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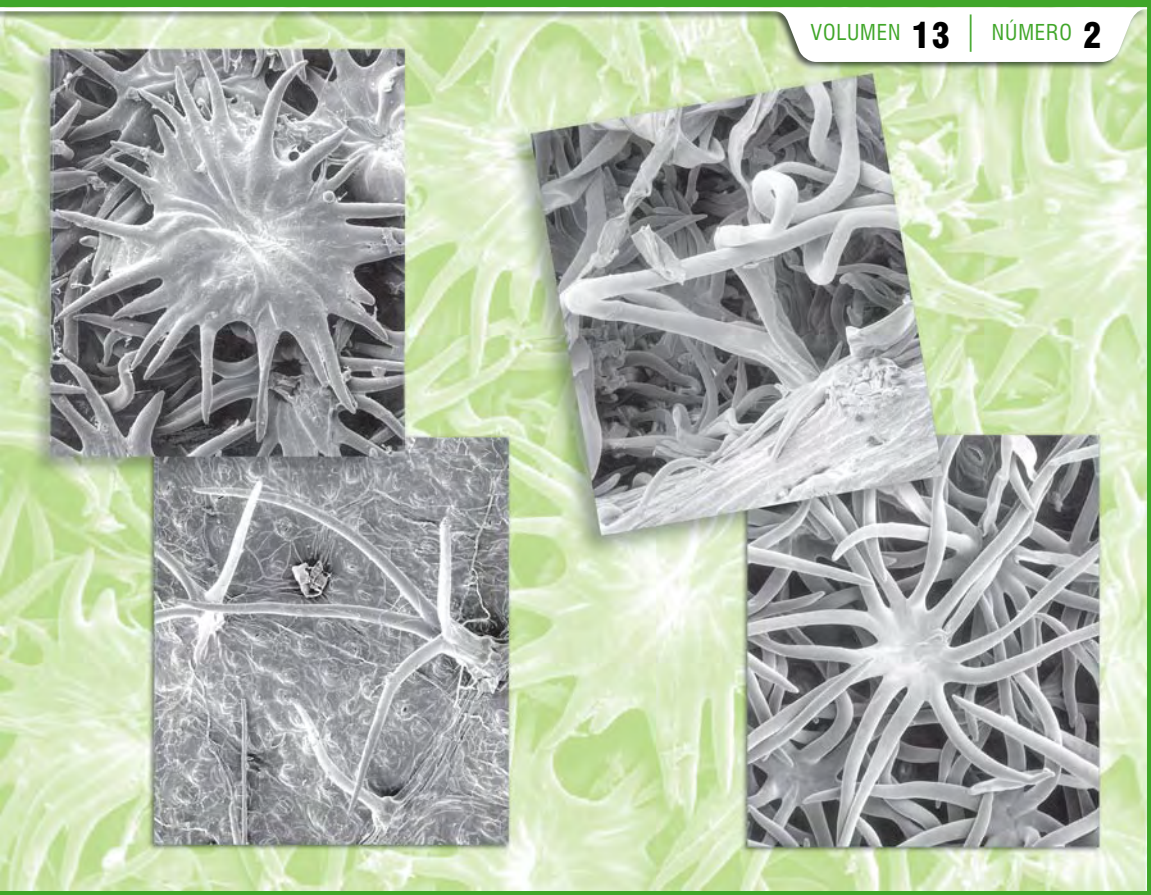

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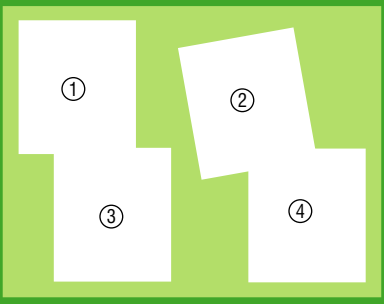

Fotomicrografías de tricomas foliares de algunas especies de *Clethra*

① *Clethra oleoides*
② *Clethra mexicana*
③ *Clethra kenoyeri*
④ *Clethra pringlei*

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Contenido

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Diversidad y distribución del *fitoplancton de agua dulce* en la Península de Yucatán, México

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Resumen

Con el objeto de determinar la composición y la diversidad del fitoplancton en doce cuerpos de agua dulce en la Península de Yucatán, México, se hizo un estudio un análisis florístico y ecológico de muestras húmedas depositadas en la Colección de Microalgas Dulceacuícolas y Marinas de la Universidad Autónoma de Yucatán (UADY). Las muestras de plancton se recolectaron durante la época de lluvias (agosto) de 1994, con el fin de obtener la composición ficológica (presencia/ausencia de las especies) en cada sitio. A pesar de que los resultados no señalan la presencia de un patrón geográfico como se esperaba, hay particularidades en la composición ficoflorística, la cual en apariencia se encuentra determinada por las condiciones hidrológicas de los cuerpos de agua estudiados. Los factores relacionados con el pH y la turbidez, junto con la temperatura, son los que influyen en la presencia o ausencia de especies. Se registraron 98 especies de microalgas, correspondientes a 60 géneros, 28 familias, 16 órdenes y cinco divisiones. Las especies con distribución más amplia fueron *Microcystis aeruginosa* Kütz., *Chlorella vulgaris* Beij., *Synedra ulna* (Nitzc.), *Dictyosphaerium pulchellum* Wood, *Gomphosphaeria aponina* Kütz. y *Microcystis protocystis* Crow.

Palabras clave: Riqueza de especies, limnología, cenote, Cyanophyta, Crysophyta, Pyrrophyta, Euglenophyta, Chlorophyta.

Abstract

In order to determine the composition and diversity of phytoplankton in twelve freshwater bodies in Mexico's Yucatan Peninsula, a floristic and ecological analysis was made of moist samples deposited in the Collection of Microalgas Dulceacuícolas y Marinas de la Universidad Autonoma de Yucatan (UADY). The samples of plankton were collected during the rainy season (August) of 1994, so as to obtain the phycological composition (presence/absence of the species) at each site. Although the results do not indicate the presence of the expected geographic pattern, there are characteristics of the phycofloristic composition that appear to be determined by the hydrological conditions of the water bodies being studied. Factors related to pH and turbidity, as well as temperature, are those that influence the presence or absence of species. Ninety-eight species of phytoplankton, corresponding to 60 genera, 28 families, 16 orders and five divisions were registered. The species with wider distribution were *Microcystis aeruginosa* Kütz., *Chlorella vulgaris* Beij., *Synedra ulna* (Nitzc.), *Dictyosphaerium pulchellum* Wood, *Gomphosphaeria aponina* Kütz. and *Microcystis protocystis* Crow.

Keywords: Species richness, limnology, cenote, Cyanophyta, Crysophyta, Pyrrophyta, Euglenophyta, Chlorophyta.

Introducción

El conocimiento que se tiene sobre la ecología de las microalgas continentales es limitado, a pesar de que las especies que forman parte del fitoplancton tienen una gran importancia dentro de las cadenas tróficas como productoras de oxígeno, bioindicadoras y hasta depuradoras de contaminación (Mora-Navarro et al. 2004).

El fitoplancton de agua dulce de la Península de Yucatán ha sido poco estudiado; los trabajos existentes están muy restringidos en escala espacial (v.gr. Sánchez-Molina & Zetina-Moguel 1993; López-Adrián & Herrera-Silveira 1994), por lo que el conocimiento que se tiene de la influencia de los parámetros ambientales (hidrológicos) en la

composición y diversidad del fitoplancton es muy limitado. Esto contrasta con la cantidad de estudios que existen en otras regiones del país, que involucran diversos aspectos y distintos grupos de microalgas (Komarkova-Legnerova & Tavera-Sierra 1996; Valadez-Cruz et al. 1996; Ibarra-Vázquez & Novelo 1997; Montejano et al. 2000, Mora-Navarro et al. op. cit.).

En el presente estudio se examinó la composición y la diversidad (riqueza de especies) del fitoplancton en doce cuerpos de agua dulce, relacionando estos parámetros bióticos con variables limnológicas (temperatura, pH, alcalinidad y conductividad eléctrica), con el fin de generar información ecológica de base sobre el fitoplancton de agua dulce de la península de Yucatán.

Materiales y métodos

Las muestras de fitoplancton analizadas corresponden a diez cenotes y dos lagunas interiores (Laguna Coba y Laguna San Antonio en Quintana Roo), ubicados en la parte norte de la Península de Yucatán (figura 1). Las muestras fueron recolectadas durante la época de lluvias (agosto) de 1994, como parte de las actividades de un proyecto (clave CONABIO MO11) enfocado en la caracterización limnológica de los cuerpos de agua dulce de la región (Herrera-Silveira et al. 1998).

En cada unidad de muestreo, se filtraron por lo menos un litro de agua, correspondientes a puntos representativos del sitio, mediante muestras superficiales directas y con una red de plancton (10µ), del 5 al 21 de agosto de 1994. Las muestras concentradas, fijadas primeramente con lugol y finalmente con formol

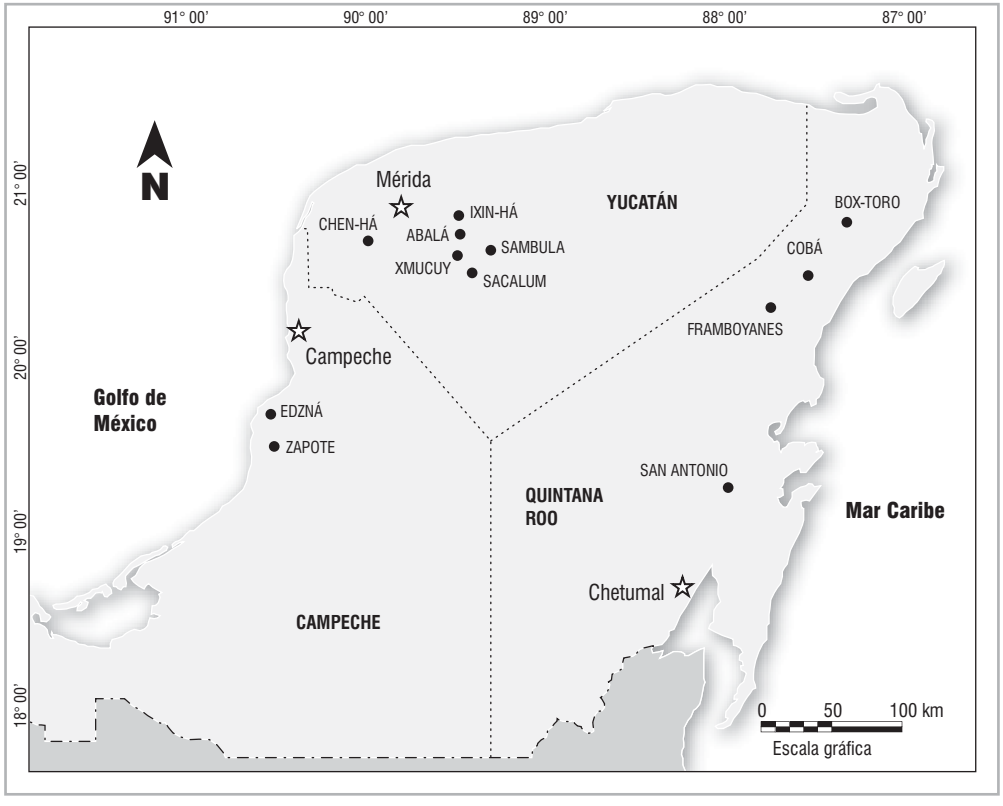

Figura 1. Ubicación de los sitios de colecta en la Península de Yucatán, México.

al 4%, se encuentran depositadas en la Colección de Microalgas Dulceacuícolas y Marinas de la Península de Yucatán (UADY), única en su tipo en el sureste de México (López-Adrián & Barrientos-Medina 2005). Las muestras húmedas, junto con los datos ambientales correspondientes (alcalinidad, conductividad eléctrica, pH y temperatura), se encuentran depositadas bajo los siguientes números de catálogo: 191, 192, 194, 195, 197, 198, 200, 209, 218, 219, 221 y 225.

Los datos sobre la composición ficológica de cada sitio se obtuvieron al revisar al menos cinco alícuotas (20 ml cada una) de la muestra conservada, las cuales se observaron en cámaras de sedimentación con la ayuda de un microscopio óptico con micrómetro integrado. El proceso de identificación se realizó con la ayuda de literatura especializada (Ettl 1978; Ettl 1983; Komarek & Fott 1983; Komarek & Kontantinos 1999).

Con los datos de composición por sitio se construyó una matriz de datos binarios (presencia/ausencia), la cual se sometió a un análisis de clasificación (cluster), con el objeto de determinar la presencia de un patrón geográfico en la composición de microalgas, utilizando como medida de asociación el índice de Baroni-Urbani y Buser y el método UPGMA como estrategia de agrupamiento (Kovach 1995). También se empleó una prueba ji-cuadrada para experimentos multinomiales para evaluar las diferencias en la diversidad taxonómica por cada división de microalgas (Zar 1984) y un análisis de correlación simple para relacionar la riqueza de especies y los parámetros limnológicos (StatSoft 1994); en ambos casos, se ajustó el nivel crítico (0.05) con el procedimiento de comparación de Holm (Manly 2001). Por último, se empleó un análisis de correspondencias canónicas (CCA) para relacionar la matriz de datos ficológicos y la matriz de datos ambientales (Ter Braak 1986).

Resultados

Se registraron 98 especies de microalgas, correspondientes a 60 géneros, 28 familias, 16 órdenes y cinco divisiones (Apéndice 1). Las divisiones más diversas fueron Chlorophyta y Chrysophyta (cuadro 1), presentándose diferencias significativas en los números de familias, géneros y especies por división taxonómica. En el apéndice se incluye la lista sistemática, junto con las localidades en las que fue registrada cada especie. Las especies con mayor distribución fueron *Microcystis aeruginosa* Kütz., *Chlorella vulgaris* Beij., *Synedra ulna* (Nitzc.), *Dictyosphaerium pulchellum* Wood, *Gomphosphaeria aponina* Kütz. y *Microcystis protocystis* Crow., con frecuencias de aparición iguales o superiores al 25%. Se observó una baja similitud entre sitios en términos de la composición microalgal (figura 2), a pesar de lo cual se puede señalar que la mayoría de los cenotes del estado de Yucatán incluidos se agrupan con el cenote Framboyanes y Laguna San Antonio (Quintana Roo), mientras que la localidad de Sacalum se agrupa con la Laguna Cobá (Quintana Roo) y el cenote ubicado en la zona arqueológica de Edzná, en Campeche.

La mayor cantidad de especies (24) se registró en el cenote Chen-Há y la menor en Ixin-Há, con sólo tres especies presentes (*Microcystis aeruginosa, M. protocystis* y *Chlorella vulgaris*). De acuerdo con el coeficiente de correlación de Spearman, la temperatura del agua es la que mejor se correlaciona con el número de especies ($r = 0.60$, $p < 0.05$), porque hay sitios con registros altos de temperatura (en particular los cenotes de Chen-há y Edzná) que presentaron un número alto de especies.

De acuerdo con los resultados del análisis de correspondencias canónicas, sólo los primeros cuatro ejes son interpretables desde el punto de vista ambiental y juntos explican el 38% de la variación en la

Cuadro 1. Diversidad taxonómica de las divisiones de microalgas registradas en el presente estudio, de acuerdo con su número de órdenes, familias, géneros y especies. Se señalan con asteriscos las diferencias significativas, de acuerdo con el procedimiento de comparación de Holm.

	Euglenophyta	Pyrrophyta	Chlorophyta	Cyanophyta	Crysophyta	X^2	P
Órdenes	1	1	6	2	6	8.37	0.0790
Familias	1	2	12	4	9	15.92	0.0030***
Géneros	2	2	25	12	18	39.31	6.4 x 10-7**
Especies	5	2	36	20	35	53.64	1.08 x 10-10*

*P< 0.0125, **P< 0.0167, ***P< 0.0250.

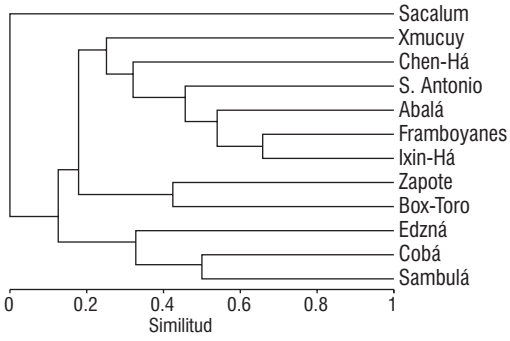

Figura 2. Similitud entre las localidades consideradas en el presente estudio, en términos de la composición ficoflorística.

composición ficológica (cuadro 2). Los dos primeros ejes canónicos (variación acumulada del 21%), señalan que existe una relación apreciable entre las propiedades limnológicas y el fitoplancton (cuadro 3). El primer eje se relaciona con cambios en la temperatura y los niveles de dureza (alcalinidad), mientras que el segundo se encuentra asociado con la conductividad eléctrica y en segundo término con el estado de acidez (pH).

De conformidad con el diagrama de ordenación, se determinó la presencia de cuatro grupos de microalgas (figura 3). El primer grupo, que incluye a *Nitzchia amphibia*, *Gomphosphaeria aponina*, *Amphora ovalis* y *C. vulgaris*, se relaciona con la temperatura del agua; *Pediastrum duplex* y *Synedra ulna* son parte del segundo grupo, correlacionado con la alcalinidad. En el tercer grupo, asociado con la conductividad eléctrica, están *Lyngbia latissima* y *Nitzchia scalaris*. Por último, *Cosmarium punctulatum* y *Selenastrum* sp. son parte del cuarto grupo, que se relaciona en cierto grado con el pH.

Cuadro 2. Resumen de los resultados del CCA. Se incluyen los porcentajes acumulativos (PA) en la variación de los datos fitoplánctico y en la relación especie-ambiente.

	Eje 1	Eje 2	Eje 3	Eje 4
Valores propios	0.84	0.79	0.70	0.64
Correlación especie-ambiente	0.99	0.98	0.99	0.98
PA datos fitoplánctico	10.80	21.06	30.11	38.35
PA relación especie-ambiente	23.54	44.76	61.29	75.00

Cuadro 3. Coeficientes canónicos y correlaciones intraconjunto de las variables limnológicas con los dos primeros ejes canónicos.

	Coeficientes canónicos		Correlaciones intraconjunto	
	Eje 1	Eje 2	Eje 1	Eje 2
Temperatura	-3.658	0.626	-0.895	-0.07
pH	0.623	-0.837	0.069	-0.624
Alcalinidad	-2.235	0.623	0.605	0.555
Conductividad eléctrica	1.512	1.252	0.193	0.908

Discusión y conclusiones

Con base en los registros que se obtuvieron, resulta evidente que las clorofitas, bacillariofitas (diatomeas) y cianofitas son las divisiones más diversas. Este patrón de diversidad había sido ya notado por otros autores (López-Adrián & Herrera-Silveira 1994; Schmitter-Soto et al. 2001), pero no en las mismas proporciones.

Del total de especies, 81 sólo se presentaron en un sitio, lo que explica la baja similitud que existe entre localidades. Por este hecho, se puede señalar que para la época de lluvias en la cual se desarrolló el trabajo de campo, los sitios incluidos en el presente estudio presentan una composición específica particular. Otros factores que pudieran explicar el patrón observado es la inclusión de sistemas acuáticos con origen similar, pero con distintos tipos de desarrollo (Herrera-Silveira & Comín 2000), así como las diferencias que pudieran presentarse entre sitios en términos de las concentraciones de nutrimentos y materia orgánica (Wetzel 1975; Reynolds 1984), aspectos que no fueron evaluados.

La temperatura es uno de los factores hidrológicos que ejercen una influencia marcada en el crecimiento y distribución de las algas (González-González 1992), como se pudo corroborar en este trabajo, ya que la temperatura del agua se correlacionó positivamente con la riqueza de especies de microalgas. Por otra parte, en escala espacial, tanto la temperatura como la conductividad eléctrica (la cual está relacionada con la turbidez del agua, según Torres-Orozco y García-Calderón 1995) son los factores principales que se relacionan con la composición de microalgas de agua dulce. Estas propiedades, junto con el pH y la alcalinidad (que son a su vez indicadores del estado de acidez de los cuerpos de agua, de acuerdo con Fott et al. 1999), pueden influir de manera notable en los grupos fitoplánctico de agua dulce de la Península de Yucatán.

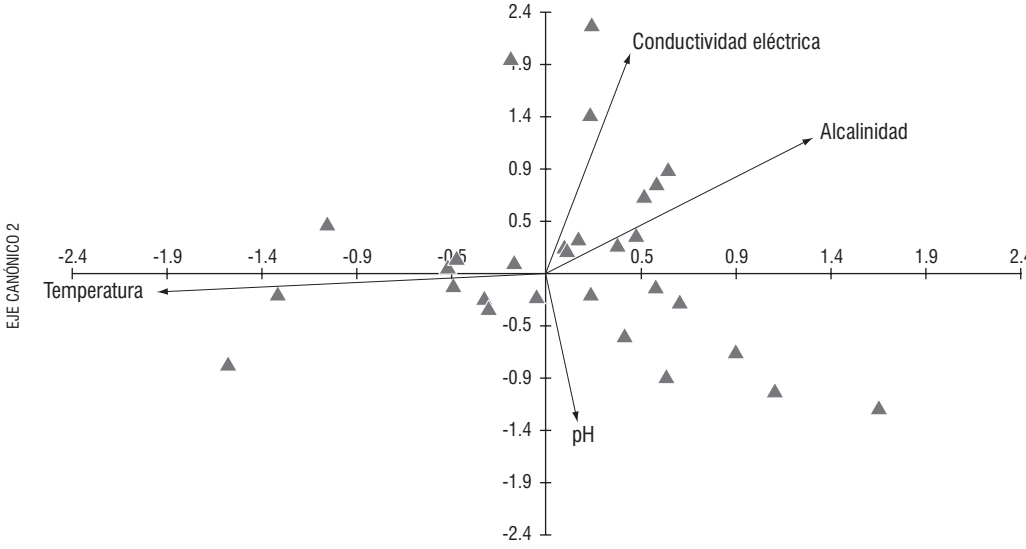

Figura 3. Diagrama de ordenación (CCA), donde se muestran las variables ambientales (flechas) y las especies de microalgas (triángulos).

No obstante que el enfoque del presente trabajo es restringido, pues sólo involucra 12 unidades de muestreo y una temporada climática, se pueden establecer ciertas tendencias. Por ejemplo, la diversidad del fitoplancton al parecer ha sido subestimada, pues se registraron 98 especies, muchas de las cuales no aparecen mencionadas en exploraciones o revisiones recientes (Sánchez et al. 2001; Schmitter-Soto et al. 2001). Los resultados indican que las diferencias limnológicas entre sitios (sobre todo en la temperatura superficial y la conductividad eléctrica) en el período de muestreo pueden explicar las diferencias en la composición fitoplanctónica. Al ser el presente trabajo una de las primeras referencias que abordan el estudio de la variación espacial de la composición del fitoplancton de agua dulce en la región, estas aseveraciones preliminares deben ser aclaradas con estudios más detallados que involucren aspectos ligados con la dinámica espacial y temporal de las comunidades de microalgas dulceacuícolas, en términos cualitativos y cuantitativos.

Agradecimientos

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Apéndice 1

Lista sistemática de las microalgas presentes en cada cuerpo de agua (en mayúsculas). El orden de las categorías supragenéricas está de acuerdo con las referencias utilizadas en el proceso de determinación. Los géneros y especies están ordenados desde el punto alfabético.

División Cyanophyta
Orden Chroococcales

Familia I. Chroococcaceae

1. *Chroococcus turgidus* (Kütz.) Nägeli, 1849 COBÁ, EDZNÁ
2. *Coelosphaerium minutissimum* Nägeli, 1849 CHEN-HÁ
3. *Gloeocapsa* cfr. *polidermatica* SACALUM

4. *Gomphosphaeria aponina* Kütz., 1836 CHEN-HÁ, COBÁ, SAMBULÁ
5. *Merismopedia minima* Beck, 1897 CHEN-HÁ
6. *Merismopedia glauca* (Ehrenberg) Kütz., 1845 XMUCUY
7. *MIcrocystis aeruginosa* (Kütz.) Kütz. ABALÁ, CHEN-HÁ, FRAMBOYANES, IXIN-HÁ, SAN ANTONIO
8. *MIcrocystis elabens* (Breb.) Kütz. CHEN-HÁ
9. *MIcrocystis protocystis* Crow (after Crow) BOX-TORO, COBÁ, IXIN-HÁ
10. *MIcrocystis viridis* (A. Brown in Rabenhorst) Lemm., 1903 SAN ANTONIO

Orden Hormogonales

Familia II. Oscillatoriaceae
11. *Lyngbia latissima* Prescott ABALÁ, COBÁ
12. *Oscillatoria formosa* Bory ex Gomont, 1827 ABALÁ
13. *Oscillatoria limosa* Ag. ex Gomont, 1892 ZAPOTE
14. *Oscillatoria printzii* Vaucher ex Gomont SAMBULÁ
15. *Phormidium subfuscum* Kütz. ex Gomont SACALUM

Familia III. Nostocaceae
16. *Pseudoanabaena catenata* Lauterb. en Bourrelly, 1972 EDZNÁ
17. *Cylindrospermopsis* cfr. *catemaco* SAN ANTONIO
18. *Cylindrospermopsis philippensis* (Taylor) SAN ANTONIO
19. *Cylindrospermopsis raciborskii* (Wolosz.) Seenayya et Subba Raju, 1972 SAN ANTONIO

Familia IV. Tubiellaceae
20. *Johannesbaptista pellucida* (Dickie) Taylor et Dronet, 1938 COBÁ

División Crysophyta
Clase Diatomophyceae (=Bacilliophyceae)
Subclase Centrophycidae
Orden Coscinodiscales (=Eupodiscales)

Familia V. Coscinodiscaceae
21. *Cyclotella meneghiniana* Kütz. CHEN-HÁ

Orden Biddulphiales

Familia VI. Anaulaceae
22. *Terpsinoe musica* Ehrenberg XMUCUY

Subclase Pennatophycidae
Orden Diatomales

Familia VII. Diatomaceae
23. *Fragilaria ulna* (Nitzch) Lange-Bertalot, 1980 BOX-TORO, COBÁ
24. *Synedra ulna* (Nitzch) Ehrenberg ABALÁ, FRAMBOYANES, XMUCUY, ZAPOTE

Orden Eunotiales

Familia VIII. Eunotiaceae
25. *Eunotia monodon* Ehrenberg, 1843 CHEN-HÁ

Orden Achnanthales

Familia IX. Achnanthaceae
26. *Achnantes inflata* (Kütz.) Grunow in Cleve & Grunow, 1880 XMUCUY
27. *Achnantes lanceolata* (Brebisson) Grunow in Cleve & Grunow, 1880 ZAPOTE
28. *Achnantes minutissima* Kütz., 1833 ZAPOTE
29. *Cocconeis placentula* Ehrenberg, 1838 ZAPOTE

Orden Naviculales

Familia X. Naviculaceae
30. *Amphora ovalis* Kütz., 1844 CHEN-HÁ, XMUCUY
31. *Amphora subcapitata* (Kisselev) Hustedt, 1959 CHEN-HÁ
32. *Cymbella turgidula* Grunow in A. Schmidt et al., 1875 ZAPOTE
33. *Diploneis interrupta* (Kütz.) Cleve, 1894 SACALUM
34. *Gyrosigma scalproides* (Rabenhorst) Cleve, 1894 ZAPOTE
35. *Gomphonema angustatum* (Kütz.) Rabenhorst, 1864 ZAPOTE
36. *Gomphonema gracile* Ehrenberg, 1838 CHEN-HÁ
37. *Navicula brockmannii* Hustedt, 1934 BOX-TORO
38. *Navicula contenta* Grunow in Van Heurck, 1884 XMUCUY
39. *Navicula cryptotenella* Lange-Bertalot, 1985 CHEN-HÁ
40. *Navicula peregrina* (Ehrenberg) Kütz., 1844 SAMBULÁ
41. *Navicula viridula* (Kütz.) Ehrenberg, 1838 CHEN-HÁ
42. *Pinnularia maior* (Kütz.) Rabenhorst, 1853 COBAY, XMUCUY

Familia XI. Epithemiaceae
43. *Denticula elegans* Kütz., 1844 BOX-TORO
44. *Denticula* aff. *kuehtzinguii* SACALUM
45. *Denticula kuehtzinguii* Grunow, 1862 CHEN-HÁ
46. *Denticula ocellata* W. Smith, 1856 CHEN-HÁ
47. *Denticula tenuis* Kütz., 1844 FRAMBOYANES

Familia XII. Nitzchiaceae
48. *Nitzchia amphibia* Grunow, 1862 CHEN-HÁ, SAN ANTONIO
49. *Nitzchia intermedia* Hantzch ex Cleve & Grunow, 1880 CHEN-HÁ
50. *Nitzchia pusilla* Grunow, 1862 emend. Lange-Bertalot, 1976 CHEN-HÁ
51. *Nitzchia scalaris* (Ehrenberg) W. Smith, 1853 COBÁ, SAMBULÁ
52. *Nitzchia sigmoidea* (Nitzch) W. Smith, 1853 EDZNÁ

Familia XIII. Surirellaceae
53. *Campylodiscus bicostatus* W. Smith in Roper, 1854 CHEN-HÁ
54. *Surirella biserata* Brébisson in Brébisson & Godey, 1836 EDZNÁ
55. *Surirella robusta* Ehrenberg, 1841 ZAPOTE

División Pyrrophyta
Clase Dynophyceae
Subclase Dinophycidae
Orden Peridiniales

Familia XIV. Peridiniaceae
56. *Peridinium gutwinskii* Woloszynska FRAMBOYANES

Familia XV. Goniaulaceae
57. *Goniaulax apiculata* (Penard.) Entz. FRAMBOYANES

División Euglenophyta
Clase Euglenophyceae
Orden Euglenales

Familia XVI. Euglenaceae
58. *Euglena acus* (O.F. Müller) Ehrenberg CHEN-HÁ
59. *Euglena spirogira* Ehrenberg EDZNÁ
60. *Phacus acuminatus* Stokes EDZNÁ
61. *Phacus pleuronectes* (O.F. Müller) Dujardin EDZNÁ
62. *Phacus tortus* (Lemm.) Skvdrtzow EDZNÁ

División Chlorophyta
Clase Chlorophyceae
Subclase Chlorophycidae
Orden Volvocales

Familia XVII. Volvocaceae
63. *Eudorina elegans* Ehrenberg, 1831 CHEN-HÁ
64. *Eudorina illinoisensis* (Kofoid) Pascher, 1927 CHEN-HÁ

Orden Chlorococcales

Familia XVIII. Chlorococcaceae
65. *Characiopsis longipes* (Kabenh.) Borzi var. westii Lemm. ABALÁ
66. *Tetraedon minimum* (A. Br.) Hansg., 1888 XMUCUY
Familia XIX. Oocystaceae
67. *Chlorella vulgaris* Beij., 1890 CHEN-HÁ, EDZNÁ, FRAMBOYANES, IXIN-HÁ
68. *Kirchneriella contorta* (Schmidle) Bohl, 1892 ZAPOTE
69. *Kirchneriella irregularis* (G.M. Smith) Kors, 1953 BOX-TORO
70. *Kirchneriella subcapitata* Kors, 1953 BOX-TORO, ZAPOTE
71. *Monoraphidium minutum* (Näg.) Kom.-Legn., 1969 ZAPOTE
72. *Oocystis solitaria* Wittr in Wittr & Nordst., 1869 CHEN-HÁ
73. *Selenastrum* sp. EDZNÁ
74. *Selenoderma* cfr. *africana* ZAPOTE
75. *Selenoderma* cfr. *skujae* Bohlin, 1897 BOX-TORO
Familia XX. Dictyosphaeraceae
76. *Botryococcus braunii* Kütz., 1849 CHEN-HÁ
77. *Botryococcus protuverans* cfr. var. *minor* COBÁ
78. *Dictyosphaerium pulchellum* Wood, 1872 BOX-TORO, SAN ANTONIO, ZAPOTE
Familia XXI. Scenedesmaceae
79. *Coelastrum microporum* Näg. in A. Br. 1855 ZAPOTE
80. *Coelastrum microporum* var. *octahedricum* (Skuja) Sodomk., 1972 EDZNÁ
81. *Scenedesmus opoliensis* P. Richt., 1896 EDZNÁ
82. *Scenedesmus quadricauda* (Turp.) Breb. sensu Chod., 1913 EDZNÁ, ZAPOTE
Familia XXII. Hydrodictyaceae
83. *Pediastrum angulosum* (Ehrenberg) ex Menegh., 1840 COBÁ
84. *Pediastrum argentinense* Bourr.& Tell in Tell, 1979 COBÁ
85. *Pediastrum duplex* Meyen, 1829 COBÁ, EDZNÁ

Orden Chaetophorales

Familia XXIII. Chaetophoraceae
86. *Pseudodendoclonium printzii* Wille, 1900 SACALUM
87. *Pseudopleurococcus botryoides* Vischer, 1933 SACALUM

Orden Siphonocladales

Familia XXIV. Cladophoraceae
88. *Cladophora fracta* Kütz., 1843 FRAMBOYANES, XMUCUY
89. *Cladophora glomerata* Kütz., 1843 ABALÁ
90. *Rhizoclonium hieroglyphycum* Kütz., 1843 ABALÁ, XMUCUY

Orden Zygnematales

Familia XXV. Zygnemataceae
91. *Spirogyra ternata* Lyng, 1820 ABALÁ

Orden Desmidiales

Familia XXVI. Closteriaceae
92. *Closterium dianae* Deflandre, 1928 FRAMBOYANES
Familia XXVII. Desmidiaceae
93. *Cosmarium margaritiferum* Deflandre, 1928 EDZNÁ
94. *Cosmarium portianum* Kieger & Bourrelly, 1956 EDZNÁ
95. *Cosmarium punctulatum* Krieger & Bourrelly, 1956 EDZNÁ, SAMBULÁ
96. *Euastrum insulare* Deflandre, 1928 EDZNÁ
Familia XXVIII. Mesotaniaceae
97. *Pseudorastrum sebaldii* Deflandre COBÁ
98. *Hyalotheca dissiliensis* Krieger & Bourrelly, 1956 COBÁ

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Forestiera corollata: una nueva especie de Oleaceae mesoamericana

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Resumen

Se propone *Forestiera corollata* X. Cornejo & E. Wallander, una nueva especie de árbol, endémica del estado de Tabasco al sudeste de México, Departamento El Petén al norte de Guatemala y Belice. Debido a su distintiva e inusual presencia de flores pistiladas con pétalos, que constituye una excepción a nivel genérico, *Forestiera corollata* es segregada de *F. rhamnifolia* Griseb., ampliamente distribuida en el Caribe.

Palabras clave: *Forestiera ecuadorensis*, *F. rhamnifolia*, flores pistiladas, pétalos.

Abstract

On account of its distinctive and unusual pistillate flowers with petals, *Forestiera corollata* X. Cornejo & E. Wallander is herewith proposed as a new tree species. It is endemic to El Petén Department, in northern Guatemala, and the adjacent state of Tabasco, in southeastern Mexico and Belize. *Forestiera corollata* is segregated from *Forestiera rhamnifolia* Griseb., widespread in the Caribbean.

Introducción

Forestiera Poir. (Oleaceae) es un género de arbustos y árboles que comprende 14 especies, que se distribuyen desde Estados Unidos hasta Panamá, Ecuador y el Caribe. Se caracteriza por presentar hojas simples, opuestas, con inflorescencias racemosas muy cortas con flores apétalas, unisexuales, las estaminadas con 2–5 estambres y frutos drupáceos (Brooks 1977; Green 1994; Pool 2001; Cornejo & Bonifaz 2006). En la revisión del género *Forestiera*, Brooks (1977:165) encontró unos especímenes que poseían inusuales flores pistiladas con pétalos, esto fue considerado una "anomalía floral" en este género, el cual se caracteriza por presentar flores apétalas, y fueron incluídos y tratados en sentido amplio bajo *Forestiera rhamnifolia* Griseb. Al realizar el estudio molecular de las especies de *Forestiera* (Wallander & Cornejo, en preparación), es notable que los mencionados especímenes de flores con pétalos de *F. rhamnifolia* s.l. no pertenecen a la especie en discusión, sino a una no descrita que necesita ser nominada. Las colecciones citadas provienen del estado de Tabasco al sudeste de México, del Departamento El Petén al norte de Guatemala y en la adyacente Belice, constituyendo su distribución geográfica un mayor soporte para esta novedad.

Forestiera corollata X. Cornejo et E. Wallander, sp. nov. TIPO: Guatemala. El Petén: Lacandon, El Caribal, bordering the river, in high forest, about 6 km SW, 5 Feb 1962 (fl), *Elias Contreras 3319* (Holótipo: NY 00818876!, isótipos: LL/TEX, MO 3726827!). Figuras 1 y 2A.

Species *Forestierae rhamnifoliae* Griseb. affinis, a qua floris pistilatis cum petalis differt.

Árbol hasta 12 m de alto y 13 cm DAP, dioico. Ramas con lenticelas orbiculares hasta elípticas, 0.2–0.8 mm de largo, blanco-cremosas; las ramas terminales subcilíndricas hasta ± complanadas, las jóvenes corto-pilosas, glabrescentes. Hojas opuestas, simples; lámina papirácea hasta delgada, cartácea, elíptica hasta oblongo-elíptica, pocas veces ovada -elíptica, 6.5–16 × 3.5–7 cm, base cuneada, ápice acuminado, margen repando o inconspicuamente dentado hasta inconspicuamente laxo-crenado hacia la porción distal de la lámina, algo lustrosa y glabra en ambos lados o haz con la nervadura media corto-pilosa, envés con numerosos y diminutos puntos glandulares-porosos, de color café, a veces algo hundidos; 8–12 pares de nervaduras secundarias, oblicuas a divergentes, prominentes en el envés, intersecundarias presentes, terciarias laxo-reticuladas, algo prominentes hasta impresas en el envés; pecíolos 5–10 mm de largo, acanalados, a veces

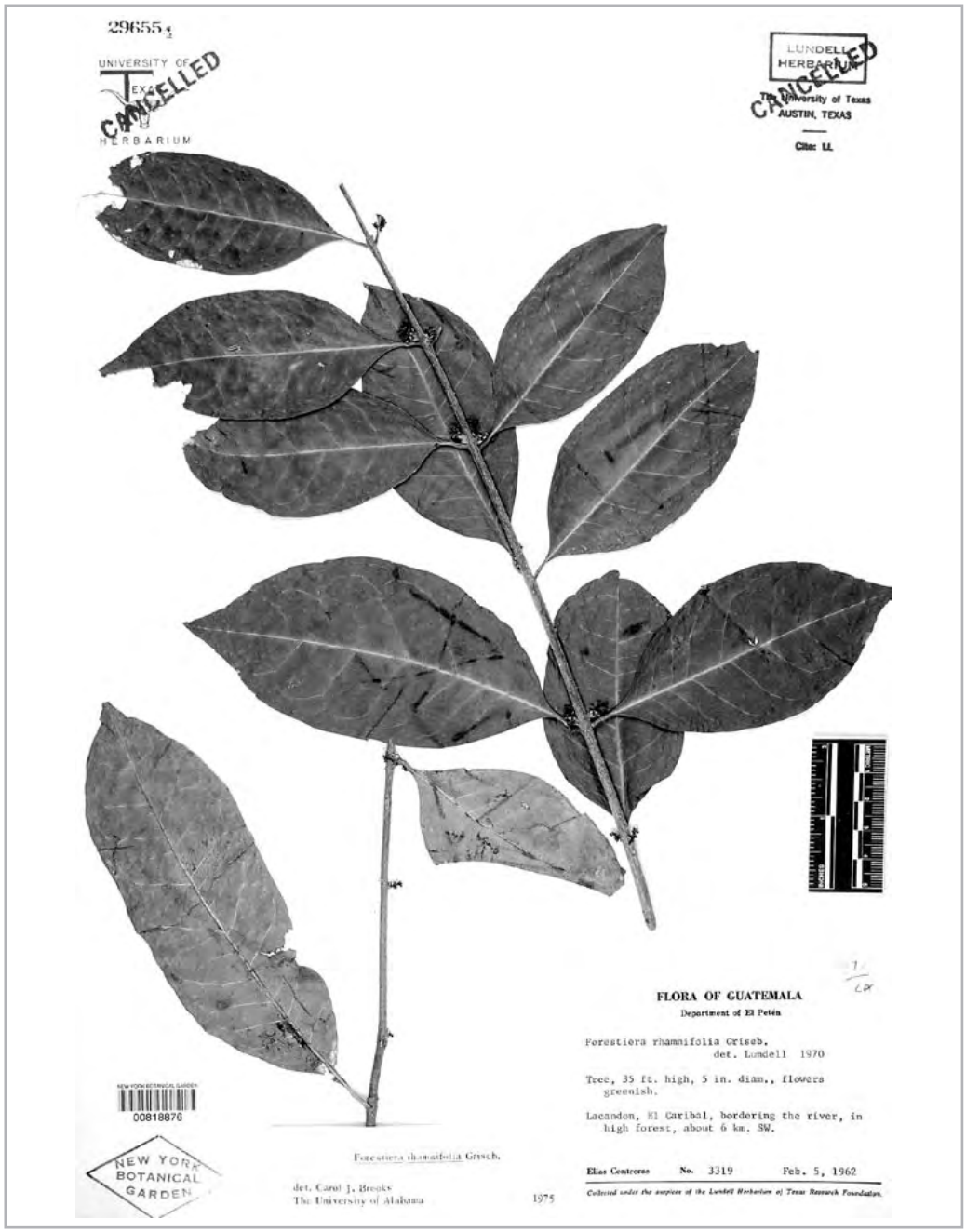

Figura 1. *Forestiera corollata* X. Cornejo & E. Wallander, el holótipo (*E. Contreras 3319*, NY).

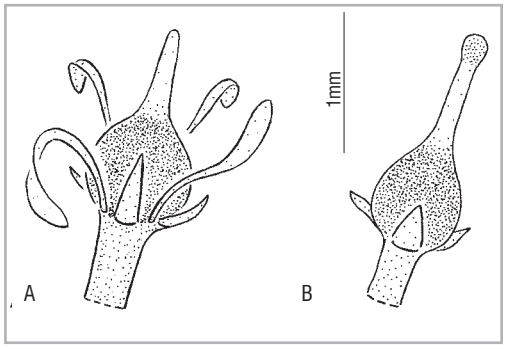

Figura 2. Flores en antesis de: A. *Forestiera corollata* X. Cornejo & E. Wallander, nótese la presencia de la corola (*E. Contreras 3319*, NY). B. *Forestiera rhamnifolia* Griseb. (*J. Shafer 13817* [Cuba], NY).

rimulosos en el lado adaxial, castaño hasta crema o crema-verdosos al secar, glabros, articulados con la rama. Inflorescencias pistiladas solitarias o en pares, racemosas, axilares y supraxilares, dispuestas a lo largo de las ramas hasta las porciones terminales, 5–10 mm de largo, verdosas (en vivo), castaño obscuras (en seco); pedúnculo con 4–6 pares de bracteolas basales, sésiles, densamente decusadas y exteriormente convexas, cartáceas, deltoides hasta elípticas, 0.5–3 × 1–2.5 mm, ápice ampliamente obtuso hasta apenas agudo, margen ciliado o glabro, amarillentas (en seco); pedúnculo 3–7 mm, raquis subtetragonal. Flores 5, 7, 9 u 11, dispuestas a lo largo del raquis en pares decusados, rematando en 3 flores terminales, la central ebracteada; las flores decusadas están subtendidas por una bráctea, divergente hasta divaricada con relación al raquis, foliosa, elíptica u obovada hasta algo oblanceolada, c. 2–3 × 1.4–2.5 mm, base cuneada, ápice obtuso a redondeado, frecuentemente erosa a ciliolada, cóncava en el lado adaxial; pedicelos c. 0.8–1.5 mm, articulados en la base y divergentes con relación al raquis, glabros; flores pistiladas c. 1.5 mm de largo, cáliz sin tubo, sépalos 4, libres, agudo-lanceolados, desiguales, 0.2–0.8 × 0.1–0.2 mm, ápice agudo, glabros; corola presente, pétalos alternisépalos, libres, lineares a lineares-oblanceolados, 1.2–2.3 × 0.1–0.2 mm, curvos al secar, glabros, pronto deciduos; estaminodios ausentes; ovario sésil, piriforme, 0.4–0.8 × 0.4–0.8 mm, negro al secar, glabro; estilo 0.4–1 mm, con frecuencia granuloso, glabro; estigma indiferenciado, ensanchado desde la posfloración. Inflorescencias e individuos estaminados desconocidos. Infructescencias 1–2.5 cm de largo, pedicelos 1–2.5 mm de largo, frutos elípticos, ca. 8–10 × 3–4.5 mm, glauco-purpuroides, glabros.

PARÁTIPOS: **Belice**. Belize District, above the mangrove, Cornhouse creek, 31 Ene 1931, *Bartlett 11283* (GH, F, NY!, US!, MICH). **Guatemala**. El Petén: Guayacán, La Pita, bordering Río San Pedro, in tintal on Guadalupe Ranch, 11 Ene 1968, *Contreras 7441* (C!, LL/TEX). El Ceibo, 11 Ene 1968, *Contreras 7447* (LL/TEX, MO!). **México**. Tabasco: Río Carrizal, 16 Dic 1888, *Rovirosa 318* (PH).

FENOLOGÍA: Florece entre diciembre y febrero; fructifica entre enero y febrero.

ETIMOLOGÍA: Su epíteto específico se refiere a su conspicuo caracter de las flores pistiladas: provista de corola (Fig. 2A).

La colección *Bartlett 11283* (Belice) posee frutos y carece de flores pistiladas. Desde el punto de vista vegetativo y geográfico concuerda con las colecciones de *Forestiera corollata*, por lo cual ha sido aquí incluida. Mayores estudios y colecciones de individuos con inflorescencias pistiladas, podrían revelar que varias de las poblaciones continentales identificadas como *F. rhamnifolia*, principalmente las localizadas a baja altitud, pertenecerían a esta especie nueva. En consecuencia, *F. corollata* tendría un mayor rango de distribución geográfica en América Central, y más aún *F. rhamnifolia* s.s., cuyo lectótipo (*Rugel 792*) proviene de Punta Brava, Cuba, podría ser una especie de distribución restringida al Caribe.

De acuerdo con los resultados moleculares (Wallander & Cornejo, en prep.), *Forestiera corollata* es afín a la sudamericana *F. ecuadorensis* X. Cornejo y C. Bonifaz, la cual presenta flores estaminadas sin corola, lamentablemente sus individuos pistilados aún son desconocidos (cuadro 1).

Cuadro 1. Diferencias morfológicas entre *Forestiera corollata* y *F. ecuadorensis*.

	***F. corollata* (pistilada)**	***F. ecuadorensis* (estaminada)**
Corola	Presente	Ausente
Ápice de la hoja	Agudo hasta acuminado, hasta 1 cm	Usualmente largo-acuminado, 1-2.5 cm
Pares de bracteolas basales	4–6	2–3

Agradecimientos

A los herbarios C, GB y MO, por el préstamo de sus colecciones, incluyendo el sintipo de *Forestiera rhamnifolia* (*Wright 2939*, MO).❖

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Foliar trichome variation in *Clethra* Subsect. Cuellaria (Clethraceae) from Mexico

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Abstract

This survey describes and illustrates the most common trichome types found in twenty species of *Clethra* from Mexico. A dissecting microscope and scanning electron microscope (SEM) were used to examine the abaxial leaf surface and to determine the significance of trichome types as taxonomic characters. Three main non-glandular trichome types occur in the genus: acicular, fasciculate and stellate. The last is considered especially representative of *Clethra*. This work reviews the taxonomy proposed by Sleumer (1967), who separated subsect. Cuellaria into four series: Glabrae, Tomentellae, Tomentosae and Ferrugineae based on leaf vestiture.

Key words: Foliar morphology, trichome structure, SEM, *Clethra*, Ericales.

Resumen

Se estudiaron e ilustraron los tricomas foliares de veinte especies de *Clethra* de México con el fin de determinar su significancia como un caracter taxonómico. Para las observaciones de la superficie abaxial se utilizaron el microscopio estereoscópico y el de barrido (SEM). Se distinguieron tres tipos principales de tricomas no glandulares en el género: acicular, fasciculado y estrellado, éste último se considera representativo de *Clethra*. Se revisó la taxonomía propuesta por Sleumer (1967) quién separó de acuerdo con el indumento foliar la subsect. Cuellaria en cuatro series: Glabrae, Tomentellae, Tomentosae y Ferrugineae.

Palabras clave: Morfología foliar, estructura de tricomas, SEM, *Clethra*, Ericales.

Introduction

The genus *Clethra* Gronov. ex L. is a monotypic and taxonomically complex genus distributed in temperate and tropical regions of both hemispheres. The number of species has been estimated as high as about 120 by Rzedowski et al. (2001). The last worldwide revision of the family was that of Sleumer (1967), who recognized just 64 species, 12 of which were mentioned as ocurring in México. The species of *Clethra* are shrubs or modest-sized to tall evergreen trees, characteristic of the temperate and tropical forests of Mexico, where the author estimates ca. 30 species occur, making that country an important center of diversity.

Clethra was first divided by DeCandolle (1839) into two sections, Euclethra and Cuellaria, using characters of stamens, style, leaf duration (deciduous vs. evergreen) and geographic distribution, the first including American Boreal and the second American Tropical species with the one species from Madeira. However, Sleumer (op. cit.), relying on better, more constant characters primarily of the seeds divided the genus differently, also into two sections. The Section Clethra (seeds not winged) included all Asian, Malasian and two North American species, and the Section Cuellaria (seeds winged). The last was subdivided into two subsections: Subsection Cuellaria (seeds circumwinged), containing all Mexican, Central and South American species, and the Subsection Pseudocuellaria (seed winged to the extremes), accomodating the Madeiran species. At the same time, Sleumer arranged Subsection Cuellaria in four series: Glabrae, Tomentellae, Tomentosae and Ferrugineae; he defined them as follows:

Series Glabrae. Young and mature leaves with the areoles or intervenium glabrous abaxially, the veins glabrous or pilose, with age completely glabrous. This series included 13 species, mostly South American, with some exceptions: *Clethra suaveolens* Turcz., *C. occidentalis* (L.) Kuntze, *C. vicentina* Standl., *C. pyrogena* Sleumer and *C. cubensis* A. Rich.

Series Tomentellae. Young and mature leaves with the abaxial surface totally covered by a tenuous tomentum more or less appressed and concolorous, formed by minute, yellowish, stellate trichomes, as only one or two strata, the inferior stratum with minute, stellate trichomes, and the superior stratum with longer stellate trichomes more or less together (tomentellous), and the reticulum slightly prominent. This series contained 16 species, mostly from Mexico and Central America and one from Cuba.

Series Tomentosae. Young and mature leaves with the abaxial surface totally covered with dense, minute, more or less appressed, stellate trichomes forming the inferior stratum; superior stratum covering all the veins with longer stellate, fasciculate trichomes. To the naked eye the surface is tomentulose, tomentose or woolly, the mature leaves glabrescent but not punctate. This series included 15 species: Mexico (6 spp.), Central America (5 spp.), South America (7 spp.), Trinidad (1 sp.) and Jamaica (2 spp.), some countries sharing the same species.

Series Ferrugineae. Young and mature leaves abaxially covered (including areoles and all veins) with minute, dense, matted, stellate trichomes, as an inferior stratum and the superior stratum with much longer, bright-red, iron oxide or pale-reddish, yellowish or reddish, fasciculate trichomes, often stipitate, to the naked eye the surface curly-villous or woolly, when completely mature glabrescent but clearly punctate. This series contained eight species, mainly South American, mostly from Peru and one Costa Rican (*Clethra consimilis* Sleumer, Table I).

This comparative study reviewing these Sleumer's series was carried out as a part of the taxonomic revision of the species of *Clethra* in Mexico.

Materials and Methods

For the examination of trichome morphology leaf material of twenty species of *Clethra* from Mexico was selected from herbarium specimens deposited at CAS, DS, F, GH, IBUG, MEXU, MICH, TEX, US, WIS and XAL; the voucher collections are cited in Table II.

For the general descriptions of foliar surface features or macro-morphology, a dissecting microscope was used; for closer observations and more precise characterizations of the trichomes or micro-morphology, a scanning electron microscopy (SEM) was used. In order to illustrate this paper, photographs showing the general aspect of the vestiture of the abaxial leaf surface and SEM images or photomicrographs were obtained.

Table I. Species of *Clethra* by series cited for Mexico by Sleumer (1967).

Glabrae	Tomentellae	Tomentosae
C. occidentalis	*C. alcoceri*	*C. lanata**
*C. suaveolens**	*C. hartwegii**	*C. macrophylla**
C. vicentina	*C. macrophylla**	*C. mexicana**
	C. occidentalis	*C. occidentalis*
	*C. oleoides**	*C. rosei**
	C. parvifolia	*C. vicentina*
	*C. pringlei**	
	C. vicentina	

*Included in this study

The concepts of macro-morphology and micro-morphology as well as the terminology of vestiture and trichome types follows Hardin (1979a, 1990, 1992), Hardin and Jones (1989), Stearn (1991) and Harris and Woolf (1994). The descriptions of the leaf morphology are arranged into the series Glabrae, Tomentellae and Tomentosae according to Sleumer's classification; the species are listed alphabetically within each taxonomic section. The series Ferrugineae was not treated in this survey, because it includes mostly South American species. The distribution of the trichomes types on the abaxial leaf surface is summarized in Table III.

Results

Most *Clethra* species have well-developed indumentum on both vegetative and reproductive organs, such as twigs, petioles, leaves (both surfaces), rachis, pedicels, sepals, petals (inner surface), ovary and capsules. However, it is the foliar trichomes that have provided important characters of great significance in the systematics of this difficult monogeneric family.

The twenty Mexican species studied here have three main types of trichomes (acicular, stellate and fasciculate) plus two more (filiform and multiradiate), which however, are not present in the majority of the species. In the genus *Clethra* glandular trichomes are absent.

Table II. Alphabetic list of species of *Clethra* from Mexico and their voucher collections for the SEM study.

Species	Collector/Herbarium	State
1. *C. chiapensis*	*Shilom Ton 621* (DS)	CHIAPAS
2. *C. conzattiana*	*González-V. 4231* (IBUG	OAXACA
3. *C. costaricensis*	*Nevling & Gómez-Pompa 1372* (F)	VERACRUZ
4. *C. fragrans*	*Pérez de la Rosa 1369* (IBUG)	JALISCO
5. *C. galeottiana*	*González-V. 4160B* (IBUG)	OAXACA
6. *C. hartwegii*	*Ramírez et al. 632* (IBUG)	JALISCO
7. *C. hondurensis*	*Matuda 1894* (DS)	CHIAPAS
8. *C. kenoyeri*	*Rzedowski 27661* (DS)	HIDALGO
9. *C. lanata*	*Rzedowski 19589* (TEX)	OAXACA
10. *C. luzmariae*	*Miranda 9225* (MEXU)	OAXACA
11. *C. macrophylla*	*Diggs & Nee 2818* (XAL)	VERACRUZ
12. *C. mexicana*	*McVaugh 9973* (LL)	MICHOACAN
13. *C. nicaraguensis*	*Breedlove 53385* (CAS)	CHIAPAS
14. *C. nutantiflora*	*Breedlove 58384* (CAS)	CHIAPAS
15. *C. oleoides*	*Breedlove 40839* (MICH)	CHIAPAS
16. *C. pachecoana*	*Breedlove & Thorne 31190* (MICH)	CHIAPAS
17. *C. pringlei*	*Sullivan 703* (TEX)	TAMAULIPAS
18. *C. rosei*	*Puga 7160* (IBUG)	JALISCO
19. *C. schlechtendalii*	*Sharp 441215* (GH)	PUEBLA
20. *C. suaveolens*	*Shilom Ton 3955* (WIS)	CHIAPAS

ACICULAR. A slender, unicellular or multicellular-uniseriate type, unbranched, more or less straight and tapered to the apex. There are two forms based on length according to Hardin (1992): the short-acicular type, 0.02–0.40 mm long, and the long-acicular, 0.41–2.5 mm long. All members of the series Glabrae and Tomentellae have at least a few acicular trichomes, manifest along the main veins of the leaf beneath, usually as upward-directed (antrorse) trichomes.

The acicular type is less noticeable when mixed with other types of trichomes, for example, with the fasciculate when they are distributed on the abaxial surface; however the acicular has the tendency to be more grouped on the major veins and in the axils of secondary veins as in most of the members of the series Tomentosae. Long-acicular trichomes may be discretely or abundantly placed throughout the lamina on the adaxial surface, leaving a pustulate surface like that characteristic of *C. costaricensis* Britton when the trichomes drop off. Acicular trichomes also commonly occur on reproductive organs as in the dense or sparse covering on the inner surface of petals, on sericeus ovaries and persisting on the surface of the mature capsule.

STELLATE. A multicellular trichome with a cluster of unicellular rays from a common base, these held horizontally and parallel to the epidermis. In *Clethra* these trichomes are minute (submicroscopic), very inconspicuous, matted and mostly flattish or somewhat erect, but the general aspect is an appressed trichome with the rays spreading in one plane. They are sessile, canescent or grayish, pale-

brown, sometimes with a reddish or ochraceous blush, with 3–17 rays. This is the commonest type of trichome found on the abaxial leaf surface in the genus.

One variant of the stellate type is the fused-stellate. It is a trichome with the rays fused beyond the base to a maximum of two-thirds the length of the ray. The union is generally asymmetrical, and the ray number is variable although usually above 10 (Hardin 1976). The species here studied showed such a trichome sessile, dull, pale-brown or ochraceous, dense and appressed to the epidermis, with 8–23 rays. The stellate and the fused-stellate types may also occur sparsely on the adaxial leaf surface.

FASCICULATE. A multicellular trichome with a cluster of 2–8 unicellular rays in a single set and the rays more or less erect (Hardin 1992). This, the most conspicuous trichome type in *Clethra*, consists of clusters of fused cells at the base, the number of cells (rays) varying according to the species (Table III). This common type is characteristic of the series Tomentosae and has been called by various authors tufted, clustered, branched or stellate. According to Hardin (op. cit.) the distinction between fasciculate and stellate types is based on the orientation of the rays, which in fasciculate are erect and in stellate horizontal. There are two frequent forms of the fasciculate, the usual stipitate-fasciculate type, in which the bases of the rays are fused into an erect stipe, and the pedestaled-fasciculate type, which has a raised epidermal base. In either case the 2–8 unicellular rays can be more or less short or very long, straight or wavy and erect or somewhat collapsed. These trichomes can be dense or sparsely distributed on the abaxial leaf surface and colored grayish, light to dark-brown or somewhat rufous as in *Clethra mexicana* DC. When the trichomes are dense, long and curly, the vestiture has a woolly appearance, for example in *C. galeottiana* Britton, *C. lanata* Mart. & Gal., *C. mexicana* and *C. rosei* Britton. These trichomes may occur mixed with the other types, such as stellate, acicular, or filiform. The fasciculate trichomes are generally the most abundant type on the twigs, petioles and rachis of the inflorescence.

In most species of *Clethra*, a combination of two or three types of trichomes occurs; however, stellate and/or stipitate-fasciculate are more or less constant within the same species though density may differ greatly. In general mature leaves have less dense vestiture on the upper surface. It is important to emphasize that a densely tomentose lower surface sometimes becomes quite glabrate. Such specimens have been called "glabrescent forms" (Sleumer 1967; González-Villarreal 1996) and occur, for example, in *C. costaricensis* and *C. lanata* of series Tomentosae and even some species of series Tomentellae like *C. pringlei* S. Watson and *C. fragrans* L. M. González & R. Ramírez. On the other hand, some species like *C. galeottiana* and *C. mexicana* exhibit a degree of persistency of the indumentum. These circumstances are in part responsible for much confusion and the creation of synonyms.

As mentioned by several authors, variations in the indumentum are possibly due to the age of the tree, the influence of local climate and soil and hybridization, giving additional taxonomic challenges. In general the most densely tomentose forms are in the drier habitats, as noticed in *Clethra rosei*, whereas shaded leaves tend to have sparse vestiture or are almost glabrous, as seen in *C. kenoyeri* Lundell and *C. fragrans*. Also, the indumentum is influenced by the age of the plant, with juvenile shoots tending to have denser indumentum on the abaxial and even on the adaxial leaf surface. As pointed out by Hardin (1979b, 1992), during blade expansion, maturation and senescence the trichomes tend to spread farther apart, and many also drop off. For taxonomic purposes the different types of trichomes and their combinations must be compared in leaves at the same state of maturity.

FILIFORM. A multicellular-uniseriate, thread-like trichome with the apex tapered to a point; slender, 0.05–2.00 mm long, generally curled or wavy (Hardin 1992). This type commonly occurs on the abaxial leaf surface, mostly confined to the midvein but sometimes on the secondary veins. It is exclusive to some members of the series Tomentosae, such as *Clethra lanata*, *C. mexicana*, *C. nicaraguensis* C. W. Ham. and *C. rosei*.

MULTIRADIATE. A multicellular, clustered or tufted, erect trichome somewhat similar to the fasciculate type, but with 8–17 rays radiating from more than one level or circle; each ray 0.05–0.15 mm long (Hardin 1992). According to Smith (2002) confusion exists in the definition of the terms multiradiate and rosulate as explained by Hardin, who used measurements to compare these trichomes types. Smith mentioned that the two types are very similar in appearance and can be separated only on the basis

of ray number, 8–20 rays for the multiradiate type and more than 21 rays for the rosulate.

In *Clethra* the multiradiate type is found most commonly on the adaxial leaf surface although sometimes it is present on the abaxial surface in some species of series Tomentellae. These trichomes are sessile, often reddish colored or pale, and when they drop off they leave a punctate mark.

Descriptions

The intent here is to characterize and illustrate the abaxial foliar surface. The series represent groups of species within *Clethra* in which the leaves have trichomes of the same generalized structure.

I. SERIES GLABRAE

Mature leaves with the abaxial surface glabrous, the midvein and secondary venation with scattered acicular trichomes or glabrous, with age the surface completely glabrous. The series contains just one species from southeastern Mexico.

Table III. Distribution of abaxial foliar trichomes types in some species of the genus *Clethra* (Clethraceae) from Mexico.

Series/Species	Stellate (Ray number)	Fused-stellate (Ray number)	Stipitate-fasciculate (Ray number)	Pedestaled-fasciculate (Ray number)
GLABRAE				
C. suaveolens	7-14			
TOMENTELLAE				
C. chiapensis		8-15		
C. conzattiana	9-16			
C. fragrans	8-13			
C. hondurensis	8-15			
C. luzmariae		8-19		
C. nutantiflora	10-17			
C. oleoides		16-23		
C. pachecoana	8-13			
C. pringlei	7-13			
C. schlechtendalii	6-13			
TOMENTOSAE				
C. costarisensis				2-7
C. galeottiana	8-9		7-8	
C. hartwegii	8-9		6-8	
C. kenoyeri				2-7
C. lanata	6-8		2-5	
C. macrophylla	3-8		2-8	
C. mexicana	7-17		2-7	
C. nicaraguensis	5-8		4-7	
C. rosei	6-9			2-8

Clethra suaveolens Turcz.

Macro-morphology. Tree, often 5–10 (–15) m or up to 65 m tall, the trunk 1 m or more dbh; **petiole** slender, flat, (3–) 10–15 (–20) mm long, reddish-brown to dark, mostly glabrous or sometimes with acicular and sessile fasciculate trichomes; **leaves** when young glabrous on both sides, with reticulate venation; **leaf blades** subcoriaceous, mostly flat, concolored or bicolored, light brown or yellowish in dry material, narrowly elliptic to elliptic-lanceolate or somewhat oblanceolate, the apex usually acute to attenuate, mucronate, sometimes rounded, the margins entire, undulate or serrulate with low incurved teeth, the base cuneate or obtuse, (1.5–) 5–15 (–19) cm long, (0.5–) 2–5 cm wide; **adaxial surface** green or yellowish when dry, totally glabrous, the midvein slightly impressed, the veins and veinlets forming a reticulate network; **abaxial surface** paler than upper surface, the epidermis smooth, lustrous with refractive epidermal cells, totally glabrous, eventually with scanty, minute, appressed, stellate trichomes, the midvein and larger veins occasionally provided with scattered short acicular or sessile fasciculate trichomes; **secondary veins** 10–15 (–17) pairs, mostly obscure, only seen as fine lines with few intermediates, some ascending, leaving the midvein at an acute angle or arching, branching before reaching the margins, the veinlets slightly impressed, forming a very thin and plane network. Figs. 1A-B.

Micro-morphology. Abaxial surface with dispersed stellate trichomes with 7–14 rays ornamented with micro-papillae or striae on the surface, the cuticle with peristomatal and other ridges; midvein and secondary veins with scattered, long, acicular trichomes. Figs. 1C-F.

Clethra suaveolens occurs in mountainous areas from the Central Plateau and Sierra Madre of Chiapas, Mexico to Honduras and Nicaragua, at elevations from 1000 to 2700 m. Typical habitats are humid oak forest, pine-oak-*Liquidambar* forest, cloud forests and montane rain forest, frequently in grassy openings and disturbed clearings.

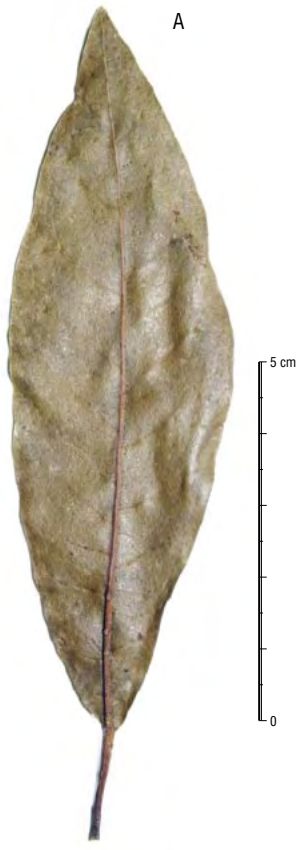
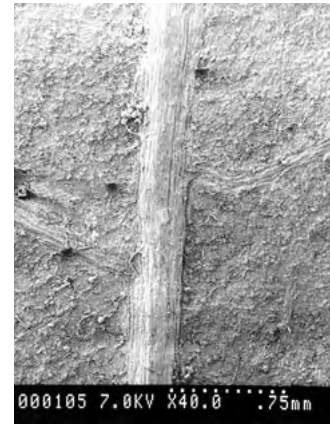


Figure 1. *Clethra suaveolens*.

C



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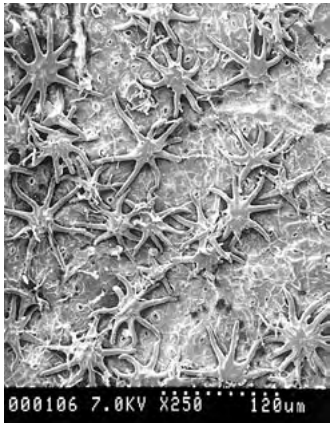


F

II. SERIES TOMENTELLAE

Mature leaves with the abaxial surface smooth to the touch, pale, yellowish or ochraceous, in appearance glabrous but actually totally covered by minute, appressed, stellate trichomes, the midvein and secondary venation with scattered, mostly antrorse, acicular trichomes, sometimes with a few fasciculate trichomes or glabrous. The series contains 10 species.

Clethra chiapensis L.M. González

Macro-morphology. Tree medium to large, 6–15 (–20) m tall; **petiole** long and slender, often flattened adaxially, (0.6–) 1.5–2.5 (–3) cm long, puberulous; **leaves** when young densely and minutely stellate above; **leaf blades** rigidly coriaceous, commonly flat, elliptic or oblanceolate to ovate-lanceolate or obovate, the apex acute, acuminate or somewhat cuspidate, often mucronate, rarely rounded, the base mostly oblique, sometimes rounded or truncate, the margins serrate to serrulate-dentate, usually extending well below the middle to near the base, rarely completely entire, the base slightly reduplicate, (2.3–) 5–10 (–15) cm long, (0.8–) 2–3 (–6) cm wide; **adaxial surface** drying olive green, with scattered, minute, pale or reddish, rosulate trichomes, becoming nearly glabrous, sometimes punctate, secondary venation impressed, the midvein with multiradiate trichomes or glabrous, the veinlets not easily discernible; **abaxial surface** dull, pale-brown, covered with minute, appressed, stellate trichomes, the midvein narrow but raised, puberulous to completely glabrous; **secondary veins** 10–13 (–18) pairs, reddish-brown, contrasting with the pale surface, almost straight or somewhat arching-ascending, forked commonly more than once and passing into the teeth, the veinlets forming a network of fine reddish-brown lines. Figs. 2A-B.

Micro-morphology. Abaxial surface covered by appressed, matted, fused-stellate trichomes with 8–15 rays ornamented with micro-papillae on the surface; midvein and secondary veins almost glabrous or with scattered fused-stellate trichomes, rarely with some short acicular trichomes. Figs. 2C-E.

Clethra chiapensis is confined to the mountainous areas of the Central Plateau of Chiapas, Mexico to adjacent Guatemala at (1500-) 2100 to 2700 m. It is found on slopes with oak-*Liquidambar*, oak-fir-pine or pine-oak-*Abies* forests and evergreen cloud forests.

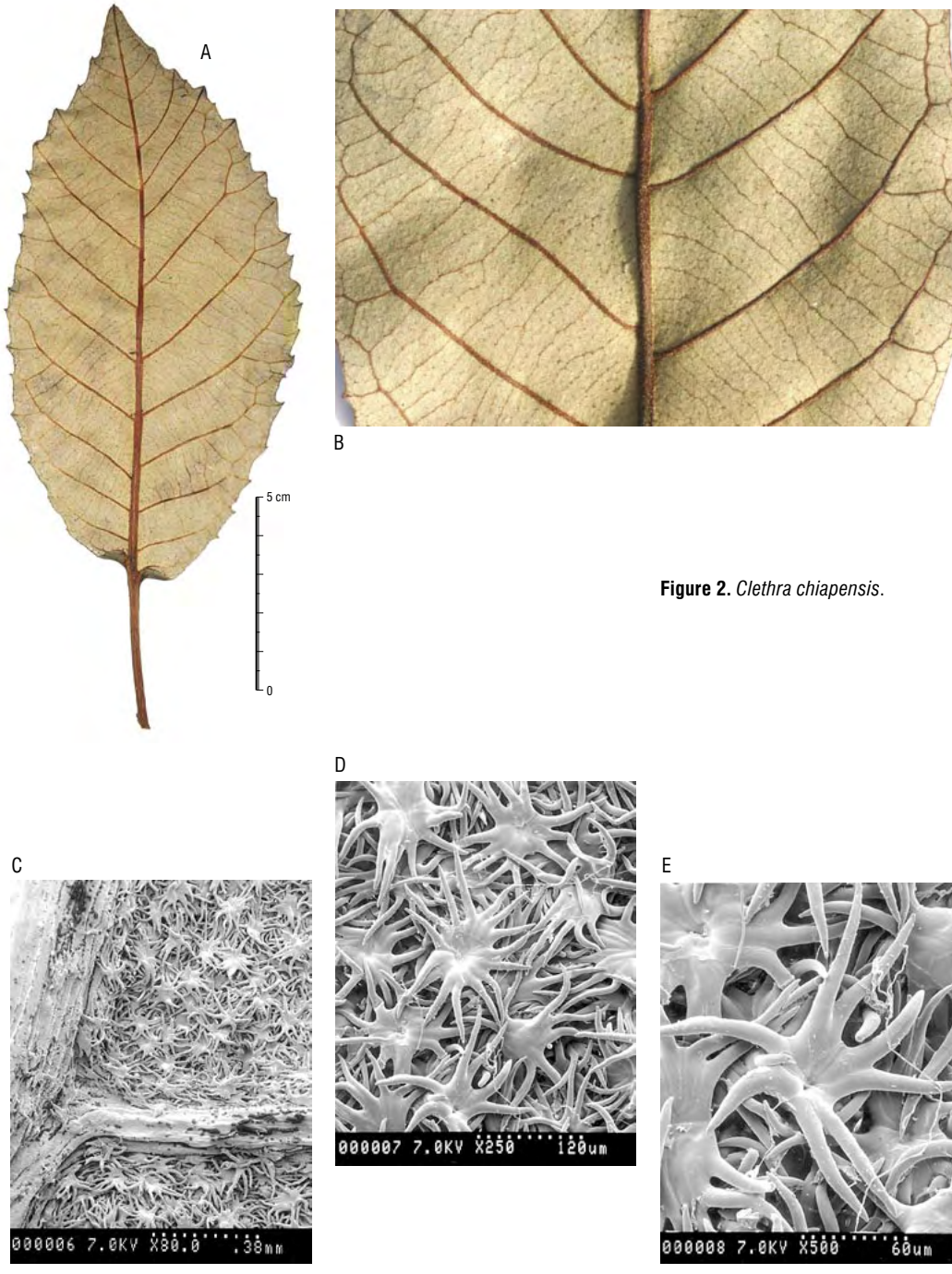


Figure 2. *Clethra chiapensis*.

Clethra conzattiana L.M. González

Macro-morphology. Tree 10–15 (–20) m tall, the trunk 15–30 cm dbh; **petiole** long and slender, (1–) 1.5–3 (–5) cm long, glabrous or with scattered stellate trichomes; **leaves** when very young densely covered with short stellate trichomes on both sides; **leaf blades** subcoriaceous, bicolored, elliptic to elliptic-oblanceolate or obovate, the apex acuminate to long-acuminate, the tip narrowly acute, aristate, rarely rounded, the base cuneate or obtuse, the margins serrate-dentate from base to apex or at least from below the middle, the teeth often curved-ascending, tipped by a stout mucro or arista, the base sometimes slightly reduplicate, (4–) 6–12 (–17) cm long, (1–) 3–5 (–9) cm wide; **adaxial surface** dark green, almost completely glabrous or with scattered, small, pale, appressed, stellate trichomes mostly on the midvein, the secondary venation well marked, the veinlets inconspicuous; **abaxial surface** noticeably paler than the upper surface, sometimes whitish or pale-brownish, covered with minute, appressed, stellate trichomes, the midvein and secondary veins provided with scattered trichomes or glabrous; **secondary veins** (15–) 20–25 pairs, slender, reddish-brown, contrasting with the much paler surface, strongly ascending or moderately arcuate, branching, passing directly into the teeth, the veinlets forming a fine reticulum of brown lines. Figs. 3A-B.

Micro-morphology. Abaxial surface covered by appressed, matted, stellate trichomes with 9–16 slender rays ornamented with micro-papillae on the surface; midvein and secondary veins almost glabrous or with very sparse stellate and acicular trichomes. Figs. 3C-E.

Clethra conzattiana is endemic to northern Oaxaca and extreme southern Puebla in the Sierra Mazateca and Sierra de Juárez mountain systems at elevations from 1700 to 2500 m. The species is found in humid forests of *Pinus*-oak with many ericads, very wet and mossy pine-*Persea* forest and cloud forests.

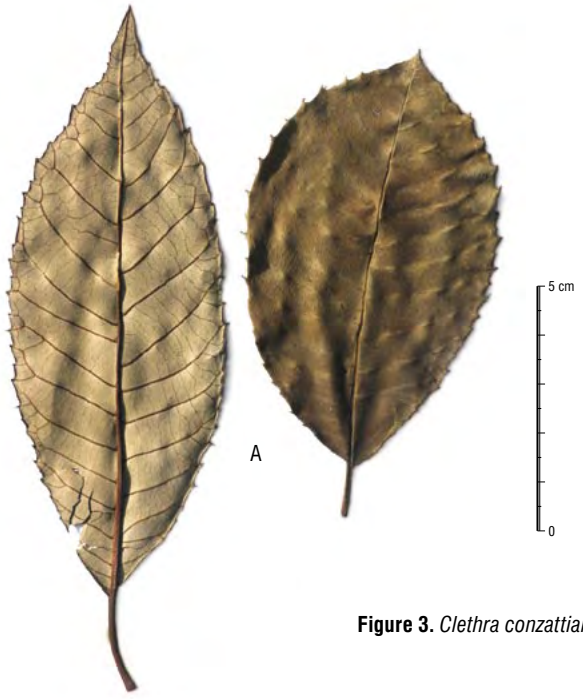
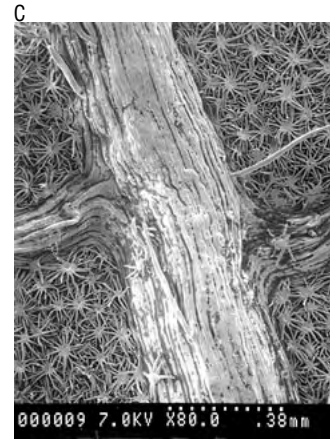
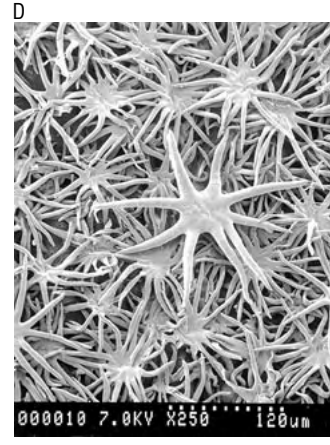
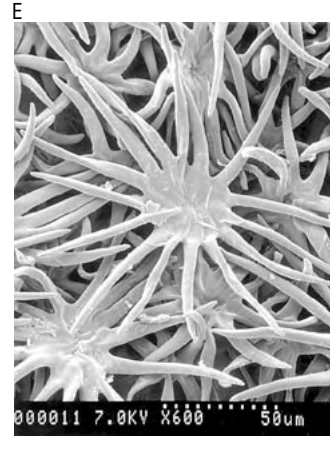


Figure 3. *Clethra conzattiana.*







Clethra fragrans L. M. González & R. Ramírez

Macro-morphology. Tree (8–) 15–20 (–40) m tall, the trunk 30–40 cm up to 1 m dbh; **petiole** slender, (10–) 15–25 (–35) mm long, terete; **leaves** when very young completely covered by appressed, rosulate trichomes on both sides; **leaf blades** subcoriaceous, bicolored, mostly flat, narrow to widely elliptic to ovate-lanceolate, rarely obovate or oblanceolate, the apex acute to acuminate or sometimes mucronate or aristate, rarely obtuse, the margins entire or sinuate, the base narrow, somewhat oblique, reduplicate, (5–) 7–12 (–21) cm long, (2–) 3–5 (–7) cm wide; **adaxial surface** dark green, lustrous, glabrous or with scattered pale, multiradiate trichomes, the midvein and secondary venation slightly impressed, the veinlets often discernible as fine lines; **abaxial surface** paler than the upper surface, often grayish or glaucous, sometimes with a brownish-yellow blush, covered with dense, minute, appressed, stellate trichomes, the midvein and secondary veins thin, somewhat prominent, with very dispersed, reddish fasciculate and rosulate trichomes plus a few acicular or almost glabrous; **secondary veins** 10–14 (–16) pairs, straight and parallel, some of them standing almost at right angles to the midvein or curved, branching and anastomosing near the margins, brown and contrasting with or the same color as the pale surface, the veinlets often forming an inconspicuous network of very fine lines. Figs. 4A-B.

Micro-morphology. Abaxial surface covered by appressed, matted, stellate trichomes with 8–13 rays ornamented with micro-papillae on the surface; along the major veins with very dispersed fasciculate trichomes with 2–4 rays, the cuticle smooth to slightly striate, with peristomatal ridges. Figs. 4C-E.

Clethra fragrans is distributed throughout the Pacific slope of the Sierra Madre del Sur in western Jalisco, Mexico at elevations from 1200 to 2300 m. It is frequently seen along roads in pine-oak forests but is also very abundant in cloud forests; on limestone as well as acidic volcanic soils.

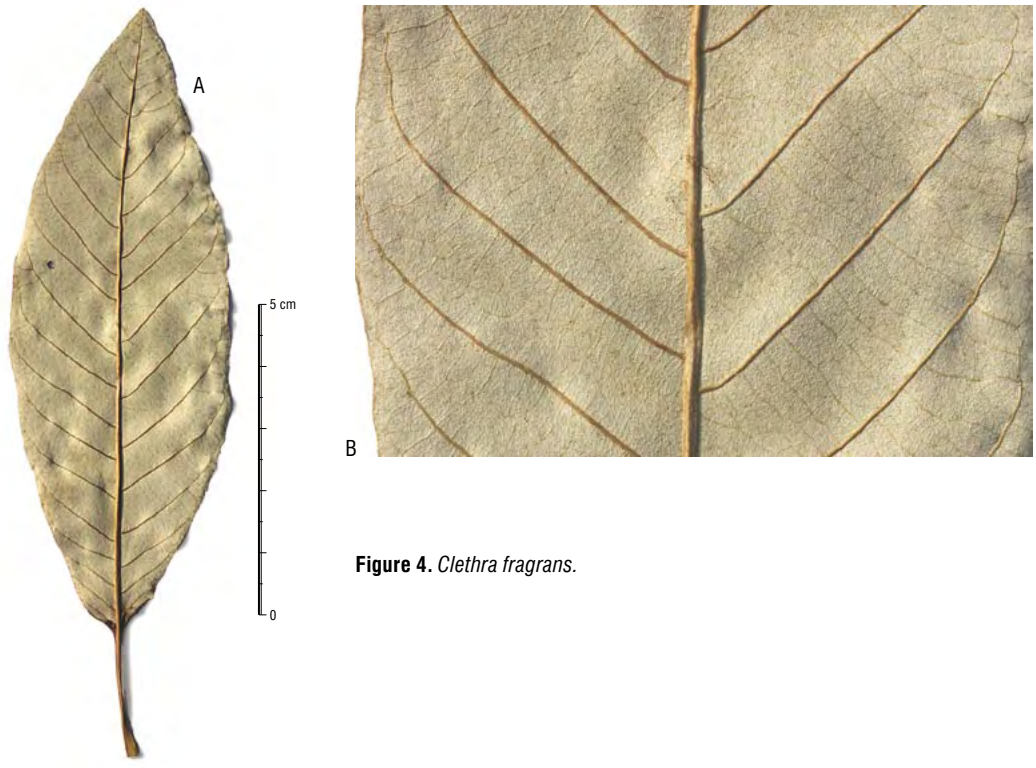


Figure 4. *Clethra fragrans.*

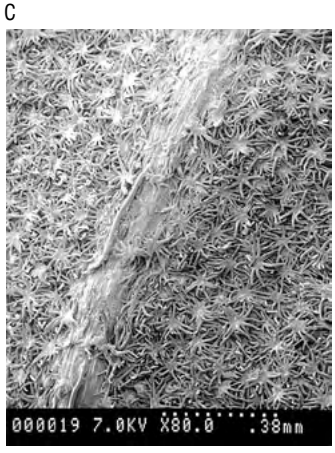
Clethra hondurensis Britton

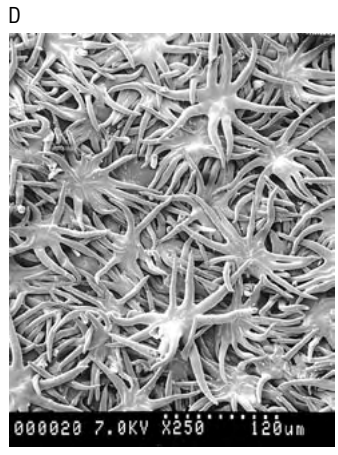
Macro-morphology. Tree, usually 8–10 m tall or to 25–40 m, the trunk 20–25 cm dbh; **petiole** long and slender, (0.8–) 1.5–2.5 (–4) cm long, laxly tomentose or puberulent; **leaves** when young densely stellate-tomentose, soon glabrescent above, densely tomentose on the larger veins below; **leaf blades** subcoriaceous, bicolored, mostly narrowly obovate or narrowly-elliptic, the apex rounded to acute with a mucro at the tip, the margins bearing marginal serrations near the apex or above the middle, the base cuneate or sub-obtuse, (4–) 7–13 (–16) cm long, (1–) 3–4 (–7) cm wide; **adaxial surface** dark green, somewhat lustrous, often punctate with multiradiate trichomes dispersed, with age glabrous or nearly so except at the base of the midvein, the larger veins evidently furrowed, the veinlets inconspicuous; **abaxial surface** paler than the upper surface, whitish to strongly pale, reddish-brown or sometimes even ochraceous, covered with minute, appressed stellate trichomes, the midvein and secondary veins narrow but prominent, puberulent, sometimes with dispersed acicular trichomes; **secondary veins** 12–14 (–16) pairs, somewhat reddish-brown, often strongly ascending, nearly straight at the base, leaving the midvein at an acute angle, the upper ones slightly curved, forked and terminating into the teeth, the veinlets forming a fine inconspicuous network. Figs. 5A-B.

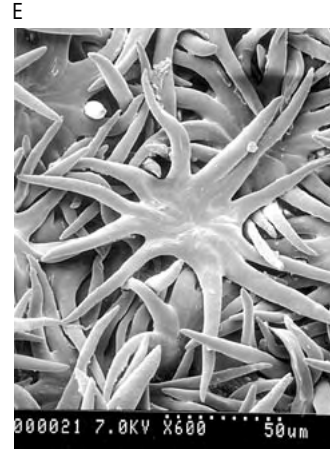
Micro-morphology. Abaxial surface entirely covered with appressed, matted stellate trichomes with 8–15 rays ornamented with micro-papillae on the surface; scattered, long, acicular trichomes restricted to the midvein. Figs. 5C-E.

Clethra hondurensis is widespread from southern Chiapas, Mexico through Guatemala, Belize and Honduras to Nicaragua. The species is found over a wide range of elevation, from 600 to 2600 m. Habitats vary from tropical rain forests to pine-oak and oak forests, usually common in disturbed areas.

Figure 5. *Clethra hondurensis.*







Clethra luzmariae L. M. González

Macro-morphology. Shrub or small **tree**, 6–10 m tall, usually spreading by horizontal underground rhizomes, thicket-forming shrubs reaching 2 m or less; **petiole** short, slender, flattened adaxially, (0.4–) 0.7–1 (–2) cm long, puberulent or somewhat pilose; **leaves** when young with scattered rosulate trichomes but almost glabrous above except for the pilose midvein; **leaf blades** rigidly coriaceous, concolored or bicolored, somewhat conduplicate, elliptic or elliptic-lanceolate, the apex acute to acuminate, sometimes mucronate or cuspidate, rarely rounded, the margins dentate-aristate (arista up to 3 mm long) mostly above the middle, in young leaves extending from near the apex to the base, rarely entire, slightly cartilaginous-thickened, sometimes evidently revolute, the base cuneate, (2.5–) 4–10 (–14) cm long, (1–) 2–3.5 (–4.5) cm wide; **adaxial surface** dark green, lustrous, often punctate or completely glabrous except the deeply furrowed midvein with acicular trichomes, the secondary veins and veinlets inconspicuous; **abaxial surface** pale-gray, covered with minute, appressed stellate trichomes, sometimes scattered, reddish multiradiate trichomes with the rays more or less erect, the midvein prominent, barely provided with acicular trichomes; **secondary veins** 9–18 pairs, slender, pale or reddish-brown contrasting with the pale surface, straight or arcuate, forked and passing directly into the teeth, the veinlets inconspicuous or absent. Figs. 6A-B.

Micro-morphology. Abaxial surface covered by appressed, matted stellate trichomes with a peltate (fused) center with 8–19 rays ornamented with micro-papillae on the surface; midvein with very dispersed, short, acicular trichomes. Figs. 6C-F.

Clethra luzmariae, an endemic species of northern Oaxaca, is very common on the Sierra de Juárez and the vicinity of Cerro Zempoaltepetl at high elevations from 2400 to 3100 m. It is found in moist oak-pine forests, in a dense ericaceous scrub in oak forests and cloud forests, as well as disturbed areas.

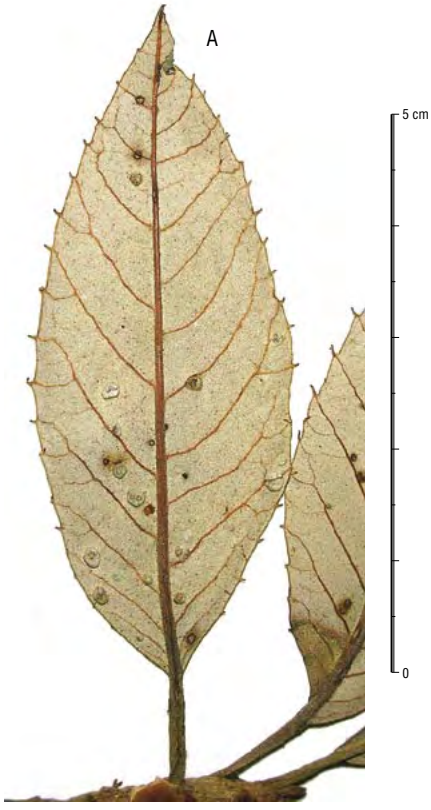
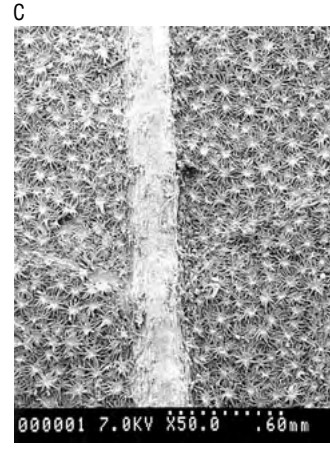
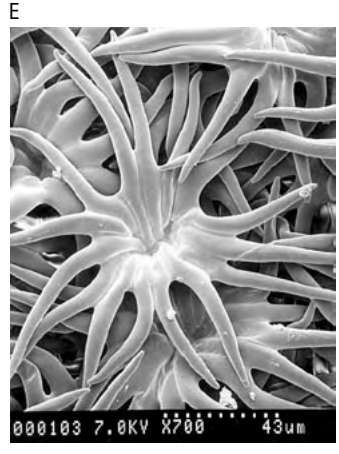
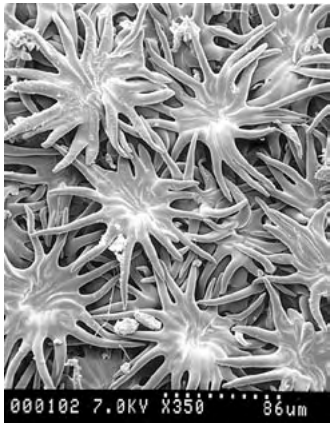
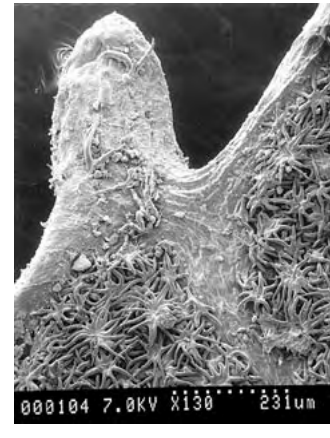


Figure 6. *Clethra luzmariae*.







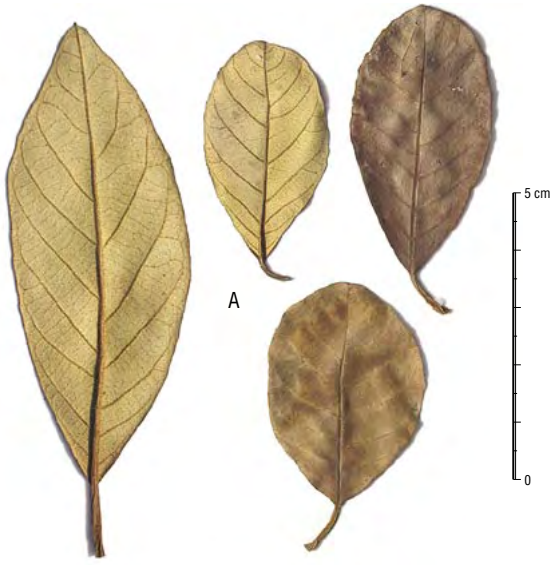


Clethra nutantiflora Standl. & L. O. Williams ex A. R. Molina

Macro-morphology. Shrub 2 m tall or small **tree**; **petiole** slender, (0.5–) 1–1.5 (–2) cm long, pilose; **leaves** when young brownish-yellow, adaxially pubescent; **leaf blades** subcoriaceous to coriaceous, bicolored, flat or somewhat conduplicate, very variable in shape even on the same branch, mostly obovate to obovate-oblong or elliptic, the apex obtuse to rounded or acute, often short acuminate, the margins entire, slightly revolute or shortly dentate, up to 8 tooth on each side above the middle or near the apex of the blade, the base mostly cuneate, sometimes obtuse, rarely slightly reduplicate, 5–10 cm long, 2.5–5 cm wide; **adaxial surface** dull when dry, punctate, with sparse, minute multiradiate trichomes, the midvein sunken, the secondary venation inconspicuous; **abaxial surface** paler than the upper surface, sometimes ochraceous, covered with minute, appressed stellate trichomes, often punctate by short, reddish-brown multiradiate trichomes with the rays more or less erect, the midvein prominent with dispersed acicular trichomes; **secondary veins** (7–) 10–15 pairs, fine, reddish-brown, covered by the indumentum, straight or arcuated, branching before the margins, some passing directly into the teeth, the veinlets very inconspicuous. Figs. 7A-B.

Micro-morphology. Abaxial surface entirely covered by appressed, matted stellate trichomes with 10–17 rays ornamented with micro-papillae on the surface; midvein with widely spaced acicular trichomes intermixed with stellate ones. Figs. 7C-E.

Clethra nutantiflora is endemic to the foothills of Mesa de Ocozocoautla, western Tuxtla Gutiérrez, Chiapas, Mexico. It occurs in steep-walled ravines, cliffs and sandstone bluffs with seasonal evergreen forest, with species of *Bouvardia*, *Bursera*, *Byrsonima*, *Clusia*, *Mastichodendron*, *Oreopanax*, *Quercus*, *Styrax*, *Ternstroemia*, and *Vaccinium*, at altitudes of 800 to 1600 m.



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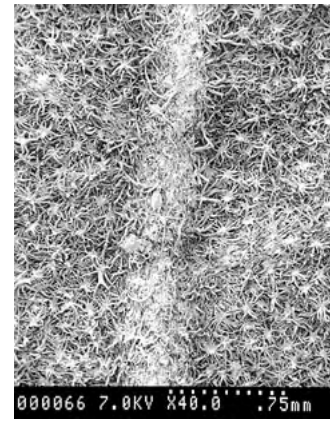

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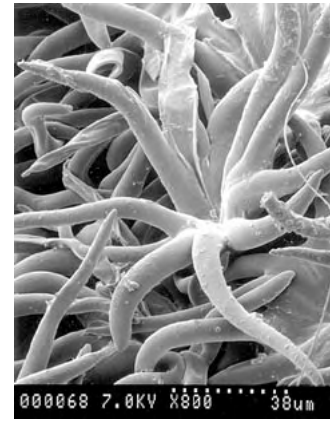


B

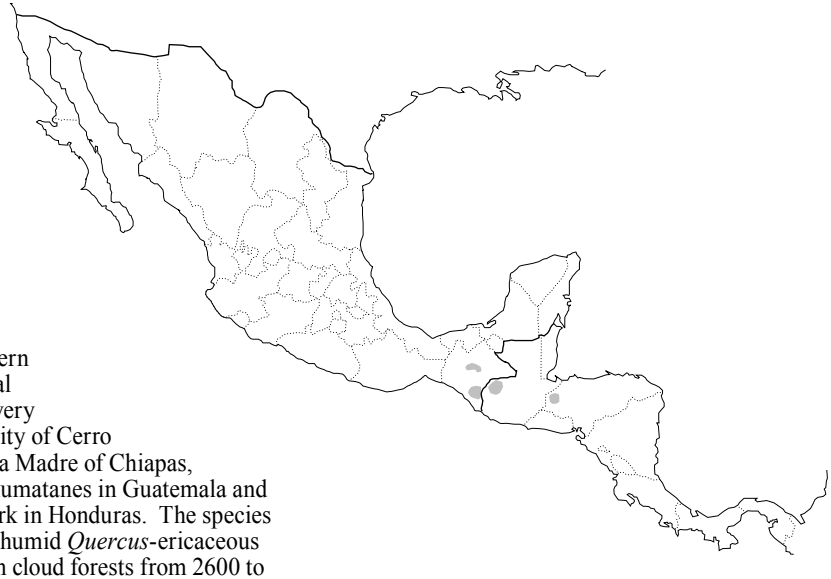
D

Figure 7. *Clethra nutantiflora.*

Clethra oleoides L. O. Williams

Macro-morphology. Small to medium **tree**, 6–8 (–15) m tall; **petiole** short, slender, (3–) 5–7 (–10) mm long, with minute, appressed stellate trichomes, densely pilose on the upper face, becoming glabrous with age; **leaves** when young almost glabrous above except for the midvein and densely covered with minute, appressed stellate-peltate trichomes below; **leaf blades** rigidly coriaceous, bicolored or concolored, often conduplicate, narrowly to broadly elliptic to elliptic-oblanceolate, occasionally obovate or oblong, the apex rounded to obtuse or acute, mucronate, the margins entire, very rarely with several minute (0.3 mm long) teeth on the margins, slightly thickened and sometimes revolute especially on young leaves, the base obtuse to cuneate, sometimes rounded, (2–) 3–7 (–10) cm long, 1–3 (–3.5) cm wide; **adaxial surface** dark green or light brown when dry, glabrous, lustrous, the midvein evidently furrowed, the secondary veins and veinlets often impressed, usually forming a rugulose network; **abaxial surface** paler than the upper surface, dull gray-brown, completely covered by dense, minute, appressed stellate trichomes with dispersed, reddish-brown multiradiate trichomes, the midvein raised, bearing a few acicular, reddish-brown trichomes mainly near the leaf base, the secondary venation obscure; **secondary veins** 8–15 pairs, forming inconspicuous, fine lines ascending or almost perpendicular to the midvein, branching and much diminished distally, the veinlets practically absent. Figs. 8A-B.

Micro-morphology. Abaxial surface entirely covered by appressed, matted stellate trichomes with a peltate (fused) center with 16–23 rays ornamented with micro-papillae on the surface; midvein with very sparse short acicular trichomes. Figs. 8C-F.



Clethra oleoides ocurrs in several disjunct areas, southern Mexico in the Central Plateau of Chiapas, very common in the vicinity of Cerro Zontehuitz and Sierra Madre of Chiapas, Mexico; Sierra Cuchumatanes in Guatemala and Celaque National Park in Honduras. The species is typically found in humid *Quercus*-ericaceous forests and evergreen cloud forests from 2600 to 3300 m.

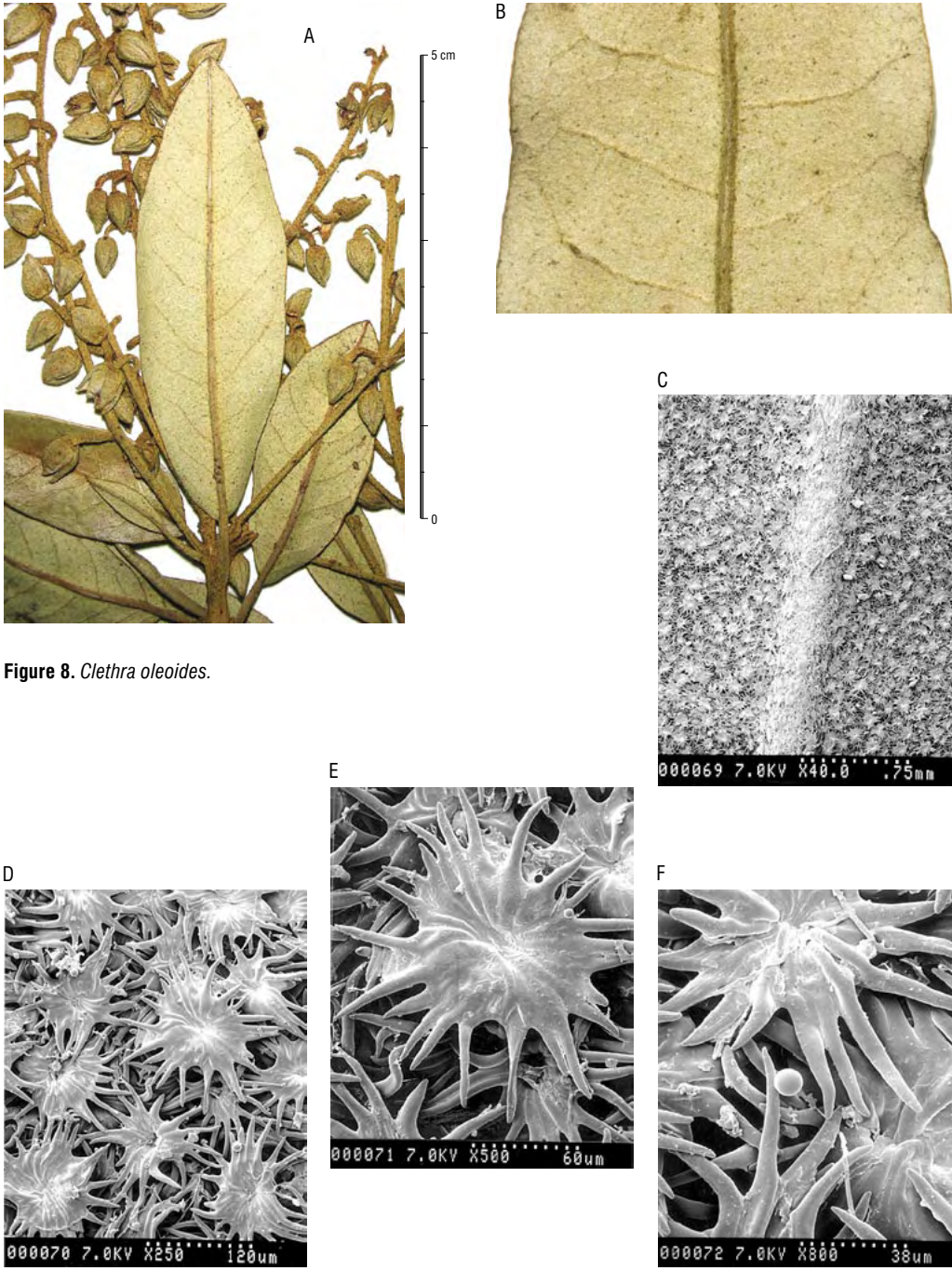


Figure 8. *Clethra oleoides.*

Clethra pachecoana Standl. & Steyerm.

Macro-morphology. Tree 6–15 (–30) m tall, with a very dense crown, often with slim trunk; **petiole** slender, 5–15 mm long, brownish-yellow to dark-brown, pubescent to puberulous; **leaves** when young with dense to sparse, rosulate trichomes of amber color, more concentrated on the midvein; **leaf blades** subcoriaceous, bicolored, mostly elliptic to narrowly elliptic, somewhat oblong or obovate, the apex acute to acuminate, very rarely rounded or obcordate, the margins entire, undulate, sometimes slightly revolute, often the young leaves with 6–12 serrations on each side, the base cuneate or truncate, evidently reduplicate, (2.5–) 5–9 cm long, (1–) 1.5–3 (–3.5) cm wide; **adaxial surface** dull green, with scattered rosulate trichomes or almost glabrous, the midvein and secondary venation furrowed, the veinlets obscure or discernible; **abaxial surface** paler than the upper surface, covered with minute, appressed stellate trichomes with some dispersed multiradiate trichomes in amber color, the midvein slender but raised, with short (0.4 mm long) acicular trichomes, the secondary venation as fine lines contrasting with the pale surface, often all the veins glabrous with age; **secondary veins** 10–15 pairs, somewhat prominent, brownish, mostly curved or sometimes straight, rarely some of them standing almost at right angles to the midvein, branching near the margins, the veinlets forming a fine network of parallel lines. Figs. 9A-B.

Micro-morphology. Abaxial surface covered with appressed, matted stellate trichomes with 8–13 rays ornamented with micro-papillae on the surface; main veins with short acicular trichomes. Figs. 9C-E.

Clethra pachecoana is known from the southernmost Mexican state of Chiapas and adjacent Guatemala to El Salvador. It grows on volcanic soils at high elevations from (1600-) 2000 to 3800 m. It is a common tree not only in cloud forests but also in humid *Quercus-Pinus* forests.

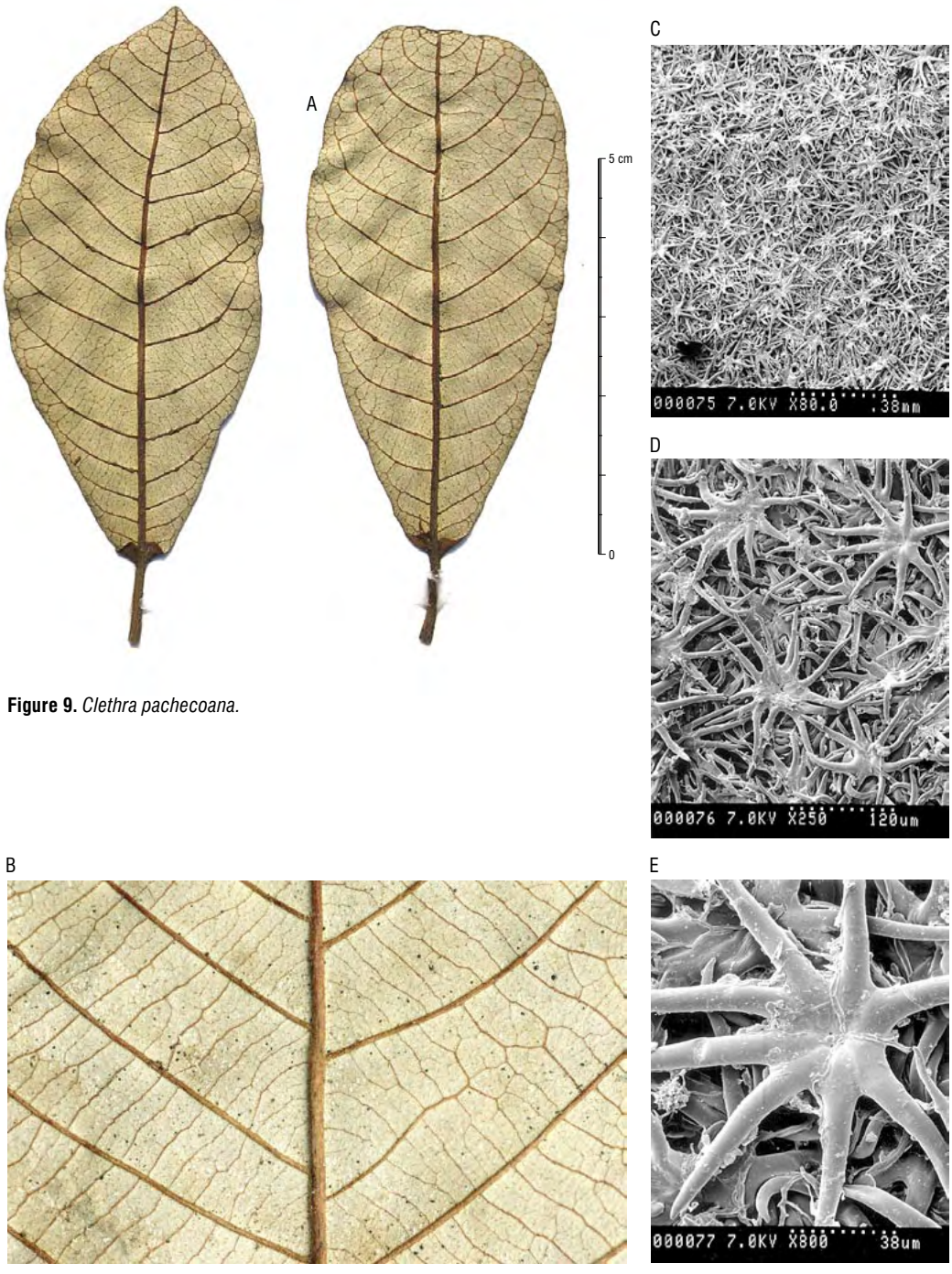


Figure 9. *Clethra pachecoana.*

Clethra pringlei S. Watson

Macro-morphology. Small to medium **tree** 6–15 m or up to 40 m tall, the trunk 25–30 (–50) cm dbh; **petiole** short, (2–) 4–7 (–15) mm long, with acicular trichomes, glabrescent with age; **leaves** when young with sparse stellate trichomes above and dense, minute stellate trichomes below; **leaf blades** subcoriaceous, bicolored, oblanceolate to elliptic or obovate, usually wider above the middle, the apex acuminate to acute, sometimes cuspidate or obtuse, the margins mostly sparsely serrulate or entire and often undulate, the base cuneate, (2–) 4–8 (–14) cm long, (0.8–) 2–3 (–6) cm wide; **adaxial surface** with scattered multiradiate trichomes to nearly glabrous except on the impressed midvein, often punctate, the secondary venation obscure or discernible; **abaxial surface** much paler than the upper surface, grayish-green or sometimes with a reddish blush, covered with minute, appressed stellate trichomes, the main veins bearing some long acicular trichomes up to 1 mm long mixed with fascicular trichomes but in general the veins glabrous; **secondary veins** 11–18 pairs, slender, reddish-brown, arching-ascending or nearly straight, branching and the branches terminating in adjacent teeth when present, otherwise anastomosing at the margins, the veinlets obscure. Figs. 10A-B.

Micro-morphology. Abaxial surface covered by appressed, matted stellate trichomes with 7–13 slender rays, the major veins with stipitate-fasciculate trichomes with 2–5 rays, the unicellular rays erect, ornamented with micro-striae; scattered, long acicular trichomes restricted to the main veins, the cuticle slightly striated with peristomatal ridges. Figs. 10C-F.

Clethra pringlei is widespread in Mexico's Sierra Madre Oriental, from the mountains of southeastern Nuevo León adjoining Tamaulipas south through San Luis Potosí, northern Querétaro and Hidalgo, with a disjunct population in central Veracruz and adjacent Puebla. An ecologically variable species, it occurs over a wide range of elevation, from 210 to 2700 m, in habitats ranging from tropical rain forests, dry to moist oak-pine forests and oak-*Liquidambar* forests to evergreen cloud forests; also in secondary vegetation.

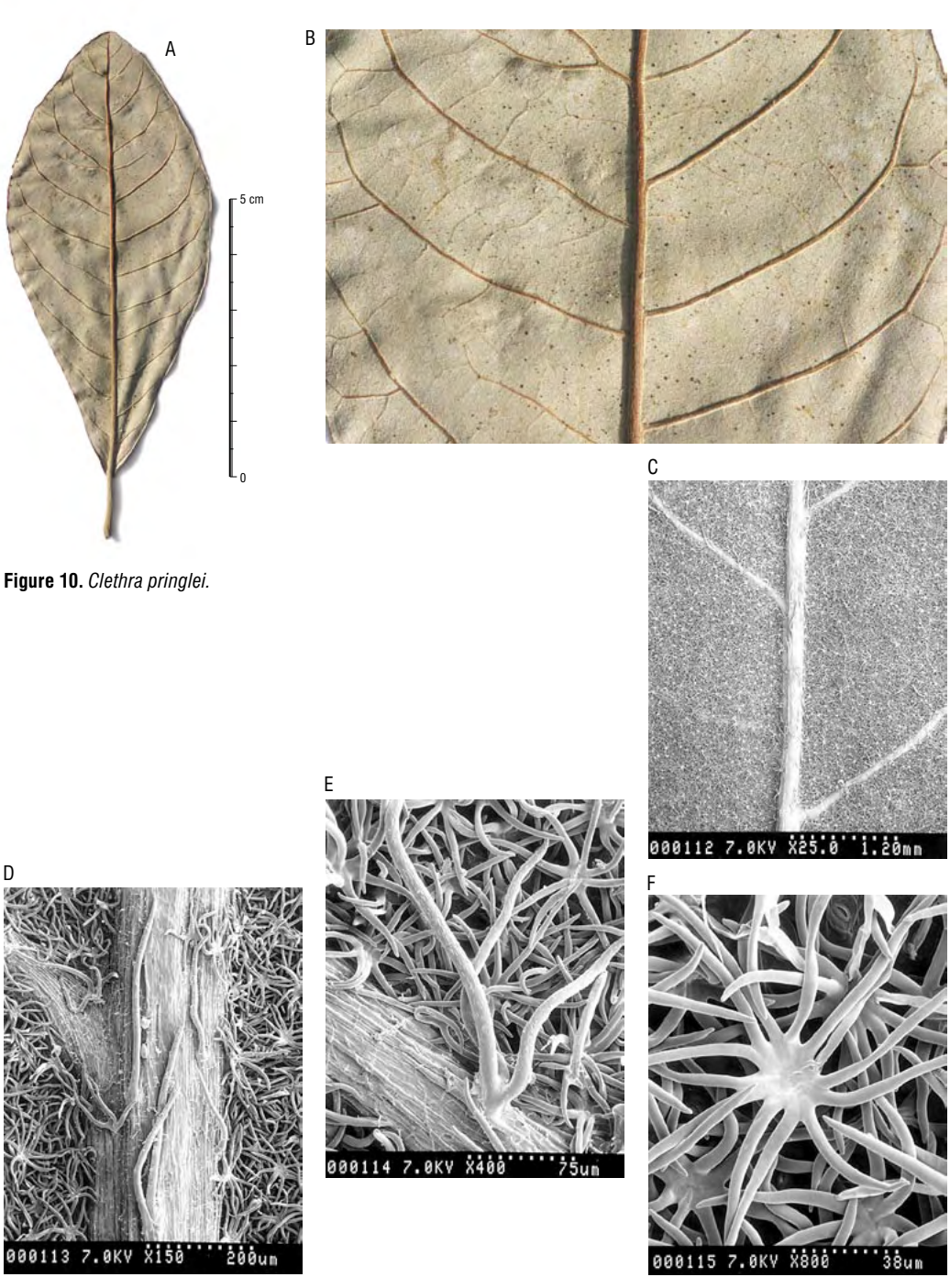


Figure 10. *Clethra pringlei.*

Clethra schlechtendalii Briquet

Macro-morphology. Tree 8–10 (–20) m tall; **petiole** slender, (0.5–) 1–2 (–2.5) cm long, stellate-tomentose to puberulous with age; **leaves** when young densely tomentose above; **leaf blades** subcoriaceous, bicolored, elliptic-lanceolate to oblong-obovate, usually considerably narrowed below the middle, the apex acute, acuminate to long-acuminate or rarely obtuse, the margins mostly serrate to less often entire, undulate, the base cuneate to rounded, sometimes oblique, (3.5–) 8–13 (–21) cm long, (1.5–) 4–6 (–9) cm wide; **adaxial surface** dark green, with small, pale multiradiate trichomes very sparse, the midvein with acicular trichomes, the secondary venation impressed, the veinlets inconspicuous; **abaxial surface** much paler than the upper surface, pale-grayish or pale-brown, covered with minute, appressed stellate trichomes, the midvein prominent and the secondary veins with sparse to many acicular trichomes; **secondary veins** (12–) 15–20 pairs, often curved-ascending, forked commonly more than once, passing into the teeth, the reddish-brown veinlets contrasting with the paler surface, evidently forming a fine network. Figs. 11A-B.

Micro-morphology. Abaxial surface covered with appressed, matted stellate trichomes with 6–13 rays ornamented with micro-papillae on the surface; midvein and secondary veins with scattered stellate trichomes with micro-papillae on the surface and long acicular trichomes intermixed but almost glabrous. Figs. 11C-E.

Clethra schlechtendalii is confined to central Veracruz and adjacent parts of Puebla and Hidalgo, Mexico. It occurs at elevations from (1000-) 1500 to 2350 m in pine-oak forests, oak forests and cloud forests, also in coffee plantations as well as disturbed areas.

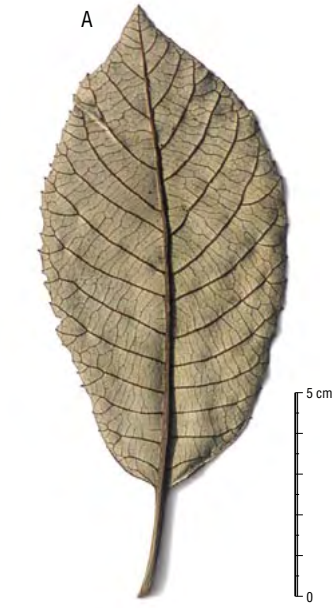
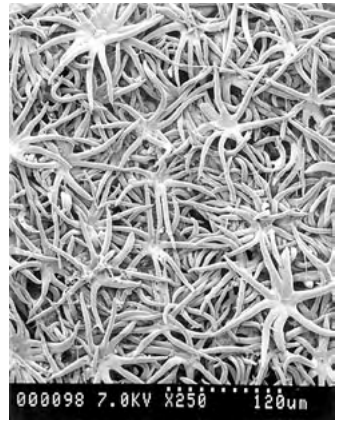
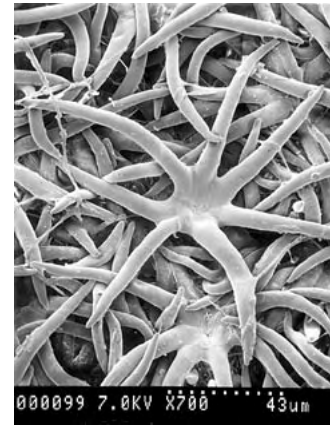


Figure 11. *Clethra schlechtendalii.*





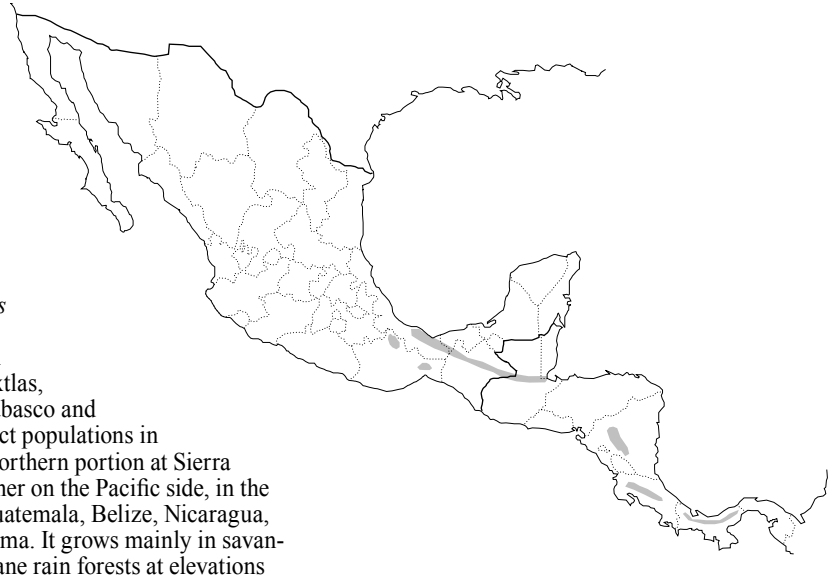
III. SERIES Tomentosae

Mature leaves with the abaxial leaf surface soft or harsh to the touch, in appearance tomentulose, tomentose or woolly. The vestiture is composed of minute, more or less appressed stellate trichomes and fasciculate trichomes either sessile, stipitate or pedestaled, often with acicular or filiform trichomes intermixed or these mainly concentrated on the major veins. The series contains nine species.

Clethra costaricensis Britton

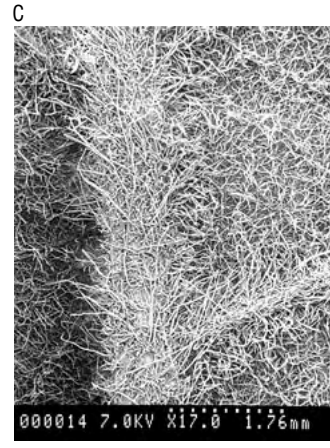
Macro-morphology. Tree 15–20 (–35) m tall, the trunk up to 1.30 m dbh; **petiole** stout, thick at the enlarged base, (0.6–) 1–1.5 (–2.5) cm long, tomentose; **leaves** when young densely tomentose on both sides; **leaf blades** subcoriaceous, bicolored, elliptic to elliptic-obovate or obovate, the apex mostly acute to acuminate, rarely rounded, mucronate or aristate, the margins often entire but aristate (arista up to 1 mm long), undulate, dentate or serrulate-aristate, the base somewhat narrowed to obtuse or truncate, 7–21 cm long, (2.5–) 3–10 cm wide; **adaxial surface** dark green, often lustrous, barely tomentose, covered with uniformly dispersed, long acicular trichomes that easily drop off, leaving a pustulate surface, multiradiate trichomes sometimes present, the midvein and secondary veins evidently furrowed and densely hispid-tomentose with acicular trichomes, the veinlets inconspicuous, often glabrescent with age; **abaxial surface** paler than the upper surface, yellowish-brown, uniformly tomentose, somewhat harsh to the touch with fasciculate and acicular trichomes intermixed, the prominent midvein with a dense vestiture of long acicular trichomes up to 1.5 mm long, as well the secondary venation; **secondary veins** 15–20 pairs, slender, usually strongly ascending at an acute angle, straight, parallel, forked commonly more than once or passing directly into the arista, the veinlets often forming a fine reticulate network. Figs. 12A-B.

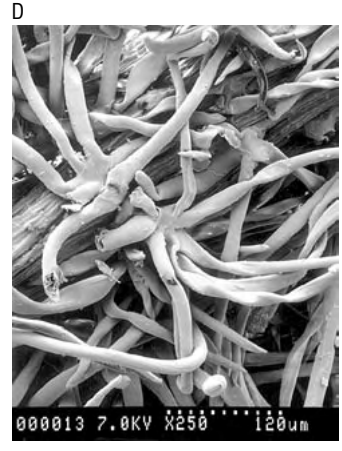
Micro-morphology. Abaxial surface densely covered by fasciculate trichomes, either sessile or pedestaled, with 2–7 rays, the unicellular rays very long, flattened and twisted (aduncate); in addition surface with long acicular trichomes but these mostly along the main veins. Figs. 12C-E.



Clethra costaricensis is widespread on the southeastern Coastal Plains, from Los Tuxtlas, Veracruz through Tabasco and Chiapas, with disjunct populations in Oaxaca, one in the northern portion at Sierra Mazateca and the other on the Pacific side, in the Chimalapas area; Guatemala, Belize, Nicaragua, Costa Rica and Panama. It grows mainly in savannas but also in montane rain forests at elevations from 200 to 1200 m, also commonly in disturbed areas.

Figure 12. *Clethra costaricensis.*





Clethra galeottiana Briquet

Macro-morphology. Tree 6–15 (–30) m tall; **petiole** slender or somewhat stout, (0.3–) 1–2 (–3) cm long, tomentose, puberulent with age; **leaves** when young densely tomentose on both sides; **leaf blades** coriaceous, bicolored, narrowly elliptic, elliptic-lanceolate, elliptic-oblong to obovate, the apex mostly acute to acuminate or obtuse to rounded, occasionally retuse, the margins often sparsely serrate or serrate-toothed (vigorous shoots markedly dentate-serrate) or entire and undulate, the base cuneate to obtuse, rounded or oblique, sometimes slightly reduplicated, (1.3–) 6–12 (–17) cm long, (0.6–) 2–5 (–6) cm wide; **adaxial surface** deep green, lustrous, rugulose, with spaced, small, reddish multiradiate trichomes, becoming glabrous and punctate, the midvein and secondary veins shallowly furrowed, the veinlets often discernible as sunken lines; **abaxial surface** permanently and closely tomentose, harsh to the touch, the vestiture pale-brown to reddish-brown, the fasciculate trichomes mostly erect and obscuring the epidermis, the midvein and secondary venation raised and densely tomentose with fascicular trichomes and acicular trichomes intermixed; **secondary veins** 10–15 (–20) pairs, ascending or straight and parallel, branching and anastomosing well within the margins or passing directly into the teeth, the veinlets forming an elevated network, often hidden by the vestiture. Figs. 13A-B.

Micro-morphology. Abaxial surface covered with appressed, matted stellate trichomes with 8–9 rays; in addition, short-stipitate fasciculate trichomes present, these with 7–8 rays ornamented with micro-papillae or micro-stria on the surface, the unicellular rays erect or wavy, some flattened. Figs. 13C-F.

Clethra galeottiana is widespread in the Sierra Madre del Sur, from Guerrero to Oaxaca and western Chiapas, Mexico. It occurs at elevations from 1800 to 3250 m in humid oak forests with dominant ericaceous shrubs, pine-oak or oak-*Abies* forests and evergreen cloud forests, also commonly in disturbed open areas.

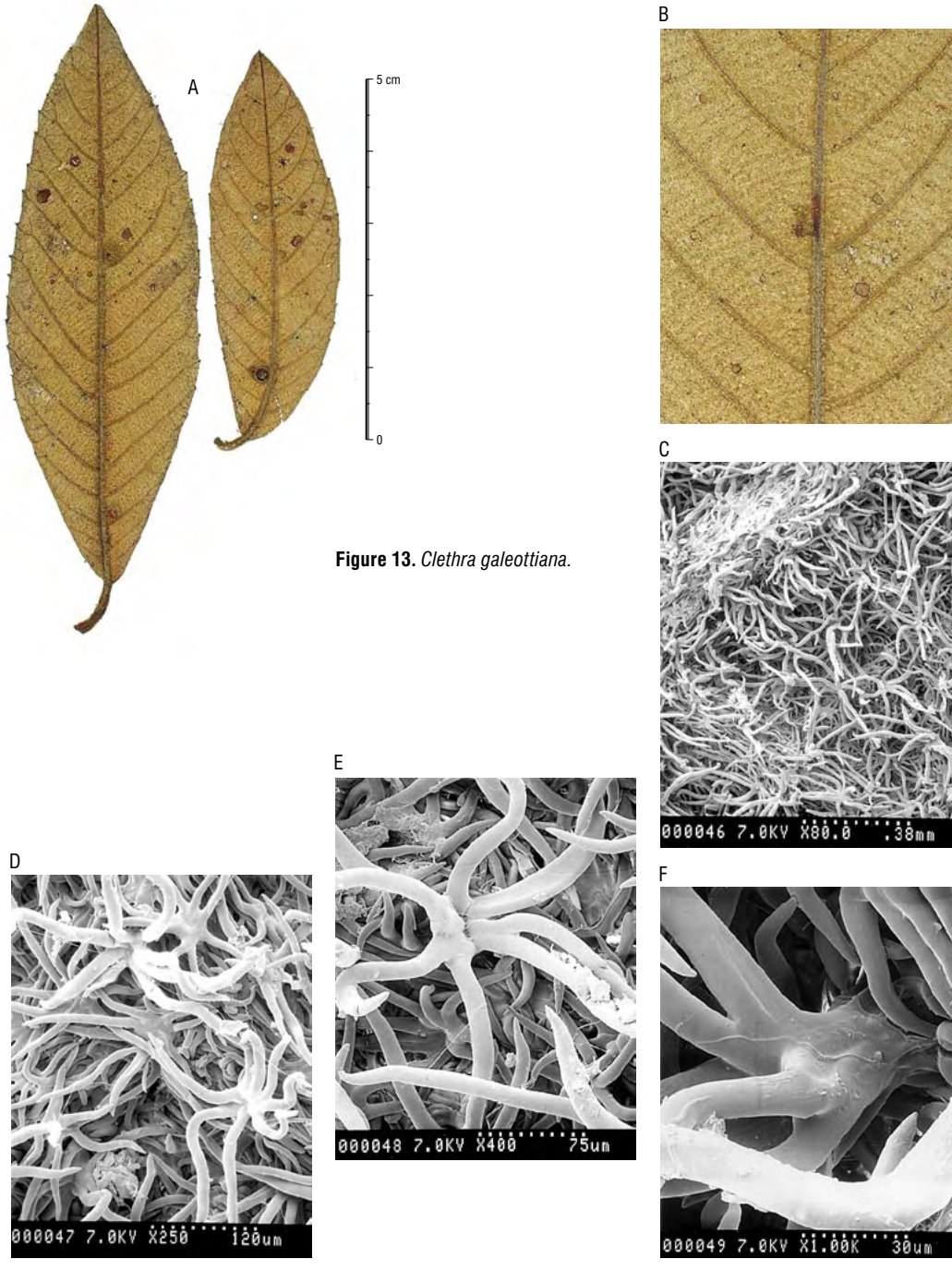
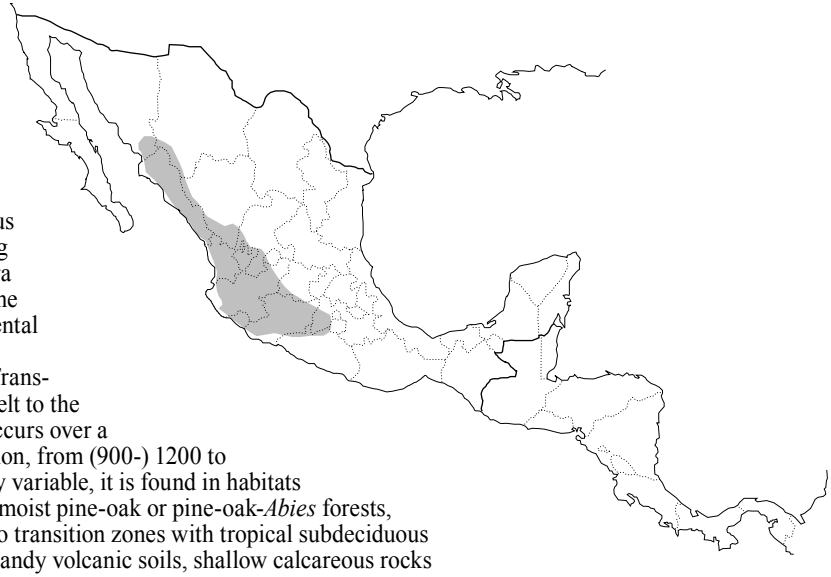


Figure 13. *Clethra galeottiana*.

Clethra hartwegii Britton

Macro-morphology. Tree mostly 5–10, but sometimes up to 30 m tall, the trunk 15–30 (–80) cm dbh; **petiole** slender to stout, (0.5–) 1–2 (–2.5) cm long, reddish-tomentose, ultimately puberulous and grayish; **leaves** when young covered with minute, pale rosulate trichomes above, densely reddish-tomentose below; **leaf blades** subcoriaceous to coriaceous, bicolored, mostly obovate, oblanceolate or elliptic, usually considerably narrowed below the middle, the apex rounded to obtuse or acute, rarely acuminate, the margins entire, undulate or serrulate-dentate in young shoots, the base cuneate or abruptly rounded, frequently reduplicate, (2.5–) 7–13 (–17) cm long, (1–) 3–7 (–10) cm wide; **adaxial surface** dark green or pale, shiny, with somewhat sparse minute multiradiate trichomes, with age almost glabrous except the midvein, the major veins furrowed, the veinlets sometimes inconspicuous; **abaxial surface** paler than the upper surface or slightly reddish-brown, covered with appressed stellate trichomes and dispersed fasciculate trichomes, the midvein and secondary venation prominent and densely reddish-tomentose, with trichomes of the fasciculate and acicular type intermixed; secondary veins (11–) 15–17 pairs, straight or ascending, branching, the veinlets forming a fine reticulate network. Figs. 14A-B.

Micro-morphology. Abaxial surface covered by appressed, matted stellate trichomes with 8–9 rays, and sparse stipitate-fasciculate trichomes with 6–8 rays ornamented with micro-papillae on the surface, the unicellular rays erect or wavy; major veins with some acicular trichomes intermixed with the fasciculate type. Figs. 14C-E.



Clethra hartwegii is one of the most widespread members of the genus in Mexico, extending from southern Sonora southward through the Sierra Madre Occidental into Jalisco, thence eastward along the Trans-Mexican Volcanic Belt to the state of Mexico. It occurs over a wide range of elevation, from (900-) 1200 to 2900 m. Ecologically variable, it is found in habitats ranging from dry to moist pine-oak or pine-oak-*Abies* forests, cloud forests and also transition zones with tropical subdeciduous forests. It grows on sandy volcanic soils, shallow calcareous rocks under cliffs or in woods on rough lava flows, moist ravines and disturbed areas.

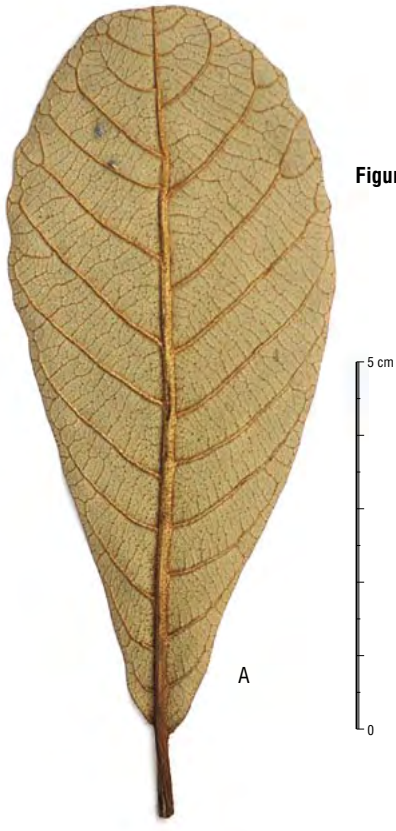
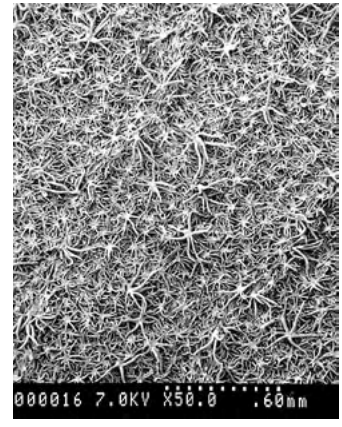


Figure 14. *Clethra hartwegii.*

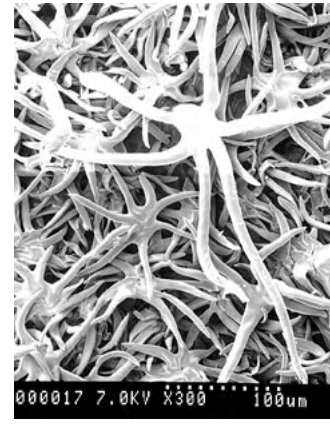
C

D



B

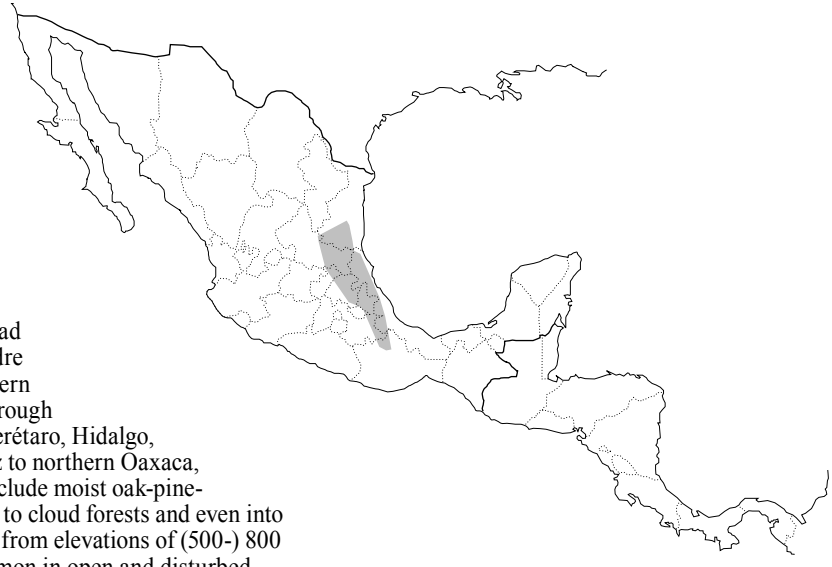
E



Clethra kenoyeri Lundell

Macro-morphology. Tree (8–) 15–20 (–40) m tall, the trunk 20–40 cm or up to 1 m dbh; **petiole** stout, (0.5–) 1–1.5 (–2.5) cm long; **leaves** when young densely tomentose on both surfaces; **leaf blades** subcoriaceous, concolored or bicolored, obovate to oblanceolate or elliptic, the apex broadly acute to acuminate, rarely rounded and apiculate, the margins often entire, undulate or minutely to coarsely serrate, the base rounded or subcordate, (3–) 10–20 (–25.5) cm long, (1–) 4.5–7.5 (–13) cm wide; **adaxial surface** dark green, somewhat lustrous, with sparse, short stellate trichomes, often finally glabrous or nearly so except for the pale-tomentose, shallowly furrowed midvein and secondary veins, the epidermis somewhat rugulose, the veinlets inconspicuous; **abaxial surface** light green or pale- to dark-brown or sometimes somewhat ferrugineous, with erect, soft stipitate-fasciculate trichomes through which a smooth, lustrous epidermis can seen, the midvein robust and raised, the veins densely to sparsely tomentose; **secondary veins** (10–) 15–20 pairs, ascending, commonly rather straight, nearly parallel, often bifurcated before reaching the margins, some passing directly into the teeth but even these veins often forked, the veinlets forming a fine reticulate network. Figs. 15A-B.

Micro-morphology. Abaxial surface sparsely covered with long-pedestaled fasciculate trichomes with 2–7 rays ornamented with micro-papillae on the surface, the unicellular rays long, slender, straight or wavy, overlapping, mainly confined to the main veins; in addition scattered, shorter acicular trichomes present, but no appressed, stellate trichomes were found; cuticle glabrous, slightly striated with peristomatal ridges. Figs. 15C-F.



Clethra kenoyeri is commonly widespread along the Sierra Madre Oriental, from southern Tamaulipas south through San Luis Potosí, Querétaro, Hidalgo, Puebla and Veracruz to northern Oaxaca, Mexico. Habitats include moist oak-pine-*Liquidambar* forests to cloud forests and even into tropical rain forests, from elevations of (500-) 800 to 2600 m. It is common in open and disturbed areas.

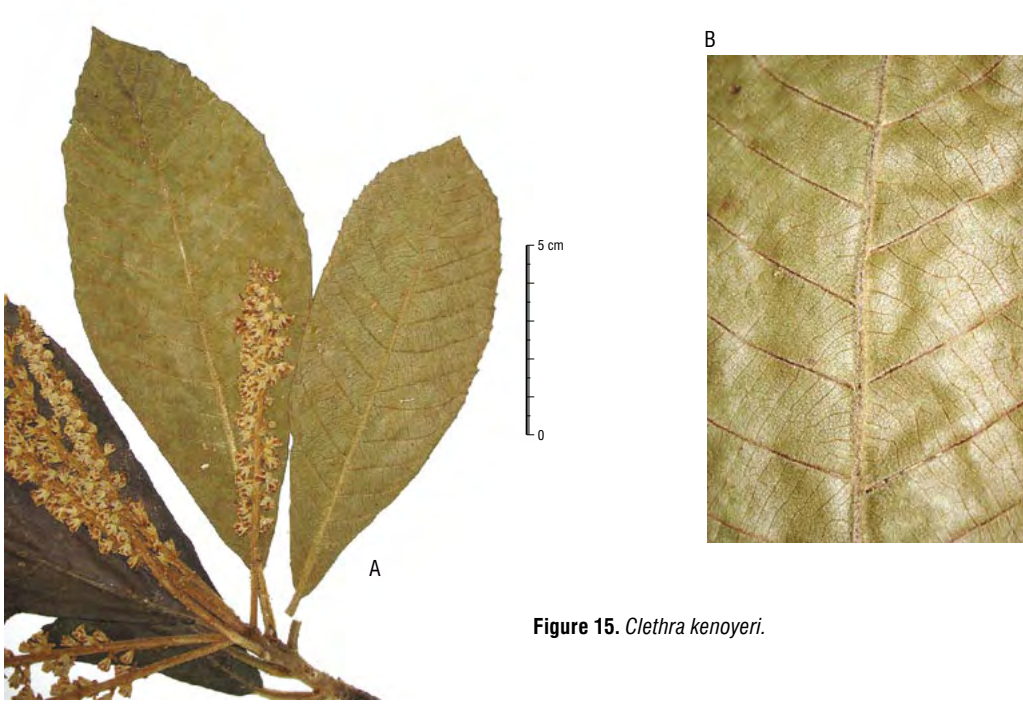
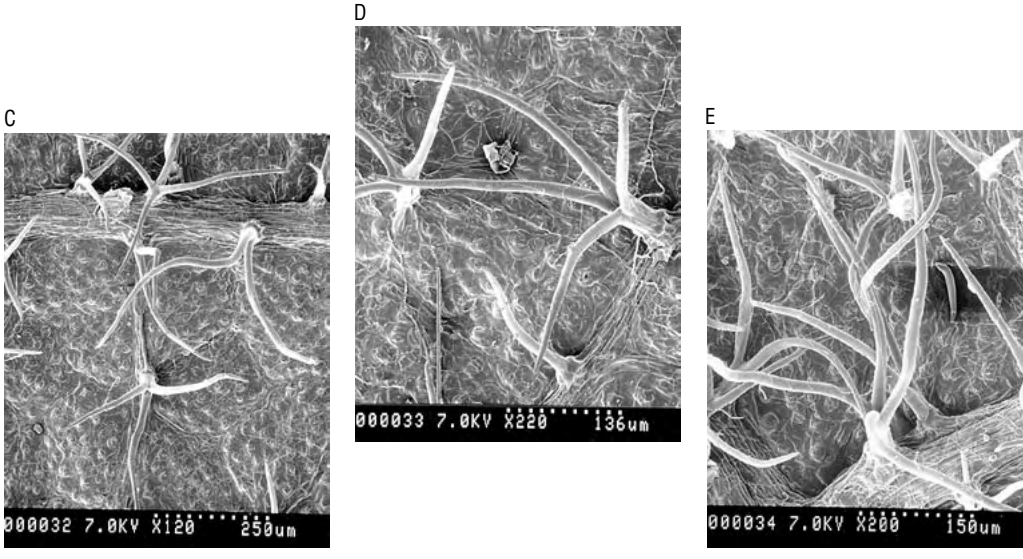


Figure 15. *Clethra kenoyeri.*



Clethra lanata Mart. & Gal.

Macro-morphology. Shrub or **tree**, 8–15 (–35) m tall; **petiole** somewhat long and slender, (0.6–) 1.5–2.5 (–4.5) mm long, densely pale-brownish tomentose; **leaves** when young heavily tomentose on both surfaces; **leaf blades** subcoriaceous, almost concolored, flat, obovate, oblong-obovate or elliptic, the apex rounded, acute or slightly acuminate, the margins entire, undulate or seldom low-toothed, the base cuneate to rounded, often oblique, (3.5–) 6–16 (–20) cm long, (1–) 3.5–8.5 (–10.5) cm wide; **adaxial surface** dark green, somewhat lustrous, with multiradiate trichomes and sparse, fine acicular trichomes sometimes punctate, becoming glabrescent, the midvein furrowed, densely tomentose, often finally glabrous except at the base, the secondary veins slightly or evidently impressed, the veinlets forming a pale, inconspicuous network; **abaxial surface** pale-brown or slightly reddish-brown, uniformly but rather sparsely soft-tomentose, through which the epidermis and the appressed stellate trichomes can be seen, often paler when becoming glabrescent and bearing just the appressed stellate trichomes, the midvein and secondary venation prominent and copiously tomentose; secondary veins (5–) 10–15 (–20) pairs, arcuate-ascending, some straight, branching and anastomosing, the veinlets forming a very fine network, often hidden by the vestiture. Figs. 16A-B.

Micro-morphology. Abaxial surface covered with scattered, appressed stellate trichomes with 6–8 rays, the unicellular rays flattened, ornamented with micro-striae on the surface, and dense to sparse, long-stipitate fasciculate trichomes with 2–5 rays, the unicellular rays slender, long, wavy, ornamented with micro-papillae on the surface; veins with scattered filiform trichomes; cuticle smooth to slightly striated or ridged but with peristomatal ridges. Figs. 16C-E.

Clethra lanata is widespread through the Sierra Madre del Sur, from southern Michoacán to Oaxaca and Chiapas, Mexico to Guatemala. It grows over a wide range of elevation from 350 to 2350 m. Habitats are quite variable, from savannas with oak-pine-*Curatella-Byrsonima* to dry or moist, pine-oak forests and even cloud forests; also common in coffee plantations.

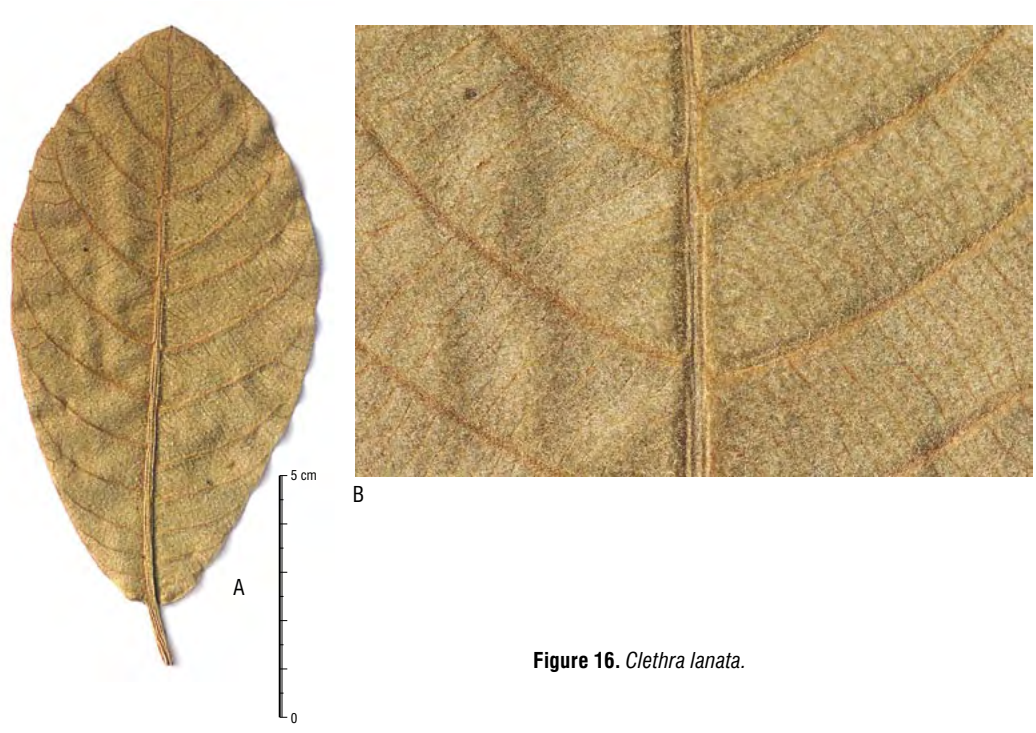


Figure 16. *Clethra lanata.*

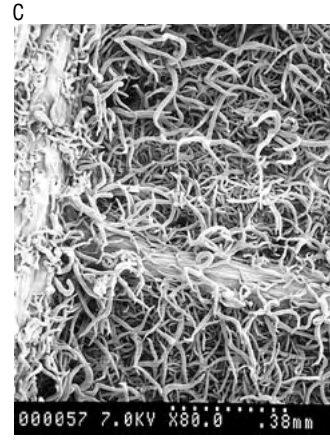
Clethra macrophylla Martens & Galeotti

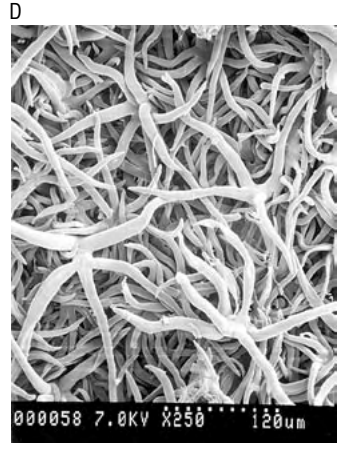
Macro-morphology. Tree 8–15 (–20) m tall, the trunk 25–30 cm or up to 1 m dbh.; **petiole** somewhat stout, (0.5–) 1.5–2.5 (–3.5) cm long, tomentose, glabrescent with age; **leaves** when young densely and finely reddish-tomentose on both surfaces; **leaf blades** subcoriaceous, bicolored, oblong-obovate to oblong-elliptic, the apex rounded to obtuse, sometimes acute to acuminate and shortly mucronate, the margins entire, undulate or toothed to serrulate-dentate, but usually entire near the base, which is rounded to subcordate, often oblique or cuneate, (3.5–) 9–16 (–25) cm long, (1.5–) 4–8 (–12) cm wide; **adaxial surface** dark green, glossy, with minute, pale stellate trichomes, finally glabrous or nearly so except for the densely tomentose midvein, the secondary venation impressed, the veinlets inconspicuous; **abaxial surface** reddish-brown, covered by pale stellate trichomes and sparse, reddish-brown stipitate-fasciculate trichomes intermixed with long acicular trichomes although these mostly concentrated along the major veins and in the vein axils, the midvein and secondary venation slender but prominent; **secondary veins** (12–) 16–18 (–22) pairs, straight or ascending, forked commonly more than once and anastomosing within the margins or passing directly into the teeth when these are present, the veinlets forming a very conspicuous network contrasting with the paler surface. Figs. 17A-B.

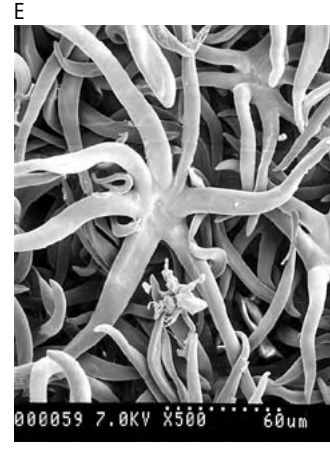
Micro-morphology. Abaxial surface densely covered with stellate trichomes with 3–8 rays, some flattened and ornamented with micro-striae on the surface, and short-stipitate fasciculate trichomes with 2–8 rays, the unicellular rays long, either erect or wavy. Figs. 17C-E.

Clethra macrophylla is well known from the central part of Veracruz and adjacent Puebla, at the junction of two important mountain systems, the Trans-Mexican Volcanic Belt and the Sierra Madre Oriental. Habitats are quite variable, because the species occurs at altitudes of (950-) 1000-2000 (-2500) m. It grows from tropical deciduous forests to oak forests, pine-oak-*Liquidambar* forests and cloud forests; usually seen in coffee plantations and open and disturbed areas.

Figure 17. *Clethra macrophylla.*



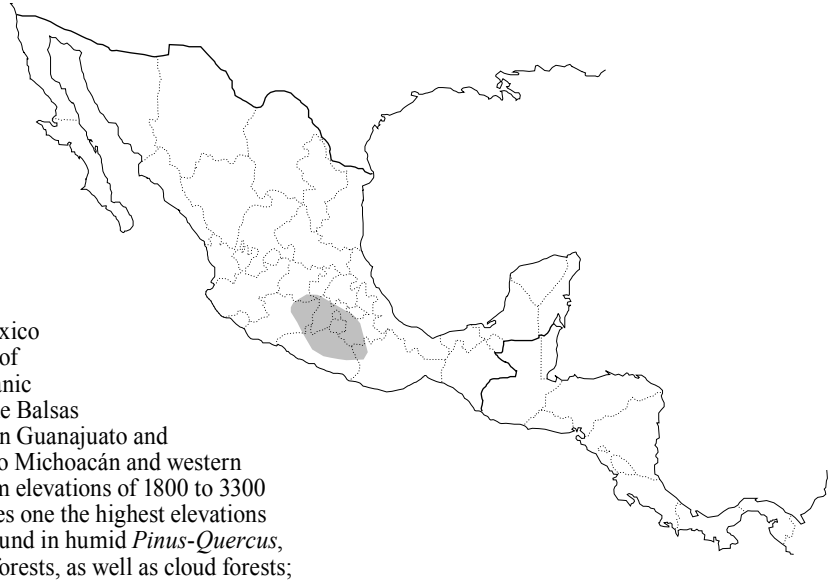




Clethra mexicana DC.

Macro-morphology. Tree (8–) 15–25 m tall, the trunk 20–30 cm or up to 1 m dbh; **petiole** long, slender or thick, (0.8–) 1.5–3 (–4.5) cm long, densely tomentose, with age usually ash-colored; **leaves** when young densely ferrugineous-tomentose, especially below and mainly along the veins; **leaf blades** usually coriaceous, bicolored, oblong-obovate or oblong-elliptic to obovate, the apex obtuse to rounded or rarely subacute, the margins entire, undulate or dentate-aristate, the base rounded to somewhat truncate or cuneate, (3.5–) 10–15 (–23) cm long, (1–) 5–8 (–12) cm wide; **adaxial surface** dark green, scattered stellate-tomentose, glabrescent, the midvein furrowed and densely tomentose, the secondary venation evidently impressed, the small veinlets forming a pale network; **abaxial surface** woolly, noticeably ferrugineous-tomentose, the long stipitate-fasciculate trichomes mixed with filiform trichomes, all veins raised and densely tomentose; **secondary veins** (12–) 14–16 (–18) pairs, moderately ascending or looping, often some of them standing almost at right angles to the midvein, branched and anastomosing near the margins, the veinlets dark-reddish-brown, forming a very conspicuous network. Figs. 18A-B.

Micro-morphology. Abaxial surface areolas covered with appressed stellate trichomes with 7–17 rays; veins densely covered with stipitate-fasciculate trichomes with 2–7 rays, the unicellular rays very long, curled throughout their length, tangled, contorted, some flattened and twisted (aduncate), ornamented with micro-striae on the surface; filiform trichomes mostly on the main veins. Figs. 18C-F.



Clethra mexicana occurs in central Mexico on the higher slopes of the Transverse Volcanic Belt and in part of the Balsas region, from southern Guanajuato and adjacent Querétaro to Michoacán and western Oaxaca. Known from elevations of 1800 to 3300 m, the species reaches one the highest elevations for the genus. It is found in humid *Pinus*-*Quercus*, pine-*Abies* and oak forests, as well as cloud forests; often in wet habitats along streams and also in disturbed open areas.

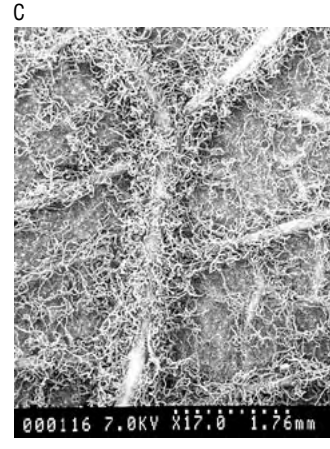
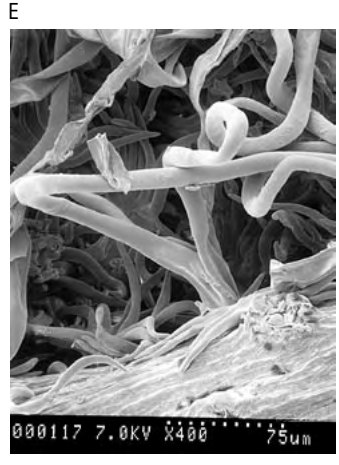
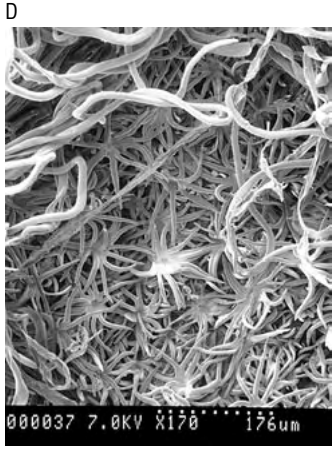


Figure 18. *Clethra mexicana.*





Clethra nicaraguensis C. W. Ham.

Macro-morphology. Tree 6–15 (–20) m tall; **petiole** long, slender, (0.5–) 1.5–2 (–3) cm long, hispid-tomentose; **leaves** when young densely tomentose on both sides; **leaf blades** rigidly coriaceous, bicolored, obovate to narrow elliptic, the apex broadly acuminate or acute, often rounded and cuspidate, the margins serrate to denticulate-aristate on the upper two thirds of the blade or entire and undulate, the base cuneate, noticeably reduplicate, (1.6–) 5–10 (–17) cm long, (0.5–) 3–5 (–8) cm wide; **adaxial surface** dark green, the epidermis lustrous and more or less rugulose, with scattered stellate trichomes, often finally glabrous or nearly so and punctate, the tomentose midvein, secondary veins and sometimes also the veinlets deeply furrowed-impressed; **abaxial surface** reddish-brown or pale-brown, covered with minute, appressed stellate trichomes, mixed with short stipitate-fasciculate trichomes, the midvein and secondary venation raised, densely reddish-tomentose; **secondary veins** 10–13 (–16) pairs, ascending, straight or curved, forked and passing directly into the teeth, the veinlets dark reddish-brown, forming a very characteristic network of parallel fine lines in sharp contrast with the paler areoles. Figs. 19A-B.

Micro-morphology. Abaxial surface covered by appressed, matted stellate trichomes with 5–8 rays ornamented with micro-papillae on the surface; veins with sparse to dense, short-stipitate fasciculate trichomes with 4–7 rays ornamented with micro-striae on the surface, the unicellular rays erect or wavy, a few filiform trichomes intermixed. Figs. 19C-F.

Clethra nicaraguensis occurs in mountainous areas from the Central Plateau to the Sierra Madre of Chiapas, Mexico to Honduras, El Salvador and Nicaragua at (800-) 1000 to 2730 m. It typically occupies steep, heavily wooded slopes with oak-pine-*Liquidambar* forests and cloud forests, also often in disturbed areas as well as oak forests.

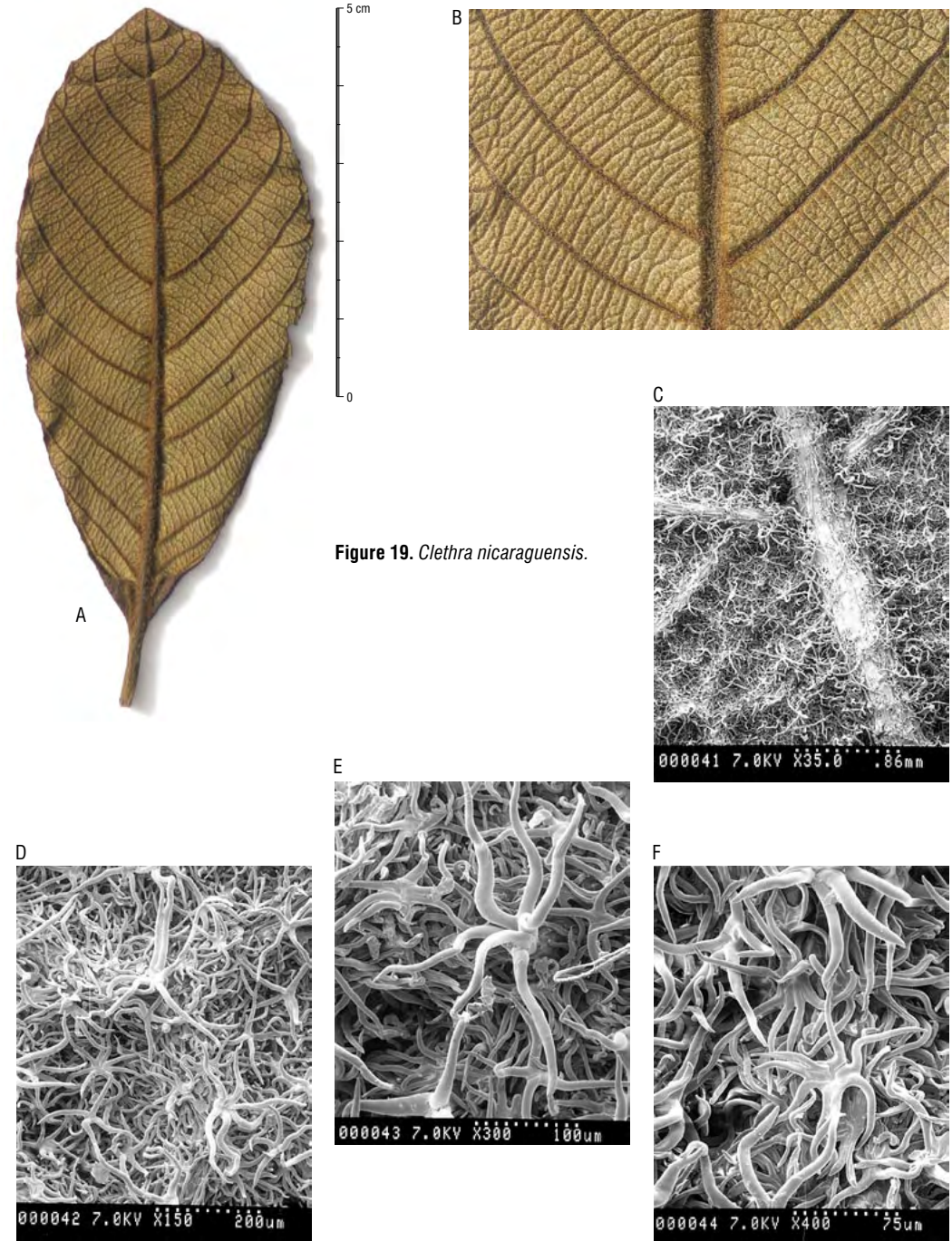
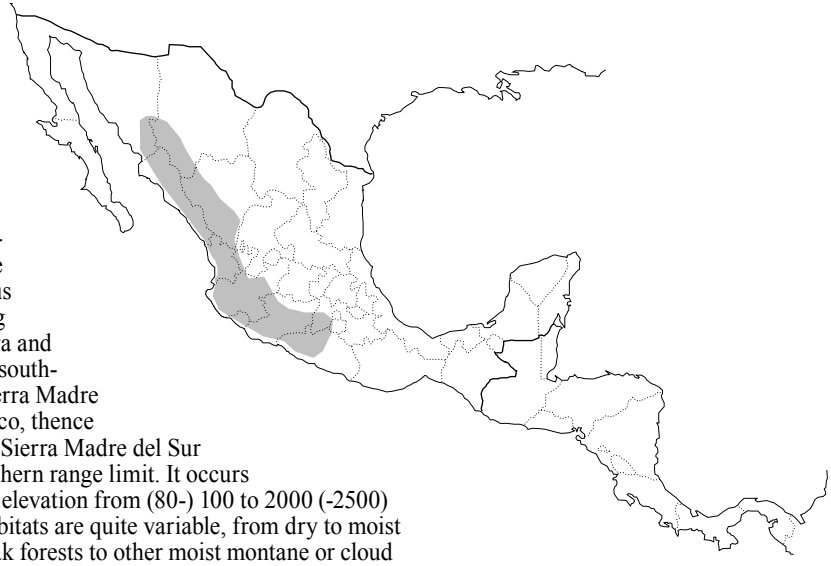


Figure 19. *Clethra nicaraguensis.*

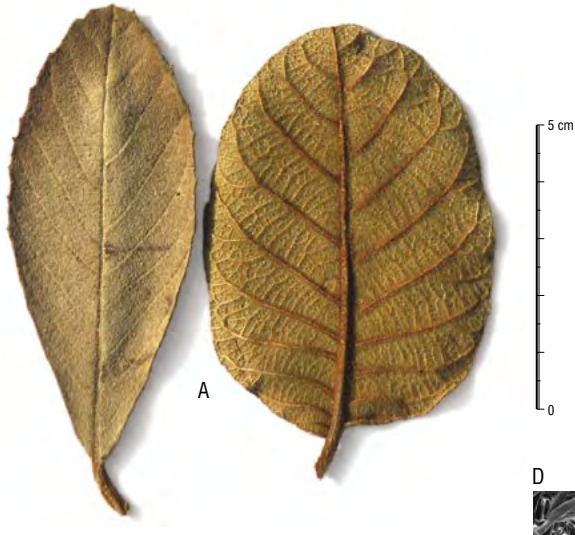
Clethra rosei Britton

Macro-morphology. Small to medium **tree** (3–) 5–10 m tall, sometimes up to 20 m, the trunk up to 50 cm dbh; **petiole** stout or long and slender, (0.5–) 1.5–2.5 (–5) cm long, with a pale-brown to reddish tomentum, glabrescent and grayish with age; **leaves** when young heavily tomentose on both surfaces; **leaf blades** commonly coriaceous, often very thick and rigid, bicolored or concolored, very variable in shape, broadly to narrowly obovate to oblanceolate, sometimes almost suborbicular or elliptic, the apex rounded to obtuse or acute, the margins entire, undulate or serrulate, the base gradually narrowed, cuneate or obtuse to rounded or somewhat cordate, (1.5–) 6–11 (–22) cm long, (0.6–) 3–6 (–12) cm wide; **adaxial surface** covered with dispersed, small, pale stellate trichomes as well stipitate-fasciculate and acicular trichomes, often finally glabrous but punctate except for the main veins, the epidermis evidently rugulose by the furrowed venation; **abaxial surface** heavily to moderately tomentose, woolly, pale-brown to red-dish-brown, becoming canescent with age, with sessile or stipitate-fasciculate trichomes mixed with filiform trichomes, all golden, crowded, tangled, closely overlapping, practically hiding the under layer of minute, pale, appressed stellate trichomes, the midvein prominent; **secondary veins** 9–14 (–21) pairs, slightly curving to strongly ascending, usually straight and parallel, branched and anastomosing, or passing into the teeth, the veinlets raised, forming a strong, prominent network, often obscured by the dense tomentum. Figs. 20A-B.

Micro-morphology. Abaxial surface covered by sparse, appressed stellate trichomes with 6–9 rays ornamented with micro-striae on the surface, as well as, dense, sessile or pedestaled-fasciculate trichomes with 2–8 rays, the unicellular rays very long, tangled, wavy, some flattened and twisted (aduncate), ornamented with micro-striae on the surface; the filiform trichomes mostly along the main veins; cuticle with peristomal ridges. Figs. 20C-E.



Clethra rosei is one of the most widespread and morphologically variable members of the genus in Mexico, extending from southern Sonora and adjacent Chihuahua southward through the Sierra Madre Occidental into Jalisco, thence southward along the Sierra Madre del Sur to Guerrero, the southern range limit. It occurs over a wide range of elevation from (80-) 100 to 2000 (-2500) m. Consequently, habitats are quite variable, from dry to moist *Pinus*-*Quercus* or oak forests to other moist montane or cloud forests; also common in savanna with *Byrsonima* and *Curatella*. It is frequent on exposed sites, cliff faces, rocky outcrops, volcanoes on lava and ash, as well as disturbed habitats.



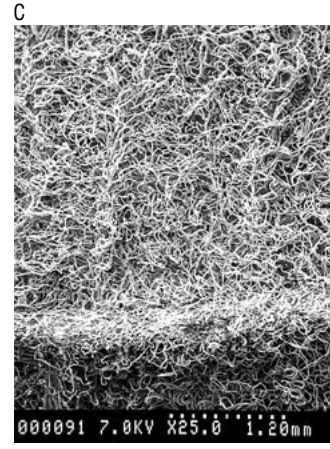


Figure 20. *Clethra rosei.*

Discussion

Combined use of a dissecting microscope and further examination with a scanning electron microscope (SEM) was employed in a detailed study of foliar surface features of vestiture and trichome morphology in *Clethra*. Three main types can be recognized: acicular (solitary), stellate and fasciculate, with their variants, and two more, the filiform and the multiradiate. All types of trichomes characteristic of the genus are non-glandular. Of the 20 species of *Clethra* of Mexico, one belongs to the series Glabrae (*C. suaveolens*), 10 to the series Tomentellae and nine to the series Tomentosae. According to Sleumer (1967) the series Ferrugineae contains South American species, mostly from Peru, with one exception in Costa Rica.

Sleumer (op. cit.) listed 13 species for the series Glabrae, most of them from South America, but four of them are not glabrous. In particular for Mexico he mentioned in addition to *Clethra suaveolens* the Jamaican *C. occidentalis* and *C. vicentina*; nevertheless, he remarks in the key "a glabrescent form" for the last, but glabrescent forms are common in many species. Moreover, he also placed *C. vicentina* in series Tomentellae and even into series Tomentosae (see Table I). Even though *C. vicentina* was not considered in this work, it clearly belongs to series Tomentellae and *C. occidentalis* to the series Tomentosae. In regard to *C. suaveolens* it was found that the abaxial leaf surface sometimes is not completely glabrous; the specimen studied showed a few minute, appressed stellate trichomes, possibly as a result of hybridization events. It is necessary to study more material and compare it with the rest of the members of series Glabrae.

Sleumer (op. cit.) included 16 species in the series Tomentellae, half of them cited for Mexico: *Clethra pringlei*, *C. oleoides*, *C. vicentina*, *C. parvifolia* Lundell, *C. alcoceri* Greenm., *C. occidentalis*, *C. hartwegii* and *C. macrophylla*. In contrast the last two as well as the Jamaican endemic *C. occidentalis* are here considered as belonging to series Tomentosae. In this work the series Tomentellae contains 10 species although not necessarily the same ones cited by Sleumer with two exceptions (*C. oleoides* and *C. pringlei*), with which I agree. Moreover, two of species he submerged in synonymy, *C. schlechtendalii* (under *C. macrophylla*) and *C. hondurensis* (under *C. occidentalis*); *C. pachecoana* was not mencioned for Mexico; and five more (*C. nutantiflora*, *C. chiapensis*, *C. conzattiana*, *C. fragrans* and *C. luzmariae*) have been discovered subsequent to his monographic work (Standley & Williams in Molina 1968; González-Villarreal 1998, 2006).

The series Tomentellae is characterized by having the abaxial leaf surface covered with minute, appressed stellate trichomes with ray number varying from 6 to 17 rays; the trichomes sometimes are arranged in several overlapping layers. In addition acicular trichomes are commonly seen on the major veins. Sometimes the fasciculate type can be present on the midvein but not usually.

Three closely related species within series Tomentellae, *Clethra chiapensis* and *C. oleoides* from Central Plateau of Chiapas and the Oaxacan *C. luzmariae*, showed the stellate variant type, having the beautifully peltate, fused center showing a higher ray number of 8 to 23 rays. All species of this unique group occupy cloud forests on mountain peaks from 2100 to 3300 m in elevation (González-Villarreal 1998). It is possible that some environmental influence exists for this particular type of trichome to be correlated with high altitudes.

Sleumer (op. cit.) included 15 species in his series Tomentosae, referring six of them to Mexico: *Clethra lanata*, *C. macrophylla*, *C. mexicana*, *C. occidentalis*, *C. rosei* and *C. vicentina*. I have removed the last species and have added five more to make a group of nine species (Table III). *Clethra costaricensis* and *C. kenoyeri* were sunk under *C. lanata* (Standley 1924; Sleumer op. cit.) however according to González-Villarreal (1996) they are good species. Finally, *C. hartwegii* was removed from series Tomentellae, and *C. nicaraguensis* was not discovered until 1985 by C. W. Hamilton.

The Mexican *Clethra hartwegii*, placed by Sleumer (op. cit.) into series Tomentellae, is better situated in series Tomentosae, judging from the presence of fasciculate-stipitate trichomes on the abaxial leaf surface. A similar relationship is suggested for *C. macrophylla*, formerly referred to series Tomentellae or series Tomentosae, but according to its trichome morphology it seems better position within the last. Sleumer considered *C. schlechtendalii* a synonomy of *C. macrophylla*, the first a completely different species from series Tomentellae. However, because the two species have similar distributions in Puebla and Veracruz, when they come into contact they appear to intergrade.

Another species of confused placement has been *Clethra galeottiana*, treated by Standley (op. cit.) as a synonym of *C. lanata*, and later by Sleumer (op.

cit.) under *C. hartwegii*. However, its recognition as a good species by González-Villarreal (op. cit.) is here confirmed; it belongs under series Tomentosae. It is clear that the vestiture of *C. galeottiana* is more dense and compact than that of *C. lanata*; furthermore it has fasciculate trichomes with a shorter stipe and higher ray number (7–8 vs 2–5). In addition *C. lanata* shows the characteristic filiform trichomes along the major veins. Owing to the general view of the vestiture of *C. lanata*, a considerable number of "woolly species" have been included in synonymy under this species, some of which I believe are good species, among them *C. costaricensis*, *C. galeottiana* and *C. kenoyeri*.

Stellate trichomes are representative of the genus *Clethra*, because they are present on the majority of the species in Mexico with two exceptions, both very distinct species from the series Tomentosae, *C. costaricensis* and *C. kenoyeri*. The first, from southern Veracruz, has a dense covering of fasciculate trichomes with 2 to 7 rays and a substantial number of long acicular trichomes intermixed. In contrast *C. kenoyeri*, distributed in the Sierra Madre Oriental, has a peculiar vestiture that consists of lax, long stipitate-fasciculate trichomes (also with 2 to 7 rays), through which a completely "glabrous" and shiny epidermis can be seen. The rest of the members of series Tomentosae, including *C. galeottiana*, *C. hartwegii*, *C. lanata*, *C. macrophylla*, *C. mexicana*, *C. nicaraguensis* and *C. rosei*, have a more complex trichome combination. In addition to the small, appressed stellate trichomes that Sleumer (1967) called the "first stratum", more evident trichomes whether stipitate-fasciculate, pedestaled-fasciculate and in some species intermixed with the acicular or the filiform type, form the "second strate". The characteristic pedestaled-fasciculate type was seen in *C. costaricensis*, *C. kenoyeri* and *C. rosei*.

Foliar trichomes provide a valuable set of analytical characters for species delimitation in *Clethra*. The vestiture as a whole, complemented with particular trichome type, enhanced in an important way the taxonomy of the species. There is, however, more work to perform, especially with the members of series Ferrugineae, which includes South American species that were not considered in this work.

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Glossary of Terms

ABAXIAL. Away from the axis or central line, turned toward the base, dorsal.

ACICULAR. Needle-shaped; acerate; stiff with pointed apex (Fig. 3C).

ADAXIAL. Toward the axis or center, turned toward the apex, ventral.

ADPRESSED. Appressed, lying flat against; oriented in parallel to the surface or axis to which attached.

ADUNCATE. Unicellular or multicellular-uniseriate, unbranched, similar to filiform type but obviously flattened and twisted throughout its length (Fig. 12E).

ANTRORSE. Directed upward (Fig. 10D).

APPRESSED. Adpressus, appressus.

AREOLE. A space marked out on a surface by cracks, ridges or a number of irregular, squarish or angular spaces.

ASPEROUS. Rough to the touch, especially when rubbed "the wrong way"; a general term without reference to trichome character.

CHARTACEOUS. Having a stiff, papery texture.

CONCOLOR. Of the same color (as the subject of comparision), uniform in color, of one color throughout.

CONDUPLICATE. Folded together lengthwise.

CORIACEUS. Leathery.

CURLY. With several bends or curvatures; tortuous; sinuous (Fig. 18C).

DEPRESSED. Sunk into the surface; somewhat flattened from above.

FASCICULATE. Thick-walled cells clustered and fused at the base, the number of rays varying from 2 to 14 in a single set and more or less erect. This trichome type may be sessile, stipitate or pedestaled.

FILIFORM. Having the shape of a thread or filament, generally curled or wavy, not twisted (Fig. 18D).

FUSED-STELLATE. A radially branched, prostrate hair with the rays fused up to two-thirds the length of the rays; sessile or stipitate (Fig. 8E).

GLABRATE. Nearly glabrous, becoming glabrous.

GLABRESCENT. Glabrate, becoming glabrous; used properly of surfaces not at first glabrous.

GLABROUS. Smooth, bald, without hair of any kind.

HIRSUTE. Covered with short, erect, stiff (but not harsh) trichomes.

HISPID. Bearing dense, erect, straight, stiff (but somewhat flexuous) trichomes; harsh to the touch (Fig. 12C).

MEMBRANACEOUS. Thin, soft and semi-transparent.

PAPILLA. Small, blunt epidermal outgrowth or projection on a surface; as ornamentation of trichome walls, micro-papillae if the wall has small rounded protrusions, and micro-striae if they are elongate (Fig. 7E).

PAPILLOSE. Covered with papillae.

PILOSE. Clothed with soft, usually long, rather straight trichomes, not dense but somewhat shaggy.

PEDESTALED. Placed on a support or foot, as a fasciculate trichome with a raised epidermal base (Fig. 15D).

PUBERULOUS. Minutely pubescent; covered with exceedingly short, fine, rather dense straight hairs at right angles to the surface.

PUBESCENT. General term meaning hairiness of any type; provided with hairs of whatever size or texture (as opposed to glabrous).

PUNCTATE. Covered with minute impressions, scarcely possessing depth, and appearing as if made by a pinpoint; dotted as if by punctures.

PUSTULA. Pustule, low projection like a blister or pimple, but larger than a papilla.

RETICULATE. Netted, marked with a network; bearing a net-like pattern represented by weak grooves or color variation outlining the veinlets.

ROSULATE. In the form of a rosette, in the case of trichomes a small tuft with many rays, each tapered to the apex; similar to multiradiate but smaller, with more rays, all the rays more spreading, and the outer ones horizontal, 0.12-0.2 mm in diameter.

RUGULOSE. Somewhat wrinkled.

RUFOUS. Reddish; dull red; rusty.

SERICEOUS. Silky, with straight, soft, long hairs, more or less appressed, often producing a satin-like sheen, especially when dense.

SOLITARY. Single; not associated with other organs of the same kind; of trichomes, long, usually straight and unicellular, often appressed; usually persisting along midrib.

STELLATE. Star-shaped; of a trichome, thick-walled, with a single set of radiating, slender rays projecting horizontally from a common center; sessile or stipitate; size and rays vary (Fig. 1F).

STIPITATE. Provided with a stipe or little stalk, e. g., a trichome with a base of fused rays elevating it above the epidermis (Fig. 10E).

STRIA. Fine linear line, streak, groove or other marking (Fig. 1E).

STRIATE (LINEATE). Marked by longitudinal lines or stripes.

STRIGOSE. With harsh, straight, stiff, short hairs, mostly appressed or weakly ascending, often with swollen bases.

TOMENTELLOUS. Minutely tomentose.

TOMENTOSE. Covered with more or less dense, matted, woolly hairs, curled and appressed.

TOMENTULOSE. Diminutive of or approaching tomentose.

VESTITURE. Any hairy covering causing a surface to be other than glabrous; indumentum.

VILLOUS (VILLOSE). Shaggy or rough with long, soft, often bent or curved (but not matted) hairs; pubescence that is coarse and bushy or unkempt.

WOOLLY (LANATE). Covered with dense, long, soft, entangled, curled trichomes, not appressed close to surface (Fig. 16C).

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