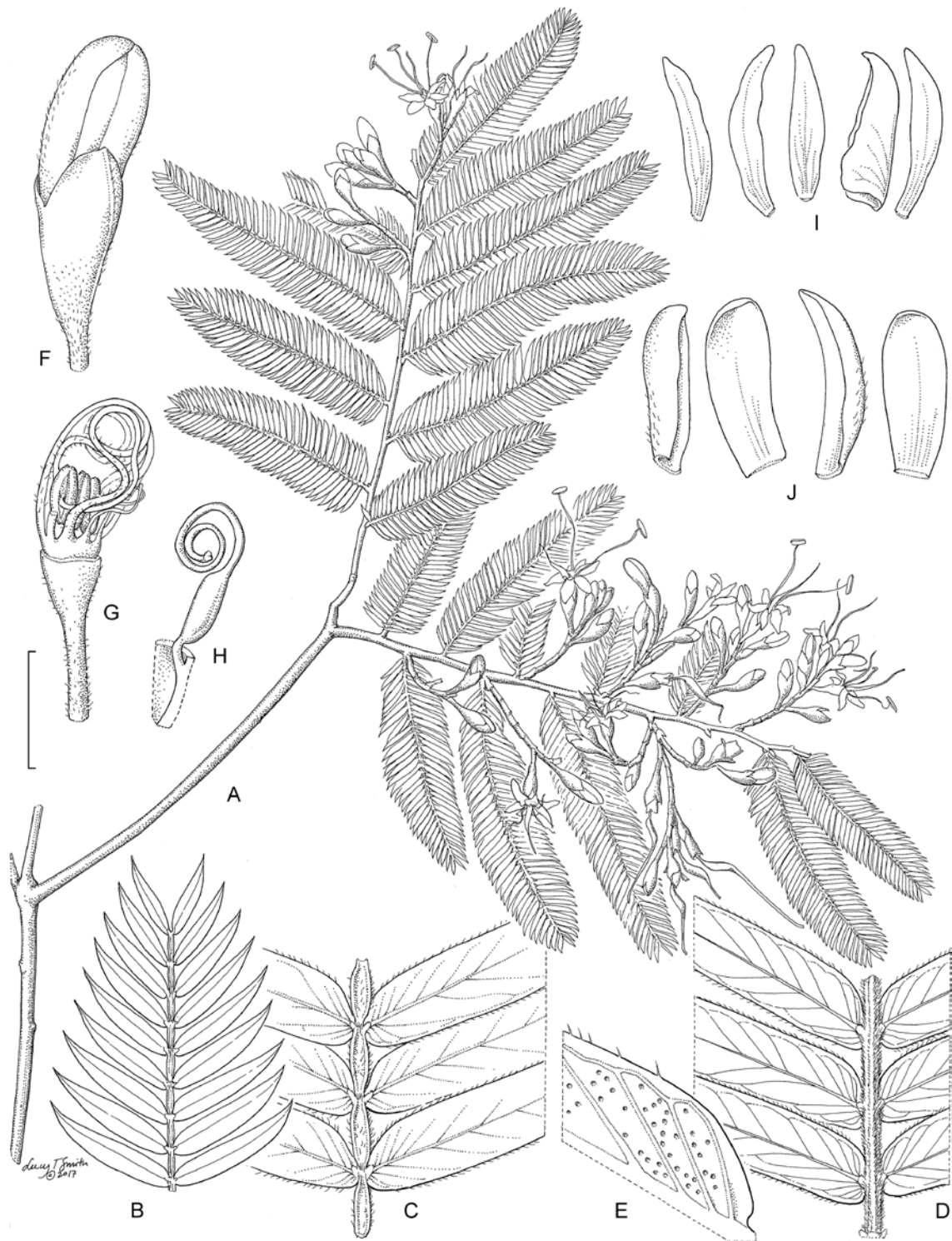


FIGURE 9. *Paloue durissima* (Ducke) Redden: A, flowering branch; B, upper portion of leaf; C, detail of upper surface of leaflets; D, detail of lower surface of leaflets; E, glands on lower surface of leaflets; F, bud; G, bud with calyx and corolla removed to show stamen packaging; H, gynoecium showing stipe attachment to hypanthium wall; I, petals; J, sepals. Scale bar length for each: A = 3 cm; B, F–J = 7 mm; C, D = 2.5 mm; E = 1 mm. Drawn from Redden 1171 (K) by Lucy Smith. Copyright © The Board of Trustees of the Royal Botanic Gardens, Kew.

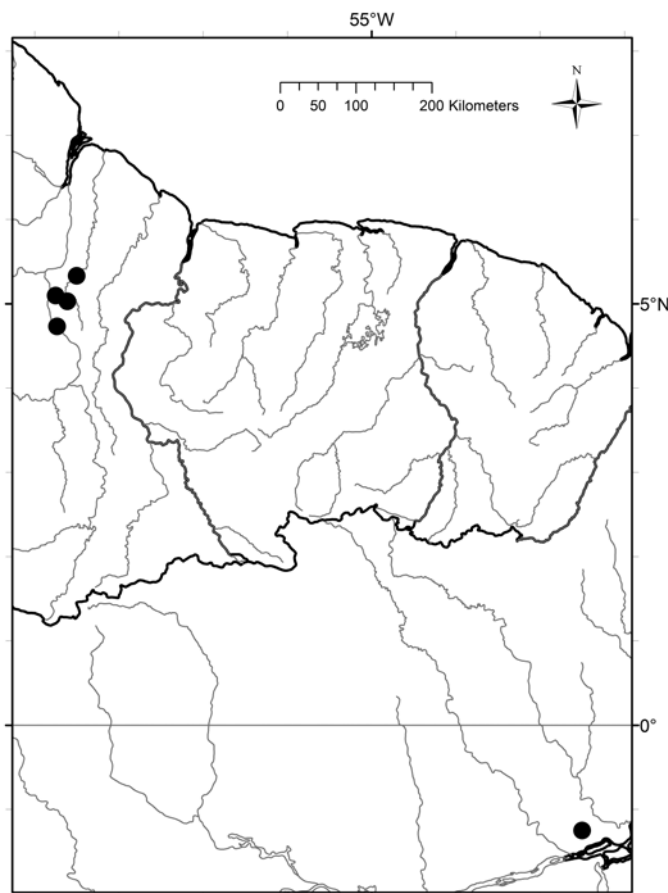


FIGURE 10. Geographic distribution of *Paloue durissima* (Ducke) Redden (dots) in Guyana and Brazil.

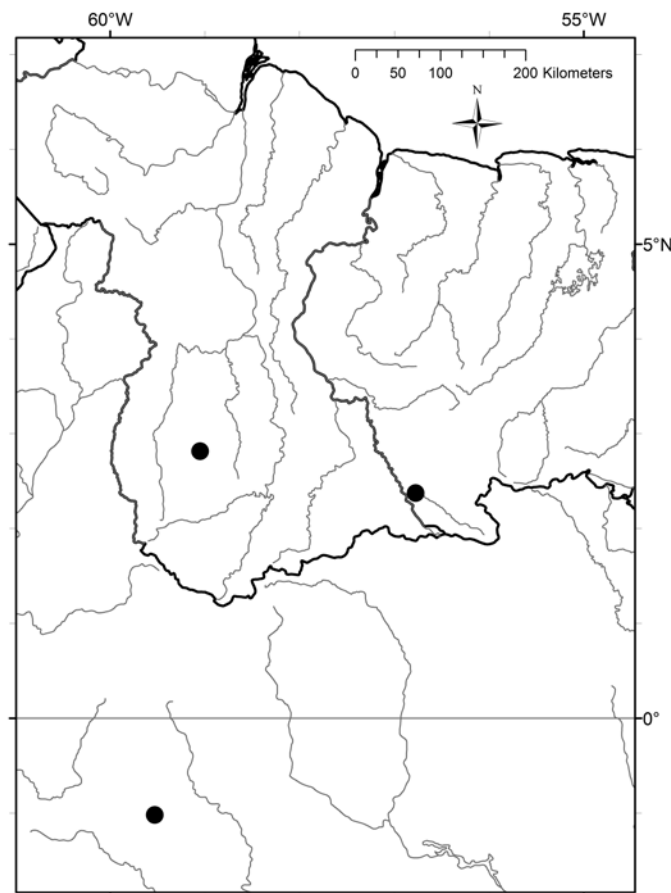


FIGURE 11. Geographic distribution of *Paloue emarginata* (R. S. Cowan) Redden (dots) in Guyana, Suriname, and Brazil.

stipe 4.5–5 mm long, glabrous; sepals 10×3.5 –5.5 mm, glabrous, elliptic, imbricate; petals 5, equal, 6.5–8 \times 1–1.5 mm, linear-lanceolate, apex acute, punctate, long-ciliate along margins; stamens 9, 3 fertile, filaments of the fertile stamens ca. 21 mm long, villose, anthers oblong, 4.5 \times 1 mm, staminodes 3–4.5 mm long, tapering toward tip, villose, filaments of stamens and staminodes connate at base for 1–2 mm; ovary 4 \times 1.5 mm, glabrous, oblong, stipe 1.5 mm long, glabrous; style 16 mm long, glabrous; stigma capitate. **Fruit** a legume, (11–)13–18 \times 4.5–5.5 cm, oblong but somewhat wider toward the apex, ca. 6–8-seeded.

DISTRIBUTION. Guyana; Suriname; Brazil: Amazonas.

PHENOLOGY. Collected in flower in June and October and in fruit in June and August.

ADDITIONAL SPECIMENS EXAMINED. **BRAZIL.** AMAZONAS: Vicinity of Rio Uatumã, Rio Pitinga, margem direita do rio, 29 Aug 1979 (fr.), *Cid et al.* 916 (K!, NY!, US!).

SURINAME. SIPALIWINI: Sipaliwini River, 0–1 km downstream from Kwamalasamutu Village, 2°22'31"N, 56°46'31"W, 213 m, 17 Jun 2004 (fl., fr.), *Hoffman* 5924 (BBS, UI, US!).

7. *Paloue fanshawei* (R. S. Cowan) Redden comb. nov.

Elizabetha fanshawei R. S. Cowan. Proc. Kon. Nederl. Akad. Wetensch. Ser. C. 79: 323–334. 1976. Type. Guyana. 107 mi along Bartica–Potaro Road, 16 Nov 1943 (fl., fr.), *D. B. Fanshawe* 1498 (holotype: NY!, image at K!, isotype K!).

FIGURES 12, 13

Tree 12–15 m tall, trunk 15–20 cm in diameter, branchlets puberulous. **Stipules** caducous, not seen. **Leaves** compound, alternate, paripinnate; petioles 3–4 mm long, minutely pubescent, rachis 5–6.5 cm long, rachis wing narrow and erect without apical projections at each leaflet insertion, minutely pubescent; **leaflets** 4–6-jugate, sessile, the blade oblong to elliptic-oblong, base inequilateral, the upper acute, lower rounded-obtuse, apex rounded, obtuse and retuse, glabrous above, below micro-punctate and near to the base a little tuft of long pilose hairs along the salient midvein. **Inflorescences** axillary racemes, 8 cm long, glabrous; bracts caducous, not seen; bracteoles oval, 14 \times 9 mm, united marginally in a tube enclosing the flower bud, glabrous;



FIGURE 12. *Paloue fanshawei* (R. S. Cowan) Redden: A, flowering branch; B, upper surface of leaflet; C, lower surface of leaflet; D, glands on lower surface of leaflet; E, fructing branch. Scale bar length for each: A, E = 3 cm; B, C = 1.5 cm; D = 1 mm. A–D drawn from *Hoffman 1069* (K); E drawn from *Fanshawe 1044* (K) by Lucy Smith. Copyright © The Board of Trustees of the Royal Botanic Gardens, Kew.

pedicel 14–16 mm long. **Flowers:** hypanthium glabrous, stipe ca. 8 mm long, tube ca. 6.5 mm long; sepals green, ca. 15 × 6–8 mm; petals 5, ovate, adaxial petal largest, ca. 27 × 16 mm, white, villose at base, the reduced petals linear, ca. 2 mm long; stamens 9, filaments 5.5 cm long, fused into a tube 3.5 mm long except at adaxial petal, villose toward base; ovary velutinous, oblong, ca. 6 × 2 mm, stipe 3 mm long, velutinous; style pilose at base. **Fruit** a legume, pilose to minutely pubescent, flat, ca. 5.5 cm long, 4–6-seeded.

DISTRIBUTION. Endemic to Guyana.

PHENOLOGY. Collected in flower in November, February and March, and in fruit in January, February, May, and October.

ADDITIONAL SPECIMENS EXAMINED. GUYANA. Mahdia River, Potaro River, 107 mi Bartica–Potaro Road, 18 Jan 1943 (fr.) *Fanshawe F1044* (K!); CUYUNI-MAZARUNI: S. Pakaraima Mts., at “Corona Falls,” ca. 20 km NW of Karasabai Village, 4°09'N, 59°41'W, 150 m, 27 Feb 1992 (fl.), *Hoffman 1069* (BRG!, K!, MO!, NY!, U!, US!); Pakaraima Mts.,

base camp 8.6 km NE of Imbaimadai on Partang River tributary, 5°46'N, 60°15'W, 650 m, 23 May 1992 (fr.), *Hoffman 1814* (BRG!, MO!, NY!, US!); base camp, small tributary of Partang River, 11.4 km NE of Imbaimadai, 5°48'N, 60°15'W, 650 m, 26 May 1992 (imm. fr.), *Hoffman 1897* (BRG!, K!, MO!, NY!, US!); West branch of Eping River, 6°00'0"N, 60°10'0"W, 122–152 m, 7 Feb 1991 (fr.), *McDowell 3895* (BRG!, K!, MO!, NY!, US!); Pakaraima Mts., Mazaruni River, 9.21 mi W of Imbaimadai to Kamarang, near Jawalla and Baimapai, 5°43'51.1"N, 60°35'15"W, 498 m, 5 Feb 2004 (fr.), *Redden 1722* (BRG!, K!, MO!, NY!, US!); Pakaraima Mts., Mazaruni River between Imbaimadai and Kamarang, near Jawalla and Baimapai; 20.2 GPS mi W and downstream of Imbaimadai, 5°43'51.1"N, 60°35'15"W, 498 m, 6 Feb 2004 (fr.) *Redden 1733* (BRG!, K!, MO!, NY!, US!); Mazaruni River base of Arawai Falls, 6°20'41.2"N, 60°34'29.1"W, 133 m, 9 Oct 2006 (fr.), *Redden et al. 4648* (K!); Warashema Mountain Range, 6°30'41.7"N, 60°25'3.7"W, 509 m, 2 Mar 2007 (f1.), *Redden 5429* (BRG!, K!, MO!, NY!, US!).

8. *Paloue* × *grahamiae* (R. S. Cowan) Redden, **comb. et stat. nov.**
(*P. induta* × *P. coccinea*)

Elizabetha grahamiae R. S. Cowan, Proc. Kon. Nederl. Akad. Wetensch. 79: 323–334. 1976. Type. Guyana. Mazaruni River, Marshall Falls, 28 Apr 1960 (fl.), *V. Graham 355* (holotype: K!).

FIGURES 14, 15, 30D

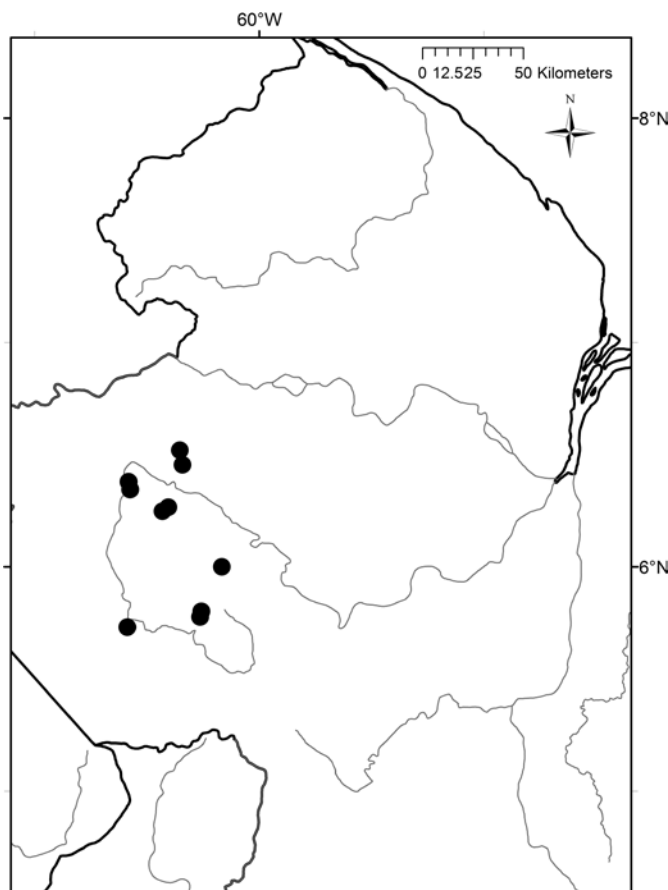


FIGURE 13. Geographic distribution of *Paloue fanshawei* (R. S. Cowan) Redden (dots) in Guyana.

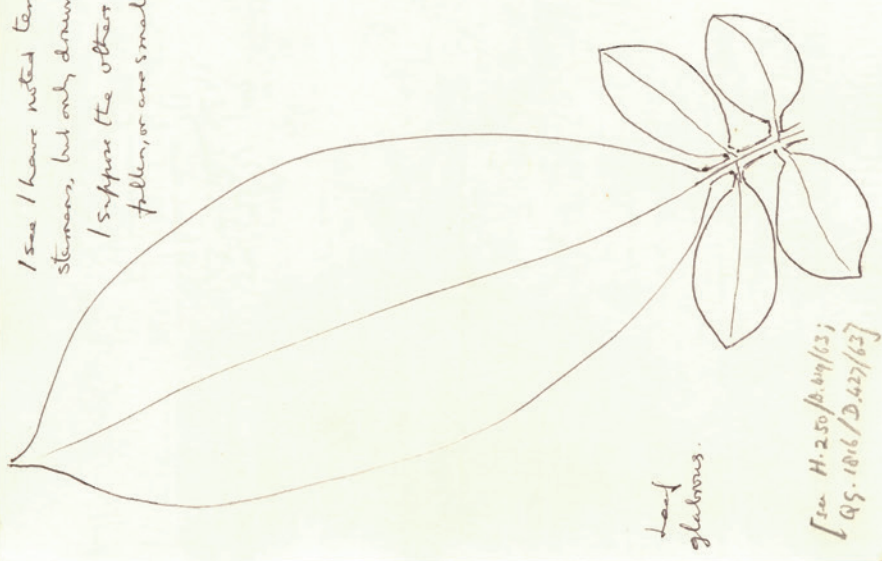
Tree 10 m tall, branchlets pubescent but becoming glabrous. **Stipules** caducous, not seen. **Leaves** compound, alternate, imparipinnate, with 1–3 lateral leaflet pairs, and a single terminal leaflet; petiole ca. 4.5 mm long, pubescent, rachis ca. 10 mm long, narrowly winged, without apical projection at leaflet insertion, the erect wing minutely pubescent; **leaflets** coriaceous, elliptic-lanceolate, sessile, glabrous, large terminal leaflet 11–12.5 × 4–5 cm, apex acute, base equal, obtuse, with paired crater-like glands at the base of the lamina, lateral leaflets 2.5–4 × 1.5–2 cm, base inequilateral, acute, apex acute, midvein salient on lower surface, secondary venation slightly raised on lower surface. **Inflorescences** terminal or axillary racemes, 6.5–9 cm long, glabrous; bracts ca. 14 × 10 mm, cucullate, oval, glabrous, apex rounded; bracteoles ca. 15 mm long, obtuse to acute; pedicels glabrous, 11 mm long. **Flowers:** hypanthium glabrous, greenish, stipe 10 mm long, tube ca. 15 × 7 mm; sepals reflexed, narrowly elliptic to oval, glabrous, 17–18 × 8–11 mm, reddish; petals 5, red, dorsal petal ca. 12 × 10 mm, elliptic, ciliate at apex, 4 other petals, long-acuminate, 11–15 × ca. 1.5 mm, apex ciliate; stamens 9, glabrous, filaments ca. 6.5 cm long, fused tube 3 mm long, anthers of three different sizes; ovary ca. 10 × 2.5 mm, velutinous, narrowly elliptic, stipe ca. 4 mm long, slightly pubescent; style glabrous except at base. **Fruit** a legume, 12–21 × 4–6 cm, pubescent, ca. 4–8-seeded.

DISTRIBUTION. Endemic to Guyana, this hybrid is found where *P. coccinea* co-occurs with *P. induta* or *P. riparia*.

Palouë x grahamii Cowan
 10/1975 R.S.C.

S. National Herbarium,

I saw 1 have noted ten (or nine) stemmers, but only drawn five. I suppose the others have fallen, or are small?



Leaf glabrous.

[See H. 250/B. 04/63; QS. 1016/D. 427/63]

K4 C4 small. A (10) or (9) joined at base only, unequal sizes, ♀ 1 with gynophore. Receptacle deeply hollowed. 2 Bractees resemble sepals. Fruit is a several seeded flat pod, with woody valves which curl when ripe.



H. 250/63
 HERB. HORT. BOT. REG. KEW.

Drawing of Miss V. Graham no. 355,
 Churchill Hills, British Guiana, April 1960.
 Comm. Miss V. Graham, 18.1.1963

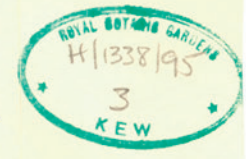


FIGURE 14. Field drawing of *Palouë x grahamii* (R. S. Cowan) Redden by Violet Graham. Illustration reproduced courtesy of the Royal Botanic Gardens, Kew.

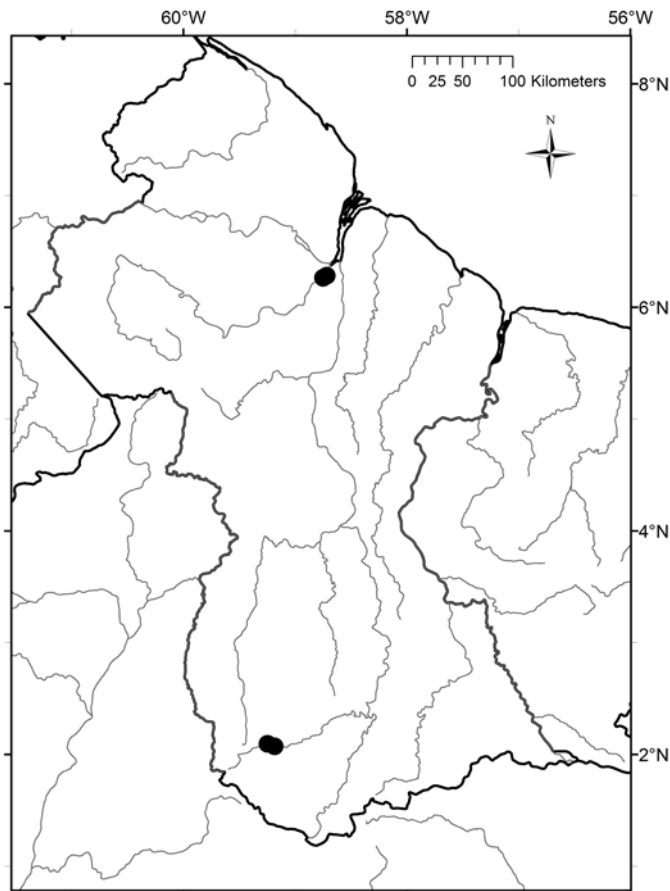


FIGURE 15. Geographic distribution of *Paloue* × *grahamiae* (R. S. Cowan) Redden (dots) in Guyana.

PHENOLOGY. Collected in flower in April and November, and in fruit in April.

NOTES. Phylogenetic analyses based on morphology and DNA sequence data from the plastid *trnL* intron and nuclear ITS provided evidence that *P. grahamiae* may be of hybrid origin (Redden, 2008; Redden *et al.*, 2010). To investigate this further, cloning experiments were conducted to check for multiple copies of ITS in the putative hybrid. Cloning yielded two distinct copies of ITS from the hybrid, which sorted with the putative parents, *P. induta* and *P. coccinea*, suggesting a recent origin of the hybrid. A specimen of *P. × grahamiae* collected in 2007 was growing in close proximity to individuals identified as *P. induta* and *P. coccinea*.

ADDITIONAL SPECIMENS EXAMINED. GUYANA. CUYUNI-MAZARUNI: Mazaruni River, Marshall Falls, ca. 20 mi from Bartica, 6°17'N, 58°43'W, 18 Nov 2005 (fl.) McDowell 5744 (BRG!, US!); 6°15'47.2"N, 58°45'1.6"W, 6 m, Redden 3307 (BRG!, K!, MO!, NY!, U!, US!). **UPPER TAKUTU-UPPER**

ESSEQUIBO: Kuyuwini River, 2°05'41.4"N, 59°14'50.8"W, 124 m, 14 Apr 2004 (fl., fr.), Redden 3090 (BRG!, K!, MO!, NY!, U!, US!); Kuyuwini River, 2°04'19.1"N, 59°10'57.9"W, 243 m, 14 Apr 2004 (fl.), Redden 3104 (BRG!, K!, MO!, NY!, U!, US!).

9. *Paloue guianensis* Aubl., Hist. Pl. Guiane 1: 365–367, pl. 141. 1775. Lectotype (here designated). French Guiana: “Forest of Guiane near the town known by the name Saint-Régis,” J. B. C. F. Aublet *s.n.* (BM!).

FIGURES 16, 17, 29E

Small shrub or tree to 10 m tall, branchlets gray/brown, glabrescent. **Stipules** caducous, linear to strap-like. **Leaves** simple, alternate, entire, blade lanceolate-oblong, 10–16 × 2.5–6 cm, apex acuminate, base acute to rounded to auriculate, usually with paired crater-like glands at the base of the lamina but sometimes these not present, blade coriaceous, glabrous; petioles 3–5 mm long. **Inflorescences** terminal or axillary racemes, 11–14 cm long; bracts orbiculate, 1 cm long, persistent or caducous; bracteoles connate, 6–10 cm long, bilobed, rounded, persistent; pedicels 6–8 mm long. **Flowers:** hypanthium 1.5–2 cm long including the stipe; sepals deep red, 15–20 × 7 mm, rounded at the apex, reflexed; petals 5, red, the three superior petals nearly equal, spatulate, 20–30 × 7 mm, or the two lateral petals much smaller, the two inferior petals filiform, 2–3 mm long, margins glabrous; stamens 9, red, filaments 4–6 cm long, connate equally to form a tube, sparsely long-pilose, anthers linear-oblong, glabrous to sparsely pilose, 3–5 mm long; ovary 1 cm long, glabrous to tomentose, stipitate, style 3–6 cm long, stigma capitate. **Fruit** a legume, 20–23 × 3–5 cm, oblong, stipitate, transversely veined, acuminate, red-brown tomentose, ca. 4–8-seeded.

DISTRIBUTION. Guyana; French Guiana; Suriname; Brazil: Amapá, Pará.

PHENOLOGY. Flowering from October to April, fruiting throughout the year (fruiting collections only unknown from January, February, and May).

NOTES. Specimens were not cited in Aublet’s protologue of *Paloue guianensis*, but a detailed drawing was included. After Aublet’s death in 1778, his herbarium was divided and put up for sale, with the main part now housed in the Banks Herbarium of the Natural History Museum (BM), and in Paris (P), with other specimens at BR, F, LIV, MO, UPS, and W (Stafleu and Cowan, 1976). One specimen at BM was assumed to be Aublet’s type of *Paloue guianensis* and is labeled as such, but no documentation as to who designated it as the type is included. Pulle (1906) and Sandwith (1937) both commented on this specimen, and Sandwith recognized the similarity between the Aublet specimen at BM and Aublet’s drawing, stating “The specimen which may with justification be taken as Aublet’s type shows a flower with three long, subequal petals which accords with his figure.” No formal designation of this specimen as the lectotype has been published, so we have made that designation here.

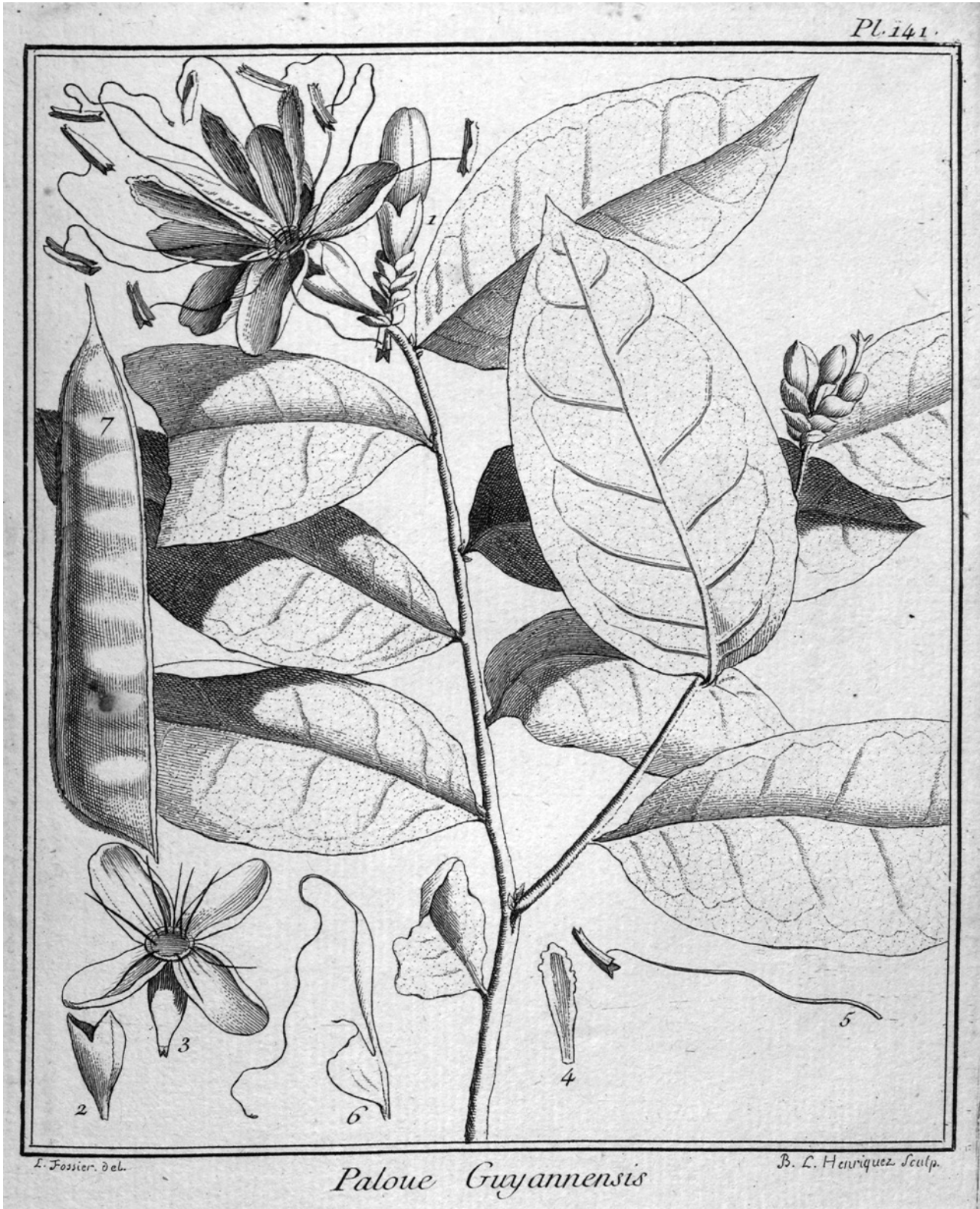


FIGURE 16. *Paloue guianensis* Aubl., reproduced from Aublet (1775: atlas 1, pl. 141): 1, inflorescence; 2, bracteoles; 3, hypanthium; 4, petal; 5, stamen; 6, ovary; 7, fruit.

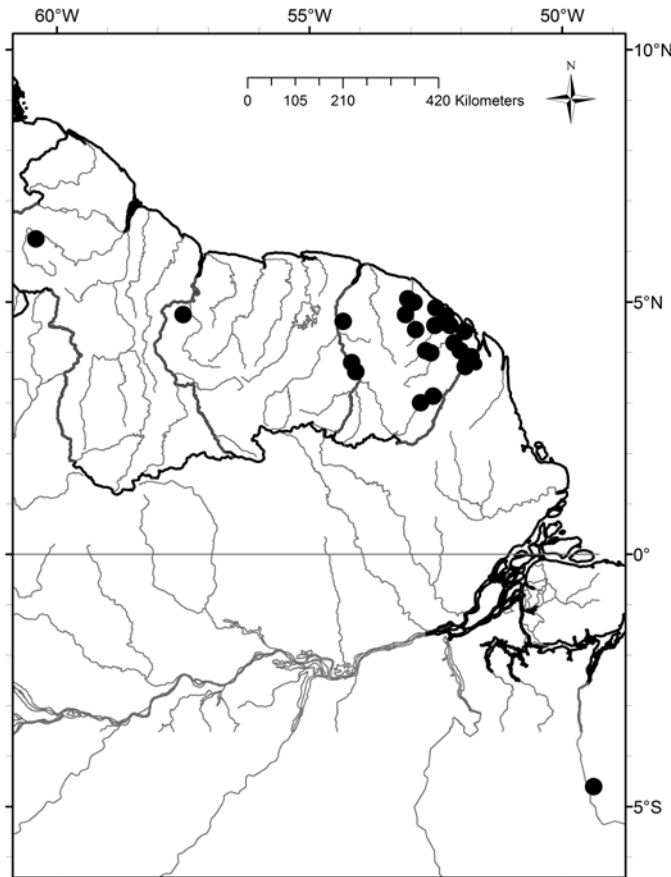


FIGURE 17. Geographic distribution of *Paloué guianensis* Aubl. (dots) across the Guiana Shield.

ADDITIONAL SPECIMENS EXAMINED. BRAZIL.

AMAPA: Rio Oiapoque, Cachoeira Grande Roche, 3°48'N, 51°53'W, 17 Jul 1960 (fr.), *Maguire et al.* 47045 (U!); Rio Oiapoque, ilha perto da cachoeira do Carratá, 1 Feb 1950 (fr.), *Fróes* 25762 (K!); PARÁ: Jacundá, 3 km toward Jatobal; area to be flooded by Tucuruí Dam, 23 Oct 1977 (fl.), *Silva et al.* AS152 (K!, MO!, U, US!).

GUYANA. UPPER DEMERARA-BERBICE: Mabura Hill area, Camudi compartment, 5°20'N, 58°10'W, 15 Mar 1996 (fl., fr.), *Roberts* 2 (U!).

SURINAME. 1862 (imm. fl.) *Kappler* 81 (L!). MAROWIJNE: Ad ripas fluv. Marowijne, 14 Feb 1949 (fl.), *Lanjouw & Lindeman* 2034 (K!, U!); NICKERIE: Area of Kabalebo Dam project, 30–130 m, 20 Nov 1981 (fl.), *Lindeman & Roon* 874 (BBS, K!, U!); SIPALIWINI: Gonini, 20 Feb 1918 (fr.), *Gonggryp* 3737 (U!).

FRENCH GUIANA. CAYENNE: SINNAMARY: Saut L'Autel-Bassin du Sinnamary, 4°45'N, 53°6'W, 25 m, 24 Mar 1994 (fl.), *Bordenave* 871 (NY!, P!, U!, US!); D. Z. de Saut-Dalles-Bassin du Sinnamary, 4°33'N, 52°53'W, 60 m, 7 Jan 1992 (fl.), *Hoff* 7211 (CAY!, NY!, P!, U!, US!); Cayenne (fl.), *von Rohr s.n.* (BM!);

Crique Gabaret-Bassin de l'Oyapock, 3°55'N, 51°48'W, 15 m, 11 Apr 1988 (fl., fr.), *Cremers* 9864 (CAY!, NY!, P, U!, US!); Trésor Reserve, 4°35'N, 52°16'W, no date (fl.), *Ek* 1579 (U!); Regina Region, eastern plateau of Montagne Tortue, 11 km WNW of Approuague River, 4°18'N, 52°22'W, 200–450 m, 14 Jun 1988 (fr.), *Feuillet* 10065 (U!); zone Crique Probert, entre Saint-Georges et le pont transfrontalier sur l'Oyapock, 3°52'50"N, 51°48'46"W, 6 m, 20 Dec 2005 (fl.), *Granville & Crozier* 17222 (CAY, K!, US); St. Georges de l'Oyapock, Crique Gabaret; en amont et en aval du Saut Emerillon, 27 Dec 1978 (jv. fr.), *Grenand* 1781 (US!); Rio Oiapoque, 3°43'N, 51°55'W in French Guiana, opposite Colonia Agricola do Oiapoque, Brazil, about 4 km N of Cricu River, 13 Aug 1960 (fr.), *Irwin & Westra* 47476 (K!, NY); Maroni, without date (fl.), *Mélinon* 18 (K!); bords de la Rivière du Maroni, 1862 (fl.), *Mélinon s.n.* (K!); Mariaflor, Oyapock, 2 Dec 1965 (fl.), *Oldeman* 1835 (U!); Riviére Comté, sur la creique Bagot, branche Nord à environ 3,700 km en amont de son embranchement, 18 Dec 1968 (st.), *Oldeman B-2054* (U!); Riviére Camopi (affluent de l'Oyapock), rives du Saut Ouayeouarou, 9 Feb 1968 (fl.), *Oldeman & Sastre* 115 (U!); Crique Alikene about 0–50 km from its confluence with River Camopi, ca. 3°10'–20'N, 52°28'–32'W, 30 Sep 1960 (fl., fr.), *Pires* 48561 (K!, U!); Fleuve Approuague, riviere Arataye, Saute Pararé, 29 Oct 1978 (fl., fr.), *Poncy* 183 (P!, U!, US!); Régina, Réserve Naturelle Des Nouragues, Camp Arataï, Rives de la riviere Arataye, 3°59'30"N, 52°35'46"W, 100 m, 20 Feb 2003 (fl., fr.), *Poncy* 1666 (K!, P!, US!); Crique Beiman sur le Maroni, 4°37'N, 54°20'W, 22 Feb 1984 (jv. fr.), *Prévost* 1717 (US!); Crique Gabrielle, 4°43'32"N, 52°17'59.2"W, 57 m, 15 Apr 2007 (fr.), *Redden* 5968 (CAY!, US!); Fleuve Moroni, Pompidou-Papaichton, 27 Dec 1978 (fl.) *Sastre* 6470 (U!); Antécume Pata, 3°15'N, 54°10'W, 134 m, 21 Feb 1991 (fl.), *Veth & Manu* 32 (U). ROURA: On road at far side of Cacao leading to town water reservoir, ca. 200–500 m from Cacao, 4°33'37.1"N, 52°27'46.8"W, 66 m, 1 Nov 2009 (fl.), *Mori et al.* 27358 (CAY!, NY!, US!).

10. *Paloué induta* Sandwith, Bull. Misc. Inform. Kew 1937(2): 106–107. 1937. Type. Guyana (as British Guiana). Upper Essequibo River: Mataruki River, between camps 1 and 2, 3 Dec 1935 (fl.), *J.G. Myers* 5801 (holotype: K!).

10a. *Paloué induta* subsp. *induta*

FIGURES 18, 30A

Medium-sized tree, 25–35 m tall, branchlets cinnamon-colored, minutely pubescent to glabrous. **Stipules** caducous, not seen. **Leaves** simple, alternate, entire, up to 11 × 3–5 cm, blade oblong-lanceolate or lanceolate, apex acuminate, base slightly rounded to cuneate with a pair of crater-like glands at the base of the lamina, one either side of the main vein, coriaceous, glabrous, petioles 3–4 mm long. **Inflorescences** solitary in axils or terminal racemes, 4–6 cm long, rachis and pedicels with short, spreading, somewhat glossy, golden hairs; bracts widely ovate, apex round-obtuse, ca. 8 mm long, outer surface densely pubescent,

caducous; bracteoles connate, bilobed, rounded, persistent, 7–10.5 mm long, with a dense, pearl-gray pubescence; pedicels 6–9 mm long. **Flowers:** hypanthium 12–25 mm long including stipe, densely pubescent with ascending, curved, short trichomes; sepals deep red on inner surface, green on outer surface, 1.3–1.5 × 0.6–1.3 cm, broadly ovate or oblong, obtuse, reflexed; petals red, glabrous, oblong or oblong-linear, largest petal acute, 13–14 × 3–5 mm, two medium-sized petals with obtuse apex, 3.5–5 × ca. 1.25 mm, two smallest petals with obtuse apex, about 1.8 × 0.75 mm, margins glabrous; stamens 9, red, filaments 4.8–5.3 cm long, uniformly connate, covered with long trichomes that weakly flex upward, anthers glabrous, 7–7.5 × 1.5 mm, the apex terminating in a little mucro that is round to obtuse, about 0.2 mm long; gynoecium tomentose, densely covered in yellow-white trichomes, stipe glabrous, style 5–6.5 cm long, base covered with trichomes similar to those on ovary. **Fruit** a legume, 11–15 × 2–4 cm; ca. 4–8-seeded.

DISTRIBUTION. Guyana; Suriname.

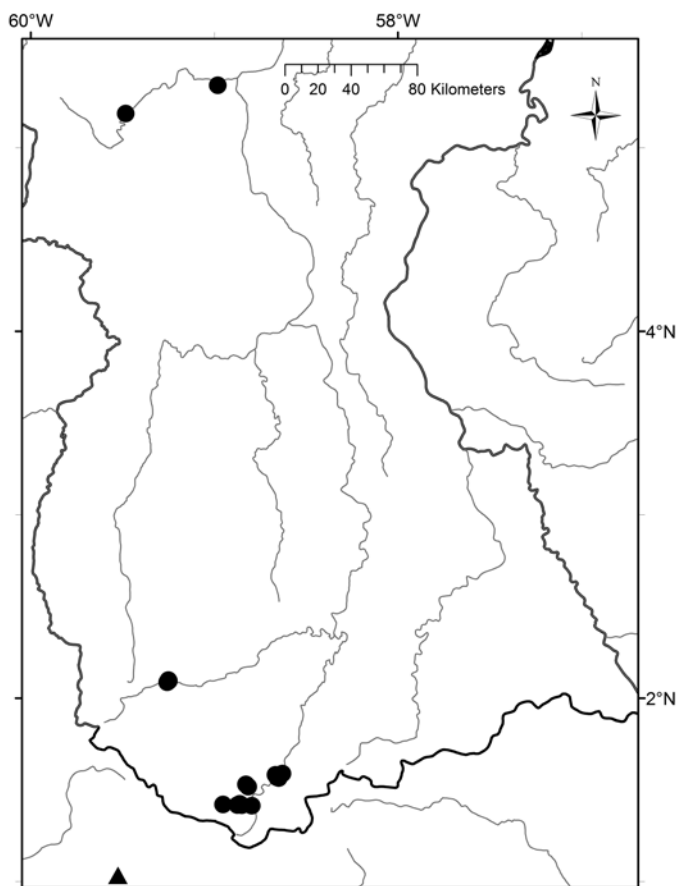


FIGURE 18. Geographic distribution of *Paloue induta* Sand with subsp. *induta* (dots) and *Paloue induta* subsp. *glabra* W. A. Rodrigues & H. C. Lima (triangle) in Guyana and Brazil.

PHENOLOGY. Flowering from September to December and in April, fruiting from March to May.

NOTES. This taxon differs from all the other species of *Paloue* in that the entire inflorescence is covered with trichomes and the ovary is distinctly villous to tomentose. *P. induta* subsp. *induta* is morphologically similar to *P. riparia* Pulle and *P. guianensis* Aubl., but *P. riparia* has smaller flowers and bracteoles and its ovaries are glabrous, and *P. guianensis* has a distinctly different petal configuration.

ADDITIONAL SPECIMENS EXAMINED. GUYANA. UPPER TAKUTU–UPPER ESSEQUIBO: Kamoia River, 0–6 km W of camp, 1°31'50"N, 58°49'40"W, 9 Nov 1996 (fl.), *Clarke 3010* (BRG!, K!, U!, US!); Kamoia Mts., 2 km S of Kamoia River, 1°31'4"N, 58°48'54"W, 13 Nov 1996 (fl.), *Clarke 3207* (BRG!, K!, NY!, US!); Essequibo River, between Camp (at confluence of Essequibo River and Onoro Creek) and Konashen Rapids, 1°35'N, 58°37'W, 18 Nov 1996 (fl.), *Clarke 3289* (BRG!, NY!, U!, US!); Sipu River, area near camp, 1°25'N, 58°57'W, 240 m, 11 Sep 1998 (fl.), *Clarke 7687* (BRG!, NY!, US!); Sipu River, 0–3 km W of camp, 1°25'17"N, 58°57'7"W, 240 m, 12 Sep 1998 (fl.), *Clarke 7790* (BRG, NY, US); Acarai Mts., Sipu River 8–10 km from juncture with Essequibo River, 0°25'N, 58°51'W, 250 m, 12 Mar 1994 (fr.) *Henkel et al. 5108* (BRG!, K!, MO!, NY!, U!, US!); Kuyuwini River, 2°5'41.4"N, 59°14'50.8"W, 124 m, 14 Apr 2004 (fr.), *Redden 3092* (BRG!, K!, NY!, US!); Parabara Village, 1.21 mi SW of village, 2°5'13.4"N, 59°15'22.6"W, 266 m, 16 Apr 2004 (fl., fr.), *Redden 3099* (BRG!, K!, NY!, US!); Parabara Village, Parabara landing, 2°5'54.5"N, 59°14'58.2"W, 238 m, 16 Apr 2004 (fl.), *Redden 3103* (BRG!, K!, NY!, US!); Essequibo River, Gunn's region, 1°33'55.7"N, 58°38'54.7"W, 236 m, 30 Apr 2004 (fr.), *Redden 3154* (BRG!, K!, NY!, US!); Essequibo River, Gunn's region, 1°34'6.6"N, 58°39'25.6"W, 235 m, 30 Apr 2004 (fr.), *Redden 3155* (BRG!, K!, NY!, US!); Sipu River, 1°25'28.2"N, 58°51'40.5"W, 225 m, 3 May 2004 (fr.), *Redden 3160* (BRG!, K!, NY!, US!); Sipu River, 1°25'28.2"N, 58°51'40.5"W, 225 m, 3 May 2004 (fr.), *Redden 3169* (BRG!, K!, NY!, US!); Chodikar River, 1°24'51.5"N, 58°47'44.5"W, 242 m, 4 May 2004 (fr.), *Redden 3189* (BRG!, K!, NY!, US!); Basin of Essequibo River, near mouth of Onoro Creek, 1°35'N, 15–24 Dec 1937 (fl.), *Smith 2652* (F!, K!, MO!, NY!, US!). **POTARO-SIPARUNI:** Micobe, along bank of Tiger Creek, 5°20'N, 59°30'W, 200 m, 20 Oct 1991 (fl.) *Tiwari 488* (NY!) Micobe, 5°20'N, 59°30'W, 200 m, 21 Oct 1991 (fl.), *Tiwari 511* (NY!, US!); Micobe, along bank of Tiger Creek, 5°20'N, 59°30'W, 200 m, 21 Oct 1991, (fr.) *Tiwari 517* (US!)

SURINAME. SIPALIWINI: Gonini River, Sep 1903 (fl., imm. fr.), *Versteeg 248* (U!).

10b. *Paloue induta* subsp. *glabra* W. A. Rodrigues & H. C. Lima, Acta Amazonica 19: 149. 1989 [1990]. Type. Brazil. Amazonas: Mun. Presidente Figueiredo-Balbina, rio Uatuma, 25 Sep 1987 (fl., fr.), *F. Matos et al. 190* (holotype: INPA 148166!; isotypes MG, RB).

Inflorescences glabrous.

DISTRIBUTION. Endemic to the state of Amazonas, Brazil.

PHENOLOGY. Collected in flower in September and in fruit in March and September.

NOTES. The subspecies, as presently circumscribed, is restricted to a very specific locality in Amazonas, Brazil (the riparian vegetation of the Uatumã and Pitinga Rivers near the UHE de Balbina). As for many specimens of *Paloue*, it is difficult to identify them to species without flowering material, and all available specimens examined were in fruit. As described, this subspecies differs from *P. induta* subsp. *induta* in that the inflorescence is glabrous and not covered in light-brown trichomes. However, other specimens of *P. induta*, as well as those of *P. riparia* and *P. guianensis*, exhibit a gradation in trichome density. The presence or absence of trichomes may prove to be an unreliable character for species and subspecies identification, but until more collections are available, subspecies *glabra* is retained as a distinct taxon. Unfortunately, herbarium material did not prove suitable for molecular analysis that might help verify the relationships among these closely related taxa.

Additional specimen examined. **BRAZIL. AMAZONAS:** Mun. Pres. Figueredo, Rio Uatumã entre rios Pitinga e Uatumã (localidade Nazare), 1–2°S, 59–60°W, 18 Mar 1986 (fr.), *Cid Ferreira et al.* 6795 (MO!, NY!).

11. *Paloue leiogyne* (Ducke) Redden comb. nov.

Elizabetha leiogyne Ducke, Bull. Mus. Nat. Hist. Paris 4: 727. 1932.

Type. Brazil. Amazonas: São Gabriel, Rio Negro, 30 Nov 1929 (fl.), *A. Ducke s.n.* (lectotype: RB 23285; isolectotypes: G, IAN, K!, NY!, R, U!, US!); remaining syntype: Serra Curicuriary, *A. Ducke s.n.* (RB 23286).

FIGURES 19, 20

Tree 15–30 m tall, branchlets pilose to tomentose. **Stipules** caducous, oblanceolate, the apex acute and mucronate, 5.5–6.5 × 0.5–1.5 cm, glabrous or slightly pubescent near the apex or base. **Leaves** compound, alternate, paripinnate; petiole (1–)2.5–3.5 mm long, terete, pilose to tomentose, rachis (12–)15–22(–26) cm long, axis pilose, narrowly alate, the wing slightly spreading, without an apical projection, puberulous, constricted at each leaflet pair insertion; **leaflets** 37–50(–57)-jugate, sessile, narrowly oblong, 19–28 × 2.5–5 mm, the base inequilateral, the apex rounded, sometimes slightly retuse, with a small caducous mucro, the margin sometimes microscopically ciliolate along one or both sides of the leaflet, a tuft of long hairs usually developed near the base of the midvein on the lower surface, midvein salient on both surfaces, the venules more or less prominulous, especially on the lower surface. **Inflorescences** usually terminal racemes, 5–7 cm long, the rachis glabrous, or pilosulose near the base or at the insertion of the pedicels; bracts rounded, 17–19 × 14–17 mm, glabrous or sometimes ciliolate; bracteoles oval, united

marginally into a tube enclosing the flower bud, glabrous, 12–18 mm long; pedicels 2–4 mm long, glabrous. **Flowers:** “greenish white with very long erect stamens” (fide Ducke, 1934); the hypanthium glabrous, stipe (3–)5–8.5 mm long, the tube 9–12 mm long, 8–10 mm in diameter; sepals pale green or the inner surfaces white, glabrous, oblong, (12–)16–17 × 6–9 mm, rounded to obtuse; petals 5, white, the dorsal one 14–18 × 10–16 mm, oblong-ovate, bi-auriculate basally, ciliate apically and villose at the extreme base on the inner side, the other four petals elliptic, ciliate apically, 15–21 × 5–7.5 mm; stamens 9, 3 fertile, white, the fertile stamen filaments 20–28 mm long, villose, joined with the sterile, glabrous filaments (these 10–11 mm long) into a tube (except at the insertion of the dorsal petals) 3–5 mm long, anthers red, elliptic, 6–7.5 × 2.5–3 mm; ovary glabrous, 8.5–10 × 2–2.5 mm, narrowly oblong, the gynophore glabrous, about 2 mm long, style 14–26 mm long, glabrous, stigma capitellate. **Fruit** a legume, oblong, ca. 20 × 5 cm, ca. 4–9-seeded.

DISTRIBUTION. Brazil: Amazonas; Venezuela: Amazonas.

PHENOLOGY. Flowering October and November, fruiting October to April.

NOTE. R. S. Cowan (1976: 336) selected the specimen *Ducke [s.n., RB] 23285* in RB as the lectotype of *Elizabetha leiogyne* from among the two syntype collections (RB 23285 and RB 23286) cited by A. Ducke in the protologue.

ADDITIONAL SPECIMENS EXAMINED. VENEZUELA. AMAZONAS: Cerro de la Neblina, Rio Yatua, 200 m, 2 Nov 1957 (fl.), *Maguire et al.* 41986 (K!, NY!, P!, RB!, US!); Rios Pacimoni-Yutua, Casiquiare, 100–140 m, 7–8 Dec 1957 (fr.), *Maguire et al.* 36705 (NY!, US!); Rios Pacimoni-Yutua, Casiquiare, 100–140 m, 25–26 Oct 1957 (fl.), *Maguire et al.* 41952 (K!, NY!, P!, U!, US!); Rios Pacimoni-Yutua, Casiquiare, 100–140 m, 9 Jan 1958 (fr.), *Maguire et al.* 42602 (NY!); Departamento Rio Negro, from Los Tambores of Comision de Limite to Caño Erubichi on Rio Baria, 1°02'N, 66°20'W, 130 m, 2 Apr 1984 (fr.), *Liesner 17125* (NY!); S. Gabriel (Waupé), R. Negro, 19 Feb 1975 (fr.), *Ribeiro 15.286 (713)* (NY!); Rio Negro, S. Gabriel, *Nascimento et al.* 148; 198 (NY!).

BRAZIL. AMAZONAS: Rio Negro, 14 Jan 1933 (sterile), *Ducke 157* (F!, MAD, NY!); Mun. São Gabriel da Cachoeira, Estrada para Camanaus, logo apos o entroncamento da Estrada para o aeroporto, 24 Nov 1987 (imm. fr.), *de Lima et al.* 3298 (MO!, NY!); Rio Negro: Rio Cauaburi, Maturacá, 5 Jul–12 Aug 1967 (st.), *Schultes 24578* (K! image, U!); Vicinity of Maturacá Mission along Rio Maturacá, 20 Oct 1970 (fr.); vicinity of Maturaca Mission, also Rio Maturaca, 20 Oct 1970 (st.), *Steyermark 104038* (K!, NY!, US!); Manaus–Caracari road, ZF-2 road, 50 m off the road, 11 Dec 1980 (st.), *Renner 59* (US!).

12. *Paloue macrostachya* (Benth.) Redden comb. nov.

Elizabetha macrostachya Benth., Fl. Bras. 15(2): 214. 1870. Type. Brazil. Gapo of Rio Paapuris, Nov 1852 (fl., fr.), *R. Spruce 2671* (holotype: K!).

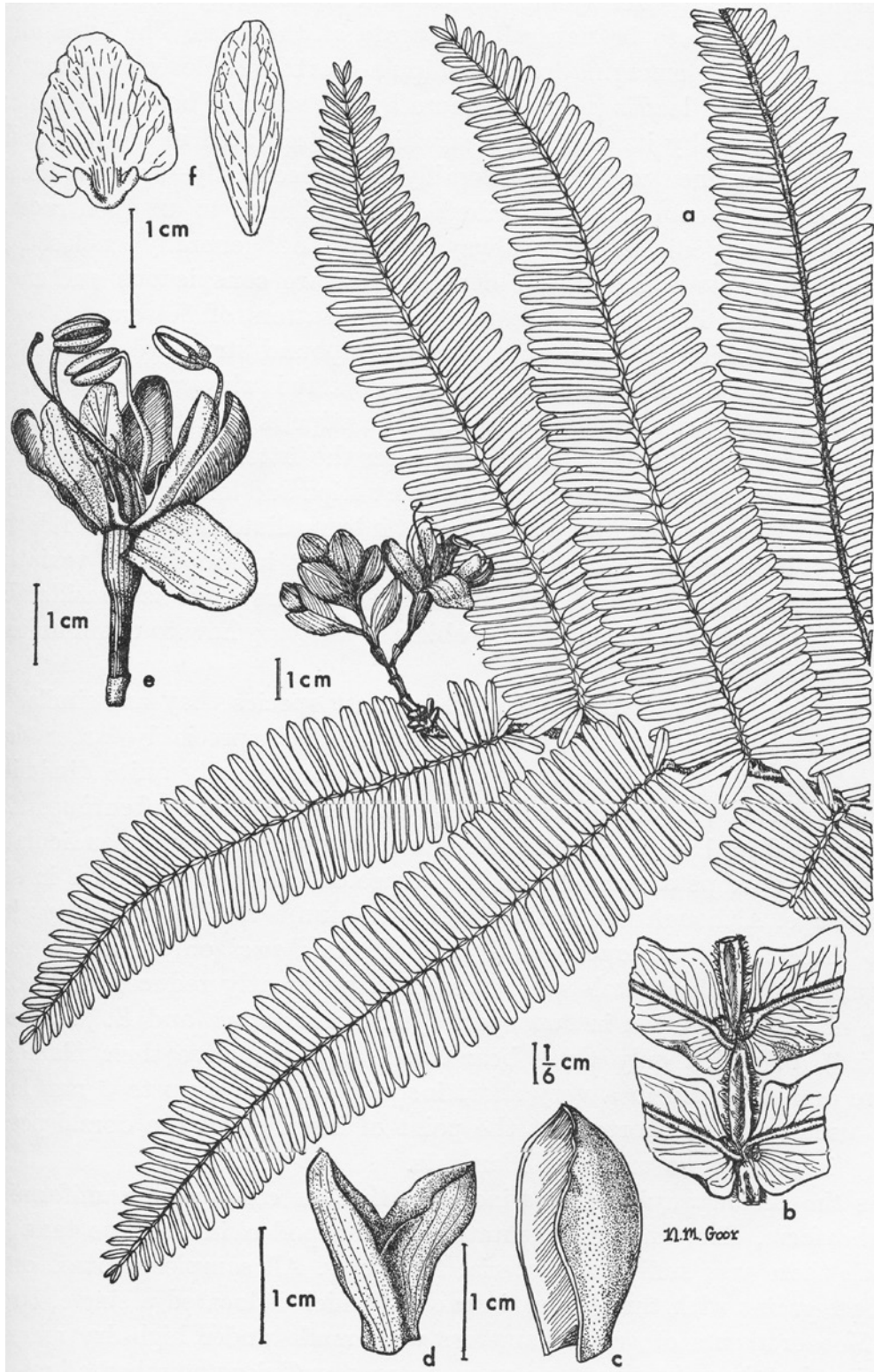


FIGURE 19. *Paloue leiogyne* (Ducke) Redden. Reproduced from Cowan (1976): a, habit; b, portion of leaf rachis; c, one bract; d, bracteoles; e, flower at anthesis with bracteoles removed; f, adaxial petal (left) and lateral or abaxial petal (right). All drawn from Maguire *et al.* 41952 by Nancy M. Goor.

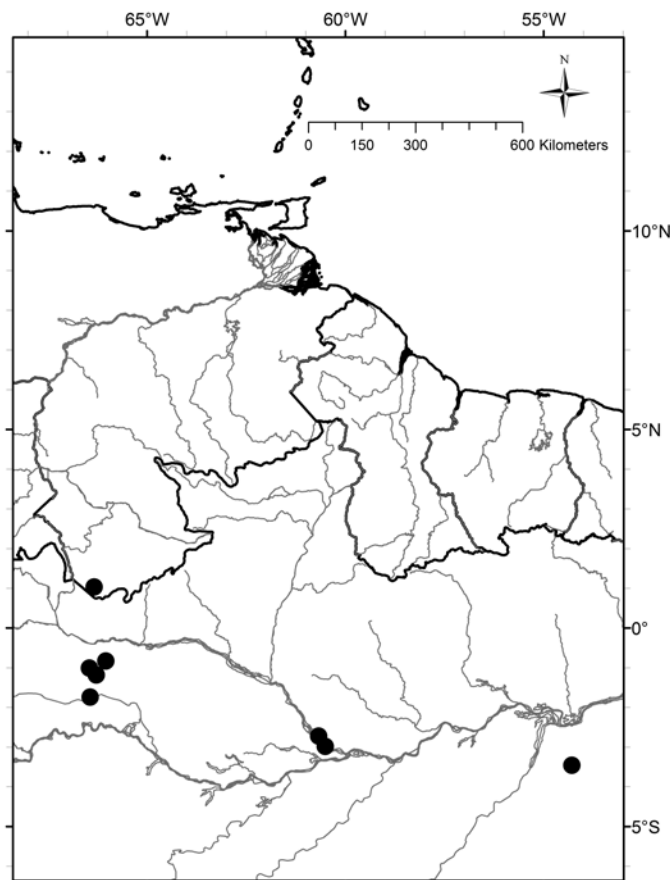


FIGURE 20. Geographic distribution of *Paloue leiogyne* (Ducke) Redden (dots) in Venezuela and Brazil.

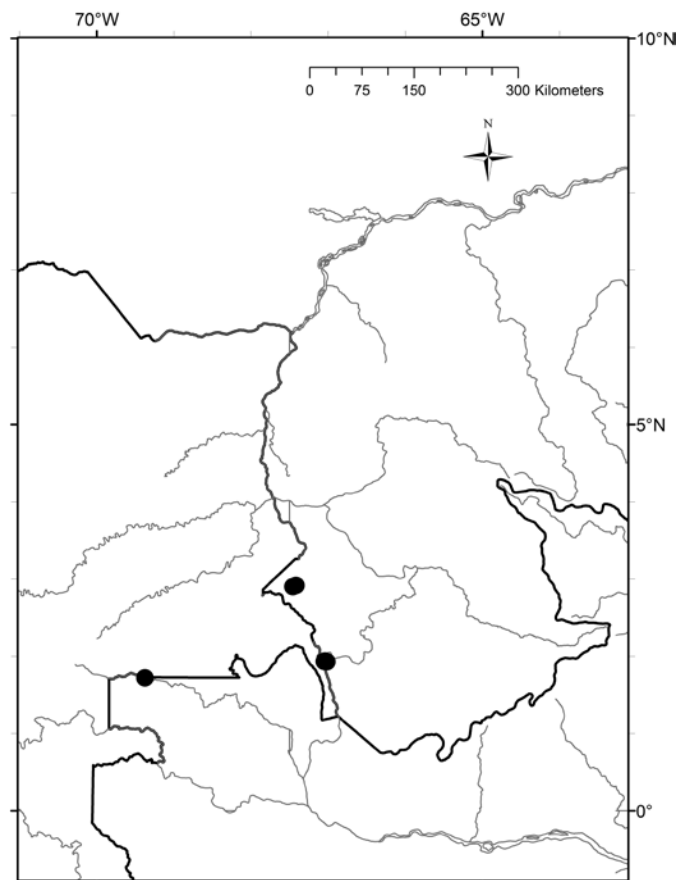


FIGURE 21. Geographic distribution of *Paloue macrostachya* (Benth.) Redden (dots) in Brazil and Venezuela.

FIGURES 21, 29B

Tree 10–15 m tall, branchlets glabrous. **Stipules** not seen. **Leaves** compound, alternate, paripinnate; petioles 9–14 mm long, terete, usually glabrous but occasionally minutely puberulous, rachis 14–28 cm long, terete, without wing or apical projections, glabrous or minutely puberulous overall or only at insertion of leaflets; **leaflets** 5–7 jugate, the petiolules 1.5–5 mm long, minutely puberulous, blades elliptic, 9.5–14 × 3.5–5 cm, the base attenuate, the upper side shorter, the apex abruptly acute to acuminate, glabrous on the upper surface, glabrous and microscopically dotted on lower surface. **Inflorescences** terminal racemes, 25–100 cm long, rachis glabrous; bracts 5–8.5 × 3.5–4.5 cm, glabrous, rigid-coriaceous, obovate, striate on the inner surface; bracteoles 5.0–5.5 × 1.5 cm, rigid-coriaceous; joined marginally for about ¾ of their length; pedicels glabrous, 11–22 mm long, longer and with a greater diameter in fruit. **Flowers**: hypanthium glabrous, woody, cylindrical, tapered basally, stipe 5–7 mm long, the tube 20–27 mm long and about 10 mm in diameter in flower, becoming about 40 mm long in fruit; sepals red, 5.5–6.0 ×

1.1–2.0 cm, more or less oblong, glabrous, the apex cucullate, the 3 petals 6.5–7.5 × 1.0–1.7 cm, glabrous, oblong, 2 petaloidia oblong, 15–17 × 6 mm; stamens 9, exserted, glabrous, the filaments about 4.5–7.5 cm long, joined basally for about 5 mm, the anthers linear, about 23 × 2 mm; ovary velvety. **Fruit** a legume, 22–28 × 5–6.5 cm, arcuate-oblong, velvety, the dorsal suture somewhat marginate, ca. 6–9-seeded.

DISTRIBUTION. Brazil: Amazonas; Venezuela: Amazonas.

PHENOLOGY. Collected in flower in November, February, March, and May, and in fruit in February, April, and May.

NOTES. *Paloue macrostachya* is a dominant tree in areas of white sands and black water in Venezuela. These areas are interspersed with areas of laterite soil, and the vegetation on the two types of soils is distinctly different. *Paloue macrostachya* only occurs on the white sands. After collecting Redden 3714, the stem was put in a bucket of water to preserve the specimen for photography. During the night a loud “pop” was heard, which was the sound of the dehiscing woody bracteoles. After bracteole dehiscence, the flower slowly emerged.

ADDITIONAL SPECIMENS EXAMINED. BRAZIL. AMAZONAS: Beira do Rio Icana, catinga alta, 12 May 1948 (fl.), *Black* 2654 (U!, US!); Rio Negro, alto Icana, vicinity, Serra Tunuhy, 15 May 1947 (fl.), *Fróes* 22282 (U!).

VENEZUELA. AMAZONAS: 3.5 km from Yavita along Yavita-Maroa Road (bearing 233°), 2°54'06"N, 67°27'27"W, 120 m, 19 Feb 1998 (fl., fr.), *Berry et al.* 6603 (MO!: 2 sheets, VEN); 3–5 km NE of San Carlos de Rio Negro, ca. 20 km S of confluence of Rio Negro and Brazo Casiquiare; 1°56'N, 67°03'W, 120 m, 1 May 1979 (fl.), *Liesner* 7128 (MO!); 3–5 km NE of San Carlos de Rio Negro, ca. 20 km S of confluence of Rio Negro and Brazo Casiquiare; 1°56'N, 67°03'W, 120 m, 4 May 1979 (fl., fr.), *Liesner* 7200 (MO!); Entre San Carlos de Rio Negro y El Solano, Departamento Río Negro, 11–17 Mar 1979 (fl.), *Marcantoni & Salcedo* 67-979 (US!); road between San Carlos and Solano, 1°55'48.8"N, 67°00'58.8"W, 101 m, 15 Feb 2005 (fl., imm. fr.), *Redden* 3714 (K!, NY!, PORT, US!, VEN); 7–9 km de Yavita hacia Pimichin, 2°55'N, 67°25–30'W, 125 m, 22 Apr 1970 (fr.), *Steyermark & Bunting* 102923 (US!, VEN!).

13. *Paloue paraensis* (Ducke) Redden comb. nov.

Elizabetha paraensis Ducke, Arch. Jard. Bot. Rio de Janeiro 3:102. 1922.

Type. Brazil. Pará: Cachoeira do Mangabal, Rio Tapajoz, 4 Sep 1916, A. Ducke 16449 (lectotype: MG, isolectotypes: G, P!, US!).

FIGURE 22

Large tree 16–30 m tall, 20 cm or more in diameter, the brachlets pilose and puberulous, the hairs more or less retrorse. **Stipules** 42–60 × 10–22 mm, oblanceolate, slightly bifid, thin, puberulous externally, glabrous within, caducous. **Leaves** compound, alternate, paripinnate; petioles 2.5–3 mm long, pilose and puberulous, rachis 9–16.5 cm long, pilosulose, narrowly winged, wing puberulous or glabrous with apical projections at leaflet insertions; **leaflets** sessile, 32–38-jugate, 17–27 × 3–5.5 mm, oblong, base inequilateral, apex truncate to rounded, retuse and mucronulate, the mucro caducous, glabrous except for a pilose patch at the base of one side of the salient midvein, venules sub-obscure. **Inflorescences** terminal, sessile, compact racemes, 4–8 cm long, the axis strigose-sericeous; bracts caducous, oval, cucullate, 15–27 × 8–15 mm, puberulous externally, glabrous within, ciliate; bracteoles 14–19 mm long, united marginally into a tube enclosing the flower bud, puberulous externally; pedicels 2–4 mm long, puberulous, hairs often retrorse. **Flowers:** hypanthium puberulous or pilosulose, stipe (6–)10–15 mm long, the cupulate tube 3–7 mm wide and deep; sepals white, the dorsal one 11–17 × 8–12 mm, oblong-oval to rotund, the other 4 oblong, 12–18 × 5–9 mm, minutely puberulous externally; petals 5, white, retuse and ciliate apically, the dorsal one triangular-ovate, 10–18 × 6–8 mm, the other four 12–18 × 4–7 mm; stamens 9, white, 3 fertile, the filaments connate in a short tube except at the adaxial petal, those of the fertile stamens 50–58 × 1.5–2 mm, glabrous, the staminodia ca. 15 mm long, glabrous; ovary narrowly oblong, velutinous, 7–10 × 1.3 mm, 8-ovulate, the stipe 5–10 mm long,

sub-sigmoid, glabrous except puberulous apically, style 34–40 mm long, glabrous, stigma capitate. **Fruit** a legume, 8–11 × 2.5–4 cm, ca. 4–6-seeded.

DISTRIBUTION. French Guiana; Suriname; Brazil: Amapá, Pará.

PHENOLOGY. Collected in flower in September, October, and January and in fruit in January.

NOTE. *Ducke* 16449, a sterile collection, was the one chosen as the type of *P. paraensis* by Ducke (1934) in his later reconsideration of his own species (Cowan, 1976).

ADDITIONAL SPECIMENS EXAMINED. FRENCH GUIANA. CAYENNE: Trois Sauts, sous le village Pina, 11 Jan 1975 (fl., imm. fr.), *Grenand* 649 (US!).

SURINAME. BROKOPONDO: Nassau Mountains, Marowijne River, 525 m, 4 Mar 1955 (st.), *Maguire* 40752 (NY!).

BRAZIL. AMAPÁ: Rio Araguari, vicinity camp 12, 1°11'N, 52°08'W, 29 Sep 1961 (st.), *Pires et al.* 51310 (NY!, US!); **PARÁ:** Belém in horto Musei culta, e regione medii fluminis Tapajoz (Igarape das Pedras, prope cataractam Furnas) introducta,

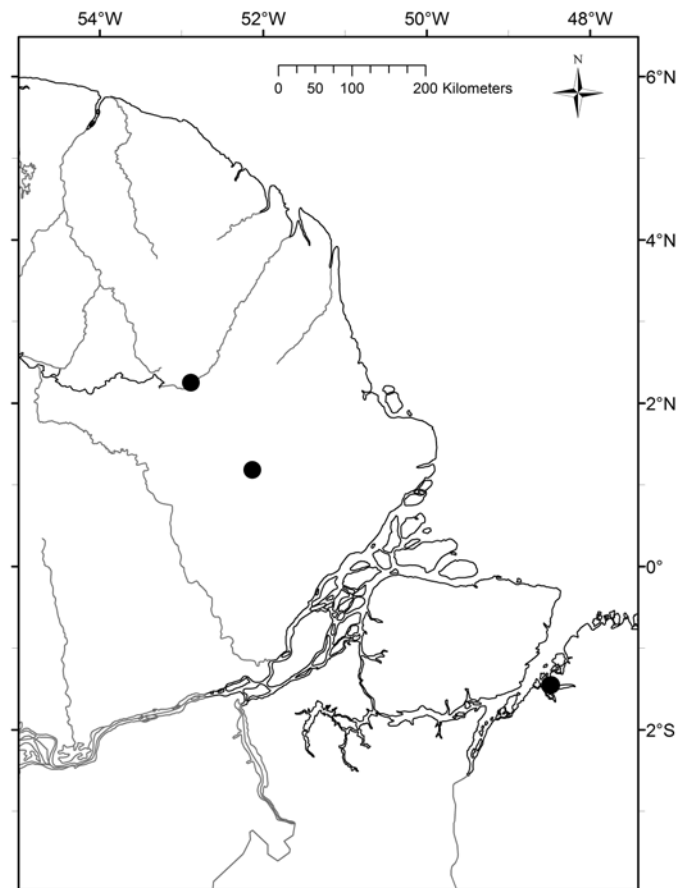


FIGURE 22. Geographic distribution of *Paloue paraensis* (Ducke) Redden (dots) in Brazil.

21 Oct 1940 (fl.), *Ducke* 591 (MO!, NY!, US!); Rio Itapacura afl. do Tapajoz, 24 Jan 1933 (st.), *Ducke* 23723 (K!, NY!); upper Cupary River, plateau between the Xingu and Tapajos Rivers, Sep 1931 (fl.), *Krukoff* 1167 (K!, NY!); upper Cupary River, plateau between the Xingu and Tapajos Rivers, Sep 1931 (st.), *Krukoff* 1184 (K!, NY!); Belem do Pará, Museu Goeldi, culta proced. Igarapi dos pedras prope Furnas, R. Tapajoz, 1936 (jv. fr.), *Sigueira* 34958 (K!, US!); Jardim Botânico Rio de Janeiro, 7 May 1984 (st.), *de Lima* 2156A (K!, NY!).

14. *Paloue princeps* (M. R. Schomb. ex Benth.) Redden comb. nov.

Elizabetha princeps M. R. Schomb. ex Benth., Hook. Jour. Bot. 2: 92. 1840. Type. Guyana. 1839 (fl., fr.). *R. Schomburgk s.n.* (holotype: K!; isotype: F!).

FIGURE 23

Medium-sized to large tree (8–)20–35(–50) m tall, trunk (25–)40–50 cm in diameter, the outer bark greenish gray, smooth, thin, the inner bark brown, branchlets pilose or pilosulose, glabrescent. **Stipules** caducous, (3.5–)4.5–9.5 × (1.1–)1.5–3.0 cm, narrowly to broadly oblanceolate, the apex rounded, entire, thin, densely puberulous on the outer surface, glabrous on the inner surface, often ciliolate on margins. **Leaves** compound, alternate, paripinnate, oblong–lanceolate; the petioles 1.5–4 mm long, terete, more or less pilosulose, occasionally glabrous, rachis (12–)20–25(–30.5) cm long, pilosulose, the narrow wing erect with apical projections at leaflet insertions, usually glabrous; **leaflets** (27–)32–40(–51)-jugate, sessile, narrowly oblong, (18–)30–47 × (3–)5–7(–8) mm, base inequilateral to obtuse, apex tapering but rounded to obtuse, glabrous except for a patch of long hairs near the base on one side of the midvein on the leaflet undersurface, often completely glabrous at maturity, micro-punctate on the lower surface, the venation sub-obscure or the midvein more or less salient. **Inflorescences** dense, strobiliform racemes, sessile, axillary or terminal, 6–11 (–15) cm long, the rachis densely pilose or strigose; bracts usually sub-rotund, infrequently oval or broadly ovate, (25–)28–3 × (22–)24–35 mm, cucullate, rounded to obtuse apically, coriaceous, pilose or pilosulose externally, glabrous within, ciliate or ciliolate; bracteoles united for about 2/3 of their length, acute, (20–)23–30 mm long, united marginally into a tube enclosing the flower bud, externally pilose and pilosulose, the inner surfaces pilose, tomentose, or strigose, at least in part; pedicels (2–)5–8 mm long, pilosulose, pilose, or tomentose. **Flowers**: hypanthium pilosulose or pilose, stipe (9–)15–20 mm long, the tube cupular, 5–11 mm long, 7–11 mm in diameter; sepals 4, white to cream-colored, 13–24 × 4–15 mm (the dorsal one broader), elliptic–oblong, oval or oblong, pilosulose externally, glabrous within; petals 5, white, except for the extreme base, which is red, the dorsal one triangular-ovate, the apex ciliate, usually emarginate, base obtuse to cordate, 1.2–2.0(–2.4) × 0.9–1.5(–2.4) cm, the other 4 petals elliptic to oval or oblong, 1.8–2.7 × 0.5–1.2 cm, glabrous; stamens 9, red, 3 fertile ones

with larger filaments, 3.0–5.8 cm long, villose at least basally, the sterile filaments glabrous, slender, 1.0–2.5 cm long, united basally with the fertile ones in a glabrous tube 0.5–1.5 mm long, anthers narrowly elliptic to oblong, 7–11 × 1.5–3 mm, glabrous, pollen grains 57–60 μm in diameter, uniformly verruculose; the ovary narrowly oblong, velutinous, 7.5–16 × 2–3.5 mm, 10–12-ovulate, the stipe (2.5–)5–8(–10) mm long, glabrous, style 2.3–4.0 cm long, glabrous, stigma capitate. **Fruit** an oblong legume, sometimes slightly arcuate, flat, narrowly bi-alate dorsally, velutinous, 17–35 × 4–6.2 cm; ca. 4–6-seeded.

DISTRIBUTION. Guyana; French Guiana; Suriname; Brazil: Amazonas, Roraima; Venezuela: Amazonas.

PHENOLOGY. Flowering from September to May, fruiting from September to April and in August.

ADDITIONAL SPECIMENS EXAMINED. **VENEZUELA.** **AMAZONAS:** Atabapo, alto Rio Orinoco, bosques riberenos medios en la planicie alluvial, 30 km al SE de le Esmeralda, 19 Feb 1990 (fl.), *Aymard* 8029 (NY!); Atabapo, alto Rio Orinoco, bosques medios a altos sobre planicie alluvial, 35 km al SE de

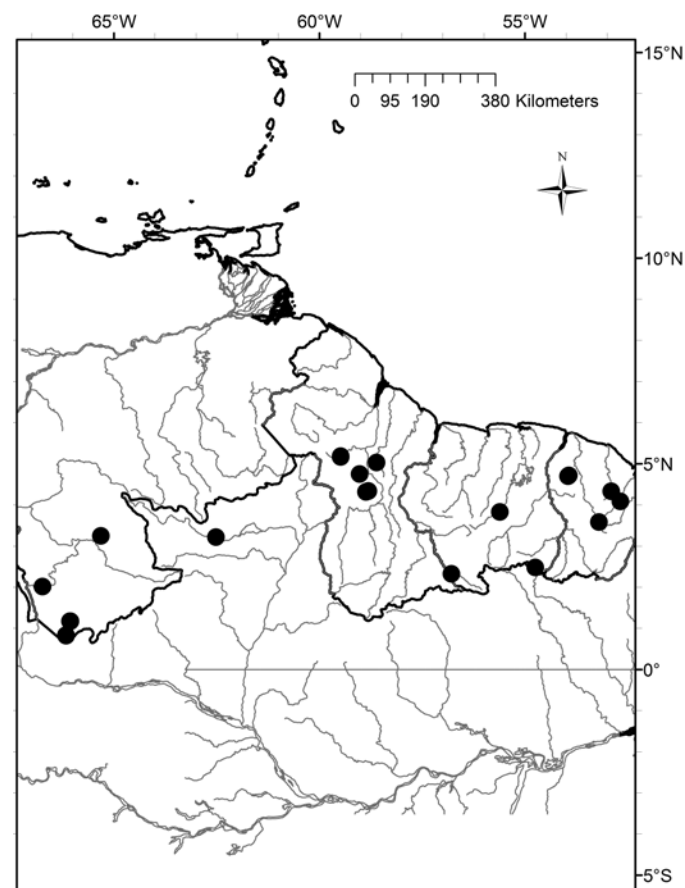


FIGURE 23. Geographic distribution of *Paloue princeps* (M. R. Schomb. ex Benth.) Redden (dots) across the Guiana Shield.

la Esmeralda, ca. 2°58'N, 65°21'W, 180 m, 16 Feb 1990 (st.), *Aymard & Delgado* 7887 (NY!); Rio Orinoco below Raudal y Salto El Tobogan, 2°14'N, 63°45'W, 370 m, 21 Nov 1989 (fl.), *Berry* 4797 (K!, MO!); Rio Mawarinuma, Neblina Base Camp, 0°50'N, 66°10'W, 140 m, 9 Feb 1985 (fr.), *Boom & Weitzman* 5718 (NY!, U!); Ugueto, 30 Sep 1951 (fl., fr.), *Croizat* 766 (NY!); without precise locality, 1951 (fl.), *Croizat* 925 (NY!); Atabapo, Salto Yureba, Cerro Yureba, lower Ventuari, 4°03'N, 66°01'W, 350 m, 15–16 Mar 1985 (fl., jv. fr.), *Liesner* 18701 (MO!); Orillas rio Tucano, aflueute del Cauaburi, 100 m, 16 Apr 1964 (fr.), *Ewel* 104 (NY!); Cerro de la Neblina, Rio Yatua, 100–140 m, 7–8 Dec 1953 (st.), *Maguire et al.* 36736 (F!, NY!, US!); Cerro de la Neblina, Río Yatua, 140 m, 14 Dec 1953 (fl.), *Maguire et al.* 36796 (F!, K!, NY!, US!); 1.5 km S of base camp, SE side of Cerro de la Neblina, 00°49'20"N, 66°09'45"W, 150 m, 12 Feb 1985 (fr.), *Nee* 30831 (NY!); Rio Negro, along Rio Baria (=Rio Mawarinuma), just upstream from base camp on SW side of Cerro de la Neblina, 00°49'50"N, 66°09'40"W, 140 m, 27 Jan 1985 (fr.), *Nee* 30573 (NY!); Rio Yatuá, 1°10'30.3"N, 66°3'25.8"W, 105 m, 4 Feb 2005 (fr.), *Redden* 3536 (PORT!, US!, VEN!); Missão Salesiana de Maturaca, R. Maturaca, afl. do R. Cauaburi, without date (st.), *Souza s.n.* (NY!); Rio Metacuni, Selvas ribereñas abajo del Salto Wãnitima, en el Caño Guacaguaca, 180–200 m, 21 Jan 1990 (fr.), *Stergios & Velazco* 14003 (MO!, NY!, PORT!); Rio Metacuni, Tepuy-Altiplanicie Sedukerawa y areas adyacentes, 3°15'N, 64°56'W, 210–650 m, 26 Jan 1990 (fr.), *Stergios & Velazco* 14256 (MO!, PORT!); Mission Rio Mavaca, 1°58'N, 65°06'W, 200–230 m, 5 Feb 1991 (fr.), *Stergios & Yanez* 15203 (NY!, PORT!); Rio Marawinuma, vicinity of Base Camp, 0°50'N, 66°10'W, 140 m, 19 Apr 1984, *Thomas & Plowman* 3151 (NY!); along Rio Marawinuma, SE of base camp, 0°50'N, 66°09'W, 140 m, 30 Apr 1984, *Thomas & Samuels* 3290 (NY!); Lower Rio Guainia, 100 m, 1942 (st.), *Williams* 14790 (F!, G, NY!, US!).

GUYANA. POTARO-SIPARUNI: Iwokrama Rainforest Reserve, Iwokrama Mts., 0–1 km SE of camp at bottom of gorge, 4°20'N, 58°48'W, 75–150 m, 24 Mar 1997 (fr.), *Clarke* 4202 (BRG!, NY!, US!); Iwokrama Mts., base camp, 4.6 km E of Georgetown–Lethem Road, Plot 1-1, 04°20'N, 58°48'W, 70–150 m, 22 Nov 1995 (st.), *Hoffman* 4877 (BRG!, NY!, US); Iwokrama Rainforest Reserve, Pakatau Falls area, old trail to Mahdia, 4°45'9"N, 59°1'21.2"W, 65 m, 30 Oct 2002 (st.), *Redden* 1104 (BRG!, K!, MO!, NY!, US!); Upper Takutu, cut line GH from Lethem to Kurupukari Road to Iwokrama Mts., 4°19'02.77"N, 58°52'01.61"W, ca. 200 m, 30 Apr 1992 (st.), *Pennington & Johnson* 431 (K!); U. Demerara-Berbice Region. Purburi Forest Reserve Camp, 5°1'48.5"N, 58°36'41.9"W, 55 m, 23 Oct 2002 (fr.), *Redden et al.* 1080 (K!).

SURINAME. BROKOPONO: In montibus, qui docuntur Nasau, 19 Mar 1949, *Lanjouw & Lindeman* 2851 (NY!). **SIPALWINI:** Tumuc Humac Mts., Talouakem, second base camp, 2°29'N, 54°45'W, 300 m, 15 Aug 1993 (fr.), *Acevedo-Rodriguez* 6044 (NY!); along Ulemari River, ca. 150 km upstream from

its confluence with Litani River, 2°46'5"N, 54°51'15"W, 175 m, 19 Apr 1998 (fr.), *Hammel et al.* 21584 (K!, MO!, US!); Upper Suriname River, Gran Lio, Awarradan vicinity, 1.5 km at 170° from tourist camp island (access from Sandu Matu Creek trailhead, 3°50'00.57"N, 55°36'51.98"W) (B. Hoffman 1.0 ha research plot ST2), 3°49'56.14"N, 55°36'39.53"W, 22 Nov 2005 (st.), *Hoffman* 6635 (US!); same locality, 19 Mar 2006 (st.), *Hoffman* 6794 (US!); Wilhelmina Gebergte, 1.5 km southeast of Juliana Top, near headwaters of West Rivier, 3°36'–3°41'N, 56°30'–56°34'W, 750 m, 26 Aug 1963 (fr.), *Irwin et al.* 55072 (NY!, U!).

FRENCH GUIANA. CAYENNE: Saut Parasol-Bassin du Sinnamary, 4°20'N, 52°54'W, 65 m, 11 Jan 1992 (fl.), *Cremers* 7323 (AAU, B, BM!, BR, CAY!, G, K!, MO!, NY!, P, U!, US!). **SAINT LAURENT DU MARONI:** Saül, Monts La Fumée, 3°37'N, 53°12'W, 200–400 m, 9 Oct 1982 (st.), *Boom & Mori* 1932 (NY!); Saül, Monts La Fumée, 3°37'N, 53°12'W, 200–400 m, 9 Oct 1982 (st.), *Boom & Mori* 1940 (NY!); Saül, Monts La Fumée, 3°37'N, 53°12'W, 200–400 m, 9 Oct 1982 (st.), *Boom & Mori* 1950 (NY!); Saül, Monts La Fumée, 3°37'N, 53°12'W, 200–400 m, 9 Oct 1982 (st.), *Boom & Mori* 1953 (NY!); Saül, Monts La Fumée, 3°37'N, 53°12'W, 200–400 m, 9 Oct 1982 (st.), *Boom & Mori* 1958 (NY!); Saül, Monts La Fumée, 3°37'N, 53°12'W, 200–400 m, 9 Oct 1982 (st.), *Boom & Mori* 1960 (NY!); Saut Parasol, Bassin du Sinnamary, 4°20'N, 52°54'W, 65 m, 11 Jan 1992 (fl.), *Hoff* 7323 (K!); Saül and vicinity, forest camp ca. 10 km ESE from Eaux Claires, 3°37'N, 53°12'W, 314 m, 4 Sep 1994 (fl.), *Mori et al.* 23777 (NY!); Nouragues Field Station and vicinity between Camp Inselberg and Saut Pararé (all collections made from 1,500–3,000 m S of Camp Inselberg), 4°05.289'N, 52°40.774'W, 23 Feb 2002 (fr.), *Mori et al.* 25433 (K!, NY!).

BRAZIL. RORAIMA: SEMA Ecological Reserve, Ilha de Maracá, Rio Puruí, 3°13'N, 62°31'W, 25 May 1987 (fl.), *Miliken & Bowles* 290 (K!, NY!); Posto Mucajai, Rio Mucajai, vicinity of Mucajai airstrip, 13 Mar 1971 (fr.), *Prance et al.* 10936 (NY!, U!, US!); Indian trail from Surucucu near Maitá Indian village, 3°20'N, 63°24'W, 14 Feb 1971 (fr.), *Prance et al.* 10517 (K!, NY!, U!); Indian trail from Surucucu, between Maitá Indian village, 3°20'N, 63°24'W, and Paramiteri Indian village, 3°25'N, 63°03'W, 20 m, 20 Feb 1971 (fr.), *Prance et al.* 10639 (K!, NY!, U!); Rio Cauaburi, between Anta and Palmito camps, 600–1,300 m, 16 Dec 1965 (fl.), *Silva & Brazão* 60669 (K!, NY!). **AMAZONAS:** Serras do Jacamin, Rio Negro, 5 Dec 1936 (fl.), *Ducke* 302 (F!, MAD, NY!), 5 Dec 1936 (fl., fr.), *Ducke* 29025 (K, 2 sheets!); Silva in declivibus montium Jacamin, Rio Negro super Santa Izabel, 5 Dec 1936 (fl.), *Ducke* 328 (NY!); Rio Curicuriary, 17 Nov 1936 (fl.), *Ducke* 34962 (K!).

15. *Paloue riparia* Pulle, Enum. Vasc. Pl. Surinam 212, pl. 10. 1906. Type. Guyana (as British Guiana). Saramacca River, near Janbasigado, Jan 1903 (fl.), *A. Pulle* 154 (holotype: U!; isotype: U!).

FIGURES 24, 25, 30B

Small to medium-sized tree, 7–10 m tall, branchlets gray-brown, glabrescent. **Stipules** caducous, not seen. **Leaves** simple, alternate, entire, ovate to oblong, 9–16 × 2.5–7 cm, apex acuminate, base rounded to acute with crater-like glands at the base of the lamina, glabrous; petioles 3–7 mm long. **Inflorescences** umbel-like, terminal racemes, 7–12 cm long, minutely puberulous or glabrate; bracts orbiculate, 5 mm long, caducous; bracteoles connate, 5 mm long, bilobed, rounded, persistent; pedicels 7–12 mm long, angular. **Flowers**: hypanthium 15 mm long including the stipe; sepals deep red, 9–11 × 6 mm, rounded at the apex, reflexed; petals 5, red, largest petal 5–7 × 3 mm, the other 4 petals very small, 1–3 × ca. 1 mm, margins pilose; stamens 9, red, filaments 5–6 cm long, connate unequally to form a tube, long-pilose; anthers oblong, glabrous, 5 mm long, , ovary 1 cm long, glabrous, style 2 cm long, stigma capitate. **Fruit** a sub-falcate legume, 11–16 × 2.5–4 cm, stipe to 2.4 cm long and 1–2 mm thick, glabrous, apex obliquely acuminate, ca. 6–8-seeded.

DISTRIBUTION. Guyana, French Guiana, Suriname.

PHENOLOGY. Flowering from September to April, fruiting from September to June.

NOTES. This species can be distinguished from the others in the genus by the small bracteoles and flowers and the glabrous anthers and gynoecium. The flowers have only one large petal and four small ones.

On numerous occasions, hummingbirds were observed feeding in the flowers of this species. The cup-shaped hypanthium was filled with liquid. Small holes at the base of the hypanthium also were observed, which may have been produced by “nectar-robbing” birds. Comparable small holes have not been observed on herbarium specimens.

ADDITIONAL SPECIMENS EXAMINED. GUYANA.

CUYUNI-MAZARUNI: Upper Mazarooni, *Appun*, 1702 (K!); *Appun*, 263 (K!); Takutu Creek to Puruni River, Mazaruni River, 8 Dec 1944 (fl., im. fr.), *Fanshawe* 4912 (K, 2 sheets!, NY!, U!); *Fanshawe* 4881 (F!, K, 2 sheets!, NY!, U!); Eping River, *Lang* 413 (NY!); *Lang et al.* 292 (F!); *McDowell* 3758 (BRG!, K!, MO!, NY!, US!); Kamakusa, *Lang et al.* 332 (F!, NY!, US!); Kuyuwini River, first base camp, 2°4'0.0"N, 59°09'32.8"W, 273 m, 21 Apr 2004 (fl., fr.), *Redden* 3106 (BRG!, K!, NY!, US!); Kamakusa, Mazaruni River, 5°56'10.3"N, 59°54'6.5"W, 64 m, 29 Sep 2004 (fl., fr.), *Redden* 3208 (BRG!, K!, NY!, US!); Mazaruni River, small rock and sand islands in river, 6°19'30.7"N, 58°42'20.3"W, 2 m, 18 Oct 2004 (fl.), *Redden* 3314 (BRG!, K!, NY!, U!, US!); Mazaruni River, 0.22 mi E of base camp, 5°53'1.2"N, 59°52'51.9"W, 89 m, 4 Oct 2004 (fl.), *Redden* 3229 (BRG!, K!, NY!, U!, US!); Mazaruni River, 0.67 mi SW of base camp, 5°48'46.4"N, 59°35'7.8"W, 64 m, 6 Oct 2004 (fl., fr.), *Redden* 3233 (BRG!, K!, NY!, U!, US!); Mazaruni River, unnamed falls (possibly Carin Crow Falls) 0.31 mi W of base camp, 5°57'17.1"N, 59°18'48.1"W, 58 m, 9 Oct 2004 (fl., imm. fr.), *Redden* 3263 (BRG!, K!, NY!, U!, US!); Mazaruni River,

small islands along river, 1.34 mi E of base camp, 5°59'52.6"N, 59°12'44.4"W, 63 m, 11 Oct 2004 (fl.), *Redden* 3281 (BRG!, K!, NY!, U!, US!); Mazaruni River, 0.78 mi NE of base camp, 6°6'34.4"N, 58°54'6.6"W, 21 m, 14 Oct 2004 (fl., imm. fr.), *Redden* 3305 (BRG!, K!, NY!, U!, US!). **POTARO-SIPARUNI:** Siparuni River, Pakutau Falls; 350 m along survey line due S from falls, 4°45'N, 59°1'W, 26 Apr 1992 (fr.), *Hoffman et al.* 1454 (BRG!, photo at K!, NY!, U!, US!); Iwokrama Rainforest Reserve, 5 km S of Siparuni River, Pakutau Plot 1, 4°45'17.2"N, 59°1'27.8"W, 8 Nov 1995 (st.), *Hoffman et al.* 4759 (BRG!, US!); Iwokrama, Siparuni River, Pakutau Falls, 5 km upstream *Mutchnick* 520 (BRG!, NY!, US!); main trail, swampy area, 0.3 mi E of White-water base camp, 4°43'54.2"N, 58°50'43.1"W, 115 m, 6 Nov 2002 (fl.), *Redden* 1161a (BRG!, K!, NY!, US!). **UPPER DEMERARA-BERBICE:** Mabura region, Central Demerara compartment, main road to Pibiri, 5°20'N, 58°30'W, 30 Nov 1992 (fl.), *Ek et al.* 614 (NY!, U!).

SURINAME. NICKERIE: Vicinity of Blanche Marie Waterfall on the Nickerie River, 4°45'30"N, 56°52'50"W, 50 m, 25 Jul 1995 (fr.), *Evans et al.* 2327 (MO!, RB-digital photo, US!); 19 Nov 1995 (fl.), *Evans et al.* 2446 (K!, MO!, US!). **SIPALIWINI:** N side of Kuruni Island, E of trail from airstrip to N branch of Kuruni River around island, ca. 30 airline km E of confluence on Corantijn River, 3°22'12"N, 57°20'36"W, 180 m, 8 Nov 1994 (fl.), *Evans et al.* 1922 (CAY!, K!, MO!, RB-digital photo, U!, US!); Coppename River, Raleigh Falls, Sept 1933 (fl., imm. fr.), *Lanjouw* 732 (L!, U!); Oever Coppename River boven Raleighvallen, 27 Nov 1954 (fl.), *Mennega* 548 (NY!, U!); Central Suriname Nature Reserve, Coppename River, Tonckens Falls, 4°25'21.7"N, 56°31'34.2"W, 60–90 m, 23 Feb 2004 (fr.) *Clarke* 11061 (US!); Central Suriname Nature Reserve, lower Rechter Coppename River, 4°18'9"N, 56°27'13.7"W, 60–90 m, 24 Feb 2004 (fr.), *Clarke* 11094 (US!); Central Suriname Nature Reserve, back channel of Coppename River at ‘Sidonkroetoe Sula’ (= sit down meeting rapids), 4°32'14.9"N, 56°30'52.5"W, 60–90 m, 9 Mar 2004 (imm. fr.), *Clarke* 11338 (US!); Central Suriname Nature Reserve, unnamed tributary of Coppename River, 200 m south of Driefoetoe Sula (= 3-ft rapids), 4°36'41.9"N, 56°30'24.6"W, 60–90 m, 10 Mar 2004 (imm. fr.), *Clarke* 11374 (US!); Upper Tapanahoni River, mouth of Paloemeu River, 11 Feb 1936 (fl.), *Rombouts* 674 (K!, U!, US!); Natuurreservaat Raleighvallen-Voltzberg op rivierover nabij GMD-kamp, 1 Nov 1972 (fl.), *Teunissen & Schulz* 13650 (K! image of sheet at U, NY!, U!). **SIPALIWINI:** Vicinity of camp on W bank of Zuid River, across river from (i.e., W and outside of) Central Suriname Nature Reserve, ca. 10 km straight-line distance SSE of Kayserberg Airstrip, 3°00'03"N, 56°27'03"W, 240 m, 14 Jun 2003 (fr.), *Evans et al.* 3516 (MO!, US!); large island in Litani River, 6 km upstream from its confluence with Marowini River to form Lawa River, 3°17'22"N, 54°06'52"W, 150 m, 1 Apr 1998 (fr.), *Hammel et al.* 21242 (K!, MO!, US!).



FIGURE 24. *Palouea riparia* Pulle. Reproduced from Pulle (1906: pl. 10, p. 212).

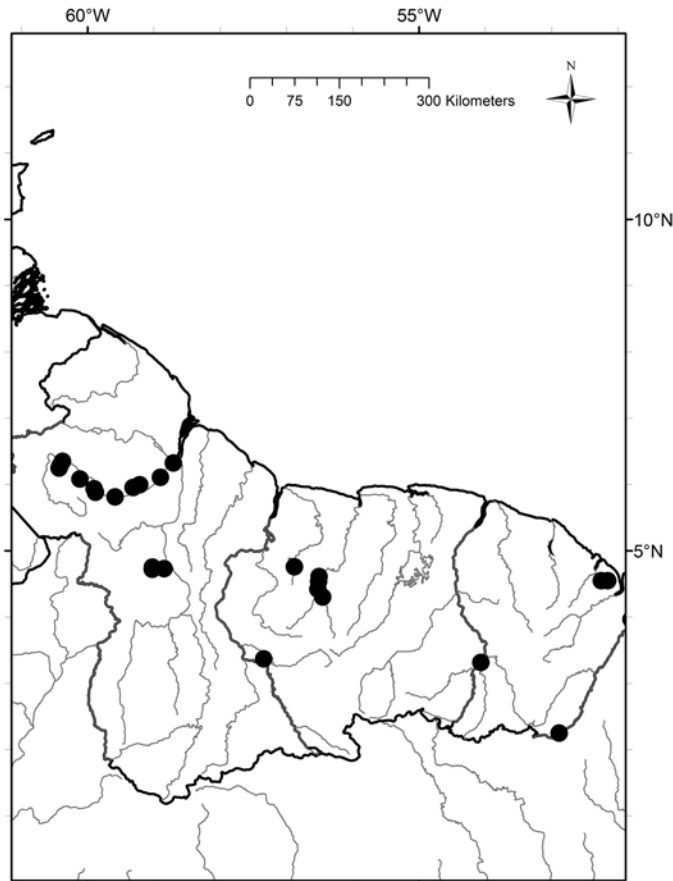


FIGURE 25. Geographic distribution of *Paloue riparia* Pulle (dots) across the Guiana Shield.

FRENCH GUIANA. CAYENNE: Montagne de Kaw sommet, 300 m, 24 Jan 2000 (fl.) *Bordenave & Raes* 5135 (CAY!, P, U!); Montagne de Kaw, 220–250 m, 12 Dec 1954 (fl.), *Cowan* 38737 (NY!, RB-digital photo, U!); *Cowan* 38814 (F!, K!, NY!, US!); CAMPOI: Trois Sauts, 13 May 1976 (fr.), *Grenand* 1285 (CAY!); Pasisit, bord de l'Oyapock, Trois Sauts, 6 Jan 1975 (fl., fr.), *Grenand* 633 (CAY!, US!).

16. *Paloue sandwithii* Redden. *Brittonia* (60) 3: 257–260. 2008. Type. Guyana. Potaro River below Waratuk Falls, 05°16'26.4"N, 59°22'46.7"W, 72 m, 5 Sep 2006 (fl.), *K. M. Redden* 4022 (holotype: BRG!; isotypes: CAY!, K!, MO!, NY!, US!).

FIGURES 26, 27, 29F

Small tree, 4–5 m tall, 20–25 cm in diameter, branchlets dark brown with waxy cuticle, glabrous. **Stipules** intrapetiolar, membranous, connate basally for at least 3 mm, distal portion

of stipule linear, 1.1–1.4 × 0.4–0.6 cm, caducous. **Leaves** simple, alternate, entire, coriaceous, dark green when fresh, elliptic-oblong, 18.5–32 × 7–11.5 cm, petiole terete, 0.5–0.7 cm in diameter, base of leaf acute-cuneate, a pair of crater-like glands at either side of the midvein at the base of the lamina, apex acuminate, 1.2–2 cm long, mucronate, venation brochidodromous, prominent especially on the lower surface. **Inflorescences** axillary and/or terminal, compact racemes, 0.5–1.5 cm long; bracts that subtend the inflorescence persistent, 5–6 × 4–5 mm, green, triangular, acute, strigulose abaxially and the margins ciliolate; floral bract 11 × 10 mm, free, ciliolate on margins but otherwise glabrous; bracteoles united almost to apex, enclosing bud except at apex, 7–9 × 6–8 mm, green, quadrangular, margins hyaline, membranous, glabrous; pedicel 4 × 2 mm, quadrangular, ca. 9 mm from insertion of bracteoles to base of hypanthium. **Flowers:** hypanthium cupular, 8 × 6 mm, glabrous; sepals 4, the adaxial sepal 12 mm long, the others 15–17 × 6–10 mm, green externally with red margins, red internally; petals 5, lateral petals 16–17 × 4–6 mm, when fresh red with white streaks, adaxial petal 18–19 × 7 mm, clawed, pale red, glabrous except for the ciliate apex, edges crispate; stamens 9, all fertile, 4–6 cm long, bright red, filaments pilose from base to apex, all united to form a tube approximately 1 mm long, anthers 7–8 × 2–3 mm, red, versatile, densely pilose along outer edge, elliptic, pollen exine verrucate; gynoecium glabrous, 9 × 2 mm at anthesis, stipe 2 mm long, glabrous, style 2.8–4 cm long, stigma capitate, minutely papillose. **Mature fruit** not seen.

DISTRIBUTION. Endemic to Guyana.

PHENOLOGY. Collected in flower in August and September; mature fruits unknown.

NOTES. *Paloue sandwithii* most resembles *P. guianensis* except it differs in having five subequal petals and large coriaceous leaves with prominent venation on their lower surfaces.

ADDITIONAL SPECIMENS EXAMINED. GUYANA. Below Kaieteur, Potaro River, Sep–Oct 1881, *Jenman* 893 (BRG!, K!); Kaieteur trail, 1 Aug 1958 (fl.), *V. Graham* 197 (K!).

17. *Paloue speciosa* (Ducke) Redden **comb. nov.**

Elizabetha speciosa Ducke, *Trop. Woods* 37: 21. 1934. Type. Brazil. Amazonas: Manaus, 2 Oct 1932 (fl., fr.), *A. Ducke* 23730 (holotype: RB; isotypes: F!, G, K!, MAD, NY!, P!, R, U!, US!).

FIGURE 28

Shrub or small tree to 6 m tall, branchlets pilosulose, glabrescent. **Stipules** caducous, thin, foliaceous, oblanceolate to obovate, 4.5 × 0.9–2.2 cm, the apex bifid, glabrous except near the apex puberulous. **Leaves** compound, alternate, paripinnate; petioles 2.5–4 mm long, erect, pilosulose, the rachis 10.5–17 cm long, narrowly winged with apical projections at each leaflet pair insertion, glabrous above, pilosulose below, rachis pilosulose beneath; **leaflets** sessile, glabrous except for the obscurely ciliolate margin, 22–34-jugate, narrowly oblong, somewhat

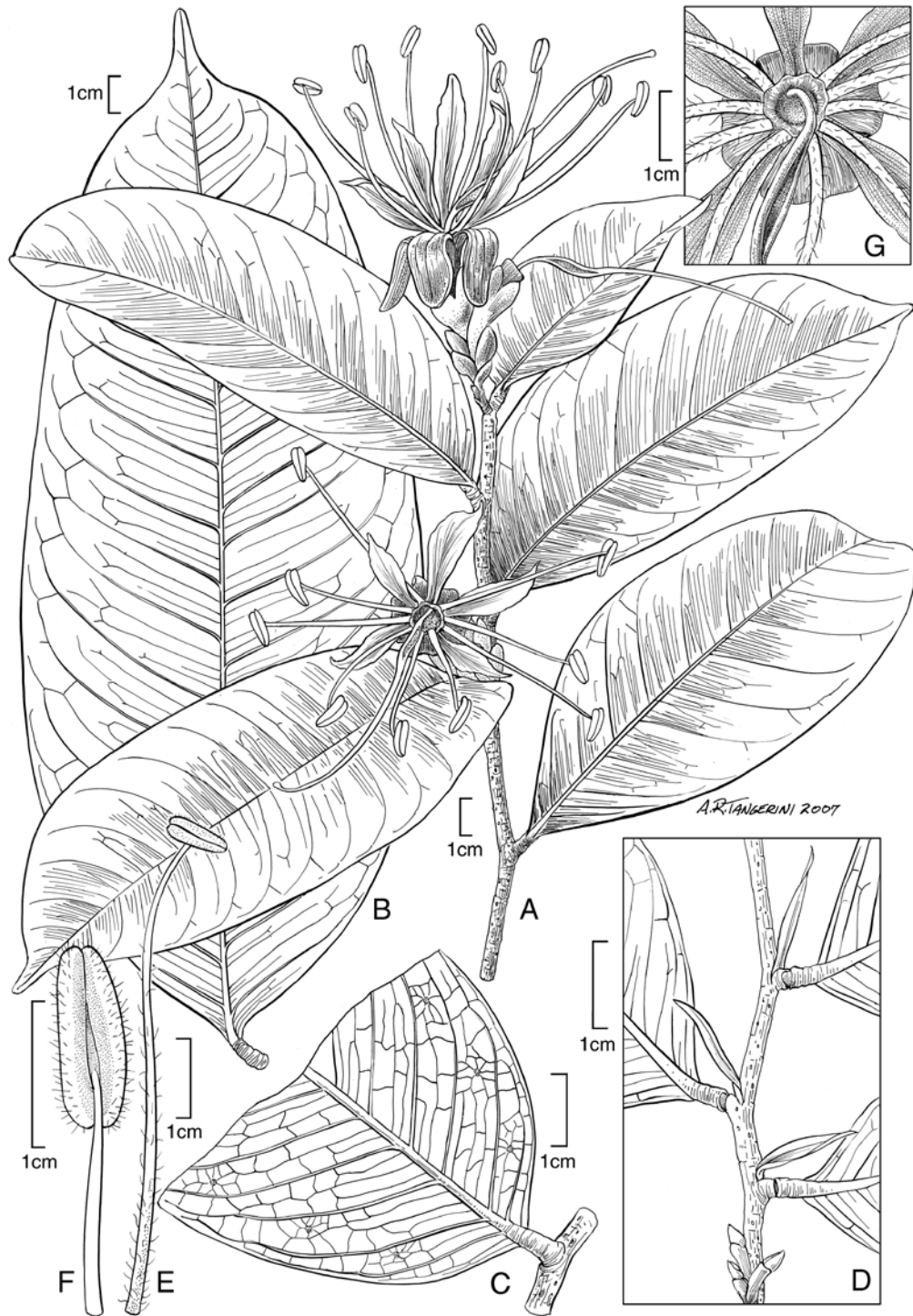


FIGURE 26. *Paloué sandwithii* Redden: A, flowering branch; B, adaxial surface of leaf showing detail of brochidodromous venation; C, paired crater-like glands on the base of the leaf lamina undersurface; D, pair of fused, intrapetiolar stipules; E, stamen filament trichomes; F, distal portion of stamen showing trichomes concentrated along the margins of the anther; G, ovary attachment on adaxial wall of hypanthium. All drawn from the holotype, *Redden 4022* (BRG), by Alice Tangerini, Smithsonian Institution.

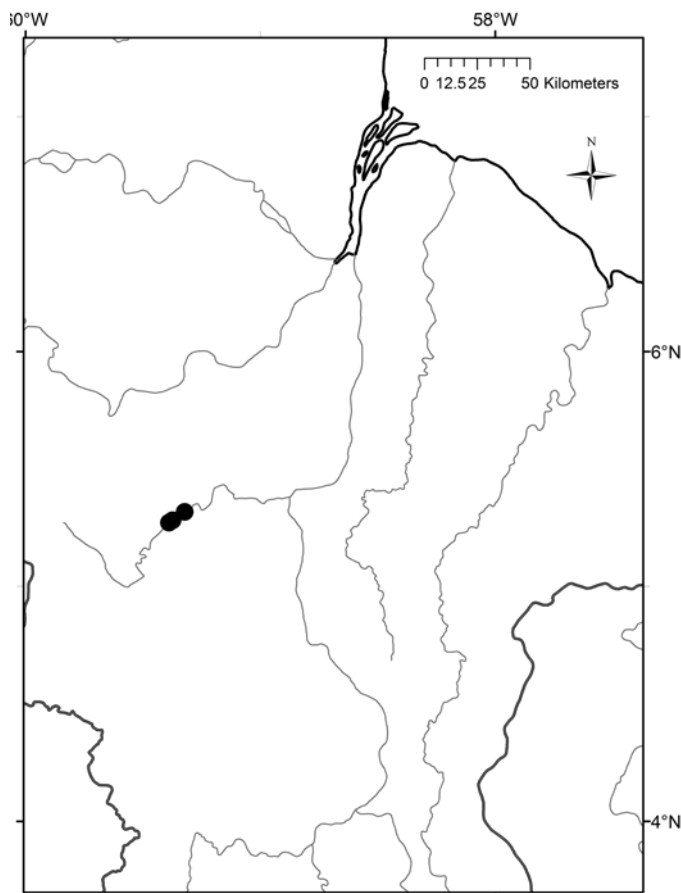


FIGURE 27. Geographic distribution of *Paloue sandwithii* Redden (dots) in Guyana.

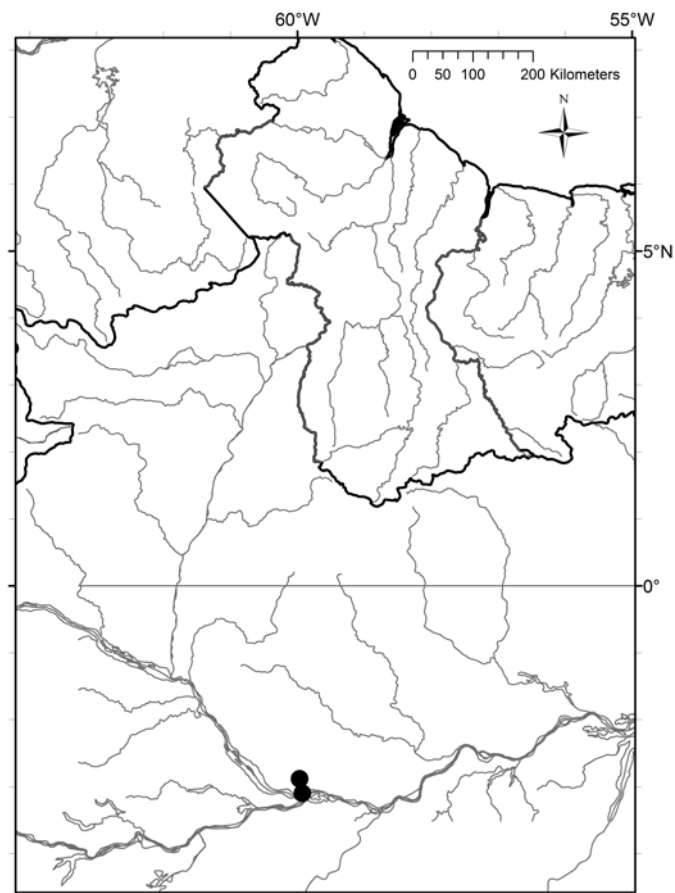


FIGURE 28. Geographic distribution of *Paloue speciosa* (Ducke) Redden (dots) in Brazil.

arcuate, 22–33 × 5–6 mm, base inequilateral, apex truncate, slightly retuse, minutely mucronulate, the mucro caducous, ciliate along upper margin near base of leaflets, the venation sub-obscure. **Inflorescences** sessile, terminal racemes, (2.2–)3.0–6.0 cm long, glabrous; bracts 10 × 6–9 mm, broadly ovate, glabrous, strongly cucullate; bracteoles 10–12 × 5–8 mm, united marginally into a tube enclosing the flower bud, glabrous, somewhat carinate, oval, obtuse; pedicels 2.5–5 mm long, glabrous, more or less compressed with the bracteole extending the length of the pedicel. **Flowers:** hypanthium glabrous, 9–16 mm long, including the stipe, 5–8 mm in diameter; sepals 4, 10–14 × 5–7 mm, glabrous, oblong, apex rounded; petals 5, red, more or less elliptic, 10–12 × 4–5 mm; stamens 9, red, 3 fertile, filaments of the 3 fertile ones 1.9–2.2 cm long, sparingly villose, the sterile ones reduced to minute staminodia, all filaments united basally into a short tube to 1 mm long; anthers narrowly elliptic, 6.5–9 × 1.5–2 mm; ovary narrowly oblong, velutinous, 6–12 × 2–3 mm, the stipe 1–1.5 mm long, glabrous except at extreme apex, style glabrous, 12–14 mm long, stigma capitate. **Fruit** a legume, 11–13 × 3–4 cm, 3–7-seeded.

DISTRIBUTION. Endemic to the state of Amazonas, Brazil.

PHENOLOGY. Collected in flower in October and in fruit in October and November.

ADDITIONAL SPECIMENS EXAMINED. **BRAZIL. AMAZONAS:** Manaus (Manoas), loco Estrada do Aleixo, silva non inundabili, 17 Oct 1935 (fl.), *Ducke* 48 (F!, K!, NY!, R, US!); Reserva Florestal Ducke, Manaus-Itacoatiara, km 26, 2°53'S, 59°58'W, 8 Nov 1995 (fr.), *Sothers et al.* 672 (K!, NY!).

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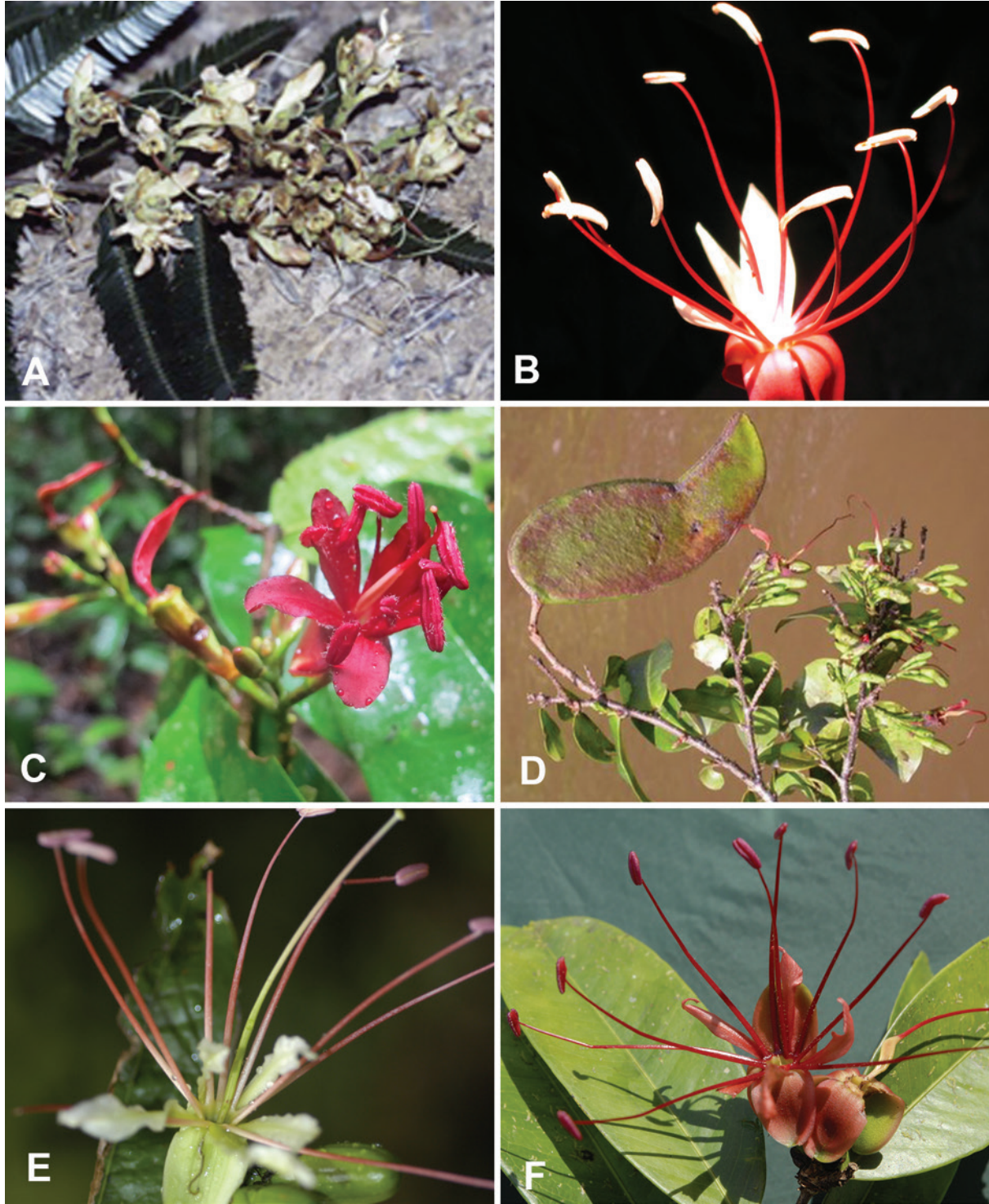


FIGURE 29. A. *Paloué durissima* (Ducke) Redden (photograph by K. Redden). B. *Paloué macrostachya* (Benth.) Redden (photograph by K. Redden). C. *Paloué brasiliensis* Ducke (photograph by B. Torke). D. *Paloué emarginata* (R. S. Cowan) Redden (photograph by B. Hoffman, for The Amazon Conservation Team). E. *Paloué guianensis* Aubl. (photograph by P. Acevedo, for Smithsonian Institution, Department of Botany). F. *Paloué sandwithii* Redden (photograph by K. Wurdack, for Smithsonian Institution, Department of Botany).

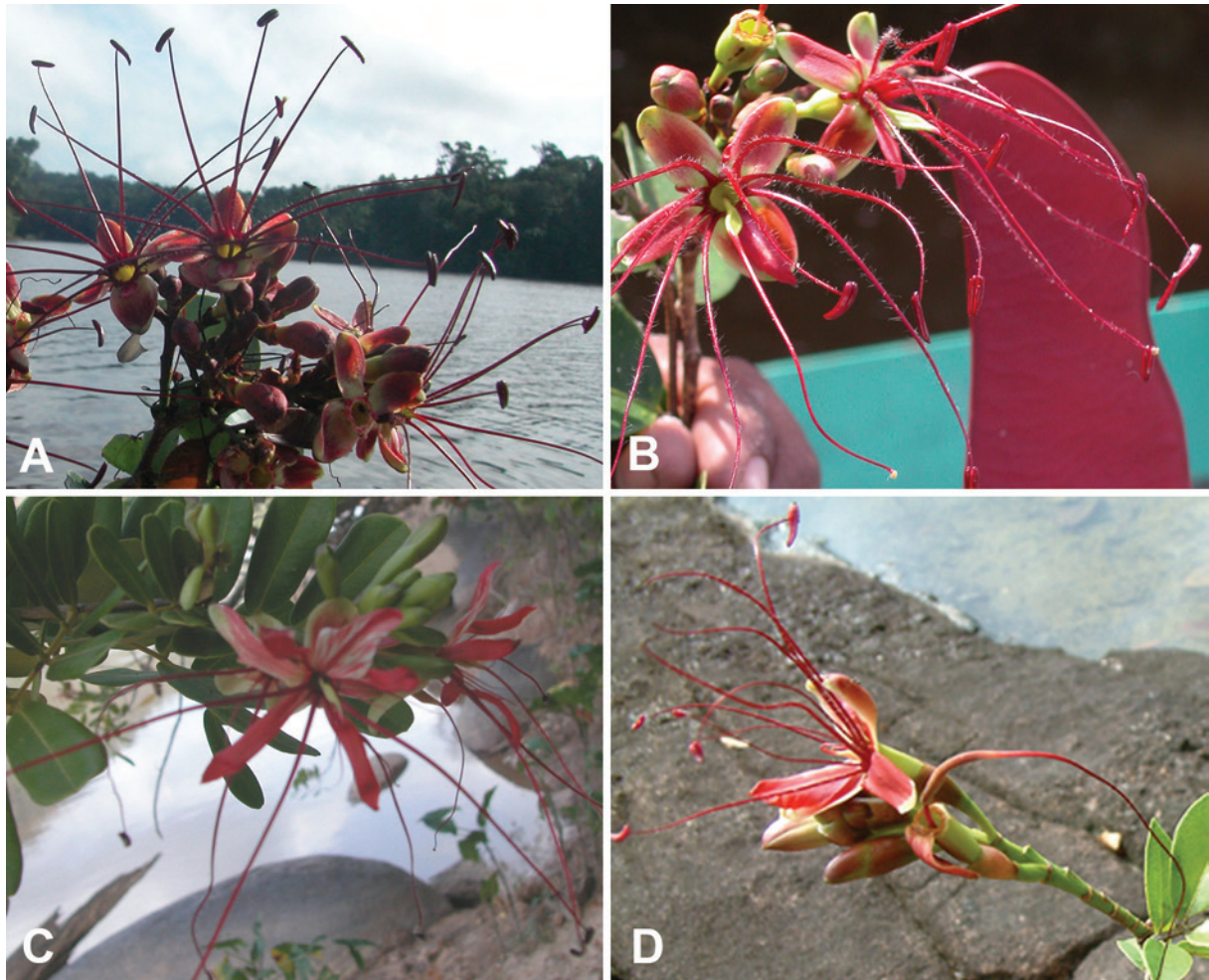


FIGURE 30. A. *Palouea induta* Sandwith subsp. *induta* (photograph by K. Redden). B. *Palouea riparia* Pulle (photograph by K. Redden). C. *Palouea coccinea* M. R. Schomb. ex Benth.) Redden (photograph by K. Redden). D. *Palouea grahamiae* (R. S. Cowan) Redden (photograph by T. McDowell).

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Appendix A:

Numerical List of Taxa

1. *P. bicolor*
 - 1a. *P. bicolor* var. *bicolor*
 - 1b. *P. bicolor* var. *velutina*
2. *P. brasiliensis*
3. *P. coccinea*
4. *P. duckei*
5. *P. durissima*
6. *P. emarginata*
7. *P. fanshawei*
8. *P. grahamiae*
9. *P. guianensis*
10. *P. induta*
 - 10a. *P. induta* subsp. *induta*
 - 10b. *P. induta* subsp. *glabra*
11. *P. leiogyne*
12. *P. macrostachya*
13. *P. paraensis*
14. *P. princeps*
15. *P. riparia*
16. *P. sandwithii*
17. *P. speciosa*

Appendix B:

List of Exsiccatae

The numbers within parentheses refer to the corresponding species number in the text and in the Numerical List of Taxa.

Acevedo-Rodriguez, P. 3266 (3), 6044 (14), 14648 (4)

Appun, C. F. 263 (15), 857 (3), 1702 (15)

Archer, W. A. 7626 (4)

Aublet, J. B. F. C. s.n. (9)

Aymard, G. 8029 (14)

Aymard, G. & Delgado, L. 7887 (14)

Beck, H. T. et al. 139 (5)

Berry, P. E. 4797 (14)

Berry, P. E. et al. 6603 (12)

Black, G. A. 2654 (12)

Boom, B. M. & Mori, S. 1932 (14), 1940 (14), 1950 (14), 1953 (14), 1958 (14), 1960 (14)

Boom, B. M. & Weitzman, A. L. 5718 (14)

Bordenave, B. N. 871 (9)

Bordenave, B. N. & Raes, N. 5135 (15)

Cid Ferreira, C. A. et al. 916 (6), 6795 (10b)

Clarke, D. C. 168 (3), 753 (5), 1327 (3), 2314 (3), 3010 (10a), 3207 (10a), 3289 (10a), 3408 (3), 3916 (3), 4202 (14), 5068 (3), 7687 (10a), 7790 (10a), 11061 (15), 11094 (15), 11338 (15), 11374 (15)

Cowan, R. S. 38737 (15), 38814 (15)

Cremers, G. 1328 (2), 5063 (2), 7323 (14), 9864 (9)

Croizat, L. 766 (14), 925 (14)

Davis, D. H. 815 (3)

de Lima, H. C. 2156A (13), 3298 (11)

Ducke, A. 48 (17), 113 (1b), 157 (11), 302 (14), 328 (14), 591 (13), 767 (4), 10882 (2), 10883 (2), 10984 (1b), 12245 (4), 16416 (2), 16449 (13), 16751 (1b), 20311 (4), 23285 (11), 23287 (1b), 23723 (13), 23726 (1a), 23727 (1b), 23729 (5), 23730 (17), 29025 (14), 34959 (1b), 34960 (1b), 34961 (1a), 34962 (14), *s.n.*, RB 10882 (2), *s.n.*, RB 108837 (2)

- Ek, R. C. *et al.* 614 (15), 1579 (9)
 Evans, R. E. *et al.* 1992 (15), 1998 (3), 2327 (15), 2446 (15), 3516 (15)
 Ewel, J. 104 (14)
- Fanshawe, D. B. 1044 (7), 1498 (7), 4881 (15), 4912 (15)
 Feuillet, C. 10065 (9)
 Fleury, M. & Pignal, M. 1691 (2)
 Fróes, R. L. 22282 (12), 25762 (9), 28100 (4)
- Gillespie, L. J. 1579 (3)
 Gonggryp, J. W. 3737 (9)
 Graham, V. 197 (16), 355 (8)
 Granville, J. J. de & Crozier F. 17222 (9)
 Grenand, P. 633 (15), 649 (13), 1285 (15), 1781 (9)
 Guppy, N. 513 (6), 172 (3)
- Hammel, B. *et al.* 21242 (15), 21584 (14)
 Henderson, A. & de Lima, J. R. do N. 604 (3)
 Henkel, T. W. 1969 (3), 3566 (3), 3662 (3), 5108 (10a)
 Hoff, M. 7211 (9), 7323 (14)
 Hoffman, B. 979 (3), 1069 (7), 1317 (3), 1814 (7), 1897 (7), 4877 (14), 5924 (6)
 Hoffman, B. *et al.* 1454 (15), 4759 (15), 6635 (14), 6794 (14)
 Hopkins, M. J. G. *et al.* 741 (3)
- Irwin, H. S. & Westra, L. Y. Th. 47476 (9)
 Irwin, H. S. *et al.* 55072 (14)
- Jansen-Jacobs, M. J. *et al.* 2273 (3), 2890 (3), 3731 (3)
 Jenman, G. S. 893 (16)
- Kappler 81 (9)
 Krukoff, B. A. 1167 (13), 1184 (13)
- Lang, H. 413 (15)
 Lang, H. *et al.* 292 (15), 332 (15)
 Lanjouw, J. 732 (15)
 Lanjouw, J. & Lindeman, J. C. 2034 (9), 2851 (14)
 Lewis, G. P. 1673 (3)
 Liesner, R. L. 17125 (11), 18701 (14), 7128 (12), 7200 (12)
 Lindeman, J. C. & de Roon, A. C. 874 (9)
 Lindeman, J. C. *et al.* 172 (3)
- Maguire, B. 40752 (13)
 Maguire, B. *et al.* 36705 (11), 36736 (14), 36796 (14), 41952 (11), 41986 (11), 42602 (11), 47045 (3)
 Marcano-Berti, L. & Salcedo, P. 67-979 (12)
 Matos, F. *et al.* 190 (10b)
 McDowell, T. 2305 (3), 2374 (3), 3758 (15), 3895 (7), 5744 (8)
 Mélinon, M. 18 (9), *s.n.* (9)
 Menega, A. M. V. 548 (15)
 Milliken, W. & Bowles, S. 290 (14), 389 (3)
 Mori, S. 24362 (3)
- Mori, S. *et al.* 23777 (14), 25433 (14), 27358 (9)
 Mutchnick, P. 520 (15), 563 (3), 672 (3), 758 (3), 987 (3)
 Myers, J. G. 3906 (3), 5801 (10a)
- Nascimento, O. C. *et al.* 148 (11), 198 (11)
 Nee, M. 30573 (14), 30831 (14)
- Oldeman, R. A. A. 1734 (2), 1835 (9), 2054 (9), 3030 (2)
 Oldeman, R. A. A. & Sastre, C. 77 (2), 115 (9), 163 (2)
- Pennington, R. T. & Johnson, I. RTP431 (14)
 Pennington, R. T. *et al.* 400 (5)
 Pires, J. M. 48561 (9)
 Pires, J. M. & Silva, N. T. 1954 (1b), 1984 (1b)
 Pires, J. M. *et al.* 51310 (13)
 Poncy, O. 183 (9), 1666 (9)
 Prance, G. T. & Ramos, J. F. 24350 (1b)
 Prance, G. T. *et al.* 9287 (3), 10517 (14), 10639 (14), 10936 (14)
 Prévost, M. F. 1717 (9)
 Pulle, A. 154 (15)
- Redden, K. M. 1080 (14), 1094 (3), 1104 (14), 1117 (3), 1161a (15), 1171 (5), 1178 (5), 1179 (3), 1180 (3), 1181 (3), 1722 (7), 1733 (7), 3018 (3), 3019 (3), 3031 (3), 3038 (3), 3045 (3), 3056 (3), 3057 (3), 3082 (3), 3088 (3), 3089 (3), 3090 (8), 3092 (10a), 3099 (10a), 3103 (10a), 3104 (8), 3106 (3), 3154 (10a), 3155 (10a), 3160 (10a), 3169 (10a), 3189 (10a), 3208 (15), 3229 (15), 3233 (15), 3263 (15), 3281 (15), 3297 (3), 3305 (15), 3307 (8), 3312 (3), 3314 (15), 3536 (14), 3714 (12), 4022 (16), 4648 (7), 5081 (3), 5429 (7), 5968 (9)
- Renner, S. S. 59 (11)
 Ribeiro, B. G. S. 15.286 (713) (11)
 Roberts, S. 2 (9)
 Rodrigues, W. A. 8730 (1b)
 Rodrigues, W. A. *et al.* 8461 (1b)
 Rombouts, H. E. 674 (15)
- Sabatier, D. & Prévost, M. F. 4674 (2)
 Sastre, C. *et al.* 6470 (9)
 Schomburgk, R. 251 (3), *s.n.* (3), *s.n.* (14)
 Schultes, R. E. 24578 (11)
 Siqueira, R. 34958 (13)
 Silva, N. T. & Brazão, U. 60669 (14)
 Silva, N. T. & Rosario, C. 3967 (2)
 Silva, N. T. *et al.* 152 (9)
 Smith, A. C. 2521 (3), 2652 (10a), 3031 (3)
 Sneathlidge, E., *s.n.*, H.A.M.P. 10.117 (2)
 Sothers, C. A. *et al.* 672 (17)
 Souza, R. *s.n.* (14)
 Spruce, R. 2671 (12)
 Stabel & Gonggryp 2861 (3)
 Stergios, B. & Velazco, J. 14003 (14), 14256 (14)

Sterigos, B. & Yanez, M. 15203 (14)

Steyermark, J. A. 104038 (11)

Steyermark, J. A. & Bunting, G. S. 102923 (12)

Teunissen, M. & Schulz, J. P. 13650 (15)

Tiwari, S. 488 (10a), 511 (10a), 517 (10a)

Thomas, W. W. & Plowman, T. 3151 (14)

Thomas, W. W. & Samuels, G. 3290 (14)

Ule, E. 8146 (3)

Versteeg 248 (10a)

Veth, B. & Manu 32 (9)

von Rohr, s.n. (9)

Williams, L. 14790 (14)

Wilson-Browne, S. J. WB136 (3)

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