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Two new species of *Caryodaphnopsis* (Lauraceae) from the Magdalena Medio, Colombia, with an updated key for the Neotropical *Caryodaphnopsis* species

Dos nuevas especies de *Caryodaphnopsis* (Lauraceae) del Magdalena Medio, Colombia, con una clave actualizada de las especies neotropicales de *Caryodaphnopsis*

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Abstract:

Background and Aims: *Caryodaphnopsis* is a tropical genus with an amphi-Pacific distribution, comprising 19 species, 10 of which Neotropical. Two new species are described from wet forest remnants on the western slopes of the Eastern Cordillera of Colombia, which is part of the Magdalena Medio biogeographical region. Their morphological relationships with Neotropical allied species are discussed.

Methods: Descriptions and illustrations of both new species were based on collections from the Santander and Boyacá departments, deposited in the herbaria of the Bogotá Botanical Garden (JBB) and the Universidad Industrial de Santander (UIS). Measurements of vegetative parts and inflorescences were taken from herbarium material. Floral structures and fruits were measured from fresh material preserved in alcohol. Threat categories were proposed according to IUCN criteria.

Key results: *Caryodaphnopsis carmensis* and *C. yariguiensis* are two species so far known only from the Magdalena Medio, Colombia. *Caryodaphnopsis carmensis* is unique because of its dense, golden pubescence on vegetative parts, leaves with subcordate base and 14-17 arcuate tertiary veins, located between the first pair of secondary veins. *Caryodaphnopsis yariguiensis* resembles *C. fieldii* but differs from the latter by the shape of leaves and the stamens with a pair of glands located between the middle portion of filament.

Both taxa are proposed as Endangered (EN). An updated key for the Neotropical *Caryodaphnopsis* species is presented, along with information about their geographic distribution.

Conclusions: The two species described are trees that yield one of the finest timbers in the Magdalena Medio and their populations are much reduced. We encourage their cultivation to promote their conservation. With these two new species, Colombia is the country with the greatest diversity of the genus (seven) and the Magdalena Medio has the highest concentration of endemic species (three).

Key words: Boyacá, conservation, Flora of Colombia, Santander, wet montane forest.

Resumen:

Antecedentes y Objetivos: *Caryodaphnopsis* es un género tropical con distribución anfipacífica, cuenta con 19 especies, 10 de ellas neotropicales. Se describen dos nuevas especies de *Caryodaphnopsis* provenientes de bosques húmedos de la vertiente occidental de la Cordillera Oriental de Colombia, que forma parte de la región biogeográfica del Magdalena Medio. Se discuten sus diferencias morfológicas con las especies afines.

Métodos: Se describen e ilustran dos nuevas especies de *Caryodaphnopsis* a partir de colecciones provenientes de los departamentos Boyacá y Santander, depositadas en los herbarios del Jardín Botánico de Bogotá (JBB) y de la Universidad Industrial de Santander (UIS). Las medidas de las partes vegetativas e inflorescencias se realizaron del material de herbario. Las estructuras florales y frutos se midieron a partir de material fresco conservado en alcohol. Se proponen sus categorías de amenaza acorde con los criterios de la IUCN.

Resultados clave: *Caryodaphnopsis carmensis* y *C. yariguiensis* son dos especies solo conocidas del Magdalena Medio, Colombia. *Caryodaphnopsis carmensis* es única por su pubescencia densa dorada en las partes vegetativas, las hojas con base subcordada y 14-17 venas terciarias, arqueadas, situadas entre el primer par de venas secundarias. *Caryodaphnopsis yariguiensis* posee caracteres que la asemejan con *C. fieldii*, pero difiere de esta última en la forma de las hojas y en los estambres con un par de glándulas situadas entre la parte media del filamento. Se propone para ambos taxones la categoría de Amenazada (EN). Se presenta una clave actualizada de las especies neotropicales, acompañada con información acerca de su distribución geográfica.

Conclusiones: Las dos especies aquí descritas son árboles que poseen una de las maderas más finas del Magdalena Medio y sus poblaciones se encuentran muy reducidas. Se propone su propagación y cultivo para promover su conservación. Con estas dos nuevas especies, Colombia es el país con mayor diversidad del género (siete), y el Magdalena Medio la región con la mayor concentración de especies endémicas (tres).

Palabras clave: Boyacá, bosque húmedo montano, conservación, Flora de Colombia, Santander.

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Introduction

Caryodaphnopsis Airy Shaw is a tropical amphi-Pacific genus of Lauraceae (van der Werff and Richter, 1985; Liu et al., 2013; Li et al., 2016), originally described from Asia (Airy Shaw, 1940). The genus shows a remarkable disjunction between Southeast Asia (southern China, Vietnam, Laos, Cambodia, the Philippines, Borneo, Malaysia, and Indonesia) and tropical America (Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, and Brazil, *sensu* Aymard and Romero-González, 2009). The Asian species were revised by Kostermans (1974), and a key of Neotropical species was published by Aymard and Romero-González (2009).

The tropical amphi-Pacific pattern has resulted from the disruption of an ancestral boreotropical distribution by Mid to Late Eocene climatic cooling, followed by relatively late immigration into Central and South America (see Li et al., 2016 for a review of this topic). According to these authors, the genus originated in the Late Cretaceous of Laurasia. However, this amphi-Pacific disjunction has two explanations: it is the result of 1) the disruption of ancestral boreotropical lineages between Eurasia and North America during the early Eocene cooling period (Li et al., 2016), and 2) the basal lineages of Lauraceae, which had established on either Gondwana or Laurasia by the Cretaceous with a divergence time of ~140 Ma (Chanderbali et al., 2001; Li et al., 2011). The latter estimation appears too old, as the earliest unquestionable lauraceous fossil is from the Cenomanian with an age of only ~100 Ma (*sensu* Li et al., 2016). In contrast, Nie et al. (2007) proposed a Late Cretaceous divergence time of *Caryodaphnopsis* at ~90 MY, which is more reliable with the comparatively basal position of the genus within the family. According to Chanderbali et al. (2001) and Li et al. (2011), *Caryodaphnopsis* and *Neocinnamomum* H. Liu, with their relatively basal positions in Lauraceae, represent the only extant taxa of the ancient Lauraceae flora documented in the middle to late Cretaceous.

Molecular analyses suggested that *Caryodaphnopsis* is monophyletic and its phylogenetic position within Lauraceae is between the *Mezilaurus* group + core Lauraceae and the *Cryptocarya* group (Li et al., 2016). In addition, an affinity between *Neocinnamomum* and *Cassytha*

L. was suggested by parsimony analyses (see Li et al., 2016, for a review of this topic). The Neotropical species of *Caryodaphnopsis* form two well-supported clades centered in two areas: Amazonia and Central America, and the Middle Magdalena region of Colombia (Li et al., 2016).

Currently, the genus encompasses 19 species (including the two new species described herein): nine in Southeast Asia and ten in Tropical America. Richter (1981) studied the bark and wood of *C. tonkinensis* (Lecomte) Airy-Shaw, and found that the genus has an interesting and very distinct wood anatomical feature among Lauraceae: the presence of pyramidal calcium oxalate crystals in the ray cells. This author commented that the Neotropical species described as *Persea inaequalis* A.C. Smith (= *Beilschmiedia inaequalis* (A.C. Smith) Kostermans) had the same characteristics of wood and bark, and this led to the recognition that *Caryodaphnopsis* was also present in the Neotropics (van der Werff and Richter, 1985; van der Werff, 2012). Also, plants of this genus have a unique lower leaf epidermis (compared with other leaves of Lauraceae) composed by an additional layer covering the lower leaf epidermis and the stomatal apparatus (Zeng et al., 2014). The origin and evolution of this unique lower epidermis may have been related to the climatic cooling and aridification process since the late Eocene (Zeng et al., 2014).

Caryodaphnopsis is characterized among genera of Lauraceae by its opposite leaves and six strongly unequal tepals, and fruits without a cupule at the apex of the pedicel (van der Werff and Richter, 1985; van der Werff, 1991, 2012). Most species have 4-locellate anthers, nine stamens, triplinerved or pinnate leaves and pear-shaped or globose fruits. Nonetheless, for generic delimitation, most of the authors used the characters that included the opposite leaves, the unequal tepals, and the unique wood anatomy (van der Werff and Richler, 1986; van der Werff and Dao, 1999).

The present work describes and illustrates two new species of *Caryodaphnopsis*, found in fragmented humid forest located in the “Serranías de Las Quinchas y Los Yariguíes”, Boyacá and Santander departments, in the biogeographical region of “Magdalena Medio”. Additionally, we present an updated key for the Neotropical species of this genus.



Materials and Methods

These two new species of *Caryodaphnopsis* were found during fieldwork between June 2015 and 2023, on the slopes of montane forest located in the Serranía de Los Yariquíes, near El Carmen de Chucurí and San Vicente de Chucurí, western Santander department, and Serranía de Las Quinchas, western Boyacá department. This discovery was made a team by botanists from the Jardín Botánico de Bogotá in the framework of the projects entitled: “Transiciones socioecológicas de los paisajes de los Andes Nororientales - conectando conocimiento para la conservación de la biodiversidad y el desarrollo rural resiliente” and “La biodiversidad de Boyacá - complementación y síntesis a través de gradientes altitudinales e implicaciones de su incorporación en proyectos de apropiación social de conocimiento y de efectos de cambio, Municipios de Tunja, Mongua, Puerto Boyacá y Otanche”.

We used a key of Neotropical species of *Caryodaphnopsis* (Aymard and Romero-González, 2009), and studied specimens deposited in the herbaria COL, JBB and UIS (herbarium acronyms cited in the text follow Thiers, 2021 continuously updated) to confirm the morphologically most similar species. In addition, digitized specimens (including type material) of other *Caryodaphnopsis* species were consulted online on several websites, including those of the Herbario Amazónico Colombiano COAH (COAH, 2021), Field Museum (F, 2023), the New York Botanical Garden (NY, 2023), the Missouri Botanical Garden (TROPICOS, 2023), the Royal Botanic Gardens, Kew (K, 2023), the Smithsonian National Museum of Natural History (US, 2023) and JSTOR (2023).

Measurements and photographs were made using a dissecting stereomicroscope (Motic SMZ-143-FBLED, Xiamen, Hong Kong) and a digital calibrator with 0.01 mm of accuracy (Mitutoyo 500-193-30CAL, Buenos Aires, Argentina). The latter device was also used to measure the vegetative parts and inflorescences (on herbarium material), and the flowers preserved in alcohol at 70%. Data on distribution gathered from herbaria (COAH, COL, FMB, JBB MO, and UDBC) labels were recorded using Arc GIS v. 10.2.1 (ESRI, 2014), and the distribution map of all Neotropical *Caryodaphnopsis* species was elaborated with coordinates taken from the labels and checking that the coordinates co-

incide with the toponyms on the labels. The specific terminology for vegetative characters, indumentum description, inflorescences, flowers, and fruit morphology follow Font-Quer (2001), and Harris and Harris (2006).

To determine the conservation status (IUCN, 2022), the extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the supporting Red List threat assessments with GeoCAT (Geospatial Conservation Assessment Tool; Bachman et al., 2011). The GeoCAT is an open source, browser-based tool that performs rapid geospatial analysis for Red List assessments. The EOO is defined by the IUCN (2022) as the minimum convex polygon encompassing all known occurrences of a species. In addition, AOO is the area within the EOO, which is comprised of 2 × 2 km grid cells containing known occurrences records.

Results

Caryodaphnopsis carmensis Humberto Mend., J. Quiroga & Díaz-Rueda, sp. nov. Figs. 1, 2.

TYPE: COLOMBIA. Santander, municipio El Carmen de Chucurí, vereda La Pitalla, finca Billete de Oro, cerca de la quebrada La Pitalla, 560 m, 6°37'8.3"N, 73°36'9.8"O, 15.II.2019, fl, *J. Quiroga-Nova 01* (holotype: JBB!, isotypes: COL!, HUA!, UIS!).

Caryodaphnopsis carmensis resembles *C. fosteri* van der Werff and *C. fieldii* Aymard & G. A. Romero, but can be differentiated from these species by the golden dense indument on internodes, apical buds, petioles and leaf blades on the adaxial surface, leaf blade oblong to oblong-elliptic, the base subcordate, with 3-5 pairs of secondary veins and with 14-17 lateral veins, prominent and branching toward margin on the adaxial surface. Also, this new species is similar to *C. tomentosa* van der Werff, but differs from it by the leaf blade oblong to oblong-elliptic, the base subcordate, 3-5 pairs of secondary nerves, and inflorescences single panicles, not or little branched from the base.

Trees 20-40 m tall, to 1.5 m in diameter at breast height (DBH), with little buttresses, bark fissured, flaking off in small plates; twigs rectangular in young parts, sub-qua-



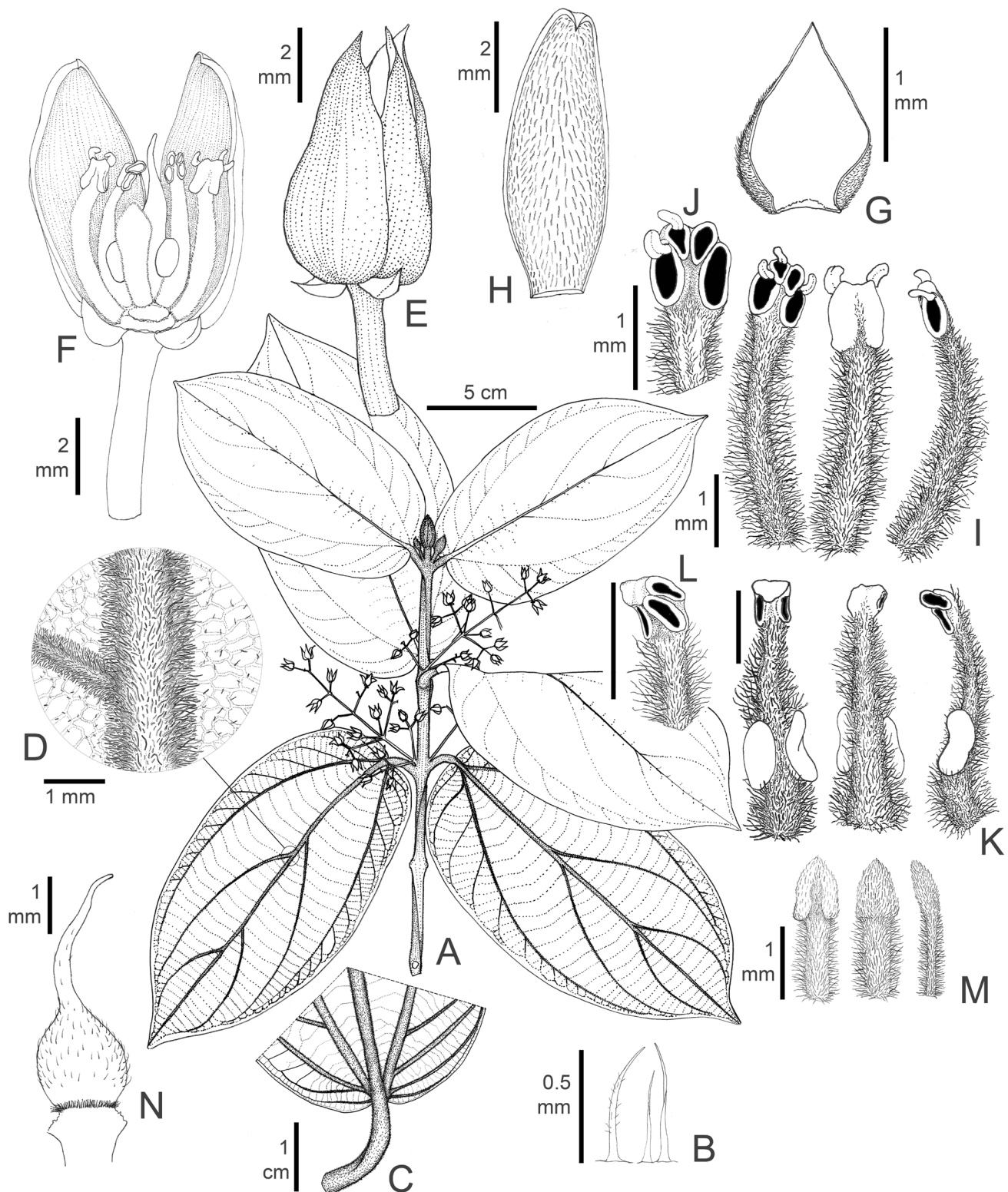


Figure 1: *Caryodaphnopsis carmensis* Humberto Mend., J. Quiroga & Díaz-Rueda. A. flowering branch; B. a trichome located on the internodes and leaves; C. view of adaxial leaf base; D. indumentum on abaxial leaf blade including tertiary veins; E. view of the flower before anthesis; F. view of the flower in anthesis without part of perianth; G. outer tepal in ventral view; H. outer tepal in ventral view; I. fertile stamens of external whorl: in ventral (left), dorsal (middle) and lateral (right) views; J. view of anthers of fertile stamens of external whorl; K. view of fertile stamens of inner whorl showing the two globose glands: ventral (left), dorsal (middle) and lateral (right) views; L. view of anthers of fertile stamen of internal whorl; M. staminodes in ventral (left), dorsal (middle) and lateral (right) views; N. pistil. Drawing by Humberto Mendoza based on *J. Quiroga-Nova 01* (JBB).

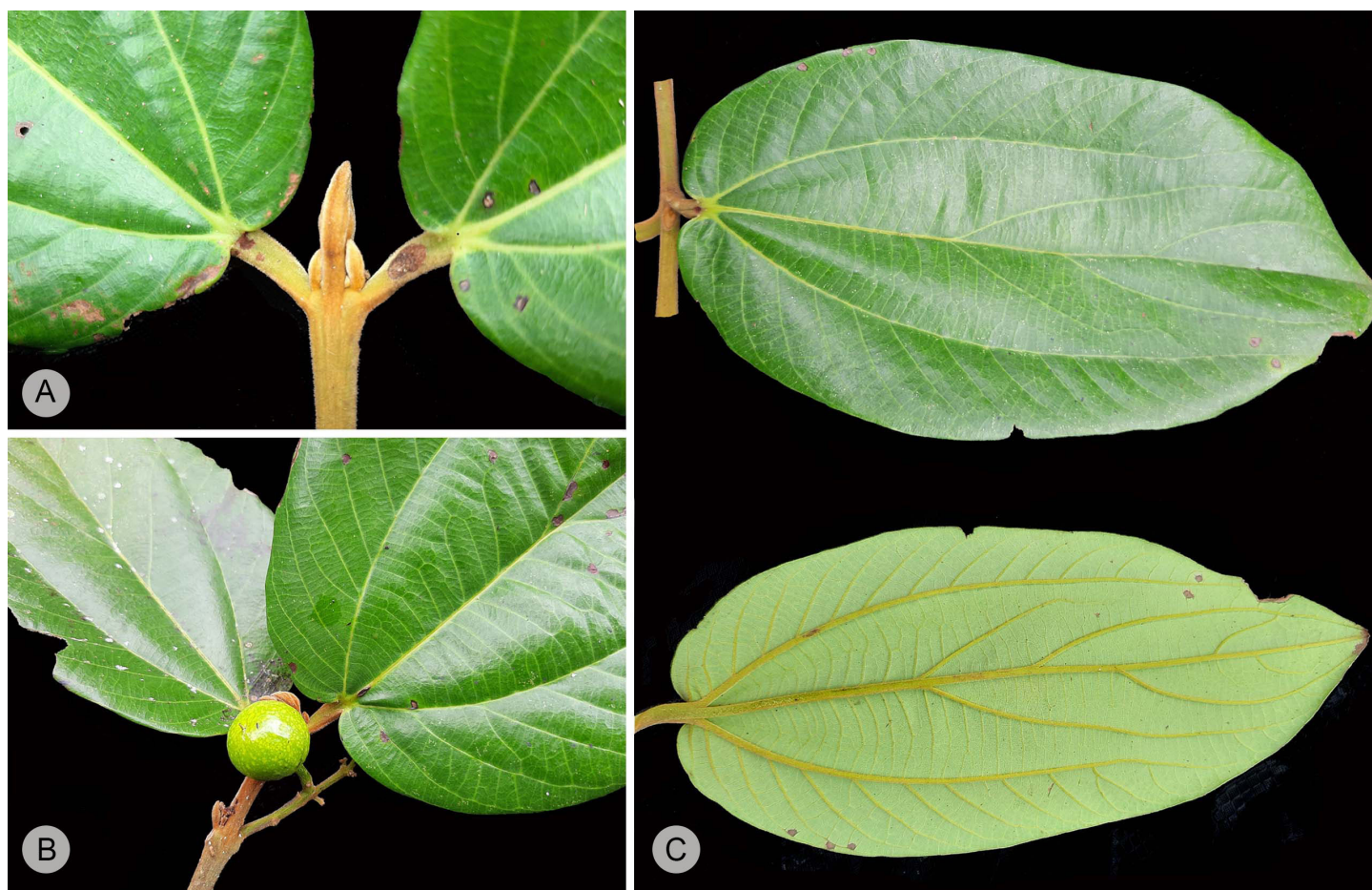


Figure 2: *Caryodaphnopsis carmensis* Humberto Mend., J. Quiroga & Díaz-Rueda. Field images: A. apical branch showing the sericeous pubescence in apical bud; B. view of adaxial and abaxial leaf base; C. branch with a fruit. Photographs by Javier Quiroga-Nova.

drangular when mature; internodes 3.7-7.6 cm long; distal internodes, terminal buds, petioles and inflorescences covered by a dense golden-brown indumentum, composed by subulate trichomes, 0.3-0.6 mm long; leaves opposite; leaf blade 12.5-23 × 8-12.5 cm, oblong, oblong-elliptic to obovate, thin coriaceous, base rounded to subcordate, apex acute, acuminate, margin entire, glabrous adaxially, with an indument like that of the internodes on veins abaxially; trinerved; midrib and secondary veins impressed on the upper surface, elevated on the lower surface; secondary veins 3-5 pairs on each side, alternate, arched and evanescent near margin; lateral veins 14-17, branching towards margin, arching upward, loop-connected and evanescent near margin, elevated on the lower surface; petiole 12-19.5 × 2-4 mm, adaxially caniculate to the apex, with an indument like that on the internodes; inflorescence a single panicle, not or little branched from the base, axillary, 1.9-

4.8 cm long, paired on distal nodes, sessile or pedunculate, central rachis with 3-5 nodes of ramification, with opposite or alternate branchlets; basal paracladia 16-40 mm long; terminal branches 1-3 flowered; bracts and bracteoles not seen; flowers pedicellate, 1.1-1.3 mm long in bud, cream-green; pedicels 3.8-6.1 mm long, tomentose; tepals 6, in two strongly unequal whorls (persisting in the early stages of the fruit); the outer 1.2-1.4 × 0.8-1.2 mm, wide-ovate, tomentose externally, glabrous internally; the inner 6.1-6.5 × 2-3.4 mm, ovate, chartaceous, pubescent on both surfaces, trichomes subulate. 0.4-0.9 mm long; stamens 12, in four whorls, each whorl with 3 stamens, three fertile whorls (9 fertile stamens), one staminodal (3 staminodes), filaments covered by subulate trichomes (0.3-0.5 mm long); the two outer fertile whorls similar in shape and size, 3.6-4.5 mm long, anther 0.9-1.1 × 0.8-0.9 mm, 4-celled in two rows; the inner whorl with 3 fertile stamens in front of outer tepals,

2.5-3.9 mm long, filament with two globose glands attached ca. 1 mm above the base, 1-1.1 × 0.5-0.6 mm, anther 0.9-1 × 0.4-0.5 mm, 4-celled in two rows; staminodes in front of the internal tepals, 1.7-2.4 mm long, anthers not celled or rarely with four cels in two rows (only seen in a single flower); pistil 3.6-4.5 mm long, 1.3-1.4 mm diameter, strigose from the middle to the apex; style ca. 2.5 mm long; stigma punctiform; fruit a globose berry, 1.3-1.4 cm diameter, green at immaturity, red when mature, seed one.

Distribution and habitat: the new species is known to occur in three localities in Boyacá and Santander departments (Colombia), in wet forests on slopes and mountains terrain, between 450-1300 m elevation in the Serranías de Los Yariguíes and Las Quinchas (Fig. 3). Both regions are located in the Magdalena Medio ecoregion, surrounded by forest with several high-value timber species such as “Cedro” (*Cedrela odorata* L., Meliaceae), “Cedro mechas” (*Cedrela fissilis* Vell., Meliaceae), “Totumillo negro” (*Minquartia guianensis* Aubl., Olacaceae), “Tagüi” (*Caryocar amygdaliferum* Mutis, Caryocaraceae), “Tamarindo” (*Uribea tamarindoides* Dugand & Romero, Fabaceae) and “Nauno” (*Pseudosamanea guachapele* (Kunth) Harms, Fabaceae).

The Magdalena Medio is an extensive inter-Andean ecoregion located in the central part of Colombia, formed by the Magdalena river and dominated by wet lowland and montane forests (Luna Uribe, 2018). This area constitutes a biodiversity hotspot (as is the case for the country; see Tietje et al., 2023), because of its high plant diversity, unique forest types and endemisms (Balcázar-Vargas et al., 2000; Restrepo et al., 2016; Luna Uribe, 2018; Mendoza et al., 2020; Ariza-Cortés et al., 2022). This region harbors several Colombian endemic genera (i.e., *Lintersemia* H. Mend., Á. Celis & M. González (Rubiaceae), *Orphanodendron* Barneby & J.W. Grimes (Fabaceae), *Romeroa* Dugand (Bignoniaceae), *Mahechadendron* W. Ariza, Cortés-Ballén & Fern. Alonso (Vochysiaceae) and numerous endemic taxa (i.e., *Andira chigorodensis* T.R. Penn. (Fabaceae), *Aphelandra fernandezii* Leonard (Acanthaceae), *Ephedranthus colombianus* Maas & Setten (Annonaceae)). However, more than 80% of its forests has been destroyed (Franco and Rodríguez, 2005; Etter and Rodríguez, 2008; Restrepo et al., 2016). The ex-

pansion of deforestation, degradation and water pollution continues (Salgado et al., 2022), with significantly greater agricultural use, pasture, selective logging, illicit crops and mining (Restrepo et al., 2021).

Etymology: *Caryodaphnopsis carmensis* is named after the municipality of El Carmen de Chucurí, Santander department, the type locality (Fig. 3). This municipality is located on the Western Andean slopes of the Eastern Cordillera of Colombia (“Cordillera Oriental”). This area is well-known for its “Cacao” plantations (*Theobroma cacao* L., Malvaceae), the impressive forests of fine timbers, and their rural civilian societies, who have resisted more than three decades of armed conflict in their region.

Phenology: this new species has been collected with flowers and fruits between December and February-March, and occasionally in May. The flowering corresponds with the dry period in this region.

Conservation status: since this species is currently known only from the type locality, and from five additional collections made around the type locality, consisting of 49 individuals, between 7-20 m high and 20-50 cm DBH, it is reported here as rare. Under IUCN Standards and Petitions Committee (IUCN, 2022) guidelines, it should be regarded as Endangered (EN) based on the criteria B1 and B2, due to the low number of known localities (six), its estimated Area of Occupancy of 24 km² and its estimated Extent of Occurrence of 573 km² (IUCN, 2022). In addition, the places where the species occurs include the last remnants of lowland inter-Andean wet forests in the Magdalena River valley region. In this area, the known occurrence is limited to fragments immersed in pastures and Cacao crops, a place where most of the fine timber trees have been cut down. Throughout this region, the deforestation process continues, sawmillers in El Carmen de Chucurí report that the largest trees have been intensively logged, and as a consequence, the populations continue to decline. Furthermore, the area where *C. carmensis* was found is not currently protected by the Colombian National Park service (Parques Nacionales Naturales de Colombia); therefore, *in situ* and *ex situ* programs are critically required.





Figure 3: Geographical distribution of Neotropical *Caryodaphnopsis* Airy Shaw species. Red point: *C. carmensis* Humberto Mend., J. Quiroga & Díaz-Rueda; yellow point: *C. cogolloi* van der Werff; dark blue point: *C. yariguiensis* Humberto Mend., Díaz-Rueda & Aymard; white point: *C. fieldii* Aymard & G.A. Romero; light blue point: *C. burgeri* N. Zamora & Poveda; green point: *C. tomentosa* van der Werff; pink point: *C. parviflora* van der Werff; purple triangle: *C. fosteri* van der Werff; light blue triangle: *C. inaequalis* (A.C. Sm.) van der Werff & H.G. Richt.; light green triangle: *C. theobromifolia* (A.H. Gentry) van der Werff & H.G. Richt.



Taxonomic notes: *Caryodaphnopsis carmensis* is characterized by a densely golden-brown indumentum on internodes, apical bud, petiole, leaf on the lower surface and inflorescence, the leaf blade is oblong to oblong-elliptic, the base is subcordate, the presence of 3-5 pairs of secondary veins along the midvein, and 14-17 tertiary veins arising from the basal secondary vein pair. This species is similar to *C. fieldii*, an endemic species from the wet montane forests located in the Coastal Cordillera, Venezuela (Aymard and Romero-González, 2009). However, the latter taxon differs in having leaf blades minutely pilose below, glabrescent when mature, with obtuse to acute base (vs. densely brown-golden pubescent with subcordate to rounded base in *C. carmensis*), rounded apex (vs. acuminate), triplennerved (vs. trinerved), one pair of secondary veins (vs. 3-5), and the inner 3-4.5 mm long, adpressed pilose externally, densely sericeous internally (vs. 6.1-6.5 mm long, pubescent on both surfaces). Additionally, this new species is morphologically related to two other taxa (*C. fosteri* van der Werff and *C. tomentosa* van der Werff). Nonetheless, *C. carmensis* differs from these two species and the other Neotropical taxa of this genus in the characters discussed in the diagnosis, Appendix, and in the key below.

Common names and uses: the names “Panelaque-mada tres venas” (because of the three conspicuous veins at the base of the leaf blade) and “Panelo” were recorded in the town El Carmen de Chucurí. The name “Panela” is coined in Colombia to well-known brown sugarcane blocks (or other shapes) widely used as a sugar substitute in the Americas, Canary Islands, India, Laos, Pakistan, Spain, and Sri Lanka (Gutiérrez-Mosquera et al., 2017). Therefore, these common names allude to the “panela” smell that its wood gives off when it is sawn. According to the local sawyers, *C. carmensis* is one of the finest timbers in the middle Magdalena valley. In the Serranía de Las Quinchas it is known as “mariposo”, “ilamá”, “ilamá hojimoto” or “pateguara”, the latter alluding to the color of the “heart” (heartwood) of the wood, which is red, like the head of the “guara” (*Cathartes aura* L., 1758). Local sawmillers report that this wood is very durable and resistant to humidity, and is used in the construction of rural houses, especially to

make planks, columns, beams and joists beams. The planks are widely used to make the “Elbas” floors. The “Elbas” are mobile structures located over the roofs of the houses to facilitate the coffee and cocoa beans drying process, the main products of the region (Fig. 4).

Additional specimens examined: COLOMBIA. Boyacá, municipio Otanche, vereda Las Quinchas, finca Chorro Negro, 794 m, 5°49'53.98"N, 74°14'20.98"O, 03.IV.2022, st, *M. Escobar-Alba* 774 (UPTC); Serranía de Las Quinchas, vereda San José de Nazareth, límites con la vereda Altazor, entre los sectores La Peña y La Recebera, 930 m, 5°49'10.0"N, 74°08'0.9"O, 08.VIII.2023, fr, *D. Díaz-Rueda et al.* 2960 (COL, CUVC, HECASA, HUA, JAUM, JBB, MEDEL, UDBC, UIS, UPTC). Santander, municipio El Carmen de Chucurí, vereda La Pitala, Finca El Tesoro, rívera de la quebrada Caño Cacho (Aguas blancas), zona centro de la Serranía de Los Yarigués, 460 m, 6°37'53.3"N, 73°35'11.6"O, 14.V.2023, fr, *D. Díaz-Rueda et al.* 2890 (COL, JAUM, JBB, HECASA, HUA, UDBC, UIS, UPTC); vereda Honduras Alto, Finca El Progreso de San Esteban, zona centro de la Serranía de Los Yarigués, 720 m, 6°39'13.9"N, 73°30'45.4"O, 15.V.2023, fl, *D. Díaz-Rueda et al.* 2908 (COL, JAUM, JBB, HUA, UDBC, UIS, UPTC); vereda El Diviso, Finca El Diviso (La Lengua), junto a la Escuela El Limón y la Tienda El Diviso, zona centro de la Serranía de Los Yarigués, 1075 m, 6°38'43.5"N, 73°31'39.2"O, 15.V.2023, fr, *D. Díaz-Rueda et al.* 2933 (JAUM, JBB, HUA, UDBC, UIS); vereda La Pitala, Finca Billete de Oro, cerca de la quebrada La Pitala, 560 m, 6°37'8.3"N, 73°36'9.8"O, 17.XII.2019, fr, *J. Quiroga* 03 (COL, FMB, HUA, JBB, UIS).

Caryodaphnopsis yariguiensis Humberto Mend., Díaz-Rueda & Aymard, sp. nov. Figs. 5, 6.

TYPE: COLOMBIA. Santander, municipio San Vicente de Chucurí, Vereda Mérida Alta, sector Varsovia, 1601 m, 6°49'19.2"N, 73°23'20.0"O, 21.XI.2021, fl, *P. Quiroga* y *G. Zabala* 84 (holotype: JBB!, isotypes: COL!, HUA!, JAUM!, UIS!).

Caryodaphnopsis yariguiensis is similar to *C. fieldii*, but can be differentiated from this species by the elliptic leaves, with acute apex, outer tepals <2 mm long, fertile





Figure 4: “Elba” house made with *Caryodaphnopsis* Airy Shaw wood. A. rural house supported by columns and joists of *C. carmensis* Humberto Mend., J. Quiroga & Díaz-Rueda; B., C., D. roof support and bed of 50 years old made with *C. yariguiensis* Humberto Mend., Díaz-Rueda & Aymard wood. Photographs by Daniel Díaz-Rueda.

stamens <2 mm long, with glands located in the middle to basal portion of the filament, fertile stamens of outer whorl ≤ 2.1 mm long, and pistil ≤ 2.6 mm long.

Trees 8-20 m tall, to 1.1 m in diameter at breast height (DBH), bark fissured, flaking off in plates; internodes 2.4-5 cm long; distal internodes rectangular and flat, lax shortly yellow pubescent, glabrescent when mature; basal nodes oblong, glabrous; apical buds densely sericeous, trichomes filiform 0.5-0.6 mm long, leaves opposite; leaf blade 8.8-22 \times 5-8.5 cm, elliptic, narrowly elliptic or oblong-elliptic, thin coriaceous, base acute or obtuse, apex obtuse, acute or slightly acuminate, margin entire, glabrous on the upper surface when young, glabrous when mature; trinerved or slightly triplennerved ca. 4 mm upward the base, midrib and

secondary veins impressed on the upper surface, elevated on the lower surface, only one pair of secondary veins, straight to apex, with 25-28 pairs tertiary veins starting on the midrib, 13-16 pair of tertiary veins, starting on the secondary veins, petiole 14-25 \times 1.2-4 mm, adaxially caniculate to the apex, pubescence white adpressed, glabrescent when mature; inflorescence 4-8 cm long, panicle, axillary, sericeous, central rachis with one to several racemes starting on the same node of ramification, each raceme without branchlets or with one ramification level; each fascicle up to 6-flowered; bracts not seen, bracteoles 0.5-0.7 mm long, triangular, densely sericeous on both sides; flowers 3.6-4 mm long in bud, cream; pedicels 2.5-5.8 mm long, dense to sparsely adpressed yellow pubescent; tepals 6, in two strongly unequal whorls (persisting in fruit); the outer 3, 1-1.1 \times 1.16-1.18 mm, ovate to wide-ovate, densely

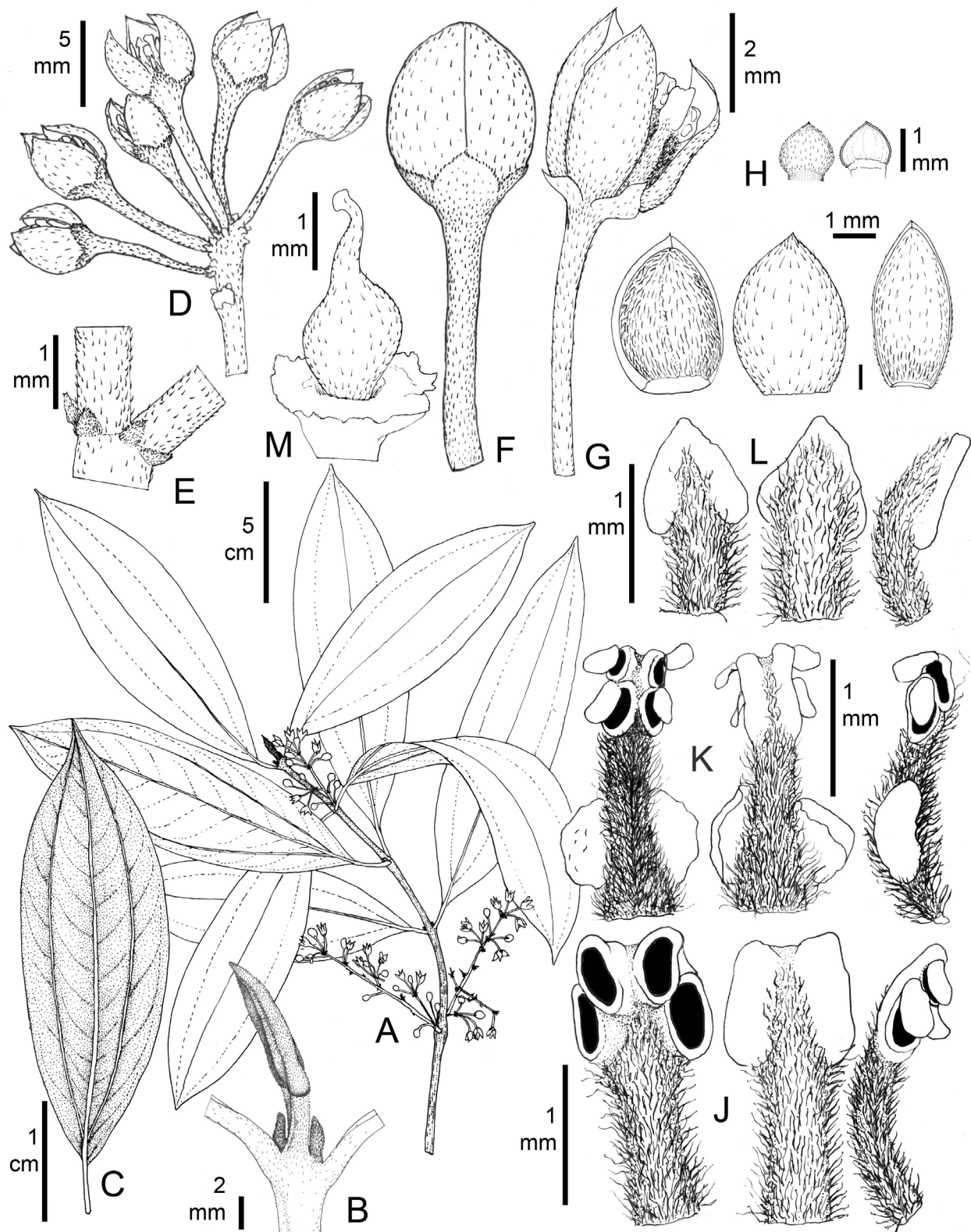


Figure 5: *Caryodaphnopsis yariguiensis* Humberto Mend., Díaz-Rueda & Aymard. A. flowering branch; B. apical bud; C. leaf blade showing the trinerved venation; D. 6-flowered fascicle; E. bracteoles; F. floral bud; G. inner tepals in ventral view; H. outer tepal in external (left) and internal (right) surfaces; I. fertile stamens of outer whorl in ventral (left), dorsal (middle) and lateral (right) views; J. fertile stamens of inner whorl in ventral (left), dorsal (middle) and lateral (right) views; K. fertile stamens of inner whorl in ventral (left), dorsal (middle) and lateral (right) views showing the two globose glands; L. staminodes in ventral (left), dorsal (middle) and lateral (right) views; M. pistil. Drawing by Humberto Mendoza based on *P. Quiroga and G. Zabala 84* (JBB).

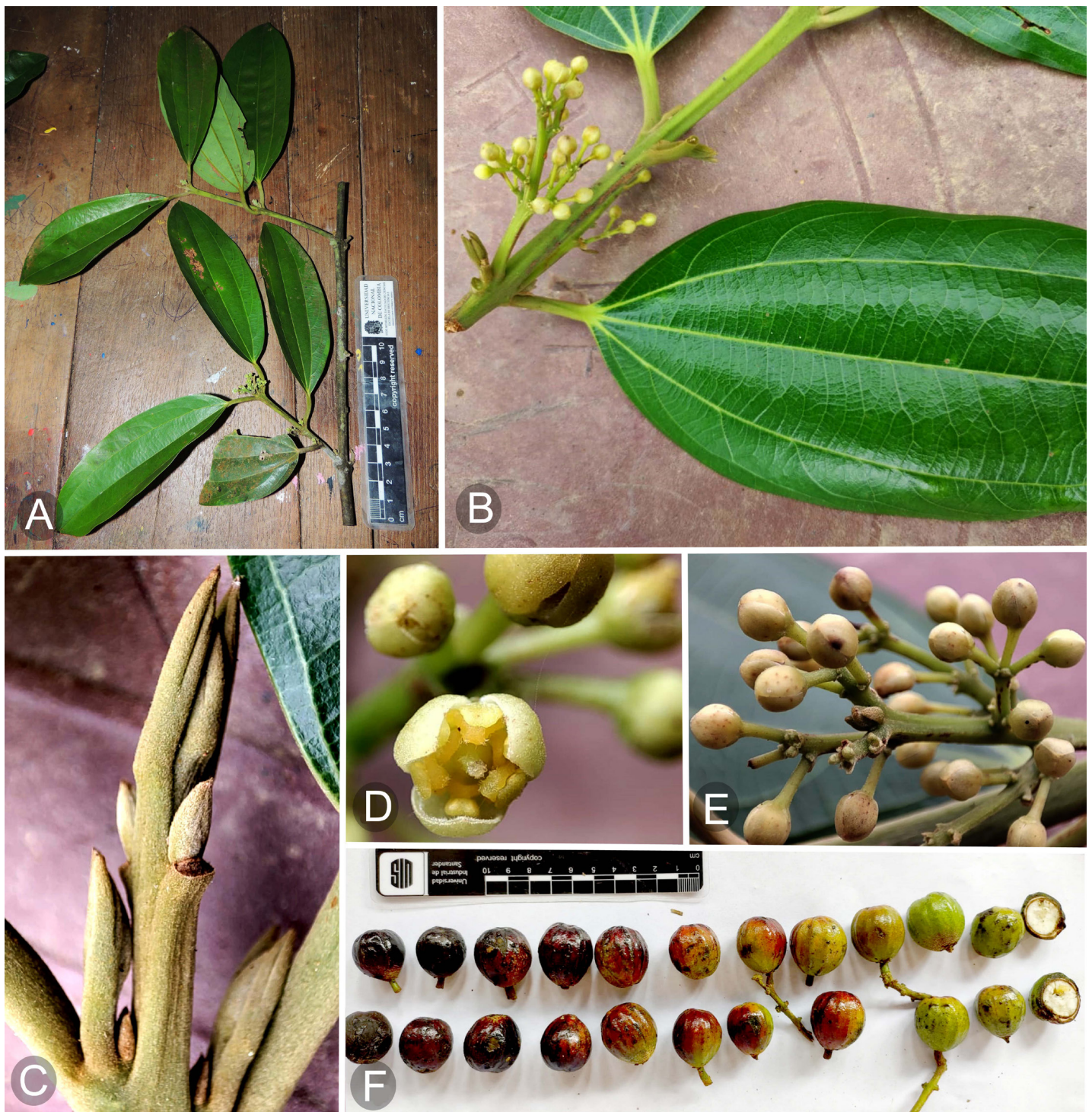


Figure 6: *Caryodaphnopsis yariguiensis* Humberto Mend., Díaz-Rueda & Aymard. Field images: A, B. detail of leaves and floriferous branch; C. apical bud; D. flower in anthesis; E. inflorescence; F. fruits at different stages of maturation. Photographs by Daniel Díaz-Rueda, Paula Quiroga and Björn Reu.

sericeous externally, glabrous internally; the inner 3, 2.9-3 × 1.9-2.2 mm, ovate, thin-chartaceous, not veined, densely sericeous on both surfaces, trichomes subulate, ca. 0.3 mm long; stamens 12 (9 fertile), filaments stout, covered

by subulate trichomes (0.3-0.4 mm long); the outer whorl with 6 fertile stamens, 2-2.1 mm long, anther 0.7-1 × 0.8-0.9 mm, 4-celled in two rows; inner whorl with 3 stamens in front of outer tepals, 1.7-1.9 mm long, filament with two

globose glands, 0.5-0.7 × 0.3-0.4 mm, attached at the middle (ca. 0.5 mm above the base), anthers 0.6-0.7 × 0.4-0.5 mm, 4-celled in two lateral rows; staminodes located in internal whorl, opposite to internal tepals, 1.5-1.6 mm long, anthers not celled; pistil 2.4-2.6 mm long, 1.1-1.2 mm diameter, sparsely adpressed pilose from the middle to the apex; style 0.9-1 mm long; stigma slightly capitate; fruit a globose berry, 2.5-2.8 cm diameter, green at immaturity, black purple when mature, seed one.

Distribution and habitat: *Caryodaphnopsis yariguiensis* occurs in several localities in Boyacá and Santander departments (Colombia). It is a relatively rare taxon in wet forests located on foothills, slopes, and mountains between 220-1700 m elevation on the western slopes of the Serranías de Los Yariguíes and Las Quinchas (Fig. 3). Both regions are located in the Magdalena Medio ecoregion. This area has forests that harbor several high-value timber species such as “Chaparro negro” (*Licaria cannella* (Meisn., Lauraceae) Kosterm.), “Punte churco” (*Aniba perutilis* Hemsl., Lauraceae), “Molinillo” (*Magnolia resupinatifolia* Aguilar-Cano & Humberto Mend., Magnoliaceae), “Pepaerruncho” (*Compsonera atopa* (A.C. Sm.) A.C. Sm., Myristicaceae) and “Cedrotagua” (*Carapa* sp., Meliaceae).

Etymology: *Caryodaphnopsis yariguiensis* is named after the Serranía de Los Yariguíes, Santander department, a region where this new species is frequent (Fig. 3). The Serranía de Los Yariguíes is located on the western slopes of the Eastern Cordillera of Colombia (“Cordillera Oriental”) in the Magdalena Medio. This area is well-known for its high biodiversity values and for being the land of Yariguíes people. The Yariguíes fiercely defended their territory and resisted the processes of conquest and colonialism until their extermination at the beginning of the 20th century (Velásquez Rodríguez y Castillo León, 2006).

Phenology: this new species was collected with flowers and fruits between November and February, and occasionally in May (the dry period in this region).

Conservation status: this species is currently known from the type locality and ten additional collections; it is

reported here as rare. Under IUCN Standards and Petitions Committee (IUCN, 2022) guidelines, it should be regarded as Endangered (EN), based on the criteria B1 and B2, its estimated Area of Occupancy (AOO) of 774 km² (with a cell size of 1 km²) and its estimated Extent of Occurrence (EOO) of 1769.87 km² (IUCN, 2022). This category applies to taxa with an AOO < 2.000 km², and with a very fragmented distribution (a local scale of B1a). This new species grows in forests with different states of conservation and disturbance, such as forests widely logged to extract timber, undisturbed forests and sometimes the individuals are found on roadsides. In addition, the area where *Caryodaphnopsis yariguiensis* occurs is currently protected by the Colombian National Park service (Parques Nacionales Naturales de Colombia), through the Parque Nacional Natural Serranía de los Yariguíes.

Taxonomic notes: *Caryodaphnopsis yariguiensis* shares morphological features (such as the sericeous indument on apical buds, tepals, and the ovary, and stout stamens) with *C. fieldii*, an endemic species from the wet montane forests located in the Coastal Cordillera, Venezuela (Aymard and Romero-González, 2009). However, the latter taxon differs in having elliptic, elliptic-oblong to oblong leaf blades and rounded apex (vs. elliptic and acute), the outer tepals 1-2 mm long, sparsely strigose externally (vs. 1-1.1 mm long, densely sericeous), the inner tepals 3-4.5 mm long (vs. 2.9-3 mm) and the stamen glands attached at the base of the filament (vs. attached at the middle of the filament). In addition, these two taxa are found in different biogeographic regions, and currently no intermediate populations are known. Moreover, this new species is morphologically related to *C. fosteri*. Nonetheless, *C. yariguiensis* differs from the latter by its distal internodes and ovary pubescent (vs. glabrous), smaller tepals and stamens, and larger ovary and fruit. This new species differs from the other Neotropical taxa of the genus in the characters discussed in the diagnosis, Appendix, and in the key below.

Common names and uses: *Caryodaphnopsis yariguiensis* is locally known as “Panelaquemada” or “Panelo”. These common names allude to the “panela” smell that the wood gives off when it is sawn. The name “Panelaquemada de Castilla” was recorded in the town El Carmen de



Chucurí. The latter is a vernacular adjective used for species that have valuable timbers for the rural communities, as well as to differentiate it from other species of the genus present in the area (i.e., *C. carmensis*, known as “Panelaquemada tres venas”). In the Serranía de Las Quinchas (Boyacá department), the peasants and the local people identified this species as “Yumbé”. The latter name is also used in El Carmen de Chucurí and other areas of the middle Magdalena valley to refer to *Caryodaphnopsis cogolloi* van der Werff.

The wood is mainly used as stakes or fence posts because of its durability and resistance to weathering and humidity. It is also applied in the construction of rural houses, especially to make planks and columns, beehives, and general furniture, such as tables and beds (Fig. 4).

Additional specimens examined: COLOMBIA. Boyacá, municipio Puerto Boyacá, vereda Las Quinchas, Finca Las Quinchas, 890 m, 5°50'6.8"N, 74°16'42.4"O, 31.VII.2019, st, *H. Mendoza et al.* 22625 (FMB, JBB). Santander, municipio Cimitarra, vereda Guineales, límites entre Cimitarra y Bolívar, 223 m, 6°07'13.2"N, 74°13'32.5"O, 14.VII.2018, st, *H. Mendoza et al.* 21450 (FMB, JBB). Municipio El Carmen de Chucurí, vereda La Pitala, Finca El Tesoro, zona centro de la Serranía de Los Yarigués, 490 m, 6°37'58.2"N, 73°35'15.7"O, 14.V.2023, fr, *D. Díaz-Rueda et al.* 2895 (COL, JAUM, JBB, HUA, UDBC, UIS, UPTC); vereda La Bodega, 1330 m, 6°40'49"N, 73°28'3"O, 25.I.2020, fl, fr, *J. Quiroga-Nova* 5 (FMB, JBB), 6 (FMB, JBB), 7 (FMB, JBB). Municipio San Vicente de Chucurí, vereda Mérida Alta, Sector Varsovia, Predio Laverde, 1523 m, 6°49'19.2"N, 73°23'20.0"O, 20.IX.2015, fl, *M. Ayala-Joya et al.* 3220 (FMB, MEDEL); Sector Siberia, Predio La Siberia, 1391 m, 6°51'23.6"N, 73°23'12.6"O, 20.IX.2015, fl, *M. Ayala-Joya et al.* 3934 (FMB); vereda Mérida Alta, Sector Varsovia, Predio Laverde, 1520 m, 6°49'19.20"N, 73°23'20"O, 15.III.2016, fl, *M. Ayala-Joya et al.* 3906 (ANDES, COL, CUVC, FAUC, HECASA, HUA, JAUM, JBB, MEDEL, UDBC, UIS, UPTC); vereda Centro, Sector La Germania, Finca Miradores, al lado de la casa, cerca al camino de Lengerke, 1440 m, 6°51'14.5"N, 73°23'14.6"O, 27.V.2022, fl, fr, *P. Cáceres, B. Reu* 17 (UIS); vereda Chanchón Alto, Finca Hato Nuevo, 1630 m, 6°54'9.7"N, 73°20'28.6"O, 6.V.2022, st, *D. Díaz-Rueda et al.* 2515 (JAUM, JBB, UDBC,

UIS); vereda Mérida Alta, Sector Varsovia, sector norte de la Serranía Los Yarigués, 1498 m, 6°52'49.0"N, 73°22'16.0"O, 21.XI.2021, fr, *P. Quiroga et al.* 81 (HUA, JAUM, JBB, UIS), 82 (HUA, JAUM, JBB, UIS); loc. cit., 1600 m, 6°49'17.1"N, 73°24'9.1"O, 21.XI.2021, fr, *P. Quiroga* 83 (JBB, UIS).

In view of the taxonomic novelties described here, a key for all *Caryodaphnopsis* species of the Neotropics is presented, partly based on the one published by **Aymard and Romero-González (2009)**.

Key to the Neotropical species of *Caryodaphnopsis*

- 1a. Leaves pinninerved 2
- 1b. Leaves triplennerved or trinerved 3
- 2a. Leaves oblong, not glaucous on the lower surface; anthers 2-celled (Amazonian Brazil, Ecuador, Peru and Colombia) *Caryodaphnopsis inaequalis* (A. C. Smith) van der Werff & Richter
- 2b. Leaves elliptic, gray-glaucous to glaucous on the lower surface; anthers 4-celled (northern biogeographical Chocó and Magdalena Medio, Colombia) *Caryodaphnopsis cogolloi* van der Werff
- 3a. Leaves glaucous on the lower surface; fruit pear-shaped (biogeographical Chocó, Colombia and Ecuador, Gorgona Island) *Caryodaphnopsis theobromifolia* (A. H. Gentry) van der Werff & Richter
- 3b. Leaves not glaucous on the lower surface, fruit globose 4
- 4a. Distal nodes and young leaves pubescent on the lower surface (trichomes erect, or suberect) 5
- 4b. Distal nodes and young leaves glabrous or sericeous on the lower surface (trichomes adpressed) 6
- 5a. Leaf base rounded or subcordate, secondary veins 3-5 pairs; inner tepals 6.1-6.5 mm long; fertile stamens 9, 2.5-4.5 mm long; anthers 4-celled (Magdalena Medio, Colombia) *Caryodaphnopsis carmensis* H. Mend., J. Quiroga & D. Díaz-Rueda
- 5b. Leaf base obtuse or acute, secondary veins 1-paired; inner tepals ca. 3 mm long; fertile stamens 6, 1.5 mm long; anthers 2-celled (Amazonian Colombia, Ecuador and Peru) *Caryodaphnopsis tomentosa* van der Werff

- 6a. Pedicel ≤ 2 mm long; inner tepals ≤ 2 mm long; fertile stamens 6, ≤ 1 mm long; anthers 2-celled; staminodia with glands (Amazonian Peru)
..... *Caryodaphnopsis parviflora* van der Werff
- 6b. Pedicel > 2 mm long; inner tepals > 3 mm long; fertile stamens 9, > 2 mm long, anthers 4-celled; staminodia without glands (Mesoamerica; Coastal Cordillera, Venezuela; Magdalena Medio, Colombia; Amazonian Bolivia, Colombia, Ecuador and Peru) 7
- 7a. Inner tepals 6.5-10 mm long; outer fertile stamens ca. 5 mm long; pistil 4.5-5 mm long, stigma bilobate (Costa Rica, Panama)
..... *Caryodaphnopsis burgeri* N. Zamora & Poveda
- 7b. Inner tepals 2.9-6 mm long; outer fertile stamens 2-4 mm long; pistil 2.4-3 mm long, stigma capitate or punctiform (Coastal Cordillera, Venezuela; Magdalena Medio, Colombia; Amazonian Bolivia, Colombia, Ecuador and Peru) 8
- 8a. Petioles slightly pilose; inner tepal 5-6 mm long, pilose inside; pistil glabrous; filaments slender, 3-4 mm long; the inner stamens with two globose glands attached ca. 1 mm above the base; ovary glabrous (Amazonian Bolivia, Colombia, Ecuador and Peru)
Caryodaphnopsis fosteri van der Werff
- 8b. Petioles densely shortly pubescent, white adpressed pubescent, glabrescent when mature; inner tepal 2.9-4.5 mm long, densely sericeous or glabrous inside; pistil pilose or strigose; filaments stout, 1.7- 2.1 mm long; the inner stamens with two globose glands attached in the lower half or at the base (Coastal Cordillera, Venezuela; Magdalena Medio, Colombia) 9
- 9a. Leaf apex rounded; inner tepal 3-4.5 mm long, densely sericeous inside, 6-veined; fertile stamens ca. 3 mm long, the inner stamens with two globose glands attached at the base (Coastal Cordillera, Venezuela)
..... *Caryodaphnopsis fieldii* Aymard & G.A. Romero
- 9b. Leaf apex obtuse, acute or slightly acuminate; inner tepal 2.9-3 mm long, glabrous inside, not veined; fertile stamens 1.7-2.1 mm long, the inner stamens with two globose glands attached ca. 0.5 mm above the base (middle) (Magdalena Medio, Colombia)
..... *Caryodaphnopsis yariguiensis* Humberto Mend., D. Díaz-Rueda & Aymard

Discussion

This contribution increases to seven the number of *Caryodaphnopsis* species known in Colombia, the country with the highest diversity of the genus in the Neotropics. Of these seven species, three are found in Amazon flooded forests (*C. fosterii*, *C. inaequalis* and *C. tomentosa*), one in the Pacific region (*C. theobromifolia*) and three endemics in the middle Magdalena valley (*C. cogolloi*, *C. carmensis* and *C. yariguiensis*). Finally, *C. carmensis* and *C. yariguiensis* are considered here to be morphological closer to the Amazonian and Central American species clade, such as *C. burgeri* and *C. fosteri*, than to *C. cogolloi*, the only species previously reported for the Magdalena Medio.

Caryodaphnopsis species richness has been continuously increasing especially over the last two decades; six *Caryodaphnopsis* species were described in the last 15 years (including the two new species described herein). This number is nearly one third (31%) of the 19 described *Caryodaphnopsis* worldwide. Increasing botanical sampling of *Caryodaphnopsis* in the wet forest areas of the Magdalena Medio may reveal the existence of more new species. However, the lack of satisfactory botanical sampling, coupled with widespread forest loss, fragmentation and disturbance, suggests the potential extinction of species before they are discovered, considered dark extinction (Boehm and Cronk, 2021). Therefore, collecting and describing new, threatened *Caryodaphnopsis* species is a necessary first step in the challenge to address their long-term conservation. Until this is done, they are invisible to science and it is not possible for them being assessed for their conservation status in order to be included in the IUCN Red List. This will improve the likelihood both that they will be proposed for conservation measures, and that such measures will be accepted (Cheek et al., 2020).

Currently, most Neotropical *Caryodaphnopsis* species are categorized as Near Threatened (NT, 2 spp.) to Endangered (EN, 3 spp.) (López-Gallego and Morales, 2020; Avendaño et al., 2021; de Kok, 2021a, b, c, d; Zamora, 2022). The three species located in the middle Magdalena valley are categorized as Endangered (*C. carmensis*, *C. cogolloi* and *C. yariguiensis*). These threatened conservation statuses are due to the loss of original habitats because of the forest transformations to productive systems (cattle



ranching, pastures, coffee and cocoa plantations), and selective logging of valuable timber throughout the region during decades.

It is important to mention that local initiatives have sought the conservation and recovery of populations of these species. The first report we have of an institutional project that included the planting of individuals of *C. yariguiensis* (before the species was described) corresponds to “Corredor de Conservación Reinita Cielo Azul” led by the PROAVES Foundation. This project reforested 613 ha, and helped to promote the ecological connection between the Serranía de los Yariguíes (Reserva Reinita Cielo Azul) and the Cerro de la Paz (Reserva Pauxi Pauxi). Between 2011 and 2013, about 3500 individuals of this species were planted, although there is currently no known quantitative evaluation of the survival of the plantations (pers. comm., Carlos Julio Rojas and Alex Monsalve, Fundación PROAVES).

Subsequently, *C. yariguiensis* was considered as VOC species (Valor Objeto de Conservación) in the Serranía de los Yariguíes National Natural Park (PNN) for being a quality timber species that had been overexploited during decades in this region (Moreno and Tinjaca, 2018; misidentified as *C. cf. burgeri*). In 2015 researchers from the Parques Nacionales Naturales de Colombia advanced a breeding initiative of *C. carmensis* (at the time unidentified) with 200 seeds (own observations). The germination rate was 10% (20), and five seedlings subsequently survived, which were planted in the Serranía de los Yariguíes National Park (own observations). Another ecological restoration project of the northern area of Serranía de los Yariguíes, between 2017 and 2018, included the planting of more than 3290 individuals of *C. yariguiensis* (Duarte-Sánchez et al., 2021). The survival rate was evaluated at 61.6% (pers. comm., Duarte-Sánchez).

In the Serranía de los Yariguíes (Santander department), a taxonomic confusion existed when referring to the timber trees known as “Panelaquemada” or “Panelo”. In fact, their taxonomic identity was uncertain, as well as whether it concerned one or several species. According to Resolution DGL No. 00188 of May 14, 2020 (whereby a ban is established for forest harvesting in the area under the jurisdiction of the “Corporación Autónoma Regional de Santander” - CAS), the species that occurs in this area

and whose wood is marketed in the region, known as “Panelaquemada” (also “Yumbé” or “Pateguara”), refers to *C. cogolloi*. The present paper clarifies that actually at least three species of the genus *Caryodaphnopsis* have timber importance and are subject to illegal logging and trading in the region. The two species described here have been propagated in ecological restoration projects implemented in the “Parques Nacionales Naturales de Colombia” and its buffer zones. However, massive propagation of the three species by public entities and organized communities in the region is suggested. For this reason, it is important to implement *ex situ* collections in botanical gardens and living collections, and if possible, to generate management plans for all species of the genus in Colombia.

Author contributions

HMC conceived the research, and wrote and edited the manuscript in Spanish, acquired all data, and reviewed the herbarium collections. JDQN, DMDR and MAJ collected the type material, field data and photographs and assisted with the threat categorization of the species and helped to write the manuscript. GA complemented the introduction, species descriptions, species key and wrote and edited the manuscript in English.

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CO - Fincas de intercambio de conocimiento” (San Vicente de Chucurí) and “Asocapayari” - Asociación de Campesinos Vecinos del Parque Natural Nacional Serranía de los Yariagués” (El Carmen de Chucurí), for the information shared about the region and the field support. We are also grateful to projects No. 8038/UIS-Minciencias and “La biodiversidad de Boyacá - complementación y síntesis a través de gradientes altitudinales e implicaciones de su incorporación en proyectos de apropiación social de conocimiento y de efectos de cambio, Municipios de Tunja, Mongua, Puerto Boyacá y Otanche”, which made it possible to make collections of the new taxa described here.

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Appendix: Comparison of diagnostic morphological characters of *Caryodaphnopsis carmensis* Humberto Mend., J. Quiroga & Díaz-Rueda, *C. yariguiensis* Humberto Mend., D. Díaz & Aymard and other Neotropical species. Measures and characters based on Zamora Villalobos and Poveda Álvarez, 1988 (*C. burgeri* N. Zamora & Poveda); van der Werff, 1988 (*C. cogolloi* van der Werff); Aymard and Romero-González, 2009 (*C. fieldii* Aymard & G.A. Romero); van der Werff, 1986 (*C. fosteri* van der Werff); Smith, 1935, van der Werff and Richter, 1985 (*C. inaequalis* (A.C. Sm.) van der Werff & H.G. Richt.); van der Werff, 2012 (*C. parviflora* van der Werff); Gentry, 1977, van der Werff and Richter, 1985 (*C. theobromifolia* (A.H. Gentry) van der Werff & H.G. Richt.); van der Werff, 1991 (*C. tomentosa* van der Werff). Characters in grey are important diagnostic characters to distinguish between species.

Characters	Species									
	<i>C. burgeri</i> N. Zamora & Poveda	<i>C. carmensis</i> Humberto Mend., J. Quiroga & Díaz-Rueda	<i>C. cogolloi</i> van der Werff	<i>C. fieldii</i> Aymard & G.A. Romero	<i>C. fosteri</i> van der Werff	<i>C. inaequalis</i> A.C. Smith	<i>C. parviflora</i> van der Werff	<i>C. theobromifolia</i> (A. H. Gentry) van der Werff & Richter	<i>C. tomentosa</i> van der Werff	<i>C. yariguiensis</i> Humberto Mend., D. Díaz-Rueda & Aymard
Branch and branchlet indument	glabrous, or sparsely sericeous	densely brown/golden pubescent	minutely ferruginous	densely short-pubescent, glabrescent when mature	pilose, glabrous when mature	glabrous	glabrous	minutely ferruginous	densely tomentose (brown)	sericeous
Leaf blade abaxial indument	glabrous	brown/golden pubescent	glaucous	minutely pilose	minutely pilose	glabrous	glabrous	glaucous	tomentose (brown)	minutely pilose
Stamen indument	pubescent	pubescent	glabrous	pubescent	pubescent	glabrous	glabrous	pubescent	pubescent	pubescent
Pistil indument	strigose	strigose	strigose	strigose	glabrous	glabrous	glabrous	strigose	puberulent	pilose
Leaf blade base	acute	rounded or subcordate	acute, obtuse	rounded, obtuse	rounded, obtuse	obtuse	acute	obtuse	acute, obtuse	obtuse, acute
Leaf blade apex	acute	acuminate	acuminate	rounded	obtuse-emarginate	obtuse	acute	obtuse	acute	obtuse, acute, slightly acuminate
Leaf blade venation	trinerved	trinerved	pinninerved	triplenerved	trinerved	pinninerved	trinerved	trinerved	trinerved	trinerved, triplenerved
Pair(s) of secondary veins	1	3-5	10-12	1	1	8-11	1	6-7	1	1
Pedicle length	2.5-9 mm	3.8-6.1 mm	2-3 mm	2-3 mm	5 mm	1.5 mm	1 mm	2.2-3.5 mm	2-3 mm	2.5-5.8 mm
Outer tepal length	1.9 mm	1.2-1.4 mm	ca. 1.5 mm	1-2 mm	1 mm	0.5 mm	0.6 mm	1 mm	ca. 1 mm	1-1.1



Appendix 1: Continuation.

Characters	Species									
	<i>C. burgeri</i> N. Zamora & Poveda	<i>C. carmensis</i> Humberto Mend., J. Quiroga & Díaz-Rueda	<i>C. cogolloi</i> van der Werff	<i>C. fieldii</i> Aymard & G.A. Romero	<i>C. fosteri</i> van der Werff	<i>C. inaequalis</i> A.C. Smith	<i>C. parviflora</i> van der Werff	<i>C. theobromifolia</i> (A. H. Gentry) van der Werff & Richter	<i>C. tomentosa</i> van der Werff	<i>C. yariguiensis</i> Humberto Mend., D. Díaz-Rueda & Aymard
Inner tepal length	6.5-10 mm	6.1-6.5 mm	ca. 4 mm	3-4.5 mm	5-6 mm	2.5 mm	2 mm	2.5 mm	ca. 3 mm	2.9-3
Fertile stamen	9	9	9	9	9	9	6	9	6	9
Fertile stamen length in outer whorl	ca. 5 mm	3.6-4.5 mm	ca. 2 mm	ca. 3 mm	ca. 3-4 mm	ca. 0.6 mm	ca. 1 mm	ca. 0.75 mm	1.5 mm	2-2.1 mm
Glandular stamen length in inner whorl	ca. 4.8 mm	2.5-3.9 mm	ca. 2 mm	ca. 3 mm	ca. 3-4 mm	ca. 0.6 mm	ca. 1 mm	0.75 mm	0.7 mm	1.7-1.9 mm
Estaminodia length in inner whorl	2-2.8 mm	1.7-2.4 mm	ca. 1 mm	1.5-2 mm	ca. 1 mm	0.8 mm	ca. 1.2 mm	ca. 0.7 mm	0.7 mm	1.5-1.6 mm
Glands position on fertile inner stamen	ca. 0.5 mm above the base	ca. 1 mm above the base	at the base	at the base	ca. 1 mm above the base	at the base	at the base	at the base?	at the base	(middle) ca. 0.5 mm above the base
Cell number of anthers	4	4	4	4	4	2	2	4	2	4
Pistil length	4.5-5 mm	3.6-4.5 mm	ca. 1.7 mm	ca. 3 mm	ca. 3 mm	not seen	1 mm	1 mm	2 mm	2.4-2.6 mm
Stigma shape	bilobate	punctiform	capitate	capitate	punctiform	punctiform	not seen	not seen	capitate	slightly capitate
Fruit length	1.8-2 cm	1.3-1.4 cm	4 cm	ca. 1.2 cm	ca. 1 cm	8.5 cm	1.5 cm	ca. 8.5-10 cm	not seen	2.5-2.8 cm
Fruit shape	globose	globose	pear-shaped	globose	globose	pear-shaped	globose	pear-shaped	not seen	globose