

FIRST REPORT OF RHABDODENDRACEAE FOR THE VASCULAR FLORA OF COLOMBIA AND THE UPPER RÍO NEGRO BASIN, WITH COMMENTS ON PHYTOGEOGRAPHY, HABITATS, AND DISTRIBUTION OF *RHABDODENDRON AMAZONICUM*

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Abstract. Rhabdodendraceae is recorded for the first time in the vascular flora of Colombia and the upper Río Negro basin, based on collections of *Rhabdodendron amazonicum* from the upper Cuyarí river, Guianá department, Colombia, and the upper Isana (Içana) river, Amazonas state, Brazil, respectively. These two localities extend considerably the northwesternly distribution of this taxon inside the Amazon Basin. Notes about the phytogeography (e.g. insights as to why this species has not yet been found between Manaus and the confluence of the Guainía and Casiquiare rivers), the habitats of *R. amazonicum*, and an updated overview of the known specimens using a geographic distribution map of this taxon is also included. The discovery of this family in the upper Río Negro region, demonstrates the value of field work through alliances between private initiatives and the Kuripaco nation.

Resumen. Se registra la familia Rhabdodendraceae para la flora vascular de Colombia y la región del alto Río Negro basándose en dos colecciones de *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber del alto río Cuyarí, departamento del Guianá y el medio río Isana (Içana), estado Amazonas, Brasil, respectivamente. Estas localidades extienden considerablemente la distribución de esta familia al noroeste de la región Amazónica. Se incluyen notas acerca de la fitogeografía (información acerca de la ausencia de esta especie entre Manaus y las confluencias de los ríos Guainía y Casiquiare), hábitats de *R. amazonicum*, y un mapa de la distribución geográfica elaborado a partir de la actualización de las colecciones de este especie. El hallazgo de *R. amazonicum* en la región del alto Río Negro demuestra el valor de los trabajos de campo realizados a través de la alianza de iniciativas privadas y el pueblo Kuripaco.

Yaakuti iipena (Kuripaco). Pakapa jnaji jaiko Rhabdodendraceae ikitsiñape Colombialiko jnite payawiya jiwidaapuliko tsakja nayu jnaji yamada naniwampe nepitana *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber aji kuwiali jiwidapuliko, departamento del Guainía jnite pamuyua Iniali (Isana), estado Amazonas, Brasil, tsakja. Jnaji jipai niniperi nayapita manupe natawiñakawa jnaji jaiko nakitsiñape jnaji wakaiteri aji noroeste lisro jliaji región Amazónica. Ninitsakja nadanampe jaikolima inakuapana (nawaupiakje linaku jliaji kuadaka kuri pakapa jnaji jnapepe jaiko itiaji Manaus jnite liukawa aji nauketaakakawa jnaji payawiya jnite katsikiali), natawiñakawa jnaji *R. amazonicum*, jnite pada mapa nakaitekawa kjereka natawiñawa jnaji jaikolima nauyawaka najnaitanda nayu jnaji nauketampe jlilipepe jliaji jaiko wakaiteli inaku. Jliaji wauketaka *R. amazonicum* payawiya jiwidapuliko likadaa wakapa kanakaidalika jliaji idejnikjeti awakadaliko napiyawaka jnaji empresa privada jnite kuripako nai.

Keywords: Rhabdodendraceae, Colombia Flora, Upper Río Negro, new family record

Rhabdodendraceae currently is a tropical family with one genus, *Rhabdodendron* Gilg & Pilg., and three species (Huber, 1909, Prance, 1972, 2004; Medeiros and Amorim, 2014); they are a significant component of some Neotropical rain forests, such as the terra-firme forests, Amazon caatingas (“campinaranas”) as well as open areas like Amazon caatinga shrubland or campinas. The genus *Rhabdodendron* has had rather a remarkable taxonomic history, summarized in Prance (1972: 3–5). Although the first species was not described until 1905, specimens eventually referred to the

genus had been collected in Brazil in the early 19th century by Carl Friedrich Philipp von Martius in 1819 and by Ludwig Riedel in 1826–1828 (Fig. 1–2).

Gilg and Pilger (1905) placed *Rhabdodendron* in Rutaceae, suggesting affinities with tribe *Cusparieae*. Species eventually transferred to *Rhabdodendron*, described by Benthham in 1853, were at first referred to *Lecostemon* Sesse & Moc. ex DC., a genus based on one of the original drawings of Mexican plants by Mociño and Sesse (Prance, 1968). Huber (1909) transferred three of

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FIGURE 1. One of the first specimens of the genus *Rhabdodendron* Gilg & Pilg., collected in the Amazon Basin by C. F. P. von Martius, representing *R. microphyllum* (Spruce ex Benth.) Huber. Image courtesy of the Herbarium—Botanische Staatssammlung München (M).



FIGURE 2. One of the first specimens of the genus *Rhabdodendron* Gilg & Pilg., collected in the Amazon Basin by L. Riedel. Image courtesy of the New York Botanical Garden (NY).

Bentham's species of *Lecostemon* to *Rhabdodendron*, and proposed a new tribe in Rutaceae, *Rhabdodendreae*; Sandwith (1943) transferred the fourth species. The genus *Rhabdodendron* was included in Rutaceae in Engler's Pflanzenfamilien (Krause, 1914). Later, Engler (1931) gave *Rhabdodendron* subfamily rank, *Rhabdodendroideae*. The genus was placed in a separate family after it was shown it differed from Chrysobalanaceae, Phytolaccaceae, and Rutaceae in many features of morphology and anatomy, which were described in detail by Prance (1968, 1972, 2002, 2004). Subsequently, a molecular phylogenetic analysis indicates a relationship with Caryophyllidae (Fay et al., 1997).

MATERIAL AND METHODS

Specimens were determined consulting relevant literature (Prance, 2005, 2009, Riviero et al., 1999). An updated database and a map of the geographic distribution of this species (Fig. 6) was compiled using information from the following databases: Tropicos (www.tropicos.org), The speciesLink Network (<http://www.splink.org.br>), Lista de espécies da Flora do Brasil (<http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB206>), Jabot (<http://www.jbrj.gov.br/jabot>), Catalog of Vascular Plant Species of Central

The occurrence of Rhabdodendraceae in the flora the Colombia, as well as the extension of their distribution in the Upper Río Negro basin, is reported here for the first time based on collections of *R. amazonicum* (Spruce ex Benth.) Huber from the Rio Cuyarí, Guainía Department (Fig. 3–5), and the upper Isana (or Içana) river, Amazonas state, Brazil. In addition, we provide morphological features that help identify this species, update information about its geographical distribution and the habitats it occupies, and give insights on why this taxon so far has not been found between Manaus and the upper Río Negro (i.e. the confluence of the Guainía and Casiquiare rivers), along the northern and eastern margin of the Río Negro.

and Northeastern Brazil (<http://sciweb.nybg.org/Science2/hcol/planalto/checklist.asp.html#>), and the Amazon Tree Diversity Network (<http://atdn.myspecies.info/>). In addition, we considered the specimens of *R. amazonicum* deposited in the following herbaria: GH, MO, US, and NY (acronyms according to Thiers, 2012). Our updated database has 288 records (Brazil: 227; Colombia: 1; French Guiana: 29; Guyana: 16; Suriname: 15); it is available from the corresponding author.

RESULTS

Rhabdodendraceae are shrubs to small evergreen trees, with exstipulate, simple, alternate leaves, gland-dotted, covered by fringed-peltate hairs, rather congested and grading into much smaller undifferentiated leaves at the beginning of each innovation. The flowers have five petals and numerous stamens with short filaments and long anthers, and a single carpel with a basal style. The fruit is a distinctive drupe held in a cup-shaped structure (like several genera of Lauraceae) formed by the persistent calyx and the swollen apex of the pedicel. Fig. 7.

Presently, three species of *Rhabdodendron* are recognized: *R. amazonicum*, a taxon hitherto well known from the Guianas, central and eastern Amazon Basin, which extends its southern range to the "Serra do Cachimbo" (on the border of Mato Grosso and Pará states), where it reaches an altitude of 600 m, in a region that represents a transition between the Amazon and the Central Planalto vegetation (Lleras & Kirkbride, 1978, Prance, 1989). The other two species have more restricted distributions: *R. macrophyllum* (Spruce ex Benth.) Huber (which includes in its synonymy the type of the genus, *R. columnare*) is limited to white sand habitats and secondary vegetation edges of terra firme forests located between the Trombetas river and Manaus, one collection from río Mojú, and *R. gardnerianum* (Benth.) Sandw., a shrub only known by fewer collections in the Cerrado habitats situated in the Northwestern portion of the Bahia and Tocantins states, Brazil (The speciesLink Network: <http://www.splink.org.br>).

Rhabdodendron Gilg & Pilg., Verh. Bot. Vereins Prov. Brandenburg 47: 152. 1905.

Type species: *R. columnare* Gilg et Pilger.

Rhabdodendron amazonicum (Spruce ex Benth.) Huber, Bol. Mus. Paraense Emilio Goeldi: Zool. 5: 427. 1909. Fig. 2–8.

Basionym: *Lecostemon amazonicum* Spruce ex Benth., Jour. Bot. Kew. Misc. 5: 295. 1853. TYPE. BRAZIL. Pará: Santarém, *R. Spruce 377* (Holotype: K; Isotypes: LD, MG, OXF, P).

Synonyms: *Lecostemon crassipes* Spruce ex Benth., Jour. Bot. Kew. Misc. 5: 295. 1853. TYPE. BRAZIL. Amazonas: Manaus, *R. Spruce 1497* (holotype: K; Isotypes: BM, CGE, M, NY, OXF, P).

Rhabdodendron crassipes (Spruce ex Benth.) Huber, Bol. Mus. Emilio Goeldi 5: 428. 1909.

Lecostemon crassipes var. *cayennense* Benth., Jour. Bot. Kew. Misc. 5: 295. 1853. TYPE: FRENCH GUIANA ["CAYENNE"]. Without any other locality, *J. Martin s.n.* (Holotype: K; isotype, BM).

Rhabdodendron duckei Huber, Bol. Mus. Emilio Goeldi 5: 428. 1909. TYPE. BRAZIL. Pará: Prope Obidos, *in sylvulis capueiras dictis*, 20 December 1903, *A. Ducke 8546* (Holotype: MG; Isotypes: BM, RB, US).

Rhabdodendron paniculatum Huber, Bol. Mus. Emilio Goeldi 5: 429. 1909. TYPE. BRAZIL. Pará: [*in sylvulis capueiras dictis prope*] Obidos, 21 November 1907, *A. Ducke 8854* (Holotype, MG; Isotypes, BM, US).

Rhabdodendron longifolium Huber, Bol. Mus. Emilio Goeldi 5: 429. 1909. TYPE. BRAZIL. Pará: [*in cacumine collinis prope*] Faro, 26 August 1907, *A. Ducke 8504* (Syntype: MG); Pará: [*in cacumine Morro do Taboleirinho ad fl.*] Mapuera, 1 December 1907, *A. Ducke 8989* (Syntype: MG).



FIGURE 3. Representative specimen of *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber from the Cuyarí river, Guainía, Colombia (Minorta-C. 991, COL). Image courtesy of the Colombian National Herbarium (COL).



FIGURE 4. Representative specimen of *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber from the Cuyarí river, Guainía, Colombia (F. Castro-Lima et al. 18215, COL). Image courtesy of the Colombian National Herbarium (COL).



FIGURE 5. Representative specimen of *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber from the Cuyarí river, Guainía, Colombia (González et al. 635, COL). Image courtesy of the Colombian National Herbarium (COL).

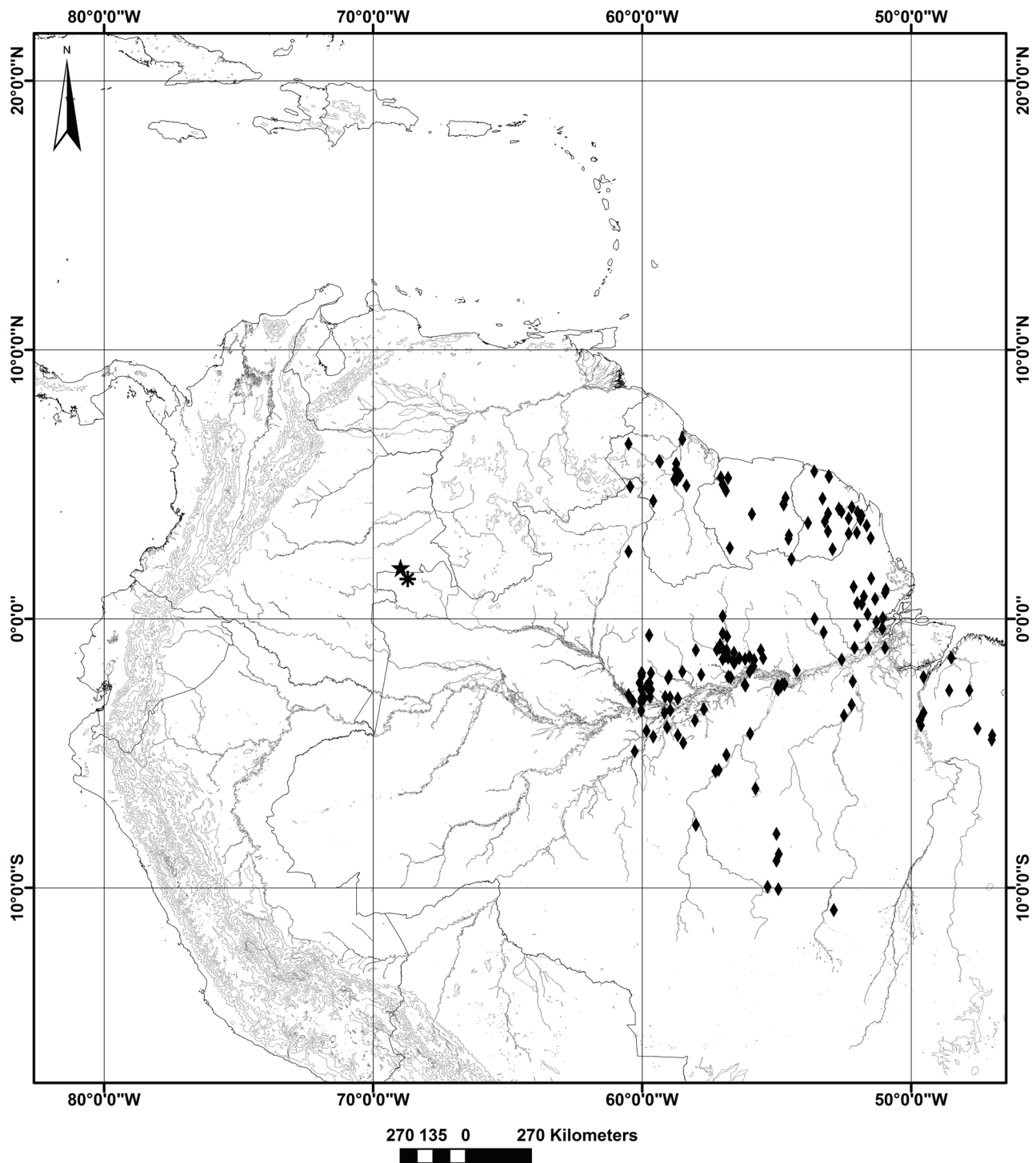


FIGURE 6. Geographical distribution of *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber (◆), with emphasis on new records from Colombia (★) and upper Río Negro of Brazil (*).



FIGURE 7. *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber. A, stem with leaves and inflorescences; B, leaf with detail of abaxial surface and lepidote scale; C, part of inflorescence; D, lateral view of flower; E, lateral view of flower with most of anthers disarticulated; F, medial section of flower (left) and gynoecium with gynobasic style (right); G, adaxial (right) and lateral (left) views of anther; H, part of infructescence; I, medial section of fruit. Drawing by B. Angell. Reprinted with permission from S. Mori and B. Angell.

Rhabdodendron arirambae Huber, Bol. Mus. Emilio Goeldi 5: 430. 1909. TYPE. BRAZIL. Pará: Alto Ariramba, campina-rana, 20 December 1906, A. Ducke 8000 (Holotype: MG).

Lecostemon sylvestre Gleason, Bull. Torrey Club 54: 68. 1927. TYPE. GUYANA. Kangaruma-Potaro Landing, dense upland bush, small tree, 15 feet high, 25–27 June 1921, H. A. Gleason 211 (Holotype: NY; Isotype: GH, K, US).

Rhabdodendron sylvestre (Gleason) Maguire, Bull. Torrey Club 75: 397. 1948.

Shrub to small trees to 15 m × 20 cm diameter, the wood with anomalous secondary phloem, the young branches with scattered peltate hairs, with a thin hard bark. Leaves oblanceolate, oblong to oblong-obovate, gradually narrowing from above middle to base, coriaceous, 20–39 × 3–10 cm, the apex acute, acuminate or mucronate, most frequently with an acuminate 2–9 mm long, gradually narrowed to a cuneate base, glabrous above, with few scattered peltate hairs beneath, not rugose on both surfaces; midrib plane to prominent above, prominent beneath; primary veins 30–45 pairs, plane to prominent above, prominent beneath, anastomosing but not forming a conspicuous marginal nerve; petioles 1.5–3.5 cm long, with scattered peltate hairs, terete, not winged. Stipules absent. Inflorescences of axillary and sometimes terminal panicles or occasionally reduced to racemes, 9–17 cm long, sparsely peltate pubescent becoming glabrous with age. Bracts and bracteoles ovate to lanceolate, persistent, 1–2 mm long, chartaceous; pedicels 6–15 mm long, glabrescent, frequently recurved, often with 2 lanceolate bracteoles. Calyx-tube turbinate-campanulate, 2–4 mm long, the lobes small but distinct, and apparent in young flowers only. Petals 5, oblong, 7–8 mm long, sepeloid, minutely punctate. Stamens ca. 45, the filaments short and flattened, persisting after flowering and then recurved; anthers linear, ca 7 mm long, basifixed, caducous. Ovary globose, glabrous. Style arising from base of ovary to one side of it, elongate, the stigmatic surface long and linear. Fruit subglobose, 6–10 mm diameter (Fig. 8); exocarp glabrous, smooth but wrinkled when dry; mesocarp very thin, fleshy; endocarp thin, bony; fragile, with median line of fracture, glabrous within.

Iconography: Prance (1968: Figures 4B [as *R. sylvestre*], 5A–B; 1972: Figures 3A, 6C–J).

Assessing distribution patterns, endemisms, and diversity of plants of the Río Negro basin as well as the core Amazon Basin continues to be a major challenge (Milliken et al., 2011; ter Steege et al., 2013; 2015, Prance, 2014; Pennington et al., 2015). The fact that enormous areas are not represented by even a single collection implies that many species distributions are still poorly known or not well understood (Nelson et al., 1990; Hopkins, 2007; Schulman et al., 2007; Cardoso et al., 2015).

Schulman et al. (2007) utilized a dataset of ca. one million herbarium collections and showed that 43% of total area of Amazonia basin is not collected, 28% is poorly explored, and only the 2% of the basin (i.e., Manaus, São Gabriel

Nomenclatural note: Comparing the protologue of *R. duckei* (Huber, 1909) with what has been cited most recently (e.g., Prance, 1968; 1972: 14), and the specimens bearing the type number in different herbaria, there seems to be a discrepancy in the type locality of *Rhabdodendron duckei*. Huber cited “*Hab. in silvulis Capueiras dictis prope Obidos*, 20 XII 03 Leg. A. Ducke 4856,” which differs from what is found, for example, on the label of an isotype at BM. The locality cited in the protologue may be a typographical error, but we have not located any possible *errata* in two separate copies of the journal. In the meantime, here we cite the locality reported in Prance (1968; 1972: 14), reflecting the label data on the different replicates of the type reported herein.

Prance (1972: 14) cited “*Rhabdodendron crassipes* var. *cayenense* [sic] Bentham,” a name never published by Bentham under that generic name, but the citation can be interpreted as a typographical error, and the listing does account for the new synonymy.

Additional Specimens examined: BRAZIL. Amazonas: Upper rio Içana, Comunidade de Jandu Cachoeira, Campinarana atrás da Pista de Aviação, 0°07'49"S, 67°05'21.1"W, May 2007, sterile, J. Stropp, P. Assunção & P. Assunção 214 (EAFM). COLOMBIA. Guainía: Panapaná, estribaciones del Cerro Campo Alegre o Guagua, ca. 3.5 km al Norte de la comunidad de Campo Alegre, 01°53'13"N, 68°58'27"O, 70 m, 01 May 2014, flowering and fruiting, V. Minorta-C., G. Aymard, F. Castro-Lima, A. Lozano, M. González y C. Villegas 991 (COL, COAH, FMB, HUA; HUAZ); F. Castro-Lima, G. Aymard, V. Minorta-C., A. Lozano, M. González y C. Villegas 18215 (COL, COAH); same locality and date, fruiting, M. González, F. Castro-Lima, G. Aymard, V. Minorta-C., A. Lozano, y C. Villegas 635 (COL, COAH, UDBC).

The species is similar to *R. macropyllum*, however it can be distinguished from the latter by the presence of secondary phloem, the leaves distinctly coriaceous, petiolate, the primary leaf veins not anastomosing and marginal vein absent (versus chartaceous, subsessile; primary leaf veins strongly anastomosing to form a marginal vein, and the wood without secondary phloem; Prance, 1972). Both species are extremely polymorphic in leaf shape and size, and also in flower dimensions, in this case, as suggested by Prance (1972: 18), perhaps accounting for the long list of synonyms referred to *R. amazonicum*.

DISCUSSION

de Cachoeira, Santarém, Iquitos) could be considering relatively well collected. Nevertheless, the Río Negro basin had been relatively well explored and studied, first by the inhabitants of this region who were able to classify the vegetation types and its most important species before the Europeans arrived (Abraão et al., 2009).

The first account of the Río Negro by European travelers came from the diary written by Gaspar de Carvajal; he was a priest who accompanied Francisco de Orellana in the first voyage down the Amazon River in 1542 (Carvajal, 1848). Subsequently, many outstanding botanists collected plants and studied the vegetation of this amazing river. The first known large collection of Amazon plants was made by

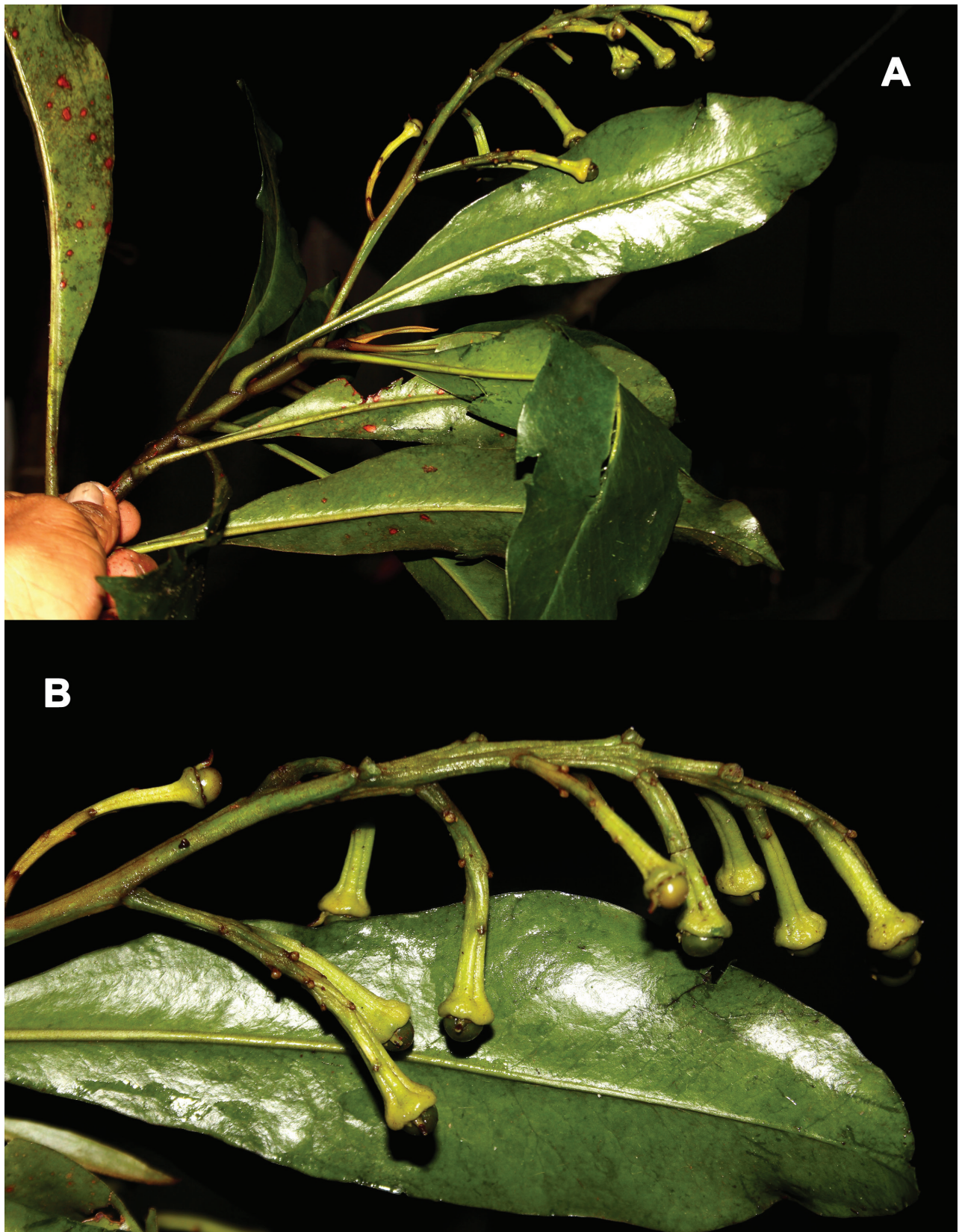


FIGURE 8. *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber. **A**, fruiting branch; **B**, close-up of the immature fruits. Photographs by Francisco Castro-Lima based on *F. Castro-Lima et al. 18215* (COL; see Fig. 4 above).

Alexandre Rodrigues Ferreira (Wurdack, 1971) during his voyage of 1783–1792. He explored the Amazon River and its main tributaries, including the Río Negro, where his itinerary notably included the Içana river (Rodrigues-Ferreira, 2008). Later, A. von Humboldt and A. G. Bonpland, traveling from the Orinoco river, reached San Carlos de Río Negro, Venezuela, in April 1800 (Huber and Wurdack, 1984). The exploration of the Río Negro basin and its most important rivers continued with the work, among others, of C. F. P. von Martius and J. B. von Spix (1819–1820), L. Reidel (1826–1828), R. H. Schomburgk (1839), P. J. Ayres (1842–1844, see Romero-González, 2016), A. R. Wallace (1851), R. Spruce (1849–1854), J. Barbosa Rodrigues (1883), G. A. E. Hübner (1903–1907, 1914), T. Koch-Grünberg (1903–1905), E. H. G. Ule (1901–1908), J. G. Kuhlmann (1918), F. von Luetzelburg (1928–1929), W. A. Ducke (1910–1932, 1933–1936, 1941–1942), E. P. Killip and A. C. Smith (1929), B. A. Krukoff (1936), J. Cuatrecasas (1939), L. I. Williams (1942), R. de Lemos Fróes (1942–1945, 1949–1952), J. A. Steyermark (1944), P. H. Allen (1945), R. E. Schultes and F. López (1947–1948), J. Murça Pires (1947–1952), G. A. Black (1947–1950), B. Maguire, J. J. Wurdack and R. S. Cowan (1950–1953), H. García-Barriga (1951), R. Romero-Castañeda (1952), A. Fernández-Pérez (1953), W. A. Rodrigues (1957–1959), B. Maguire, J. Murça Pires, and J. A. Steyermark (1965), N. T. Silva and U. Brazão (1966), P. Maas (1971), G. T. Prance (1971), J. Zarucchi and M. Balick (1975), K. Kubitzki (1975), R. Liesner and H. Clark (1977), and B. Stergios (1981). Besides this amazing amount of field work, thousands of plant collections from the Amazon River (including some from the Río Negro) and the Guayana Shield were products of the eight expeditions to the Amazon Basin conducted by B. A. Krukoff in 1923–1950 (Landrum, 1986), the twenty five expeditions sponsored by the bi-national plant collecting program “Projeto Flora Amazônica” (Prance et al., 1984), the interdisciplinary and multi-national I.V.I.C. project (which represents the most detailed study ever conducted of Amazon caatinga and terra-firme forests in the Upper Río Negro; Medina et al., 1977), and the Neblina expeditions (Brewer-Carías, 1988). In addition, supplementary work was carried out by the Biological Diversity of the Guiana Shield Program (Funk, 2007), and the twenty five years of botanical exploration in the Colombia Amazon conducted by the SINCHI Institute (Cárdenas-López et al. 2007a). As a result, currently there exists a relatively good understanding of the structure and floristic composition of the Río Negro basin (Dezzeo et al., 2000; Córdoba y Etter, 2001; Rudas et al., 2002; Boubli, 2002; Cárdenas-López, 2007; Cárdenas-López et al., 2007b, 2014; Aymard et al., 2009; Aymard, 2011; Medina and Cuevas, 2011; Stropp et al., 2011, 2013; Pombo de Souza, 2012).

The Río Negro basin harbors a considerable number of regional endemics (Lleras, 1997; Clark et al., 2000, Aymard et al., 2009), no doubt due to its unique habitats, such as diverse terra-firme forests and the peculiar scrub-savanna locally called “sábanas de arenas blancas,” (Spanish) or “campina de solo arenoso” (Portuguese), and the Amazonian caatinga or campinarana forest (Prance, 2001

and references therein). This type of vegetation growing in white-sand and often near black-water rivers is frequent in the Guianá and Río Negro basins. They occupy small areas in the lower Río Negro (Rodrigues, 1961; Takeuchi, 1961, 1962) but are much more extensive in the upper basin, where they are subject to partial or total seasonal flooding (Klinge and Medina, 1979; Prance, 1989, 2001; Huber, 1995a,b). The soils are acidic, deep, sandy spodosols or quartzitaments; the parent material is characterized by a subsurface accumulation of humus that is complexed with aluminum and iron (Herrera, 1985; Dubroeuq and Volkoff, 1998; Schargel et al., 2000).

Rhabdodendron amazonicum has been found in the Guianas over ferro-bauxite soils (e.g. Lely region, 500–700 m, Suriname) and also growing in sandy loam soils not subject to flooding such as Wallaba communities dominated by *Eperua falcata* Aubl. located in the Bartica-Potaro area, and in forests with high presence of *Morabukea* (*Mora gonggripaii* (Kleinh.) Sandw.), and Greenheart (*Chlorocardium rodiei* (R. H. Schomb.) Rohwer, Richt. & van der Werff) situated in the Mabura Hill region. In Brazil (including the foothills of Roraima) this species is found through the central to eastern Brazilian Amazon, where it is quite frequent along campina aberta and campinarana forests (e.g., Amazonas: Manaus-Caracará Highway; Pará: Rio Mapuera, Tucuruí, Oriximiná), in terra-firme forests growing in clay soils (e.g., Amapá: Matapí, Macapá, Pará: Monte Dourado, Rio Cuieiras), and in disturbed areas such as forests growing on road sides. The wide variety of habitats where *R. amazonicum* is found strongly indicates that this species is not a white sand specialist as was suggested recently (García-Villacorta et al., 2016). The same wide habitat preference is found in many other species frequent in forests that grow in white sand in the upper Río Negro region, such as *Aldina kunhardtiana* Cowan, *Eperua leucantha* Benth., *E. purpurea* Benth., *Dendroponax neblinae* Maguire, Steyermark & Frodin, *Helianthostylis steyermarkii* C. C. Berg, *Pentamerista neotropica* Maguire, *Sloanea floribunda* Spruce ex Benth., *Tetrameranthus duckei* R. E. Fr., *Hebepetalum humirifolium* (Planch.) Benth., *Erisma micranthum* Spruce ex Warm., and *Asteranthos brasiliensis* Desf., all considered soil generalists (Aymard et al., 2009), suggesting that plant communities growing in white-sand and terra-firme forests growing in clay soils in the upper Río Negro basin may have a common evolutionary history.

We show here that *Rhabdodendron amazonicum* also occurs in Amazonian caatingas or campinaranas of the middle Río Negro basin, specifically in the middle Içana river, Brazil, and the upper Cuyarí river, Colombia (Fig. 3–5); the latter is a black-water river the basin of which includes largely unexplored flooded and non flooded forests (Aymard and Castro-Lima, 2015). The collection from the Içana river was made during inventories made to compare the tree communities of white-sand and terra-firme forests, and included plots established in Amazonian caatinga forests in the vicinity of São Gabriel de Cachoeira and the Içana river (Stropp et al., 2011, 2013). These authors neither realized the phytogeographic significance of the collection nor presented information to distinguish

the caatingas around São Gabriel de Cachoeira from those in the the Içana river. The collection from the Cuyarí river, reported herein, was made in a tall Amazonian caatinga forest, with a close canopy which let little light filter to the understory. At this site, the primary dominant species were *Hevea rigidifolia* (Spruce ex Benth.) M. Arg., *Mezilaurus caatingae* van der Werff, *Caraipa longipedicellata* Steyerl., and *Micropholis maguirei* Aubrév.

When the geographical distribution of *R. amazonicum* is plotted and analyzed (Fig. 6), it is evident that the species is known from the Río Negro basin from only the two collections cited above, and that apparently it is absent from a large area between Manaus and the confluence of the Guainía and Casiquiare rivers, two points ca. 1000 km apart and encompassing basically the northern and eastern bank of the Río Negro, dominated mainly by habitats where this species has been previously collected (e.g., Amazonian caatinga, “campina de solo arenoso,” and terra-firme forest). It would be easy to treat the absence of *R. amazonicum* from this large area as a collection artifact, which we regard as an unlikely explanation given the largest number of exceptional plant collectors who have worked in this particular area in the last 250 years, since the age of exploration in the Neotropics began.

Nonetheless, despite the lack of tools to reconstruct phylogenies (e.g., material for DNA extraction) and of information about dispersal biology (although the fruits are most likely dispersed by animals, especially birds: see Prance, 2002; 2004), here we would like to explore an alternative hypothesis to explain the peculiar distribution of *R. amazonicum* in the Río Negro basin based on palaeobotanical records and paleoclimatic events. It is already well known that vegetation responds to factors such as temperature, precipitation, and atmospheric CO₂ and fluctuating dry seasons, all resulting in changes in plant communities (Mayle et al., 2004; Colinvaux, 2005; Jaramillo et al., 2010).

Rhabdodendron amazonicum could be a representative of a relictual flora, the former range of which was reduced by extreme nutrient deficiency, frequent fires, unfavorable soil-water conditions (Klinge and Cuevas, 2000), and the influence of the Last Glacial Maximum (LGM) some 21,000–18,000 years ago (Hooghiemstra et al., 2002; Mayle et al., 2009). During this period, the climate was very dry and cool, factors that generated severe aridity in this region and, as a result, the structure and floristic composition of the forest vegetation changed in several areas of the Amazon Basin (Hooghiemstra et al., 2006; Wesseling et al., 2010), where forest was substituted by savannah and others types of low vegetation such as shrublands (Mayle et al., 2004; Gosling et al., 2009; Absy et al., 2014). Furthermore, Levine et al. (2016) demonstrated that water stress operating at the scale of individual plants, combined with spatial variation in soil texture can explain observed patterns of variation in ecosystem biomass, composition, and dynamics across the Amazon region, and strongly influences the ecosystem’s resilience to changes in the length of the dry season. Bush et al. (2004) provided the strongest evidence, resulting from

palynological studies conducted in the upper Río Negro (São Gabriel de Cachoeira, Brasil), that many species disappeared from this region as a consequence of climate instability. These authors found pollen of *Alnus* Mill., *Gordonia* J. Ellis, *Hedyosmum* Sw., *Myrsine* L., *Podocarpus* Pers., and *Weinmannia* L. (taxa that currently are common in the Andes), mixed with genera of the lowlands (e.g., *Caryocar* L., *Cedrela* P. Browne, *Guarea* F. Allam. ex L., *Pachira* Aubl., and *Pouteria* Aubl.; Bush et al., 2004). This profile shows that Andean taxa were abundant in the Upper Río Negro basin 45,000–12,000 years ago and that, during this period, this portion of Amazonia had high levels of diversity due to the boundary conditions that sustained rainforests: relatively low seasonality, high precipitation, and an edaphically heterogeneous substrate (ter Steege et al., 2010). Later, between 12,000 years ago and the present, pollen of these genera (and also *Cedrela*) completely vanished. Currently, with the exception of a few *Podocarpus* species, and *Gordonia fruticosa* (Schard.) H. Keng, none of these Andean genera are present in the lowland flora of the upper Río Negro. *Podocarpus* is a broad-leafed conifer with a primarily southern hemispheric and the Andean mountain distribution (de Laubelfels, 2004); it is tolerant to dry and cool climates (Mayle et al., 2004). *Podocarpus tepuiensis* J. Buchholz & N. E. Gray was found in the lowlands of the southern Orinoco basin of Venezuela, neighboring the Río Negro basin (in Río Temi, a tributary of the Atabapo river, at ca. 100 m, running north and parallel to the San Miguel river, a tributary of the Guainía and therefore of the Río Negro; Berry and Aymard, 1997; de Laubelfels, 2004). In addition, *Podocarpus magnifolius* Buchholz & N. E. Gray and *P. celatus* de Laubenf. had been collected in Northwestern portion of Amazon Basin of Colombia (Araracuara) and in Loreto-Perú (Vásquez, 1997), respectively, and *P. aracaensis* de Laubenf. & Silba, was described from Araçá (de Laubelfels and Silba, 1988), an outlying tepui within Brazil (Prance and Johnson, 1992). This evidence shows that the Río Negro region and other places of the Amazon Basin housed a set of species before the Last Glacial Maximum (LGM), that many have since disappeared, and that a few others, components of a relictual flora, survive in specific habitats such as the communities over very acidic soils (Punyasema et al., 2011). As postulated above, *Rhabdodendron amazonicum* easily could be another representative of a flora with formerly a much more widespread distribution in the Río Negro region, but that currently is restricted to a few and unique habitats and sites.

The first occurrence of Rhabdodendraceae reported herein for the flora of Colombia and the flora of the Upper Río Negro (NW of Amazonas state, Brazil) greatly expands the geographical distribution and improves the family-level information of the flora of Colombia (Bernal et al., 2016; Rangel, 2015), and our knowledge of the geographical range of *Rhabdodendron*, an interesting Neotropical genus. The family so far is absent in Venezuela, Ecuador, Perú, Bolivia, as well as the Southeastern and Northwestern Amazon Basin regions (Gentry, 1983). The latter is an area that comprises a large portion of the Amazon Basin of Colombia, Ecuador

and Perú, considered one of the world's last zone of high biodiversity with an extraordinary number of species across taxa and where large tracts of forests still remain largely intact (Pitmann et al., 2008; Bass et al., 2010). The absence of this family in southeastern and northwestern Amazonia could be related with the the Pebas wetland system (Hoorn et al., 2010; Sacek, 2014), which may also have played a role as a dispersal barrier for pre-Pebas groups, that could account for the well-known pattern of Andean-centred vs. Amazonian-centred biodiversity (Gentry, 1982; Antonelli and Sanmartín, 2011).

The Río Negro basin has outstanding global conservation significance due to its extraordinary biodiversity and the potential to sustain this biodiversity in the long term because of its large size and wilderness nature, and the probability of maintaining wet, rainforest conditions while anticipated climate change-induced drought intensifies in the Western

Amazon. However, further mining activities, selective logging, and new road developments will threaten its as yet unvalued conservation status. These findings help to form the scientific basis for policy recommendations, including stopping new destructive events, and creating more areas off-limits to large-scale development in adjacent regions of the three countries that comprise the basin. Finally, this report is yet another example that demonstrates the need for continued taxonomic and floristic studies in regions where there are large geographic gaps in the knowledge of Amazonian flora, so that there is adequate planning for conservation and sustainable use of regional biota. Advances in documentation of the Upper Río Negro flora will only be achieved through institutional and private partnerships, improvements in training, and continued field work mounting new expeditions with many researchers working in collaboration with the local people.

LITERATURE CITED

- ABRAÃO, M. B., G. H. SHEPARD JR., B. W. NELSON, J. C. BANIWA, G. ANDRELLO, AND D. W. YU. 2009. Baniwa vegetation classification in the white-sand Campinarana habitat of the Northwest Amazon. Pages 83–115 in L. M. JOHNSON AND E. HUNN, EDS. *Landscape Ethnoecology: Concepts of biotic and physical space*. Berghahn Books, New York and Oxford.
- ABSY, M. L., A. M. CLEEF, C. D'APOLITO, AND M. F. F. DA SILVA. 2014. Palynological differentiation of savanna types in Carajás, Brazil (southeastern Amazonia), *Palynology* 38: 78–89.
- ANTONELLI, A. AND I. SANMARTÍN. 2011. Why are there so many plant species in the Neotropics? *Taxon* 60: 403–414.
- AYMARD, G. 2011. Bosques húmedos macrotérmicos de Venezuela. *Biollania* (Edición Especial) 10: 36–46.
- AND F. CASTRO-LIMA. 2015. A second tree species of *Ampelozizyphus* (Rhamnaceae), from the upper Cuyarí river basin, Guainía (Colombia). *Harvard Papers in Botany* 20: 161–166.
- , R. SCHARFEL, P. BERRY, AND B. STERGOS. 2009. Estudio de los suelos y la vegetación (estructura, composición florística y diversidad) en bosques macrotérmicos no-inundables, estado Amazonas, Venezuela (aprox. 01°30'–05°55'N; 66°00'–67°50'E). *Biollania* (Edición Especial) 9: 6–251.
- BARMAN, R. J. 1971. The Forgotten Journey: Georg Heinrich Langsdorff and the Russian Imperial Scientific Expedition to Brazil, 1821–1829. *Terrae Incognitae* 3: 67–96.
- BASS, M. S., M. FINER, C. N. JENKINS, H. KREFT, D. F. CISNEROS-HEREDIA, S. F. MCCracken, N. C. A. PITMAN, P. H. ENGLISH, K. SWING, G. VILLA, A. DI FIORE, C. C. VOIGT, AND T. H. KUNZ. 2010. Global Conservation Significance of Ecuador's Yasuní National Park. *PloSone* 5: 1–22.
- BERNAL, R., S. R. GRADSTEIN, AND M. CELIS, EDS. 2016. Catálogo de plantas y líquenes de Colombia. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá. <http://catalogoplantascolumbia.unal.edu.co>
- BERRY, P. E. AND G. AYMARD. 1997. A historic portage revisited. *Biollania* (Edición Especial) 6: 263–274.
- BOUBLI, J. P. 2002. Lowland floristic assessment of Pico da Neblina National Park, Brazil. *Plant Ecology* 160: 149–167.
- BREWER-CARÍAS, C. 1988. Cerro de la Neblina: Resultados de la Expedición 1986–1987. Fundación para el Desarrollo de las Ciencias Físicas, Matemáticas y Naturales, Caracas.
- BUSH, M., P. E. DE OLIVEIRA, P. A. COLINVAUX, M. C. MILLER, AND J. E. MORENO. 2004. Amazonian paleoecological histories: one hill, three watersheds. *Paleoecography, Palaeoclimatology, Palaeoecology* 214: 359–393.
- CÁRDENAS-LÓPEZ, D., ED. 2007. Flora del Escudo Guayanés en Inírida (Guainía, Colombia). Instituto Amazónico de Investigaciones Científicas Sinchi. Bogotá, Colombia.
- , R. LÓPEZ, C. A. MARÍN, J. C. ARIAS, AND S. SUA. 2007a. Botánica en la Amazonia Colombiana: doscientos años después de Martius. *Revista Colombia Amazónica* 2: 71–100.
- , J. S. BARRETO, J. C. ARIAS, U. G. MURCIA, C. A. SALAZAR, AND O. MÉNDEZ. 2007b. Caracterización y tipificación forestal de ecosistemas en el municipio de Inírida y el corregimiento de Cacahual (Guainía); una zonificación forestal para la ordenación de los recursos. Sinchi y Corporación para el Desarrollo Sostenible del Norte y el oriente Amazónico, Bogotá.
- , N. CASTAÑO, AND S. SUA. 2014. Flora de la Estrella Fluvial Inírida. Pages 90–100 in F. TRUJILLO, J. S. USMA, AND C. A. LASSO, EDS. *Biodiversidad de la Estrella Fluvial Inírida*. World Wildlife Fund Colombia, CDA, Fundación Omacha, Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Colombia. Bogotá D.C.
- CARDOSO, D., J. G. CARVALHO SOBRINHO, C. E. ZARTMAN, D. L. KOMURA, AND L. P. QUEIROZ. 2015. Unexplored Amazonian diversity: rare and phylogenetically enigmatic tree species are newly collected. *Neodiversity* 8: 55–73.
- CLARK, H., R. LIESNER, P. E. BERRY, A. FERNÁNDEZ, G. AYMARD, AND P. MAQUIRINO. 2000. Catálogo anotado de la flora del área de San Carlos de Río Negro, Venezuela. *Scientia Guianae* 11: 101–316.
- CARVAJAL, DE FR. G. 1848. Descubrimiento del río de las Amazonas según la relación hasta ahora inédita del viaje de Francisco de Orellana (editado por J. T. Medina). E. Rasco, Sevilla.
- COLINVAUX, P. A. 2005. The Pleistocene vector of Neotropical diversity. Pages 78–106 in E. BERMINGHAM, C. W. DICK, AND C. MORITZ, EDS. *Tropical Rainforests: Past, Present and Future*. The University of Chicago Press, Chicago, Illinois.
- CÓRDOBA, M. P. AND A. ETTER. 2001. Flora. Pages 102–107 in A. ETTER, L. G. BAPTSITE, M. CÓRDOBA, Y. MUÑOZ, A. REPIZZO, M. ROMERO, M. ALVÁREZ, F. ESCOBAR, F. FERNÁNDEZ, H. MENDOZA, AND A. ROJAS, EDS. *Puinawai y Nukak*. Caracterización ecológica de dos reservas nacionales naturales de la Amazonia Colombiana. Pontificia Universidad Javeriana, Colciencias, Instituto A. von Humboldt y Fundación FES. Bogotá, Colombia.
- DEZDEO, N., P. MAQUIRINO, P. E. BERRY, AND G. AYMARD. 2000. Principales tipos de bosques en el área de San Carlos de Río Negro, Venezuela. *Scientia Guianae* 11: 15–36.

- DE LAUBENFELS, D. J. 2004. Podocarpaceae. Pages 297–300 in P. E. BERRY, K. YATSKIEVYCH AND B. K. HOLST, EDS. *Flora of the Venezuelan Guayana*, Vol. 8. Missouri Botanical Garden, St. Louis, Missouri.
- AND J. SILBA. 1988. Notes on Asian and Trans-Pacific Podocarpaceae II. *Phytologia* 65: 329–332.
- DUBROEUCQ, D. AND B. VOLKOFF. 1998. From Oxisols to Spodosols and Histosols: Evolution of the soil mantles in the Río Negro basin (Amazonia). *Catena* 32: 245–280.
- ENGLER, A. 1931. Rutaceae. A. ENGLER AND K. PRANTL, EDS. *Die natürlichen Pflanzenfamilien*, ed 2, 19a: 187–359.
- FAY, M. F., K. M. CAMERON, G. T. PRANCE, M. D. LLEDÓ, AND M. W. CHASE. 1997. Familial relationships of *Rhabdodendron* (Rhabdodendraceae): plastid *rbcl* sequences indicate a Caryophyllid placement. *Kew Bull.* 52: 923–932.
- FUNK, V. A. 2007. *The Guiana Shield: 20 years and counting*. *The Plant Press* 10 (2): 1, 12–15.
- GARCÍA-VILLACORTA, R., K. G. DEXTER, AND T. PENNINGTON. 2016. Amazonian white-sand forests show strong floristic links with surrounding oligotrophic habitats and the Guiana Shield. *Biotropica* 48: 47–57.
- GENTRY, A. H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden* 69: 557–593.
- . 1993. *A Field Guide to the Families and Genera of Woody Plants of Northwest South America*. Conservation International, Washington, D.C.
- GILG, E. F. AND R. K. F. PILGER. 1905. Rutaceae in R. Pilger, *Beiträge zur Flora der Hylea nach den Sammlungen von E. H. G. Ule*. *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* 47: 152–154, Tafeln II–III.
- GOSLING, W. D., F. E. MAYLE, N. J. TATE, AND T. J. KILLEEN. 2009. Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. *Review of Palaeobotany and Palynology* 153: 70–85.
- HERRERA, R. 1985. Nutrient cycling in Amazonian forests. Pages 95–105 in G. T. PRANCE AND T. E. LOVEJOY, EDS. *Key Environments: Amazonia*. Pergamon Press, Oxford.
- HOOGHIEMSTRA, H., V. M. WIJNINGA, AND A. M. CLEEF. 2006. The paleobotanical record of Colombia; implications for biogeography and biodiversity. *Annals of the Missouri Botanical Garden* 93: 297–325.
- , T. VAN DER HAMMEN, AND A. CLEEF. 2002. Paleoeología de la flora boscosa. Pages 43–58 in M. R. GUARIGUATA AND G. H. KATTAN, EDS. *Ecología y conservación de bosques Neotropicales*. Editorial Libro Universitario Regional, Costa Rica.
- HOPKINS, M. J. G. 2007. Modeling the known and unknown plant biodiversity of the Amazon Basin. *Journal of Biogeography* 34: 1400–1411.
- HOORN, C., F. P. WESSELINGH, H. TER STEEGE, M. BERMÚDEZ, A. MORA, J. SEVINK, I. SANMARTÍN, A. SÁNCHEZ-MESEGUER, C. ANDERSON, J. FIGUEROA, C. JARAMILLO, D. RIFF, F. R. NEGRI, H. HOOGHIEMSTRA, J. LUNDBERG, T. STADLER, T. SÄRKINEN, AND A. ANTONELLI. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330: 927–931.
- HUBER, J. 1909. *Rhabdodendron*. *Materiales para a flora amazonica*, VII, *Plantae Duckeanae austro-guyanenses*. *Boletim do Museu Paraense “Emílio Goeldi”* 5: 424–431.
- HUBER, O. 1995a. Geographical and Physical Features. Pages 1–61 in P. E. BERRY, B. HOLST AND K. YATSKIEVYCH, EDS. *Flora of the Venezuelan Guayana*, Vol. 1. Missouri Botanical Garden, St. Louis, and Timber Press, Portland, Oregon.
- . 1995b. Vegetation. Pages 97–160 in P. E. BERRY, B. HOLST AND K. YATSKIEVYCH, EDS. *Flora of Venezuelan Guayana* Vol. 1. Missouri Botanical Garden, St. Louis, and Timber Press, Portland, Oregon.
- AND J. J. WURDACK. 1984. History of botanical exploration in Territory Federal Amazonas, Venezuela. *Smithsonian contributions to Botany* 56: 1–83.
- HUMBOLDT, A. VON. 1818–1819. *Personal Narrative of Travels to the Equinoctial Regions of the New Continent, during the years 1799–1804*. Translated by H. M. Williams. H. G. Bohn, London.
- JARAMILLO, C., C. HOORN, S. A. F. SILVA, F. LEITE, F. HERRERA, L. QUIROZ, R. DINO, AND L. ANTONIOLI. 2010. The origin of the modern Amazon rainforest: implications of the palynological and palaeobotanical record. Pages 317–334 in C. HOORN, F. P. WESSELINGH, EDS. *Amazonia, Landscape and Species Evolution*. Blackwell Publishing, Oxford.
- KLINGE, H. AND E. CUEVAS. 2000. Bana: Una comunidad leñosa sobre arenas blancas en el alto Río Negro, Venezuela. *Scientia Guianae* 11: 37–49.
- AND E. MEDINA. 1979. Río Negro caatingas and campinas, Amazonas States of Venezuela and Brazil. Pages 483–488 in R. L. SPECHT, ED. *Heathlands and Related Shrublands*. Elsevier Scientific Publications, Co., New York.
- KRAUSE, K. 1914. Rutaceae. A. ENGLER AND K. PRANTL, *Die natürlichen Pflanzenfamilien*, *Ergänzungsheft* 3, *Nachtr.* 4: 157.
- LANDRUM, L. R. 1986. The life and botanical accomplishments of Boris Alexander Krukoff. *Advances in Economic Botany* 2: 1–96.
- LLERAS, E. 1997. Upper Río Negro region (Brazil, Colombia, Venezuela). Pages 333–337 in S. D. DAVIES, V. H. HEYWOOD, O. HERRERA-MACBRYDE, J. VILLA-LOBOS, AND A. C. HAMILTON, EDS. *Centres of Plant Biodiversity volumen 3: The Americas*. World Wildlife Fund for Nature and The World Conservation Union, Cambridge, U.K.
- LLERAS, R. AND J. H. KIRKBRIDE JR. 1978. Alguns aspectos da vegetação da serra de Cachimbo. *Acta Amazonica* 8(1): 51–65.
- LEVINE, N. M., K. ZHANG, M. LONGO, A. BACCINI, O. L. PHILLIPS, S. L. LEWIS, E. ALVÁREZ-DÁVILA, A. C. SEGALIN DE ANDRADE, R. J. W. BRIENEN, T. L. ERWIN, T. R. FELDPAUSCH, A. L. MONTEAGUDO, P. NÚÑEZ V., A. PRIETO, J. E. SILVA-ESPEJO, Y., AND P. R. MOORCROFT. 2016. Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *PNAS* 113: 793–797.
- MAYLE, F. E., M. J. BURN, M. POWER, AND D. H. URREGO. 2009. Vegetation and fire at the last glacial maximum in tropical South America. Past climate variability in South America and surrounding regions. Pages 89–112 in F. VIMEUX, F. SILVESTRE, AND M. KHODRI, EDS. *Developments in Paleoenvironmental Research* 14. Springer, Berlin.
- MAYLE, F. E., D. J. BEERLING, W. D. GOSLING, AND M. B. BUSH. 2004. Responses of Amazonian ecosystems to climatic and atmospheric carbon dioxide changes since the last glacial maximum. *Philosophical Transactions of the Royal Society B* 359: 499–514.
- MEDeiros, H. AND A. M. A. AMORIM. 2014. *Rhabdodendraceae in Lista de Espécies da Flora do Brasil*. Jardim Botânico do Rio de Janeiro. Available at: <http://floradobrasil.jbrj.gov.br/jabot/floradobrasil/FB206> (accessed February 11, 2016).

- MEDINA, E., R. HERRERA, C. JORDAN, AND H. KLINGE. 1977. The Amazon project of the Venezuelan Institute for Scientific Research. *Natural Resources* 13: 4–6.
- AND E. CUEVAS. 2011. Complejo Caatinga Amazónica: Bosques pluviales esclerófilos sobre arenas blancas. *Biollania* (Edición Especial) 10: 36–46.
- MILLIKEN, W., D. ZAPPI, D. SASAKI, M. HOPKINS M., AND T. R. PENNINGTON. 2011. Amazon vegetation: How much don't we know and how much does it matter? *Kew Bulletin* 65: 1–19.
- NELSON, B. W., C. A. C. FERREIRA, M. F. DA SILVA, AND M. L. KAWASAKI. 1990. Endemism centres, refugia and botanical collection density in Brazilian Amazonia. *Nature* 345: 714–716.
- PENNINGTON, T., M. HUGHES, AND P. W. MOONLIGHT. 2015. The origins of tropical rainforests hyperdiversity. *Trends in Plant Science* 20: 693–695.
- PITMAN, N. C., H. MOGOLLÓN, N. DÁVILA, M. RÍOS, R. GARCÍA-VILLACORTA, J. GUEVARA, T. BAKER, A. MONTEAGUDO, O. PHILLIPS, R. VÁSQUEZ-MARTÍNEZ, M. AHUITE, M. AULESTIA, D. CARDENAS, C. CERÓN, P. A. LOIZEAU, D. NEILL, P. NUÑEZ, W. PALACIOS, R. SPICHTER, AND E. VALDERRAMA. 2008. Tree community change across 700 km of Lowland Amazonian Forest from the Andean Foothills to Brazil. *Biotropica* 40: 525–535.
- POMBO DE SOUZA, M. M. 2012. Estrutura e composição das comunidades de arvores na bacia do alto Río Negro. Master's Thesis, Instituto Nacional de Pesquisas da Amazônia-INPA, Manaus, Brazil.
- PRANCE, G. T. 1968. The systematic position of *Rhabdodendron* Gilg & Pilg. *Bulletin du Jardin botanique de l'État à Bruxelles* 38: 127–146.
- . 1972. *Rhabdodendraceae*. *Flora Neotropica* 11: 1–22. Hafner, New York.
- , B. W. NELSON, M. FREITAS DA SILVA, AND D. C. DALY. 1984. Projeto Flora Amazônica: Eight years of binational botanical expeditions. *Acta Amazonica* (Supl. 1/2): 5–29.
- PRANCE, G. T. AND D. M. JOHNSON. 1992. Plant collections from the Plateau of Serra do Aracá (Amazonas, Brazil) and their phytogeographic affinities. *Kew Bulletin* 47: 1–24.
- . 1989. American tropical forests. Pages 99–132 in H. LIETH AND M. J. A. WERGER, EDS. *Tropical Rain Forest Ecosystems, Ecosystems of the World* 14B. Elsevier, Amsterdam, the Netherlands.
- . 2001. Amazon Ecosystems. Pages 145–157 in S. ASHER-LEVIN, ED. *Encyclopedia of Biodiversity* Vol. 1: A–C. Academic Press, New York.
- . 2002. *Rhabdodendraceae*. Pages 339–341 in K. KUBITZKI, ED. *The Families and Genera of Vascular Plants* Vol. V. Flowering Plants: Dicotyledons. Malvales, Capparales and non-betain Caryophyllales. Springer, Berlin.
- . 2004. *Rhabdodendraceae*. Pages 321–322 in N. P. SMITH, S. A. MORI, A. HENDERSON, D. W. M. STEVENSON, AND S. V. HEALD, EDS. *Flowering Plants of the Neotropics*. The New York Botanical Garden, Princeton University Press, Princeton, New Jersey.
- . 2005. *Flora da Reserva Ducke, Amazonas, Brasil: Rhabdodendraceae*. *Rodriguesia* 56 (86): 183–185.
- . 2009. Neotropical *Rhabdodendraceae*. In W. MILLIKEN, B. KLITGÅRD AND A. BARACAT. (2009 onwards), *Neotropikey—Interactive key and information resources for flowering plants of the Neotropics*. <http://www.kew.org/science/tropamerica/neotropikey/families/Rhabdodendraceae.htm> (accessed May 2016).
- . 2014. That glorious forest (exploring the plants and their indigenous uses in Amazonia). *Memoirs of the New York Botanical Garden* 113: 1–214.
- PUNYASENA, S. W., J. W. DALLING, C. JARAMILLO, AND B. L. TURNER. 2011. Comment on “The response of vegetation on the Andean flank in Western Amazonia to Pleistocene climate change.” *Science* 333: 1825a–b.
- RANGEL-CH. J. O. 2015. La riqueza de las plantas con flores de Colombia. *Caldasia* 37: 279–307.
- RIBEIRO, S. DA J. E. L., M. J. G. HOPKINS, A. VINCENTINI, C. A. SOTHERS, M. A. DA COSTA, J. M. DE BRITO, M. A. DE SOUZA, L. H. P. MARTINS, L. G. LOHMANN, P. A. ASSUNÇÃO, E. DA C. PEREIRA, C. FERNANDES DA SILVA, M. R. MESQUITA, AND L. C. PROCÓPIO. 1999. *Flora da Reserva Ducke* (Guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia Central. INPA-DFID, Manaus Brazil.
- RODRIGUES, W. A. 1961. Aspectos fitossociológicos das caatingas do Río Negro. *Boletim do Museu Paraense “Emílio Goeldi,” Nova serie, Botanica* 15: 3–41.
- RODRIGUES-FERREIRA, A. 2008. Carta e inventario enviados desde Barcelos el 17 de abril de 1786. Pages 80–86 in J. P. MONTEIRO SOARES Y C. FERRÃO, EDS. *Viagem ao Brasil de Alexander Rodrigues Ferreira Vol. III [Correspondência 1a parte (1779–1788); “Transcrição, Establecimiento do Texto e Notas” de J. Pereira da Silva]*. Kapa Editorial, Petrópolis.
- ROMERO-GONZÁLEZ, G. 2016. Pedro Joaquim Ayres—Un personaje lleno de misterios en la historia del estado Amazonas de Venezuela. *Boletín de Historia de las Geociencias en Venezuela* 120: 1–84.
- RUDAS, A., A. PRIETO, AND O. RANGEL. 2002. Principales tipos de vegetación de La Ceiba (Guainía), Guayana Colombiana. *Caldasia* 24: 243–365.
- SACEK, V. 2014. Drainage reversal of the Amazon River due to the coupling of surface and lithospheric processes. *Earth and Planetary Science Letters* 401: 301–312.
- SANDWITH, N. Y. 1943. New and noteworthy Polypetalae from British Guiana. *Journal of the Arnold Arboretum* 24: 218–226.
- SCHARGEL, R., G. AYMARD, AND P. BERRY. 2000. Características y factores formadores de spodosoles en el sector Maroa–Yavita, Amazonía Venezolana. *Revista UNELLEZ de Ciencia y Tecnología* 18(1): 85–96.
- SCHULMAN, L., T. TOIVONEN, AND K. RUOKOLAINEN. 2007. Analyzing botanical collecting effort in Amazonia and correcting for it in species range estimation. *Journal of Biogeography* 34: 1388–1399.
- STROPP, P., P. VAN DER SLEEN, P. P. ASSUNÇÃO, A. LOPES DA SILVA, AND H. TER STEEGE. 2011. Tree communities of white-sand and terra-firme forests of the upper Río Negro. *Acta Amazonica* 41: 521–544.
- , ———, C. A. QUESADA, AND H. TER STEEGE. 2013. Herbivory and habitat association of tree seedlings in lowland evergreen rainforest on white-sand and terra-firme in the upper Río Negro. *Plant Ecology & Diversity* 7: 255–265.
- TAKEUCHI, M. 1961. The structure of the Amazonian vegetation III. Campina forest in the Río Negro region. *Journal Fac. Sci. Univ. Tokyo* 8(2): 27–35.
- . 1962. The structure of the Amazonian vegetation IV. High Campina forest in the upper Río Negro. *Journal of the Faculty of Science: University of Tokyo, Section 3, Botany* 8(5): 279–288.

- TER STEEGE, H., N. C. A. PITMAN, T. J. KILLEEN, W. F. LAURANCE, C. A. PERES, J. E. GUEVARA, R. P. SALOMÃO, C. V. CASTILHO, I. LEÃO AMARAL, F. DIONÍZIA DE ALMEIDA MATOS, LUIZ DE SOUZA COELHO, WILLIAM E. MAGNUSSON, OLIVER L. PHILLIPS, DIOGENES DE ANDRADE LIMA FILHO, MARCELO DE JESUS VEIGA CARIM, MARIANA V. IRUME, M. PIRES MARTINS, J.-F. MOLINO, D. SABATIER, F. WITTMANN, D. CÁRDENAS LÓPEZ, J. RENAN DA SILVA GUIMARÃES, A. MONTEAGUDO MENDOZA, P. NÚÑEZ VARGAS, A. G. MANZATTO, N. FARIAS COSTA REIS, J. TERBORGH, K. R. CASULA, J. C. MONTERO, T. R. FELDPAUSCH, E. N. HONORIO CORONADO, A. J. DUQUE MONTOYA, C. E. ZARTMAN, B. MOSTACEDO, R. VÁSQUEZ, R. L. ASSIS, M. BRILHANTE MEDEIROS, M. FRAGOMENI SIMON, A. ANDRADE, J. L. CAMARGO, S. G. W. LAURANCE, H. E. MENDONÇA NASCIMENTO, B. S. MARIMON, B. H. MARIMON JR., F. COSTA, N. TARGHETTA, I. C. GUIMARÃES VIEIRA, R. BRIENEN, H. CASTELLANOS, J. F. DUVENVOORDEN, H. F. MOGOLLÓN, M. TERESA FERNANDEZ PIEDADE, G. A. AYMARD C., J. A. COMISKEY, G. DAMASCO, N. DÁVILA, R. GARCÍA-VILLACORTA, P. R. STEVENSON DIAZ, A. VINCENTINI, T. EMILIO, C. LEVIS, J. SCHIETTI, PRISCILA SOUZA, A. ALONSO, F. DALLMEIER, L. VALLE FERREIRA, D. NEILL, A. ARAUJO-MURAKAMI, L. ARROYO, F. ANTUNES CARVALHO, F. COELHO SOUZA, D. DANTAS DO AMARAL, R. GRIBEL, B. GARCIA LUIZE, M. PETRATI PANSONATO, E. VENTICINQUE, P. FINE, M. TOLEDO, C. BARALOTO, C. CERÓN, J. ENGEL, T. W. HENKEL, E. M. JIMENEZ, P. MAAS, M. C. PEÑUELA MORA, P. PETRONELLI, J. D. CARDENAS REVILLA, M. SILVEIRA, J. STROPP, R. THOMAS-CAESAR, T. R. BAKER, D. DALY, M. RÍOS PAREDES, N. FERREIRA DA SILVA, A. FUENTES, P. MØLLER JØRGENSEN, J. SCHÖNGART, M. R. SILMAN, N. CASTAÑO ARBOLEDA, B. BARÇANTE LADVOCAT CINTRA, F. CORNEJO VALVERDE, A. DiFIORE, J. F. PHILLIPS, T. R. VAN ANDEL, P. VON HILDEBRAND, E. MARQUES BARBOSA, L. C. DE MATOS BONATES, D. DE CASTRO, E. DE SOUSA FARIAS, T. GONZALES, J.-L. GUILLAUMET, B. HOFFMAN, Y. MALHI, I. P. DE ANDRADE MIRANDA, A. PRIETO, A. RUDAS, A. R. RUSCHELL, N. SILVA, C. I. A. VELA, VINCENT A. VOS, E. L. ZENT, S. ZENT, A. CANO, M. TRINDADE NASCIMENTO, A. A. OLIVEIRA, H. RAMIREZ-ANGULO, J. FERREIRA RAMOS, R. SIERRA, M. TIRADO, M. N. UMAÑA MEDINA, G. VAN DER HEJDEN, E. VILANOVA TORRE, C. VRIESENDORP, O. WANG, K. R. YOUNG, C. BAIDER, H. BALSLEV, N. DE CASTRO, W. FARFAN-RÍOS, C. FERREIRA, C. MENDOZA, I. MESONES, A. TORRES-LEZAMA, L. E. URREGO GIRALDO, D. VILLARROEL, R. ZAGT, M. N. ALEXIADES, K. GARCIA-CABRERA, L. HERNANDEZ, I. HUAMANTUPA-CHUQUIMACO, W. MILLIKEN, W. PALACIOS CUENCA, S. PANSINI, D. PAULETTO, F. RAMIREZ AREVALO, A. FELIPE SAMPAIO, E. H. VALDERRAMA SANDOVAL, AND L. VALENZUELA GAMARRA. 2015. Estimating the global conservation status of more than 15,000 Amazonian tree species. *Science Advances* 1 (10): 1–10.
- TER STEEGE, H., ATDN (Amazon Tree Diversity Network: collective author), AND RAINFOR (The Amazon Forest Inventory Network: collective author). 2010. Contribution of current and historical processes to patterns of tree diversity and composition of the Amazon. Pages 349–359 in C. HOORN AND F. P. WESSELINGH, EDS. *Amazonia, Landscape and Species Evolution*. Blackwell Publishing, Oxford.
- _____. ET AL. 2013. Hyperdominance in the Amazonian tree flora. *Science* 342: 225–335.
- THIERS, B. 2012. Index Herbarium. A Global Directory of Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium. Electronic database accessible at <http://sweetgum.nybg.org/ih/> (accessed February 20, 2016).
- VÁSQUEZ, R. 1997. Flórula de las reservas Biológicas de Iquitos. Perú. *Annals of the Missouri Botanical Garden* 63: 1–1046.
- WESSELINGH F. P, C. HOORN, S. B. KROONENBERG, A. ANTONELLI, J. G. LUNDBERG, , H. B. VONHOF, AND H. HOOGHIEMSTRA. 2010. On the origin of Amazonian landscapes and biodiversity: a synthesis. Pages 421–431 in C. HOORN AND F. P. WESSELINGH, EDS. *Amazonia, Landscape and Species Evolution*. Blackwell Publishing, Oxford.
- WURDACK, J. J. 1971. The Melastomataceae collections of A. R. Ferreira. *Taxon* 20: 595–596.