Octavia sessiliflora DC. and Mussaenda glomerulata Lam. ex Poir., two obscure taxa from French Guiana synonymous with members of the Alibertia group (Rubiaceae, Gardenieae)

Piero G. DELPRETE

Herbier de Guyane, UMR AMAP, Institut de Recherche pour le Développement (IRD), boîte postale 165, F-97323 Cayenne, French Guiana (France) piero.delprete@ird.fr

Claes PERSSON

Department of Biological and Environmental Sciences, University of Gothenburg, P.O. Box 461, S-405 30 Göteborg (Sweden) claes.persson@bioenv.gu.se

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ABSTRACT

During the process of completing the Rubiaceae Juss. treatment for the *Flora* of the Guianas, two little-known taxa described from material collected in French Guiana, Mussaenda glomerulata Lam. ex Poir. and Octavia sessiliflora DC., needed to be studied in order to establish their true identity. Mussaenda glomerulata was first studied by Lamarck and later published by Poiret (1797), based on specimens collected by L. C. Richard; a specimen of M. glomerulata was found in the Lamarck herbarium, which is here selected as lectotype. Mussaenda glomerulata was concluded to be synonymous with Amaioua corymbosa Kunth. Because M. glomerulata has priority over Amaioua corymbosa, the new combination Amaioua glomerulata (Lam. ex Poir.) Delprete & C. Persson, comb. nov. is here proposed. The obscure *Octavia* DC. was published by Candolle based on specimens with ovaries and fruits. After a detailed analysis of the type specimens, we inferred that the flowers of Octavia are always terminal, although sometimes they might appear axillary because of overtopping axillary shoots (pseudoaxillary). Additionally, what Candolle interpreted as 8-merous fruits is a misinterpretation, and they are instead fleshy berries with eight seeds. With these new observations in mind, we concluded that Octavia sessiliflora is synonymous with Cordiera triflora A.Rich in DC. Full synonymy, typification of the taxa involved and representative specimens of this species are here presented.

KEY WORDS Mussaenda, Amaioua, Octavia, Cordiera, Lasianthus, Gardenieae, Lasiantheae, Rubiaceae, French Guiana, Neotropics, lectotypification.

RÉSUMÉ

Octavia sessiliflora *DC. et* Mussaenda glomerulata *Lam. ex Poir., deux taxons obscurs provenant de Guyane française synonymes de deux membres du groupe* Alibertia (*Rubiaceae*, *Gardenieae*).

Pendant le processus d'achèvement du traitement des Rubiaceae Juss. pour la Flora of the Guianas, deux taxons peu connus et décrits à partir de matériel collecté en Guyane française, Mussaenda glomerulata Lam. ex Poir. et Octavia sessiliflora DC., ont du être étudiés afin de confirmer leur vraie identité. Mussaenda glomerulata a été initialement examiné par Lamarck et ensuite publié par Poiret, en utilisant du matériel collecté par L. C. Richard; un échantillon de M. glomerulata a été trouvé dans l'herbier de Lamarck, et choisi comme lectotype. Mussaenda glomerulata est reconnu comme synonyme d'*Amaioua corymbosa* Kunth. Parce que *M. glomerulata* a priorité sur Amaioua corymbosa, la nouvelle combinaison Amaioua glomerulata (Lam. ex Poir.) Delprete & C. Persson, comb. nov. est ici proposée. L'obscur Octavia DC. a été publié par Candolle, décrivant des échantillons avec ovaires et fruits, et précisant que ce taxon possède des fleurs solitaires pouvant être terminales où bien à l'apex de courts rameaux axillaires. Il y a également décrit des drupes rondes avec huit pyrènes, et rapprochait ce taxon de Pyrostria Comm. ex A. Juss. Mais, après une analyse détaillée des échantillons types, nous avons déduit que les fleurs d'Octavia sont toujours terminales, bien que parfois pouvant apparaître axillaires, à cause de la croissance des rameaux axillaires (pseudoaxillaires). Ainsi, les fruits que Candolle a interprétés comme drupes octomères sont le résultat d'une fausse interprétation, et ce sont plutôt des baies charnues avec huit graines. À partir de ces nouvelles observations, nous avons conclu qu'Octavia sessiliflora est un synonyme de Cordiera triflora A.Rich in DC., et la synonymie complète, la typification des taxons concernés, ainsi que les spécimens représentatifs de cette espèce sont ici présentés.

MOTS CLÉS Mussaenda, Amaioua, Octavia, Cordiera, Lasianthus, Gardenieae, Lasiantheae, Rubiaceae, Guyane française, Néotropiques, lectotypification.

INTRODUCTION

During the process of writing the Rubiaceae Juss. treatment for the Flora of the Guianas, two obscure taxa described from specimens collected in French Guiana, Mussaenda glomerulata Lam. ex Poir. and Octavia sessiliflora DC., needed to be studied in order to establish their identity. Both taxa were described from collections made at the end of the 18th century, and are kept in the historic sections of the Paris and Geneva herbaria, that cannot be sent out on loan. This might be one of the reasons that kept these taxa in their unresolved taxonomic situation. Therefore, considerable work was necessary by the staff of these herbaria in order to locate the specimens for this study (see acknowledgements). A short history of the specimens, typifications and conclusions based on our comparative analyses of the two taxa are presented below.

SYSTEMATICS

Mussaenda Glomerulata

Mussaenda glomerulata was first studied by Lamarck and later published by Poiret (1797) in the monumental Encyclopédie méthodique. Poiret (1797: 393, 394), after the short Latin description "Mussenda [sic] glomerulata Lam. herb. Mussenda foliis ovatoacutis; floribus terminalibus, glomerulatis." wrote (liberal translation from French): "I am only mentioning this plant, because it seems to have a strong relation with the *Mussenda* [sic], as far it is possible for me to judge from the dry and incomplete specimen that I examined. This specimen was communicated to Lamarck by [Louis Claude] Richard, who collected it in French Guiana. It has the habit of Tachia guianensis Aubl. [Gentianaceae], and has all the characters of a Rubiaceae [although Tachia Aubl. has axillary, solitary flowers]. Its young branches

are cylindrical, a little striated, lightly velutinous, with opposite, petiolate leaves, with blades ovate, acute, more than 10 inches long and up to three inches wide, narrower at base, round and wider at apex, terminating with an obtuse tip. Petioles and abaxial side of the leaves are covered with brown velvet; they are almost glabrous and with a lighter color below, marked by strongly impressed, simple, alternate [secondary] veins, with smaller transverse, much more numerous [tertiary] veins. Flowers are united in terminal branches of a densely glomerulate unit. The peduncles are simple, short, and covered, as the calyces, by a many white to silvery hairs. The calyx is campanulate, divided at mouth by five or six acute teeth. The corolla is tubular, whitish, lightly velvety outside; its tube is not much longer than the calyx. The stamens vary from five to six." Sprengel (1824), probably without seeing the original specimens, transferred this taxon to *Rondeletia glomerulata* (Lam. ex Poir.) Spreng., with the following short description: "Foliis ovatis obtusiusculis, floribus terminalibus glomerulatis pedunculatis hirsutis. Guiana. (Mussaenda glomerulata Lam.)." However, the reasons that lead Sprengel to transfer this taxon to Rondeletia L. are unknown to us. Candolle (1830: 372) returned it to Mussaenda, although as a species non satis notae, citing "Rondeletia glomerulata Spreng. Syst. 1, 707" as a synonym and without any further comment. Lemée (1954: 518) maintained it as Rondeletia glomerulata and as present in French Guiana, citing the page corresponding to Candolle's treatment. Steyermark (1967: 249), even more synthetically, wrote: "Stated as coming from the "Guiana" but no material seen." This series of switches between Mussaenda and Rondeletia, accompanied by synthetic notes, is probably due to the fact that no type material has been examined by these specialists, in order to assign this taxon to a definitive position.

Searching for type specimens of *Mussaenda glo-merulata*, the first step was to look in the Lamarck herbarium (P-Lam) at the Muséum national d'Histoire naturelle, Paris. The folder of *Mussaenda glome-rulata* contains one sheet without specimens, where are glued three labels (Fig. 1A): the bottom one is older, and bears Lamarck's handwriting (in ink) "Indeterminée – Rubiacée donnée par M^r. Rich. –

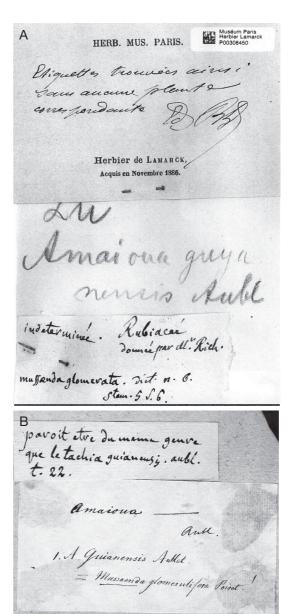


Fig. 1. — Mussaenda glomerulata Lam. ex Poir.: A, labels present in the folder of M. glomerulata (as "Mussenda glomerata" [sic]); the middle label, written in pencil, indicates the connection to "Amaioua guyanensis" [sic]; B, labels of the lectotype of M. glomerulata (= Amaioua corymbosa Kunth); the note indicating a certain similarity to Tachia guianensis Aubl. is the same observation found in the original description of Mussaenda glomerulata.

Mussenda [sic] glomerata [sic], dict. n°6 – Stam. 5, S. 6." [Undetermined – Rubiaceae – donated by Mr. [Louis Claude] Richard – Mussanda [sic Mussaenda] glomerata [sic, should be glomerulata], dictionary n° 6 [sic, should be 4], 5 or 6 stamens]; the middle label (written in pencil), of unknown author, says "Amaioua guyanensis [sic] Aubl.", and the upper label, handwritten (in ink) by Edmond Bonnet (signed "Ed. B.") says "Étiquettes trouvées ainsi sans aucune plante correspondante" [labels found here without any corresponding plant] and bears the stamp "Herbier de Lamarck, acquis en Novembre 1886" [Lamarck herbarium, acquired in November 1886]. Edmond Bonnet (1848-1922) was a botanist and herbarium curator, who was responsible to organize the Lamarck Herbarium between 1887 and 1902. With these indications, a further search in the Amaioua Aubl. folder of the Lamarck herbarium lead to a specimen that corresponds entirely to the material missing from the folder of Mussaenda glomerulata. This specimen has two labels (Fig. 1B): the lower one saying "Amaioua _____ Aubl. – 1. A. guianensis Aublet = Mussaenda glomerulifera [sic] Poiret!" and the upper one, probably handwritten by Poiret, saying "pavoit être du même genre que le Tachia guianensis Aubl. – t. 22." [seems to be of the same genus of Tachia guianensis Aubl. – t. 22]. Both labels represent a direct connection to the missing specimen and to Poiret's original description; therefore, this specimen is here selected as the lectotype of *Mussaenda glomerulata*. Additionally, it is obviously a species of *Amaioua*, with a male inflorescence, as the flowers have no ovary. In the Guianas only two species of *Amaioua* are present: *A. corymbosa* Kunth and A. guianensis Aubl.; the former is distinguished from the latter by the leaf blades with (4-)5-7(-9) secondary veins each side (vs with (5-)8-12(-14) secondary veins each side in A. guianensis), and male inflorescence cymose, with (2-)3 branches (vs fasciculate). Therefore, the specimen in question is Amaioua corymbosa, and we conclude that the two taxa are synonymous. Because the name Mussaenda glomerulata has priority over Amaioua corymbosa, a new combination is necessary, which is proposed below. In addition, full synonymy, selected specimens examined, and observations about the ecology and distribution of this species are presented below.

Family RUBIACEAE Juss. Genus *Amaioua* Aubl.

Amaioua glomerulata (Lam. ex Poir.) Delprete & C.Persson, comb. nov. (Fig. 2)

Mussaenda glomerulata Lam. ex Poir., Encyclopédie méthodique, Botanique 4: 393 (1797). — Rondeletia glomerulata (Lam. ex Poir.) Spreng., Systema Vegetabilium 1: 707 (1824). — Type: French Guiana, s.d. [1781-1785], L.C. Richard s.n. (lecto-, P-Lam [P00308470!], here designated).

Amaioua corymbosa Kunth in Humb. & Bonpl., Nova Genera et Species Plantarum 3: 419 (1820). — Type: Venezuela, Cumanacoa, Humboldt & Bonpland s.n. (holo-, P-Bonpl.!).

Amaioua fagifolia Desf., Mémoires du Muséum national d'Histoire naturelle (Paris) 6: 14 (1820). — Type: French Guiana, s.d., J. Martin s.n. (syn-, P[2 specimens], P-Juss.!).

SPECIMENS EXAMINED. — Mexico. Chiapas, Mun. Las Margaritas, W side of Laguna Miramar, E side of San Quintín, 350 m, 11.II.1973, fr., *Breedlove 33144* (NY). Belize. Cayo, near Augustine, 450 m, 26.VIII.1980, fem. fl., *Whiteford 2222* (BM).

Nicaragua. Comarca de El Cabo Río Leicus, 28 km SW of Waspan, 66 m, 25.VIII.1965, fem. fl., *Molina R. 15200* (NY).

Guatemala. Izabal, Sto. Tomás de Castilla, c. 30 km SW of town, Sinai, 15°39'N, 88°35'W, 15.III.1988, fr., Marshall et al. 396 (NY).

Panama. Panama, Las Perlas, San José Island, 19.VII.1967, male fl., *Stimson 5328* (NY).

Guyana. Kanuku Mts, Rupunini R., Crabwood Cr., 29.VI.1995, fr., *Jansen-Jacobs et al. 4278* (CAY, GB, NY). — Rupununi Distr., Kuyuwini Landing, Kuyuwini R., 10.X.1992, imm. fr., *Jansen-Jacobs et al. 2832* (CAY, L, NY). Suriname. Distr. Suriname, Zanderij Savanne, *Hekking 901* (L). — Mapane Creek, area near camp 8, *Schulz 7548* (L, NY).

French Guiana. Sinnamary, Brigandin, 26.III.1993, imm. fr., *Puig 12055* (CAY). — Basse crique Courouaïe (affluent du Bas Approuague), à 5 km en amont des Deux Fourches, 15.I.1970, imm. fr., *Oldeman B-2766* (CAY).

DISTRIBUTION AND ECOLOGY

Distributed from Mexico and Cuba to Colombia, Venezuela, the Guianas, and Brazil. It is found in low scrub forest, seasonally deciduous forest, or savanna forest on white sand, lateritic clay soil, brown sand on rocky substrate, sometimes along creeks on alluvial soils, from sea level to 800 m altitude.

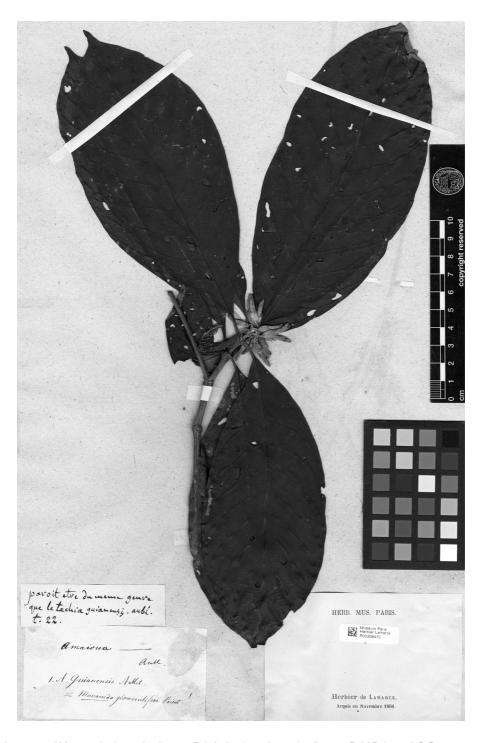


Fig. 2. — Lectotype of Mussaenda glomerulata Lam. ex Poir. (= Amaioua glomerulata (Lam. ex Poir.) Delprete & C. Persson, comb. nov.) preserved at the Lamarck Herbarium (P-Lam, P00308470).

OCTAVIA SESSILIFLORA (FIGS 3; 4)

The little-known, monotypic genus *Octavia* DC. was described by Candolle (1830) from fruiting specimens collected in French Guiana by Jean-Baptiste Patris. Patris (1734-1786) resided in French Guiana from 1764 until his death, and his collections were later included in Candolle's herbarium (G-DC). Many labels of Patris specimens bear the handwriting "Cayenne", but this was added later by Candolle, although most Patris' collections were made in many localities throughout French Guiana (and not just Cayenne). In the incomplete description of Octavia, Candolle wrote that its calyx is "globose" and truncate, that the ovary has a fleshy disk, and that the drupes are globose, fleshy and with eight oneseeded pyrenes (hence the generic name). He added that the flowers are solitary at the apex of axillary short shoots (although the flowers of Octavia were unknown to him), and suggested an affinity to *Pyrostria* Comm. ex A. Juss. because of its 8-pyrenate fruits. Kuntze (1891: 290) transferred Octavia sessiliflora to Nonatelia Aubl. section *Mephitidia* (Reinw. ex Blume) Kuntze, as Nonatelia sessiliflora (DC.) Kuntze (along with Nonatelia moralesii (Griseb.) Kuntze [= Lasianthus lanceolatus (Griseb.) Urb.]) because of its axillary inflorescence, and suggested that this section should be transferred to Lasianthus Jack. After these two works, this taxon fell into general oblivion, and no other botanist attempted to establish its identity and systematic position, probably because of the scanty specimens deposited at the Candolle herbarium (G-DC) at Geneva, and the G-DC restrictions to send specimens on loan. Only a few citations about *Octavia* appeared in the 20th century, and Robbrecht (1988) and Govaerts et al. (2012) maintained Octavia as a synonym of Lasianthus.

There are three specimens of *Octavia* at the G-DC herbarium, all collected by Patris, and therefore all type specimens, which are all terminal branchlets with solitary young ovaries and mature fruits. Their growth habit follows that of the Aubréville model (Hallé *et al.* 1978), which is a reiteration of growth through axillary buds located below the terminal flowers (the axillary

shoot becomes the bearer of a new apical bud); this growth habit is common in many Rubiaceae genera, and in many other plant families. The stipules are narrowly triangular or narrowly ovate at base and acute to acuminate at apex; however, Candolle interpreted them as "bracts" and described them as "ovate-oblong, acuminate, erect, much shorter than the petiole, deciduous" (free translation from Latin: Candolle 1830: 464). The leaf blades are ovate, elliptic, to oblong-elliptic, c. 7-13 × 3-5 cm, round to acute at base, and acute to acuminate at apex, the acumen is narrowly triangular, sometimes slightly falcate, 1-2 cm long, and with 6-8(-9) secondary veins on each side.

Candolle's interpretation of the flower position in Octavia is somewhat confusing, as he wrote that its "flowers are sessile, solitary, ebracteate, axillary or at shoot apex" (free translation from Latin: Candolle 1830: 464). A careful analysis of the type specimens revealed that flowers (young ovaries, lacking corollas and style) and fruits are instead always terminal; however, some of them are subtended by a lateral branch originated from an axillary bud located a few nodes below them (becoming the bearer of the new apical bud, see above), and giving the false impression that flowers and fruits are axillary. Because of this, Candolle interpreted flowers and fruits as either axillary or terminal, but, in fact, they are consistently terminal (or pseudoaxillary).

Candolle wrote that the fruits of Octavia are drupes with eight one-seeded pyrenes. However, this statement has two errors that could be due to interpretation of the dry specimens. First, a detailed analysis of the outer surface and a longitudinal section of the "pyrenes" revealed that they are in fact seeds with a papery seed coat (with longitudinal cells), fleshy albumen and narrowly cylindrical embryo (Fig. 3). Second, the presence of eight seeds does not automatically mean that the fruits are 8-locular. In fact, several genera of the tribe Gardenieae have ovaries with pseudo-walls, and the pseudolocules might be erroneously interpreted as true locules. Consequently, Candolle's interpretation of an 8-locular fruit is a misinterpretation of a

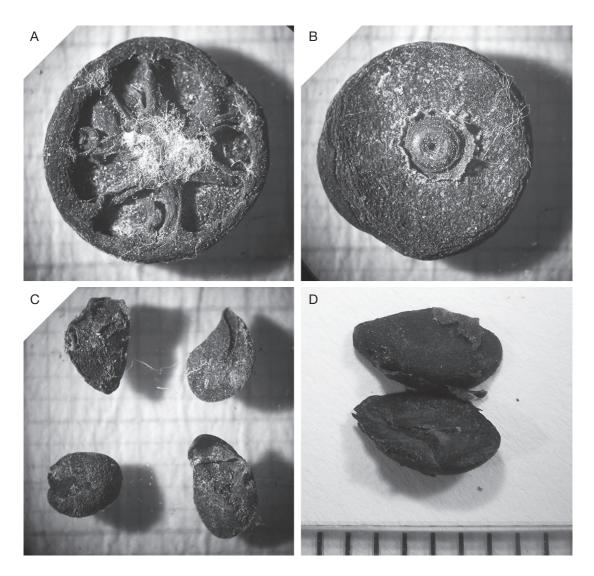


Fig. 3. — Octavia sessiliflora DC. (= Cordiera triflora A.Rich. in DC.): **A**, cross section of the fruits, showing eight "chambers" (false septa); **B**, fruit seen from the top, showing disk and permanent calyx; **C**, seeds; **D**, detail of one seed longitudinally cut, showing parts of the exotesta. Material references in Fig. 4.

2-3(4)-locular fruit with 2-3(-5) seeds per locule, with chambers separated by pseudo-walls. Therefore, the fruits of *Octavia* are fleshy berries with eight seeds (Fig. 3). With these characters in mind, a quick search through the Rubiaceae genera occurring in the Guianas, pointed to the genus *Cordiera* A.Rich in DC., and more specifically to *C. triflora* A.Rich in DC., which is

the type of the genus and coincidentally its type specimen was also collected in French Guiana. As *Cordiera* is a dioecious genus (with female individuals bearing solitary flowers with fertile ovaries, and male individuals with multiflorous inflorescences and flowers with fertile male parts), the type specimens of *Octavia sessiliflora* are in fact female branches of *C. triflora*.

As indicated above, there are three sheets preserved at the Candolle herbarium (G-DC), all bearing the herbarium number G00310467. Sheet N. 3 (Fig. 4) has three labels, all in Candolle's handwriting: the first saying "Rubiaceae - Guettarda? - Cayenne" (although this might not be the collection locality), the second "Bacca – 8 loc. - loculis 1 spermis", and the third "Octavia sessiliflora DC." Also, at the bottom of this specimen there is a little envelope containing several fruits and seeds; some of the fruits were cut transversally, showing the eight rooms that Candolle interpreted as eight locules. Because this is the only specimen that bears the handwriting "Octavia sessiliflora", Candolle's synthetic diagnosis of the fruit and an envelope with fruits and seeds, we select this sheet as the lectotype of this taxon.

Additionally, several South American taxa have been treated as synonymous with Cordiera triflora by Persson & Delprete (Delprete 2010), although without a complete explanation of their typification and synonymisation (due to the synthetic style of the floristic treatment); therefore we are here presenting a short explanation of the typification and synonymy of this species. Standley (1929, 1931) and Krause (1908) did not present any comparison with C. triflora when they described Alibertia steinbachii Standl., A. benensis Standl. and A. tenuifolia K.Krause, respectively; however, the descriptions of these three taxa are well within range of variation of *C. triflora* as here circumscribed, and therefore they are confirmed to be synonymous and are here typified. Also, the lectotype of *C. triflora*, selected by Persson & Delprete (Delprete 2010), is a specimen preserved at the Paris General herbarium (P), and was collected by Louis Claude Marie Richard in French Guiana. An isolectotype specimen, once belonging to the Franqueville herbarium, was later included in P and then transferred to F. The label of this specimen has Achille Richard's handwriting: "Cordiera triflora Rich., Rive du Kourou, Guyane, legit Cl. Richard." Also, Steyermark (1965: 226) incorrectly cited the type of Cordiera triflora as: "In ripis fluvii Kourou, British Guiana, Poiteau, Richard 365 (B, photo NY)." However, in this short citation he succeeded to make several mistakes. First, the specimen was collected in French Guiana and

not in "British Guiana" as he wrote. Second, he misinterpreted the name "Poiteau," which is not the name of the locality but the collector's name of the specimen at the Berlin Herbarium. Third, he cited "Richard 365" but L.C. Richard never used any collection or herbarium number. This confusion can be clarified by examining the image of the specimen cited by Stevermark, which was preserved at the Berlin herbarium (destroyed during the second World War), and now available at the "Berlin Negatives" website of the Field Museum (2011). This specimen was in fact collected by Poiteau, and "365" is the Negative N. assigned by Macbride when he photographed the specimen, just before the second World War; therefore, this specimen should be cited as "French Guiana, s.d., P.A. Poiteau s.n. (B, destroyed), Negative N. 365," and it is not a type specimen. In conclusion, taking into account the information presented above, full synonymy and typification of Cordiera triflora are presented below.

Cordiera triflora A.Rich. (Figs 3; 4)

In DC., Prodromus 4: 445 (IX.1830) (reimpr. Mémoire sur la famille des Rubiacées 223: pl. 20, fig. 2 [XII.1830]; reimpr. Mémoires de la Societé d'Histoire naturelle de Paris, series 3, 5: 223, pl. 20, fig. 2 [1834]). — Alibertia triflora (A.Rich.) K.Schum. in Mart. et al., Flora Brasiliensis 6 (6): 392 (1889). — Cordiera trifolia Steud., orth. var., Nomenclator Botanicus, 2nd ed., 1: 419 (1840). — Type: French Guiana, Kourou R., L.C.M. Richard s.n. (lecto-, P [P03821428], selected by Persson & Delprete in Delprete [2010]; iso-, F, K).

Octavia sessiliflora DC., Prodromus 4: 464 (1830). — Nonatelia sessiliflora (DC.) Kuntze, Revisio Generum Plantarum 1: 290 (1891). — Type: French Guiana, without locality, s.d. [1781-1785], Patris s.n. (lecto-, G-DC [sheet 3], here designated; isolecto-, G-DC [sheets 1; 2]).

Alibertia tenuifolia K. Krause, Verhandlungen des Botanischen Vereins der Provinz Brandenburg 50: 106 (1908).
— Type: Brazil, "Amazonas" (Acre), Rio Juruá Miry (Rio Jurua Mirim), IX.1901, male fl., Ule 5843 (holo-, B, destroyed; lecto-, MG, here designated; isolecto-, G[2], HBG, K, L; photo-B at F, GH, MO, NY, RB).

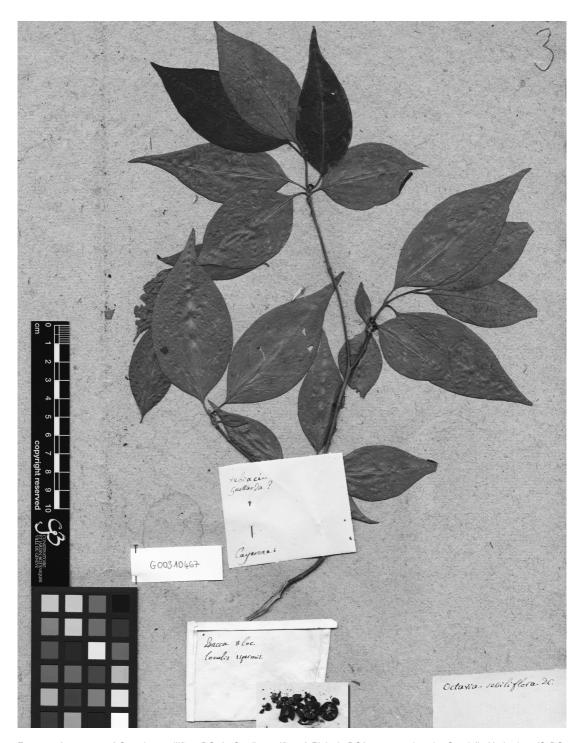


Fig. 4. — Lectotype of Octavia sessiliflora DC. (= Cordiera triflora A.Rich. in DC.), preserved at the Candolle Herbarium (G-DC, G00310467, Sheet N. 3).

Alibertia steinbachii Standl., Publications of the Field Columbian Museum, Botanical Series 4: 287 (1929). — Type: Bolivia, Santa Cruz, Prov. Sara, Buenavista, 9.X.1924, male fl., Steinbach 6597 (holo-, F 573427; iso-, A, BM, G, GH, MO, NY, S).

Alibertia benensis Standl., Publications of the Field Columbian Museum, Botanical Series 7: 291 (1931). — Type: Bolivia, Beni, San José, between Trinidad and Santa Cruz, IX.1926, male fl., Wendermann 2580 (holo-, B, destroyed; lecto-, S, here designated; isolecto-, LPB, MO, frag-B at F, frag-S at F).

SPECIMENS EXAMINED. — Venezuela. Terretorio Federal Amazonas, Cerro de La Neblina, along Río Mawarinuma, upstream from Neblina Base Camp, 0°50'N, 66°10'W, 140 m, 2.V.1984, fr., *Stein et al. 1709* (MO, VEN).

Guyana. Upper Takatu-Upper Essequibo Region, SE Kanuku Mts, Mt Ishtaban, 3°15'N, 59°25'W, 300-500 m, 26.VI.1989, fr., *Gillespie et al. 1876* (MO, NY, US). — Potaro-Siparuni Region, 6.5 km NE of Suruma village, 4°10'N, 59°01'W, 400 m, 3.V.1992, imm. fr., *Hoffman et al. 1563* (CAY, MO, NY, US).

Surinam. Goudkreek, Corantyn, 17.X.1916, Stahel & Gonggrijp BW 3585 (L).

French Guiana. Lower Oyapock River, NE face Piton Rocheux, Haut de Crique Armontabo, 300-350 m, 22.II.1981, *Cremers 7079* (CAY[2], NY, UB). — Kourou, s.d., *Richard s.n.* (F [ex P], P n.v., photo-P at A[2]). Ecuador. Morona-Santiago, Cordillera Cutucú, 2°40'S, 78°W, c. 1000 m, 17.XI-5.XII.1944, male fl., *Camp 1072* (NY[2], US).

Peru. Amazonas, mouth of Río Santiago, 160 m, XI.1924, fl., *Tessmann 4443* (NY, frag-B at F). — Junín, Rondayacu, 35 km S of San Ramón in Tulumayo valley, 1850 m, 5.VI.1983, fr., *Gentry et al. 41480* (GB, MO, USM). — Loreto, above Pongo de Manseriche, Left bank of Río Santiago, 200 m, 4.XII.1931, male fl., *Mexia 6210* (BM, CAS, F, G[2], GB[2], GH, MO, NY, S, UC, US).

Brazil. Amapá, Mun. Calçoene, BR-156 in vicinity of goverment rd camp Carnot, 53-72 km WNW of Calçoene, 2°33'-38'N, 51°16'W, 11.XII.1984, fr., *Rabelo et al. 2972* (NY, US). — Amazonas, Mun. Humaitá, near Livramento on Rio Livramento, 12.X-6.XI.1934, imm. fr., *Krukoff 6993* (A, BM, F, K, MO, NY, S, US; frag at F). — Mato Grosso, Sto. Antonio do Leverger, Engenho Velho, 24.III.1983, male fl., *Carreira et al. 655* (NY). — Tocantins, Mun. Palmeiras de Tocantins, rd to Rio Curiacaca from BR-153, 6°38'S, 47°33'W, 200 m, 12.I.2008, fr., *Silva & Moreira 12551* (CEN, UFG).

Bolivia. Beni, Iténez, Magdalena, 4 km W, 10.XI.1993, fl.-fr., Moraes et al. 1720 (GB, LPB). — Santa Cruz, Ichilo, 1.2 km S of Buena Vista, 17°29'S, 63°39'W, c. 350 m, 9.X.1996, fem. fl., Persson & Gustafsson 302 (GB, NY, S), male fl., 303 (GB, LPB, S). — Prov. Sara, Buenavista, 500 m, 14.XII.1920, Steinbach 5219 (GH, NY, frag-B at F).

DISTRIBUTION AND ECOLOGY

Occurring in tropical South America, primarily at the region bordering the Amazon Basin (circum-Amazonian distribution), in Venezuela, the Guianas, Brazil (from Amapá through Tocantins, Mato Grosso and Mato Grosso do Sul), and along the western slopes of the Andes in Peru and Bolivia. It grows in undercanopy of forests, thickets and at forest margins, both on *terra firme* and on sandy alluvial soil, from 200 to 2000 m altitude.

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GOVAERTS R., RUHSAM M., ANDERSSON L., ROBBRECHT

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