

A NEW SPECIES OF *NEEA* (NYCTAGINACEAE: *PISONIEAE*) FOR THE FLORA OF COLOMBIA

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Abstract. *Neea gustaviaefolia*, a new species from the wet forests from “Sierra de La Macarena” and upper “Guaviare” river regions of Colombia (Guaviare and Meta departments) is described, illustrated, and its morphological relationships are discussed. This new species is a small tree of 6 m tall, on the basis of its alternate, oblanceolate larger leaves and a shorter terminal cymes inflorescence, verticillate (with three opposite primary branches), it does not appear to be closely allied to any other *Neea* species. This new species shares several other features with five species (*N. alumnorum*, *N. brevipedunculata*, *N. floribunda*, *N. itanhaensis* and *N. verticillata*). Morphologically, however, it is comparable to *N. alumnorum* and *N. itanhaensis* but it differs in its leaves, inflorescences, staminal perianth, and stamens number. In addition, ecological, floristic, and geological notes about the “La Sierra de La Macarena” are included. A key for identifying species of *Neea* to Colombia is also provided. *Neea gustaviaefolia* is remarkable for its alternate, large leaves (30–65 × 10–20 cm), in an otherwise predominantly opposite, small to medium (4–25 × 2–8 cm) leaved genus, and it increases to 27 the number of species of the genus to Colombia flora.

Keywords: *Neea*, Nyctaginaceae, “Sierra de La Macarena,” alternate leaves, wet forest

Resumen. *Neea gustaviaefolia* de bosques húmedos de la Sierra de La Macarena y la cuenca alta del río Guaviare de Colombia (departamentos de Guaviare y Meta) es descrita, ilustrada, y sus relaciones morfológicas son discutidas. Por sus hojas alternas, grandes, oblongoeladas y la inflorescencia cimada verticilada, muy corta terminal, (con tres ramas primarias opuestas), *Neea gustaviaefolia* no se relaciona con ninguna de las otras especies de *Neea*. Esta nueva especie comparte algunos caracteres morfológicos con cinco especies (*N. alumnorum*, *N. brevipedunculata*, *N. floribunda*, *N. itanhaensis*, *N. verticillata*). Sin embargo, morfológicamente, es comparable con *N. alumnorum* and *N. itanhaensis* de las cuales difiere en sus hojas, inflorescencias, perianto estaminal, y el número de los estambres. Se presentan notas ecológicas, florísticas y geológicas acerca de la Sierra de La Macarena y una clave de las especies del género en Colombia. *Neea gustaviaefolia* es notable por sus hojas alternas, muy grandes, en un género donde predominan las hojas opuestas, de tamaños pequeño a mediano. Este nuevo hallazgo eleva a 27 el número de especies del género para la flora de Colombia.

Palabras claves: *Neea*, Nyctaginaceae, Sierra de La Macarena, hojas alternas, bosques húmedos

Neea Ruiz & Pav. (1794: 52), is a genus considered part of Nyctaginaceae, Pisonieae (Heimerl, 1934; Douglas and Spellenberg, 2010; Rossetto et al., 2019a, Rossetto and Caraballo-Ortiz, 2020). It is the most diverse and representative genus in Nyctaginaceae, distributed throughout tropical and subtropical areas around the world, with ca. 400 species and thirty-one genera (Bittrich and Kühn, 1993; Douglas and Manos, 2007). The genus has a Neotropical distribution and ranges from southern Florida, central to southern Mexico through Central America, the Caribbean, Colombia, Venezuela, Guianas, Ecuador, Peru, Brazil, Bolivia and Paraguay (Damascena and Coelho, 2009 Onwards; Ulloa Ulloa et al., 2018 Onwards) and comprises ca. 84 species (World Checklist of Vascular Plants; kew.org).

Neea is most diverse throughout the Amazon and Guayana bioregions, where the species are found in lowland (“terra firme”) vegetation and montane forests. Several species are found over rocky slopes and oligotrophic soils derived from the Precambrian crystalline basement of the Guayana Shield (e.g., *N. grandis* Steyererm. & Maguire, *N. neblinensis* Steyererm. & Maguire), and drained by black

waters rivers (e.g., *N. clarkii* Steyererm., *N. mapourioides* Steyererm.) on non-flooded forests known as “caatinga Amazonica”, “campina” or “campinarana” (Steyermark and Aymard, 2003; da Silva Costa et al., 2021). The remaining species appear to require more specific habitats, like foothills in the low to medium altitude (500–1500 m) mountains of the Andes, along the Pacific Coast of Colombia and Ecuador, the dry forests, and xerophytic ecosystems a well. Several species have wide geographic distributions (e.g., *N. amplifolia* Donn. Sm., *N. divaricata* Poepp. & Endl., *N. floribunda* Poepp. & Endl., *N. ovalifolia* Spruce ex J. A. Schmidt), whereas others are endemic to particular geographical areas, such as some species found only in Caribbean islands (Ulloa Ulloa et al., 2018 Onwards), or in Southeast Brazil (Furlan & Giulietti, 2014; Rossetto et al., 2019b; Rossetto and Ferraz, 2020).

Ethnobotanical information about *Neea* in the lowlands is not commonly found in the literature. Burger (1983) reported that the fruits of *Neea* ssp. are used for coloring in Costa Rica. The bark of *Neea brevipedunculata* Steyererm., *N. clarkii* Steyererm., *N. mapourioides* Steyererm. and *N. robusta*

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Steyerm. is crushed and used by Arawak groups (i.e., Baniwa, Kuripako) in the upper Rio Negro region of Colombia and Venezuela to treat snake, spider, and ant bites. These species are known with the local name of “Palo de culebra” (Steyermark and Aymard, 2003). Guillermo Klug observed that the Indians of the Putumayo and Caquetá departments, Colombia paint their teeth black with the leaves of *N. parviflora* Poepp. & Endl. by chewing them, to preserve them from infection. Also, he noticed that these Indians have very sound and strong teeth, this taxon is known as “Yanamuco” (*G. Klug 1955*, MO; Jan–Feb 1931).

Neea is characterized by its dioecious condition, the leaves are commonly opposite, sometimes verticillate, rarely alternate, and the staminate perianth is usually urceolate, sometimes tubular to ellipsoid or infundibuliform with the stamens included, the pistillate perianth has stigmas only rarely exerted, and the pistil sessile or narrowed at the base.

Neea is closely related to *Guapira* Aublet (1775: 308): both genera have unarmed stems and branches and fleshy anthocarps. These two genera have traditionally been treated as distinct taxa based on the shape of the staminate perianth and the stamen position in the perianth, which is exerted in *Guapira* and inserted in *Neea* (Standley, 1937; Burger, 1983; Steyermark and Aymard, 2003; Harling, 2010). Burger (1983) was the first to recommend that both genera should be united under *Guapira*. Molecular evidence indicates that these genera form a single lineage (Douglas and Manos, 2007; Rossetto et al., 2019a), and that exerted stamens is a homoplastic character (Rossetto et al., 2019a). However, other researchers (Chagas and Costa Lima, 2020) considered that these studies are based on a small sample of species (20%), and the resulting data still do not represent a robust phylogenetic support to demonstrate that these entities should be merged. Nevertheless, morphologically, *Guapira* and *Neea* can be distinguished by the state characters presented in Burger (1983), Harling (2010), Pool (2001), DeFilipps and Maina (2003) and Steyermark and Aymard (2003).

Throughout the years, *Neea* has been infamously known to be one of most difficult genera among Neotropical flowering plant genera (Standley, 1931; Douglas and Spellenberg, 2010). These authors pointed out that many

diagnostic characters are not well represented in herbarium specimens, which, combined with the relatively sparse collections of these often-dioecious plants, has meant that species in this genus remain poorly understood. In addition, most exsiccatae differ in one or several characters from one another, but without any discernible coordination (Harling, 2010), and many mis-identified collection have been accumulated in herbaria for decades (Steyermark, 1987). These authors assumptions partially are true. Nonetheless, after studying this group for the last two decades, it is obvious that an additional problem is the absence of experts in this group (*Pisonieae*) that are familiar with the bulk of the ca. 190 species.

Steyermark and Aymard (2003) identified two taxonomically useful inflorescence characters that separate species: 1) inflorescence cauliflorous or ramiflorous on the old stem versus inflorescence axillary or terminating the stem or its branches; 2) the junction of lowest axes of inflorescences with summit of peduncle enlarged, 2.5–4 mm wide versus the junction of lowest axes of inflorescence with summit of peduncle not manifestly enlarged, 0.8–2 mm wide.

No comprehensive monograph of *Neea* has been completed, although the genus has been largely treated for Flora of Peru (Standley, 1937), Flora of Guatemala (Standley and Steyermark, 1946), Flora of Panama (Woodson et al., 1961), Flora of Belize and Petén region (Lundell, 1962), Flora of Costa Rica (Burger, 1983), Flora of Nicaragua (Pool, 2001), Flora of the Guianas (DeFilipps and Maina, 2003), Flora of the Venezuelan Guayana (Steyermark and Aymard, 2003), *Manual de Plantas de Costa Rica* (González-Rámirez, 2007), Flora of Ecuador (Harling, 2010), and Flora of Brazil (Furlan & Giulietti, 2014).

The present contribution increases the number of *Neea* species known from Colombia (to 27 species) and Venezuela (29), the two countries with the highest number of species in the genus. In this geographical and taxonomical context, *N. spruceana* Heimerl is treat here as different from *N. oppositifolia* Ruiz & Pav., *N. laetevirens* Standl. is considering a synonymy of *N. psychotrioides* Donn. Sm., *N. divaricata* Poepp. & Endl. and *N. virens* Poepp. ex Heimerl are recognized as validate species, and the record of *N. nigricans* Fawc. & Rendle is based in Choisy (1849).

MATERIAL AND METHODS

This work is based on morphological (using a dissecting stereomicroscope) and herbarium studies in COAH, COL, GH, HUA, MO, NY, MEDEL, PORT, and VEN (herbarium codes after Thiers, 2019). Perhaps one of the most commonly consulted public datasets (Global Biodiversity Information Facility (GBIF; www.gbif.org) was not used in this work since recent research has found that 29–90% of the records are potentially erroneous, with large variation across taxonomic groups (Zizka et al., 2020). However, the world checklist of vascular plants (WCVP) was consulted: this dataset is a comprehensive list of scientifically described plant species, compiled over four decades, from peer-reviewed literature, authoritative scientific databases, herbaria and observations, then reviewed by experts (Govaerts et al., 2021).

Historical taxonomic literature on *Neea* was examined using Biodiversity Heritage Library website (<http://www.biodiversitylibrary.org>). In particular, the protologues in Choisy (1849), Schmidt (1872), Heimerl (1891, 1897, 1914, 1932, 1934), and Huber (1909) were examined. Current bibliography on *Neea* were scrutinized, mainly the treatments of Nyctaginaceae in the Flora of the Guianas (DeFilipps and Maina, 2003), the Flora of the Venezuelan Guayana (Steyermark and Aymard, 2003), the Flora of Ecuador (Harling, 2010) and Flora of Brazil (Furlan & Giulietti, 2014). Also, the checklists: *Nuevo Catálogo de la Flora Vasculare de Venezuela* (Aymard, 2008), *Catálogo de plantas y líquenes de Colombia* (Bernal, 2016) and *Catálogo de las plantas con flores de la Amazonia colombiana*

(Infante-Betancour and Rangel-Ch., 2018) were reviewed. Type specimens of *Neea* species involved in this study were examined using on-line images from JSTOR Global Plants (<https://plants.jstor.org/>). In addition, International Plant Names Index (<https://www.ipni.org/>) and Tropicos (<http://legacy.tropicos.org/Home.aspx>) were also consulted to update the current nomenclature and geographical information.

The specific terminology for vegetative characters, vestiture description, inflorescences, flowers, and fruit

morphology follow Font-Quer (2001), Harris and Harris (2006), and Endress (2010).

To determine the conservation status of *N. gustaviaefolia* (according to IUCN categories and criteria; IUCN, 2017), the extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the supporting Red List threat assessments with GeoCAT (Bachman *et al.* 2011), constantly updated through the <https://www.kew.org/science/our-science/projects/geocat-geospatial-conservation-assessment-tool>.

TAXONOMY

Neea gustaviaefolia Aymard, *sp. nov.*

TYPE: COLOMBIA. Meta. Sierra de La Macarena, sector Oriental, selvas densas entre los ríos Güejar y Sansa, 2°52'N; 73°54'O, 500–1000 m, 24 Agosto 1950 (fl), *Jesús Medardo Idrobo 481* (Holotype: COL). Fig. 1–2.

Neea gustaviaefolia can be distinguished from all other species previously described for the genus by the combination of the following characters: small tree, ca. 6 m tall, oblanceolate leaves, secondary veins 15–17; canaliculate on the upper surface, elevated on the lower surface, inflorescence with shorter and stout peduncle, 10–40 × 4–7 mm, compound by terminal cymes, with three opposite, verticillate primary branches, staminal perianth tubular, sparsely ferruginous pubescent outside and stamens 9.

Small *tree* 6 m tall, 6–10 cm diameter; branches glabrous, fistulous, striate, bark flaking off when mature. *Leaves* alternate, glabrous, pale green (olive) to brown when dried and opaque on both surfaces, blades 40–46 × 10–15 cm, coriaceous, oblanceolate, glabrous on both surfaces, with sparsely yellow dots on the lower surface, apex acute, base acute-attenuate, margins entire, revolute, venation pinnate; midvein and secondary veins canaliculate on the upper surface, elevated on the lower surface; secondary veins brochidodromous, 15–17 pairs, arcuated and convergent towards margin and linking 5–7 mm to the margin, tertiary veinlets obscure on the upper surface, elevate on the lower surface, forming large areoles, petiole stout, 1.5–2.5 × 0.3–0.5 cm. *Staminate inflorescences*, 7–10 × ca. 11 cm, terminal cymes, erect, peduncle 1–4 cm × 0.4–0.7 mm, thickened, striate, glabrous; with three opposite, verticillate primary branches, 4–4.5 × 0.2–0.4 cm, glabrous, each branch with two basal bracts (lanceolate, ca. 3 × ca. 1 mm, glabrous), these branches, above formed 2–4 alternate secondary axes, 8–16 mm long, shortly dense ferruginous, bearing a solitary flower or groups of three flowers born along the length of these axes. bracts at base of secondary axis lanceolate, ca. 1 mm long, ferruginous on both sides. *Staminate perianth* sessile, subtended by 1–3 bracteoles, often unequal at flower base, 0.50–0.60 mm long, acute, covered with ferruginous trichomes outside, glabrous inside; perianth 3–4 × 1–1.5 mm, tubular, sparsely adpressed ferruginous outside, more dense at the base, glabrous inside, 5-lobed, open lobes acute; stamens 9, included, filaments 0.5–1 mm long, unequal, connate at the base, glabrous, anthers 0.5–0.8 mm, oblong, glabrous; pistillode ca. 2 mm long, glabrous. *Pistillate flowers* and anthocarps not seen.

Phenology: this new species has been collected with flowers in bud and open flowers in June and August.

Etymology: the epithet *gustaviaefolia* is coined after the large and oblanceolate leaves of the species that resemble the leaves of the great majority of the species of the genus *Gustavia* L. (Lecythidaceae).

Distribution and ecology: the species is hitherto known to occur in primary or secondary wet forest at 100–1000 m elevation, located in “Serranía de La Macarena” and SE of San José del Guaviare, in the Meta and Guaviare departments (Fig. 2). The type locality, the “Serranía de La Macarena” is an isolated mountain range separated by about 40 km at their northern extreme from the East Andes. The range, ca. 120 km long and 30 km wide, is oriented from north to south. The highest elevation reaches 1,250 m, the highest point of the Orinoquia region. According to Pinson *et al.* (1962) and Díaz-Merlano (2016), the basement rocks on the east side of the Macarena include the Precambrian granite of the Guyana shield in the Guaviare River valley, and the San José del Guaviare region. The rocks of the shield are overlaid by sandstones and conglomerates of the Vaupés formation of lower Paleozoic to the lower Oligocen age. The origin of the Macarena range is associated with the dragging of a block of the Cordillera Oriental with a rupture plane related to the Algeciras-La Uribe faults. The proposed boundary of the Orinoquia-Amazonia watersheds allows the segregation of the set of blocks associated with the Amazon from Southwest to Northeast with the Amazonas, Putumayo, Caquetá and Vaupés blocks or mountain range block. Therefore, the boundary between the two natural regions is marked by the beginning of the Inírida block that together with the Guaviare, Vichada, Tomo and Arauca blocks define (based on the watersheds), the Amazonian and Orinocense regions of Colombia (Jaramillo and Rangel-Ch., 2014; Rangel-Ch. and Infante-Betancour, 2018). This natural region is well known by its four interesting biogeographical types of vegetation: the lowland a medium forests with presence of numerous Amazonian and Guayana elements (e.g., *Calycophyllum spruceanum* (Benth.) Hook. f ex K. Schum., Rubiaceae; *Justicia macaranensis* Leonard, Acanthaceae; *Petrea maynensis* Huber, Verbenaceae), the Andean region closely relate with the slopes of the Colombian Eastern Cordillera, the Orinoquia savannas, and a sector dominated by tepui-like vegetation, located on top of La Macarena mountains (Stevenson *et al.*, 2004). A phytosociological study performed in this region (Romero-V. *et al.*, 2011),

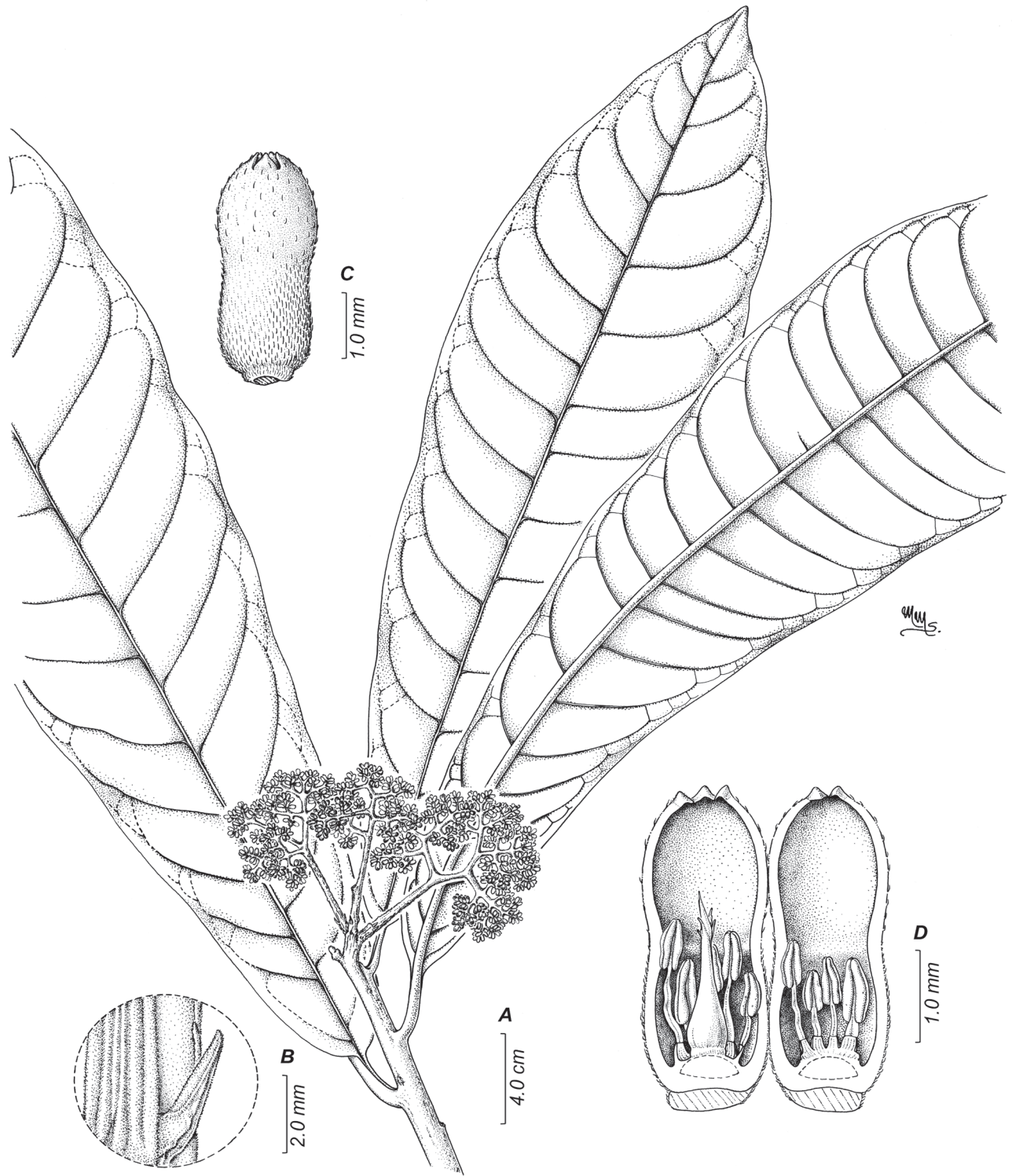


FIGURE 1. *Neea gustaviaefolia* Aymard **A**, habit showing the branch of staminate plant and larger oblanceolate alternate leaves; **B**, basal bract located on primary branches; **C**, frontal view of the staminate perianth bud; **D**, inside the staminate perianth in longitudinal section showing the stamens and the sessile pistillode. Based on the holotype.

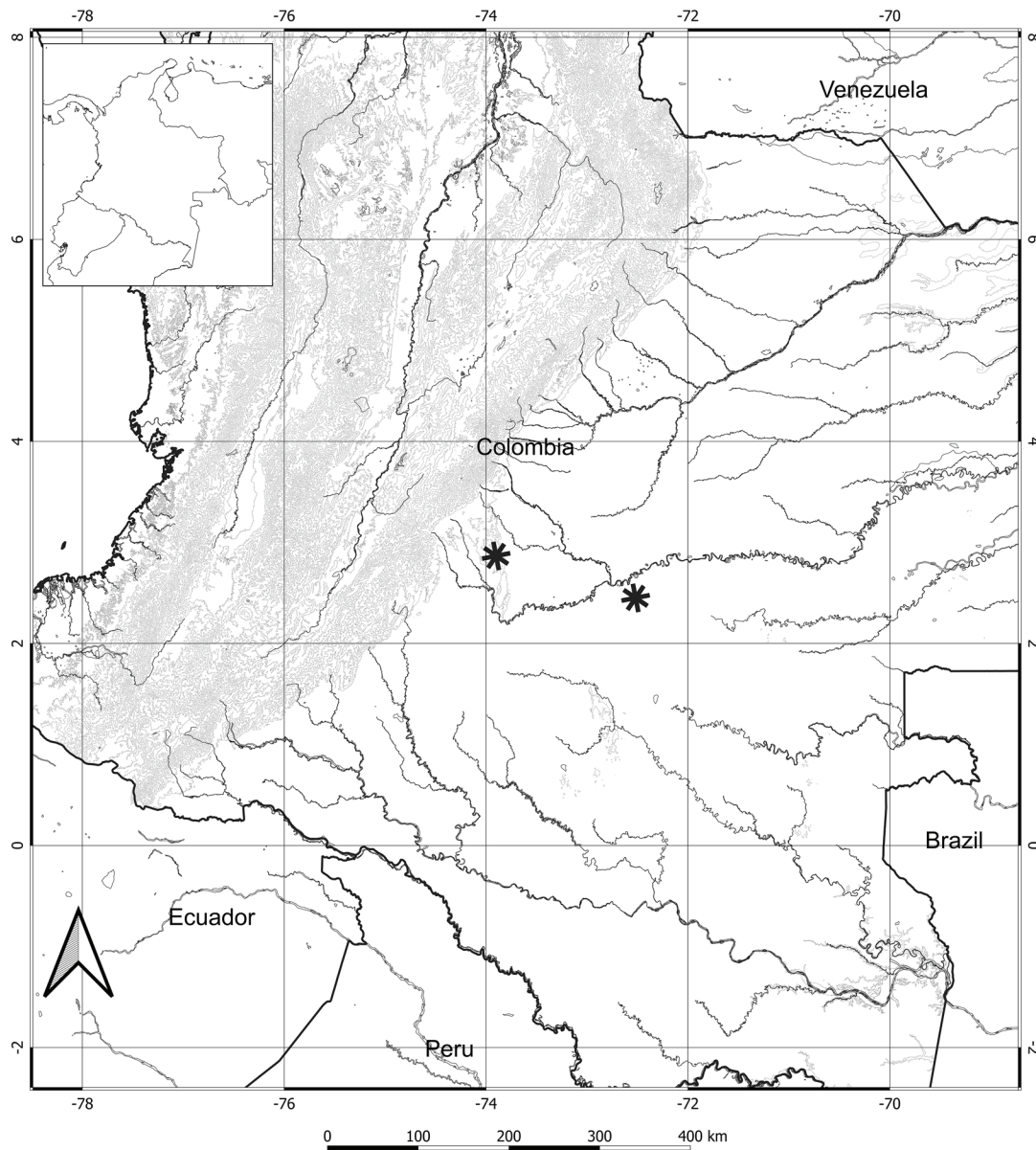


FIGURE 2. Geographical distribution of *Neea gustaviaefolia* Aymard.

classified the forest vegetation as a large formation made up of palm communities of *Socratea exorrhiza* (Mart.) H. Wendl. (Arecaceae) and *Iryanthera hostmannii* (Benth.) Warm (Myristicaceae). This syntaxonomic unit encompasses two formations: (1) forests located between 475–550 m dominated by *Batocarpus orinocensis* H. Karst. (Moraceae) and *Pseudosenefeldera inclinata* (Müll. Arg.) Esser (Euphorbiaceae) and (2) palm communities at 380–450 m dominated by *Syagrus orinocensis* (Spruce) Burret (Arecaceae) and *Virola elongata* (Benth.) Warm. (Myristicaceae).

Colombia has among the highest plant diversity, types of vegetation, and number of endemic species in the world (Rangel-Ch., pers. com., 2021). Infante-Betancour and Rangel-Ch. (2018a) reported 760 species, in 411 genera and

95 families of plants for “Sierra de La Macarena,” in only 1.472 collections that covered 1.087 km². This highly diversity is associated by the interrelation among the Andes system, with the Orinoquia and Amazonian complexes (Infante-Betancour and Rangel-Ch. (2018b)). It is one the less documented world’s biodiversity hotspots and yet is threatened by road building, deforestation, and general degradation (for a review see: Murillo-Sandoval et al., 2021).

Additional specimen examined: COLOMBIA. Guaviare: San José de Guaviare, vereda Triunfo II, Finca El Silencio de Juan Gordillo, bosque secundario, 02°27'3.96"N; 72°31'4.2"W, 200 m, 25 June 2003. *Rene López-L., Mario Coy & Armando Lucena* 8255 (COAH).

Conservation status. Currently, this species is only known from the type and one additional collection, and

it is reported here as rare species. However, under IUCN (2017) guidelines two localities constitute deficient data (DD) to determine its conservation status. Nevertheless, it should be regarded as Endangered (EN) based on the criterion B1ab(iii)+2ab(iii), due to the lower number of known localities (two) and to its smaller estimated Area of Occupancy, with just 12,000 km², an estimated Extent of Occurrence of 120,406 km² (IUCN, 2017), and the continuous deforestation and degradation of the ecosystems of the “Sierra de La Macarena” and the area located south of San José de Guaviare. These areas had been highly deforested during the last five decades, especially in the years through the post-conflict period. This expansion happens more quickly and without regulation, with significantly greater agricultural and cattle ranching patch sizes due the emergence of illegal land uses, that unfortunately accelerate land cover change in the coming years (for a review see: Murillo-Sandoval et al., 2021). Although conservation status assessments can still be carried out for species with such low numbers of collections (Rivers et al. 2011), it may be hard to determine whether an appearance of rarity in a species is due to the lack of data or to its actual rarity. In addition, the region where *N. gustaviaefolia* was found, “Parques Nacionales Naturales Sierra de La Macarena y Tinigua” are apparently well protected by Colombian National Park service (*Parques Nacionales Naturales de Colombia*).

Given its alternate (in a predominantly opposite-leaved genus), oblanceolate larger leaves and a shorter terminal cymes inflorescence, verticillate (with three opposite primary branches), it does not appear to be closely allied to any other *Neea* species. However, this new species does share several features with five species (*N. alumnorum* M.Pignal, Soares Filho & Romaniuc, *N. brevipedunculata* Steyerl., *N. floribunda* Poepp. & Endl., *N. itanhaensis* E. F. S. Rossetto & J. R. Ferraz and *N. verticillata* Ruiz & Pav.). By its inflorescence structure (shorter peduncle with three opposite verticillate primary branches) and larger, oblanceolate alternate leaves, *N. gustaviaefolia* represents a unique combination of features that does not occur in any species of the genus. According with Rossetto et al. (2019b), only four species so far have verticillate inflorescences (*N. amplexicaulis* Dwyer & M.V.Hayden, *N. pendulina* Heimerl, *N. uleana* (Heimerl) Furlan, *N. theifera* Oerst.). Morphologically, this new species is relatively comparable to *N. alumnorum* M.Pignal, Soares Filho & Romaniuc from Bahia state, Brazil (Pignal et al., 2013) and *N. itanhaensis* E. F. S. Rossetto & J. R. Ferraz from São Paulo state, Brazil (Rossetto et al., 2019b). Nevertheless, it differs from the five species mentioned (*N. alumnorum*, *N. brevipedunculata*, *N. floribunda*, *N. itanhaensis* and *N. verticillata*) in the vegetative and reproductive characters discussed in the diagnosis, in Table 1, and to Colombian taxa in the following key.

KEY TO SPECIES OF *NEEA* FOUND IN COLOMBIA

(MODIFIED FROM STEYERMARK AND AYMARD, 2003; ENDEMIC SPECIES INDICATED WITH THE SYMBOL “◆”).

- 1a. Leaves alternate. 2
- 1b. Leaves opposite, subopposite, verticillate or subverticillate in whorls of 3 or 4 5
- 2a. Inflorescence cauliflorous on the old stem or ramiflorous. . . *N. floribunda* (Amazonas, Antioquia, Caquetá, Guaviare, Meta, Putumayo, Vaupés)
- 2b. Inflorescence axillary or terminating the stem or its branches 3
- 3a. Leaves coriaceous, oblanceolate, 40–46 × 10–15 cm, secondary veins 15–17, impressed and canaliculate on the upper surface; brown when dried; inflorescence subumbellate. *N. gustaviaefolia* (Guaviare, Meta) ◆
- 3b. Leaves thickly papyraceous, chartaceous or subcoriaceous, elliptic to broadly-elliptic or obovate-rotundate, 7.5–30 × 2.5–12 cm, secondary veins 6–10, obscure or slightly evident on the upper surface, bright-green, yellow or yellowish-green; inflorescence corymbose or paniculate 4
- 4a. Tree 10 m tall; leaves elliptic, elliptic-rotundate or obovate-rotundate, thickly papyraceous or subcoriaceous, apex long-caudate, acumen ca. 2 cm long, secondary veins 10–12; inflorescence paniculate; peduncle stout, ca. 4.5 × 0.3–0.4 cm *N. darienensis* (Antioquia and Chocó department)
- 4b. Shrub to treelet to 6 m tall; leaves elliptic to broadly-elliptic, chartaceous, apex acute to acuminate, acumen ca. 1 cm long; secondary veins 6–8; inflorescence corymbose; peduncle 1–2(–5.6) × 0.2 cm. *N. virens* (Amazonas, Antioquia, Caquetá, Chocó, Magdalena, Putumayo)
- 5a. Leaves verticillate, subverticillate or ternate. 6
- 5b. Leaves opposite or subopposite. 13
- 6a. Inflorescence cauliflorous on the old stem or ramiflorous 7
- 6b. Inflorescence axillary or terminating the stem or its branches 8
- 7a. Leaves oblong-elliptic to elliptic or broadly elliptic, apex acute to cuspidate; peduncle 0.5–3 cm long; anthocarp 1.6–2 cm long, oblong-ellipsoid. *N. floribunda* (Amazonas, Antioquia, Caquetá, Guaviare, Meta, Putumayo, Vaupés)
- 7b. Leaves lanceolate, lanceolate-elliptic to narrowly elliptic or oblanceolate, apex acuminate; peduncle 4–6 cm long; anthocarps 1.4–1.7 cm long, oblong. *N. verticillata* (Amazonas, Caquetá, Meta)
- 8a. Branches, petioles, leaves on the lower surface (more evident in the midrib and secondary veins), inflorescences and bracteoles densely ferruginous tomentose *N. woronowii* (Chocó, Santander) ◆
- 8b. Branches, petioles, leaves on the lower surface, inflorescences and bracteoles glabrous, sparsely puberulent or minutely adpressed-ferruginous 9
- 9a. Leaves lanceolate, lanceolate-elliptic to narrowly elliptic or oblanceolate; anthocarps 1.4–1.7 cm long, oblong *N. verticillata* (Amazonas, Caquetá, Meta)
- 9b. Leaves elliptic, narrowly elliptic, obovate-elliptic, oblanceolate or oblong; anthocarps 0.4–1.2 cm long. 10

KEY TO SPECIES OF *NEEA* FOUND IN COLOMBIA CONT.

10. Leaves membranaceous to chartaceous; inflorescence 10–17 cm long, with a slender, filiform and elongate rachis, ca. 0.5 mm wide 11
- 10b. Leaves coriaceous; inflorescence 2–8 cm long, rachis stout, 1–3 mm wide 12
- 11a. Leaves oblong to elliptic, 12–25 × 5–9 cm; staminate perianth tubular anthocarp ellipsoid to obovoid . *N. laxa* (Amazonas, Guaviare, Meta)
- 11b. Leaves narrowly elliptic, elliptic or oblanceolate; 4–12 × 2–4 cm; staminate perianth ovoid-urceolate; anthocarp ellipsoid or narrowly ovoid *N. delicatula* (very probably in Antioquia and Chocó departments; in Darién, Colombian-Panamanian border).
- 12a. Staminate perianth tubular-elliptic; pistillate perianth tubular; anthocarps broadly ellipsoid or lanceolate *N. psychotrioides* (Antioquia, Cauca, Chocó, San Andrés, Providencia y Santa Catalina, Valle?)
- 12b. Staminate perianth urceolate, sometimes infundibuliform; pistillate perianth suburceolate, campanulate or infundibuliform; anthocarps narrowly ellipsoid or oblong *N. spruceana* (Amazonas, Antioquia, Casanare, Guaviare, Guanía, Meta, Putumayo)
- 13a. Leaves sessile or nearly so, the petiole 1 mm long; inflorescence terminal, or both axillary and terminal on the stem. 14
- 13b. Leaves petiolate, the petiole 0.3–6.5 cm long; inflorescence either cauliflorous on the old stem, ramiflorous, axillary or terminal on the branches. 15
- 14a. Leaves usually obtuse at base; young stem with subspreading rufous-brown hairs; inflorescence both axillary and terminal on the stem. *N. ignicola* (Vichada)
- 14b. Leaves amplexicaul, clasping the stem, base rotundate-truncate or cordate; young stem glabrous; inflorescence terminal *N. amplexicaulis* (Chocó)
- 15a. Inflorescence cauliflorous on the old stem 16
- 15b. Inflorescence axillary or terminating the stem or its branches 20
- 16a. Staminate perianth urceolate, ferruginous basally outside; stamens 5–13 *N. verticillata* (Amazonas, Caquetá, Meta)
- 16b. Staminate perianth tubular, subinfundibuliform or infundibuliform, glabrous or minutely sparsely puberulent outside; stamens 6–9. 17
- 17a. Leaves ovate, ovate-elliptic, ovate-lanceolate or lanceolate, 4–15 × 1.5–6 cm; main secondary veins 16–25, subhorizontal or ascending at an angle < 20° *N. ovalifolia* (Guaviare, Guanía?, Magdalena)
- 17b. Leaves oblanceolate-elliptic, oblanceolate, lanceolate-elliptic, obovate, oblong, or oblong-ovate, 8–45 × 3–18 cm, main secondary veins 8–14, ascending at an angle usually > 30°. 18
- 18a. Leaves 8–12.5(–15) × 2.5–4.5(–5.5) cm; staminate perianth subinfundibuliform; stamens 8 *N. clarkii* (Caquetá, Guanía?)
- 18b. Leaves 10–45 cm long × 3.5–16 cm; staminate perianth tubular or infundibuliform; stamens 7–10. 19
- 19a. Principal secondary leaf veins 6–8 each side, slightly elevated on lower surface; staminate perianth infundibuliform *N. brevipedunculata* (Antioquia, Guanía)
- 19b. Principal secondary leaf veins 8–12 each side, conspicuously elevated on lower surface; staminate perianth tubular *N. floribunda* (Amazonas, Antioquia, Caquetá, Guaviare, Meta, Putumayo, Vaupés)
- 20a. Leaves broadly rounded or submarginate at the apex, obovate or elliptic-obovate; perianth subcampanulate; anthocarps usually costate or striate longitudinally *N. obovata* (Amazonas, Caquetá, Guanía, Vaupés)
- 20b. Leaves mainly acute to acuminate or long-caudate at the apex, of shapes other than above; perianth mainly tubular to ellipsoid, subinfundibuliform, infundibuliform, campanulate, suburceolate or urceolate; anthocarps not costate or striate longitudinally 21
- 21a. Main secondary veins of leaf blades 17–26 each side. 22
- 21b. Main secondary veins of leaf blades generally 6–16 each side. 25
- 22a. Stems and branches hirsute or hirtellous; leaves hirsute to reddish hirsute-tomentose on the lower surface; inflorescences densely reddish hirsute with patent trichomes 23
- 22b. Stems and branches glabrous or sparsely pilose; leaves, glabrous or ferruginous puberulent on the lower surface; inflorescences sparsely ferruginous. 24
- 23a. Leaves bullate on the upper surface, all blade hirsute to hirtellous on the lower surface; bracteoles filiform, ciliate at margin, staminate perianth 5–8 × 3–6 mm *N. hirsuta* (Bolívar)
- 23b. Leaves not bullate on the upper surface; midrib and secondary veins hirsute on the lower surface; bracteoles oblong to lanceolate, glabrous to puberulous; staminate perianth 3–4 × ca. mm. *N. parviflora* (Amazonas, Caquetá, Chocó, Putumayo)
- 24a. Leaves ovate, ovate-elliptic, ovate-lanceolate or lanceolate, main secondary veins subhorizontal or ascending at an angle < 20°, relatively close together, 3–4 mm apart; petioles 5–19 mm long *N. ovalifolia* (Guaviare, Guanía?, Magdalena)
- 24b. Leaves oblong-elliptic, main secondary veins ascending at an angle usually > 30°, petiole ca. 8 mm long. *N. constrictoides* (Cundinamarca)
- 25a. Branches, petioles, leaves on the lower surface (more evident in the midrib and secondary veins), inflorescences and bracteoles densely ferruginous tomentose *N. woronowii* (Chocó, Santander) ♦
- 25b. Branches, petioles, leaves on the lower surface, inflorescences and bracteoles glabrous, sparsely puberulent or minutely adpressed-ferruginous. 26
- 26a. Staminate perianth ferruginous-puberulent or moderately ferruginous-pubescent toward base 27
- 26b. Staminate perianth glabrous, tomentose, sometimes sparsely puberulous near base, or minutely papillate apically. 28
- 27a. Leaves lanceolate-elliptic or oblanceolate-elliptic, densely black punctate on the lower surface; bracteoles subtending the flowers ovate-deltoid, 3–4 mm long, densely ferruginous tomentose outside; staminate perianth subinfundibuliform, moderately ferruginous-pubescent *N. clarkii* (Caquetá, Guanía?)
- 27b. Leaves oblong to oblong-elliptic, without black punctations on the lower surface; bracteoles subtending the flowers linear-lanceolate, ca. 1 mm long, sparsely brown-puberulous outside; staminate perianth oblong-urceolate, sparsely ferruginous-puberulent *N. divaricata* (Amazonas, Antioquia, Bolívar, Guaviare, Huila, Putumayo, Risaralda, Valle)

KEY TO SPECIES OF *NEEA* FOUND IN COLOMBIA CONT.

- 28a. Leaves with secondary veins 6–16; inflorescence paniculately or corymbiform and irregularly branched; staminate perianth 4–10 × 1.5–4 mm. 29
- 28b. Leaves with secondary veins 5–7; inflorescence umbellately or trichotomously branched; staminate perianth 2–3.5 × 0.8 mm 38
- 29a. Leaves yellow, yellowish, green-yellowish or yellow-brown when dried, shiny on the upper surface 30
- 29b. Leaves green, dark green, dark brown or black when dried, dull on the upper surface 32
- 30a. Leaves elliptic, broadly-elliptic, elliptic-rotundate or obovate-rotundate; inflorescence with short a thick raquis, 1–6.5 cm long, 1–4 mm wide. 31
- 30b. Leaves elliptic-lanceolate, oblong-lanceolate, oblong, elliptic, ovate-elliptic or ovate; inflorescence with a slender, longer and filiform and elongate rachis, 8–17 cm long, ca. 0.5 mm wide wide 32
- 31a. Leaves elliptic, elliptic-rotundate or obovate-rotundate, thickly papyraceous or subcoriaceous; peduncle ca. 4.5 cm long, 3–4 mm wide... *N. darienensis* (Antioquia and Chocó department)
- 31b. Leaves narrowly to broadly oblong-elliptic, membranaceous, peduncle 1.5–6 cm long, ca. 1.0 mm wide. *N. virens* (Amazonas, Antioquia, Caquetá, Chocó, Magdalena, Putumayo)
- 32a. Leaves elliptic-lanceolate or oblong-lanceolate, 5–23 × 2–9 cm; petiole 2–10 mm long; inflorescence corymbiform, 3–5 × ca. 4 cm; staminate perianth broadly urceolate, yellow, yellowish or green, 5–5.5 cm long, glabrescent outside *N. anisophylla* (Cundinamarca, Magdalena)
- 32b. Leaves oblong, elliptic, ovate-elliptic or ovate, 15–31 × 5–16 cm; petiole 0.6–5 cm long; inflorescence paniculate, 10–17 × 2–3 cm; staminate perianth tubular, purple to red, 5–10 mm long, sparsely puberulent outside. *N. laxa* (Amazonas, Guaviare, Meta)
- 33a. Leaves 4–7 × 1.2–4 cm; petioles 4–6 mm long; branches, petioles and inflorescences white tomentellous; inflorescence ca. 2 cm long, staminate perianth 4–5 × ca. 1 mm. *N. nigricans* (Bolívar, San Andrés, Providencia y Santa Catalina)
- 33b. Leaves longer than 10 × 6 cm; petioles 1–6.5 cm long; branches, petioles and inflorescences glabrous or minutely adpressed ferruginous; inflorescence longer than 5 cm long, staminate perianth 4–10 × 1–3 mm. 34
- 34a. Leaves abruptly narrowed to the apex, tapering gradually to the base, staminate perianth 6–10 mm long, oblong-urceolate or tubular-elliptic 35
- 34b. Leaves acute, acuminate to cuspidate or obtuse at the apex, rounded, cuneately-acute or short-cuneate at the base, staminate perianth 4–7 mm long, urceolate, suburceolate, tubular or tubular-ellipsoid 36
- 35a. Staminate perianth oblong-urceolate, sessile to subsessile, pedicels ca. 1 mm long; pistillate perianth infundibuliform; anthocarps ellipsoid *N. amplifolia* (Antioquia, Chocó, Magdalena)
- 35b. Staminate perianth tubular-elliptic, pedicellate, pedicels 2–4 mm long, pistillate perianth tubular; anthocarps broadly ellipsoid or lanceolate. *N. psychotrioides* (Antioquia, Cauca, Chocó, San Andrés, Providencia y Santa Catalina, Valle?)
- 36a. Leaves broadly elliptic, sometimes orbicular, 15–30 × 8–18 cm, tertiary veinlets evanescent on upper leaf surface; staminate perianth tubular, ellipsoid, bracteoles subtending the flowers ca. 1 mm long, linear to linear-lanceolate *N. macrophylla* (Amazonas, Antioquia, Caquetá, Guaviare, Meta, Putumayo, Vaupés)
- 36b. Leaves obovate, elliptic-lanceolate or elliptic-oblong, 8–24 × 4–9.4 cm, tertiary veinlets conspicuously reticulate and subelevated on upper leaf surface; staminate perianth urceolate, suburceolate, sometimes subinfundibuliform 37
- 37a. Leaves coriaceous, petioles 1–3.5 cm long; bracteoles subtending the flowers ca. 2 mm long, deltoid; staminate perianth suburceolate; stamens 9–10. *N. robusta* (Amazonas, Caquetá, Guaviare, Guianía, Meta, Vaupés)
- 37b. Leaves membranaceous to subcoriaceous, 0.4–1.5 cm long; bracteoles subtending the flowers 0.5–1 mm long, triangular-lanceolate; staminate perianth urceolate, sometimes infundibuliform; stamens 5–6 *spruceana* (Amazonas, Antioquia, Casanare, Guaviare, Guianía, Meta, Putumayo)
- 38a. Junction of lowest axes of inflorescences with summit of peduncle enlarged, 2.5–4 mm wide *N. clarkii* (Caquetá, Guianía?)
- 38b. Junction of lowest axes of inflorescence with summit of peduncle not manifestly enlarged, 0.8–2 mm wide. 39
- 39a. Staminate perianth 3–4.5 × 1.5 mm, densely ferruginous tomentose outside; petiole and young stem sparsely puberulent; leaves drying brown; principal secondary veins 10–12 each side. *N. sebastianii* (Caquetá, Guianía)
- 39b. Staminate perianth 6.5–7 × 2.8–3 mm, with minute, sparse to moderate ferruginous outside; petiole and young stem glabrous; leaves drying blackish brown; principal secondary veins 6–8 each side *N. mapourioides* (probably Guianía, it has been collected just across the Colombia border in San Carlos de Río Negro, Amazonas state, Venezuela)

TABLE 1. Comparison of diagnostic morphological characters of *Neea gustaviaefolia* Aymard and related species (based on Pignal et al., 2013).

CHARACTER	<i>N. ALUMNORUM</i>	<i>N. BREVIPENDUNCULATA</i>	<i>N. FLORIBUNDA</i>	<i>N. GUSTAVIAEFOLIA</i>	<i>N. ITANHAENSIS</i>	<i>N. VERTICILLATA</i>
Habit	Small to medium tree, 2.5–8(–20.5) m tall	Small to medium tree, 6–20 m tall	Shrubs to small tree 3–6 m tall	Small tree, ca. 6 m tall	Shrubs to small trees, 1.5–5.0 m tall	Small tree, 4–6 m tall
Leaves disposition	Alternate, rarely sub-verticillate	Opposite	Opposite, sub-verticillate, rarely alternate	Alternate	Opposite	Verticillate, opposite, sometimes alternate
Leaves shape and size	Oblanceolate, elliptic or ovate; 36–63 × 8–13.5 cm	Ovate, oblanceolate, or elliptic-oblong; 10–22 × 5–12.5 cm	Ovate-elliptic or oblanceolate; 15–42 × 7.5–13.8 cm	Oblanceolate; 40–46 × 10–15 cm	Oblanceolate, elliptic or obovate-elliptic; 11.5–37.5 × 4–11 cm	Oblong-lanceolate or elliptic-oblong; 25–40 × 7–10.5 cm
Secondary veins	(17–)20(–23); impressed on the upper surface, elevated on the lower surface	6–8; impressed on the upper surface; slightly elevated on the lower surface	6–7; elevated on both surfaces	15–17; canaliculate on the upper surface, elevated on the lower surface	12–20; impressed on the upper surface, elevated on the abaxial surface	14–15; elevated on both surfaces
Inflorescence attachment	Cauliflorous	Cauliflorous on the old stem or ramiflorous	Cauliflorous on the old stem or ramiflorous, sometimes terminal	Terminal	Terminal	Terminal
Inflorescence disposition	Peduncle 2.5–4 cm; primary branches opposite or subopposite	Peduncle 1–1.5 cm long; primary branches subfasciculate or subumbellate	Peduncle 0.5–3 cm; primary branches subopposite	Peduncle 1–4 cm long; with three opposite verticillate primary branches	Peduncle ca. 12.5 cm long; with three-five opposite verticillate primary branches	Peduncle 4–6 cm long; primary branches alternate to subopposite
Staminate perianth	Urceolate; ca. 7 × 4 mm, glabrescent	Tubular; ca. 3.7 × 1.5 mm, glabrous	Urceolate; ca. 5 × 3 mm, puberulent	Tubular; 3–4 × 1–1.5 mm, sparsely pubescent	Ellipsoid urceolate; 8–11 × 8–4.5 mm, glabrescent	Tubular; 3 × 1.6 mm, puberulent
Stamen	8–9	7	6(–9)	9	6–8	unknown

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