

Circumscription and nomenclature of *Hiraea barclayana*, H. reclinata, and H. ternifolia (Malpighiaceae), and of seven species misassigned to them

C. Anderson¹

Key words

Central America Colombia Hiraea Malpighiaceae Mexico Venezuela

Abstract A review of collections from Mexico to northern South America that had been primarily determined as H. barclayana, H. reclinata, and H. ternifolia, or synonyms, showed them to include ten species. Misinterpretations were caused by superficial morphological similarities and traditional nomenclatural errors. The species now recognized include six previously described: H. barclayana, H. hookeriana (formerly included in H. reclinata), H. reclinata, H. sanctae-marthae, H. ternifolia, and H. transiens. Four new species are proposed: H. mcvaughii, H. silvicola, and H. venezuelana; H. trianae was previously recognized at varietal level and is elevated to species. A neotype is chosen for *H. reclinata*. Lectotypes are designated for *H. velutina* (= *H. barclayana*) and four synonyms of H. reclinata: H. borealis, H. borealis var. glandulifera, H. obovata var. angustifolia, H. obovata var. latifolia forma glandulifera. Full descriptions and synonymies as well as a key are presented. All species are illustrated.

Published on 8 August 2016

INTRODUCTION

The genus Hiraea Jacq. comprises over 60 species found from Mexico to Argentina, except Chile. It is characterised by epipetiolar stipules and umbellate axillary inflorescences. For the majority of species the basic inflorescence unit is a 4-flowered umbel, solitary or arranged in ternate or sometimes biternate cymes; the remainder have multi-flowered umbels, the numerous pedicels radiating from one point. The bilaterally symmetrical flowers have yellow petals. The fruit is a schizocarp breaking into three samaras, which, except in a few species, are butterfly-shaped, i.e., the nut bearing two large lateral wings and a dorsal crest or winglet. Although the genus is easily recognized, the species are not so readily determined, owing to subtle morphological distinctions as well as nomenclatural misinterpretation and confusion.

This study is focussed on taxa with inflorescences based on 4-flowered umbels gathered from southern Mexico to northern Colombia and northern Venezuela to which the names H. reclinata Jacq., H. barclayana Benth., H. velutina Nied., and H. ternifolia (Kunth) A.Juss. have been most commonly attached. Also included are three collections from Brazil that were tentatively assigned to H. ternifolia. Determinations had been based largely on the presence or absence and nature of abaxial laminar vesture. In general, plants with sparsely pubescent to glabrous laminas had been assigned to H. reclinata (or one of its synonyms: H. borealis Nied., H. obovata (Kunth) Nied., H. purpusii Brandegee) or to H. transiens Nied. Plants with the abaxial laminar surface densely velutinous were determined as H. barclayana, H. velutina, or H. ternifolia.

Presence or absence of abaxial laminar vesture is a useful character in Hiraea; however, in many species any abaxial pubescence often thins gradually and is eventually shed as the leaf ages, though generally some of the vesture is retained on and near the costa and secondary veins. Onset of flowering may

occur before or at the time the new leaves emerge. Collections of this stage often consist of bare branches crowded with numerous condensed inflorescences, and perhaps a flush of young leaves (e.g., Fig. 5a) and/or a few old leaves that seem to lack vesture. Among the taxa under consideration here, such collections are often labelled as *H. reclinata* (or a synonym) only because any retained leaves appear to be glabrous to the casual observer, although closer examination would reveal remnants of distinctive vesture.

TAXONOMIC HISTORY

Correct application of names was also obscured by the influential publications of Franz Niedenzu and José Cuatrecasas. Niedenzu's interpretations of Hiraea (1906, 1928) suffered from the paucity of collections available to him and his lack of opportunity to study the collections and types at BM, K, and P. Many more collections of Hiraea had accumulated by the time Cuatrecasas (1958) prepared his review of Hiraea in Colombia; yet, he also did not have the chance to study all pertinent collections and types. Niedenzu, in his revision of Hiraea (1906), was particularly uncertain about the identity of *H. barclayana*. He noted in a footnote that he had not seen an 'authentic' specimen, and that H. barclayana might be the same as his new H. velutina. In his revision of Mascagnia (1908) he published the combination Mascagnia barclayana (Benth.) Nied., but with a question mark and footnoted observation "Forsan potius" vera Hiraea affinis H. ternifoliae". He returned H. barclayana to Hiraea in his monograph of the Malpighiaceae for Das Pflanzenreich (1928). For plants with sparsely pubescent to glabrous leaves Niedenzu recognized H. borealis, H. reclinata (including H. hookeriana A.Juss.), and H. obovata (including H. barclayana), and as well as his H. transiens (1906), based on diverse syntypes from Colombia, Peru, and Venezuela. To the listings of specimens for the last name, he added collections from Brazil (Bahia) and Bolivia, which further confused the application of the name *H. transiens*. For plants with velutinous

© 2016 Naturalis Biodiversity Center

You are free to share - to copy, distribute and transmit the work, under the following conditions:

Attribution:

You must attribute the work in the manner specified by the author or licensor (but not in any way that suggests that they endorse you or your use of the work).

Non-commercial: You may not use this work for commercial purposes.

No derivative works: You may not alter, transform, or build upon this work.

For any reuse or distribution, you must make clear to others the license terms of this work, which can be found at http://creativecommons.org/licenses/by-nc-nd/3.0/legalcode. Any of the above conditions can be waived if you get permission from the copyright holder. Nothing in this license impairs or restricts the author's moral rights.

¹ University of Michigan Herbarium, 3600 Varsity Drive, Ann Arbor, MI 48108, USA; e-mail: chra@umich.edu.

vesture Niedenzu recognized H. ternifolia and H. velutina. Under H. ternifolia he included as synonyms H. wiedeniana A.Juss. and H. houlletiana A.Juss., which are both synonyms of H. macrophylla (Colla) P.L.R.Moraes & Guglielmone, a species of eastern Brazil (C. Anderson 2014). His H. velutina (1906) is based on disparate syntypes, here assigned to H. barclayana and H. ternifolia. Cuatrecasas (1958) in his treatment of the Malpighiaceae for Colombia placed H. velutina within H. ternifolia. Like Niedenzu, he included H. hookeriana and H. barclayana under H. reclinata and also listed H. transiens as an additional synonym. Cuatrecasas & Croat (1981) in the account of Malpighiaceae for the Flora of Panama maintained this synonymy for H. reclinata and added Tetrapterys panamensis Seem. and the combination Hiraea panamensis (Seem.) Griseb., which are here considered synonyms of H. barclayana. As in some other genera of Malpighiaceae that have calyx glands, populations of Hiraea may include individuals in which such glands are absent. Niedenzu (1906, 1928) recognized this difference at the level of variety and Cuatrecasas (1958) of forma; however, this variability does not merit taxonomic recognition.

NOTES ON MORPHOLOGY

In all species treated, the tertiary veins of the leaf blades are spaced well more than 1 mm apart, and higher-order veins are clearly visible (Fig. 3e). These aspects immediately exclude the partly sympatric glabrous *H. fagifolia* (DC.) A.Juss., in which the scalariform tertiary veins are very closely spaced, c. 1 mm or less apart, and higher-order veins are not evident. The size of leaves of vegetative branches often greatly exceeds those found on branches bearing inflorescences; the largest dimensions given in the descriptions are commonly taken from mature leaves of sterile or fruiting specimens. Shape is also quite variable (e.g., Fig. 3a, b, d); the youngest laminas are often the narrowest. The hairs found in *Hiraea* vary from sessile or subsessile and straight to wavy or V-shaped to distinctly stalked and Y- or T-shaped, the latter with the trabecula (the cross-piece) straight to wavy.

The basic inflorescence is a ternate cyme of 4-flowered umbels, although one or both lateral branches may be suppressed occasionally. In some species the inflorescence is biternate (Fig. 2c), and in a few both forms may occur. In most genera of Malpighiaceae the pedicel is subtended by a pair of bracteoles and is borne on a peduncle subtended by a bract. In Hiraea, the floriferous peduncle is absent, and the flower is borne on a pedicel subtended by a pair of bracteoles and a bract (Fig. 3f). The term 'peduncle' in *Hiraea* denotes the axis subtending an umbel. The cyme may be subsessile or borne on an inflorescence axis. The lateral peduncles are usually borne on rudimentary axes, subtended by a pair of bracts, whereas the central peduncle is sessile. In a few species, all peduncles are sessile. As a rule, the crowded inflorescences borne on leafless branches are condensed, and have shorter axes and pedicels than inflorescences borne in the axils of expanded leaves (Fig. 1a, b, 2a, b). Measurements of flowers and embryos given in the descriptions are taken from herbarium material revived with Pohl's solution (Pohl 1965).

CONCLUSIONS AND KEY

The aspect of the abaxial laminar surface proves to be indeed a useful character for identification, if used with care. Review of the collections found under the bewildering array of names shows them to belong to ten species. In four species the abaxial laminar vesture is persistent and velutinous. These include *H. barclayana* (Mexico to northern Colombia and adjacent

Venezuela), H. ternifolia (Panama, Colombia, north-western Venezuela), H. trianae (Colombia; elevated from varietal rank), and a novelty, H. silvicola C.E.Anderson (Brazil). In three species the abaxial vesture is composed of all or in part of T-shaped hairs, i.e., mixed with sessile or Y-shaped hairs, which thins as the leaves mature: H. mcvaughii C.E.Anderson (Mexico; here newly described), H. hookeriana (northern Venezuela, Trinidad and Tobago), and H. venezuelana C.E.Anderson (western Venezuela; another novelty). In another three species any abaxial pubescence consists of only sessile to subsessile hairs. In H. reclinata (Mexico to Colombia) the abaxial vesture is usually sparse already in expanding leaves; the mature leaves are mostly glabrescent to glabrous. In H. transiens (Colombia, northern Venezuela) the hairs on the abaxial surface are persistent but so small that the leaf seems glabrous to the unaided eye. Added to these is *H. sanctae-marthae* C.V.Morton (north-western Colombia) in which the laminas are abaxially densely silvery sericeous at the time of flowering and fruiting; however, this distinctive vesture thins after the reproductive phase, and sterile specimens with older leaves have been mistaken for H. reclinata. These ten species may be separated with the following key.

- Laminas abaxially evenly velutinous, the hairs all Y- and Vshaped or with some T-shaped hairs intermixed 2
- 2. Laminas adaxially velutinous, eventually glabrescent; leaves ternate or sometimes opposite; inflorescences ternate cymes to variously branched. Panama (Darién), Colombia, Venezuela (Mérida) 7. H. ternifolia
- Laminas adaxially sericeous when young (or also with some Y- and T-shaped hairs in *H. barclayana*), soon glabrous; leaves opposite; inflorescences ternate cymes
- Laminas bullate, petioles 11–23 mm long, bearing stipules at middle to distal 1/4; inflorescences 1–2 per leaf axil, umbels 4–6-flowered. — Colombia (Cundinamarca, Norte de Santander, Tolima) 9. H. trianae
- 3. Laminas plane, petioles 5–15.5 mm long, bearing stipules in basal 1/3–1/4 (occasionally at middle in *H. barclayana*); inflorescence 1 per leaf axil, umbels 4-flowered 4
- 4. Styles pubescent in basal 1/4–1/2; posterior petal c. 4 mm long and wide, margin glandular-digitate-fimbriate; hairs of abaxial vesture V- or Y-shaped, stalk to 0.05 mm long, arms 0.1–0.2 mm long, T-shaped hairs absent. Brazil (Maranhão, Pará)............................... 6. *H. silvicola*
- 5. Mature laminas abaxially appearing glabrous to the naked eye, but evenly covered with minute appressed hairs 0.1–0.3(–0.5) mm long; inflorescences biternate, all peduncles sessile, sometimes with an additional peduncle inserted below one or both lateral axes (Fig. 8d). Northern Colombia to northern Venezuela 8. *H. transiens*
- 5. Mature laminas abaxially densely sericeous at time of flowering and fruiting, or glabrous, or with scattered sessile, subsessile, or stalked hairs, hairs/trabecula (0.3–)0.5–2.2 mm long; inflorescences ternate cymes (or also some biternate in *H. hookeriana*, *H. venezuelana*), central peduncle sessile, lateral peduncles sessile or subtended by a rudimentary axis, without additional peduncles 6

- 6. Laminas on fertile branches abaxially densely silvery sericeous, the epidermis hidden, the vesture thinning with age, eventually glabrescent but usually some of the vesture retained near the costa and secondary veins; stipules at base of petiole. Colombia (Atlántico, Magdalena) 5. H. sanctae-marthae
- 7. Young laminas adaxially with T-shaped hairs, soon glabrous, abaxially tomentose; mature laminas abaxially with abundant T-shaped hairs, not bullate. Mexico (Colima, Guerrero, western Jalisco, Nayarit, southern Sinaloa)

- 9. Inflorescence 1 per leaf axil (rarely 2), a ternate cyme with all umbels 4-flowered; base of lamina truncate in smaller leaves to cordate and auriculate in larger ones; petiole with a pair of glands at apex or just below it (rarely glands absent), bearing stipules at the middle to basal 1/4; mature laminas abaxially with scattered sessile to subsessile hairs to glabrous, T-shaped hairs absent. Southern Mexico to north-eastern Colombia 4. H. reclinata
- 9. Inflorescences 1–2 per leaf axil, a ternate cyme with the lateral umbels (5–)6-flowered, central umbel 4-flowered, occasionally some cymes biternate and all umbels 4-flowered; base of lamina cuneate to briefly truncate in largest leaves; petiole with a pair of glands at apex or up to 1.5–2 mm below apex, bearing stipules at the middle to distal 1/3; mature laminas abaxially with a mixture of scattered sessile, subsessile, and T-shaped hairs to glabrous. Venezuela (Aragua, Barinas, Lara, Yaracuy) 10. *H. venezuelana*

TAXONOMIC TREATMENT

1. Hiraea barclayana Benth. — Fig. 1; Map 1-3

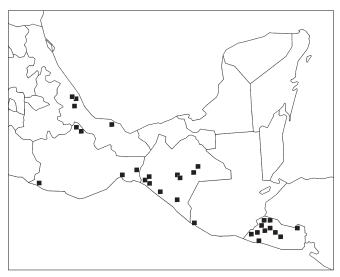
Hiraea barclayana Benth. (1844) 75. — Mascagnia barclayana (Benth.) Nied. (1908) 29. — Type: Barclay 1127 (holo K-hb. Benth.; iso BM, K-hb. Hook., MO), 'Libertad in Columbia' [El Salvador, La Libertad, La Libertad], Apr. 1837 (Belcher 1843).

Tetrapterys panamensis Seem. (1853) 92. — Hiraea panamensis (Seem.) Griseb. (1858) 100. — Type: Seemann 1215 (holo BM; iso K), Panama, Veraguas, near Santiago de Veraguas, 1849.

Hiraea velutina Nied. (1906) 6. — Type: Galeotti s.n. (lecto, here designated MICH; isolecto BR), Mexico, Oaxaca, Pinotepa [Nacional], 1839 (McVaugh 1978).

Woody vine, shrub or twining shrub, or small tree to 4 m; stems densely velutinous when young, becoming glabrous. *Leaves* opposite. Laminas of the larger leaves 6–18 by 3–10 cm, elliptical to obovate, apex mucronate or emarginate-mucronate, base truncate in smaller leaves to cordate or auriculate in larger ones, adaxially densely and loosely covered with straight to wavy ses-

sile to subsessile hairs, often intermixed with an understory of V- and Y-shaped hairs, soon glabrescent to glabrous, abaxially velutinous, the hairs mostly Y-shaped but also V-shaped, with a few T-shaped hairs intermixed, stalk to 0.2 mm long, arms of Y- and V-shaped hairs 0.1-0.5 mm long, often uneven, trabecula of T-shaped hairs 0.5-1.4 mm long, mostly straight; margin without glands or with scattered glands 0.2-0.3 mm diam in the distal 1.3 or only near apex; adaxially costa slightly impressed and secondary veins not or very slightly impressed, abaxially costa and secondary veins prominent. Petioles 5-11 by 1.3-2 mm, velutinous, with a pair of glands at apex, each gland 0.5-1.5 mm long. Stipules 2.3-4 mm long, borne in basal 1/3-1/4 of petiole or occasionally at middle. Inflorescences solitary axillary ternate cymes of 4-flowered umbels; umbel without a gland in the centre; inflorescence axis 0-2.5 mm long, bracts 1.2–2.5 mm long and wide; lateral axes 0–3 mm long, subtended by a pair of bracts 1.5-2.5 mm long and wide; peduncles (0.5–)1–8(–11) mm long; bracts and bracteoles subtending pedicels 1.2-2 mm long and wide; pedicels (7-)10-20(-26) by 0.4-0.5 mm, densely covered with sessile to T-shaped hairs (stalk to 0.1 mm); axes and abaxial surface of bracts and bracteoles densely sericeous. On leafless branches inflorescences usually crowded and condensed, sessile to subsessile, pedicels 7-10 mm long. Sepals 2-2.5 by 1.5-2 mm, triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands 1.8-2 mm long, or all sepals eglandular. Petals yellow, glabrous; lateral petals with the claw 2.5-3 mm long, limb of anterior-lateral petals 6-7.5 mm long and wide, of posterior-lateral petals 6.5-8 mm long and wide, all orbicular, margin irregularly and finely denticulate to erose or sometimes subentire but with a few teeth, longest teeth to 0.2(-0.4) mm long; posterior petal with the claw 3-3.5 mm long and thicker than that of lateral petals, limb 5.5-6.5 mm long and wide, orbicular, margin of the distal 1/3-1/2 dentate-fimbriate to lacerate, the proximal 1/2-2/3 erose to subentire, fimbriae 0.2-1 mm long, longest at apex. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament 3.5-4.5 mm long, anther 1.1-1.3 mm long; stamens opposite anterior-lateral petals: filaments 3-3.3 mm long, anthers 0.6–1.1 mm long; stamens opposite anteriorlateral sepals: filaments 3.3-4 mm long, anthers 1-1.1 mm long; stamens opposite posterior-lateral petals: filaments 2.5–3 mm long, anthers 0.6-1 mm long; stamens opposite posteriorlateral sepals: filaments 3.2-4 mm long, anthers 0.8-1 mm long; stamen opposite posterior petal: filament 2-2.7 mm long, anther 0.5-0.8 mm long. Styles incurved, glabrous; anterior



Map 1 Distribution of *Hiraea barclayana* Benth. in Mexico, Guatemala and El Salvador.

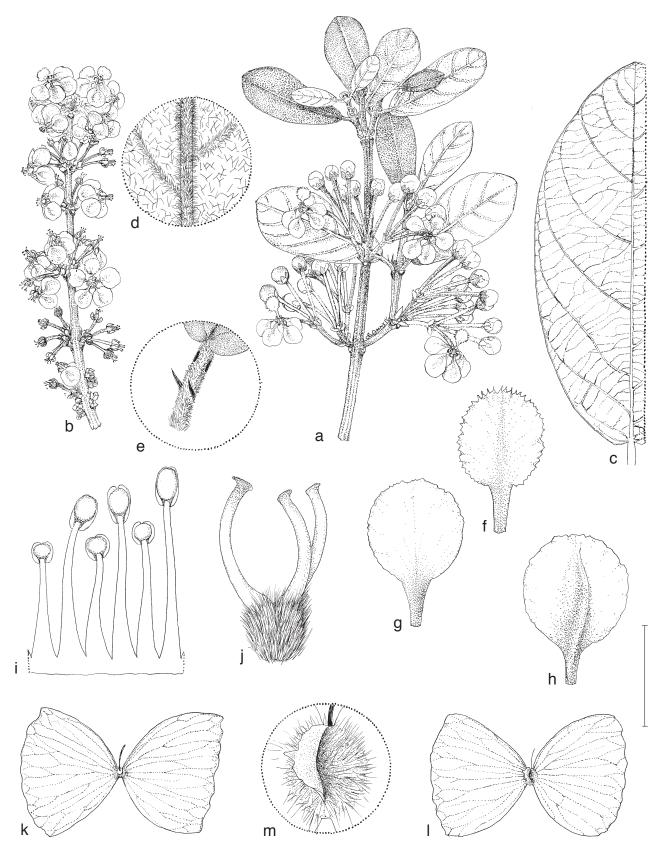
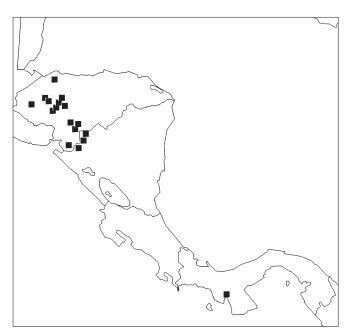


Fig. 1 Hiraea barclayana Benth. a. Flowering branch; b. condensed inflorescences on leafless branch; c. large leaf, abaxial view; d. detail showing abaxial vesture of lamina; e. base of lamina, adaxial view, and petiole with a pair of glands and a pair of stipules; f. posterior petal; g. posterior-lateral petal; h. anterior-lateral petal; i. portion of androecium, first stamen at left opposite posterior petal; j. gynoecium, anterior style at left; k. samara, adaxial view; l. samara, abaxial view; m. detail of samara showing dorsal winglet (from: a, f–j. Edwards 606, F; b. Renderos 139, MO; c–e. Molina 941, GH; k–m. Villacorta 10859, MO). — Scale bar: a–c = 4 cm; d, m = 4 mm; e = 1.3 cm; f–h = 6.7 mm; i–j = 2.7 mm; k–l = 2 cm. — Drawn by Karin Douthit.



Map 2 Distribution of *Hiraea barclayana* Benth. in Honduras, Nicaragua and Panama.

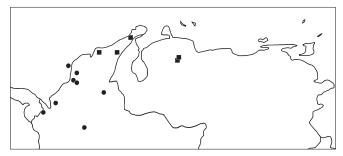
style 3.3-4.2 by 0.4-0.5 mm, apex extended into a spur (0.05-)0.2-0.3 mm long; posterior styles 3.3-4.2 by 0.3-0.5 mm, apex extended into a spur (0.02-)0.1-0.2 mm long or sometimes without a spur. Ovary 1.3-1.5 mm long, densely villous. *Samara* butterfly-shaped; lateral wings (1.5-)2.5-3.3 by 1.5-2.3 cm; dorsal wing or crest 0.2-4.5 mm high, subentire or erose or coarsely dentate; nut subspherical, 3.5-4.5 mm diam, areole 1.5-2 mm diam. Embryo subspherical to spherical, 3.6-4.2 mm diam.

Distribution — Southern Mexico (Veracruz, Oaxaca, Chiapas) to northern Nicaragua (Chinandega, Madriz, Nuevo Segovia), one collection from Veraguas, Panama (type of *Tetrapterys panamensis*), northern Colombia (La Guajira, Magdalena), north-western Venezuela (Lara, Zulia).

Habitat & Phenology — In thickets and shrublands, tropical deciduous and subdeciduous forest, seasonal evergreen forest, pine-oak forest; sea level to 1050(–1300) m; collected in flower and fruit from February to June (one flowering collection from December).

Notes — The spreading/erect vesture on the abaxial surface of the lamina of H. barclayana immediately separates it from the partly sympatric *H. reclinata*, in which the laminas are usually glabrous or have appressed hairs. The new leaves of H. barclayana are densely pubescent on both surfaces, but as the lamina expands, the adaxial surface is soon glabrescent to glabrous. The abaxial vesture persists and is composed largely of V- and Y-shaped hairs (the arms commonly unequal) as well as some T-shaped hairs. The aspect of the vesture changes with the growth of the leaf. The abaxial surface of youngest laminas has the arms of the closely spaced hairs intertwining. As the leaf expands the vesture thins and becomes evenly velutinous, and gradually sparser in older leaves. Only in the oldest leaves is the laminar vesture eventually sloughed off; such leaves superficially appear glabrous but some of the distinctive hairs remain, especially near and on the costa and secondary veins, particularly at and near the base of the lamina.

The ranges of *H. reclinata* and *H. barclayana* are largely sympatric, but *H. barclayana* is much less frequently collected. Surprisingly, it is not known from Costa Rica, a country that saw years of intensive collecting in anticipation of the Manual de Plantas



Map 3 Distribution of *Hiraea barclayana* Benth. (■) in Colombia and Venezuela and *H. reclinata* Jacq. (●) in Colombia.

de Costa Rica (*Malpighiaceae* by W.R. Anderson 2007b). The type of *Tetrapterys panamensis* appears to be the only record of *H. barclayana* in Panama. Triana & Planchon (1862) cite the name under *H. barclayana*, as does Hemsley (1879), who had access to this type (as well as that of *H. barclayana*). Niedenzu (1928) saw neither type and in his treatment of *Tetrapterys* lists Seemann's name under "species incertae mihi invisae" as well as, with question mark, in the synonymy for *H. obovata* [= *H. reclinata*]. Cuatrecasas & Croat (1981) in the Flora of Panama cite *Tetrapterys panamensis* and the combination in *Hiraea* as synonyms of *H. reclinata*.

In the protologue the type of *H. barclayana* is said to have come from 'Libertad in Columbia' (Bentham 1844), which led Triana & Planchon (1862) to include H. barclayana in their Prodromus of the Colombian flora. Hemsley (1879) states 'San Salvador, Libertad', which is the locality given on the BM isotype. The labels of the duplicates at Kew say only 'Libertad', but the labels with the isotypes at MO note 'Mexico' as the country of origin. The late William R. Anderson left unpublished notes concerning the type locality and confirmed that it is the port of La Libertad in El Salvador. Captain Belcher (1843; 1: 32-36) in his "Narrative..." of the voyage describes arriving from Nicaragua at "Libertad" in April 1837 and going overland to San Salvador before returning to the port and proceeding to Mexico. Barclay's specimens are branches bearing fruits and mature leaves. The abaxial vesture was described by Bentham as sparse, which likely led some readers to equate H. barclayana with H. reclinata (and synonyms). One of the two isotypes at MO is a mixture of H. barclayana and a legume.

Niedenzu (1906) based *H. velutina* on three syntypes: *Galeotti s.n.* from Oaxaca, Mexico, *Seler & Seler 1800* from Chiapas, Mexico, and *Lehmann 4636* from Antioquia, Colombia. The *Galeotti* duplicate at MICH is here designated as lectotype of *H. velutina*, and the name thus becomes a synonym for *H. barclayana*. Both the lectotype and isolectotype are annotated by Niedenzu. *Lehmann 4636* belongs to *H. ternifolia*. I did not find any duplicates of *Seler & Seler 1800*; Niedenzu's syntype at B was destroyed. Because it was obtained in Chiapas, it is most likely referable to *H. barclayana*. Until William R. Anderson realized the correct application of the names *H. barclayana* and *H. reclinata* during his floristic work on *Malpighiaceae*, starting in the 1970s, collections of *H. barclayana* were commonly determined as *H. velutina*.

2. Hiraea hookeriana A.Juss. — Fig. 2; Map 4

Hiraea hookeriana A.Juss. (1840) 258. — Type: B. de Sch. s.n. [Baron von Schack] (holo K), Trinidad and Tobago, Trinidad.

Woody vine, scandent shrub to 6 m, or small tree 3-4(-8) m; stems densely sericeous when young, becoming glabrous. *Leaves* opposite. Laminas of the larger leaves 5-15 by 2-7.5

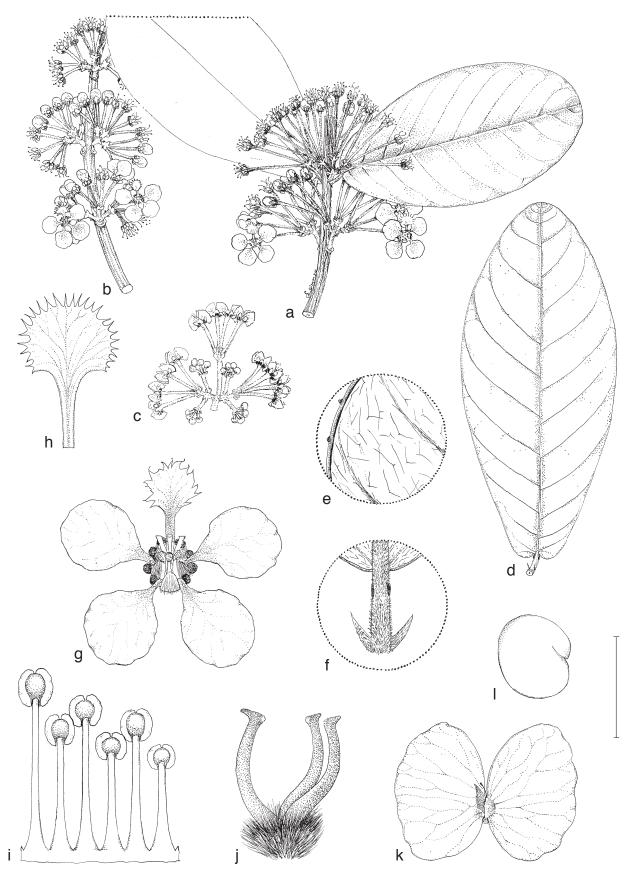
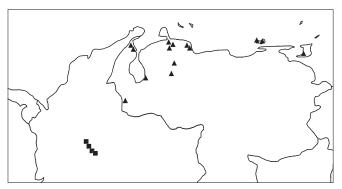


Fig. 2 Hiraea hookeriana A.Juss. a. Flowering branch; b. condensed inflorescences on leafless branch; c. inflorescence with tertiary branching (biternate cyme); d. large leaf; e. detail showing abaxial vesture of lamina and two marginal glands; f. base of lamina, abaxial view, and petiole with a pair of glands and a pair of stipules; g. flower with lacerate posterior petal; h. posterior petal with dentate-fimbriate margin; i. portion of androecium, first stamen at right opposite posterior petal; j. gynoecium, anterior style at left; k. samara, abaxial view; l. embryo (from: a, d-f, h-j. Sugden 1212, K; b. Britton 2916, US; c. Bunting 12895, NY; g. Steyermark & González 113617, MO; k. Sugden 1234, MO; l. Medina 825, VEN). — Scale bar: a-d = 4 cm; e, l = 4 mm; f = 8 mm; g = 1 cm; h-j = 2.7 mm; k = 2.7 cm. — Drawn by Karin Douthit.

cm, narrowly elliptical to narrowly oblanceolate or narrowly oblong to elliptical or obovate, apex mucronate or emarginatemucronate, base truncate in smaller leaves to slightly cordate in larger ones, mature laminas coriaceous and bullate, adaxially with sessile to subsessile hairs when young, soon glabrescent to glabrous, abaxially with subsessile to T-shaped hairs and sometimes also with a few Y-shaped hairs when young, soon glabrescent but often hairs retained on the costa and secondary veins especially toward the base, the oldest laminas eventually glabrous, hairs with a stalk (0.05–)0.1–0.3 mm long, trabecula of T-shaped hairs 0.5-2.2 mm long, straight or wavy, arms of Y-shaped hairs 0.2–0.6 mm long, uneven; margin eglandular or with scattered glands 0.2-0.4(-0.5) mm diam in distal 1/4-1/2or only near apex; costa and secondary veins impressed adaxially and prominent abaxially. Petioles (2-)3-9 by 1.5-2.5 mm, densely sericeous, with a pair of glands at apex or in the distal 1/3 (in very short petioles sometimes at about the middle), each gland 0.5-1.7 mm long. Stipules 2-4.5(-5) mm long, borne at or slightly above base or sometimes to basal 1/3 (rarely near the middle) of petiole. Inflorescences solitary axillary ternate cymes of 4-flowered umbels or sometimes biternate; umbel without a gland in the centre; inflorescence axis 0-6(-8) mm long, bracts 2-2.5 by 1.5-2 mm; lateral peduncles borne on axes 0-2.5 mm long, subtended by bracts 1-1.5 mm long and wide; peduncles (1.5-)3-11.5(-15.5) mm long, the lateral usually longer than the central one; bracts and bracteoles subtending pedicels 1-2 mm long and wide; pedicels 8-24 by c. 0.5 mm, densely covered with sessile to T-shaped hairs (stalk to 0.1 mm); axes and abaxial surface of bracts and bracteoles densely sericeous. On leafless branches inflorescences usually crowded and condensed, sessile to subsessile, pedicels 8-12 mm long. Sepals 1.8-2.5 by 1.5-2.5 mm, triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands 1–1.3(–2) mm long, or all eglandular. Petals yellow, glabrous; lateral petals with the claw 1.5-2.5 mm long, limb 6.5-7.5(-8) mm long and wide, orbicular, margin subentire to irregularly minutely denticulate, teeth to 0.1 mm long; posterior petal with the claw 3-4 mm long and thicker than that of lateral petals, limb 5-6 mm long and wide, orbicular, margin variably lacerate-dentate-fimbriate, teeth/fimbriae to 0.4(-0.7) mm long, those at apex minutely glandular or eglandular. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament 3-4 mm long, anther 1–1.4 mm long; stamens opposite anterior-lateral petals: filaments 2-3 mm long, anthers 0.8-1 mm long; stamens opposite anterior-lateral sepals: filaments 2.7-3.5 mm long, anthers 0.9-1 mm long; stamens opposite posterior-lateral petals: filaments 2-2.5 mm long, anthers 0.6-0.8 mm long; stamens opposite posterior-lateral sepals: filaments 2.5-3.2 mm long, anthers 0.9-1 mm long; stamen opposite posterior petal: filament 1.8-2.3 mm long, anther 0.5-0.6 mm long. Styles incurved, glabrous; anterior style 2.5-4 by 0.4-0.5 mm,



Map 4 Distribution of *Hiraea hookeriana* A.Juss. (▲) and *H. trianae* (■).

apex extended into a spur 0.2–0.3 mm long; posterior styles 2.5–3.8 by 0.3–0.4 mm, apex extended into a spur 0.1–0.2 mm long. Ovary 1–1.5 mm long, densely villous. *Samara* butterfly-shaped; lateral wings 2–3 by 1.5–2 cm; dorsal wing 2–3.5 mm long, 1–3 mm high, subentire or coarsely dentate; nut subspherical, 3–3.5 mm diam, areole c. 1.4 by 1.5–2 mm. Embryo spherical, 3–3.5 mm diam.

Distribution — Northern Venezuela (Falcón, Nueva Esparta, Portuguesa, Táchira, Yaracuy, Zulia), Trinidad.

Habitat & Phenology — In wet evergreen and semi-evergreen riverine forest, thickets, and matorral; sea level to 1300 m; collected in flower in February, April through June, August, and October (in bud in December and January), in fruit from April to June, August, October, and November.

Notes — Traditionally *H. hookeriana* was equated with *H. reclinata* in the literature (e.g., Grisebach 1860, Niedenzu 1906, 1928, Cuatrecasas 1958) and in the herbarium. It differs in its distinctive coriaceous bullate laminas, in which the costa and secondary veins are deeply impressed adaxially. The abaxial vesture is composed mostly of T-shaped hairs mixed with some Y-shaped and subsessile hairs, which are gradually abraded. The older laminas become glabrescent and eventually glabrous, but commonly some of the characteristic hairs are retained on and along the costa and secondary veins. *Hiraea hookeriana* differs from the sympatric *H. venezuelana* in its bullate leaves, stipules placed at or near the base of the petiole, and in its inflorescences bearing only 4-flowered umbels.

The shape of the posterior petal of *H. hookeriana* varies from lacerate to having the margin drawn out into fimbriae, these eglandular or minutely gland-tipped. Fig, 2g, h shows the extremes, but in many specimens the margin is intermediate, with the apex more irregularly divided than the lateral margins. The lateral petals are usually subentire but may be minutely denticulate.

3. Hiraea mcvaughii C.E.Anderson, sp. nov. — Fig. 3; Map 5

Differt a *H. reclinata* laminae foliorum adaxaliter et abaxaliter pilos T-formes ferens; petalo postico margine apice dentato vel lacero-dentato et basi denticulato. — Type: *McVaugh 15228* (holo MICH; iso MEXU, US), Mexico, Nayarit, Mirador de Aguila, c. 14 mi N of Tepic, 600 m, 8 July 1957.

Etymology. The specific epithet honours Rogers McVaugh (1909–2009), foremost student of the flora of western Mexico, who collected the type.

Woody vine, shrub or twining shrub, or small tree to 3 m; stems sericeous when young, becoming glabrous. Leaves opposite. Laminas of the larger leaves 5-17.5 by 3-10 cm, elliptical to obovate, apex apiculate-mucronate, mucronate, or emarginate-mucronate, base truncate in smaller leaves to cordate or auriculate in larger ones, adaxially densely covered with subsessile to T-shaped hairs (stalk to 0.1 mm) when young, soon glabrous, abaxially tomentose when young, the vesture soon thinning, when mature with T-shaped hairs, stalks (0.05–)0.1–0.2 mm long, trabecula 1–2 mm long, straight to wavy; margin with a few scattered glands c. 0.2 mm diam near apex or glands absent; costa slightly impressed adaxially and prominent abaxially, secondary veins not impressed adaxially and prominent abaxially. Petioles 5-11 by 1.2-2 mm, densely sericeous, with a pair of glands at apex, each gland 0.5–1 mm long. Stipules 1.5-4.5 mm long, borne near the base to the middle of the petiole. *Inflorescences* solitary axillary ternate cymes of 4-flowered umbels; umbel without a gland in the centre; inflorescence axis 0-3 mm long, bracts 1.5-2.5 mm long and wide; lateral peduncles borne on axes 0-4 mm long, subtended by bracts 1.5–2 mm long and wide; peduncles 1–12 mm long; bracts and bracteoles subtending pedicels 1.3–2 mm long and wide; pedicels (9-)12-26 by 0.4-0.5 mm, densely

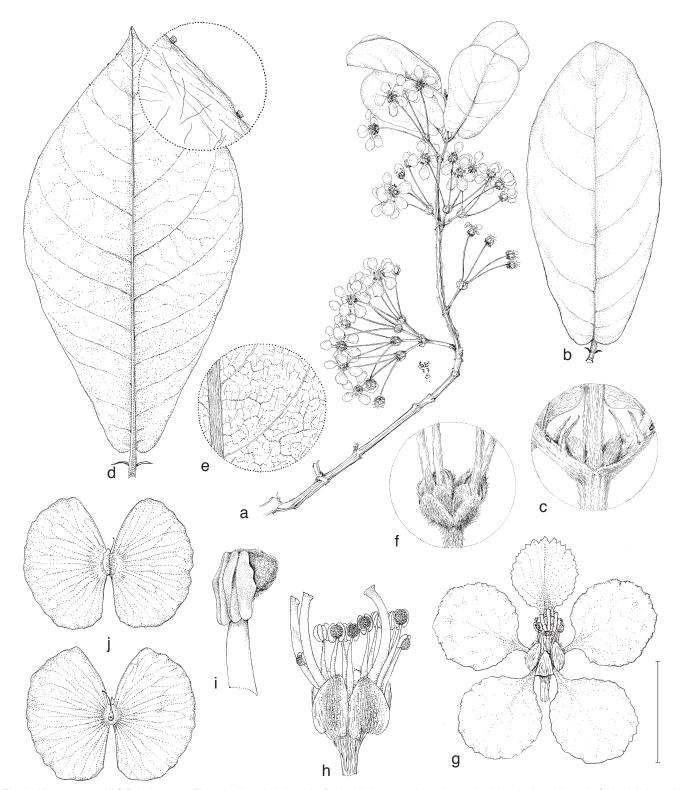
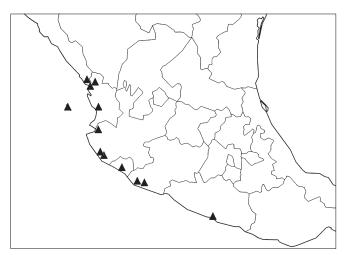


Fig. 3 *Hiraea mcvaughii* C.E.Anderson. a. Flowering branch; b. large leaf, adaxial view; c. node to show epipetiolar stipules; d. large leaf, abaxial view, with detail showing vesture and marginal glands; e. enlargement of abaxial leaf surface to show reticulate venation; f. base of umbel; g. flower, posterior petal uppermost; h. flower with petals removed, anterior style at right; i. anther and portion of filament; j. samaras, abaxial view (above) and adaxial view (below) (from: a-c, f-i. *McVaugh 15228*, MICH; d-e, j. *McVaugh 15257*, MICH). — Scale bar: a-b = 4 cm; c, g = 8 mm; d = 4 cm (4 mm); e = 1.6 cm; f = 5.7 mm; h = 4 mm; i = 1.3 mm; j = 2.7 cm. — Drawn by Karin Douthit.

covered with sessile to T-shaped hairs (stalk to 0.1 mm); axes, abaxial surface of bracts and bracteoles densely sericeous. Sepals 2-2.5(-2.8) by 2-2.5 mm, triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands 1-2 mm long, or all sepals eglandular. Petals yellow, glabrous; lateral petals with the claw 2.5-3 mm long, limb of anterior-lateral petals 8-8.5 mm long and wide, orbicular, margin subentire to minutely denticulate, teeth to 0.1 mm long, or with a few larger teeth (to 0.3 mm) at apex, limb

of posterior-lateral petals 7–8 mm long and wide, orbicular, margin irregularly denticulate or only at apex and otherwise subentire, teeth to 0.2(–0.4) mm long; posterior petal with the claw 3–4 mm long and thicker than that of lateral petals, limb 7–7.5 mm long and wide, orbicular, margin irregularly dentate to dentate-lacerate, teeth to 0.5–1.2 mm long, longest at apex. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament 3.8–4.5 mm long, anther 1.1–1.3 mm long; stamens opposite anterior-lateral petals: filaments 3.5–4



Map 5 Distribution of Hiraea mcvaughii C.E.Anderson.

mm long, anthers 0.9–1 mm long; stamens opposite anterior-lateral sepals: filaments 3.8–4.5 mm long, anthers 1–1.2 mm long; stamens opposite posterior-lateral petals: filaments 2.5–3 mm long, anthers 0.8–1 mm long; stamens opposite posterior-lateral sepals: filaments 3.5–4 mm long, anthers 0.9–1.1 mm long; stamen opposite posterior petal: filament 2–2.5(–3) mm long, anther 0.6–0.8 mm long. Styles incurved, glabrous, 4–4.5 by 0.4–0.5 mm; apex of anterior style extended into a spur 0.1–0.3 mm long; apex of posterior styles extended into a spur 0.05–0.1 mm long. Ovary 1–1.5 mm long, densely villous. *Samara* butterfly-shaped; lateral wings 3.2–3.3 by 2–2.3 cm; dorsal wing a crest c. 1.5 mm high, coarsely dentate; nut subspherical, 4–5 mm diam, areole 2–2.3 mm diam. Mature seed not seen.

Distribution — Coastal regions of western Mexico (Colima, Guerrero, Jalisco, Michoacán, Nayarit and adjacent Sinaloa). Habitat & Phenology — In tropical deciduous and subdeciduous forest, and roadside thickets; sea level to 600 m; collected in flower in February, May to August (one collection from December), in fruit in June to August.

Representative specimens. Mexico, Colima, Mpio. Ixtlahuacán, brecha Ixtlahuacán-La Presa. 1 km NE de Ixtlahuacán. Santana & Cervantes 286 (IBUG, MICH). Guerrero, sea cliffs west of Acapulco, Clark 7178 (NY, US); Puerto Marqués, Acapulco, Sept. 1952, Ramírez C. s.n. (MEXU). Jalisco, Mpio. La Huerta, Estación de Biología de Chamela, 2 km SE sobre la carretera Puerto Vallarta-Barra de Navidad, Ayala 667 (CAS, MICH); Estación de Biología de Chamela, Bullock 1352 (MEXU, MICH, MO), 1585 (MICH, TEX); Mpio. La Huerta, km 56, carr. B. Navidad Pto. Vallarta, Bullock 1712 (CAS, MICH); Mpio. La Huerta, Los Angeles de Tenacatita, González & Gúzman 939 (MEXU); Mpio. La Huerta, Estación de Biología de Chamela, Magallanes 713 (MEXU, MICH), 2977 (MEXU, MICH, TEX). Michoacán, Mexican Hwy 200 between Playa Azul and Tecomán, Colima, 6 km W of Maruhuata, Miller & Téllez V. 3089 (MICH); trail from Atizupa to San Pedro N of Hwy 200, Murray & Johnson 1454 (MICH). Nayarit, Mpio. Tepic, Aguamilpa, 4 km antes La Presa, N21°40' W104°34', Flores F. 1859 (MICH); Tres Marías Islands, María Magdalena, 28 June 1963, Grant s.n. (DS); W of Ingenio, Gregg 1039 (MO); Mirador de Aguila, c. 14 mi N of Tepic, McVaugh 15257 (MICH); Acaponeta, Rose 1507 (GH, NY, US). Sinaloa, Rosario, 26-29 July 1897, Rose s.n. (US).

Note — *Hiraea mcvaughii* is a species of the coastal regions of western Mexico and not sympatric with *H. barclayana*, with which it was commonly placed, often as '*H. velutina*'. It is readily separated from *H. barclayana* and *H. reclinata* by the persistent abaxial laminar pubescence composed of T-shaped hairs. The dense abaxial vesture of the youngest leaves thins quickly, and mature laminas bear T-shaped hairs with straight to wavy trabecula. The hairs are never appressed, as in *H. reclinata*, nor predominantly Y-shaped, as in *H. barclayana*.

4. Hiraea reclinata Jacq. — Fig. 4; Map 3, 6, 7

Hiraea reclinata Jacq. (1760) 4, 21, non Hiraea reclinata Blanco (1837). — Triopterys reclinata (Jacq). Cav. (1790) 431. — Malpighia reclinata (Jacq). Colla (1824) 85. — Type: H.H. Smith 1508 (neo, here designated MICH; isoneo MO, NY, UC, US), Colombia, Magdalena, near Masinga, 250 ft, 22 Mar. [1898–1899].

Malpighia obovata Kunth (1822 '1821') 146. — Hiraea kunthiana A.Juss. (1840) 258, nom. superfl. — Hiraea obovata (Kunth) Nied. (1906) 7, non Hiraea obovata Huber (1902). — Hiraea obovata (Kunth) Nied. var. latifolia Nied. (1906) 7, nom. superfl. — Hiraea obovata (Kunth) Nied. var. latifolia Nied. forma eglandulosa Nied. (1906) 7, nom. superfl. — Type: Humboldt & Bonpland s.n. (holo P-HBK, image), Colombia, Antioquia, [Puerto] Nares. Hiraea obovata (Kunth) Nied. var. latifolia forma glandulifera Nied. (1906) 7. — Type: Pittier 9882 [J.D. Smith 6975] (lecto, here designated US; isolecto G), Costa Rica, Puntarenas, sur les bords du Río Coto, Mar./Apr. 1896. Hiraea obovata (Kunth) Nied. var. angustifolia Nied. (1906) 7. — Type: Tonduz 13955 (lecto, here designated US; isolecto K), Costa Rica, Guanacaste, dans les buissons à Nicoya, Jan. 1900.

Hiraea borealis Nied. (1906) 5. — Hiraea borealis Nied. var. eglandulosa Nied. (1906) 6, nom. superfl. — Type: Gaumer 66 (holo B†; lecto, here designated K), Honduras, Islas de la Bahía, 'Island of Ruatan' [Roatán], [1885]. Hiraea borealis Nied. var. glandulifera Nied. (1906) 6. — Type: Gaumer 67 (holo B†; lecto, here designated GH), Mexico, Quintana Roo, Cozumel Island, 20 Apr. 1885. [The duplicate at K has eglandular sepals.]

Hiraea purpusii Brandegee (1922) 184. — Type: Purpus 8731 (holo UC-214375; iso GH. MO, NY, UC, US), Mexico, Veracruz, Camerón, Apr. 1922.

Woody vine to 25 m or scandent shrub or treelet to 4(-7) m; stems densely sericeous when young, becoming glabrous. Leaves opposite. Laminas of the larger leaves 6-25.5 by 3-12 cm, narrowly to broadly elliptical or obovate, apex mucronate or emarginate-mucronate to apiculate (occasionally acuminate), base truncate in smaller leaves to cordate and auriculate in larger ones, adaxially densely loosely sericeous when very young, soon glabrescent to glabrous, abaxially sericeous, usually sparsely so, when young, and soon glabrescent to glabrous but often hairs retained on and along the costa and secondary veins, entirely glabrous in oldest laminas, hairs 0.3-1(-2) mm long, sessile or subsessile, straight or wavy; margin without glands or sometimes with a few scattered glands c. 0.2 mm diam in distal 1/3 or only near apex; costa and secondary veins slightly or not impressed adaxially, prominent abaxially. Petioles 4-18 by 1.5-2.5 mm, densely sericeous, with a pair of glands at apex, each gland 0.6-1.5(-1.8) mm long, or rarely glands absent. Stipules 2-4.6 mm long, borne at middle to basal 1/4 of petiole, in young leaves or on very short petioles sometimes nearer the base. Inflorescences solitary (rarely 2) axillary ternate cymes of 4-flowered umbels; umbel without a gland in the centre; inflorescence axis 0-3(-5) mm long, bracts 1.5-2.5mm long and wide; lateral peduncles borne on axes 0.5-2.5 mm long, subtended by bracts 1.2–2 mm long and wide; peduncles 0.5–8(–11) mm long; bracts and bracteoles subtending pedicels 1.2-1.5(-2) mm long and wide; pedicels (7-)9-29 by c. 0.3 mm, densely covered with sessile to T-shaped hairs (stalk to 0.05 mm); axes and abaxial surface of bracts and bracteoles densely sericeous. On leafless branches inflorescences usually crowded and condensed, sessile to subsessile, pedicels 7–10 mm long. Sepals 2-2.5 by 1.8-2 mm, triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands 1.5-2 mm long, or all sepals eglandular, or rarely all sepals glandular (or the anterior sepal with only one gland). Petals yellow, glabrous; lateral petals with the claw 2-2.5 mm long, limb 6-7(-8) mm long and wide, orbicular, margin of anterior-lateral petals subentire, margin of posterior-lateral petals subentire or minutely and irregularly denticulate, teeth to 0.1(-0.2) mm long; posterior petal with the claw (2.2–)2.5–3 mm long and thicker than that of lateral petals, limb 5.5-6 mm long and wide, orbicular, margin irregularly denticulate-fimbriate (sometimes coarsely), teeth/fimbriae to 0.5 mm long, longest at apex, diminishing toward base,

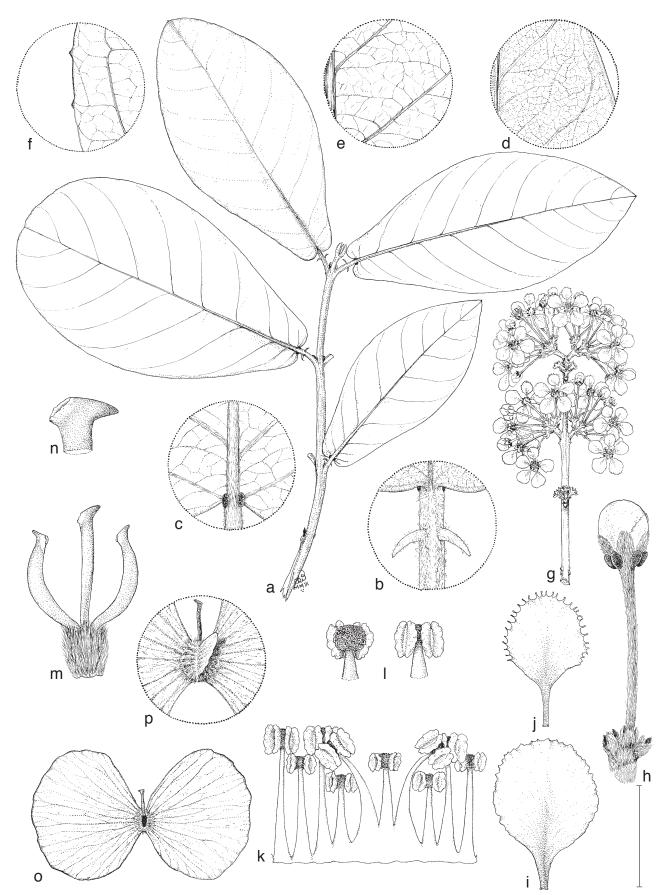
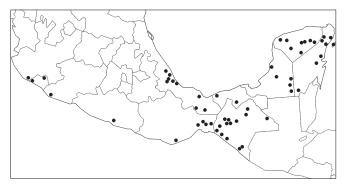


Fig. 4 *Hiraea reclinata* Jacq. a. Leafy branch; b. petiole with a pair of stipules, adaxial view; c. base of lamina and apex of petiole with glands, abaxial view; d. detail of lamina, adaxial view; g. leafless branch bearing inflorescences; h. flower bud; i. posterior-lateral petal; j. posterior petal; k. androecium, stamen fifth from right opposite posterior petal; l. anthers, abaxial view (left) and adaxial view (right); m. gynoecium, anterior style in centre; n. terminal portion of a style; o. samara, adaxial view; p. nut of samara bearing dorsal winglet (from: a-n. *H.H. Smith 1508* p.p. [collected in March], MICH; o, p. *H.H. Smith 1508* p.p. [collected in June], NY). — Scale bar: a, g = 4 cm; b-e, h, p = 8 mm; f = 4 mm; i, j = 2 cm; k, m = 2.7 mm; l = 2 mm; n = 1.3 mm; o = 1.6 cm. — Drawn by Karin Douthit.



Map 6 Distribution of Hiraea reclinata Jacq. in Mexico.

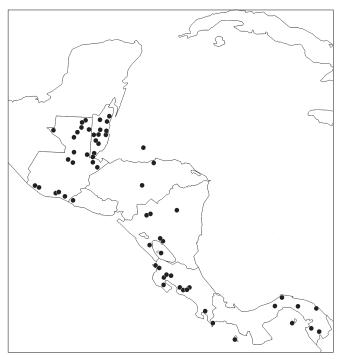
occasionally gland-tipped. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament 3.5-4.5 mm long, anther 1.1–1.3 mm long; stamens opposite anterior-lateral petals: filaments 3-3.5 mm long, anthers 0.5-0.7(-0.9) mm long; stamens opposite anterior-lateral sepals: filaments 3-3.7 mm long, anthers 0.6-1.3 mm long; stamens opposite posteriorlateral petals: filaments 2–2.8 mm long, anthers 0.5–0.8(–1) mm long; stamens opposite posterior-lateral sepals: filaments 3-4 mm long, anthers 0.7-1 mm long; stamen opposite posterior petal: filament 2–2.5 mm long, anther 0.5–0.7 mm long. Styles incurved, glabrous; anterior style 3.2-4.2 by 0.4-0.5 mm, apex extended into a spur (0.05-)0.2-0.3 mm long; posterior styles (3–)3.5–4.2 by 0.4–0.5 mm, apex extended into a spur (0.05–)0.1–0.2 mm long. Ovary 1.2–1.5 mm long, densely villous. Samara butterfly-shaped; lateral wings (1.5–)2.5–3.3 by 1.5–2.3 cm; dorsal wing or crest 0.2–4.5 mm high, subentire or erose or coarsely dentate; nut subspherical, 3.5-4.5 mm diam, areole 1.5-2 mm diam. Embryo subspherical to spherical, 3.6-4.2 mm diam.

 $\label{eq:Distribution} \textbf{--} \ \textbf{Western and southern Mexico}, \textbf{Central America}, \textbf{northern Colombia}.$

Habitat & Phenology — In wet and dry primary and secondary forest, often along rivers and streams, also in thickets and scrub; sea level to 860 (–1000) m; collected in flower and fruit mostly from January through June, a few flowering collections from September to November.

Notes — Hiraea reclinata is greatly variable throughout its diverse habitats and broad range, from southern Mexico to northern Colombia. Typical plants have leaves with short petioles and elliptical to obovate, glabrous laminas with a cordate to auriculate base and a mucronate apex. The petiole bears a pair of glands at or near the apex, but occasionally the glands are absent, even among some leaves of the same branch. The stipules are usually borne at the middle to basal 1/4 of the petiole. The laminas of emergent leaves bear straight to wavy hairs that are mostly sessile or subsessile and are usually soon shed, more gradually abaxially than adaxially and sometimes patchily, but hairs are often retained on and along the costa and the proximal secondary veins abaxially. Whereas the adaxial vesture is initially dense, usually even the youngest leaves are abaxially only sparsely pubescent, except for the major veins and along the margins. Occasionally, the vesture is more tardily shed, and mature laminas are thinly and/or patchily sericeous (the epidermis always visible) abaxially or rarely on both surfaces (e.g., J.D. Smith 2547, Escuintla, Guatemala; Matuda 2181, Chiapas, Mexico).

The inflorescence is a single ternate cyme of 4-flowered umbels, which is commonly subsessile, but may be borne on an axis to 5 mm long. The peduncles bearing the umbels also are mostly short but occasionally measure 10 mm or more.



Map 7 Distribution of Hiraea reclinata Jacq. in Central America.

Less variation is shown in the flowers, except in the ornamentation of the styles. In most flowers the styles bear a pronounced spur 0.2-0.3 mm long, that of the anterior is usually longer than those of the posterior styles; however, occasionally the spur is barely expressed and only c. 0.05 mm long.

Niedenzu (1906) followed Jussieu (1840, 1843) and Grisebach (1860), who applied the name *H. reclinata* to collections from Trinidad and Tobago that belong to *H. hookeriana*, a species with distinctive bullate leaves and abaxial vesture composed of mostly T-shaped hairs. In his monograph of the family, Niedenzu (1928) changed his interpretation by adding three collections from Colombia: *Schlim 524 (H. transiens)* and *H.H. Smith 1515*, 1516 (*H. reclinata*). He used the name *H. obovata* for collections from Central America now assigned to *H. reclinata* and erected *H. borealis* to accommodate two Gaumer collections, from Roatán Island (Islas de la Bahía, Honduras) and Cozumel Island (Quintana Roo, Mexico). *Hiraea borealis* was subsequently often applied to specimens of *H. reclinata* from Mexico.

A neotype is chosen here for *H. reclinata*, because no authentic material was found. Specimens of the neotype collection are all labelled as dating from March; the NY duplicate also carries the perforated collection tag with the years '1898–99'. An additional specimen at NY labelled *H.H. Smith 1508* is dated as 'May 30' and not part of the neotype gathering. See Allen (1904) and Ayers & Boufford (1988) for details of H.H. Smith's collecting activities in Colombia.

Niedenzu (1906) cited two syntypes for *H. obovata* var. *angustifolia*, *J.D. Smith* 2554 from Guatemala and *Tonduz* 13955 from Costa Rica. Because his variety is defined by leaf and calyx characters, the duplicate of *Tonduz* 13955 at US is here designated as lectotype. Niedenzu noted that the Guatemalan specimen he saw (now destroyed) lacked leaves.

5. Hiraea sanctae-marthae C.V.Morton — Fig. 5; Map 8

Hiraea sanctae-marthae C.V.Morton (1933) 87. — Type: Walker 1211 (holo US; iso MO, WIS), Colombia, Magdalena, Río Frío, Quebrada Rodríguez, Santa Marta, 15 Mar. 1925.

Woody vine to 8 m or shrub to 3 m; stems densely sericeous when young, becoming glabrous. *Leaves* opposite. Laminas

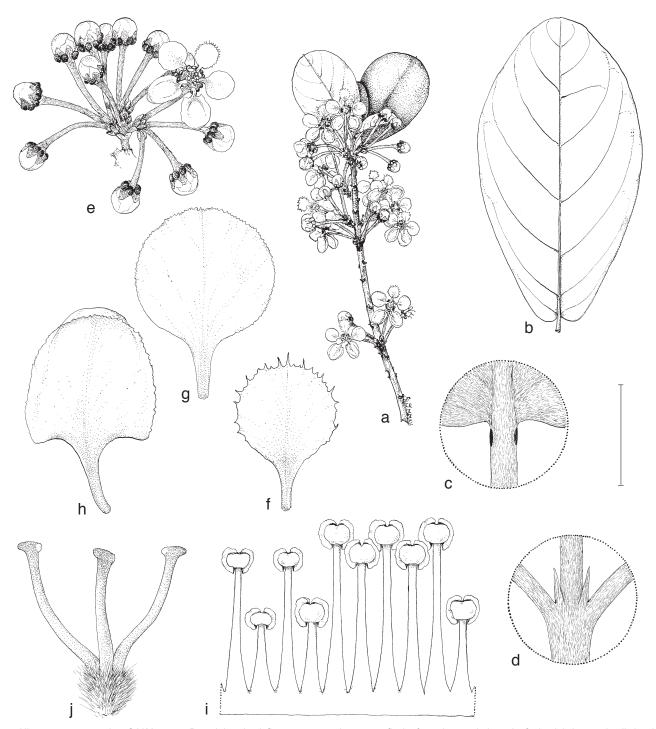
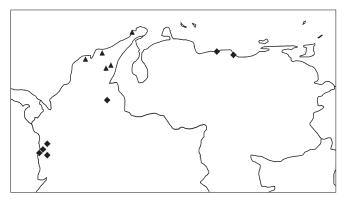


Fig. 5 Hiraea sanctae-marthae C.V.Morton a. Branch bearing inflorescences and at apex a flush of new leaves; b. large leaf, abaxial view; c. detail showing dense abaxial vesture of lamina and a pair of glands at apex of petiole; d. detail showing stipules borne at base of petioles; e. inflorescence; f. posterior petal; g. posterior-lateral petal; h. anterior-lateral petal; i. androecium, stamen second from left opposite posterior petal; j. gynoecium, anterior style in centre (from: a. Haught 3743, US; b-h. Smith 1514, GH; i-j. Walker 1211, US). — Scale bar: a-b = 4 cm; c-d = 8 mm; e = 1 cm; f-h = 4 mm; i-j = 2.7 mm. — Drawn by Karin Douthit.

of the larger leaves 6.5–20 by 3–8.5 cm, elliptical to obovate, apex mucronate, base slightly cordate, adaxially sericeous when very young, soon glabrous, abaxially densely silvery sericeous and the epidermis hidden, hairs 0.3–1.2 mm long, sessile or subsessile, straight or wavy, with age the vesture thinning and older laminas becoming thinly sericeous and eventually glabrate; margin without glands or sometimes with a few scattered glands c. 0.2 mm diam near apex; costa and secondary veins not or slightly impressed adaxially, prominent abaxially. Petioles 3–8 by c. 2 mm, densely sericeous, with a pair of glands at apex, each gland 0.7–1.2 mm long. Stipules 1.5–3 mm long, borne at base of petiole. *Inflorescences* solitary axillary ternate cymes of 4-flowered umbels; umbel without a gland in the cen-

tre; inflorescence axis 0–1.5 mm long, bracts 0.8–1.7 and wide; central peduncle 1–6 mm long; lateral axis 0–0.5 mm long, subtended by bracts 1.2–2 mm long and wide; lateral peduncles 0.5–7.5 mm long; bracts and bracteoles subtending pedicels 1–2 mm and wide, triangular; pedicels 11–25 by c. 0.3 mm; axes, abaxial surface of bracts and bracteoles, and pedicels densely sericeous. Sepals 1.8–2.2 by 1–1.5 mm, triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands c. 1.5 mm long, prominent, or all sepals eglandular, or all sepals glandular. Petals yellow, glabrous; lateral petals with the claw 2–2.5 mm long, limb of anterior-lateral petals 5.5–6.5 mm long and wide, orbicular, margin subentire, limb of posterior-lateral petals 5–5.5



Map 8 Distribution of *Hiraea sanctae-marthae* C.V.Morton (\blacktriangle) and *Hiraea transiens* Nied. (\spadesuit).

mm long and wide, orbicular, margin minutely and irregularly denticulate, especially distally, sometimes subentire; posterior petal with the claw c. 2.5 mm long and thicker than that of lateral petals, limb c. 5 mm long and wide, orbicular, margin irregularly dentate-fimbriate, teeth/fimbriae 0.2–0.3(–0.5) mm long. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament 3.5-5 mm long, anther 1.1-1.3 mm long; stamens opposite anterior-lateral petals: filaments 3-4 mm long, anthers 0.8-1 mm long; stamens opposite anteriorlateral sepals: filaments 3.5-4 mm long, anthers 1-1.3 mm long; stamens opposite posterior-lateral petals: filaments 2.5-3 mm long, anthers (0.5–)0.8 mm long; stamens opposite posterior-lateral sepals: filaments 3-4 mm long, anthers 0.8-1 mm long; stamen opposite posterior petal: filament 2-2.5 mm long, anther 0.5-0.6 mm long. Styles incurved, glabrous, 3-3.5 by 0.4-0.5 mm; apex of anterior style extended into a spur c. 0.3 mm long; apex of posterior styles extended into a spur 0.1-0.2 mm long. Ovary 1-1.5 mm long, densely villous. Mature samara not seen; immature samara butterfly-shaped, dorsal wing present.

Distribution — Northern Colombia (Atlántico, Cesar, Magdalena).

Habitat & Phenology — In dry forest and thickets; sea level to 200 m; collected in flower in April and October, in young fruit in May.

Notes — Flowering and fruiting specimens of H. sanctaemarthae are easily distinguished from all other species here discussed by the silvery appressed vesture on the abaxial surface of the laminas, which is so dense that the epidermis is hidden. Yet, this distinctive vesture eventually thins. Old leaves become abaxially thinly sericeous to eventually glabrate; they may appear glabrous to the unaided eye and lead to confusion with H. reclinata. The retained hairs are generally aligned and parallel, unlike in *H. reclinata*, where the retained hairs are scattered. Also, in *H. sanctae-marthae* the stipules are at the base of the petiole. Three collections by Gentry and collaborators from Cesar are sterile and show the transition of the abaxial indumentum. This change is especially well shown in Gentry et al. 60742 (MO), which consists of two branches, one of which terminates in a young internode with a smaller leaf that shows the typical dense vesture; the other leaves show the gradual thinning. Such an abrupt change in abaxial vesture from very dense to glabrescent or glabrous is also observed in some other species of Hiraea, e.g., H. idroboana Cuatrec., H. buntingii W.R.Anderson, and other *Malpighiaceae*, e.g., *Stigmaphyllon* crenatum C.E.Anderson (C. Anderson 1997). Collections of H. sanctae-marthae with the dense abaxial vesture evident have been misidentified as H. velutina, and those in which the vesture was not obvious as H. hookeriana or H. reclinata.

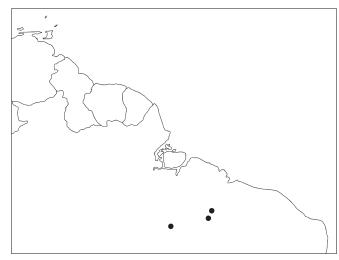
The holotype and WIS isotype are numbered '1211', but the MO duplicate is numbered '11'. All other data agree, and the specimens appear to be from the same gathering.

6. Hiraea silvicola C.E.Anderson, sp. nov. — Fig. 6; Map 9

Differt a *H. ternifolia* foliis oppositis, stylis basi pubescentibus, et petalo postico late triangulari, c. 4 mm longo et lato. — Type: *Lobo et al. 307* (holo MICH; iso MG), Brazil, Maranhão, Mpio. Santa Luzia, margens da estrada da Fazenda Cacique já próximo a ferrovia Carajás, 17 Mar. 1983.

Etymology. The specific epithet refers to the forest habitat.

Scandent shrub to 5 m; stems densely sericeous when young, becoming glabrous. Leaves opposite. Laminas of the larger leaves 6.5-17.5 by 3.5-12 cm, elliptical to obovate, apex obtuse- or emarginate-mucronate or sometimes apiculate, base acute to truncate, adaxially sericeous when very young, soon glabrous, abaxially velutinous, hairs V- or Y-shaped, stalk to 0.05 mm long, arms 0.1-0.2 mm long; margin with scattered glands 0.2-0.3 mm diam in distal 1/4-3/4 or only a few near apex or glands absent; costa and secondary veins not impressed adaxially, prominent abaxially. Petioles 7-15.5 by 1.5-2 mm, densely velutinous, with a pair of glands at apex to 1.5 mm below apex, each gland 0.7–1 mm long. Stipules 2–3 mm long, borne at middle to basal 1/4 of petiole. Inflorescences solitary axillary ternate cymes of 4-flowered umbels; umbel without a gland in the centre; inflorescence axis 0.5-1 mm long, bracts c. 1 mm long and wide; lateral peduncles sessile like the central one; peduncles 2-5 mm long; bracts and bracteoles subtending pedicels 1-1.2 by 0.8-1 mm; pedicels 10-13 by c. 0.5 mm; axes, abaxial surface of bracts and bracteoles, and pedicels densely sericeous. Sepals 1.7-1.8 by c. 2 mm, broadly triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands c. 1.5 mm long. Petals yellow, glabrous; lateral petals with the claw 2-2.3 mm long, limb of anterior-lateral petals c. 6 mm long and wide, orbicular, margin subentire, limb of posterior-lateral petals c. 5.5 mm long and wide, orbicular, margin subentire; posterior petal with the claw c. 3 mm long and thicker than that of lateral petals, limb c. 4 mm long and wide, broadly triangular, margin glandular-digitate-fimbriate, fimbriae to 0.4(-0.5) mm long. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament c. 2.5 mm long, anther c. 1.1 mm long; stamens opposite anterior-lateral petals: filaments c. 2.1 mm long, anthers c. 1.1 mm long; stamens opposite anterior-lateral sepals: filaments c. 2.5 mm long, anthers c. 1.1 mm long; stamens opposite posterior-lateral petals: filaments c. 2 mm long, anthers c. 0.9 mm long; stamens opposite posterior-lateral sepals: filaments c. 2.5 mm long, anthers c. 1 mm



Map 9 Distribution of Hiraea silvicola C.E.Anderson.

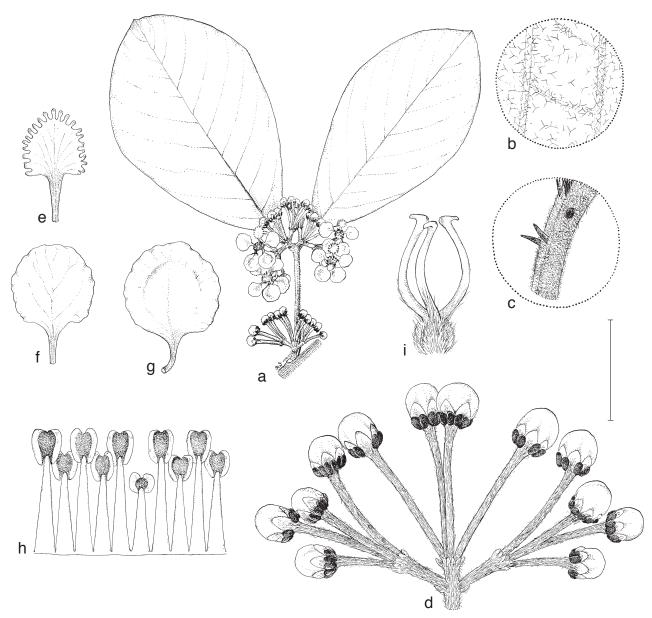


Fig. 6 Hiraea silvicola C.E.Anderson. a. Flowering branch; b. detail of abaxial leaf surface; c. portion of petiole with gland and a pair of stipules; d. inflorescence; e. posterior petal; f. posterior-lateral petal; g. anterior-lateral petal; h. androecium, stamen fifth from right opposite posterior petal; i. gynoecium, anterior style in centre (all: Lobo et al. 307, MICH). — Scale bar: a = 4 cm; b = 2 mm; c-d = 8 mm; e-g = 6.7 mm; h-i = 2.7 mm. — Drawn by Karin Douthit.

long; stamen opposite posterior petal: filament c. 1.6 mm long, anther c. 0.6 mm long. Styles incurved, 3–3.5 by c. 0.3 mm, anterior style with scattered hairs in the proximal 1/3–1/2, apex extended into a spur c. 0.2 mm long; posterior styles with scattered hairs in the proximal 1/4, apex extended into a spur c. 0.1 mm long. Ovary c. 1 mm long, densely villous. Mature samara not seen; immature samara butterfly-shaped, dorsal wing present.

Distribution — Brazil (Maranhão, Pará).

Habitat & Phenology — In forest; collected in flower in March, in young fruit in October.

Additional specimens examined. BRAZIL, Maranhão, Mpio. Grajaú, 52 km S of Arame, 78 km N of Grajaú along Hwy 006, S05°12' W46°12', Schatz et al. 928 (MG, MICH). Pará, Serra dos Carajás, Serra Norte, 5 km NE of AMZA Exploration Camp, c. S06° W50°15', Berg et al. 542 (MICH).

Note — Collections of *H. silvicola* were tentatively placed with *H. ternifolia* only because the laminas are abaxially persistently though finely velutinous. The hairs that compose the vesture range from sessile (V-shaped) to having a tiny stalk at most 0.05 mm long (Y-shaped); T-shaped hairs are absent. *Hiraea silvicola* also differs in its opposite phyllotaxy, leaves,

and inflorescences. The laminas are adaxially sericeous when young and not bullate when mature. The inflorescence is a solitary ternate cyme with all umbels 4-flowered. In most species the lateral peduncles are usually borne on a rudimentary lateral axis, but in *H. silvicola* the peduncles are all sessile (Fig. 6d).

7. Hiraea ternifolia (Kunth) A.Juss. — Fig. 7; Map 10

Hiraea ternifolia (Kunth) A.Juss. (1840) 257. — Malpighia ternifolia Kunth (1822 '1821') 146. — Hiraea ternifolia (Kunth) A.Juss. var. granatensis Nied. (1906) 10, nom. superfl. — Hiraea ternifolia (Kunth) A.Juss. var. granatensis Nied. subvar. humboldtiana Nied. (1906) 10, nom. superfl. — Type: Humboldt & Bonpland s.n. (holo P-HBK; iso P), Colombia, Cundinamarca, prope Pandi.

Hiraea ternifolia (Kunth) A.Juss. var. eglandulosa Triana & Planch. (1862)
330. — Type: Triana s.n. [5568-3] (lecto, designated by Cuatrecasas 1958:
P; isolecto BR, COL, G, K, MO, NY, US), Colombia, Tolima, Mariquita, entre Piedras et Ibaqué.

Hiraea platytriphylla Hochr. (1910) 276. — Type: Holton 802 (lecto, designated by W.R. Anderson 2007a: NY; isolecto G, GH, K), Colombia, 'Magdalena'

Woody vine to 2 m or small tree to 6 m; stems densely velutinous when young, becoming glabrous. Leaves ternate or sometimes

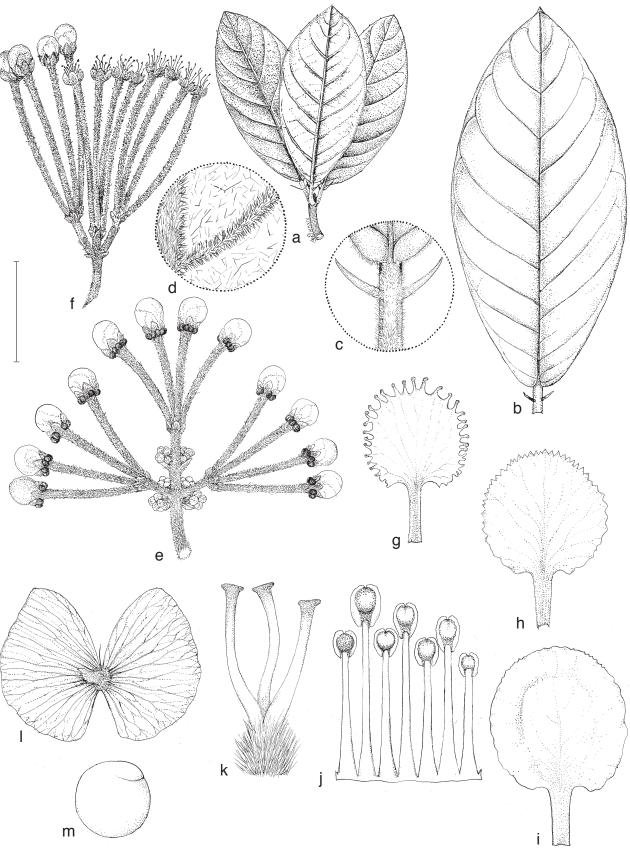
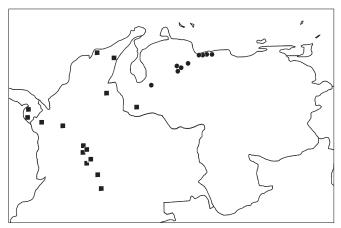


Fig. 7 Hiraea ternifolia (Kunth) A.Juss. a. Stem apex with ternate leaves; b. large leaf, adaxial view; c. base of lamina and apex of petiole with a pair of glands (almost hidden by vesture) and a pair of stipules, adaxial view; d. detail showing abaxial vesture of mature lamina; e. triternate cyme, the lateral umbels of each ternate unit in bud; f. ternate cyme; g. posterior petal; h. posterior-lateral petal; i. anterior-lateral petal; j. androecium, first stamen at right opposite posterior petal; k. gynoecium, anterior style at right; l. samara, abaxial view; m. embryo (from: a. García Barriga 11845, NY; b-d. García Barriga 11697, NY; e, g-k. Uribe U. 2987, US; f. Schlim 515, P; k-l. Whitefoord & Eddy 486, MO). — Scale bar: a-b = 4 cm; c = 8 mm; d = 4 mm; e-f, l = 2 cm; g-i, m = 5.7 mm; j-k = 2.7 mm. — Drawn by Karin Douthit.



Map 10 Distribution of *Hiraea ternifolia* (Kunth) A.Juss. (■) and *H. venezuelana* C.E.Anderson (●).

opposite. Laminas of the larger leaves 7-19 by 3.5-9.5 cm, elliptical to slightly obovate, apex mucronate or apiculate, base truncate to slightly cordate, mature laminas coriaceous and bullate, adaxially velutinous, eventually glabrescent, abaxially velutinous, hairs mostly Y-shaped but mixed with V-shaped hairs, stalk of Y-shaped hairs to 0.02-0.2 mm long, arms of V- and Y-shaped hairs 0.05–0.4 mm long, often unequal; margin with scattered glands 0.2-0.3 mm diam in distal 1/4-1/3(-1/2); costa and secondary veins impressed adaxially, prominent abaxially. Petioles 6-25 by 2-3.5 mm, densely velutinous, with a pair of glands at apex to 2 mm below apex, each gland 1-1.2 mm long. Stipules 2.5-5.5 mm long, borne usually at the middle or sometimes to basal 1/3 of the petiole (or nearer the base; Chocó, Darién). Inflorescences 1-2 per leaf axil, basically a ternate cyme bearing 4-6-flowered umbels but often additionally branched, the most complex (Fig. 7e) composed of three ternate units (Fig. 7f), at times not all axes expressed and the inflorescence then various; umbels without a gland in the centre, sometimes loosely arranged and bearing the 5th and/or 6th pedicel and associated bract and bracteoles on the peduncle below the 4 terminal flowers; inflorescence axis 0-9.5 mm long, bracts 1.5-2.5 mm long and wide; secondary axes 0-5.5 mm long, subtended by bracts 1.2-2 mm long and wide; peduncles 0.5-9 mm long; pedicels 18-30 (to 35 mm in fruit) by 0.4-0.5 mm, densely covered with sessile to T-shaped hairs (stalk to 0.1 mm); axes and abaxial surface of bracts and bracteoles densely sericeous. Sepals 2.2-2.5 mm long and wide, triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands 1.5-1.6 mm long, or all sepals eglandular. Petals yellow, glabrous; lateral petals with the claw 2.5-3 mm long, limb of anterior-lateral petals 7-8 mm long and wide, orbicular, margin subentire to irregularly shallowly denticulate, teeth to 0.05(-0.1) mm long; limb of posterior-lateral petals 6–7 mm long and wide, orbicular, margin denticulate, teeth to 0.3(-0.5) mm long; posterior petal with the claw 3-3.5 mm long and thicker than that of lateral petals, limb 5.5-6.5 mm long and wide, orbicular, margin glandulardigitate-fimbriate, fimbriae to 0.8(-1) mm long, longest at apex. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament 3.5-4.5 mm long, anther 1.2-1.3 mm long; stamens opposite anterior-lateral petals: filaments 3-4 mm long, anthers 0.8-1 mm long; stamens opposite anteriorlateral sepals: filaments 3.3-3.7 mm long, anthers 1-1.2 mm long; stamens opposite posterior-lateral petals: filaments 2.5-3.5 mm long, anthers 0.8-1 mm long; stamens opposite posterior-lateral sepals: filaments 3-3.1 mm long, anthers 1–1.1 mm long; stamen opposite posterior petal: filament 2–2.8 mm long, anther 0.6-0.7 mm long. Styles glabrous, 3-3.7 by 0.4–0.5 mm; anterior style slightly incurved, apex extended into a spur 0.1–0.2 mm long; posterior styles incurved, apex extended into a spur 0.05–0.1 mm long. Ovary 1–1.5 mm long, densely villous. *Samara* butterfly-shaped; lateral wings 2.8–3.2 by 2–2.2 cm; dorsal wing or crest 0.2–5.5 mm high, coarsely dentate; nut subspherical, 4.5–5.5 mm diam, areole 2.2–3 mm diam. Embryo subspherical to spherical, 4.5–4.7 mm diam.

Distribution — Panama (Darién), Colombia (Cesar, Cundinamarca, Chocó, Meta, Norte de Santander, Tolima), Venezuela (Mérida).

Habitat & Phenology — Lowland forest; 150–1700 m; collected in flower February to May, July, September, and December, in fruit in March, May, September, and November.

Notes — Hiraea ternifolia is unusual in its ternate phyllotaxy, complex inflorescences, and the velutinous vesture covering nearly all vegetative structures. As a rule the leaves are ternate but sometimes are opposite. For example, Lehmann 4636 is one of two syntype collections of H. velutina; the duplicate that Niedenzu saw at B (destroyed, photo F) consists of a leafy branch that is ternate, and a leafless flowering sprig with opposite leaf scars. The duplicates at K and US consist of branches with opposite leaves. Another example is found among the duplicates of Whitefoord & Eddy 486. The sheet at F consists of three branches, one of which has opposite leaves; the specimens at MEXU and MO are all ternate. The ternate arrangement is also found in the compound inflorescences, which may be triternate (Fig. 7e); however, not all axes are necessarily expressed, and the inflorescences vary from ternate cymes to variously branched complex units. The central umbel is usually 4-flowered, but the lateral umbels are often 6-flowered, as is sometimes the central umbel as well. The laminas are velutinous on both surfaces; the adaxial vesture is eventually sloughed off though mostly retained on the costa, but the abaxial hairs are persistent. Mature laminas are bullate, with the costa and secondary veins deeply impressed adaxially. Cuatrecasas (1958) indicated the COL duplicate of Triana s.n. [5568-3] as isotype of Hiraea ternifolia var. eglandulosa. Yet, this collection is one of three syntypes cited by Triana & Planchon (1862), and therefore Cuatrecasas's choice is one of lectotypification. Triana's and Planchon's types for the names published in 1862 are at P, and the specimen at P is thus the lectotype.

8. Hiraea transiens Nied. — Fig. 8; Map 8

Hiraea transiens Nied. (1906) 8. — Type: Triana s.n. (lecto, designated by W.R. Anderson 2007a: G; isolecto BM, COL, K, NY), Colombia, Chocó, Istmo de San Pablo [= Istmina], 100 m, 1853 (Dugand 1944).

Woody vine to 1 m or scandent shrub to 2 m; stems sericeous when young, soon glabrous. Leaves opposite. Laminas of the larger leaves 7.5–18 by 5–8 cm, elliptical to broadly obovate, apex mucronate to acuminate-mucronate, base acute to briefly truncate, adaxially sericeous when very young but soon glabrous, abaxially appearing glabrous to the naked eye but sparsely and finely sericeous, eventually patchily glabrescent, oldest laminas glabrous but often hairs retained on and along the costa and secondary veins, the hairs 0.1-0.3(-0.5) mm long, sessile, straight; marginal glands absent or sometimes with scattered glands 0.2 mm or less diam near apex; costa and secondary veins not or slightly impressed adaxially, prominent abaxially. Petioles 8-13.5 by 1.5-1.8 mm, densely sericeous, with a pair of glands at apex or 1-1.5 mm below apex, each gland 0.6-1.2 mm long. Stipules 2-3.5 mm long, borne at middle to distal 1/4 of petiole. Inflorescences 1-2 axillary biternate cymes of 4-flowered umbels; umbel without a central gland; inflorescence axis 2-8 mm long, bracts 1-2 by 1-1.5 mm; central peduncle 3-7.5 mm long; lateral axes to 3 mm long,

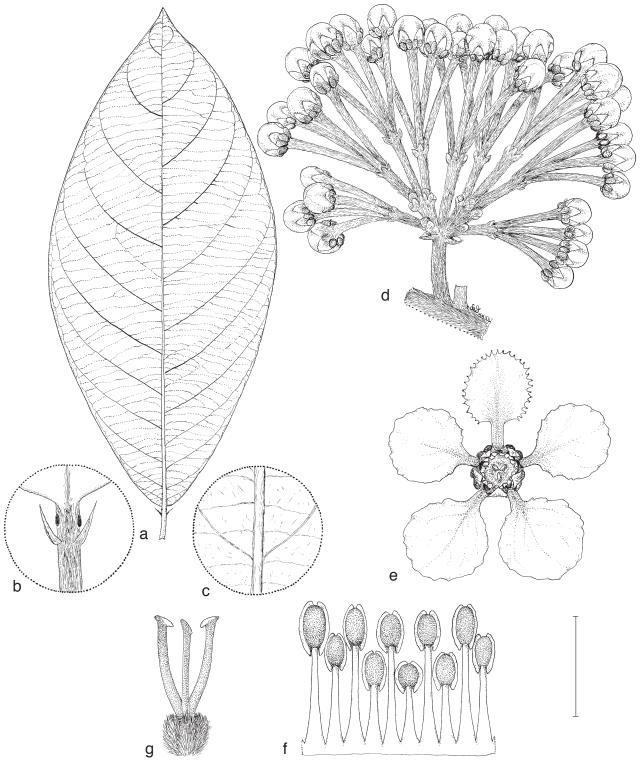


Fig. 8 *Hiraea transiens* Nied. a. Large leaf, abaxial view; b. petiole and lamina base, adaxial view, showing a pair of glands and a pair of stipules; c. detail of abaxial leaf surface; d. inflorescence in bud; e. flower, posterior petal uppermost; f. androecium, stamen fifth from right opposite posterior petal; g. gynoecium, anterior style in centre (all from: *Acevedo-R. et al. 6863*, MICH). — Scale bar: a = 4 cm; b, d = 8 mm; c = 4 mm; e = 5.7 mm; f, g = 2.7 mm. — Drawn by Karin Douthit.

subtended by bracts 0.5 by 1.5 mm, each lateral axis terminating in three sessile peduncles 2.5–7.5 mm long, bracts 0.5 by 1.5 mm; bracts and bracteoles subtending pedicels 0.5 by 1.5 mm; pedicels 9.5–14 by 0.3 mm; axes, abaxial surface of bracts and bracteoles, and pedicels densely sericeous; sometimes an additional lateral peduncle 2–5.5 mm long inserted below one or both lateral axes. Sepals 1.5–2 mm long and wide, triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands 1.3–1.5 mm long, or all eglandular. Petals yellow, glabrous; lateral petals

with the claw 2–2.5 mm long; limb of anterior-lateral petals 5–6.5 mm long and wide, orbicular, margin subentire to irregularly minutely denticulate, limb of posterior-lateral petals 4.5–5.5 mm long and wide, orbicular, margin subentire to irregularly minutely denticulate especially toward apex, teeth to 0.01 mm long; posterior petal with the claw c. 3 mm long and thicker than that of lateral petals, limb 4–5 mm long and wide, orbicular, margin glandular-dentate-fimbriate, fimbriae to 0.5 mm long. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament (2.5–)3.5 mm long,

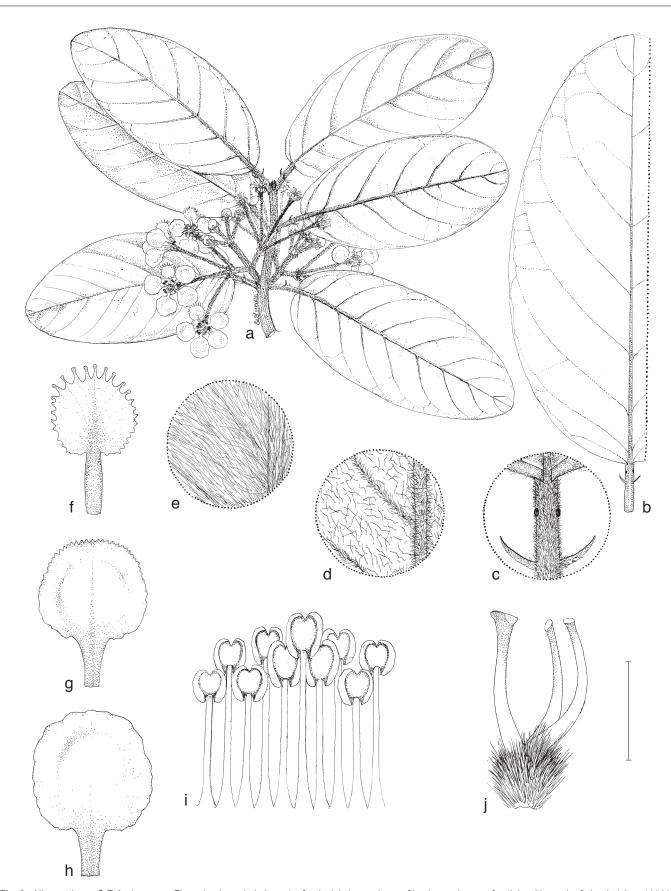


Fig. 9 Hiraea trianae C.E.Anderson. a. Flowering branch; b. large leaf, adaxial view; c. base of lamina and apex of petiole with a pair of glands (almost hidden by vesture) and a pair of stipules, adaxial view; d. detail showing abaxial vesture of mature lamina; e. detail showing dense adaxial vesture of young lamina; f. posterior petal; g. posterior-lateral petal; h. anterior-lateral petal; i. androecium, first stamen at left opposite posterior petal; j. gynoecium, anterior style at left (from: a-d, f-g. Barclay et al. 3474, US; e. Triana s.n., G). — Scale bar: a-b = 4 cm; c = 8 mm; d-e = 4 mm; f-h = 6.7 mm; i-j = 2.7 mm. — Drawn by Karin Douthit.

anther (1.1–)1.5 mm long; stamens opposite anterior-lateral petals: filaments (2.1–)2.8–3 mm long, anthers (0.8–)1.1–1.3 mm long; stamens opposite anterior-lateral sepals: filaments (2.5–)3.3–3.5 mm long, anthers 1–1.3 mm long; stamens opposite posterior-lateral petals: filaments (1.5–)2.5–2.6 mm long, anthers (0.8–)1.2 mm long; stamens opposite posterior-lateral sepals: filaments (2.5–)3.3–3.5 mm long, anthers 0.8–1 mm long; stamen opposite posterior petal: filament 1.5–2.3 mm long, anther 0.5–0.6 mm long. Styles slightly incurved, glabrous, (2.5–)3.5–4 by c. 0.4 mm; apex of anterior style extended into a spur 0.1–0.2 mm long; apex of posterior styles extended into a spur 0.05–0.1 mm long. Ovary 0.8–1 mm long, densely villous. Mature *samara* not seen; immature samara butterfly-shaped, dorsal wing present.

Distribution — Northern Colombia (Antioquia, Chocó, Norte de Santander) and northern Venezuela (Distrito Federal, Miranda).

Habitat & Phenology — In forest, one collection (*Acevedo et al. 6863*) from mangrove swamp; sea level to 200 m; collected in flower in February to April, June, September, November; in young fruit in February.

Note — *Hiraea transiens* is partly sympatric with *H. reclinata* and is often misidentified as that species (or '*H. obovata*'). The abaxial surface of the lamina looks glabrous to the naked eye but is covered with tiny appressed hairs, mostly 0.1–0.2 mm long. The hairs are eventually abraded. The oldest leaves are mostly glabrous, although often some hairs are retained along the costa and secondary veins, especially toward the base. *Hiraea transiens* also differs from *H. reclinata* in its biternate inflorescences, which sometimes bear one or two additional pedunculate umbels below the lateral axes (Fig. 8d).

9. Hiraea trianae C.E.Anderson, sp. nov. — Fig. 9; Map 4

Differt a *H. ternifolia* foliis oppositis, laminae adaxaliter sericeae, et petalo postico margine apice digitato-fimbriato basi denticulato. — Type: *Barclay et al. 3474* (holo US; iso COL, US, WAG), Colombia, Cundinamarca, S of Silvania on toll road to Fusagasugá, near km 37, turn W and proceed for 4 km on road to Tibacuy, 1300 m, 30 May 1972.

Hiraea ternifolia (Kunth) A.Juss. var. robustior Cuatrec. (1958) 401. — Type: García-Barriga 12313 (holo US; iso COL, US), Colombia, Cundinamarca, al oeste de Guadas, camino de herradura entre Guadas y el Alto de Aguaclara, hacienda 'Paramillo', 1040–1320 m, 24 July 1947.

Hiraea ternifolia (Kunth) A.Juss. var. robustior Cuatrec. forma glandulosa Cuatrec. (1958) 401. — Type: Mutis 2060 (holo US; iso MA, online image), Colombia, without locality.

Etymology. The specific epithet honours José Jerónimo Triana (1834–1890), whose collections and writings greatly advanced comprehension of the Colombian flora.

Woody vine to 30 m; stems densely sericeous when young, becoming glabrous. Leaves opposite. Laminas of the larger leaves 7.5–17 by 4.5–9.5 cm, elliptical, apex mucronate, base truncate to slightly cordate, mature laminas coriaceous and bullate, adaxially with sessile to subsessile hairs when young, soon glabrescent to glabrous but with some hairs retained on and along the costa and secondary veins, abaxially velutinous mixed with scattered T-shaped hairs, stalk to 0.2 mm long, arms of Y-shaped hairs 0.1–0.3 mm long, trabecula of T-shaped hairs 0.5-1.5 mm long, often crisped and intertwined; margin with scattered glands 0.2-0.3 mm diam in distal 1/4-1/2; costa and secondary veins impressed adaxially, prominent abaxially. Petioles 11–23 by 2–3 mm, densely velutinous, with a pair of glands at apex to 3 mm below apex, each gland 0.8–1.3 mm long, sometimes glands absent. Stipules 2.2–4 mm long, borne at middle to distal 1/4 of petiole. *Inflorescences* 1–2 axillary ternate cymes, central umbel 4-flowered, lateral umbels 4-6-flowered; umbel without a gland in the centre; inflorescence axis

1–4.5 mm long, bracts 1.5–1.8 mm long and wide; all peduncles sessile but the laterals ones often with a bract c. 1.5 mm long near the base; peduncles 2.5-13.5 mm long; bracts and bracteoles subtending pedicels 1.5–2 by 1.3–1.5 mm; pedicels 19-26 by 0.5-10 mm, densely covered with sessile to T-shaped hairs (stalk to 0.1 mm); axes and abaxial surface of bracts and bracteoles densely sericeous. Sepals 2.2-2.8 mm long and wide, triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands 1–1.5 mm long, or all sepals eglandular. Petals yellow, limb of posterior petal streaked with red, glabrous; lateral petals with the claw 2.5-3 mm long, limb of anterior-lateral petals c. 8 mm long and wide, orbicular, margin subentire, limb of posteriorlateral petals c. 7 mm long and wide, orbicular, margin finely denticulate distally, teeth to 0.1 mm long, subentire proximally; posterior petal with the claw 3.5-4 mm long and thicker than that of lateral petals, limb 6-6.5 mm long and wide, orbicular, margin glandular-digitate-fimbriate at apex, fimbriae to 0.8(-1) mm long, grading into denticulate toward the base, the teeth decreasing in size, erose near the base. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament c. 4 mm long, anther c. 1.3 mm long; stamens opposite anterior-lateral petals: filaments c. 3.5 mm long, anthers 1.2-1.3 mm long; stamens opposite anterior-lateral sepals: filaments c. 3.8 mm long, anthers c. 1.2 mm long; stamens opposite posterior-lateral petals: filaments 2.7-3 mm long, anthers 1.2 mm long; stamens opposite posterior-lateral sepals: filaments 3.5-3.8 mm long, anthers c. 1 mm long; stamen opposite posterior petal: filament c. 2.5 mm long, anther c. 0.9 mm long. Styles glabrous, 3.5–3.7 by 0.4–0.5 mm; anterior style slightly incurved, apex extended into a spur 0.1–0.2 mm long; posterior styles incurved, apex extended into a spur 0.05-0.1 mm long. Ovary c. 1.5 mm long, densely villous. Samara not seen.

Distribution — Colombia (Cundinamarca, Norte de Santander, Tolima).

Habitat & Phenology — In forest; 600–1320 m; collected in flower in May and July.

Additional specimens examined. Colombia, Cundinamarca, Junca, 1200 m, Triana 3377 (G, K). Norte de Santander, 'Provincia de Ocaña', Schlim 324 6 712 (COL). Tolima, Mariquita, 600 m, Triana 1202 (US). Without locality, Mutis 5772 (US).

Notes — Hiraea trianae was first described by Cuatrecasas (1958) as a variety of *H. ternifolia*, with which it shares abaxially velutinous leaves. It is here elevated to species level. It differs from H. ternifolia by its abaxial laminar pubescence, composed of sessile to subsessile hairs. The initially dense vesture is sloughed off in patches, and older leaves are glabrescent to eventually glabrous, though some hairs of usually retained along the costa. None of the collections seen exhibit ternate phyllotaxy. The inflorescence is a simple ternate cyme, one or two per leaf axil. The posterior petal is glandular-digitatefimbriate only at the apex; the rest of the margin grades from denticulate to erose toward the base. Cuatrecasas named his variety 'robustior' to emphasize the thicker inflorescence axes and pedicels evident in the collections he saw. Yet, all of those have young inflorescences in bud or the flowers beginning to open. As inflorescences mature, the pedicels elongate and become thinner. This transition is well shown in the holotype.

The type collection, *Barclay et al. 3474*, was distributed as annotated by Cuatrecasas as *H. sclerophylla* Cuatrec., doubtlessly owing to an unfortunate error in handling annotation labels. *Hiraea sclerophylla* is immediately separated from *H. trianae* by the appressed abaxial laminar vesture.

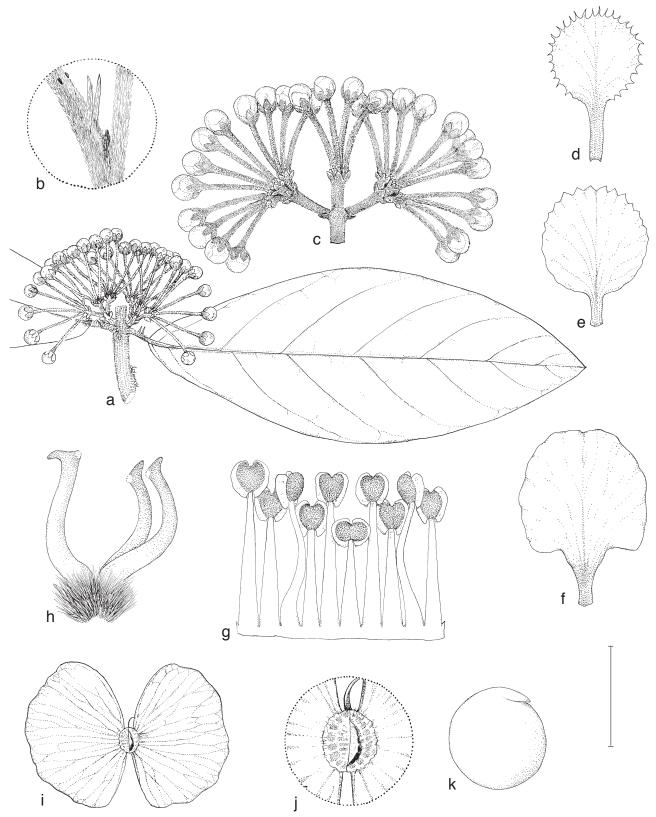


Fig. 10 Hiraea venezuelana C.E.Anderson. a. Portion of stem with a large leaf and two inflorescences, each a ternate cyme; b. petiole with a pair of glands and a pair of stipules; c. inflorescence with the lateral branches also ternately branched; d. posterior petal; e. posterior-lateral petal; f. anterior-lateral petal; g. androecium, abaxial view, the stamen fifth from right opposite posterior petal; h. gynoecium, anterior style at left; i. samara, abaxial view; j. detail of samara showing dorsal winglet; k. embryo (from: a, d-h. Benítez de Rojas 2739, MICH; b. Romero 574, MY; c. Saer 473, VEN; i-k. Badillo 1999, MY). — Scale bar: a = 4 cm; b, j = 8 mm; c = 1.3 cm; d-f = 5.7 mm; g, h = 2.7 mm; i = 2 cm; k = 4 mm. — Drawn by Karin Douthit.

10. *Hiraea venezuelana* C.E.Anderson, *sp. nov.* — Fig. 10; Map 10

Differt a *H. reclinata* umbellis lateralibus floribus (5–)6; laminae foliorum majorum basi cuneatae vel anguste truncatae, abaxaliter pilos T-formes et pilos appressos ferens. — Type: *C. Benitez de Rojas 2739* (holo MICH; iso F, VEN), Venezuela, Aragua, Dtto. Girardot, Parque Nacional Henri Pittier, por la vía hacia Choroní, vertiente sur, 1000–1200 m, 19 May 1980.

Woody vine, small shrub, or treelet; stems sericeous when young, soon glabrous. Leaves opposite. Laminas of the larger leaves 6-17 by 2.5-7 cm, elliptical to oblanceolate, apex acute to rounded, mucronate, base cuneate to briefly truncate in largest laminas, adaxially sericeous when very young, soon glabrous, abaxially with a sparse mixture of subsessile and mostly T-shaped hairs, eventually glabrescent, the oldest glabrous but often some hairs retained on and along the costa and secondary veins, stalk of hairs 0.05-0.1 mm long, trabecula 0.5-1.5 mm long, straight or wavy; margin with scattered glands 0.2-0.3 mm diam in distal 1/4-1/2 or sometimes only near apex or eglandular; costa and secondary veins not or slightly impressed adaxially, prominent abaxially. Petioles (6.5-)7-15(-21) by 1-2 mm, densely sericeous, with a pair of glands at apex or up to 1.5(-2) mm below apex, each gland 0.5-1 mm long. Stipules 1.8-4 mm long, borne at middle to distal 1/3 of petiole. Inflorescences 1-2 axillary ternate and sometimes also biternate cymes; inflorescence axis 0.5-3.5 mm long, bracts 0.8-2 by 0.8-1.5 mm; lateral axes 1-2 mm long, subtended by bracts 0.5-0.7 mm long and wide; in ternate cymes peduncles 1.5-6.5 mm long, the central peduncle usually shorter than the lateral two, central umbel 4-flowered, lateral umbels (5-)6-flowered; in biternate cymes the tertiary axes 1-2 mm long, bearing peduncles 1-2 mm long and subtended by bracts 0.7 by 0.5 mm, central and lateral umbel 4-flowered; umbels without a gland in the centre; bracts and bracteoles subtending pedicels 1-2 by 0.8-1.5 mm; pedicel (8-)17-22(-25) by 0.4-0.5 mm; axes, abaxial surface of bracts and bracteoles, and pedicels densely sericeous. On leafless branches, inflorescences often crowded and condensed, sessile to subsessile, pedicels 8-11 mm long. Sepals 1.8-2 mm long and wide, triangular, adaxially glabrous, abaxially sericeous; anterior sepal eglandular, the lateral four biglandular, glands 1.5–1.8 mm long, or all sepals eglandular. Petals yellow, glabrous; lateral petals with the claw c. 2 mm long; limb of anterior-lateral petals 6.5-7 mm long and wide, orbicular, margin subentire, limb of posterior-lateral petals 5.5-6.5 mm long and wide, orbicular, margin subentire but apex irregularly dentate, teeth to 0.2 mm long; posterior petal with the claw 3-3.5 mm long and thicker than that of lateral petals, limb 5-5.5 mm long and wide, orbicular, margin glandularfimbriate, fimbriae to 0.4(-5) mm long. Stamens glabrous, filaments basally connate. Stamen opposite anterior sepal: filament 3-3.5 mm long, anther c. 1 mm long; stamens opposite anterior-lateral petals: filaments c. 2.5-3 mm long, anthers c. 0.9 mm long; stamens opposite anterior-lateral sepals: filaments 3-3.3 mm long, anthers 0.9-1 mm long; stamens opposite posterior-lateral petals: filaments 2.3-2.5 mm long, anthers 0.8-0.9 mm long; stamens opposite posterior-lateral sepals: filaments 2.5-3 mm long, anthers 0.8-0.9 mm long; stamen opposite posterior petal: filament 2-2.2 mm long, anther c. 0.6 mm long. Styles incurved, glabrous; anterior style 3.3-3.7 by 0.4-0.5 mm, apex extended into a spur 0.1-0.2 mm long; posterior styles 3.2-3.5 by 0.4-0.5 mm, apex extended into a spur 0.05-0.1 mm long. Ovary c. 1.5 mm long, densely villous. Samara butterfly-shaped; lateral wings 2.5-3 by 1.7-2.5 cm; dorsal wing a crest to 1.2 mm high, coarsely dentate or denticulate; nut subspherical, 4-4.5 mm diam, areole 2-2.5 mm diam. Embryo spherical, 4-4.5 mm diam.

Distribution — Northern Venezuela (Aragua, Barinas, Lara, Yaracuy).

Habitat & Phenology — In forest, matorral, and at roadsides; sea level to 1300 m; collected in flower in April and May, in fruit in April through August.

Additional specimens examined. VENEZUELA, Aragua, Rancho Grande, Parque Nacional, Badillo 1999 (MY); 4–5 km NE de Bahía de Cata, por la vía hacia Cuyagua, Carnevali et al. 513 (VEN); along R. Chuao, Pittier 12180 (A, NY, US, VEN); Dtto. Girardot, carretera Cata-Cuyaga, Romero 567 (MY); Dtto. Girardot, carretera Maracay-Ocumare de la Costa, Parque Nacional Henri Pittier, Romero 574 (MY). Barinas, vicinity of Barinitas, Lasser 44 (US); Quebrada de Paranguleta, Lasser 66 (VEN). Lara, entre La Piedad y Sarare, Saer 423 (F, VEN); enter Cujicito y Sarare, Saer 454 (F, VEN). Yaracuy, Dtto. Nirgua, San Vincente, Benítez de Rojas 2367 (MO, MY, VEN); 5 km N of Salom, Gentry & Puig-Ross 14386 (MICH, VEN).

Note — *Hiraea venezuelana* is distinctive in its inflorescences. The ternate cymes, 1–2 per leaf axil, bear (5–)6 flowers in the lateral umbels. Leafless flowering branches may have some condensed biternate cymes mixed in among the ternate cymes (e.g., *Pittier 12180, Romero 574, Saer 423*). In such biternate cymes, all umbels are 4-flowered, and the most distal umbels are essentially sessile (Fig. 10c). *Hiraea venezuelana* superficially resembles *H. reclinata*, but the young laminas are abaxially covered with a mixture of sessile, subsessile, and T-shaped hairs. In *H. reclinata* the hairs are appressed, and all umbels are 4-flowered. The petioles of *H. venezuelana* have a pair of glands sometimes at the apex but mostly on the petiole, up to 2 mm below the apex, and the pair of stipules is placed at the middle to the distal 1/3.

Acknowledgements I am indebted to the late William R. Anderson for sharing his insights on *Hiraea* and *Malpighiaceae* in general, and am grateful for the comments and corrections provided by Barry Hammel and an anonymous reviewer. Karin Douthit drew the handsome illustrations. I thank the directors, curators, and staff of the following herbaria for providing access to their collections and for many courtesies shown during visits: A, BM, BR, CAS, CHAPA, COL, DS, DUKE, ENCB, F, G, GH, IBUG, K, MER, MEXU, MG, MICH, MO, MY, MYF, NY, P, TEX, U, UC, US, VEN, W, WAG, WIS, XAL. This study was supported in part by a grant from the National Science Foundation to the University of Michigan (DEB-0543909).

REFERENCES

Allen JA. 1904. Report on mammals from the district of Santa Marta, Colombia, collected by Mr. Herbert H. Smith, with field notes by Mr. Smith. Bulletin of the American Museum of Natural History 20: 407–468.

Anderson C. 1997. Monograph of Stigmaphyllon (Malpighiaceae). Systematic Botany Monographs 51: 1–313.

Anderson C. 2014. Hiraea cuneata, H. macrophylla, and four new species confused with them: H. hatschbachii, H. occhionii, H. reitzii, and H. restingae (Malpighiaceae). Edinburgh Journal of Botany 73: 361–378.

Anderson WR. 2007a. Lectotypification of names of Malpighiaceae – I. Contributions from the University of Michigan Herbarium 25: 83–93.

Anderson WR. 2007b. Malpighiaceae. İn: Hammel BE, et al. (ed), Manual de Plantas de Costa Rica, vol. 6. Monographs in Systematic Botany from the Missouri Botanical Garden 111: 253–312.

Ayers TJ, Boufford DE. 1988. Index to the vascular plant types collected by H.H. Smith near Santa Marta, Colombia. Brittonia 40: 400–432.

Belcher E. 1843. Narrative of a voyage round the world: performed in Her Majesty's ship Sulphur, during the years 1836–1842. London.

Bentham G. 1844. Malpighiaceae. In: Bentham G, The botany of the voyage H.M.S. Sulphur, 74–75. London.

Blanco M. 1837. Flora de filipinas. Manila.

Brandegee TS. 1922. Plantae Mexicanae Purpusianae, XI. University of California Publications in Botany 10: 181–188.

Cavanilles, AJ. 1790. Nona dissertatio botanica. Madrid.

Colla LA. 1824. Hortus ripulensis. Turin.

Cuatrecasas J. 1958. Prima flora colombiana. Malpighiaceae. Webbia 13: 343–664

Cuatrecasas J, Croat TB. 1981 '1980'. Family 93, Malpighiaceae. In: Woodson Jr RE, et al. (ed), Flora of Panama – Part VI. Annals of the Missouri Botanical Garden 67: 851–945.

Dugand A. 1944. Itinerarios botánicos de José Jerónimo Triana. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 5: 483–489.

Grisebach A. 1858. Malpighiaceae. In: Martius KFP (ed), Flora brasiliensis, 12, 1: 1–108. Leipzig, Munich.

Grisebach A. 1860. Malpighiaceae. In: Grisebach A, Flora of the British West Indian Islands: 114–122. London.

Hemsley WB. 1879. Malpighiaceae. In: Hemsley WB, Biologia centraliamericana. Botany 1: 145–157. London.

Hochreutiner BPG. 1910. Critical notes on new or little known species in the Herbarium of the New York Botanical Garden. Bulletin of the New York Botanical Garden 6: 262–299.

Huber J. 1902. Materiaes para a flora amazonica. Boletim do Museu Paraense de Historia Natural e Ethnographia (Museu Goeldi) 3: 400–446. Jacquin NJ. 1760. Enumeratio systematica plantarum. Leiden.

Jussieu A. 1840. Malpighiacearum synopsis, monographiae mox edendae prodromus. Annales des Sciences Naturelles. Botanique. Sér. 2, 13: 247–291, 321–338.

Jussieu A. 1843. Monographie de la famille des Malpighiacées. Archives du Muséum d'Histoire Naturelle, Paris 3: 5–151, 255–616, pl. 1–23.

Kunth CS. 1822 '1821'. Malpighiaceae. In: Humboldt FHA, Bonpland AJ, Kunth CS, Nova genera et species plantarum (quarto ed.), text: 5: 145–174, plates 445–452. Paris.

McVaugh R. 1978. Galeotti's botanical work in Mexico: the numbering of his collections and a brief itinerary. Contributions from the University of Michigan Herbarium 11: 291–297.

Morton CV. 1933. Two new species of Hiraea from Colombia. Proceedings of the Biological Society of Washington 46: 87–90.

Niedenzu F. 1906. De genere Hiraea. Verzeichnis der Vorlesungen am Kgl. Lyceum hosianum zu Braunsberg im Winter-Semester 1906/7: 1–17.

Niedenzu F. 1908. De genere Mascagnia. Arbeiten aus dem botanischen Institut des Kgl. Lyceum hosianum in Braunsberg: 1–29.

Niedenzu F. 1928. Malpighiaceae. In: Engler A (ed), Das Pflanzenreich, IV. 141: 1–870. Leipzig.

Pohl RW. 1965. Dissecting equipment and materials for the study of minute plant structures. Rhodora 67: 95–96.

Seemann B. 1853. The botany of the voyage of H.M.S. Herald. London. Triana JJ, Planchon JE. 1862. Prodromus florae Novo-granatensis. Annales des sciences naturelles. Botanique sér. 4, 18: 258–381.

IDENTIFICATION LIST

The numbers following the collectors numbers refer to the following species:

1 = H. barclayana 3 = H. mcvaughii 5 = H. sanctae-marthae 7 = H. ternifolia 9 = H. trianae 2 = H. hookeriana 4 = H. reclinata 6 = H. silvicola 8 = H. transiens 10 = H. venezuelana

Acevedo-Rodríguez et al. 6863: 8 – Acosta & Acosta 344: 4 – Aguilar H. 294: 4; 328: 4 – Alfaro 3142: 4 – Almeda & Utley 802: 4 – Alvarez 672: 4 – André K912: 7 – Añez 17: 2 – Apollinaire (Bro.) 78: 7 – Araquistain & Moreno 2851: 4 – Arnason & Lambert 17308: 4; 17528: 4 – Arvigo 226: 4; 748: 4 – Avenado D. & Juan 141: 4 – Aviles 2222: 4 – Ayala 667: 3; 91-97B: 3 – Aymard & Ortega 2531: 2.

Badillo 1999: 10 – Balick 1925: 4 – Barclay 1127: 1 – Barclay et al. 3474: 9 – Barlow 6/13: 4 – Bartlett 12696: 4; 12709: 4; 12782: 4 – Benítez de Rojas 2367: 10; 2739: 10 – Berg et al. 542: 6 – Bernardi 7707: 2 – Bernoulli & Cario 3011: 4 – Blackmore & Chorley 3726: 1 – Breedlove 9977: 4; 24646: 1; 24647: 1; 24672: 1; 50731: 1; 50866: 4; 56273: 1; 57959: 4 – Brenes 22477: 4 – Britton 2916: 2 – Bullock 1352: 3; 1585: 3; 1712: 3 – Bunch 426: 1 – Bunting 10152: 2; 10279: 2; 12895: 2; 12904: 1 – Bunting & Licht 708: 4 – Burnham 967: 4; 974: 4.

Cabrera 2140: 4; 4968: 4; 7885: 4; 8397: 4; 8632: 4; 8739: 4; 11418: 4; 11460: 4 - Callejas et al. 10010: 8 - Calzada et al. 10185: 4 - Carballo 293: 1 - Carlson 653: 1; 2072: 4 - Carnevali et al. 513: 10; 4491: 4 - Chan 2362: 4 - Chan V. & Flores 589: 4 - Chater 4: 4 - Chavarría 491: 4; 605: 4; 762: 4; 1227: 4; 1247: 4; 2020: 4 - Clark 7178: 3 - Contreras 206: 4; 3529: 4; 5758: 4; 6754: 4; 6866: 4; 8649: 4; 9716: 4; 9735: 4; 10822: 4 - Coronado & Rueda 3754: 1 - Coronado & Soriano 620: 1 - Coronado & Velásquez 14: 4 - Cortes 258: 1 - Cowan 2985: 4 - Croat 5026: 4; 5592: 4; 5614: 4; 5719: 4; 5927: 4; 7210: 4; 7747: 4; 9225: 4; 14028: 4; 23550: 4; 34674: 4 - Cuadros V. 2152: 4; 4393: 4.

D'Arcy 3934: 4; 4050: 4 - Daniel 9552: 1 - Daubenmire 648: 4; 714: 4 - Davidse et al. 20408: 4; 30680: 4 - Dorantes 511: 1 - Dugand 5112: 4; 6276: 5; 6288: 5 - Dugand & García Barriga 2392: 4 - Dugand & Petén 809: 5 - Duke 10673: 4; 15327: 7 - Duno de Stefano et al. 1966: 4 - Durán 198: 4; 971: 4 - Dwyer 10795: 4.

Echeverry E. 3464: 7 – Edwards 146: 1; 606: 1 – Erlanson 70: 4 – Escalante 86: 4

Flora Falcón 588: 2; 596: 2 – Flores F. 1859: 3 – Fonnegra G. 1578: 1 – Forero & León 150: 4 – Forero et al. 9396: 7 – Foster 1385: 4; 1771: 4; 2152: 4. Galdames 2743: 4 – García-Barriga 11697: 7; 11845: 7; 12313: 9 – Gaumer 66: 4; 67: 4; 1040: 4; 2410: 4; 24250: 4 – Gentle 1199: 4; 1241: 4; 1637: 4; 2584: 4; 5259: 4; 5260: 4; 5535: 4; 6215: 4; 6751: 4; 7569: 4 – Gentry 3329: 4; 3345: 4; 41198: 2; 79387: 4 – Gentry & Cuadros 57143: 5; 68107: 4 – Gentry & Puig-Ross 14386: 10 – Gentry & Woodruff 71486: 4 – Gentry et al. 34821A: 4; 60672: 4; 60691: 5; 60742: 5 – Ginés 3618: 2 – Gómez D. 994: 4 – Gómez-Pompa & Nevling 1268: 4 – González & González L67: 1 – González & Gúzman 939: 3; 8874: 3 – González & Villacorta 24: 1 – Grayum et al. 11189: 4 – Gregg 1039: 3 – Guerrero C. 1193: 4.

Hammel 7244: 7 – Hammel et al. 18899: 4 – Haught 3743: 5; 4043: 1; 4785: 4 – Hazlett 1597: 1 – Hernández G. 1024: 4; 1046: 4; 2472: 4 – Hernández M. 219: 4 – Hladik 359: 4 – Holton 802: 7 – Hughes 338: 1 – Hunnewell 14710: 4.

Jahn 378: 2 – Janzen 10906: 4; 10934: 4; 11714: 4; 11760: 4; 12199: 4; 12389: 4 – Jiménez 2075: 4 – Jiménez M. 3926: 4 – Johnston 732: 4. Kalbreyer 651: 8 – King 18: 1.

Lankeseter 1320: 4 – Lara 108: 1 – Lasser 44: 10; 66: 10 – Laughlin 817: 4 – Lent 599: 1 – Liesner 338A: 4; 5009: 4 – Linares & Martínez 2618: 1 – Linden 1148: 7 – Lira C. 816: 4; 832: 4 – Lobo et al. 307: 6 – López

57: 4 – López F. 917: 1 – Lott 2549: 3; 3438: 3 – Lundell 3363: 4; 3370: 4; 4084: 4; 7408: 4; 15737: 4.

MacDougall 30: 1 – Magallanes 713: 3; 2977: 3 – Martínez 712: 1 – Martínez & Téllez 12765: 4 – Martínez M. 1535: 4 – Martínez S. 12016: 4; 18440: 4; 27531: 4 – Matuda 17526: 4 – Maya J. 1708: 1; 3043: 1; 3220: 1; 3237: 4 – McPherson 870: 4 – McVaugh 15228: 3; 15257: 3; 15773: 4 – McVaugh & Koelz 1532: 4; 1711: 4 – Meave & Howe 1381: 4 – Medina 2: 2; 825: 2 – Meléndez L. 29: 4 – Méndez Ton 5882: 4 – Miller & Téllez V. 3089: 3 – Miranda 5327: 4; 5351: 4 – Molina 1525: 1; 11901: 1 – Molina R. 941: 1; 2723: 1; 6995: 1; 7805: 1; 7894: 1; 8009: 1; 8478: 1; 11885: 1 – Molina R. & Molina 31516: 1 – Monterrosa 878: 1 – Moraga 906: 4 – Morales 1474: 4; 4154: 4; 6153: 4 – Morales & Salazar 1472: 4 – Moreno 25695: 4 – Moritz 1678: 8 – Morton 7105: 1 – Murray & Johnson 1427: 4; 1454: 3 – Mutis 2363: 7; 2432: 7; 4221: 7; 5772: 9.

Nava Z. 1874: 4 – Navarro 133: 4 – Nelson & Romero 4561: 4; 4562: 4 – Nelson et al. 239: 1.

Opler 98: 4; 679: 4; 1750: 4.

Panero 5755: 4 – Pascual 1044: 4 – Peck 431: 4 – Pérez J. 603: 3; 1908: 3 – Pfeiffer & Skog 3083: 3 – Pinto et al. 273: 7 – Pittier 3519: 4; 5563: 4; 5566: 4; 6529: 4; 6531: 4; 9882: 4; 12180: 10 – Puch & Narváez 497: 4 – Purpus 26: 1; 6422: 4; 8283: 1, 4; 8731: 4; 10152: 1; 10525: 1; 16335: 4. Quigley 900: 4 – Quintero 1728: 7.

Renderos 139: 1 – Reyes & Chavarría 97: 4; 109: 4 – Reyes G. 4539: 4; 4713: 4 – Robleto 825: 4 – Rodríguez 1804: 4 – Romero 567: 10; 574: 10 – Romero-Castaneda 8067: 4; 9637: 4 – Rosales 210: 4; 310: 4; 416: 4; 616: 4; 727: 4 – Rose 1507: 3 – Rueda et al. 14015: 1 – Ruhfel 13: 4 – Ruiz Z. 3191: 2 – Rzedowski 15478: 4.

Saer 423: 10; 454: 10 – Salvador C. 2457: 1 – Sanabria & Simá 386: 4 – Sandino 2988: 1 – Sandoval 358: 4; 386: 4 – Santana & Cervantes 286: 3 – Saunders 259: 4 – Schatz et al. 928: 6 – Schipp S447: 4 – Schlim 324 or 712: 7; 516: 7; 524: 8; 712: 9 – Schmalzel 295: 4 – Seemann 1215: 1 – Sermeño 137: 4 – Shattuck 1162: 4 – Smith, H.H. 1507: 1, 4; 1508: 4; 1514: 5; 1515: 4; 1516: 4 – Smith, J.D. 2547: 4; 2554: 4; 6975: 4 – Smith, R.F. V3653: 1; V4012: 1; V8653: 1 – Snedaker C-6: 4 – Sousa 988: 1; 2413: 1 – Standley 9328: 4; 21226: 1; 25874: 1; 31446: 4; 55014: 1; 64793: 4; 79042: 4; 87408: 4; 87561: 1 – Standley & Chacón P. 5863: 1; 5942: 1 – Standley & Padilla V. 2560: 1 – Starr 58: 7 – Stevens et al. 7420: 4; 17389: 4; 27294: 4 – Stevenson 257: 7 – Steyermark 45658: 4; 45769: 4; 45898: 4; 45916: 4 – Steyermark & Davidse 116261: 8 – Steyermark & Gonzales 113617: 2 – Steyermark et al. 122580: 2; 123032: 2 – Sugden 1212: 2; 1234: 2.

Téllez 1838: 4; 2048: 4; 2280: 4; 2546 : 4; 2687: 4; 8700: 1 – Tonduz 13896: 4; 13955: 4 – Triana 1202: 9; 3377: 9 – Trujillo 1386: 2 – Tún Ortíz 931: 4; 1107: 4; 1808: 4.

Ucan 2502 – Uribe U. 2510: 7; 2987: 7.

Valerio et al. 229: 4 – Van der Werff & Wingfield 3436: 2 – Ventura A. 7995: 1; 8490: 4; 12678: 1; 17241: 4 – Villacorta 1085: 1 – Von Sneidern 5764: 4. Walker 1211: 5 – Watson 37: 4 – Wendt & Hernández G. 5663: 4 – Wendt et al. 3796: 4; 3807: 4 – Whitefoord 3113: 4; 9172: 4; 10356: 4; 10407: 4 – Whitefoord & Eddy 486: 7 – Williams 18176: 1 – Wilson 164: 4 – Wingfield 8605: 2; 8935: 2; 8946: 2 – Wingfield et al. 12684: 2; 12697: 2. Zamudio R. 330: 4.