



TWO NEW TAXA OF *CLETHRACEAE*: SECT. *CUELLARIA*, SER. *TOMENTOSAE*) FROM HONDURAS

DOS NUEVOS TAXONES DE *CLETHRACEAE*: SECT. *CUELLARIA*, SER. *TOMENTOSAE*) DE HONDURAS

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Abstract

Background: As part of the taxonomic revision of the genus *Clethra* in Central America, two new species from Honduras were discovered. The two new species described here have been confused mainly with *C. lanata*, *C. mexicana* and *C. salvadorensis*.

Question: Are foliar trichomes useful to distinguish species?

Taxon: Species of *Clethra*.

Study site: Central and southern mountain ranges of Honduras.

Methods: Relevant literature on *Clethra* was reviewed and specimens from six herbaria were examined. Type material from all morphologically similar species, as well as those taxa with which the two new species have previously been confused were compared.

Results: *Clethra albertinae* and *C. standleyana* are described and illustrated as new and endemic species from Honduras, both belong to ser. *Tomentosae*. *Clethra albertinae* is most closely related to *C. licanoides*, a species endemic to Guatemala, and *C. standleyana* is most closely related to *C. nicaraguensis*, a widespread species that occurs from Mexico (Chiapas) to Nicaragua. Based on the IUCN Red List a conservation assessment of Vulnerable and Endangered is recommended for both new species. An updated list and key to the nine species of *Clethra* for the flora of Honduras is proposed.

Conclusions: The foliar trichomes turned out to be diagnostic and in combination with characters of the inflorescences can be used to separate all Honduran species of *Clethra*. In Central America, Honduras is the third country with the most species rich of this genus after Guatemala and Costa Rica.

Key words: Endemism, Mesoamerica, new species, taxonomy, foliar trichomes.

Resumen

Antecedentes: Como parte de una revisión taxonómica sobre el género *Clethra* en Centroamérica, se descubrieron dos especies nuevas de Honduras. Las dos especies nuevas se han confundido en el pasado principalmente con *C. lanata*, *C. mexicana* y *C. salvadorensis*.

Pregunta: ¿Son útiles los tricomas foliares para distinguir especies?

Taxón: Especies de *Clethra*.

Sitio de estudio: Cordilleras del centro y sur de Honduras.

Métodos: Se revisó la literatura relevante sobre *Clethra* y se examinaron especímenes de seis herbarios. Se comparó con material tipo de las especies morfológicamente similares, así como aquellos taxones con los que las dos especies nuevas se habían confundido.

Resultados: *Clethra albertinae* y *C. standleyana* se describen e ilustran como especies nuevas y endémicas de Honduras, ambas pertenecen a la ser. *Tomentosae*. *Clethra albertinae* está más estrechamente relacionada con *C. licanoides*, una especie endémica de Guatemala, y *C. standleyana* está más estrechamente relacionada con *C. nicaraguensis*, una especie muy extendida que se encuentra desde México (Chiapas) hasta Nicaragua. Con base en la Lista Roja de la UICN se recomienda una evaluación de conservación de Vulnerable y en Peligro para ambas especies nuevas. Se propone una lista actualizada y clave de las nueve especies de *Clethra* para la flora de Honduras.

Conclusiones: Los tricomas foliares resultaron ser diagnósticos y en combinación con caracteres de las inflorescencias pueden usarse para separar todas las especies hondureñas de *Clethra*. En Centroamérica, Honduras es el tercer país con mayor riqueza de especies de este género después de Guatemala y Costa Rica.

Palabras clave: Endemismo, Mesoamérica, nuevas especies, taxonomía, tricomas foliares.



The Clethraceae, a small family in the order Ericales (Anderberg & Zhang 2002, Berazaín-Iturralde 2006) is composed of two genera, *Clethra* Gronov. ex L. and *Purdiaeae* Planch., and includes 85 species (The Plant List 2013: www.theplantlist.org). The genus *Purdiaeae* is being represented by one species in Central America, 12 species in Cuba, and two species in South America (Berazaín-Iturralde 2004). In contrast, the genus *Clethra* is widespread, occurring from temperate to tropical regions in eastern Asia and American with a single exception (*C. arborea* Aiton) in Madeira. The number of species varies according to different authors: 64-65 species (Sleumer 1967, WFO (<http://www.worldfloraonline.org/taxon/wfo-4000008596>), 120 species (Calderón de Rzedowski 2001), ca. 85 species (Fior *et al.* 2003), and 73 to 79 species (Gustafsson 2004, POWO: www.plantsoftheworldonline.org). According to Sleumer (1967) the genus has been divided into two sections based mainly on a character of the seed. North American, Asian and Malasian species, characterized by wingless seeds, belong to sect. *Clethra*, whereas Mexican, Central America, and South American species distinguished by winged seeds, constitute the sect. *Cuellaria*. Later Sleumer (1967) subdivided sect. *Cuellaria* into subsect. *Cuellaria* and subsect. *Pseudocuellaria*, the latter including solely the Madeiran species. He mentions that subsect. *Cuellaria* has a wide distribution in Mexico (12 spp.), Central America (12 spp.), South America (19 spp.), and the Greater Antilles (three species: *C. cubensis* A.Rich., *C. alexandri* Griseb., and *C. occidentalis* (L.) Kuntze). However, for Mexico González-Villarreal (2007) reported about 30 species and Vickery (2021) cited 16 species for Mesoamerica. Recent taxonomic studies suggest that the number is likely to increase as in the case of Mexico and Central America.

Members of *Clethra* consists of evergreen or deciduous shrubs, medium-sized or even tall trees 1-20 m high. The leaves are alternate, simple, entire, coriaceous or subcoriaceous, finely to coarsely toothed (as often seen in young blades), their surfaces glabrous or with vestiture. The inflorescences are terminal panicles or racemes, these straight or slightly bent with bracts mostly deciduous after anthesis and pedicels slightly accrescent in fruit. Flowers are perfect, poucliform, white to yellow-white, and fragrant, the sepals entire, becoming lignified, glabrous or hairy internally, the petals free with margin erose-fimbriate, glabrous or hairy internally, and the ovary superior. Fruits are a loculicidal, trigonous capsule with persistent sepals and style. Seeds are numerous, small, flattened, winged all around (González-Villarreal 2009).

According to Sleumer (1967), *Clethra* subsect. *Cuellaria* is subdivided into four series: *Glabrae*, *Tomentellae*, *Tomentosae* and *Ferrugineae*, based mainly on differences in leaf vestiture. The latter contains only South American species. Indument types have been investigated in numerous plant groups and have been widely used to define species groups and circumscribe species (*e.g.*, Fagaceae: Hardin 1976, Ericaceae: Hardin & Gensel 1982, Juglandaceae: Hardin & Stone 1984, Betulaceae: Hardin & Bell 1986, Fagaceae: Valencia-Ávalos & Delgado-Salinas 2003, Scareli-Santos *et al.* 2013).

According to González-Villarreal (2007) who has studied the foliar trichomes in 20 species of *Clethra*, five types of trichomes are reported: acicular, stellate, fasciculate, filiform and multiradiate. 1) Acicular - simple, slender, short to long, appressed, obliquely erect, completely patent or less noticeable when mixed with other types of trichomes (*e.g.*, fasciculate). It has the tendency to be more grouped on the major veins. The acicular type is found in most *Clethra* species. 2) Stellate - a minute, matted, appressed, pale trichome with the rays spread out in a plane, found mainly on the abaxial surface. These are characteristics of the series *Tomentellae*, although they also occur in the series *Glabrae* and *Tomentosae*. Members of the latter, show a bistratate vestiture abaxially, composed by stellate trichomes (as inferior stratum) mixed with acicular and fasciculate that appear as superior stratum. This stratum is the most conspicuous and diverse. 3) Fasciculate - is a cluster of rays in a single set where the rays are free, erect or wavy. The lower part is connate into a kind of stem called stipe that can be short or long. The number of rays varies and is decisive to distinguishing species. 4) Multiradiate - a minute, reddish or pale trichome, somewhat similar to the fasciculate trichome. These trichomes usually occur on the adaxial surface. 5) Filiform - is a thread-like trichome generally curled or wavy, commonly occurs on the abaxial surface. It is exclusive to some members of the series *Tomentosae*. For taxonomic use the different types and their combination must be compared in leaves of the same state of maturity, since young leaves show a denser vestiture and some hairs tend to fall.

Members of series *Tomentosae* present the greatest taxonomic problems in the circumscription of species, in particular those from Mexico and Central America. One reason, the most significant one, is the lack of study of trichome morphology. Another is the presence of glabrescent variants in species normally densely tomentose, for example, in the cases of *Clethra lanata* Mart. & Gal., *C. mexicana* DC., and *C. salvadorensis* Britton. As a matter of fact, most collections of tomentose species from Central America and even some from South America have been misidentified, annotated, and cited with one (or more) of these three names. All taxa examined for this study were confused. The process of extricating and renaming misidentified species, once completed, resulted in a residuum of the unassigned material that constitutes the bases for the two new species proposed in this paper.

Material and methods

Relevant literature on *Clethra* for the area was consulted, including the *Monographia Clethracearum* by Sleumer (1967), and floras such as *Flora of Guatemala* (Standley & Williams 1966), *Flora of Nicaragua* (Hamilton 2001), and *Flora Mesoamericana* (Vickery 2021).

This review of the genus *Clethra* was carried out at the Wisconsin State Herbarium (WIS) and is based on critical study of specimens received on loan from F, MEXU, MO, NY, and US. Additionally, for comparision of similar species as well as for updating the list of names and synonymy of Honduran *Clethra*, all type material of species reported for Central America was studied, which involved specimens from A, BM, BR, C, DS, F, GH, K, L, M, MEXU, MICH, MO, NY, S, TEX, U, UC, and US (acronyms according to Thiers 2015). This reworking of a considerable number of specimens enabled construction of a key for the identification of all species known to be present in the country.

All measurements and morphological characters were taken from herbarium material. A dissecting microscope (Nikon SMZ 745, model 2016148, with 50 × magnification) was used for the investigation of indumenta. Trichome nomenclature is that proposed by Hardin (1976) and followed by González-Villarreal (2007).

The distribution map was constructed in Quantum GIS ver. 3.16.2 (qgis.osgeo.org) using coordinates provided on specimen labels. The data were projected into a map of administrative divisions from Global Administrative Areas ver. 4.0 (GADM 2021) and a topographic map generated from WorldClim (Fick & Hijmans 2017). Conservation status was determined using the geospatial conservation assessment tool GeoCAT (Bachman *et al.* 2011) and applying the IUCN red list criteria (IUCN 2022).

Results

***Clethra albertinae* L.M.González, sp. nov.** ([Figures 1-2, 5](#)). *Type*: Honduras, departamento de Ocotepeque, between El Agua Caliente and Machuca, highway to Guatemala and Honduras border, 1,000 m, abundant in pine forest, tree 3-5 m, flowers white, 4/9/1975, A. Molina R. & A.R. Molina 31084 (Holotype: F).

Diagnosis. *Clethra albertinae* is morphological similar to *C. licanioides* Standl. & Steyermark, from which it differs by the shorter petioles, 0.3-0.8 (-1.5) cm long (vs (1-) 2-3 (-3.5) cm long), covered by long acicular and fasciculate trichomes (vs multiradiate and fasciculate trichomes); adaxial leaf surface covered by stellate trichomes of 4-15 rays and dispersed, sessile-fasciculate trichomes of (2-) 4-8 rays (vs stellate trichomes of 4-8 rays and short-stipitate fasciculate trichomes of 4-8 (-10) rays); abaxial leaf surface covered by short-stipitate fasciculate trichomes of 2-7 (mostly 4) rays, mixed with sessile-fasciculate trichomes of 7-9 rays and long acicular trichomes, as superior stratum (vs short-stipitate fasciculate trichomes of 2-8 (-10) rays, mixed with acicular trichomes); flowers with sepals glabrous internally (vs densely tomentose); filaments 2-3 mm long, glabrous (vs (2.5-) 3.5-4 mm long, pilose); style 2-3 mm long, glabrous (vs 5-6 mm long, pilose); fruit 5-8 mm in diameter (vs 8-20 mm in diameter).

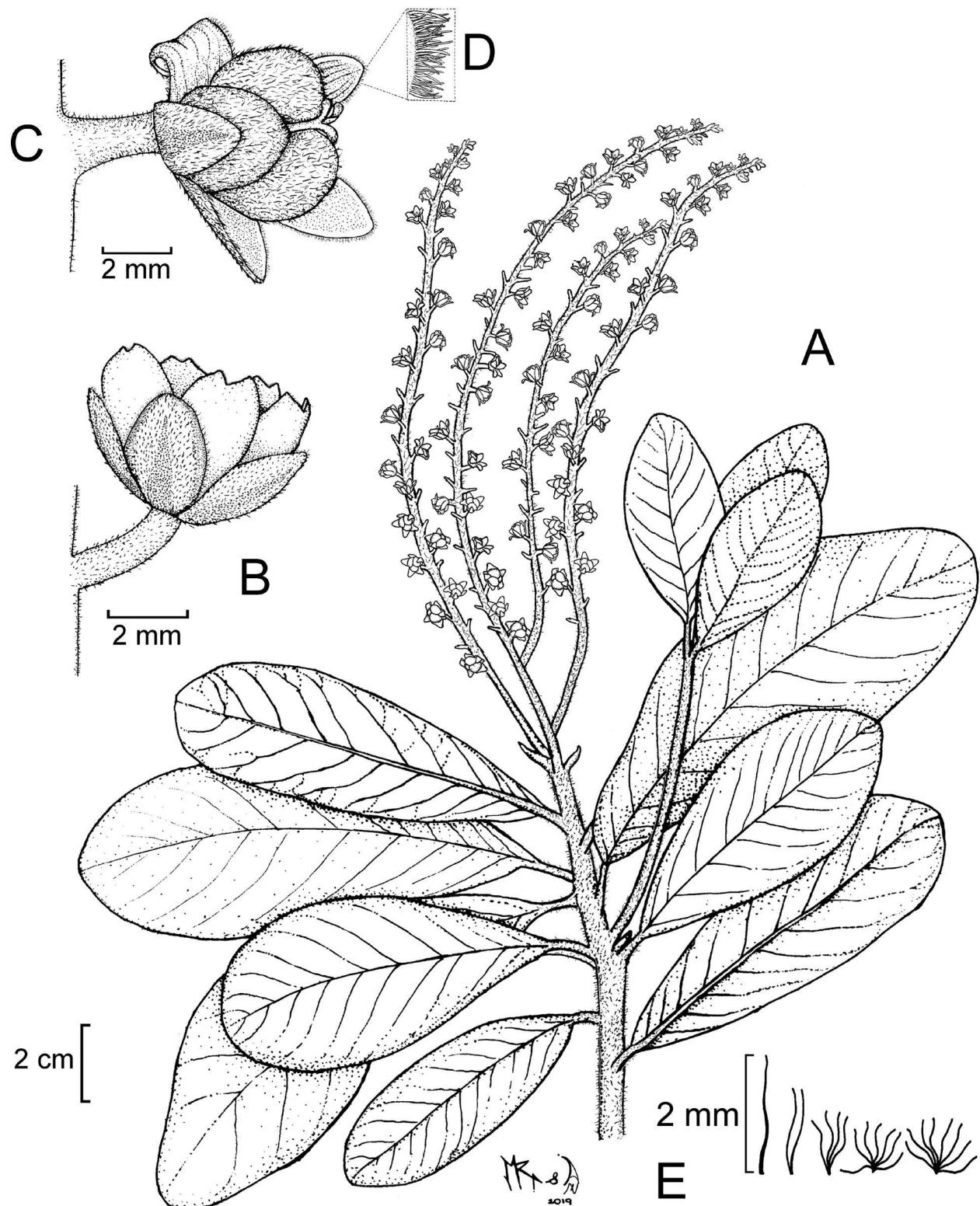


Figure 1. *Clethra albertinae*. A. Branchlet with inflorescence. B. Flower. C. Immature fruit. D. Detail of sepal margin. E. Trichomes of abaxial leaf surface, long acicular, short-stipitate fasciculate of 2-4 rays and sessile-fasciculate of 7-9 rays. Illustration by Anna Paizani Guillén and José Manuel Ramírez Amezcuá, based on the holotype (A. Molina & A.R. Molina 31084).

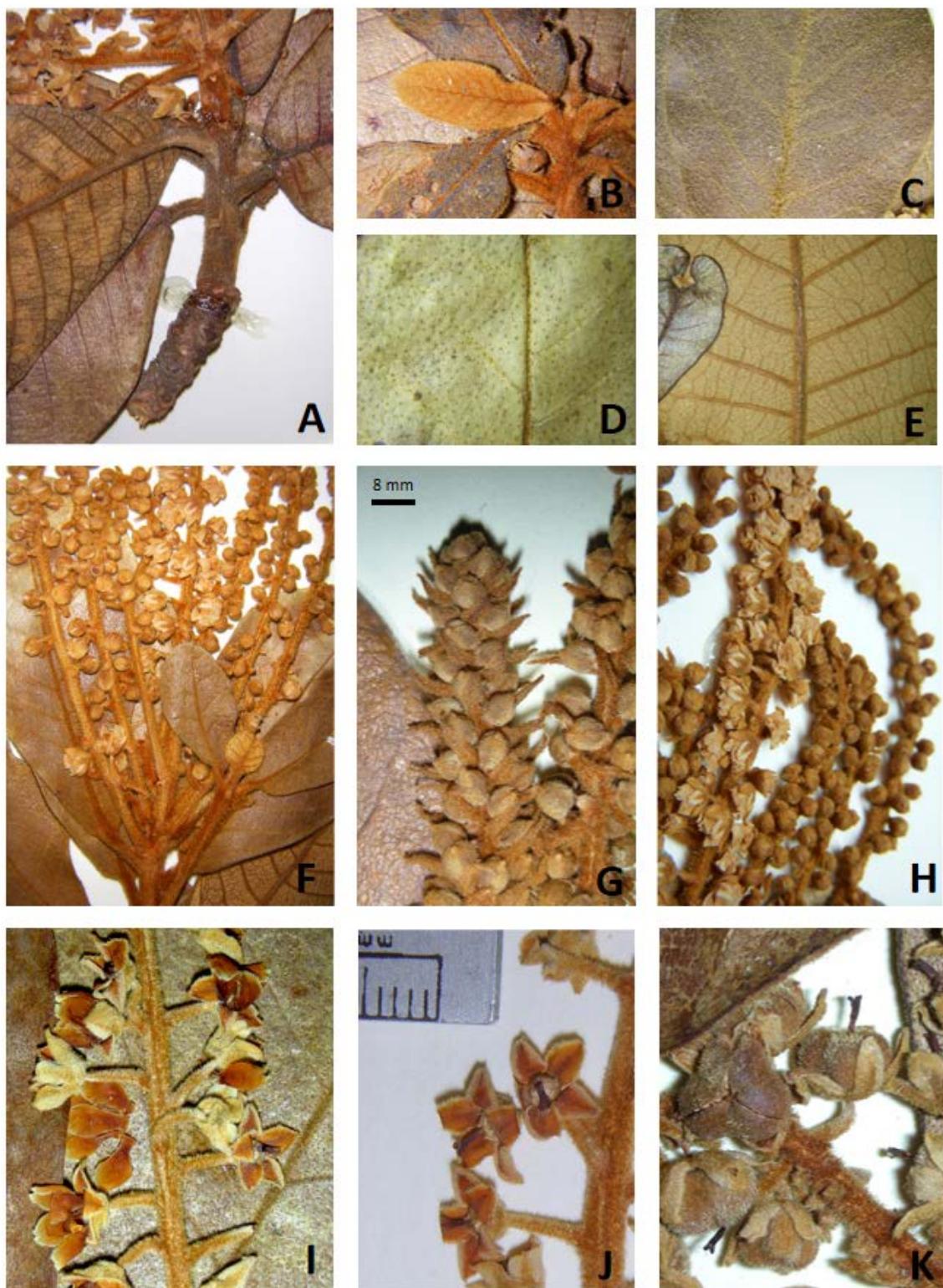


Figure 2. *Clethra albertinae*. A. Detail of the indumentum on petioles and branchlet of the present year. B. Detail of the tomentum of young leaves. C-D. Portions of adaxial leaf surface, with age showing the punctate indumentum. E. Portion of abaxial leaf surface. F. Flowering branchlet. G. Flowers in prefloration and bracts. H. Inflorescence fragment. I. Inflorescence fragment showing flowers with fimbriate-ciliate petals. J. Detail of the reflexed sepals, showing the glabrous internal surface. K. Rachis with immature fruits.

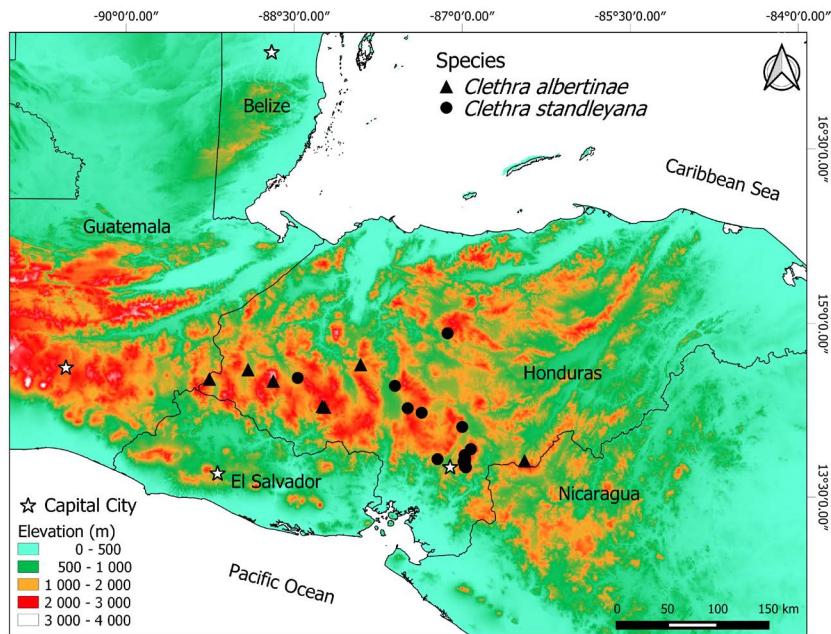


Figure 5. Distribution map of *Clethra albertinae* and *C. standleyana* in Honduras.

Description. Shrubs or medium-sized trees (3-) 5-12 m tall; branchlets somewhat robust, 4.5-7.5 mm in diameter, densely and tightly tomentose, covered mainly by sessile-fasciculate trichomes mixed with acicular trichomes, yellowish-brown to reddish-brown, becoming canescent-puberulous or glabrous, the epidermis not exfoliate, with prominent foliar scars. Leaves coriaceous, when young densely reddish-brown tomentose on both sides, in age concolorous or bicolorous; petiole somewhat short and thick especially at the base, angular, 0.3-0.8 (-1.5) cm long, densely and tightly tomentose, covered mainly by acicular trichomes mixed with sessile-fasciculate trichomes of 4-8 or more rays; leaf blades obovate or obovate-elliptic to widely elliptic, (4.5-) 6-16 × 2.5-8.5 cm, apex widely rounded to obtuse, base rounded or somewhat truncate or cuneate, margins entire, rarely with 1-6 minute teeth on the whole leaf, sometimes cupped, concave beneath; adaxial surface covered by stellate trichomes of 4-15 rays and dispersed, sessile-fasciculate trichomes of (2-) 4-8 rays, the rays fine, long, erect, collapsed or wavy and all tangled, on young leaves forming a dense mat, at maturity glabrous and evidently punctate except for the tomentose midvein, all veins furrowed and well marked, giving a rough surface; abaxial surface light-brown to yellowish-brown, soft-tomentose, covered by minute, pale, appressed-stellate trichomes as inferior stratum, the superior stratum formed by short-stipitate fasciculate trichomes of 2-7 (mostly 4) rays, the rays long, fine, wavy or twisted, overlapping but not entangled, mixed with some shorter, sessile-fasciculate trichomes of 7-9 rays, and long acicular trichomes (1.2-2 mm long), these mostly concentrated along the thick midvein, the veinlets elevated; secondary veins 10-15 on each side, mostly arched-ascending, branching several times before reaching the margins. Inflorescences an elongate and slightly curved panicle of 4-8 racemes, 10-15 (-25) cm long, loosely-flowered; rachis somewhat thick, with a dense yellowish-brown tomentum, ribbed; bracts navicular, (3-) 5-8 mm long, longer than the flowering pedicels or the same size, basal bracts up to 10 mm long, apex acute to acuminate, densely tomentose, dropping off early; pedicels slender, straight, (3-) 4-6 mm long, tomentose; sepals ovate to ovate-oblong, 3-5 × 2 mm, apex of the internal lobes acute, the external lobes obtuse to acute, margins long-ciliate, tomentose, glabrous but puberulous at apex internally, reflexed in fruit; petals entirely free, obovate, (4-) 5-6 × 3-3.5 mm, margin fimbriate-ciliate, rarely completely entire (Evans 1289, MO), internally pilose at the base; filaments filiform, 2-3 mm long, slightly enlarged at the base, flattened laterally, glabrous; anthers sagittate, 1.2-1.5 (-2) mm long, with a small appendix at the base; ovary 2-2.5 mm in diameter, densely sericeous; style short, 2-3 mm long, glabrous. Fruit a depressed-globose, trigonous capsule, when immature 7-8 mm in diameter, on a pedicel 6-8 mm long. Seeds unknown.

Distribution, ecology, and phenology. *Clethra albertinae* is apparently endemic to Honduras, where it is currently known from the southern-central mountainous areas. The plant is located from Ocotepeque department in the convergence of El Salvador and Guatemala to El Paraiso department, near the border with Nicaragua. It is a common to abundant tree in the pine and pine-*Liquidambar* forests, along trails in secondary shrubby vegetation and at edges of steep banks. It occurs at (850-) 1,000-2,300 m elevation, reaching its highest known limit at Celaque National Park in the cloud forest. In the area of Siguatepeque, it grows sympatrically with *C. hondurensis* Britton and *C. vicentina* Standl. The species flowers almost all year.

Conservation status. The GeoCAT tool (Bachman *et al.* 2011) estimated the Extent of Occurrence (EOO) of *Clethra albertinae* was calculated as 7,973 km², and its Area of Occupancy (AOO) as 28 km², based on cells of 2 × 2 km. Following IUCN (2022) criteria, EOO and AOO results place *C. albertina* in the vulnerable (VU) and endangered (EN) categories, respectively.

Etymology. The specific epithet honors Albertina Rodríguez, usually cited as Albertina R. Molina, who with her husband Antonio Molina R. carried out botanical explorations in Central America, contributing greatly to the knowledge of the flora of Honduras. They made the type collection of the species here described.

Additional specimens examined. Honduras, Departamento de Comayagua, barranco El Socorro near Siguatepeque, 1,350 m, 18/4/1951, P.H. Allen 6222 (F). Departamento de Copán, 42 km S of Santa Rosa de Copán, 850 m, 15/7/1971, W.E. Harmon & J.A. Fuentes 6461 (MO). Departamento de El Paraíso, municipio de Oropolí, aldea El Corralito, 1,280-1,400 m, 3/5/2000, A. Molina R. *et al.* 34915 (MEXU, MO). Departamento de Intibucá, Camaco, Yamaranguila, 2/7/1973, J.R. Martínez 144 (MO). Departamento de Lempira, San Manuel Colohete to Cerro Sucte, Parque Nacional Celaque, 14° 30' N, 88° 41' W, 2,300 m, 18/2/1993, R. Evans 1289 (MO). Departamento de Ocotepeque, cascada de Yamaranguila, 1,800 m, 7/4/1956, A. Molina R. 6365 (F, NY, US).

Discussion

Specimens of *Clethra albertinae* have frequently been confused with *C. lanata*, *C. licanoides*, *C. mexicana*, and *C. salvadorensis*, probably due to the superficial appearance of the leaf indumentum, generating a chaotic taxonomic situation. The concept of *C. mexicana* has been widely misapplied by several authors. In fact, the species is endemic to central Mexico, where its distribution is restricted to the Trans-Mexican Volcanic Belt and part of the Balsas region. It grows from humid pine-oak-*Abies*, oak forests to the cloud forest at 1,800-3,300 m elevation (González-Villarreal 2007). With respect to *C. lanata* and *C. salvadorensis*, they are, in fact, morphologically closely related. They have been cited in synonymy under *C. mexicana* by Standley & Williams (1966), Berendsohn *et al.* (2009); and Vickery (2021), who also added to the list *C. bimatrata* Standl. & Steyermark, *C. costaricensis* Britton, *C. nicaraguensis* C.W.Ham., and *C. panamensis* Standl. & L.O.Williams, complicating this situation even more. However, Berendsohn *et al.* (2009) argued that if *C. mexicana* is truly a Mexican species, then *C. lanata* is a valid species that includes *C. salvadorensis*. Previously, Sleumer (1967: 161) had already accepted *C. lanata*, placing *C. costaricensis*, *C. panamensis*, and *C. salvadorensis*, among other species from South America and the Caribbean, in its synonymy. In contrast, Hamilton (2001) also accepted *C. lanata* but listed *C. costaricensis* as the only synonym. *Clethra lanata*, another endemic species from Mexico, is morphologically unrelated to *C. mexicana* and has a very different geographical distribution and habitat. *Clethra lanata* is confined to the Sierra Madre del Sur, occurring in a variety of habitats from savannas to the moist pine-oak forest at 350-2,350 m elevation. Regarding *C. salvadorensis*, this is a species with a wider distribution, from Mexico (Chiapas) to Costa Rica, growing in semi-evergreen montane forest at 1,000-1,800 m elevation.

In Honduras, it is found in Lempira, La Paz, and Choluteca departments, growing at 1,300 m elevation. The correct taxonomic characterization of all these species has been confirmed on the basis of detailed examinations of trichomes, each of which is distinguished by a characteristic combination of trichomes.

Clethra albertinae is probably related to the Guatemalan *C. licanoides*. Both have robust branchlets, coriaceous leaf blades, these mostly obovate with the adaxially surface punctate with age and yellowish-brown to reddish tomentum abaxially. Also, for their elongated inflorescences with a robust rachis and pedicels 4-6 mm long. In fact, *W.E. Harmon & J.A. Fuentes* 6461 and *A. Molina R. & A.R. Molina* 31084 (the type of *C. albertinae*) have been cited as *C. licanoides* by Vickery (2021), along with one additional collection, *W.E. Harmon & J.A. Fuentes* 6360 (MO) from Distrito Central, not seen.

In [Table 1](#) diagnostic features of *Clethra albertinae* are compared with *C. licanoides* and also with those species with which it has most often been confused, all in the series *Tomentosae*. Additionally, it is worth noting that the flowers in *C. albertinae* have the sepals glabrous internally (vs densely tomentose) and the petals are less hairy internally than in *C. licanoides*. Also, *C. licanoides* has pilose filaments, an unusual feature in subsect. *Cuellaria* according to Sleumer (1967: 45), who pointed out that “in all species in this subsection the filaments are glabrous”. However, pilose filaments can also be present in *C. lanata*, as well as pilose styles. The fruits of *C. licanoides* become very large, some reaching up to 20 mm in diameter, whereas those of *C. albertinae* are 5-8 mm in diameter.

Clethra standleyana L.M.González, sp. nov. ([Figures 3-5](#)). *Type*: Honduras, Departamento de El Paraíso, Manzaraqua road southwest of Güinope, about 1,400 m, steep bank in quebrada, shrub 1-2 m, common, corolla white, 2/6/1951, *P.C. Standley* 28508 (Holotype: F; Isotype: F).

Diagnosis. *Clethra standleyana* is closely related to *C. nicaraguensis*, from which it differs by the shorter petioles, soft-tomentose, (8-) 1-1.5 cm long (vs hispid-tomentose, (0.5-) 1.5-2 (-3) cm long); leaf blade base unfolded (vs noticeably infolded); adaxial leaf surface covered by dispersed, stellate trichomes of 5-10 rays and sessile-fasciculate trichomes of 2-7 rays (vs dispersed, stellate trichomes of 8-16 rays, mixed with sessile-fasciculate trichomes of (2-) 4-8 rays); veinlets abaxially slightly raised or not (vs noticeably raised, forming an elevated network); inflorescences a loosely-flowered panicle, rachis slender, with soft yellowish-brown tomentum (vs densely-flowered raceme or panicle, rachis thick, with hispid-ferrugineous tomentum); flowers with petals pilose internally at the base (vs glabrous or with few hairs internally at the base).

Description. Shrubs or medium-sized trees (1-) 5-10 m tall, commonly gnarled; branchlets somewhat robust, 5-8 mm in diameter, densely and tightly tomentose, covered mainly by sessile-fasciculate trichomes mixed with acicular trichomes, yellowish-brown to reddish-brown, becoming puberulous-canescens to glabrous, often canaliculate, epidermis not exfoliating, with foliar scars. Leaves coriaceous to subcoriaceous, when young reddish-brown adaxially, in age bicolorous; petiole somewhat long and slender, angular, (0.8-) 1-1.5 cm long, densely and tightly tomentose, covered mainly by acicular trichomes mixed with some sessile-fasciculate trichomes of 2-9 fine rays; leaf blades very variable in shape, obovate to obovate-oblong, narrow to widely elliptic or oblong-elliptic, 5-15 (-16.5) × (2.5-) 4-8 cm, apex rounded to obtuse or acute, base narrowly rounded to truncate or sometimes cuneate, margins mostly entire, undulate, occasionally serrulate; adaxial surface in appearance glabrous but covered by dispersed, stellate trichomes of 5-10 rays, mixed with sessile-fasciculate trichomes of 2-7 erect rays, glabrescent with age, all veins evidently furrowed, giving a rough surface, the midvein densely covered with long acicular trichomes (up to 1.2 mm long) and fasciculate trichomes, especially near the base; abaxial surface evidently paler, yellowish-brown to ochraceous, somewhat rough to the touch, covered by minute, pale, appressed-stellate trichomes as inferior stratum, the superior stratum formed by short-stipitate fasciculate trichomes of (2-) 4-8 rays, the rays long, fine, amber, erect or wavy, mixed with acicular trichomes, all more or less the same size, overlapping, somewhat tangled but not hiding the minute stellate trichomes, the secondary veins raised particularly the midvein, veinlets slightly raised or not; secondary veins 10-15 on each side, mostly arched-ascending or sometimes straight and elevated, branching several times before reaching the margins, bearing mostly acicular trichomes. Inflorescences an elongate and straight panicle of 5-10 racemes, 10-25 cm long, loosely-flowered; rachis slender, with a dense yellowish-brown tomentum, ribbed; bracts subulate, (2.5-) 3-5 × 1.5-2 mm, longer than the flowering pedicels, apex acute, sometimes long-acuminate, densely tomentose, dropping off early; pedicels slender, bent or straight, 1-2 (-4) mm long, tomentose; sepals ovate-

Table 1. Comparative morphology of *Clethra albertinae* with the related *C. licanoides* and other species with which it has been confused.

Character/taxon	<i>C. albertinae</i>	<i>C. licanoides</i>	<i>C. lanata</i>	<i>C. salvadorensis</i>
Petiole	Densely tomentose, 0.3-0.8 (-1.5) cm long, with acicular and fasciculate trichomes.	Tomentose, (1-) 2-3 (-3.5) cm long, with multiradiate and fasciculate trichomes.	Densely tomentose, (0.6-) 1.5-2.5 (-4.5) cm long, with acicular and fasciculate trichomes.	Densely tomentose, (0.8-) 1-2 (-3) cm long, with fasciculate trichomes.
Leaves				
Base	Rounded or somewhat truncate or cuneate.	Narrowly rounded to cuneate, slightly to strongly infolded.	Cuneate to rounded, often oblique.	Cuneate, strongly infolded.
Adaxial surface	Stellate trichomes of 4-15 rays and dispersed sessile-fasciculate trichomes of (2-) 4-8 rays.	Stellate trichomes of 4-8 rays and short-stipitate fasciculate trichomes of 4-8 (-10) rays.	Stellate trichomes of 2-6 (-8) rays mixed with long-stipitate fasciculate trichomes of 4-6 (mostly 4) rays and sparsely, fine, acicular trichomes.	Stellate trichomes of 2-7 rays mixed with fasciculate trichomes of 2-8 rays and acicular trichomes.
Abaxial surface	Soft to the touch, with short-stipitate fasciculate trichomes of 2-7 (mostly 4) rays mixed with some sessile-fasciculate trichomes of 7-9 rays and long acicular trichomes.	Rough to the touch, with short-stipitate fasciculate trichomes of 2-8 (-10) rays mixed with acicular trichomes.	Soft to the touch, with long-stipitate fasciculate trichomes of 2-5 rays mixed with long acicular trichomes.	Soft to the touch, mostly acicular trichomes, sometimes sessile-fasciculate trichomes of 2-5 rays.
Inflorescence	Panicle, rachis thick with dense yellowish-brown tomentum.	Panicle, rachis thick with dense reddish to rusty tomentum.	Panicle, rachis slender with dense to sparse yellowish-brown tomentum.	Raceme, rachis slender with dense yellowish-brown tomentum.
Sepals (internally)	Glabrous but puberulous at the apex.	Puberulous.	Puberulous.	Puberulous.
Petals (internally)	Pilose at the base.	Pilose to densely pilose at the base, rarely glabrous.	Densely pilose at the base.	Densely pilose at the base.
Filaments	2-3 mm long, glabrous.	(2.5-) 3.5-4 mm long, densely pilose.	(1.5-) 2-3 mm long, glabrous, rarely pilose.	1.5-2 (-2.5) mm long, glabrous.
Style	2-3 mm long, glabrous.	5-6 mm long, pilose.	(1.5-) 2-3 (-4) mm long, densely to scarcely pilose or glabrous.	2-3 mm long, glabrous.

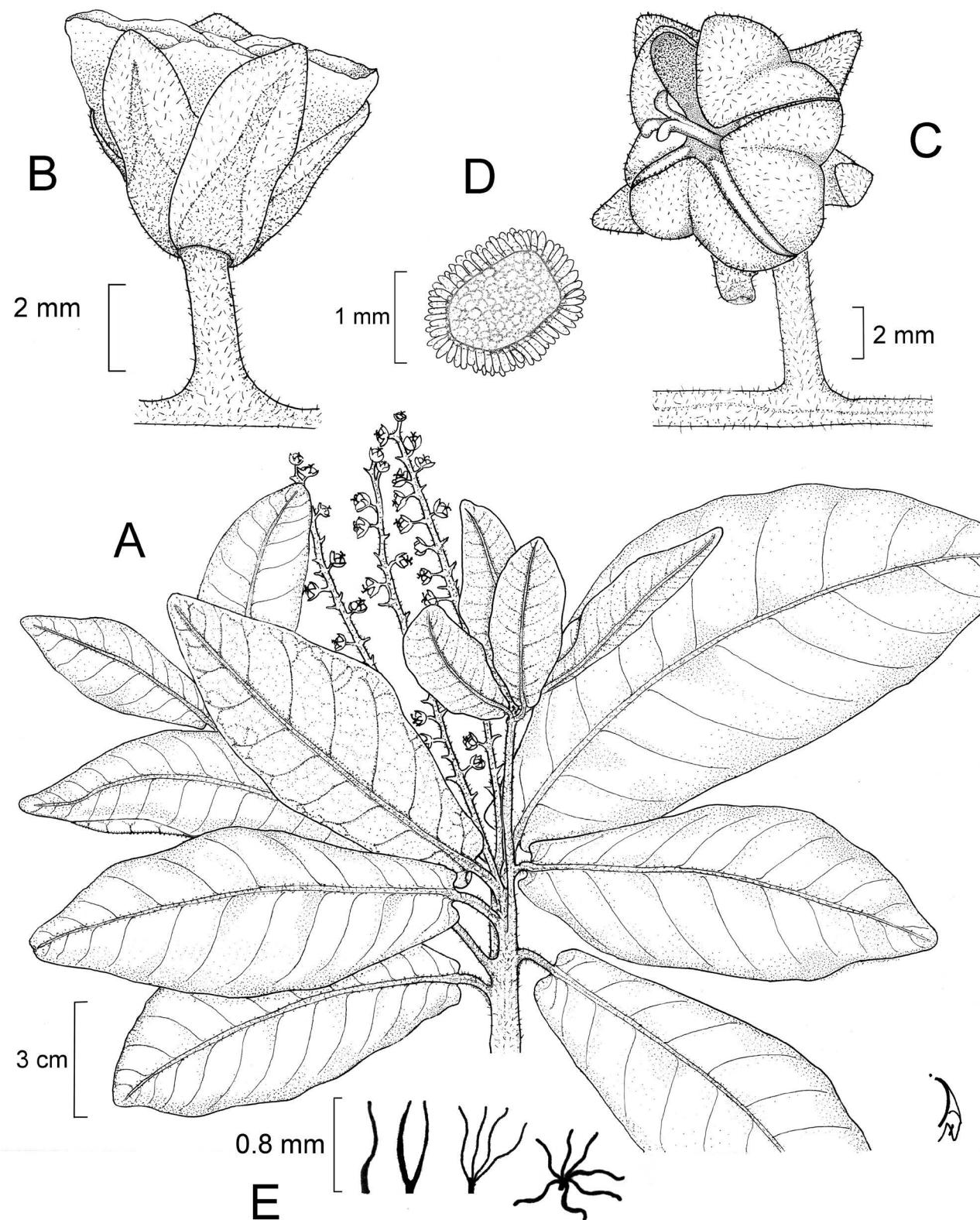


Figure 3. *Clethra standleyana*. A. Branchlet with inflorescence. B. Flower. C. Mature dehisced capsule. D. Seed showing the elongated and flattened testa cells all around. E. Trichomes of abaxial leaf surface, long acicular and short-stipitate fasciculate of (2-) 4-8 rays. Illustration by Anna Paizani Guillén, based on the holotype (P.C. Standley 28508).

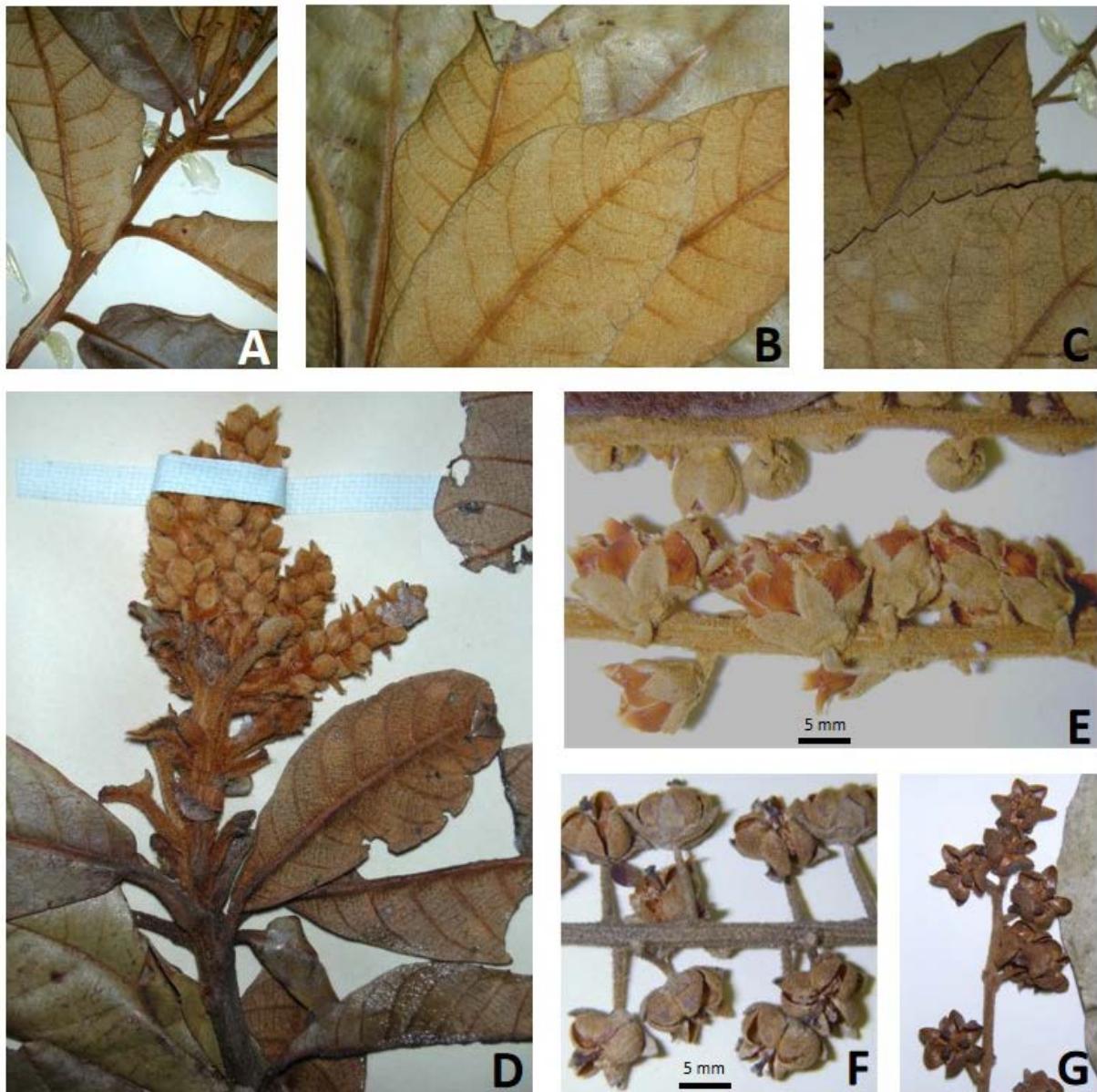


Figure 4. *Clethra standleyana*. A. Detail of the indumentum on petioles and branchlet. B. Detail of the adaxial and abaxial surface of the blade. C. Margins low serrate-dentate (occasionally). D. Flowers in prefloration and bracts. E. Part of an inflorescence. F-G. Rachis with fruits.

oblong, 4-5.5 × 2-3 mm, apex of the internal lobes acute, the external lobes obtuse to rounded, margins long-ciliate, tomentose, puberulous internally; petals entirely free, obovate, 4-6 × 3-4 mm, margin deeply fimbriate to fimbriate-ciliate, internally pilose at the base; filaments filiform, 2.5-3 mm long, slightly enlarged at the base, flattened laterally; anthers sagittate, 1.3-1.5 mm long; ovary 2-3 mm in diameter, densely sericeous; style elongate, 2-4 mm long, sometimes pilose at the base. Fruit a depressed-globose, trigonous capsule, when mature 3-4 × 8-10 mm, on a pedicel 6-7 mm long. Seeds numerous, circular or elliptic, flattened, 1.5-1.8 × 0.8-1.5 mm.

Distribution, ecology, and phenology. *Clethra standleyana* is endemic to Honduras, where it is restricted to the south-central cordilleras. It is a common to abundant, slender tree with dark green leaves, lustrous on upper surface, growing in the open pine forest on rocky hillsides heavily grazed and open dry pine grassland. Also, it is frequent

on steep banks and along creeks in shallow ravines, growing on sandy soil. It occurs mostly at 1,000-1,500 m elevation but as low as 800 m in the Amarateca Valley region. The species flowers throughout the year but mostly from November to February; fruiting from June to September.

Conservation status. Using GeoCAT tool (Bachman *et al.* 2011) estimated the Extent of Occurrence (EOO) of *Clethra standleyana* was calculated as 10,684 km², and its Area of Occupancy (AOO) as 52 km², based on cells of 2 × 2 km. Following the IUCN (2022) criteria, EOO and AOO results place *C. standleyana* in the vulnerable (VU) and endangered (EN) categories, respectively.

Etymology. The given specific epithet honors Paul Carpenter Standley (1884-1963), in recognition of his monumental contributions: *Trees and shrubs of Mexico*, *Flora of Costa Rica*, *Flora of Guatemala*, and several contributions to the floras of Honduras and Panama. He described fourteen species of *Clethra* from Mexico (2 spp.), Guatemala (6 spp.), Honduras (3 spp.), El Salvador (1 sp.), Costa Rica (1 sp.) and Panama (1 sp.); furthermore, he made the type collection of the species here described.

Additional specimens examined. Honduras, departamento de Comayagua, trail from Finca Sansón to Cerro Sansón, near Guaimaca, 18/2/1955, M.C. Carlson 3164 (F, MEXU, NY, US); carretera a La Pirámide [N Comoyagua], 1,500 m, 28/6/1964, A. Molina R. 14383 (F, LL, NY); La Pirámide, 1,500 m, 28/6/1964, A. Molina R. 14394 (F, NY); ca. Cuesta La Cocona, entre Comoyagua y Siguatepeque, 1,212 m, 8/4/1951, L.O. Williams & A. Molina R. 17633 (F). Departamento de El Paraíso, municipio de Güinope, 2.5 mi S of the intersection of El Zamorano-Morolica and Güinope, 4 km airline WSW of Güinope, 13° 51' 50" N, 86° 58' 43" W, 1,370 m, 16/6/1994, G. Davidse *et al.* 35006 (MO, WIS); municipio de San Lucas, ca. 6 mi S of Manzaraqua, between El Zamorano & Morolica, 13° 46' 04" N, 86° 58' 37" W, 1,250 m, 16/6/1994, G. Davidse *et al.* 35034 (MO, WIS); Río Yeguare [E of Zamorano] ca. 14° N, 87° W, 1,400 m, 3/2/1957, A. Molina R. 7585 (F); entre Manzaraqua y San Lucas, 1,500 m, 4/7/1962, A. Molina R. 10744 (F, NY); entre San Lucas y Manzaraqua, 1,500 m, 4/7/1962, A. Molina R. 10751 (F); entre Manzaraqua y San Lucas, 1,500 m, 4/7/1962, A. Molina R. 10754 (F); Tapahuasca, between Manzaraqua and San Lucas, 1,400 m, 24/11/1966, A. Molina R. 18752 (F, NY, US); 2 km NW of Güinope, near Manzaraqua, 1,390 m, 27/2/1949, P.C. Standley 17248 (F); Las Casitas [E of Marale], 1,400-1,500 m, 25/10/1951, P.C. Standley 29032 (US); cerro El Zapotillo, between Zamorano and Güinope, 4600 ft [1,400 m], 4/7/1962, G.L. Webster *et al.* 11974 (F, MEXU, MO); 3 km NW of Güinope, 1,400 m, 27/2/1949, L.O. Williams & D. Merrill 15697 (F); near Manzaraqua, 1,400 m, 7/2/1956, L.O. Williams & A. Molina R. 19017 (F). Departamento de Francisco Morazán, Amarateca Valley, near Zambrano, 800 m, 5/9/1968, A. Molina R. 22659 (F, NY); 12 km NE of Sabana Grande, near Los Artillos, 1,000 m, 23/12/1947, L.O. Williams & A. Molina R. 13592 (F).

Discussion

Herbarium material of *Clethra standleyana* has been annotated and even cited in the literature as several distinct morphological entities, including *Clethra lanata*, *C. macrophylla* Martens & Galeotti, *C. mexicana*, *C. occidentalis* (L.) O.Kuntze, *C. salvadorensis* and even *C. hondurensis*.

P.C. Standley 28508, the type, originally was determined as *Clethra salvadorensis* and later, in 1965, annotated as *C. mexicana* by L.O. Williams, as was L.O. Williams & D. Merrill 15697. Soon thereafter, Standley's collection was cited by Sleumer (1967: 163) as *C. lanata* along with Molina 7585, Standley 17248, Williams & Merrill 15697 (cited as *Merrill & Williams*), and Williams & Molina 17633, 13592, as well as Williams & Molina 19017 (not seen). Other collections of *C. standleyana* that were mentioned in *Flora Mesoamericana* by Vickery (2021) as *C. mexicana* are G. Davidse *et al.* 35006, 35034. Earlier in 1992, he had annotated A. Molina R. 10744, 18752 (F, NY) as *C. mexicana* as

accepted name, even though they were not cited. For comments about *C. salvadorensis*, *C. mexicana* and *C. lanata*, see discussion under *C. albertinae*.

On the other hand, *G.L. Webster et al. 11974* was first considered to be *Clethra occidentalis* but annotated as *C. macrophylla* by C.H. Hamilton in 1983 and later yet as *C. occidentalis* (incl. *C. macrophylla*) by Vickery in 1990. Nonetheless, the duplicate at F has this remark made as well by Vickery in 1992: “*C. mexicana* DC (verging towards *C. occidentalis*)”.

P.C. Standley 29032 was treated differently, having been identified initially as *Clethra hondurensis* before being referred by Sleumer (1967: 160) to *C. occidentalis* and later by T. Duncan in 1973 as *C. hondurensis*. However, *C. hondurensis* is a member of the series *Tomentellae*, characterized by leaf blades with abaxial surface soft, pale, yellowish or ochraceous-colored with vestiture composed by only one stratum of minute, appressed-stellate trichomes. A few additional acicular trichomes may be present on midvein and secondary venation. *Clethra hondurensis* also occurs in Belize, Guatemala and Nicaragua (González-Villarreal 2007).

According to Sleumer (1967), *Clethra occidentalis* is a wide-ranging species occurring in Jamaica, Mexico, and Central America. Regarding this opinion there are disagreements. Duncan (1979) in a numerical analysis demonstrated that *C. occidentalis* as circumscribed by Sleumer (1967) is composed of distinct morphological and geographical entities. His results demonstrated that *C. occidentalis* occurs only in Jamaica, as other previous authors (e.g., Britton 1914) believed.

The confusion with *Clethra macrophylla* may have been due to the leaf shape (oblong-elliptic) margins (entire, undulate or serrulate) combined with elongated inflorescences having bracts longer than the flowering pedicels. However, *C. standleyana* differs mainly in the leaf indumentum and geographical distribution. *Clethra macrophylla* is another endemic species from Mexico, occurring in central Veracruz and adjacent Puebla, at the juncture of two important mountain systems, the Trans-Mexican Volcanic Belt and the Sierra Madre Oriental.

Despite the long mixup in which *Clethra standleyana* was immersed, it is more closely related morphologically to *C. nicaraguensis*. They share robust branchlets, coriaceous bicolored leaves with secondary veins furrowed above and raised below, although the vestiture of *C. standleyana* is more yellowish to ochraceous-colored and that of *C. nicaraguensis* more reddish or rusty. Both have fasciculate trichomes of 4-8 rays as superior stratum abaxially. In [Table 2](#) diagnostic features of *C. standleyana* are compared with *C. nicaraguensis* and *C. macrophylla*, two of the species with which it was confused. *Clethra nicaraguensis* has a relatively wide geographical distribution from southern Mexico (Chiapas) to Nicaragua. In Honduras, it has a greater distribution than *C. standleyana*, being found in Comayagua, Copan, Itibuca, La Paz, Ocotepeque and Olancho departments, where it grows above 1,600 m elevation in mostly humid forests.

It is possible that *Clethra standleyana* can be introgressed with *C. vicentina*, a species widely distributed in Honduras, where the two become sympatric. *A. Molina R. 10744* and *G.L. Webster et al. 11974* from El Paraiso department not only show dark-colored petioles, as commonly seen in *C. vicentina*, but also less prominent venation and glabrescent surfaces.

In the Americas, as in Asia, *Clethra* is essentially a mountain-inhabiting genus, and in Honduras, one of the most mountainous countries in Central America, the genus is mostly concentrated in the mountain systems of Comayagua, Lempira, Morazan, Ocotepeque and El Paraiso departments. Originally, four taxa were described for this country: *C. caloneura* Standl. & L.O.Williams, *C. hondurensis*, *C. molinae* Standl. & L.O.Williams, and *C. viridifolia* Standl. & L.O.Williams, *C. hondurensis* in 1914 and the others in the 1950s (Nelson-Sutherland 2001). However, after revision of the genus by Sleumer (1967), these names were reduced to synonymy, leaving only three accepted names, as follows: *C. occidentalis* (*C. hondurensis*, *C. caloneura*), *C. vicentina* (*C. molinae*, *C. viridifolia*) and *C. lanata*. More recently, in *Flora Mesoamericana* Vickery (2021) reports seven species for Honduras: *C. gelida* Standl., *C. hondurensis* (*C. caloneura*, *C. nutantiflora* Standl. & L.O.Williams, *C. obliquinervia* Standl. & Steyermark.), *C. licanoides*, *C. mexicana* (*C. bimatrata*, *C. costaricensis*, *C. lanata*, *C. nicaraguensis*, *C. panamensis*, *C. salvadorensis*), *C. pachecoana* Standl. & Steyermark., *C. suaveolens* Turcz. (*C. glaberrima* Lundell, *C. matudae* Lundell, *C. nubium* Standl. & L.O.Williams, *C. vulcanicola* Standl.) and *C. vicentina*. However, it is evident from his synonymy that species have

Table 2. Comparative morphology of *Clethra standleyana* with the related *C. nicaraguensis* and other species with which it has been confused.

Character/taxon	<i>C. standleyana</i>	<i>C. nicaraguensis</i>	<i>C. macrophylla</i>	<i>C. mexicana</i>
Petiole	Soft-tomentose, (0.8-) 1-1.5 cm long.	Hispid-tomentose, (0.5-) 1.5-2 (-3) cm long.	Tomentose, (0.5-) 1.5-2.5 (-3.5) cm long.	Densely tomentose, (0.8-) 1.5-3 (-4) cm long.
Leaves				
Blade	Obovate to obovate-oblong, narrowly to widely elliptic or oblong-elliptic.	Narrowly elliptic to obovate.	Oblong, obovate to oblong-elliptic.	Oblong-obovate or oblong-elliptic to obovate.
Apex	Rounded to obtuse or acute.	Acute to acuminate, sometimes rounded and cuspidate.	Rounded to obtuse, sometimes acute to acuminate.	Obtuse to rounded or rarely subacute.
Base	Narrowly rounded to truncated or sometimes cuneate, unfolded.	Cuneate, noticeably infolded.	Rounded or subcordate, often oblique, rarely cuneate, unfolded.	Rounded to truncated or cuneate, rarely slightly infolded.
Margins	Mostly entire, undulate, occasionally serrulate.	Mostly serrulate or dentate, sometimes entire and slightly revolute.	Entire, toothed or serrulate-dentate.	Entire, undulate or serrulate-dentate.
Adaxial surface	Stellate trichomes of 5-10 rays mixed with sessile-fasciculate trichomes of 2-7 rays.	Stellate trichomes of 8-16 rays mixed with sessile-fasciculate trichomes of (2-) 4-8 rays.	Multiradiate trichomes.	Stellate trichomes of 10-13 or more rays mixed with sessile-fasciculate trichomes of (2-) 8-10 rays.
Abaxial surface	Stipitate-fasciculate trichomes of (2-) 4-8 rays, stipite short, the rays amber, erect or wavy, mixed with acicular trichomes.	Stipitate-fasciculate trichomes of (2-) 4-8 rays, stipite short, the rays reddish, erect or wavy with acicular trichomes on main veins.	Stipitate-fasciculate trichomes of (2-) 5-9 rays, stipite short, the rays reddish-brown, erect with acicular trichomes on main veins.	Stipitate-fasciculate trichomes of 2-7 rays, stipite long, the rays reddish-brown, curled, tangled, contorted, mixed with filiform trichomes.
Inflorescence	Loosely-flowered panicle, rachis slender with yellowish-brown tomentum.	Densely-flowered raceme or panicle, rachis thick with ferruginous tomentum.	Lax to densely-flowered panicle, rachis thick with reddish-brown tomentum.	Lax to densely-flowered raceme, rachis thick with reddish to ferruginous tomentum.
Sepals (internally)	Puberulous.	Puberulous.	Puberulous.	Glabrous but puberulous at the base.
Petals (internally)	Pilose at the base.	Glabrous or with few hairs at the base.	Glabrous or with few hairs at the base.	Glabrous.

been gratly confused. For example, four of these seven accepted species do not grow in Honduras. *Clethra gelida*, a Costa Rican endemic, was confused with the morphologically similar *C. oleoides* L.O.Williams, another species which also occurs at high elevations in the cloud forest and subparamo. *Clethra linanioides*, (as cited *Harmon 6461, 6360, Molina 31084*), is endemic to Guatemala, it has been confused with *C. albertinae*. *Clethra mexicana* as mentioned before is endemic to Mexico. So far known, *C. pachecoana* is distributed through part of the northern Central American volcanic arc from southern Guatemala to El Salvador.

My study of *Clethra*, including the two new endemic species described herein, brings to nine the number of species known for Honduras, making it the third most diverse country in Central America after Guatemala and Costa Rica. The accepted taxa are included in three series, as shown below. A revised synonymy appears in parentheses.

Series *Glabrae*

Clethra pyrogena

Clethra suaveolens (*C. viridifolia*)

Series *Tomentellae*

Clethra hondurensis (*C. caloneura*)

Clethra oleoides

Clethra vicentina (*C. molinae*)

Series *Tomentosae*

Clethra albertinae

Clethra nicaraguensis

Clethra salvadorensis

Clethra standleyana

Of all these species, *Clethra hondurensis* and *C. vicentina* have the widest distributions, each being present in ten departments, where they are established in different types of vegetation along wide altitudinal gradients. *Clethra hondurensis* grows in pine-oak, pine and rain forest areas at 200-2,000 m elevation. Locally, it is known as “concha de lagarto”, “nance de cerro” and “pepenance”. It also occurs in Guatemala, Belize and Nicaragua. *Clethra vicentina* grows in the oak-pine forest and cloud forest at 900-2,200 m elevation, at its lowest elevation inhabiting subtropical dry forest. Regionally it is known as “sapotillo”. It is also distributed in Mexico (Chiapas), Guatemala, El Salvador and Nicaragua.

In contrast, there are two species with restricted distributions in Honduras. *Clethra oleoides* is found in the highest region of the country, growing in Celaque National Park in the cloud forest at 2,400-2,850 m elevation, where it can be sympatric with *C. suaveolens*. *Clethra oleoides* also occurs in two disjunct areas of Mexico (Guerrero, Chiapas) and in Guatemala. *Clethra pyrogena* Sleumer is known solely from Pico Bonito National Park, where collected once (*Thomas Hawkins 891* at MO, WIS) in the cloud forest at 1,100-1,600 m elevation. It is also known from Costa Rica and Panama. An identification key to these nine species is presented below.

Key to species of Clethra in Honduras

1. Abaxial leaf surface glabrous or with a vestiture comprised of one stratum made up of minute, appressed-stellate trichomes.
2. Mature leaves with the abaxial surface green or pale-green color, lustrous, glabrous, the midvein and secondary venation with scattered acicular trichomes or glabrous..... Ser. *Glabrae*
3. Adaxial leaf surface dull brown, with stellate trichomes, secondary veins narrow and furrowed; leaves mostly widely elliptic, obovate or lanceolate with apex acuminate or obtuse, margins serrate-dentate, the teeth 0.5-1 mm long; petals glabrous internally; filaments 1.2-1.5 (-2) mm long; style 1.5 mm long. Occurs at elevations between 1,100-1,600 m..... *C. pyrogena*
3. Adaxial leaf surface green or pale-green, totally glabrous or with scattered, small stellate trichomes, secondary

veins inconspicuous; leaves narrowly elliptic to elliptic-lanceolate or oblanceolate with apex acute, margins entire, undulate or serrulate with low incurved teeth; petals densely pilose internally; filaments 2-3 mm long; style 1.5-2.5 (-3) mm long. Occurs at elevations between 1,500-2,700 m. *C. suaveolens*

2. Mature leaves with the abaxial surface pale, yellowish or ochraceous-colored, dull, totally covered by minute, appressed-stellate trichomes, the midvein and secondary venation with scattered, mostly antrorse acicular trichomes, sometimes with few fasciculate trichomes or glabrous. Ser. *Tomentellae*

4. Petiole less than 1 cm long; leaf blades often conduplicate, 3-7 (-10) × 1-3.5 cm; abaxial leaf surface with appressed-stellate-peltate trichomes; inflorescences short, less than 15 cm long. Occurs at elevations between 2,400-2,850 m. *C. oleoides*

4. Petiole 1.5-2.5 (-4) cm long; leaf blades flattened, 7-15 (-21) × 3-7 cm; abaxial leaf surface with appressed-stellate trichomes; inflorescences elongated, (8-) 15-25 cm long. Occurs at elevations between 200-2,200 m.

5. Leaf margins entire, undulate or rarely obscurely toothed; leaves mostly elliptic to ovate-lanceolate, rarely obovate, apex acute to acuminate, base infolded underneath; bracts usually shorter than the flowering pedicels; pedicels (2.5-) 4-7 (-9) mm long. *C. vicentina*

5. Leaf margins irregularly serrate from above the middle to the apex; leaves mostly narrow obovate or narrowly elliptic, apex rounded or acute, base not infolded underneath; bracts usually longer than the flowering pedicels; pedicels 1.5-3 (-4) mm long. *C. hondurensis*

1. Abaxial leaf surface tomentulose, tomentose or wooly, the vestiture comprised of two strata. The superior stratum formed by fasciculate trichomes that are either sessile or stipitate, often with acicular trichomes intermixed, the inferior stratum is made up of minute, more or less appressed-stellate trichomes. Ser. *Tomentosae*

6. Adaxial leaf surface with veins slightly impressed; abaxial leaf surface mostly with acicular trichomes, sometimes fasciculate trichomes as superior stratum. *C. salvadorensis*

6. Adaxial leaf surface with veins deeply furrowed impressed; abaxial leaf surface mostly fasciculate trichomes mixed with acicular trichomes as superior stratum.

7. Abaxial leaf surface soft-tomentose, with short-stipitate fasciculate trichomes of 2-7 (mostly 4) rays, mixed with some shorter, sessile-fasciculate trichomes of 7-9 rays and long acicular trichomes; bracts navicular, (3-) 5-8 mm long; sepals glabrous but puberulous at apex internally, reflexed in fruit. *C. albertinae*

7. Abaxial leaf surface rough-tomentose, with long stipitate-fasciculate trichomes of (2-) 4-8 rays and no acicular trichomes mixed; bracts subulate, 3-5 (-8) mm long; sepals completely puberulous internally, not reflexed in fruit.

8. Petiole 1.5-2 (-3) cm long, hispid-tomentose, covered mainly by fasciculate trichomes mixed with acicular and multiradiate trichomes, all persistent; leaves with margins serrate to denticulate-aristate on the upper two-thirds, sometimes entire and undulate, base cuneate, noticeably infolded; adaxial leaf surface with stellate trichomes of 8-16 rays and sessile-fasciculate trichomes of (2-) 4-8 rays; abaxial leaf surface with robust short-stipitate fasciculate trichomes as superior stratum, the veinlets forming a very characteristic network of parallel fine lines; petals glabrous or with few hairs at the base internally. Plants from elevations between 1,600-2,200 m. *C. nicaraguensis*

8. Petiole (0.8-) 1-1.5 cm long, soft-tomentose, covered mainly by acicular trichomes mixed with some sessile-fasciculate trichomes, with age glabrescent; leaves with margins entire, undulate or sometimes low serrate-dentate, base narrowly rounded to truncate or sometimes cuneate, unfolded; adaxial leaf surface with stellate trichomes of 5-10 rays and sessile-fasciculate trichomes of 2-7 rays; abaxial leaf surface with short-stipitate fasciculate trichomes as superior stratum, the veinlets not forming a network of parallel fine lines; petals pilose at the base internally. Plants from elevations between 800-1,000 m. *C. standleyana*

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