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The *Rudgea hostmanniana* complex (Rubiaceae) in the Guiana Shield region

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Abstract

A taxonomic revision of the *Rudgea hostmanniana* complex in the Guiana shield region is presented. This group includes species with sheathing stipules bearing dorsal appendages, thick glabrous leaves lacking domatia, inflorescences thyrsoid to glomerulate but not regularly dichotomous, a calyx tube absent or very short, a corolla tube 2–7(–13) mm long, and fruits usually brownish when immature and turning red or orange at maturity. Eight species are recognized, among which *Rudgea billietiae*, endemic to Kaw Mountain in French Guiana, is newly described and illustrated; it is assessed as Endangered according to IUCN criteria. The other species are *R. bolivarensis*, *R. cornigera*, *R. coussareoides*, *R. hostmanniana*, *R. maypurensis*, *R. pungens*, and *R. tanaosepala*. A key to the species is presented, as well as a table summarising their diagnostic characters.

Keywords: Brazil, French Guiana, Guyana, Kaw Mountain, Neotropical Region, new species, Palicoureeae, Psychotrieae, Rubioideae, Suriname, Venezuela

Introduction

Rudgea Salisbury (1807: 327) is a Neotropical genus including at least 120 species (Zappi 2003) which are mostly shrubs or small trees of forest undergrowth. The genus has been placed either in tribe Psychotrieae (Schumann 1891, Robbrecht 1988, Andersson 2002, Lachenaud 2019) or in the segregate tribe Palicoureeae (Robbrecht & Manen 2006, Razafimandimbison *et al.* 2014). It is closely related to *Notopleura* (Bentham in Oersted 1853[“1852”]: 37) Bremekamp (1934: 289), which it resembles in having stipules provided with appendages, but differs from it by the non-succulent habit and usually terminal inflorescences (Taylor 2001). *Rudgea* is also related to *Palicourea* Aublet (1775: 172) *sensu lato* (including *Psychotria* subg. *Heteropsychotria* Steyermark 1972: 484) and *Eumachia* A.P. de Candolle (1830: 478), but these genera have stipules without appendages, and those of *Palicourea* are usually bifid, which is not the case in *Rudgea* (Taylor *et al.* 2015). Other characters of *Rudgea* (and of Psychotrieae in the broad sense) are a valvate corolla aestivation, presence of raphides, bilocular ovaries with a single erect ovule in each locule, and drupaceous fruits (Razafimandimbison *et al.* 2014).

The main centers of diversity of the genus are northwestern South America, and the Atlantic forest of Brazil (Zappi 2003). The taxonomy of the genus is poorly known in some parts of its range, particularly in the Guianas. Steyermark (1967) presented a conspectus of the species from Venezuela, the three Guianas and northern Brazil (a few species from outside this region were also included in his treatment), but no more recent regional revision is available. The checklist of Funk *et al.* (2007) mentions 18 *Rudgea* species from the three Guianas, among which two, *R. corniculata*

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Bentham (1850: 462) and *R. sandemanii* Sandwith (1949: 263) are actually misidentified (Lachenaud *et al*. 2022). On the other hand, two other species occurring in the Guianas, *R. coussareoides* (Standley 1931: 441) C.M.Taylor, Bruniera & Zappi (2015: 4) and *R. pungens* (Steyermark 1972: 677) C.M.Taylor, Bruniera & Zappi (2015: 4), have recently been transferred from *Psychotria* Linnaeus (1759: 906) to *Rudgea*.

The authors' work on the genus, in the perspective of its treatment for the *Flora of the Guianas*, has shown the existence of several new species, six of which have been described elsewhere (Lachenaud *et al*. 2022), and uncovered additional taxonomic issues. The current paper deals with one particular group where considerable confusion has occurred: the *Rudgea hostmanniana* Bentham (1850: 459) complex. This group includes species with sheathing stipules bearing dorsal appendages, thick glabrous leaves without domatia, inflorescences thyrsoid to glomerulate but not regularly dichotomous, calyx tube absent or very short, relatively short corolla tube (usually ≤ 7 mm long, rarely up to 13 mm) and fruits usually brownish when immature and turning red or orange at maturity. Within this group *R. hostmanniana* is both the earliest described species and the most widespread. The remaining species have much narrower ranges, and most of them have been confused with *R. hostmanniana* either in the literature or in herbaria. Steyermark (1967, 1988) recognised a number of species in this complex that have later been included in *R. hostmanniana* (Zappi & Steyermark 2004). Two species from French Guiana, *R. pungens* and the new species *R. billietiae* O. Lachenaud, described below, are peripheral to this group and differ from the rest by their particularly long and narrow stipular sheath. *Rudgea pungens* is further aberrant by its large foliaceous bracts surrounding the inflorescence and relatively long corolla tube; its affinities have long remained obscure, but the discovery of *R. billietiae*, with stipules resembling *R. pungens* but inflorescences resembling *R. hostmanniana*, provides a missing link connecting it to the rest of the group.

In the process of describing *Rudgea billietiae* and comparing it with related species, it was realized that considerable confusion existed in the application of the name *R. hostmanniana*, and that most of the taxa synonymized with the latter were worth reinstating. Therefore, we present here a revision of the *R. hostmanniana* complex in the Guiana Shield region (i.e. the three Guianas, eastern Venezuela, and northern Brazil), which is both the center of diversity of the complex, and the area where most taxonomic confusion has occurred. It must be noted that several species from outside this region appear to be closely related to or part of the *R. hostmanniana* complex, for instance *R. crassifolia* Zappi & E. Lucas (2001: 745) from Eastern Brazil, *R. marginata* Standley (1930a: 154) from Colombia, *R. nebulicola* Steyermark (1967: 414) from eastern Venezuela, and *R. pittieri* Standley (1940: 211) from Panama. Because some of them are poorly known to us, and their taxonomic status is not disputed, they are not dealt with in this paper.

In the present treatment eight species of the *R. hostmanniana* complex are recorded from the Guiana Shield region: *R. billietiae* O. Lachenaud (*sp. nov.*), *R. bolivarensis* Steyermark (1967: 415), *R. cornigera* Bremekamp (1934: 304), *R. coussareoides*, *R. hostmanniana* (represented by the type subspecies), *R. maypurensis* Standley (1930b: 72), *R. pungens*, and *R. tanaosepala* Sandwith (1933: 334). Complete descriptions are provided for each species. A key to the species is presented, and their distinctive characters are summarised in a Table. The morphology of the stipules (Fig. 1), and in particular the position of their appendages, was found to be a very good diagnostic character to separate similar species. Other characters that proved useful are the shape and size of the calyx lobes, indumentum of the corolla, presence or absence of a dorsal corniculum on the corolla lobes (Fig. 2), pyrenes, and leaf venation.

Material and methods

This paper is based on a study of the herbarium collections from BM, BR, CAY, G, K, L, P and U (Thiers 2022); some collections from GB, MO and INPA were also studied on loan. Types specimens from other herbaria were consulted online. Three of the species (*Rudgea billietiae, R. hostmanniana* and *R. pungens*) were also studied in the field in French Guiana. The descriptions were prepared from herbarium specimens, material preserved in alcohol, and field notes. All collections cited have been seen, unless otherwise stated. The terminology adopted for the morphological descriptions follows Radford *et al.* (1974), Robbrecht (1988), Zappi (2003) and Taylor *et al.* (2015). The width mentioned for the various organs is the maximum width, which for the stipules refers to the basal interpetiolar portion. The following abbreviations are used: fl. (flowers), fr. (fruits), imm. fr. (immature fruits), st. (sterile). The conservation status assessment was established following the procedures and terminology of the IUCN Red List Categories and Criteria (IUCN 2012), with the extent of occurrence and area of occupancy estimated by the Geospatial Conservation Assessment Tool (GeoCAT) using a 2 km cell width (Bachman *et al.* 2011). The maps were produced with DIVA-GIS 7.5.0.

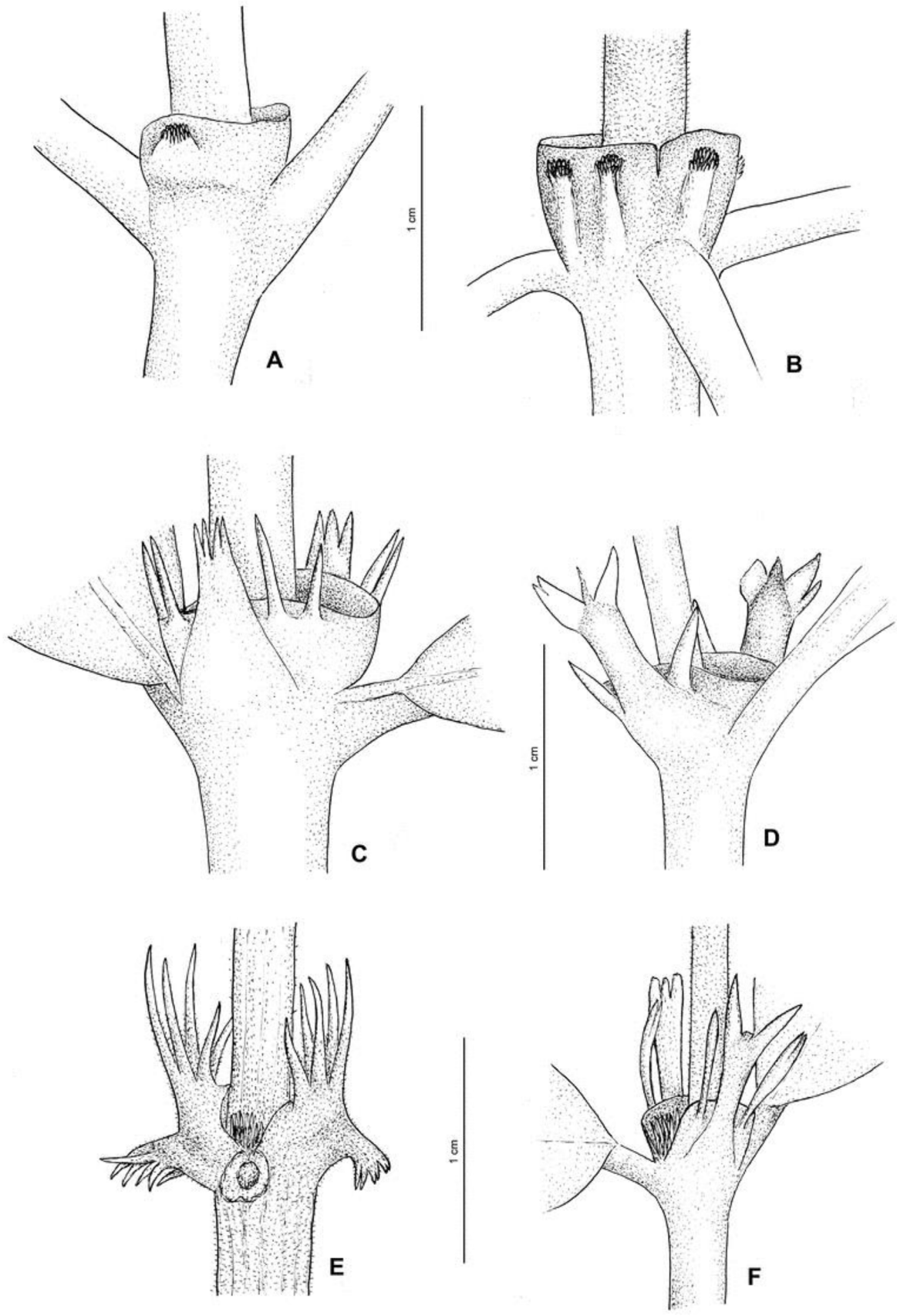

FIGURE 1. Stipules in the *Rudgea hostmanniana* complex. A, *R. bolivarensis*; B, *R. coussareoides*; C, *R. cornigera*; D, *R. hostmanniana* subsp. *hostmanniana*; E, *R. maypurensis*; F, *R. tanaosepala*. A from *Mutchnick 1620* (K), B from *Diaz et al. 7727A* (K), C from *Schulz 7539* (U), D from *Lachenaud 1011* (BR), E from *Williams 12972* (K), F from *Clarke & Hoffman 584* (U). Drawing by O. Lachenaud.

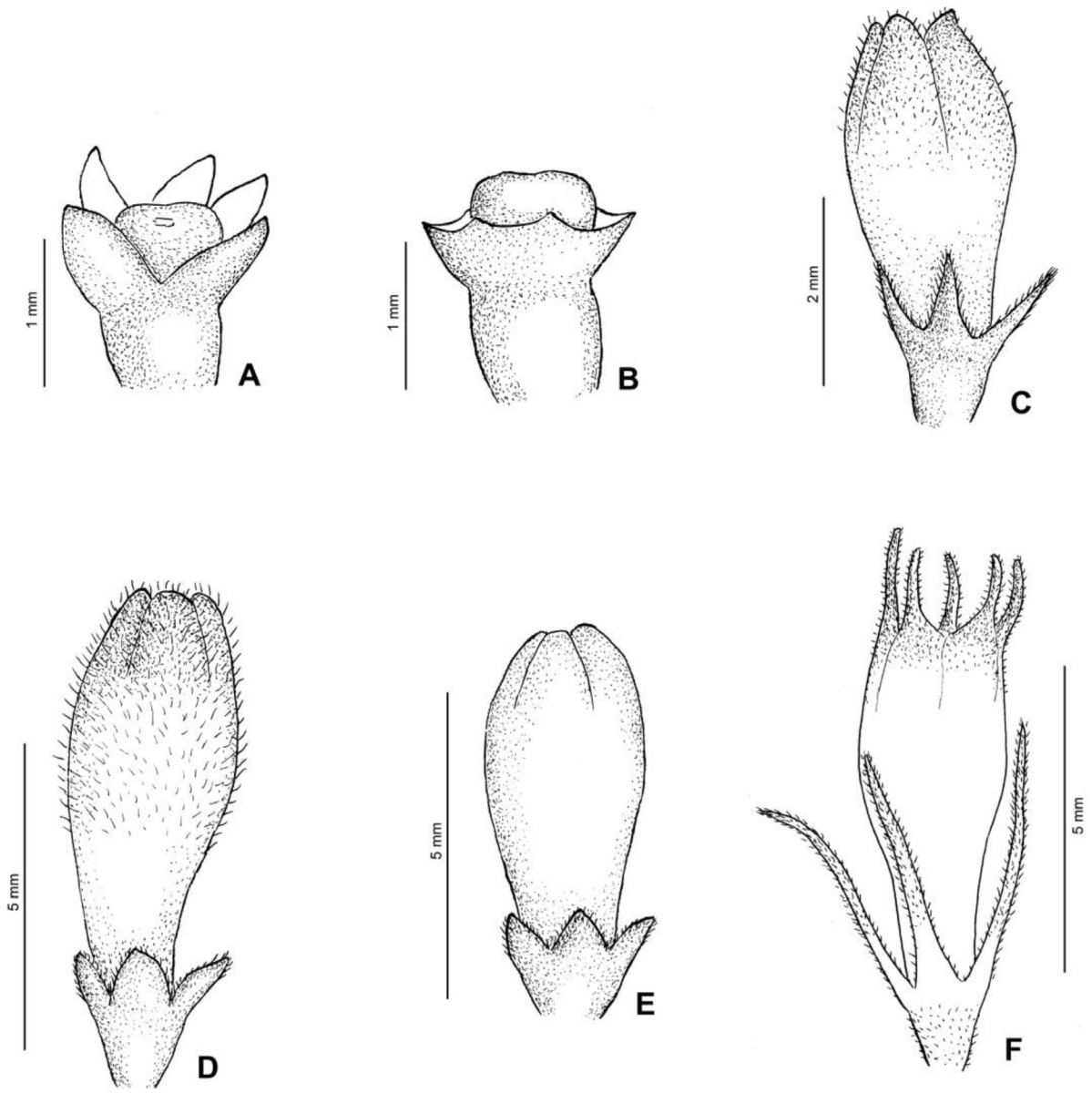

FIGURE 2. Calyx and corolla in the *Rudgea hostmanniana* complex. A, *R. bolivarensis*, calyx; B, *R. coussareoides*, calyx; C, *R. cornigera*, flower bud; D, *R. hostmanniana* subsp. *hostmanniana*, flower bud; E, *R. maypurensis*, flower bud; F, *R. tanaosepala*, flower bud. A from *Henkel 5675* (U), B from *Liesner 24924* (K), C from *Procter 4769* (U), D from *Lachenaud 981* (BR), E from *Plowman 13733* (K), F from *Clarke & Hoffman 584* (U). Drawing by O. Lachenaud.

Taxonomic treatment

The taxonomic accounts for each species are presented below in an alphabetical order, and preceded by an identification key.

Key to the species

1. Leaves ternate; stipular appendages all dorsal and shorter than sheath (Fig. 1B) (Guyana, Venezuela, N. Brazil, Peru) ..... ***R. coussareoides***
- Leaves opposite; stipular appendages exceeding sheath, except in *R. bolivarensis*.....2
2. Stipules narrowly tubular with sheath longer than broad (but often splitting very early at flower-bearing nodes); inflorescences glabrous, sometimes with large foliaceous bracts; corolla lobes corniculate, glabrous outside 3
- Stipules with sheath broader than long; inflorescences puberulous (rarely glabrous in *R. maypurensis*), never with large foliaceous

bracts; corolla lobes not corniculate, or, if corniculate, pubescent or puberulous outside at least near the apex 4

3. Stipules with dorsal appendages inserted near the base; inflorescence subcapitate with large foliaceous imbricate bracts 10–20 x 2–7 mm; corolla tube 13 mm long (French Guiana) ..... ***R. pungens***
- Stipules with dorsal appendages inserted in upper half; inflorescence distinctly branched with small subulate bracts 3–5 mm long; corolla tube 6 mm long (French Guiana: Kaw Mountain) ..... ***R. billietiae***

4. Stipules ± truncate with appendages shorter than sheath (Fig. 1A); leaves thickly coriaceous, with conspicuously reticulate tertiary venation; corolla lobes glabrous outside and not corniculate (Venezuela, Guyana, N Brazil) ..... ***R. bolivarensis***
- Stipules with appendages exceeding sheath; leaves with tertiary venation usually rather obscure; corolla lobes corniculate except in *R. maypurensis* 5

5. Stipules with dorsal appendages recurved, free at base or shortly connate into a keel (Fig. 1E); leaves slightly cordate to rounded at base; corolla lobes not corniculate; pyrenes dorsally verrucose (Venezuela, N Brazil, ?SE Colombia)..... ***R. maypurensis***
- Stipules with appendages all erect, the dorsal ones connate into a keel (Fig. 1C–D & F); leaves cuneate to obtuse at base, never cordate; corolla lobes corniculate; pyrenes not verrucose dorsally 6

6. Calyx lobes 3–5 mm long, linear (Fig. 2F); bracts 5–7 mm long, linear to narrowly lanceolate; corolla lobes usually with linear appendages (rarely these short and blunt); fruits ellipsoid to globose; leaf blade with secondary veins weakly ascending (Guyana) ..... ***R. tanaosepala***
- Calyx lobes 0.7–2 mm long, semicircular to subulate (Fig. 2C-D); bracts usually < 3 mm long, or if longer (to 10 mm in *R. hostmanniana*) then relatively broad; corolla lobes with short and blunt appendages; fruits obovoid, rarely subglobose; leaf blade with secondary veins usually strongly ascending.....7

7. Stipules with central keel much exceeding the lateral appendages (Fig. 1D); leaves acute (rarely obtuse) at base, with petiole 0.5–2 cm long; inflorescence pyramidal or rarely hemispherical; calyx lobes triangular to semicircular (Fig. 2D); corolla tube 3–5 mm long (widespread) ..... ***R. hostmanniana***
- Stipules with central keel roughly equalling the lateral appendages (Fig. 1C); leaves obtuse at base, with petiole 0.2–0.8 cm long; inflorescence hemispherical; calyx lobes subulate to narrowly triangular (Fig. 2C); corolla tube 5–7 mm long (Guyana, Suriname) ..... ***R. cornigera***

1. *Rudgea billietiae* O. Lachenaud, ***sp. nov.*** Fig. 3 & 4

Foliis glabris crassis venulis inconspicuis, stipulis basi connatis et dorso appendiculatis, fructibusque statu immaturo brunneis deinde rubris Rudgeae pungenti, R. hostmannianae, R. cornigerae *et* R. tanaosepalae *affinis. A* Rudgeae pungenti *differt bracteis multo minoribus, 3–5 mm longis, inflorescentiis manifeste ramosis et corollae tubo multo breviore, 6 mm longo (vs. 13 mm longo); ab alteris speciebus stipulis longiore tubulosis in vaginam 7.5–12 mm longis (vs. 2–5 mm longis) connatis, praeterea inflorescentiis glabris (vs. puberulis) distinguitur.*

Type:—FRENCH GUIANA. Route de Kaw, pk 33, sentier vers les grottes, 4 December 2000 (fl.), *F. Billiet & B. Jadin 7456* (holotype, BR! [BR000000907382]; isotypes, CAY! [CAY014905, CAY014906], MO n.v., NY n.v.).

Much-branched shrub 1.75–3 m tall; trunk pale grey; branches ascending; twigs glabrous, 1–2 mm thick, soon covered with a pale straw-coloured bark. *Stipules* 9–15 × 2.5–4.5 mm, glabrous, marcescent and soon corky, consisting of a narrow tubular sheath 7.5–12 mm long (usually split at flower-bearing nodes) bearing ca. 12 terminal linear appendages 1.5–4 mm long, and 6–8 early caducous dorsal appendages 1 mm long, forming a very short decurrent keel inserted in the upper half of the stipule. *Leaves* opposite; petioles 0.2–1 cm long, glabrous; blades elliptic, 4.7–13.5 × 1.3–5.5 cm, decurrent on petiole at base, gradually acuminate at apex, very thick and easily cracking in the fresh state, entirely glabrous, drying greyish-green to yellowish; midrib concave above; secondary veins 6-11 on each side of midrib, strongly ascending, forming an angle of ca. 45° with the midrib; tertiary veins invisible in fresh material, sometimes faintly prominent in dry material; domatia absent. *Inflorescences* terminal in rather contracted panicles, 1–4 cm long, erect, white in flower and green in fruit, glabrous; peduncle terete, 0.5–1.6 cm long; branched part 0.5–2.4 × 1.3–3.5 cm; secondary branches 3–4 per node, 0.2–1 cm long; bracts linear or narrowly lanceolate, 3–5 × 0.3–1.5 mm, entire or dentate in lower half, shortly ciliate in upper part. *Flowers* sessile, 5-merous. *Hypanthium* obconical, 0.5–0.8 mm long, glabrous. *Calyx* tube extremely reduced, lobes linear to narrowly triangular, 1.5–2 × 0.3–0.6 mm, very acute at apex, glabrous or ciliate. *Corolla* white, hypocrateriform; tube funnel-shaped, 6 mm long, 0.5–1 mm wide at base, 2–3 mm wide at mouth, glabrous outside, pubescent inside at the distal portion below the mouth; lobes triangular, 4–5 × 2 mm, glabrous on both sides, with broad, rounded dorsal cornicula 0.7–1 mm long. *Stamens* white, exserted; filaments exserted beyond the corolla mouth by 3 mm; anthers 1.2 × 0.3 mm. *Disk* shortly cylindrical, 0.7 mm long, glabrous. *Style* included, 5 mm long, glabrous; lobes 0.8 mm long, stigmatic surface papillose. *Fruits* ellipsoid, 6–7 × 5–6 mm when dry, dark red-brown and hard when immature, bright cherry red and soft when mature, glabrous, sessile or with very short pedicel ≤ 0.5 mm long, crowned with persistent calyx 1.5 mm in diameter. *Pyrenes* plano-convex, hemi-ellipsoid, 6.5 × 5 mm, dorsal side with 3 hardly distinct longitudinal ridges, smooth between the ridges, ventral side smooth. *Seeds* with a deep T-shaped ventral furrow.

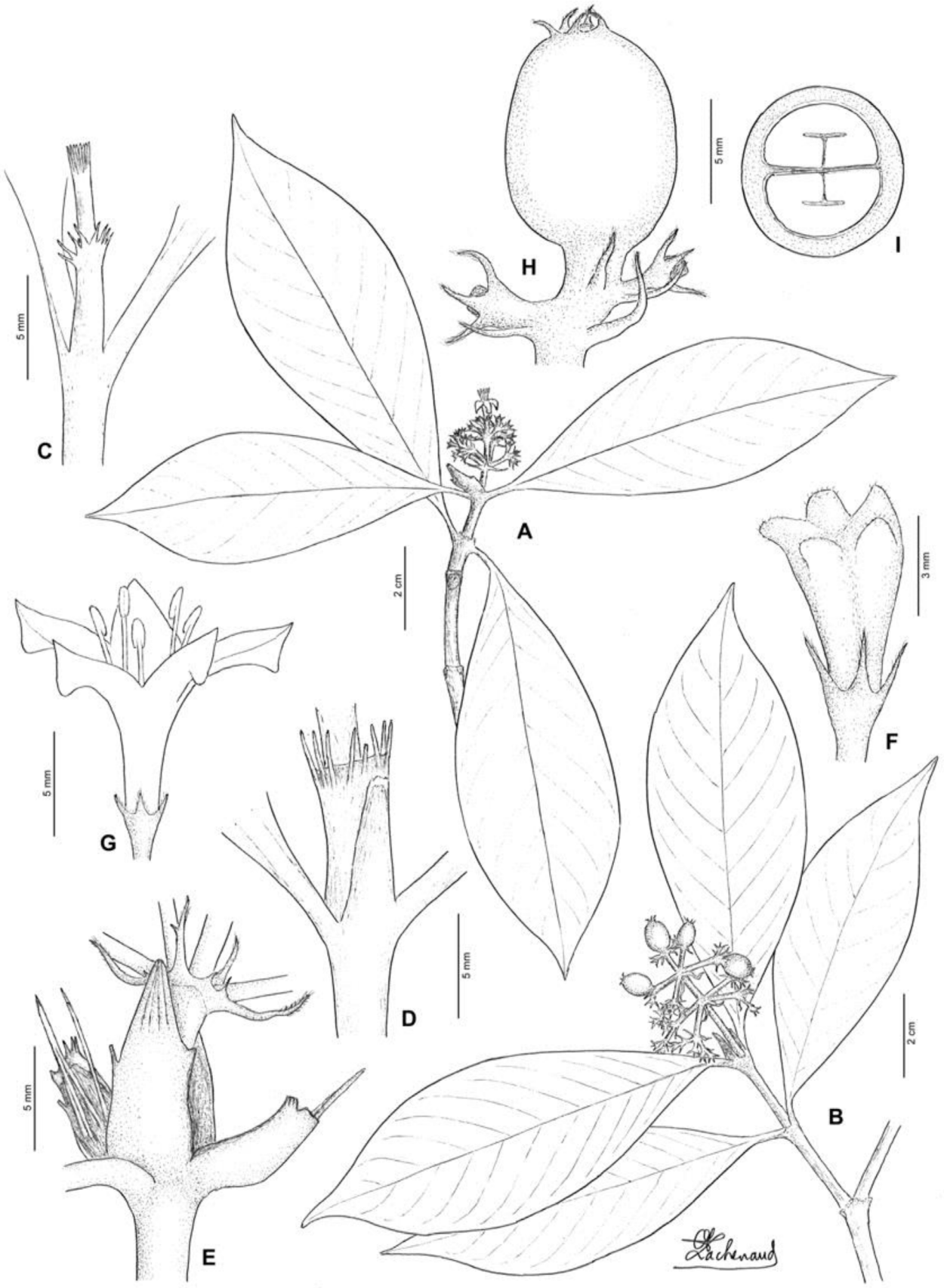

FIGURE 3. *Rudgea billietiae*. A, flowering branch; B, fruiting branch; C, terminal bud; D, stipules of an older node (dorsal appendages fallen off); E, base of inflorescence and broken stipules of the upper node; F, flower bud; G, flower; H, fruit and portion of infructescence; I, cross-section of fruit. A, E, G from *Billiet & Jadin 7456* (BR), B–C and H–I from *Lachenaud 1643* (BR), D, F from *Lachenaud 1878* (BR). Drawing by O. Lachenaud.

FIGURE 4. *Rudgea billietiae*. A, inflorescence; B, fruiting branch; C, immature fruits; D, leaf abaxial side; E, terminal bud; F, stipules from older node; G, mature fruits. Voucher collections: A *Billiet & Jadin 7456*, B–F *Lachenaud 1643*, G *Lachenaud 1878*. Photo A by F. Billiet, photos B–G by O. Lachenaud.

Distribution and ecology:—This species is endemic to the Kaw mountain in northeastern French Guiana (Fig. 5) where it occurs exclusively in low, open canopy forest on lateritic crust, 150–300 m in elevation. It is locally abundant in this habitat, which only covers small areas on the ridge of the mountain.

Phenology:—Flowers have been collected in December (beginning of first rainy season) which is probably the main flowering period; a single inflorescence was also seen in June, among a mostly fruiting population (*Lachenaud 1878*), which is probably a case of flowering asynchrony. Fruits have been collected in November (once, immature) and were seen in abundance from February to late June at least (OL pers. obs.). They apparently take about six months to mature. They are already full-sized in February, but still hard and brown, and remain so for a long time; they start to turn soft and red in late June (OL pers. obs.).

Eponymy:—This species is named after the Belgian botanist Frieda Billiet, collector of the type. Together with her husband Bernard Jadin (1948–2012), she made important plant collections in French Guiana between 1981 and 2009, several of which have been described as new species, e.g., *Philodendron billietiae* Croat (1995: 24), *Oryctanthus guianensis* Kuijt (2011: 465) and *Rudgea jadinii* O. Lachenaud (Lachenaud *et al.* 2022: 168).

Conservation status assessment:—Endangered [EN B1ab(iii) & 2ab(iii)]. *Rudgea billietiae* has a very restricted range, being endemic to the ridge of the Kaw Mountain in French Guiana, where it grows in low stunted rainforest on lateritic crust. Its extent of occurrence (EOO) is calculated to be 68 km², which falls within the limit for Critically Endangered under criterion B1, while its area of occupancy (AOO) is estimated to be 24 km², within the limit for Endangered status under criterion B2 (the actual AOO is however certainly < 5 km², because its habitat only occurs as small isolated patches). The species is known from 13 specimens representing six occurrences and one subpopulation; one occurrence is protected in the Réserve Naturelle des marais de Kaw-Roura, the others have no official protection status. The area where it is found harbours important bauxite and gold deposits; mining projects have been abandoned in 2008 but may resurface in the future, and represent the main threat to the species. Another potential threat comes from touristic development and the building of related infrastructures. Forest exploitation is also ongoing in part of its range, but unlikely to represent a major threat to this species, which occurs in areas of low forest with few exploitable trees. In view of all these factors, a decline in habitat extent and quality is projected. The six occurrences represent five locations in the sense of IUCN, and the species qualifies for Endangered status under the conditions B1ab(iii) & 2ab(iii). The species is recommended for inclusion on the list of protected plants in French Guiana, and particular measures should be taken to protect its habitat, which harbours several other threatened species.

Notes:—Specimens of *Rudgea billietiae* have for a long time been confused in herbaria with either *R. hostmanniana* or *R. pungens*. In the vegetative state *R. billietiae* is very similar to the latter, which also has stipules connate into a long narrow tube (a character not always easy to see on herbarium specimens, because the stipules of the flower-bearing nodes tend to split early) and can only be separated by the position of the dorsal appendages of the stipules, which are inserted in their upper half in *R. billietiae* and near their base in *R. pungens*. The two species differ markedly in their inflorescences, especially in the development of their bracts (much larger in *R. pungens*) and in the size of the corolla tube, which is about twice longer in *R. pungens*. They also seem to have different ranges, *R. pungens* being apparently absent from the Kaw Mountain. In inflorescence structure and corolla length *R. billietiae* resembles *R. hostmanniana*, *R. cornigera* and *R. tanaosepala*, but these have much shorter stipular sheaths and puberulous inflorescence axes (glabrous in *R. billietiae*). Differences between all these species are summarised in Table 1.

It is not known whether the flowers of *R. billietiae* are heterostylous: only two collections with open flowers have been seen (the type and *Martin s.n.*) and both are of the brevistylous form.

Three specimens collected in the late XVIIIth or early XIXth centuries, *Leblond s.n.*, *Martin s.n.* and *Richard s.n.*, have no precise locality; the two former are labelled "Cayenne", but this indication was often used for the whole of French Guiana at that time. They may well have come from the Kaw Mountain, which is only about 50 km from Cayenne and was already accessible at that time. The Richard collection is a mixture, including two branches of *R. pungens* (one flowering, one fruiting) and one of *R. billietiae* (fruiting), collected at different times of the year and probably in different places.

Additional Specimens Examined (paratypes):—FRENCH GUIANA. Montagne de Kaw, E end ca. 10 km from end of road, 4°32'N 52°07'W, 10 March 1994 (fr.), *L. Andersson, C. Gustafsson, C. Persson & J. Rova 1949* (CAY); Montagne de Kaw, 13 May 1985 (fr.), *C. Feuillet 2244* (CAY, P); Montagne de Kaw, forêt dense sur versant nord, à proximité de la route, 5 km E de Camp Caïman, 14 June 1979 (st.), *J.-J. de Granville 2978* (CAY, P); Montagne de Kaw, extrémité est, versant sud, 3 November 1985 (imm. fr.), *J.-J. de Granville 8244* (CAY, P, U); Montagne de Kaw, sentier des grottes, 23 February 2014 (imm. fr.), *O. Lachenaud 1643* (BR, CAY, MO, P); same locality, 4°33'15"N 52°10'18"W, 28 June 2014 (fl. buds & fr.), *O. Lachenaud 1878* (BR, CAY, MO, P); Montagne de Kaw, Amazon Lodge, 4°33'35.1"N 52°12'20.7"W, 23 August 2017 (st.), *O. Lachenaud 2639* (BR, CAY, MO); Montagne de Kaw, au pk 30.5, à gauche de la route, 3 January 2019 (st.), *O. Lachenaud 2689* (BR, CAY); Route de Fourgassié, peu après le croisement de la route de Kaw, 3 January 2019 (fallen fl.), *O. Lachenaud 2695* (BR, CAY); "Cayenne", no date [ca. 1800], *J.B. Leblond s.n.* (G); "Cayenne", no date [ca. 1800] (fl.), *J. Martin s.n.* (BM [3 sheets], K [2 sheets]); no locality or date (fr.), *L.C.M. Richard s.n.* (P [P04008549], mixed with *R. pungens*; see notes above).

2. *Rudgea bolivarensis* Steyermark (1967: 415). Fig. 1A, 2A

Type:—VENEZUELA. State of Bolivar, Gran Sabana, along wooded portion of quebrada tributary to Río Kukenan, south of Mount Roraima, 1005–1065 m, 2 October 1944 (fr.), *J.A. Steyermark 59118* (holotype, VEN! [VEN15991]; isotype, NY! [NY00133207]).

Much-branched shrub or *tree* 3–15 m tall; twigs 3–5 mm thick, glabrous, soon covered with a pale buffish-straw bark. *Stipules* 3.5–5 × 3–10 mm, glabrous, marcescent but soon damaged, consisting of a ± truncate sheath (usually split at flower-bearing nodes) bearing on each side of the node a dense mass of 10–25 thick aculeiform dorsal appendages 1–1.3 mm long, shorter than the sheath and inserted between 1/3 and 2/3 of its length from the base. *Leaves* opposite; petioles 0.3–2 cm long, glabrous; blades elliptic, 4–18.5 × 1.8–9 cm, acute to rounded at base, obtuse to hardly acuminate at apex, very coriaceous with thickened margin, entirely glabrous, drying olive brown to olive green; midrib slightly concave above; secondary veins 7–12 on each side of midrib, moderately ascending, forming irregular loops 1.5–8 mm from the margin; tertiary venation densely reticulate and prominent below (at least in the dry state); domatia absent. *Inflorescences* terminal, in rather lax panicles, 6.5–14 cm long, erect, minutely spreading-puberulous (the peduncle ± glabrous); peduncle terete, 4.5–8.5 cm long; branched portion 1.5–5.5 × 3.5–7.8 cm; secondary branches 3–4 per node, 0.4–2.8 cm long; bracts minute, ca. 0.7 x 0.5 mm long, triangular to linear, puberulous. *Flowers* sessile, 5(–6)-merous. *Hypanthium* cylindrical, 0.7 mm long, glabrous. *Calyx* tube extremely reduced, lobes triangular to narrowly elliptic, 0.5–1 × 0.3–0.5(–1) mm, obtuse to acute at apex, glabrous or minutely ciliate at apex. *Corolla* only known in young bud stage; tube glabrous outside, villose at distal portion inside; lobes not dorsally corniculate, glabrous outside. *Stamens* not seen. *Disk* shortly cylindrical, 0.3 mm long, glabrous. *Style* not seen. *Fruits* obovoid to ellipsoid, 5.5–9 × 4–6 mm when dry, green when immature, bright orange when mature, glabrous, sessile or with pedicel < 1 mm long, crowned by the persistent calyx 1.5–2 mm in diameter, i.e. not markedly accrescent. *Pyrenes* plano-convex, hemi-obovoid, 6–8 × 4.5–5.5 mm, dorsal side faintly ridged with 3–4 dorsal and 2 lateral ridges, smooth between the ridges, ventral side smooth. *Seeds* with a deep T-shaped ventral furrow.

Distribution and ecology:—This species occurs in southeastern Venezuela (Mt. Roraima area) and adjacent Guyana and Brazil (Fig. 5), in forest/savanna edges, at 700–1100 m altitude.

Phenology:—Specimens with flower buds were collected in December; and with fruits in June-July (immature), October and December (mature or nearly so).

Notes:—The original description of this species was based on two specimens, one from Venezuela, and one from Brazil. Several additional specimens from Guyana have since been found, and represent a new record for the country. Strangely enough, two Guyanan specimens (*Henkel et al. 5675*, *Henkel & Chin 5709*) have coordinates falling in Brazil, which may be due to an error either of country or of coordinates reported on the label. Mature flowers are still unknown.

Zappi & Steyermark (2004: 808) included *Rudgea bolivarensis* in synonymy under *R. hostmanniana*, which is similar in inflorescence and fruit characters. The stipules of *R. bolivarensis*, however, are very different and diagnostic, bearing only dorsal appendages that are shorter than the sheath (all other species of the complex have the stipular appendages exceeding the sheath, except *R. coussareoides*, which is easily recognized by its ternate leaves). *Rudgea bolivarensis* also differs from *R. hostmanniana* by having the corolla glabrous outside, leaves more coriaceous with a conspicuously thickened margin and an evident tertiary venation, and pyrenes with much less prominent dorsal ridges. The supposed differences in inflorescence structure, mentioned by Steyermark (1967), are actually not reliable; he described the pedicels of *R. bolivarensis* as 5–8 mm long, but the flowers are sessile and the fruits are sessile or subsessile (pedicel < 1 mm long).

Additional Specimens Examined:—BRAZIL. **Roraima** ["Rio Branco"]: along igarapé 5 km SE of Serra Sabang, 720 m, 16–18 December 1954 (fl. buds & fr.), *B. Maguire & C.K. Maguire 40276* (NY, VEN).

GUYANA. Pakaraima Mountains, Upper Ireng R. watershed, Malakwalai-Tipu, 300 m downslope from NE escarpment, 4°48'N, 60°18'W, 1100 m, 17 July 1994 (imm. fr.), *T.W. Henkel, M. Chin & L. Williams 5675* (CAY, U); Pakaraima Mountains, upper Ireng River watershed, E bank Kaalmang River at base of Achiknang, 4°59'N, 60°08'W, 700 m, 19 July 1994 (imm. fr.), *T.W. Henkel & M. Chin 5709* (K); Pakaraima Mountains, upper Ireng River, hills 2–3 km E of Cipo settlement, 4°48'N, 60°2'W, 760 m, 12 October 1994 (fr.), *P. Mutchnik, T.W. Henkel & L. Williams 1* (K); Northern Pakaraimas, Koa Valley, Annuyeng Creek from mouth to falls, 4°39'48"N, 59°48'33"W, 834 m, 10 June 1995 (imm. fr.), *P. Mutchnick 1620* (K).

3. *Rudgea cornigera* Bremekamp (1934: 304). Fig. 1C, 2C.

Type:—SURINAME. Watramiri, 22 June 1910 (fl.), *B.W.* [=*Bureau v.h. Boschwezen*] *4728* (lectotype, first-step designated by Steyermark (1967: 4166), **second-step** U! [U0006284], **here designated**; isolectotypes BR [BR0000024941754]!, G! [without barcode], MO [MO-797272, MO-797610]!).

Much-branched shrub 2–6 m tall, main stem up to 4 cm in diameter; twigs glabrous, 3–4 mm thick, soon covered

with a pale buffish-straw bark. *Stipules* 6–12 × 5–12 mm, glabrous, marcescent and soon corky, consisting of a short basal sheath 3–5 mm long (usually split at flower-bearing nodes) bearing on each side of the node 1–2 linear lateral appendages 2.5–5 × 0.5–1 mm, and a central keel 4–9 × 2–4 mm, about equalling the latter and divided into 4–7 often unequal appendages 1–3.5 mm long, the lateral ones usually connate, longer than the central ones. *Leaves* opposite; petioles 2–8 mm long, glabrous; blades elliptic to slightly oblanceolate, (8.5–)10.2–22 × (1.7–)2.8–9.6 cm, gradually narrowed towards an obtuse base, strongly acuminate at apex, very thick, entirely glabrous, drying greyish-green to olive brown; midrib concave above; secondary veins 8–11 on each side of midrib, usually strongly ascending, forming loops well away from the margin; tertiary veins lax and slightly prominent in dry specimens (probably invisible in the fresh state); domatia absent. *Inflorescences* terminal, in lax to fairly condensed hemispherical panicles, 2.4–12.5 cm long, erect, sparsely spreading-puberulous; peduncle terete, 0.8–6.5 cm long; branched portion 1.5–6 × 1.8–7 cm; secondary branches (2–)3–4 per node, 0.3–2 cm long; bracts 1.5–3 × 0.3–1.5 mm, triangular to subulate, entire or irregularly dentate, shortly pubescent especially on the margins. *Flowers* sessile, 5-merous, heterostylous, fragrant. *Hypanthium* obconical, 0.5 mm long, glabrous. *Calyx* tube extremely reduced, lobes triangular to subulate, 0.7–1.2 × 0.3–0.5 mm, acute at apex, shortly pubescent especially on the margins. *Corolla* white, hypocrateriform; tube cylindrical to narrowly funnel-shaped, 5–7 mm long, 0.8–1.3 mm wide at base, 2–4 mm wide at mouth, glabrous outside, with a ring of dense short hairs at the insertion of the stamens inside; lobes narrowly elliptic, 3–5 × 1–2.5 mm, puberulous outside at least near the apex, papillose inside, with obtuse dorsal cornicula 0.5–1 mm long. *Stamens* subsessile with anthers tips reaching the corolla mouth in long-styled flowers, or fully exserted with filaments 1 mm long in short-styled flowers; anthers 1.8–2 × 0.4 mm. *Disk* shortly cylindrical, 0.5 mm long, glabrous. *Style* just as long as corolla tube in both morphs, 5–6.5 mm long, glabrous; style branches 1 mm long, stigmatic surface papillose. *Fruits* obovoid, 7–11 × 4.5–8 mm when dry, brown when immature, orange to red when mature, glabrous, sessile, crowned with persistent calyx 1.5–2.5 mm in diameter. *Pyrenes* plano-convex, hemi-obovoid, 7.5–8 × 4.5–5 mm, dorsal side with 3 ridges, smooth between the ridges, ventral side smooth. Seeds with a deep T-shaped ventral furrow.

Distribution and ecology:—Northern Suriname and central Guyana (Fig. 5). The species occurs in dry forest, mixed evergreen forest, *Mora* forest, and rocky areas along creeks, often on brown sand, 0–700 m elevation.

Phenology:—Specimens with flowers were collected in May (buds), August and October-December; and with fruits in all months of the year, except June and August.

Notes:—This species closely resembles *Rudgea hostmanniana*, and the two have often been regarded as synonyms in herbaria, although the synonymy seems not to have been officially published. Steyermark (1967: 399) in his dichotomous key separated them only by the size of the petiole, supposed to be 2–5 mm in *R. hostmanniana* and 8–15 mm in *R. cornigera*. In fact, the two species must have been inverted in the key, since *R. cornigera* has petioles not exceeding 8 mm in length, usually shorter than those of *R. hostmanniana*. A detailed study of the material available showed that petiole length is not a reliable character to separate the two taxa; however, more significant differences exist (see Table 1) and *R. cornigera* should therefore be maintained as a separate species. It is also similar to *R. tanaosepala*, which has a partly overlapping geographic range (for differences see the key and Table 1).

The heterostyly in *Rudgea cornigera* is of an unusual type, where the style is about as long as the corolla tube in both morphs, and only the position and length of the stamens varies. This is another difference with *R. hostmanniana*, which shows reciprocal heterostyly.

Bremekamp (1934: 304) cited several syntypes in the original description of *Rudgea cornigera*: *B.W. 1862, 2227, 2457, 2662, 3356 & 4728*, *Samuels 430* and *Versteeg 515*. Steyermark (1967: 416) cited *B.W. 4728* as type, which is to be interpreted as a first-step lectotypification, but did not specify the herbarium of deposit. The sheet in U (barcode U0006284), where Bremekamp worked, is here selected as a lectotype.

Additional Specimens Examined:—GUYANA. Holmia, November 1909 (fl.), *A.W. Bartlett 8731* (K); Kamarang to Waramadou trail, 5°50’N, 60°39’W, 23 January 1996 (imm. fr.), *D. Clarke 789* (CAY, U); Region Potaro-Siparuni, Paramakatoi, 0.5-4 km from trail to Maikwak & Kowatipu, 4°43’N 59°42’W, 22 February 1996 (imm. fr.), *D. Clarke & Grose 1197* (U); 20 m from Saydak creek, 11 April 1979 (fr.), *P.J. Edwards 1220* (K, P); Mabura region, YaYa creek, 5°20’N, 58°30’W, 25 November 1992 (fl. buds), *R.C. Ek 586* (U); 85 miles Bartica – Potaro road, 3 November 1947 (fl. buds), *D.B. Fanshawe* in *Forest Department 5545* (K); Upper Demerara River, September 1887 (fl. buds & fr.), *G.S. Jenman 4054* (K); Pakaraima Mts, Kamarang, 5°52’N, 60°38’W, 8 November 1979 (fl.), *P.J.M. Maas & L.Y.T. Westra 3973* (K, U); Mabura Hill, 5°19’N, 58°28’W, 27 October 1981 (fl.), *P.J.M. Maas, E.A. Mennega & B.J.H. ter Welle 5884* (K, U); Blackwater Creek camp, 5°12’N, 59°10’W, 23 May 1991 (fr.), *T. McDowell, C.M. Kelloff & A. Stobey 4903* (CAY); Potaro River, left margin on portage trail on second set of rapids above Chenapou, 5°0’50.3”N 59°39’3.1”W, 18 March 2014 (fr.), *F.A. Michelangeli, Z. Narine, J. Isaacs, N. Carter & P. Lewis 2293* (NY); Mabura Hill Area, 5°20’N 58°40’W, 6 June 1986 (fl.), *J.J. Pipoly & R. Boyan 7593* (CAY, P); Pakaraima Mts, Mazaruni River,

17 GPS miles W of Imbaimadai to Kamarang, 5°42’58”N, 60°32’34”W, 4 February 2004 (fr.), *K.M. Redden, C. Perry, C. Paul & M. Lyle 1680* (P); Mazaruni River above ABC Falls, 6°4’N, 60°37’W, 16 February 2004 (imm. fr.), *K.M. Redden, M. Lyle, R. Williams, C. Perry & C. Paul 2807* (CAY, K); Mabura Hill, 180 km SSE of Georgetown, Ya-ya Creek, 11 March 1988 (fr.), *H. ter Steege, P. de Jager, J.M.C. Potters & W.N.J. Ursem 238* (U); mouth of Suru-a-gu-puh River, 12 September 1960 (fr.), *S.S. Tillett & C.L. Tillett 45389* (K, U).

SURINAME. Palisadeweg, 17 October 1949 (fl. & fr.), *B.B.S. 278* (K, U); Bosch Reserve Watramiri, 5 December 1916 (fr.), *Bureau v.h. Boschwezen 2502* (U); Bosch Reserve Zanderij I, 17 October 1917 (fl.), *Bureau v.h. Boschwezen 3356* (INPA, U); Watramiri, 2 August 1916 (fallen fl.), *B.W. 2227* (L); Watramiri, 8 February 1917 (imm. fr.), *B.W. 2662* (BR, G); Mapane, 9 June 1970 (fl. & fr.), *C.J. Gieteling 104* (WAG); Forest Reserve Zanderij 1, 31 July 1933 (fr.), *J. Lanjouw 353* (INPA, K, U); Jodensavanne – Mapane Kreek area (Suriname R.), 16 March 1953 (fr.), *J.C. Lindeman 3519* (U); ibid., 5 May 1953 (fr.), *J.C. Lindeman 3805* (U); Coppename River, near Bitagron, along S road of Surocto base, 6 August 1954 (fl.), *J.C. Lindeman 6437* (U); Along Rijsdikweg, ca. 25 km S of Paramaribo, 28 October 1954 (fl. buds), *J.C. Lindeman 6625* (U); Kabo, distr. Saramacca, October 1978 (fr.), *J. Procter 4769* (U); Forest of Zanderij, 31 May 1916 (fl. buds), *J.D. Samuels 430* (K, L, P); hoog droogl. bos bij Kamp 8, 23 December 1955 (fl.), *J.P. Schulz 7539* (U); pr. Paramaribo, June 1904 (fl. buds), *G.M. Versteeg 515* (U); “e regione Para”, s.d. (fr.), *H.R. Wullschlaegel 994* (BR).

4. *Rudgea coussareoides* (Standley) C.M. Taylor, Bruniera & Zappi (2015: 45, p. 4 [E-publication]). – *Psychotria coussareoides* Standley (1931: 441). **–** *Palicourea coussareoides* (Standley) Delprete & J.H. Kirkbride (2016: 417). Fig. 1B, 2B.

Type:—VENEZUELA. Amazonas, slopes of Mount Duida, Agüita, 4000 ft [ca. 1220 m], 1928–29 (fl. buds), *G.H.H. Tate 919* (holotype, NY! [NY00132650]).

Rudgea tillettii Steyermark (1967: 416).

Type:—GUYANA. Porkknocker Camp 2 on Partang River, about 19 miles from mouth, Merume Mountains, 625 m, 28 June 1960 (fl. buds), *S.S. Tillett, C.L. Tillett & R. Boyan 43934* (holotype, NY! [2 sheets, NY00133238, NY00133239], isotypes K! [K000005080], VEN! [VEN64649]).

Psychotria coussareoides var. *ciliata* Steyermark (1972: 496).

Type:—VENEZUELA. Bolivar: Cerro Venamo (parte SO), 950–1000 m, 10 January 1964 (fl. buds), *J.A. Steyermark, G.C.K. Dunsterville & E. Dunsterville 92929* (holotype, VEN! [VEN62981], isotype, NY! [NY00132651]).

Shrub or tree 1.5–7 m tall; twigs glabrous, 1.5–3 mm thick, soon covered with a brown corky bark. *Stipules* 2.5–7 × 4.5–10 mm, glabrous, marcescent but soon damaged, consisting of a truncate sheath bearing 6 groups (2 between every pair of leaves) of ca. 10 thick aculeiform dorsal appendages 0.5–1 mm long, shorter than the sheath and inserted between 2/3 and 3/4 of its length from the base. *Leaves* ternate; petioles 0.8–2.5 cm long, glabrous; blades elliptic, 6.2–21 × 1.2–7 cm, decurrent on petiole at base, acuminate at apex, coriaceous with slightly recurved margin, entirely glabrous, drying olive brown to dark brown; midrib slightly prominent above; secondary veins 8–11 on each side of midrib, weakly to moderately ascending, forming irregular loops 0.5–2 mm from the margin; tertiary venation prominently reticulate (at least in the dry state) and concolorous below, the veins 1–2 mm apart; domatia absent. *Inflorescences* terminal, pale green to purplish (at least in the fruiting stage), in pyramidal panicles, 5.7–13.5 cm long, erect, minutely spreading-puberulous; peduncle terete, 2.2–4.2 cm long; branched portion 3.5–10.5 × 3–8 cm; secondary branches (2–)3–4 per node, 1.2–2 cm long; bracts of basal node resembling small leaves, 8–27 × 1–5.5 mm, narrowly elliptic, glabrous, the other bracts minutely triangular, 1–2.5 × 0.5–2 mm, entire or dentate, glabrous to puberulous. *Flowers* sessile, 5-merous, fragrant. *Hypanthium* cylindrical, 0.8–1 mm long, glabrous. *Calyx* shortly cupuliform, glabrous to puberulous; tube 0.3–0.7 mm long; lobes triangular, 0.2–0.3 mm long. *Corolla* white, hypocrateriform; tube funnel-shaped, 2–2.5 × 1.2–1.8 mm, glabrous to papillose outside, densely villose inside except towards the base; lobes narrowly triangular, 2.5–3 × 1–1.5 mm, acute at apex, glabrous outside, papillose inside. Stamens mostly included with only the tips exserted, anthers 1 × 0.5 mm. *Disk* cylindrical, 0.3–0.7 mm long, glabrous. *Style* exserted, 4.5–5.5 mm long, bilobed, glabrous. *Fruits* ellipsoid to subglobose, 5.5–8 × 4–5.5 mm when dry, green or greyish-blue when immature, dark purple when mature, glabrous, sessile or with pedicel < 2 mm long, calyx not markedly enlarged, 1.3–2.5 mm wide. *Pyrenes* plano-convex, hemi-ellipsoid, 7–7.5 × 5–5.5 mm; dorsal side faintly and irregularly ridged, slightly granulose, ventral side smooth. *Seeds* with a deep T-shaped ventral furrow.

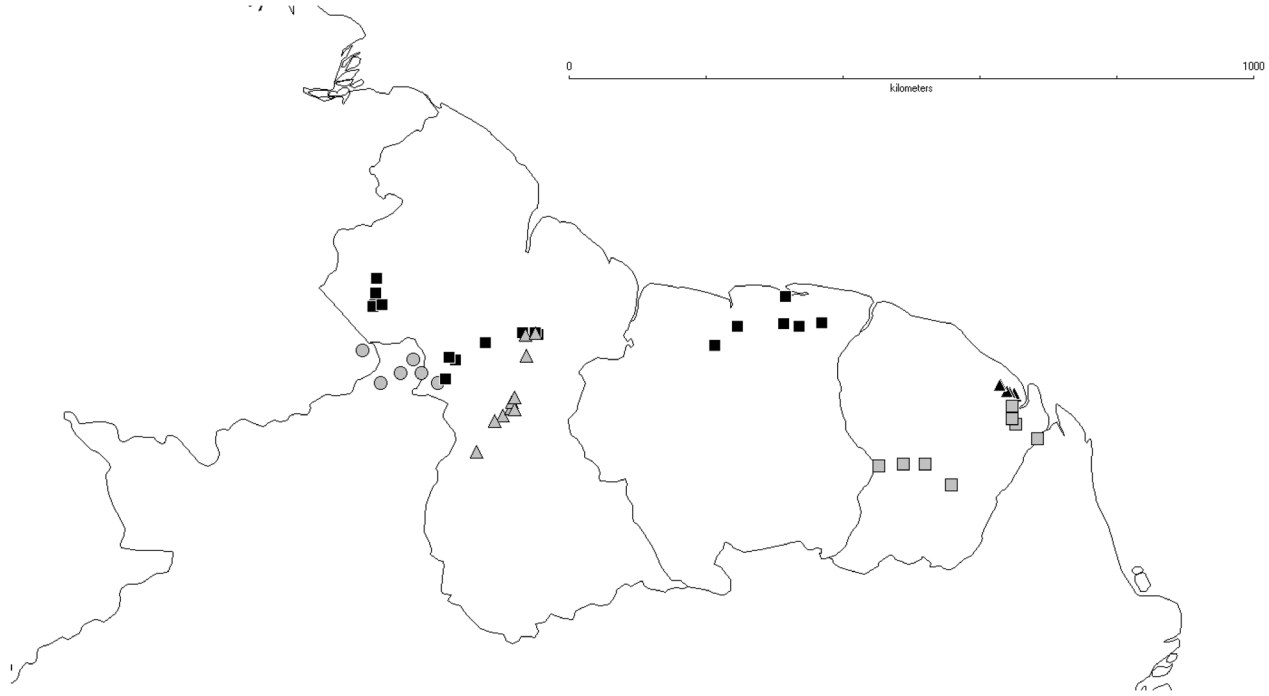

FIGURE 5. Distribution of *Rudgea billietiae* (black triangles), *R; bolivarensis* (grey circles), *R. cornigera* (black squares), *R. pungens* (grey squares) and *R. tanaosepala* (grey triangles).

FIGURE 6. Distribution of *Rudgea coussareoides* (squares), *R. hostmanniana* subsp. *hostmanniana* (triangles) and *R. maypurensis* (circles).

Distribution and ecology:—Occurring in western Guyana, eastern Venezuela, and northern Brazil (Amazonas) and apparently in disjunct populations in Amazonian Peru (Fig. 6); in tepui slope forests, sometimes on riverbanks, mostly 700–1500 m but as low as 300 m altitude in Peru.

Phenology:—Flowers in October (buds), January-February, and June; fruits in January, April and October-November.

Notes:—The systematic position of this species, which has only recently been transferred to *Rudgea* from

Psychotria (Taylor *et al.* 2015) has long been unclear. It appears that it is part of the *R. hostmanniana* complex, and in particular closely resembles *R. bolivarensis* in stipule morphology. It is easily separated from the latter – and from all species of *Rudgea* in the Guiana Shield region – by its ternate, rather than opposite, leaves. Furthermore, its stipules bear two separate groups of appendages between every leaf pairs (as opposed to one in *R. bolivarensis*) and its inflorescences are also more slender than in *R. bolivarensis*.

It is unclear whether the flowers of this species are heterostylous; only two specimens with open flowers have been seen, and both seem to pertain to the long-styled form.

A specimen from Brazil, cited below, represents a new record for the country; though it was seen in photograph only, this identification is without any doubt. A previous record of this species from French Guiana (Funk *et al.* 2007, as *Psychotria coussareoides*) is presumably based on the specimen *R.A.A. Oldeman & C. Sastre 88* (CAY), which is *Coussarea sp*. No authentic material of *R. coussareoides* from French Guiana has been seen by the authors.

Additional Specimens Examined:—BRAZIL. **Amazonas:** Manacapuru, margen do lago grande, operação Radam, ponto 4, 9 October 1976 (fl. buds), *T.R. Bahia 219* (F n.v., NY, photo K).

GUYANA. Upper Mazaruni River region, Karowtipu Mountain, 5°45'N, 60°35'W, 1000 m, 25 April 1987 (fr.), *B.M. Boom & D. Gopaul 7728* (MO); Pakaraima Mountains, Mount Wokomung, Wusupubaru Creek, 2 km from juncture with Suruwubaru Creek, 5°03'N, 59°53'W, 975–1125 m, 13 February 1993 (fl.), *T.M. Henkel, M. Chin & W. Ryan 1326* (MO); Pakaraima Mountains, Mount Wokomung, headwaters of Wusupubaru Creek, 5°03'N, 59°53'W, 975–1125 m, 15 February 1993 (fl.), *T.M. Henkel, M. Chin & W. Ryan 1385* (NY).

PERU. **Amazonas:** Distrito Imaza, comunidad Aguaruna Putuim, Anexo de Yamayakat, 700–750 m, 21 January 1996 (fr.), *C. Díaz S., H. Osores, H. Díaz & D. Díaz 7727A* (K).

VENEZUELA. **Amazonas:** Distrito Atabapo, Cerro Marahuaca, 3°43'N, 65°30'W, 1200 m, 16 October 1988 (fr.), *R. Liesner 24924* (K); Distrito Atabapo, Cerro Huachamacari, 3°49'N, 65°43'W, 800–1300 m, 5 November 1988 (fr.), *R. Liesner 25881* (K).

5. *Rudgea hostmanniana* Bentham (1850: 459) subsp. ***hostmanniana***. Fig. 1D, 2D, 7A–C.

Type:—SURINAME. Without locality, 1843 (fl.), *F.W.R. Hostmann 548* (lectotype, first-step designated by Steyermark (1967: 413), **second-step** K! [K000579485], **designated here**; isolectotypes BM! [BM000832001], G! [G00436709, G00436710], GH! [GH00094434, 00094435], P! [P04008004]).

Rudgea intercedens Müller Argoviensis (1881: 205)**, *syn. nov.***

Type:—BRAZIL. [Pará]: Without locality, *s.d.* [1785] (fl.), *L.C.M. Richard s.n.* (lectotype, P! [P03985391], **designated here**; isolectotype, G! [G00436705]).

Much-branched shrub 1–5(–8) m tall; twigs glabrous, 2–4 mm thick, soon covered with a pale buffish-straw bark. *Stipules* 7–13 × 3–8.5 mm, glabrous, marcescent and soon corky, consisting of a basal sheath 3–5 mm long (usually split at flower-bearing nodes) bearing on each side of the node 1–2 narrowly triangular lateral appendages 2–5 × 0.3–1 mm, and a central keel 5–10 × 1.2–2 mm, much exceeding the latter and divided into 2–8 terminal appendages 2–3 mm long, these often grouped in two phalanges. *Leaves* opposite; petioles 0.5–2 cm long, glabrous; blades elliptic to slightly oblanceolate, 8.5–20(–22) × 2–7.8(–12) cm, acute or rarely obtuse at base, obtuse to shortly acuminate at apex, very thick, entirely glabrous, drying yellowish-green to olive brown; midrib flat or concave above; secondary veins 8–12 on each side of midrib, rather strongly ascending, forming very inconspicuous loops 1.5–5 mm from the margin; tertiary venation invisible in the fresh state, sometimes prominent but very lax in the dry state; domatia absent. *Inflorescences* white, terminal, in lax to rather condensed, pyramidal or rarely hemispherical panicles, 5.2–18 cm long, erect, shortly spreading-puberulous, the peduncle often glabrescent; peduncle terete, 3–11 cm long; branched portion 1.7–11 × 2.4–8.5 cm; secondary branches (2–)3–4 per node, 0.5–3 cm long; bracts triangular to lanceolate, 2.5–10 × (0.7–)1.5–3 mm, entire or the lower ones often dentate at base, acute at apex, glabrous to sparsely pubescent. *Flowers* sessile, 5-merous, heterostylous. *Hypanthium* obconical, 0.7 mm long, glabrous. *Calyx* tube extremely reduced, lobes triangular to semi-circular, 0.7–2 × 0.5–0.8 mm, acute to rounded at apex, glabrous to sparsely pubescent externally, ciliate on the margins. *Corolla* white, fragrant, hypocrateriform; tube narrowly funnel-shaped, 3–5 mm long, 1–1.2 mm at base, 2–3 mm wide at mouth, glabrous to densely villous outside, densely villous at upper half inside; lobes narrowly triangular, 3–4 × 1.2–1.5 mm, densely villous to sparsely pubescent outside at least near the apex, papillose inside, with hemispherical to conical dorsal cornicula ≤ 0.7 mm long. *Stamens* included and subsessile in long-styled flowers, or long exserted with filaments 3–4 mm long in short-styled flowers; anthers 1–1.2 x 0.3 mm. *Disk* shortly

cylindrical, 0.6 mm long, glabrous. *Style* exserted, 5.5–6 mm long in long-styled flowers, or as long as corolla tube, 4.5–5 mm long in short-styled flowers; lobes 0.8–1.5 mm long, stigmatic surface papillose. *Fruits* obovoid or rarely subglobose, 5.5–10 × 5.5–7.5 mm when dry, green when immature, becoming orange-red later (said to turn black at full maturity), glabrous, sessile, crowned with persistent calyx 1–2 mm in diameter, i.e. not markedly accrescent. *Pyrenes* plano-convex, hemi-ellipsoid to hemi-obovoid, or rarely hemispherical, 5.5–9 × 4.5–8.5 mm, dorsal side with 3–4 prominent and 2 lateral ridges, smooth between the ridges, ventral side smooth. *Seeds* with a deep T-shaped ventral furrow.

FIGURE 7. A–C, *Rudgea hostmanniana*. A, inflorescence; B, leaf abaxial side; C, fruits. D–F, *Rudgea pungens*. D, infructescence, top view; E, infructescence, lateral view; F, stipule. Voucher collections: A–C, plant not collected (Kourou, French Guiana), D–F *Lachenaud 1720*. A–C Photos by P. Petronelli, D–F photos by O. Lachenaud.

Distribution and ecology:—Widespread and common in the three Guianas, occurring also locally in eastern Venezuela, and apparently disjunctly in the Brazilian state of Acre (Fig. 6); occurs mostly in riparian forest and in low coastal forest on white sands, occasionally also on granitic outcrops in the interior, from sea level to 850 m in elevation. Another subspecies, *R. hostmanniana* subsp. *freemanii* (Sprague & R.O.Williams ex R.O.Williams & Cheesman 1928: 39) Steyermark (1967: 414) is found in similar habitats in Trinidad, Tobago, Grenada, and the coastal cordillera of Venezuela.

Phenology:—Flowering specimens were collected throughout the year; fruiting specimens throughout the year, except December–January, with a peak in August–September.

Notes:—This species is here circumscribed in a narrower sense than previously (e.g., Zappi & Steyermark 2004; Bruniera 2015), and as thus includes only two subspecies, which distributions are discussed above. It is similar to *Rudgea billietiae*, *R. bolivarensis*, *R. cornigera, R. maypurensis* and *R. tanaosepala*, and has frequently been confused with all of them. Differences between these species are summarised in Table 1; especially diagnostic for *R. hostmanniana* is the shape of the stipules, with the dorsal keel long exceeding the lateral appendages (Fig. 1D). An illustration of *R. hostmanniana* (sensu stricto) may be found in the *Flora de Venezuela* (Steyermark 1974, fig. 166) and is quite accurate, although the tertiary leaf veins are usually less apparent than depicted on the figure.

The above species description is based on subsp. *hostmanniana*. Subspecies *freemannii* is very similar to subsp. *hostmanniana*, differing only by the densely puberulous hypanthium and outer surface of the calyx, which is a rather slight but apparently constant character. The length of the peduncle, used as an additional diagnostic character by Steyermark (1967) actually shows much overlap between the two taxa. Not all authors have accepted the distinction of subsp. *freemannii*, for instance Acevedo-Rodriguez & Strong (2012: 842) considered it a synonym of *R. hostmanniana*. Zappi & Steyermark (2004) recognized three subspecies, although the third one, subsp. *maypurensis* (Standley) Zappi (in Zappi & Steyermark 2004: 808), is here reinstated in its original specific rank.

The original description of *Rudgea hostmanniana* is based on several syntypes: *Hostmann 548* from Surinam, *Rob. Schomburgk 12* and *Rich. Schomburgk 2* from Guyana (or more likely Roraima state, Brazil), and *Lockhart s.n.* from Trinidad, the latter belonging to subsp. *freemannii*. The second and third syntype actually represent the same collection (van Dam 2002: 100) since the Schomburgk brothers travelled together and often used separate numbers for the same gathering. Steyermark (1967: 413) cited *Hostmann 548* as type, which is to be treated as a first-step lectotypification (Art. 9.10 of the *Code*) because he did not indicate the herbarium of deposit. The specimen of this collection in K, which is presumably the one studied by Bentham, is here selected as the second-step lectotype.

Müller Argoviensis (1881: 205), in the original description of *Rudgea intercedens*, did not explicitly cite a type, and he only indicated "Habitat in Brasilia (ex hb. Juss., in hb. Rich., nunc in hb. Franq.)". A specimen from the Richard herbarium in P, which is annotated *R. intercedens* probably in Müller's hand, and bears the indication "Brasiliae – herb. Juss.", is here selected as lectotype. This specimen matches *R. hostmanniana* in every detail; the synonymy of the two species, which Zappi (2003: 585) already noted to be strongly similar, was recognized by Bruniera (2015) in her thesis, and is here formally established.

The fruits of *Rudgea hostmanniana* are usually red or orange; two specimen labels report that they turn black at maturity (*Davidse 4110; Tostain et al. 1884*) but this indication remains to be confirmed in the field. As far as is known, in all other species of the complex the mature fruits are red.

A collection from Colombia, *M.B. Monsalve 741* (GB), cited as *Rudgea hostmanniana* subsp. *hostmanniana* by Bruniera (2015: 137) probably represents a new species; its stipules lack the characteristic central keel of *R. hostmanniana* and its inflorescences have unusually large bracts. No authentic collection of *R. hostmanniana* from Colombia has been seen by the authors, although the species could be expected in the southeastern region of the country.

Additional Specimens Examined:—BRAZIL. **Amazonas:** Km 1–5 road Boca do Acre – Rio Branco, 24 September 1966 (fl.), *G.T. Prance, B.S. Pena, J.F. Ramos & E.R. Videcki Jr 2534* (U).

FRENCH GUIANA. NE foot of Montagne des Pères, 5 km S of Kourou, 5°06'N, 52°36'W, 11 March 1994 (fl. & fr.), *L. Andersson, C. Gustafsson, C. Persson & J. Rova 1954* (CAY, GB, K); Saut Dalles, Bassin du Sinnamary, 5°27'N, 53°01'W, 24 September 1992 (fl.), *B. Bordenave 236* (CAY, P, U); Saut l'Autel, Bassin du Sinnamary, 4°42'N 52°58'W, 25 October 1992 (fl. buds), *B. Bordenave 391* (CAY, P); ibid., 4°45'N, 53°06'W, 10 March 1994 (fl. & fr.), *B. Bordenave 806* (CAY, P, U); Malmanoury, 5 February 1995 (st.), *L. Cadamuro & F. Solacroup 242* (CAY); Fusées Sondes, 20 February 1995 (fr.), *L. Cadamuro & F. Solacroup 292* (CAY); Diamant, 22 February 1995 (st.), *L. Cadamuro & F. Solacroup 340* (CAY); Kikiwi, 2 March 1995 (st.), *L. Cadamuro & F. Solacroup 349* (CAY) & *358* (CAY); Crique Canceler, 5°26'N, 53°02'W, 8 December 1996 (fl.), *G. Cremers, F. Crozier & M. Hoff 14474* (P, U); Rivière de Kourou, March 1875 (fl. & fr.), *J. Crevaux s.n.* (P); village Boni de Assici, bassin du Maroni, 3°49'N,

54°12’W, 17 March 1989 (fl. & fr.), *M. Fleury 773* (CAY); Piste de Saint-Elie, 20 February 1985 (fr.), *P.-M. Forget 276* (CAY); Lieu-dit Maya, route de la Carapa, 4°56’59”N, 52°26’30”W, 1 March 2007 (fr.), *S. Gonzalez 1095* (CAY); rive du Grand Inini vers Bicade, 21 August 1970 (fr.), *J.-J. de Granville C-31* (CAY, P, U); îlets du Saut Emérillon sur le Grand Inini, 27 August 1970 (fr.), *J.-J. de Granville C-107* (CAY, P); bordure du Grand Inini, à Dégrad Nicole, 4 September 1970 (fr.), *J.-J. de Granville B-3657* (CAY, P); Rivière Petite Ouaqui, entre Saut Macaque et Saut Baille-Nom, 12 July 1973 (fl.), *J.-J. de Granville B-4954* (CAY, P, U); Rivière Grande Ouaqui, à 8 km de son confluent avec la Petite Ouaqui, 13 July 1973 (st.), *J.-J. de Granville 1814* (CAY, P); Rivière Petite Ouaqui, “Saut Baille Nom”, 14 July 1973 (st.), *J.-J. de Granville 1829* (CAY, P, U); Fleuve Mana, Saut Fracas, 23 July 1981 (fl. buds), *J.-J. de Granville 4640* (CAY, P); Rivière Mana, Gros Saut, 25 July 1981 (fr.), *J.-J. de Granville 4654* (CAY, P, U); Rivière Grand Inini en aval et en amont de Dégrad Fourmi, 13 September 1985 (fr.), *J.-J. de Granville 8180* (CAY, P, U); Site Ariane 4 - Crique Karouabo, C.S.G., 11 May 2007 (st.), *J.-J. de Granville 17387* (CAY); Crique Arouany, 22 August 1962 (fl. & fr.), *F. Hallé 632* (CAY, K, P); Saut Takari-Tanté, Bassin du Sinnamary, 4°37’N, 52°56’W, 16 November 1989 (fl.), *M. Hoff 5864* (CAY, U); Saut Aïmara, Bassin du Sinnamary, 16 January 1992 (fl.), *M. Hoff 7576* (CAY); Rivière Iracoubo, entre roche Hirondelle et Carbet Gendarmerie, 28 December 2010 (fl.), *O. Lachenaud 981* (BR, CAY, MO); Kourou, Campus du CIRAD, 30 December 2010 (st.), *O. Lachenaud 1011* (BR, CAY); “Cayenne”, no date (fl.), *J.B. Leblond s.n.* (G); without locality, 1859, *F.M.R. Leprieur s.n.* (G); Haute Mana, en amont de Gros Saut, 29 August 1981 (fr.), *C. Moretti 1259* (CAY, P); entre Saut Vata et Saut Bérard, 22 September 1965 (fr.), *R.A.A. Oldeman 1541* (CAY, P, U); Fleuve Sinnamary, ca. 4 km en amont sur la Crique Tigre, 4 August 1967 (fr.), *R.A.A. Oldeman B-1153* (CAY, P); Fleuve Sinnamary, ca. 6 km en amont sur la Rivière Courcibo, 8 August 1967 (fr.), *R.A.A. Oldeman B-1188* (CAY, P); Rivière Courcibo à ca. 1.5 km en amont su Saut Caouène, 10 August 1967 (fr.), *R.A.A. Oldeman B-1202* (CAY, P, U); Fleuve Kourou, ca. 700 m en amont du Saut Léodate, 25 September 1967 (fr.), *R.A.A. Oldeman B-1388* (CAY, P, U); Fleuve Sinnamary, Saut Bois Blanc, 22 April 1969 (fl.), *R.A.A. Oldeman B-2305* (CAY, P, U); without locality, 1820 (fl.), *G.S. Perrottet s.n.* (G, P); without locality, July 1824 (fl.), *P. A. Poiteau s.n.* (K); Kourou, Campus Silvolab, 5°10’N, 52°39’W, 8 April 2001 (fl.), *M.-F. Prévost & M. Fournier 4151* (BR, CAY, G, K, P, U); ibid., 16 April 2001 (fr.), *M.-F. Prévost & D. Sabatier 4154* (CAY, G, K, MO, P); ad montem Macouriae, s.d. (fl.), *L.C.M. Richard s.n.* (P); près de Saut Macaque, rives du Grand Ouaqui, 12–14 September 1961 (fr.), *R. Schnell 12153* (P); Crique Ouaqui, September 1961 (fr.), *Service Forestier (BAFOG) 7769* (CAY, P, U), *7807* (CAY, P, U); Forêt de Maya, route de la Carapa, Macouria, 31 March 2008 (fr.), *O. Tostain, T. Deville & V. Pelletier 1884* (CAY).

GUYANA. Towakaima Falls, Barama River, 7°18’N 59°59’W, 3 October 1996 (fr.), *T. R. van Andel, E. Samuels, N. George & M.A.J.P. Smeets 1692* (U); Mabaruma, Aruku River, 11 March 1945 (fl.), *D.B. Fanshawe FD 5129* (K, U); Kaow Island, Essequibo River, 13 July 1943 (fr.), *Forest Department 4132* (K); SE Kanuku Mountains, 3°03’N, 59°25’W, 25 June 1989 (fr.), *L.J. Gillespie, D. Gopaul & Peterson 1824* (K, U); Surama Lake, 4 km NE of Surama Village, 3 May 1992 (fl.), *B. Hoffman, D. Allicock & T. Allicock 1567* (CAY); Kanuku Mts, Moco Moco R., 3°18’N, 59°39’W, 19 July 1995 (fr.), *M.J. Jansen-Jacobs, C. Simmons, A. Jacobs-Brouwer, V. James & R. Andrew 4574* (CAY, K, P, U); Upper Essequibo Region, Rewa River, Spider Mountains, 3°08’N, 58°32’W, 17 September 1999 (fl.), *M.J. Jansen-Jacobs, B.J.H. ter Welle, P.P. Haripersaud, O. Muller & M. van der Zee 5955* (U); ibid., 20 September 1999 (fl.), *M. J. Jansen-Jacobs, B.J.H. ter Welle, P.P. Haripersaud, O. Muller & M. van der Zee 6015* (CAY, K, P, U); Mazaruni River, September 1880 (fl.), *G.S. Jenman 765* (K); Essequibo River, October 1881 (fl.), *G.S. Jenman 1193* (K); Bartica, November 1888 (fl.), *G.S. Jenman 4675* (K, U); Mazaruni River, August 1889 (fr.), *G.S. Jenman 5440* (K); no locality, 1841 (fl.), *Rob. Schomburgk 12* (BM, K, P); Isorova Hill, June 1912 (fr.), *F. A. Stockdale 247* (K); Cuyuni River, Crab Fall, 30 April 1933 (fl.), *T.G. Tutin 16* (BM, K).

SURINAME. Without locality, 1841 (fl.), *Berthoud-Coulon 197* (BM), *198* (BM); in districtu Surinamensi Para, February–April 1844 (fl.), *A. Kappler 1455* (P); ibid., *A. Kappler 1485* (G, P, U); Coppename River, near Raleigh Falls, 13 September 1933 (fr.), *J. Lanjouw 814* (INPA, K, U); along Kort en Duur Creek, tributary of Perica River, 29 November 1953 (fl.), *J.C. Lindeman 5117* (BR, U); Saramacca River Headwaters, Jacob Kondre, 16 June 1944 (fr.), *B. Maguire 23833* (BR, K, P, U); Paramaribo, 23 May 1916 (fr.), *J.S. Samuels 317* (K, L); in sylvis Paraensis prope Onoribo, 8 March 1838 (fl.), *F. Splitgerber 665* (L); fluv. Corantijn, Kaboerie - Winana, 27 October 1916 (fr.), *G. Stahel & J.W. Gonggrijp 2985* (U); Corantyne River, near Mac Claren, 23 January 1963 (fl.), *J. G. Wessels Boer 555* (P, U); Paramaribo, 1851 (fr.), *H. R. Wullschlaegel 242* (BR); “Para”, no date (fl.), *H. R. Wullschlaegel 995* (BR).

VENEZUELA. **Miranda:** 3 km SW of Araguita, along road between Caucagua and Altigracia de Orituco, 17 November 1973 (fr.), *G. Davidse 4110* (L); Catalina, May 1896 (fl. buds), *H.H. Rusby & R.W. Squires 209* (BM); ibid., May 1896 (fl.), *H.H. Rusby & R.W. Squires 444* (K).

6. *Rudgea maypurensis* Standley (1930b: 72). – *Rudgea hostmanniana* subsp. *maypurensis* (Standley) Zappi (in Zappi & Steyermark 2004: 808). (Figs. 1E, 2E)

Type:—VENEZUELA. Amazonas: Maypures, June 1854 (fr.), *R. Spruce 3615* (holotype, K! [K000447196]; isotype, P! [P04008962]; fragment, G! [G00436708]).

R. corocoroensis Steyermark (1988: 349), ***syn. nov.***

Type:—VENEZUELA. Amazonas, Dpto. Atures, 5–8 km NW of settlement of Yutajé, 3 km W of Rio Coro-Coro, W of Serranía de Yutaje, 5°40'N, 66°09'W, 700–1000 m, 10 March 1987 (fl.), *R. Liesner & B. Holst 21827* (holotype MO! [MO-2049858]; isotypes, F! [N°2030267], NY! [NY00133209], PORT! [PORT34149], U! [U0006286], US! [US00153756]).

Much-branched shrub 1–4 m tall; twigs densely patent-puberulous or more rarely glabrous, 1.5–3 mm thick, soon covered with a pale straw-coloured bark, becoming greyish on older stems. *Stipules* 3–10 x 3–5.5 mm, densely patent-puberulous to glabrous, marcescent and soon corky, consisting of a basal sheath 1–3 mm long (usually early split) bearing on each side of the node 4–6 erect linear terminal appendages 2–7 mm long, and 4–10 recurved dorsal appendages 1-3 mm long, these often connate at base into a short keel. *Leaves* opposite; petioles 0.1–0.7 cm long, patent-puberulous to glabrous; blades elliptic, 2.8–12 × 1–8.8 cm, slightly cordate to rounded at base, obtuse to hardly acuminate at apex, very thick, entirely glabrous, drying yellowish-green (or the young leaves blackish-green); midrib flat or concave above; secondary veins 6–11 on each side of midrib, rather strongly ascending, hardly prominent; tertiary venation not or hardly distinct; domatia absent. *Inflorescences* terminal, in rather condensed pyramidal panicles, 1.8–8.8 cm long, erect, shortly spreading-puberulous or more rarely glabrous; peduncle terete, 1–6.5 cm long; branched portion 0.8–3.5 × 1–3 cm; secondary branches (2–)3–4 per node, 0.4–2.7 cm long; bracts 1.5–5 × 0.7–2 mm, triangular to lanceolate, entire or often dentate at base, acute at apex, glabrous outside, pubescent inside. *Flowers* sessile, 5-merous, heterostylous. *Hypanthium* obconical, 0.7 mm long, glabrous. *Calyx* tube extremely reduced, lobes triangular, 0.5–1.8 × 0.5–0.7 mm, acute or obtuse at apex, densely ciliate. *Corolla* white (the lobes sometimes pale yellow), hypocrateriform; tube narrowly funnel-shaped, 3–4 mm long, 1–1.2 mm wide at base, 1.7–2 mm wide at mouth, glabrous outside, villose in the upper part inside; lobes narrowly triangular, 2.5 x 1.3 mm, glabrous to puberulous at apex outside, papillose inside, not corniculate dorsally. *Stamens* included, with subsessile anthers in long-styled flowers, or well-exserted, with filaments 3 mm long, in short-styled flowers; anthers 1.5 x 0.3 mm. *Disk* cylindrical to slightly conical, 0.5–0.8 mm long, glabrous. *Style* exserted, 6 mm long in long-styled flowers, or included, ca. 3.5 mm long in short-styled flowers, glabrous or densely pubescent in the distal half; lobes 0.5–1 mm long, stigmatic surface papillose. *Fruits* obovoid to subglobose, 4.5–6 × 4–5.5 mm when dry, green when immature, orange to red when mature, glabrous, sessile, crowned with persistent calyx 1–1.5 mm in diameter. *Pyrenes* plano-convex, hemi-obovoid, 5–5.5 × 4.2–5 mm, dorsal side with 2–4 prominent to very weak longitudinal ridges, slightly verrucose, ventral side ± smooth. *Seeds* with a deep T-shaped ventral furrow.

Distribution and ecology:—Restricted to southeastern Venezuela (Amazonas state) and adjacent northwestern Brazil (Amazonas state), and probably eastern Colombia (Fig. 6); occurs in dry forests bordering granitic rocks ("lajas") where it is locally abundant, at 85–200 m in elevation.

Phenology:—Specimens with flowers were collected in March–April, with immature fruits in April–May, and with mature fruits in June–August and once in November.

Notes:—This taxon, treated as a subspecies of *Rudgea hostmanniana* by Zappi & Steyermark (2004), is distinct enough to retain its original species status. It differs from *R. hostmanniana* by its stipules (compare Fig. 1D & 1E), its corolla lobes that are not corniculate at apex, and its pyrenes that are dorsally verrucose (Table 1). The leaves are also more coriaceous and shiny than in *R. hostmanniana*, with an often slightly cordate base and a usually shorter petiole, and the fruits are generally smaller. An illustration of this taxon (as *R. hostmanniana* subsp. *maypurensis*) has been published by Zappi & Steyermark (2004: fig. 618).

The original description of *Rudgea maypurensis* was published in Standley (1930b: 72), not in Standley (1931: 434) as incorrectly cited by Steyermark (1967: 411). The flowers are here described for the first time; they are mentioned neither in the protologue, nor in any of the subsequent descriptions (Standley 1930b: 72; Steyermark 1967: 411, 1974: 1070-1071; Zappi & Steyermark 2004: 808–809).

The type specimen of *Rudgea corocoroensis* was only seen in photograph, which is sufficient to establish that it agrees with *R. maypurensis* in all essential characters, particularly the diagnostic stipules, although the petioles are longer than usual for the species; the two names are therefore synonymized here. Steyermark (1988: 350) described the stipules of *R. corocoroensis* as having "5-7 rigid aculeae arising at or just below the sheath summit", apparently

omitting the dorsal appendages that are clearly present, and the calyx tube as 2 mm long, which is instead much smaller. He considered *R. corororoensis* as related to *Rudgea morichensis* Steyermark (1967: 424) but the latter is quite different, e.g. in its deeply cupular calyx and prominent tertiary leaf veins, and does not seem to belong to the *R. hostmanniana* complex.

The types of both *Rudgea maypurensis* and *R. corocoroensis* have glabrous twigs, petioles and inflorescences; in all other collections seen these parts are shortly patent-puberulous.

A collection from Brazil, cited below, is a new record for the country; although it is sterile and was only seen on photograph, its identification is without any doubt. A specimen from Colombia, *Cuatrecasas 4052*, referred to this species with some doubt by Steyermark (1967: 411), has not been seen for this revision.

Additional Specimens Examined:—BRAZIL. **Amazonas:** vicinity of Pico Rondon, Perimetral Norte Highway km 211, 1°32'N 62°48'W, 2 February 1984 (st.), *G.T. Prance, I.L. do Amaral, J.J. Pipoly, A.S. Tavares, C.D.A. da Mora & A. Cress 28731* (NY).

VENEZUELA. **Amazonas:** 8 km S of Puerto Ayacucho, estación de piscicultura, 5°36'N, 67°37'W, 13–15 April 1978 (fl.), *G. Davidse & O. Huber 14888* (K); Raudal d'Atures, 1 August 1887 (fr.), *Gaillard 36* (P); Estación de Piscicultura de Puerto Ayacucho, 5°37'N, 67°37'W, 15 April 1977 (st.), *O. Huber 617* (K); ibid., 15 April 1977 (fl.), *O. Huber 617a* (K); ibid., 15 April 1977 (imm. fr.), *O. Huber 617b* (K); 1–2 km E of Hotel Amazonas, Puerto Ayacucho, 8 November 1953 (fr.), *B. Maguire, J.J. Wurdack & G.S.Bunting 36034* (K); 6 km N of Puerto Ayacucho on road to El Burro, 26 April 1984 (fl.), *T. Plowman 13733* (K); ibid., *T. Plowman 13742* (K); Cerro Piapoco, cerca del km 12–13 de la carretera Puerto Ayacucho–Sanariapo, 31 July 1967 (fr.), *L. Ruiz-Terán 4444* (BR, K); Puerto Ayacucho, 18 May 1940 (fr.), *L. Williams 12972* (K).

7. *Rudgea pungens* (Steyermark) C.M. Taylor, Bruniera & Zappi (2015: 45, p. 4). – *Psychotria pungens* Steyermark (1972: 677). (Fig. 7 D–F).

Type:—FRENCH GUIANA. Without locality, s.d., *F.M.R. Leprieur 118* (holotype, P! [P00837150]; probable isotype (unnumbered collection), G! [G00418599, G00418600]).

Shrub 0.3–2 m tall, with nearly horizontal branches; twigs glabrous, 1–1.5 mm thick, soon covered with a pale straw-coloured bark. *Stipules* 8–16(–20) × 1–7 mm, glabrous, marcescent and soon corky, consisting of a narrow tubular sheath 5–9(–12) mm long (usually split at flower-bearing nodes) bearing 8–15 terminal linear appendages 3–8 mm long, and 5–7 dorsal linear appendages 0.5-3 mm long, forming a very short decurrent keel inserted 1–3 mm above the base of the stipule. *Leaves* opposite; petioles 0.2–0.6 cm long, glabrous; blades elliptic, 6.5–14.5(–16) × 1.8–4.5(–5.5) cm, acute or obtuse at base, gradually long-acuminate at apex, very thick, entirely glabrous, drying olive green to olive brown; midrib concave above; secondary veins 5–10 on each side of midrib, strongly ascending, forming an angle of 45–60° with the midrib; tertiary veins invisible in fresh leaves, sometimes slightly prominent when dry; domatia absent. *Inflorescences* terminal, subcapitate and involucrate, ca. 8-flowered, patent to sub-erect, glabrous, sessile or pedunculate; peduncle (when present) terete, to 1 cm long; flower-bearing portion 1.3–2.2 × 1.4–3.5 cm, secondary branches apparently absent or extremely reduced in flower, to 2 mm long in fruit; bracts pale green, numerous and imbricate in several rows, 10–20 × 2–7 mm, lanceolate, entire, acute at apex, glabrous or shortly ciliate, erect or patent, persistent in fruit. *Flowers* sessile, 5-merous, heterostylous. *Hypanthium* obovoid, 1.5 mm long, glabrous, *Calyx* tube 0.5–1 mm long, glabrous; lobes linear to narrowly triangular, 1.2–3.5 × 0.5–1 mm, glabrous or ciliate. *Corolla* white, tube narrow and almost cylindrical, 13 mm long, 1 mm wide at base, 1.5–2.5 mm wide at mouth, glabrous outside (inside not seen); lobes narrowly triangular, 2.5 × 1 mm, glabrous, with short, obtuse dorsal appendage 0.5 mm long. *Stamens* included in long-styled flowers, or exserted with filaments exceeding corolla throat by 1 mm in short-styled flowers; anthers 2.3 × 0.3 mm. *Disk* shortly cylindrical, 0.5 mm long, glabrous. *Style* exserted, exceeding corolla mouth by 1.5 mm in long-styled flowers, or included in short-styled flowers. *Fruits* ovoid with truncate apex, 11 × 7–8 mm when fresh, 7–10 × 5–7 mm when dry, dark red-brown and hard when immature, cherry red when mature, glabrous, sessile, crowned with persistent calyx 2.5–4 mm in diameter. *Pyrenes* plano-convex, hemi-obovoid to hemi-ellipsoid, 9 × 6.5 mm, dorsal side smooth, ventral side smooth. *Seeds* with a deep T-shaped ventral furrow.

Distribution and ecology:—This species is only known from French Guiana (Fig. 5), where it occurs on the main summits of the central Inini-Camopi chain (Mts Atachi Bacca to Mts Bakra) and disjunctly at low altitudes in the northeast; it should be expected in adjacent parts of Suriname and Brazil. It is apparently restricted to relatively low forests on rocky substrates, 5-800 m in elevation, and is locally abundant.

Phenology:—Flowering collections were made in January, May and August; fruiting collections in January, March–April (full-sized, but still hard) and August (mature fruits). As in the similar *Rudgea billietiae*, the fruits probably take several months to mature.

Notes:—This species, originally described in *Psychotria* (Steyermark 1972), was recently transferred to *Rudgea* (Taylor *et al.* 2015) but its affinities within the genus were still unclear. Taylor and Bruniera (2018) mentioned its similarity to the *R. bracteata* J.H. Kirkbride (1981: 97) group, especially because of the well-developed bracts, but members of that group have larger fruits, and stipules with a prominent dorsal keel and without marginal appendages. The involucrate inflorescences and narrowly tubular stipules of *R. pungens* are unusual characters in *Rudgea*, but the discovery of *R. billietiae*, with similar stipules and lax inflorescences, links it to *R. cornigera, R. hostmanniana* and *R. tanaosepala*, which have lax inflorescences and shorter stipular sheaths. The differences between these species are summarised in Table 1.

The original description of the species was based on a single specimen without fruits or corollas, and is therefore incomplete on several points. The species is now known from additional complete material, which allows to present here a full description; only the interior of the corolla tube cannot be described, because the flowers are too few for a dissection to be made. The dimensions in brackets refer to a vegetative collection (*Granville 4002*) from Mount Bakra, French Guiana, which has slightly larger leaves and stipules; though it almost certainly belongs to this species, confirmation with reproductive material from the same area would be reassuring.

Specimens Examined:—FRENCH GUIANA. Crique Kapiri – RN2, bassin de l'Approuague, 4°07'N, 52°05'W, 11 January 1991 (fallen fl.), *G. Cremers 11474* (CAY); savane-roche [inselberg] Virginie, 4°11'N, 52°08'W, 18 February 2009 (fallen fl.), *C. Delnatte, F. Billiet, J.-J. de Granville & B. Jadin 1682* (CAY); Fleuve Sinnamary, rive droite, layon ONF (n°7) direction Sud, à 7 km du fleuve, 1 May 1969 (fl.), *J.-J. de Granville 128* (CAY); sommet des Monts Atachi Bacca, 4 March 1971 (fr.), *J.-J. de Granville 765* (CAY, P); Monts Galbao, 10 km WSW Saül, 14 March 1973 (imm. fr.), *J.-J. de Granville 1534* (CAY, P); Monts Bakra, versant Sud, 5 km WSW du pic Coudreau, 28 September 1980 (st.), *J.-J. de Granville 4002* (CAY, P); Montagne Bellevue de l'Inini, zone centrale, 23 August 1985 (fl. & imm. fr.), *J.-J. de Granville, L. Allorge, G. Cremers, A.R.A. Görts-van Rijn & J.F. Kodjoed 7770* (BR, CAY, P); Crique Gabaret, bassin de l'Oyapock, Saut Mérignan, 13 April 1988 (fallen fl.), *J.-J. de Granville 10275* (CAY); Monts Atachi Bacca, versant Nord, 9 km au SE de Gobaya Soula, 3°33'N, 53°55'W, 12 January 1989 (fl.), *J.-J. de Granville, G. Cremers, J.I. Hagemann, B.E. Leuenberger, R.W. Sanders & M. Sangrey 10616* (CAY, P); Monts Atachi Bacca, est du plateau sommital, 3°33'N, 53°55'W, 22 January 1989 (fr.), *J.-J. de Granville, G. Cremers, J.I. Hagemann, B.E. Leuenberger, R.W. Sanders & M. Sangrey 10861* (CAY, P); layon Régina – Kaw, 4°21'W–52°08'W, 7 August 1997 (fallen fl.), *V. Hequet 688* (CAY); Route Régina – Saint Georges, piste de la savane-roche [inselberg] Virginie, 4°11'05"N, 52°08'13"W, 6 April 2014 (fr.), *O. Lachenaud 1720* (BR, CAY, L, MO, P); without locality, s.d. (fl.), *L.C.M. Richard s.n.* (P [P04008549], mixed with *R. billietiae*); sommet nord du Mont Galbao, 29 January 1978 (fallen fl.), *Tay 91* (MPU).

8. *Rudgea tanaosepala* Sandwith (1933: 334). Fig. 1F, 2F.

Type:—GUYANA. Simuni Creek, Rupununi River, 25 August 1931 (fl.), *T.A.W. Davis* in *Forest Department 2149* (holotype, K! [2 sheets, K000447201, K000447202]).

Much branched shrub 2–7 m tall; twigs glabrous or minutely puberulous, 2–2.5 mm thick, soon covered with a pale straw-colored bark. *Stipules* 6.5–12 × 2–4.5 mm, glabrous or minutely puberulous, marcescent and soon corky, consisting of a short basal sheath 2–3.5 mm long (usually split at flower-bearing nodes) bearing on each side of the node one bifid lateral appendage 3–5.5 × 0.5 mm, and a central keel (4.5–)7–13 × 1–2 mm, the latter usually bifid for 2.5–4 mm long (rarely ± irregularly fimbriate) with each of the lobes divided in 3–5 linear appendages 1–2.5 mm long. *Leaves* opposite; petioles 0.1–0.7 cm long, glabrous or minutely puberulous; blades oblanceolate to narrowly elliptic, 7–20.7 × 1.8–7.2 cm, obtuse to rounded at base, gradually acuminate at apex, very thick, entirely glabrous, drying greyish-green; midrib concave or flat above; secondary veins 7–11 on each side of midrib, weakly ascending and forming loops 2–3 mm before margin; tertiary veins very lax and slightly prominent when dry (probably invisible when fresh); domatia absent. *Inflorescences* terminal, paniculate or rarely glomerulate, 0.8–4.4 cm long, erect, puberulous; peduncle terete, 0.1–2.4 cm long; flower-bearing portion 0.5–2.2 × 1.4–3.3 cm; secondary branches 3–4 per node, to 1.2 cm long, rarely absent; bracts 5–7 × 0.7–1.2 mm, linear to narrowly lanceolate, entire or with linear lateral teeth, sparsely and shortly puberulous outside. *Flowers* sessile, 5-merous, heterostylous, fragrant. *Hypanthium* obconical to almost cylindrical, 0.8 mm long, glabrous. *Calyx* tube extremely reduced, lobes linear, 3–5 × 0.7–1.2 mm, shortly and

sparsely puberulous outside. *Corolla* white, hypocrateriform; tube narrowly infundibuliform, 6–7 mm long, 1–1.3 mm wide at base, 1.5–3 mm wide at mouth, glabrous outside, with a ring of dense short hairs at stamens insertion inside; lobes triangular to narrowly elliptic, 3.5–5 × 1–1.5 mm, puberulous outside at the apex, minutely papillose inside, with narrowly cylindrical (or rarely short and obtuse) dorsal cornicula (0.5–)1–1.5 mm long. *Stamens* included in long-styled flowers, or exserted with filaments exceeding corolla mouth by 2–5 mm and anthers 2.2 × 0.4 mm in short-styled flowers. *Disk* shortly cylindrical, 0.5 mm long, glabrous. *Style* exserted, 9–10 mm long in long-styled flowers, or included, 6 mm long, in short-styled flowers, lobes with papillose stigmatic surface. *Fruits* globose to ellipsoid, 7–11 × 7–11 mm when dry, dark brown (presumably immature) to red or orange (mature), glabrous, sessile, crowned with slightly accrescent persistent calyx 2.5 mm wide. *Pyrenes* plano-convex, hemi-ellipsoid or hemi-obovoid, 7–7.5 × 6.5 mm, dorsal side with 3 often very faint ridges mostly visible at the base, smooth between the ridges, ventral side smooth. *Seeds* with a deep T-shaped ventral furrow.

Distribution and ecology:—A species endemic to central Guyana (Fig. 5), locally common in the middle Essequibo River basin; it grows in lowland forest on white or brown sand, sometimes along streams, at 80–500 m elevation.

Phenology:—Flowering specimens were collected in August and October–November; and fruiting specimens in February–April and September–October.

Notes:—This species was for a long time only known from the type (cf. Steyermark 1967: 407). It is now fairly well represented in herbaria, where most of the specimens had so far been mistaken for the closely similar and much more widespread *Rudgea hostmanniana*. The species is distinctive, within the *R. hostmanniana* complex, by its long and very narrow calyx lobes (Fig. 2F; Table 1); the secondary leaf veins are also less ascending than in other species, though a few specimens of *R. cornigera* approach *R. tanaosepala* in this respect.

The inflorescences in *R. tanaosepala* are quite variable; they are usually well-branched, but sometimes the ramifications are very short or absent (e.g. *Hoffmann et al. 1488*; *Maas et al. 5885*). Specimens from the south of the range, including the type, have usually glabrous vegetative parts (rarely the twigs are sparsely puberulous) and corolla lobes with narrowly cylindrical, 1–1.5 mm long dorsal cornicula. The more northern specimens (*Ek et al. 602, 772; Maas et al. 5885*) have minutely puberulous twigs, stipules and petioles, and corolla lobes with shorter and broader dorsal cornicula, ca. 0.5 mm long; it is possible that they represent a separate infraspecific taxon.

Records of *R. tanaosepala* from French Guiana (Funk *et al.* 2007) are based on misidentified collections of the recently described *R. glomerulata* Zappi & O. Lachenaud (Lachenaud *et al.* 2022: 159). The latter differs from *R. tanaosepala* and other species of the *R. hostmanniana* complex by its stipules lacking dorsal appendages, large and deeply laciniate bracts 9–28 × 2.5–3.5 mm, longer corolla tube, 18–20 mm long that is entirely glabrous within, longer calyx tube 1.5–4 mm long, bipartite disk, yellow to yellow-orange fruits, and densely pubescent twigs, petioles and abaxial side of leaf veins.

A collection from the Bakhuis Mountains, in Suriname, *Bordenave, Doerga, van Troon & James 8619* (BBS n.v., CAY) resembles the variants of *Rudgea tanaosepala* with glomerulate inflorescences, but has smaller leaf blades, 5–7 × 0.8–1.7 cm, and stipules with four subequal dorsal appendages on each side and no dorsal keel. It presumably represents a new species, but the material is very poor, with only leaves, hypanthia and calyces.

Specimens Examined:—GUYANA. Iwokrama Rainforest Reserve, Iwokrama Mts, 4°20'N, 58°50'W, 22 November 1995 (fl.), *D. Clarke & B. Hoffmann 584* (CAY, U); Iwokrama Rainforest Reserve, Moco Moco II Creek, 20 mi. SW of Kurupukari on Kurupukari – Annai road, 4°25'N, 58°49'W, 24 March 1996 (fr.), *D. Clarke 1431* (CAY, U); Iwokrama International Rainforest Reserve, Iwokrama Mts, 4°19'N 58°47'W, 22 September 1996 (fr.), *D. Clarke 2492* (CAY, K, U); Iwokrama Rainforest Reserve, Iwokrama Mountains, 4°19'N, 58°47'W, 22 September 1996 (fr.), *D. Clarke 2516* (CAY, U); Iwokrama Rainforest Reserve, N of Surama, 4°10'N, 59°03'W, 20 May 1995 (fr.), *C. Ehringhaus 126* (CAY); Mabura region, West Pibiri compartment, 5°20'N, 58°30'W, 28 November 1992 (fl.), *R.C. Ek 602* (U); Mabura region, Pibiri compartment, main road, 5°01.95'N, 58°37.73'W, 20 March 1993 (fr.), *R.C. Ek, B. Gravendeel, B. Robers & M. Elsinga 772* (U); Region Potaro-Siparuni, Annai – Karupukari road, 18 km N of Surama village cut off, 0.5 km W of road, 4°14'N, 58°56'W, 29 April 1992 (imm. fr.), *B. Hoffman, T. Pennington & C. Capellaro 1488* (CAY, U); Mabura Hill, 5°19'N 58°38'W, 27 November 1981 (fl.), *P.J.M. Maas, A. Mennega & B.J.H. ter Welle 5885* (U); Iwokrama Reserve, Essequibo watershed, Georgetown–Lethem road, Mount Daniel transect, 4°28'26"N, 58°47'05"W, 27 February 1995 (fr.), *P. Mutchnik 973* (K).

TABLE 1. Diagnostic characters of species in the *Rudgea hostmanniana* complex (significant characters in **bold**).

	R. billietiae	***R. bolivarensis***	***R. cornigera***	***R. coussareoides***	***R.hostmanniana***	***R. maypurensis***	***R. pungens***	***R. tanaosepala***
Stipule sheath	7.5–12 mm long, longer than broad	3.5–5 mm long, broader than long	3–5 mm long, broader than long	2.5–7 mm, broader than long	3–5 mm long, broader than long	1–3 mm long, broader than long	5–12 mm long, longer than broad	2–3.5 mm long, broader than long
Stipule appendages	long terminal appendages + short dorsal ones inserted in upper half of the stipule	all dorsal and shorter than sheath, in 2 groups (1 between every pair of leaves)	central keel + lateral appendages of about the same length	all dorsal and shorter than sheath, in 6 groups (2 between every pair of leaves)	central keel + much shorter lateral appendages	erect terminal appendages + **recurved dorsal appendages**, keel not or hardly distinct	long terminal appendages + short dorsal ones inserted in lower half of the stipule	central keel + slightly shorter lateral appendages
Leaves	opposite	opposite	opposite	**ternate**	opposite	opposite	opposite	opposite
Petiole length	2–10 mm	3–20 mm	2–8 mm	8–25 mm	5–20 mm	1–7 mm	2–6 mm	1–7 mm
Leaf base	decurrent	acute to rounded	obtuse	decurrent	acute (rarely obtuse)	obtuse to **slightly cordate**	acute to obtuse	obtuse to rounded
Tertiary veins (dry state)	not or weakly prominent	very prominent	weakly prominent	very prominent	not or weakly prominent	invisible	not or weakly prominent	weakly prominent
Inflorescences	ramose (sometimes shortly), glabrous	ramose, puberulous	ramose, puberulous	ramose, puberulous	ramose, puberulous	ramose, glabrous to puberulous	subcapitate, glabrous	ramose or not, puberulous
Bracts	linear to lanceolate 3–5 × 0.3–1.5 mm	triangular, ca. 0.7 × 0.5 mm	subulate to triangular, 1.5–3 × 0.3–1.5 mm	triangular, 1–2.5 × 0.5–2 mm (except leaf-like basal pair)	triangular to lanceolate, 2.5-10 × (0.7–)1.5–3 mm	triangular to lanceolate, 1.5–5 × 0.7–2 mm	large and foliaceous, 10–20 × 2–7 mm	linear to lanceolate, 5–7 × 0.7–1.2 mm
Calyx lobes	1.5–2 mm, subulate	0.5–1 mm, triangular to narrowly elliptic	0.7–1.2 mm, triangular to subulate	0.2–0.3 mm, triangular	0.7–2 mm, triangular to semi-circular	0.5–1.8 mm, triangular	1.2–3.5 mm, linear to subulate	3–5 mm, linear
Corolla tube length	6 mm	only buds seen	5–7 mm	2–2.5 mm	3–5 mm	3–4 mm	**13 mm**	6–7 mm
Corolla lobes abaxial side	corniculate, glabrous	not corniculate, glabrous	corniculate, puberulous at least near apex	not corniculate, glabrous	corniculate, pubescent at least near apex	not corniculate, glabrous or puberulous at apex	corniculate, glabrous	corniculate, puberulous near apex
Heterostyly	reciprocal (either style or stamens exserted)	? (flowers only known in bud)	**non-reciprocal** (style ± of same length but stamen position variable)	? (only long-styled morph seen)	reciprocal (either style or stamens exserted)	reciprocal (either style or stamens exserted)	reciprocal (either style or stamens exserted)	reciprocal (either style or stamens exserted)
Fruits	ellipsoid	obovoid to ellipsoid	obovoid	ellipsoid to subglobose	obovoid (rarely subglobose)	obovoid	ovoid	ellipsoid to globose
Dorsal side of pyrenes	very faintly ridged	faintly ridged	strongly ridged	faintly ridged	strongly ridged	faintly to strongly ridged and **verrucose**	smooth	ridged, sometimes faintly
Calyx width on fruit (mm)	1.5	1.5–2	1.5–2.5	1.3–2.5	1–2	1–1.5	**2.5–4**	ca. 2.5
Distribution	French Guiana	W Guyana, SE Venezuela, NW Brazil	Guyana, Suriname	Guyana, Brazil, Venezuela, Peru	Guianas, E Venezuela, northern Brazil	SE Venezuela, NW Brazil, Colombia (?)	French Guiana	Guyana

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