

10 PRELIMINARY FLORA MESOAMERICANA TREATMENT OF *GUATTERIA*

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ABSTRACT

For the Annonaceae treatment of *Flora Mesoamericana* the genus *Guatteria* was studied. 32 species are recognised, of which two are undescribed.

To be submitted to Flora Mesoamericana

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INTRODUCTION

For the Annonaceae treatment of *Flora Mesoamericana* the genus *Guatteria* was studied.

MATERIALS AND METHODS

Herbarium material was investigated from the following herbaria: CR, F, INB, K, MO, NY, PMA, SCZ, U, and US. Measurements as a rule were made on dried material. Measurements on material in spirit are given between accolades { }. Colour indications and descriptions of surface structures are based on dried material, unless stated otherwise. The density of the indument is indicated by using the following gradations: densely, rather densely, and sparsely. The photographs that accompany the descriptions are representative for the species described.

GUATTERIA RUIZ & PAV.

Trees or shrubs, very rarely lianas, covered with simple hairs to glabrous. Leaves with the midrib impressed (rarely flat or raised) on the upper side. Inflorescence axillary (rarely terminal), among leaves, 1-few-flowered, pedicels with suprabasal articulation, bracts 2, below the articulation. Flowers bisexual, cream, white, green, yellow, brown to orange, medium-sized; sepals 3, valvate, free or connate at the base; petals 6, free, mostly subequal, imbricate, much longer than the sepals; stamens numerous, not septate, connective shield discoid; staminodes absent; carpels numerous, free, ovule 1, basal. Fruit apocarpous, consisting of numerous, indehiscent, fleshy, stipitate monocarps; seed 1, not arillate.

Literature: Fries, R.E. *Acta Horti Berg.* 12(3): 291-540

KEY TO THE SPECIES

1. Flowers terminal.
 2. Inflorescence many-flowered; pedicels 15-65 mm long; leaves 10-22 x 3-7 cm; petals 25-40 mm long.
Mexico, Guatemala.....7. *G. anomala*
 2. Flowers solitary; pedicels 6-12 mm long; leaves 5-8 x 2-3.5 cm; petals 7-9 mm long.
Panama.....2. *G. acrantha*
1. Flowers axillary.
 3. Young twigs densely covered with erect hairs.
 4. Leaf base cordate.
 5. Lower side of leaves covered with reddish brown, soft hairs, upper side glabrous except for a hairy midrib; pedicels 9-17 mm long; monocarps 50-75. Costa Rica15. *G. pudica*
 5. Both sides of leaves covered with rough hairs; pedicels 20-40 mm long; monocarps 10-15.
Panama.....24. *G. aff. tomentosa*
 4. Leaf base acute, obtuse, or attenuate.
 6. Midrib raised on the upper side of the leaf; leaves narrowly oblong-elliptic.
Panama, Costa Rica.....8. *G. chiriquiensis*
 6. Midrib impressed to flat on the upper side of the leaf; leaves narrowly ovate to narrowly obovate.
 7. Leaves verrucose.
 8. Sepals 15-20 mm long; monocarps 20-30 mm long; stipes 2-3 mm long.
Costa Rica, Panama.....22. *G. talamancana*
 8. Sepals up to 10 mm long; monocarps up to 16 mm long; stipes 3-10 mm long.
 9. Monocarp/stipes: 2.3-3; monocarps 9-16 mm long; stipes 3-7 mm long; young twigs often zigzagging. Costa Rica, Panama.....14. *G. oliviformis*
 9. Monocarp/stipes: 1.2-1.6; monocarps 8-12 mm long; stipes 5-10 mm long; young twigs straight.
 10. Petioles 1-5 x 2-4 mm; leaves 18-42 x 5-13 cm; petals 13-32 mm long.
Nicaragua, Costa Rica, Panama.....3. *G. aeruginosa*
 10. Petioles 3-9 x 1-2 mm; leaves 10-17 x 3-5 cm; petals 10-12 mm long.
Panama.....26. *G. zamorae*

7. Leaves not verrucose.
- 11. Young twigs distinctly winged; flower buds distinctly pointed (see also *G. recurvisepala*); petals brown to chocolate-coloured; leaves coriaceous. Panama.....**1. *G. aberrans***
 - 11. Young twigs terete; flower buds rounded; petals green to yellow, sometimes brownish (in *G. recurvisepala*); leaves chartaceous (sometimes coriaceous in *G. recurvisepala*).
 - 12. Sepals 2-5 mm long; petals canary yellow; leaves greenish when dried. Panama.....**5. *G. allenii***
 - 12. Sepals 5-13 mm long; petals green, brown to yellow (but never canary yellow); leaves never greenish when dried;
 - 13. Sepals appressed to patent; upper side of leaves covered with erect hairs. Panama.....**23. *G. tomentosa***
 - 13. Sepals recurved; upper side of leaves glabrous except for the hairy midrib.
 - 14. Leaves 11-14 x 3-5 cm; sepals 5-7 mm long; seeds pitted. Nicaragua to Panama.....**10. *G. dolichopoda***
 - 14. Leaves 15-32 x 5-13 cm; sepals 6-11 mm long; seeds smooth. Costa Rica, Panama.....**16. *G. recurvisepala***
3. Young twigs covered with appressed hairs or glabrous.
- 15. Young twigs distinctly winged. Costa Rica, Panama.....**4. *G. alata***
 - 15. Young twigs terete.
 - 16. Leaves mostly folded when dried. Panama.....**11. *G. jefensis***
 - 16. Leaves never folded when dried.
 - 17. Leaves distinctly rounded at the apex, densely verrucose. Panama.....**19. *G. rotundata***
 - 17. Leaves acuminate or sometimes acute at the apex, sometimes verrucose.
 - 18. Monocarps sessile or very shortly stipitate (stipes up to 3 mm long).
 - 19. Leaves 18-33 x 5-10 cm, densely verrucose on the lower side. Panama.....**20. *G. sessilicarpa***
 - 19. Leaves 7-20 x 3-6 cm, not or sparsely verrucose on the lower side.
 - 20. Monocarps globose, 20-25 mm diam.; pedicels 10-18 mm long. Costa Rica.....**27. *G. sp. 1***
 - 20. Monocarps ellipsoid, 10-14 x 4-8 mm; pedicels 3-7 mm long. Costa Rica.....**17. *G. reinaldii***
 - 18. Monocarps distinctly stipitate with stipes >3 mm long.
 - 21. Monocarps distinctly beaked at the apex; petiole 15-20 mm long. Costa Rica.....**18. *G. rostrata***
 - 21. Monocarps rounded to minutely apiculate at the apex; petiole mostly much shorter than 15 mm (but see under *G. slateri*).
 - 22. Young stems mostly zigzagging; secondary veins raised on the upper side of the leaves.
 - 23. Monocarps/stipes: 3.4-5; leaves verrucose.....**25. *G. verrucosa***
 - 23. Monocarps/stipes: 0.7-2.6; leaves not verrucose.
 - 24. Monocarp/stipes: 1.6-2.6; stipes 3-6 mm long; upper side of leaves glabrous. Panama.....**21. *G. slateri***
 - 24. Monocarp/stipes: 0.7-0.8; stipes 8-14 mm long; upper side of leaves with a hairy midrib. Costa Rica.....**9. *G. costaricensis***
 - 22. Young stems straight; secondary veins impressed or raised on the upper side of the leaves.
 - 25. Secondary veins raised.
 - 26. Basal margins revolute; monocarps 40-75; seeds slightly pitted. Costa Rica, Panama.....**13. *G. lucens***
 - 26. Basal margins not revolute; monocarps 10-20; seeds brain-like. Mexico.....**12. *G. galeottiana***
 - 25. Secondary veins impressed.
 - 27. Pedicels 35-50 mm long; sepals 4-5 mm long. Panama.....**28. *G. sp. 2***
 - 27. Pedicels 10-35 mm long; sepals 3-12 mm long. Throughout Central America.....**6. *G. amplifolia***

DESCRIPTIONS OF SPECIES OF GUATTERIA

1. *Guatteria aberrans* Erkens & Maas, *Blumea* 51(2): 201. f. 1. (2006). Holotype: Panama, *Maas & al.* 9570 (U).

Trees 8-25 m. Young twigs densely covered with erect, curly, brown hairs, soon glabrous. Leaves 15-32 x 4-9.5 cm, narrowly elliptic to sometimes narrowly ovate, coriaceous, not verrucose, sparsely covered with appressed hairs above, soon glabrous, sparsely covered with appressed hairs below; base obtuse; apex acuminate (acumen 10-20 mm long); midrib flat to slightly impressed above; secondary veins distinct, 15-22 per side, prominent above. Petioles 5-10(-15) x 2-3 mm, decurrent as prominent ridge in young twigs. Flowers solitary or in pairs; pedicels 7-20 mm, densely covered with erect, curly, brown hairs. Sepals 7-12 x 5-8 mm, triangular to very broadly triangular, patent, but soon becoming completely reflexed, outer side densely covered with erect, curly, brown hairs. Petals brown to chocolate-coloured, unequal, outer ones narrowly elliptic, 13-27(-32) x 5-9 mm, inner ones narrowly triangular-ovate, 15-23(-32) x 7-13 mm, outer side densely covered with erect, curly brown hairs. Stamens ca. 1 mm, connective shield glabrous. Carpels 30-40. Monocarps 10-40, green maturing blue-black, 10-16 x 7-9 mm, ellipsoid, sparsely covered with erect, brown, curly hairs, soon glabrous, apex apiculate, stipes 9-15 x 1-2 mm. Seed 10-12 x 5-6 mm, ellipsoid, smooth. *Forest.* (P (*Maas & al.* 9564, U). 0-540 m. (Panama, pacific coast of Colombia).

Guatteria aberrans is highly typical by its pointed flower buds (a feature only sometimes seen in *G. recurvisepala*), its chocolate-brown petals, and by its reddish coloured leaf base after drying. Judging from the material we have studied it seems that the petals in this species stay always closed, a feature not known in the genus.

It is noteworthy that the Colombian material has longer pedicels (15-20 mm) than the Panamanian material (7-12 mm).

2. *Guatteria acrantha* Erkens & Maas, *Blumea* 51 (2): 202. t. 1 & f. 2, 3 (2006). Holotype: Panama, *Rivera* 355 (SCZ).

Trees or shrubs 5-20 m. Young twigs sparsely covered with appressed hairs, soon glabrous. Leaves 5-8 x 2-3.5 cm, narrowly obovate to narrowly elliptic, chartaceous, not verrucose, glabrous above, rather densely covered with appressed hairs below; base attenuate; apex rounded or very shortly and bluntly acuminate; midrib flat to slightly impressed above; secondary veins distinct, 6-9 per side, flat to slightly prominent above. Petioles 1-3 x 1 mm. Flowers solitary, terminal; pedicels 6-12 mm, densely covered with appressed, brown hairs. Sepals 3-5 x 3-4 mm, ovate-triangular to deltate, appressed to reflexed, outer side densely covered with appressed, brown hairs. Petals greenish, subequal, obovate, 7-9 x 5-7 mm, outer side densely covered with appressed, brown hairs. Stamens 1-1.5 mm, connective shield papillate. Carpels 15-20. Monocarps ca. 10, green, 7-10 x 3-4 mm, narrowly ellipsoid, subglabrous, apex apiculate, stipes 1-2 x 1 mm. Seed ca. 8 x 3 mm, narrowly ellipsoid, pitted. *Cloud forest.* P (*Deago & al.* 265, PMA). 900-1500 m. (Endemic).

Guatteria acrantha is unique by its terminal, minute flowers and by its very tiny, mostly roundish-tipped leaves.



Top: *Guatteria aberrans* Erkens & Maas (Maas 9570, U).

Bottom: *Guatteria acrantha* Erkens & Maas (Deago 265, INB).

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3. *Gutteria aeruginosa* Standl., *Publ. Field Columbian Mus., Bot. Ser.* 4(8): 206 (1929). Holotype: Panama, *Cooper 526* (F).

Trees 5-20 m. Young twigs densely covered with erect, brown hairs. Leaves 18-42 x 5-13 cm, narrowly oblong-elliptic to narrowly obovate, chartaceous, densely verrucose, sparsely covered with appressed hairs above, but midrib densely covered with erect, brown hairs, densely to sparsely covered with erect, brown hairs below; base acute to obtuse, often slightly decurrent into the petiole; apex acuminate (acumen 10-20 mm long); midrib flat to impressed above; secondary veins distinct, 12-24 per side, flat to prominent above. Petioles

1-5 x 2-4 mm. Flowers solitary; pedicels 13-30 mm, densely covered with erect, brown hairs. Sepals 4-10(-16) x 5-9(-14) mm, broadly ovate-triangular, appressed, later becoming reflexed, outer side densely covered with appressed and erect, brown hairs. Petals yellowish green to creamy yellow, subequal, ovate-oblong to ovate-trullate, 13-32(-35) x 6-22(-27) mm, outer side densely covered with appressed and erect, brown hairs. Stamens 1.5-2 mm, connective shield densely papillate to hairy. Carpels ca. 50. Monocarps 20-50, green, maturing purple-black, 8-12(-15) x 4-6(-9) mm, ellipsoid, subglabrous, apex apiculate, stipes 5-10 mm. Seed 8-10 x 4-5 mm, ellipsoid, brain-like. *Forest. N* (*Rueda & al. 5796*, MO); CR (*Maas & al. 9427*, U); P (*Gordon 5*, MO). 0-1200 m. (Endemic).

Gutteria aeruginosa is typical by its dense indument of erect, brown hairs and its densely verrucose leaves. The basal part of the pedicels is often provided with 2-3 remnants of bracts. The material from Nicaragua, the Heredia region in Costa Rica and the Bocas del Toro region in Panama is less verrucose, but matches all other features of *G. aeruginosa* well. Non-verrucose material from Bocas del Toro might belong to *G. panamensis* (for differences see under the latter species).

4. *Gutteria alata* Maas & Setten, *Proc. Ned. Kon. Ned. Akad. Wetensch. C.* 91(3): 250. f. 8-9 (1988). Holotype: Panama: *Alverson & al. 1955* (WIS).

Trees 5-30 m. Young twigs with sharp wings decurrent from the petioles, sparsely to rather densely covered with appressed, brown hairs, soon glabrous. Leaves 18-34 x 10-16 cm, obovate to elliptic, coriaceous, rather densely to densely verrucose, sparsely covered with appressed hairs to glabrous above and below; base acute to obtuse, decurrent as wings on the petiole; apex very shortly acuminate (acumen ca. 5 mm long); midrib impressed above, keeled below; secondary veins distinct, 17-20 per side, flat to prominent above. Petioles 10-15 x 5-7 mm. Flowers solitary; pedicels 12-33 mm, densely covered with appressed, pale brown hairs. Sepals 10-13 x 9-10 mm, broadly ovate, appressed, outer side densely covered with appressed, pale brown hairs. Petals yellow, equal, very broadly ovate, 13-15 x 10-13 mm, outer side densely covered with appressed hairs. Stamens 1.5-2 mm, connective shield papillate. Carpels 20-30. Monocarps 6-20, green to purple, 18-24 x 12-15 mm, ellipsoid, sparsely covered with appressed, brown hairs to glabrous, apex rounded to apiculate, stipes 4-22(-30) x 1.5-3 mm. Seed 15-19 x 7-8 mm, ellipsoid to ovoid, pitted to striate. *Forest. CR* (*Zamora ?*, INB?); P (*McPherson 13675*, U). 300-900 m. (Endemic).

Gutteria alata is very typical by its strongly winged stems and by its broad and obovate to elliptic, very shortly acuminate leaves.

There are several soon falling bracts (below the articulation) in this species.

5. *Guatteria allenii* R.E. Fr., *Ark. Bot. n.s.* 1(6): 336 (1950). Holotype: Panama, *Allen 1900* (S).

Trees or rarely shrubs (1-)4-12 m. Young twigs densely covered with erect, brown hairs, soon glabrous. Leaves 10-21 x 3-8 cm, narrowly elliptic to narrowly obovate, chartaceous, not verrucose, often greenish when dry, sparsely covered with appressed and erect hairs to glabrous above, rather densely covered with erect, brown hairs below; base acute; apex acuminate (acumen 5-20 mm long); midrib flat to slightly impressed above; secondary veins distinct, 8-12 per side, slightly prominent above. Petioles 2-7 x 1-2 mm. Flowers solitary, sometimes in pairs; pedicels 8-20 mm, densely covered with appressed, brown hairs. Sepals 2-5 x 3-5 mm, broadly ovate-triangular, reflexed, outer side densely covered with appressed, brown hairs. Petals yellowish green, maturing canary yellow, equal, oblong-ovate, 10-15(-25) x 5-9(-15) mm, outer side densely covered with appressed hairs. Stamens 1-2 mm, connective shield densely hairy. Carpels 40-60. Monocarps 25-50, green, maturing black, 9-11 x 4-5 mm, ellipsoid, sparsely covered with appressed hairs, apex apiculate, stipes 4-8 x 1 mm. Seed 9-10 x 4 mm, ellipsoid, brain-like. *Forest. P* (*Maas & al. 9543*, U). 700-1100 m. (Endemic).

Guatteria allenii is very distinct by its canary yellow flowers. In the herbarium it can at first glance be recognized by its greenish leaves, a feature rarely seen in Central American *Guatteria*.

6. *Guatteria amplifolia* Triana & Planch., *Ann. Sci. Nat., Bot. sér.* 4.17: 35 (1862). Holotype: Panama, *Fendler 3* (K).

Guatteria diospyroides Baill. subsp. *diospyroides*; *G. diospyroides* Baill. subsp. *hondurensis* R.E. Fr.; *Guatteria jurgensenii* Hemsl.; *G. inuncta* R.E. Fr. var. *inuncta*; *G. inuncta* R.E. Fr. var. *caudata* R.E. Fr.; *G. inuncta* R.E. Fr. var. *minor* R.E. Fr.; *G. platypetala* R.E. Fr.

Trees or shrubs 2-12, rarely up to 20 m. Young twigs sparsely to rather densely covered with appressed hairs or glabrous. Leaves 13-40 x 4-15 cm, narrowly ovate to narrowly obovate, sometimes ovate or elliptic, chartaceous, not verrucose, glabrous above, sparsely covered with appressed hairs to glabrous below; base obtuse, cordate (with basal margins inflexed), to acute; apex acuminate (acumen 5-30 mm long); midrib impressed above; secondary veins distinct, 12-20 per side, impressed to flat above. Petioles 4-13 x 1-7 mm. Flowers solitary, sometimes in pairs; pedicels 10-25(-40) mm, rather densely to sparsely covered with appressed hairs. Sepals 3-12 x 4-10 mm, broadly ovate-triangular, reflexed to appressed, outer side rather densely to densely covered with appressed hairs. Petals green, maturing yellow, equal, oblong-ovate to oblong-obovate, 10-25 x 5-15 mm, outer side densely covered with appressed hairs. Stamens 1-2 mm, connective shield papillate. Carpels 75-100. Monocarps (25-)50-75, green, maturing red to finally black, 7-10 x 3-6 mm, ellipsoid, sparsely covered with appressed hairs to glabrous, apex distinctly apiculate, stipes 5-20(-25) x 1 mm. Seed 7-10 x 4-6 mm, ellipsoid, slightly pitted. *Forest. M* (*Murray & Johnson 1384*, U); *G* (*Marshall & al. 336*, U); *H* (*Maas & al. 8492*, U); *B* (*Davidse & Holland 36721*, U); *N* (*Stevens 12476*, U); *CR* (*Maas & al. 7964*, U); *P* (*Maas & al. 9533*, U). 0-1100 m. (Mesoamerica).

Guatteria amplifolia is without any doubt the most problematic and complex species of *Guatteria* in Central America and it is with some hesitation that we united the several names under this species.

Typical *G. amplifolia* is encountered throughout Panama and is characterized by very large leaves and petioles with the secondary veins distinctly impressed on the upper



Top: *Guatteria allenii* R.E. Fr. (Maas 9543, U).

Bottom: *Guatteria amplifolia* (McPherson 11898, U). For more examples of this species, also see figure 1 in chapter 6 (page 106).

side; furthermore the leaf base is obtuse to cordate with the basal margins somewhat inflexed. Towards the West, in Costa Rica, Nicaragua, and all other western Central American countries, leaves and petioles tend to be smaller, and the secondary veins are less impressed to even flat on the upper side. Moreover, the leaf base is mostly acute, although obtuse leaf bases are also sometimes found. As all these changes are quite gradual we consider it to fall within the variation of one species, namely *G. amplifolia*.

It has been noted, in the field as well as in herbarium material, that the sepals of the Panamanian material are sometimes persistent as a calyx around the pedicel.

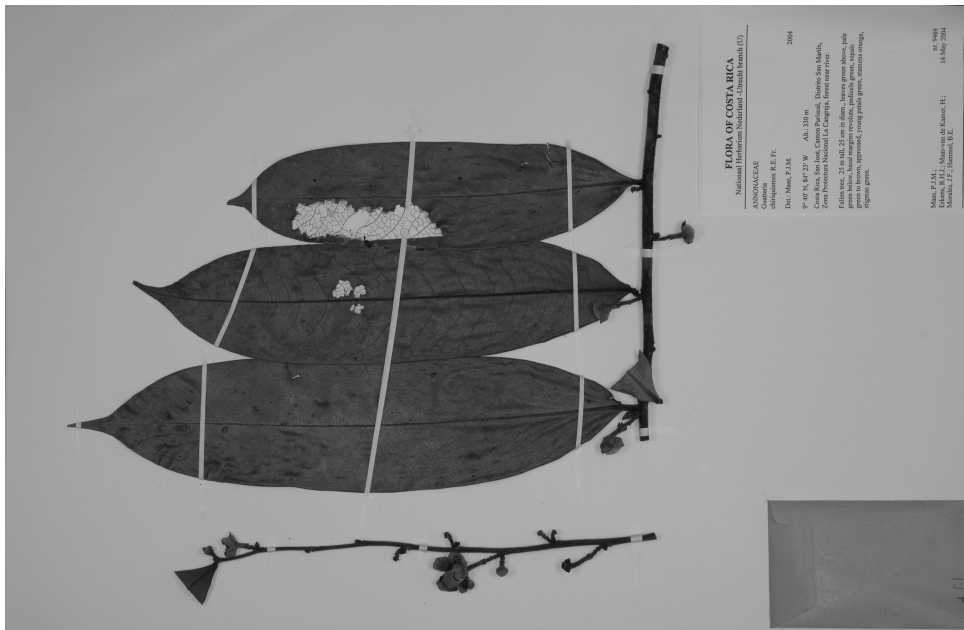
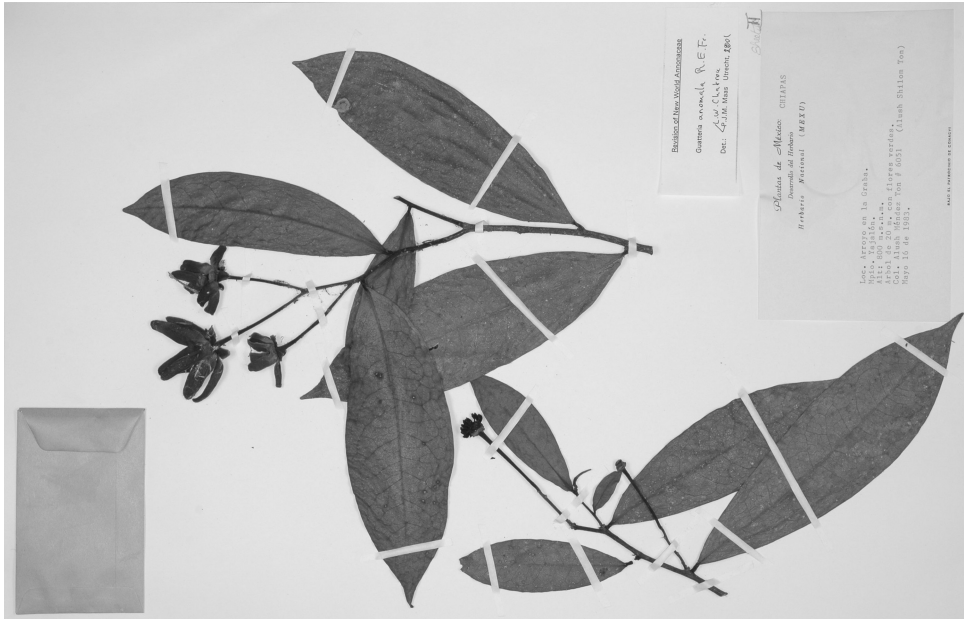
7. *Gutteria anomala* R.E. Fr., *Acta Horti Berg.* 12(3): 524. t. 1a-f (1939). Holotype: Guatemala, *von Tuerckheim 7816* (B).

Trees 10-60 m, with deeply fluted stems. Young twigs rather densely covered with appressed, white hairs, very soon glabrous. Leaves 10-22 x 3-7 cm, narrowly obovate to narrowly elliptic, chartaceous, not verrucose, glabrous above and below; base acute, attenuate; apex shortly acuminate (acumen 2-10 mm long); midrib impressed above; secondary veins distinct, 9-13 per side, prominent above. Petioles 3-9 x 2-3 mm. Flowers in a terminal, many-flowered inflorescence up to 10 cm long; pedicels 15-65 mm, sparsely covered with appressed, white hairs. Sepals 5-8 x 4-7 mm, broadly ovate-triangular, reflexed, outer side densely covered with appressed and erect, curly, white hairs. Petals green with red inner base, equal, narrowly ovate to narrowly oblong-ovate, 20-40 x 6-13 mm, outer side densely covered with appressed and erect, curly, white hairs. Stamens 1-1.5 mm, connective shield densely papillate. Carpels 25-35. Monocarps 5-15, red, maturing black, 15-30 x 5-15 mm, narrowly ellipsoid, glabrous, apex rounded, stipes 5-12 x 2-3 mm. Seed 15-25 x 8-9 mm, shape, brain-like. *Forest. Ch (Méndez Ton 6051, U); G (von Tuerckheim 7816, B).* 0-950 m. (Mexico to Guatemala).

Gutteria anomala is very typical by its several-flowered and terminal inflorescence! This species is thought to be the largest tree within the genus and is reported to be up to 60 m high with a d.a.p. of 169 cm. It needs to be compared with *G. grandiflora*.

8. *Gutteria chiriquiensis* R.E. Fr., *Kongl. Svenska Vetensk. Acad. Handl. ser. 3.* 24(10): 11 (1948). Holotype: Panama, *Pittier 5748* (US).

Trees 5-25 m. Young twigs slightly winged, densely covered with a velutinous indument of long-persisting, erect, brown hairs. Leaves 13-32 x 3-7 cm, narrowly oblong-elliptic, chartaceous, not verrucose, rather densely covered with erect, brown hairs above, densely covered with a velutinous indument of erect, brown hairs below; base acute to almost obtuse, sometimes slightly oblique; apex acuminate (acumen 5-25 mm long); midrib flat apically, becoming distinctly raised basally; secondary veins distinct, 13-15 per side, prominent above. Petioles 1-5 x 1-2 mm. Flowers solitary or in pairs; pedicels 20-35 mm, densely covered with appressed and erect, brown hairs. Sepals 5-7 x 5-7{-9} mm, broadly ovate-triangular, appressed, outer side densely covered with appressed, brown hairs. Petals yellow to cream, equal, narrowly oblong-ovate, 10-15{-25}x 10-12{-15}mm, outer side densely covered with appressed hairs. Stamens 1-2 mm, connective shield glabrous. Carpels 75-100. Monocarps 15-40, dark purple to black, 7-10 x 3-5 mm, ellipsoid, sparsely covered with appressed hairs, particularly near the apical part, apex apiculate, stipes 5-8 x 1 mm. Seed 6-8 x 4 mm, ellipsoid, slightly pitted to striate. *Forest. CR (Maas & al. 9469, U); P (Pittier 5132, US).* 0-500 m. (Endemic).



Top: *Guatteria anomala* R.E. Fr. (Mendez Ton 6051, U).

Bottom: *Guatteria chiriquiensis* R.E. Fr. (Maas 9469, U).

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Guatteria chiriquiensis is easily recognizable by its almost oblong leaves, its short petioles, and by its midrib which is raised on the upper side, the last feature very rarely seen in the genus. The basal leaf margins are mostly revolute.

Two scars are often visible below the articulation of the pedicel, as the result of two fallen bracts.

9. *Guatteria costaricensis* R.E. Fr., *Acta Horti Berg.* 12(3): 514. f. 34b (1939). Holotype: Costa Rica: Oersted 146 (C).

Guatteria costaricensis R.E. Fr. var. *endresii* R.E. Fr.

Trees or shrubs 3-10 m. Young twigs often zigzagging, rather densely to sparsely covered with appressed, brown hairs, soon glabrous. Leaves 7-17 x 2-6 cm, narrowly elliptic, sometimes slightly falcate, chartaceous, not verrucose, drying greyish or brownish black, rather densely covered with erect hairs along the midrib above, sparsely covered with appressed, brown hairs below; base acute; apex acuminate (acumen 5-10 mm long); midrib flat to impressed above, often keeled below; secondary veins distinct, 8-14 per side, prominent above. Petioles 3-7 x 1-2 mm. Flowers solitary; pedicels 10-20 mm, rather densely to finally sparsely covered with appressed, brown hairs. Sepals 3-4 x 3-6 mm, deltate to shallowly ovate-triangular, reflexed, outer side sparsely covered with appressed, brown hairs, upper margins densely so. Petals cream to yellow, equal, ovate to rhombic, 10-14 x 8-9 mm, outer side densely covered with appressed hairs. Stamens 1.5-2 mm, connective shield densely papillate. Carpels ca. 75. Monocarps 30-40, green when young, 7-10 x 4-5 mm, ellipsoid, sparsely covered with appressed hairs, soon glabrous, apex apiculate, stipes 8-14 x 1 mm. Seed 8-9 x 3-4 mm, ellipsoid, pitted to brainlike. *Forest.* CR (Grayum & Hammel 5524, U), P (Folsom 4878, MO). 600-1600 m. (Endemic).

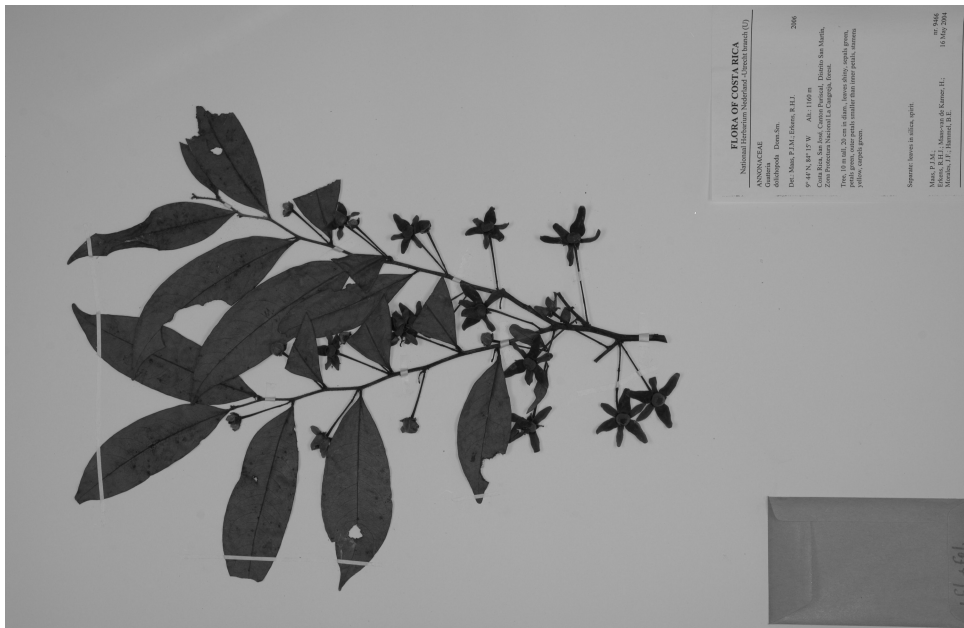
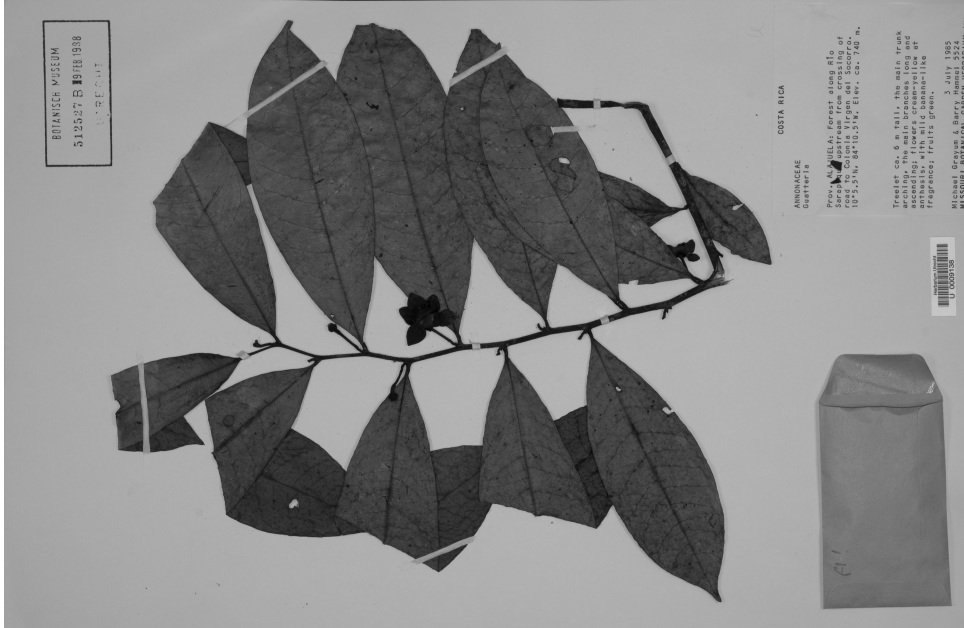
Guatteria costaricensis has often been confused with *G. oliviformis*, but is aberrant by its non-verrucose leaves, its indument of appressed hairs on its young twigs, its longer stipes, its smaller sepals and seeds and its greyish or brownish black leaves after drying.

The Panamanian material of *G. costaricensis* seems to resemble the small leaved material of *G. slateri*. For the differences with *G. slateri* see under that species.

10. *Guatteria dolichopoda* Donn. Sm., *Bot. Gaz.* 23: 2 (1897). Lectotype: Costa Rica, *Donnell Smith* 6429 (US).

Guatteria dolichopoda Donn. Sm. var. *microsperma* R.E. Fr; *G. tonduzii* Diels var. *tonduzii*; *G. tonduzii* Diels var. *leptopus* R.E. Fr..

Trees or shrubs 3-20 m. Young twigs rather densely to sparsely covered with erect, brown hairs ca. 0.5 mm long, finally glabrous. Leaves 11-14 x 3-5 cm, narrowly elliptic, sometimes narrowly ovate, chartaceous, not verrucose, glabrous above, but primary vein and sometimes the secondary veins covered with erect, brown hairs, sparsely covered with erect (and appressed), brown hairs below; base acute to attenuate; apex acuminate (acumen 10-20 mm long); midrib impressed to flat above; secondary veins indistinct, 10-15 per side, flat to slightly prominent above. Petioles 2-6 x 1 mm. Flowers solitary, sometimes in pairs; pedicels 30-60 mm, rather densely to sparsely covered with erect hairs, becoming almost glabrous in fruit. Sepals 5-7 x 3-6 mm, ovate-triangular, reflexed, outer margins rolled inwards, outer side rather densely to sparsely covered with appressed hairs. Petals green, maturing yellow, subequal, narrowly oblong-elliptic to narrowly ovate, 14-30 x 4-11 mm, outer side densely to rather densely covered with appressed, white hairs, particularly



Top: *Guatteria costaricensis* R.E. Fr. (Grayum 5524, U).

Bottom: *Guatteria dolichopoda* Donn. Sm. (Maas 9466, U).

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towards the base. Stamens 1.5-2 mm, connective shield minutely papillate. Carpels 60-100. Monocarps 75-100, black, 7-11 x 4-5 mm, ellipsoid, sparsely covered with appressed hairs, soon becoming glabrous, apex apiculate, stipes 15-20 x 1 mm. Seed 6-9 x 4-5 mm, ellipsoid, pitted. *Forest. CR* (Maas & al. 9466, U); P (Maas & al. 9509, U). 0-1600 m. (Mesoamerica, Colombia (Chocó)).

Guatteria dolichopoda is recognized by its quite long pedicels and young twigs covered with erect hairs ca. 0.5 mm long. It has often been confused with *G. tomentosa*; see under that species.

11. *Guatteria jefensis* Barringer, *Ann. Missouri Bot. Gard.* 71: 1186 (1984). Holotype: Panama, Hammel 6302 (MO).

Shrubs or trees 1-6 m. Young twigs sparsely covered with appressed hairs, soon glabrous. Leaves 7-20 x 3-7 cm, ovate to elliptic, coriaceous, often folded when dry, not verrucose, sparsely covered with erect hairs along midrib and secondary veins above, sparsely covered with appressed hairs below; base obtuse; apex shortly acuminate (acumen to 10 mm long); midrib impressed above; secondary veins distinct, 10-13 per side, impressed to flat above. Petioles 3-8 x 1-3 mm. Flowers solitary or in pairs; pedicels 15-50 mm, densely covered with appressed hairs. Sepals 5-8 x 5-7 mm, broadly ovate-triangular, appressed, finally becoming patent to slightly reflexed, margins revolute, outer side densely covered with appressed hairs. Petals yellowish green to yellow, equal, broadly ovate to obovate, 10-15(-20) x 7-15 mm, outer side densely covered with appressed hairs. Stamens 1-2 mm, connective shield glabrous, sometimes slightly umbonate. Carpels 40-50. Monocarps 25-50, green, maturing blackish purple, 10-13 x 5-7 mm, ellipsoid, glabrous, apex rounded or apiculate (apicle nipple-shaped, ca 1 mm long), stipes 4-8 x 1-2 mm, distinctly constricted at the apex. Seed 8-11 x 5-6 mm, ellipsoid, slightly pitted. *Dwarf cloud forest.* P (Valdespino & al. 685, U). 800-1000 m. (Endemic).

Guatteria jefensis, one of the many narrow endemics of Cerro Jefe, is easily distinguished by its thick, often folded leaves and by its constricted stipes.

12. *Guatteria galeottiana* Baill., *Adansonia* 8: 268 (1868). Holotype: Mexico, Liebmann 16 (C).

Trees 2-10 m. Young twigs sparsely covered with appressed hairs, soon glabrous. Leaves 10-15 x 3-5 cm, narrowly elliptic, rarely somewhat obovate, chartaceous, not verrucose, often bright green when dry, shiny, glabrous above, glabrous below, except for some hairs along the midrib; base attenuate; apex acuminate (acumen 10-20 mm long); midrib flat above; secondary veins distinct, 8-15 per side, slightly raised above. Petioles 4-8 x 1-2 mm. Flowers solitary; pedicels 25-50 mm, sparsely covered with appressed hairs to glabrous. Sepals 4-5 x 4-5 mm, deltate, reflexed, outer side rather densely covered with appressed hairs. Petals yellowish green, subequal, ovate, 12-15 x 6-7 mm, outer side rather densely covered with appressed hairs. Stamens 1-2 mm, connective shield papillate. Carpels 20-40. Monocarps 10-20, green, maturing black, 10-13 x 5-6 mm, narrowly ellipsoid, sparsely covered with appressed hairs to glabrous, apex apiculate, stipes 9-17 x 1 mm. Seed 9-12 x 4-5, ellipsoid, brain-like. *Forest. M* (Oaxaca, Veracruz; Trigós 3057, MO). 0-500(-900) m. (Endemic).

Guatteria galeottiana is an endemic from the Veracruz and Oaxaca regions in Mexico. It can be recognized by its leaves that often dry bright green, its long pedicels, the narrowly ellipsoid and apiculate monocarps, and its almost perpendicular secondary



Top: *Guatteria jefensis* Barringer (Valdespino 685, U).

Bottom: *Guatteria galeottiana* Baill. (Beaman 6121, U).

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venation. All these characters fit the type very well. However, the collections from Oaxaca (e.g. *Hernández 1695*) differ somewhat by having rounder monocarps and a somewhat more ascending secondary venation, but further fall within the description of this species.

13. *Guatteria lucens* Standl., *Trop. Woods* 42: 22 (1935). Holotype: Panama, *Cooper 280* (F).

Guatteria dumetorum R.E. Fr.

Trees 8-38 m. Young twigs densely to sparsely covered with appressed hairs, soon glabrous. Leaves 10-21 x 2-6 cm, narrowly elliptic to narrowly obovate, chartaceous, densely or not verrucose, shiny above, glabrous above, sparsely, sometimes rather densely covered with appressed hairs below; base long-attenuate, basal margins often revolute; apex acuminate (acumen 5-15 mm long); midrib impressed above, often keeled below; secondary veins distinct, 11-20 per side, prominent above. Petioles 5-11 x 1-2 mm. Flowers solitary, rarely in pairs; pedicels 7-35 mm, densely, but soon sparsely covered with appressed hairs. Sepals 2-5 x 2-4 mm, deltate to shallowly triangular, reflexed, outer side densely covered with appressed hairs. Petals yellow, orange, to greenish red, subequal, narrowly ovate to rhombic-ovate, 10-19 x 3-9 mm, outer side densely covered with appressed hairs. Stamens ca. 1 mm, connective shield papillate. Carpels 75-100. Monocarps 40-75, green, red, to finally black, 5-12 x 3-7 mm, narrowly ellipsoid to ellipsoid, rather densely to sparsely covered with appressed hairs to glabrous, apex apiculate, stipes 5-20 x 0.5-1 mm. Seed (5-)7-12 x 3-5 mm, narrowly ellipsoid, slightly pitted. *Forest*. CR (*Maas & al. 9486*, U); P (*Maas & al. 9561*, U). 0-900 m. (Endemic).

Guatteria lucens is well characterized by shiny leaves with a long-attenuate base, and by its prominent venation on the upper leaf side.

Most of the costarican material of this species investigated by us is characterized by non-verrucose to slightly verrucose leaves, and fits *G. lucens* fairly well. Most investigated collections of Panama, and some specimens of the Osa Peninsula in Costa Rica, however, have distinctly verrucose leaves and fall within the concept of *G. dumetorum*. As all other features of these Panamanian collections fit *G. lucens* very well, for this moment we have united both species under the oldest name, namely *G. lucens*.

14. *Guatteria oliviformis* Donn. Sm., *Bot. Gaz.* 23: 1 (1897). Syntypes: Costa Rica, *Tonduz 1740* (CR, US) and *Tonduz 7802* (CR, US).

Trees 5-25 m. Young twigs often zigzagging, densely covered with long-persistent, erect, brown hairs. Leaves 10-20 x 3-7 cm, narrowly elliptic to narrowly obovate, coriaceous to slightly chartaceous, rather densely to densely verrucose, often drying blueish green, densely covered with erect, brown hairs along the midrib above, becoming glabrous, densely covered with erect, brown hairs below; base acute to obtuse; apex acuminate (acumen 5-15 mm long); midrib impressed to slightly raised above; secondary veins distinct, 8-12 per side, slightly prominent above. Petioles 3-7 x 1-2 mm. Flowers solitary, sometimes in pairs; pedicels 7-25 mm, densely to sparsely covered with erect, brown hairs. Sepals 5-7 x 5-9 mm, very broadly to shallowly ovate-triangular, reflexed, outer side rather densely to sparsely covered with appressed, whitish hairs. Petals yellowish green to yellow, equal, ovate to elliptic, 12-16{-25} x 7-10{-15} mm, outer side densely covered with appressed and erect, whitish hairs. Stamens 2-2.5 mm, connective shield densely papillate. Carpels 40-50. Monocarps 10-50, green, maturing purplish black, 9-16 x 6-11 mm, ellipsoid, somewhat wrinkled, glabrous, apex rounded or apiculate, stipes

3-7 x 1-2 mm. Seed 9-12 x 6-7 mm, ellipsoid, rough. *Forest. CR (Maas & al. 9471, U); P (Maas & al. 9510, U). (0-)1200-2200 m. (Endemic).*

Guatteria oliviformis could be confused with *G. costaricensis*. For differences see under the latter.

Several collections from La Amistad, Costa Rica (*Angulo 374, Chinchilla 181 and Acosta 2411*) are somewhat aberrant from the general *G. oliviformis* appearance because they lack verrucose leaves. They do match the description of *G. oliviformis* in all other respects.

15. *Guatteria pudica* N. Zamora & Maas, *Bot. Jahrb. Syst.* 122: 244. f. 3-5 (2000). Holotype: Costa Rica, *Herrera 4026 (INB).*

Trees 4-13 m. Young twigs densely covered with a long-persisting indument of erect, reddish brown hairs. Leaves 10-28 x 5-10 cm, narrowly elliptic to narrowly oblong-elliptic, chartaceous, not verrucose, glabrous above, but midrib vein densely covered with erect, reddish brown hairs, densely covered with erect, reddish brown hairs below; base obtuse to slightly cordate, basal margins revolute; apex acuminate (acumen 10-20 mm long); midrib impressed to flat above; secondary veins distinct, 7-16 per side, impressed to slightly prominent above. Petioles 3-8 x 2-3 mm. Flowers solitary; pedicels 9-17 mm, densely covered with erect and appressed, reddish brown hairs. Sepals 5-8 x 5-8 mm, broadly ovate-triangular, appressed to slightly reflexed, outer side densely covered with appressed hairs. Petals yellowish green to yellow, equal, broadly ovate to rhombic, 10-20 x 9-18 mm, outer side densely covered with appressed, reddish brown hairs. Stamens 1.5-2 mm, connective shield papillate. Carpels 75-100. Monocarps 50-75, wine-red when ripe, 8-11{-13} x 4-6{-8} mm, ellipsoid, sparsely covered with appressed hairs, apex apiculate, stipes 5-10 x 1 mm. Seed 7-8 x 4 mm, ellipsoid, pitted. *Forest. CR (Maas & al. 9495, U). 0-500 m. (Endemic).*

Guatteria pudica is probably closest to *G. chiriquiensis*, with which it shares a long-persistent indument of erect, brownish hairs on most of its vegetative parts. It differs, however, by an obtuse to slightly cordate leaf base, its narrowly elliptic to narrowly oblong-elliptic leaves, and by its midrib which is impressed to flat (instead of raised) on the upper side of the lamina.

16. *Guatteria recurvisepala* R.E. Fr., *Acta Horti Berg.* 12(3): 447. f. 19e (1939). Holotype: Costa Rica, *Skutch 4234 (S).*

Trees 4-30 m. Young twigs densely covered with long-persisting erect, brown hairs. Leaves 15-32 x 4-13 cm, narrowly oblong-elliptic to narrowly obovate, chartaceous to coriaceous, not verrucose, glabrous above, but midrib densely covered with erect, brown hairs, densely (to rather densely) covered with erect, brown hairs below; base obtuse, rarely acute, sometimes slightly oblique; apex acuminate (acumen 5-25 mm long); midrib flat above; secondary veins distinct, 11-18 per side, flat to slightly prominent above. Petioles 5-13 x 2-4 mm. Flowers in a several-flowered inflorescence or solitary; pedicels 15-40 mm, densely covered with erect, brown hairs. Sepals 6-11 x 7-11 mm, broadly ovate-triangular, soon strongly reflexed, outer side densely covered with appressed, brown hairs. Petals yellowish green, yellow, to brown, equal, obovate to rhombic, 15-30{-45} x 10-15{-25} mm, outer side densely covered with appressed, brown hairs. Stamens 1.5-2 mm, connective shield papillate, slightly umbonate. Carpels 75-100. Monocarps 50-75, green, maturing purple-black, 7-10 x 5-6 mm, ellipsoid, sparsely covered with appressed hairs, apex



Top: *Guatteria pudica* N. Zamora & Maas (Maas 9495, U).

Bottom: *Guatteria recurvisejala* R.E. Fr. (Maas 9483, U).

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apiculate, stipes 8-20 x 0.5-1 mm. Seed 7-8 x 4-5. mm, ellipsoid, smooth. *Forest. N* (Stevens 19831, MO); CR (Maas & al. 9483, U); P (Galdames & al. 2281, MO). 0-110 m. (Mesoamerica, pacific coast of Colombia, Venezuela, Guyana).

Guatteria recurvisepala can be distinguished by a combination of: strongly recurved sepals and its indument of erect, brown hairs on most of its vegetative parts (although the indument varies from densely to rather densely hairy). The flower buds in this species are sometimes slightly pointed, a feature only known from *G. aberrans*.

17. *Guatteria reinaldii* Erkens & Maas, *Blumea* 51(2): 206. f. 4. (2006). Holotype: Panama, Aguilar & al. 2031 (INB).

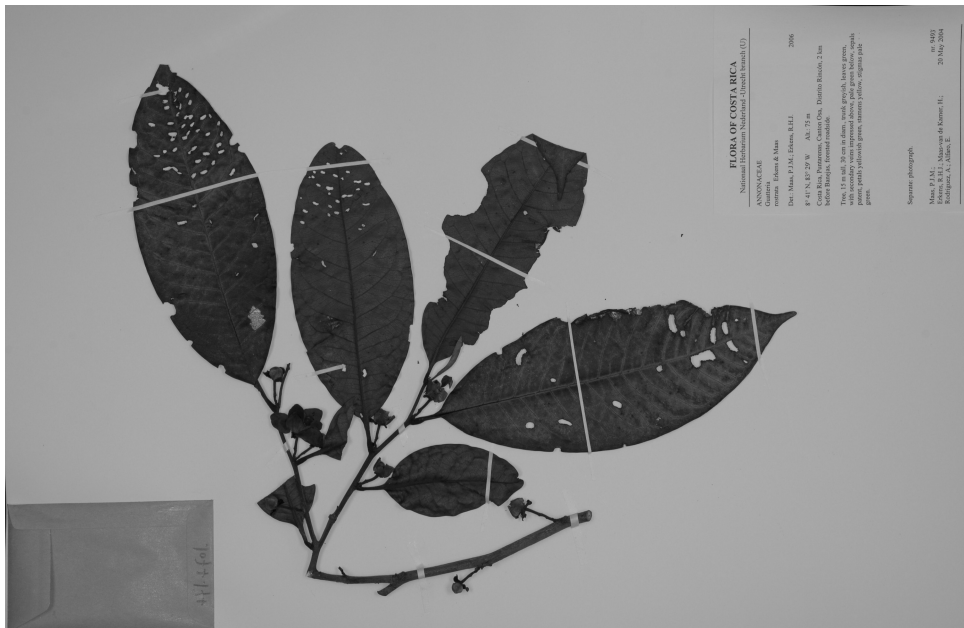
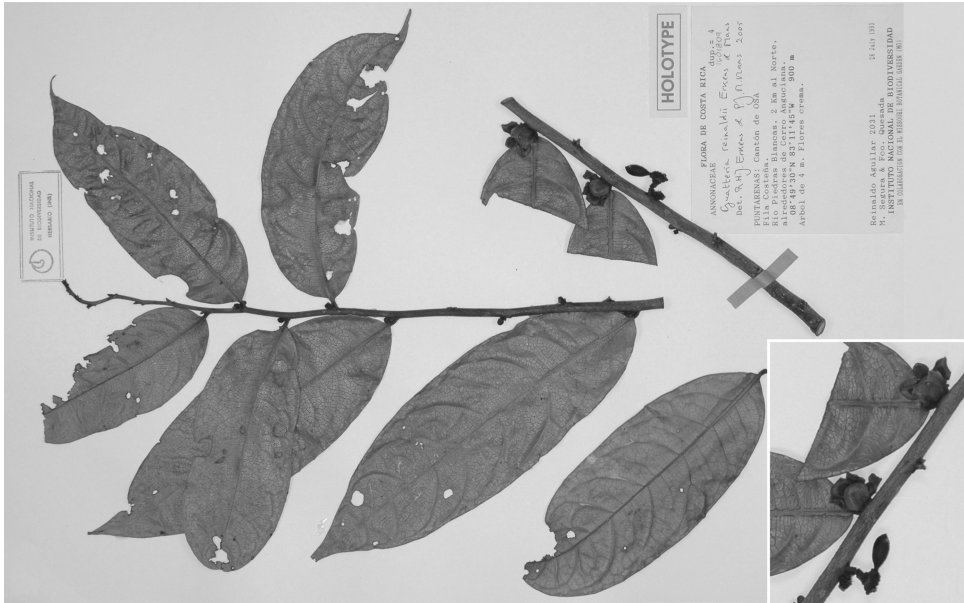
Trees 4-10 m. Young twigs rather densely covered with appressed hairs, soon glabrous. Leaves 13-20 x 4-6 cm, narrowly ovate to narrowly elliptic, chartaceous, sparsely or not verrucose above, shiny above, glabrous above, except for some hairs along primary vein, sparsely to rather densely covered with appressed hairs below; base obtuse; apex acuminate (acumen 10-15 mm long); midrib flat to raised above; secondary veins distinct, 6-10 per side, strongly prominent above. Petioles 2-4 x 1-2 mm. Flowers solitary or in pairs; pedicels 3-7 mm, densely covered with appressed, dark brown hairs. Sepals ca. 6 x 6 mm, deltate, appressed, outer side densely covered with appressed, dark brown hairs. Petals cream, equal, ovate-triangular, 8-14 x 8-11 mm, outer side densely covered with appressed, dark brown hairs. Stamens 2-2.5 mm, connective shield papillate. Carpels not counted. Monocarps <10, purple-black, 10-14 x 4-8 mm, narrowly ellipsoid, sparsely covered with appressed hairs, apex rounded or apiculate, stipes 1-3 x 1 mm. Seed 11 x 7 mm, ellipsoid, pitted. *Forest. CR* (Aguilar & al. 2031, U). 900 m. (Endemic).

Guatteria reinaldii, a poorly known Costarican species, can be recognized by its very shortly stipitate monocarps and short pedicels. This species at first sight resembles *G. pudica* but its parts are generally smaller in size. Both species occur in the Osa area and probably are closely related.

18. *Guatteria rostrata* Erkens & Maas, *Blumea* 51(2): 210. t. 2 & f. 5. (2006). Holotype: Costa Rica, Aguilar & al. 3654 (U).

Trees 7-20(-30) m. Young twigs densely covered with appressed hairs, soon glabrous. Leaves 18-28 x 7-11 cm, elliptic to obovate or narrowly so, chartaceous, not verrucose, dull above, glabrous above, rather densely covered with appressed hairs below; base attenuate and decurrent into the narrowly winged petiole; apex acuminate (acumen 10-20 mm long); midrib impressed above; secondary veins distinct, 16-19 per side, prominent above. Petioles 15-20 x 2-3 mm. Flowers solitary or in pairs; pedicels 15-35 mm, densely covered with appressed hairs, finally subglabrous. Sepals 7-12 x 5-10 mm, triangular, patent, outer side rather densely covered with appressed hairs. Petals green to yellowish green, unequal, outer ones ovate, 14-22 x 10-15 mm, inner ones oblong-elliptic to ovate, 10-15 x 5-9 mm, outer side densely covered with appressed hairs. Stamens ca. 2 mm, connective shield densely papillate. Carpels 20-30. Monocarps 5-15, green, maturing red to purple-black, 15-18 x 6-7 mm, narrowly ellipsoid, sparsely covered with erect hairs, soon glabrous, apex rostrate (beak 1-2 x 1-2 mm), stipes 7-10 x 1 mm. Seed ca. 15 x 7 mm, ellipsoid, apex slightly pointed, slightly tuberculate. *Forest. CR* (Maas & al. 9493). 0-350 m. (Endemic).

Guatteria rostrata can be distinguished by its beaked (=rostrate) monocarps,



Top: *Guatteria reinaldii* Erkens & Maas (Aguilar 2031, INB).

Bottom: *Guatteria rostrata* Erkens & Maas (Maas 9493, U).

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combined with rather large leaves and extremely large petioles (15-20 mm long).

The monocarps of *Gentry 65385* (MO) from Colombia (Chocó) resemble the ones from this species quite well. However, because the collection seen only consisted of infructescences, it could not be identified with certainty as *G. rostrata*.

19. *Gutteria rotundata* Maas & Setten, *Proc. Ned. Kon. Ned. Akad. Wetensch. C.* 91(3): 255. f. 11 (1988). Holotype: Panama, *Nee & Tyson 10999* (MO).

Trees 5-20 m. Young twigs sparsely covered with appressed hairs, soon glabrous. Leaves 5-14 x 2-5 cm, obovate to obovate-elliptic, coriaceous, rather densely verrucose on both sides, glabrous above, rather densely covered with appressed hairs below; base acute, extreme base attenuate and decurrent on petiole; apex shortly acuminate, obtuse to broadly rounded, the extreme tip obtuse; midrib flat above, keeled below; secondary veins distinct, 7-12 per side, prominent above. Petioles 6-8 x 2 mm. Flowers solitary; pedicels 4-10 mm, rather densely covered with appressed hairs. Sepals 3-4 x 4-5 mm, broadly ovate-triangular, appressed, outer side rather densely covered with appressed hairs. Petals green to yellow, unequal, outer ones ovate-elliptic to rhombic, 10-17 x 4.5-12 mm, inner ones slightly smaller, outer side rather densely covered with appressed hairs. Stamens 1-2 mm, connective shield papillate. Carpels 6-10. Monocarps and seeds unknown. *Forest. P (McPherson 8475, U)*. 0-500 m. (Endemic).

Gutteria rotundata is unique by its leaves, the apex of which is mostly distinctly rounded.

20. *Gutteria sessilicarpa* Maas & Setten, *Proc. Ned. Kon. Ned. Akad. Wetensch. C.* 91(3): 257. f. 13-15 (1988). Holotype: Panama, *Mori & Kallunki 5037* (MO).

Trees 5-20 m. Young twigs rather densely covered with appressed hairs, soon glabrous. Leaves 18-33 x 5-10 cm, narrowly elliptic to narrowly obovate, coriaceous, rather densely verrucose, particularly below, glabrous above, except for some hairs at base and primary veins, and ciliate along basal margins, sparsely covered with appressed hairs to glabrous below; base acute, extreme base decurrent along petiole, basal margins often revolute; apex acuminate (acumen 5-10 mm long); midrib impressed above, keeled below; secondary veins distinct, 17-20 per side, slightly prominent above. Petioles 4-12 x 3-4 mm. Flowers solitary; pedicels 7-18 mm, rather densely to sparsely covered with appressed hairs. Sepals 7-9 x 8-10 mm, deltate, reflexed, outer side densely covered with appressed hairs. Petals green, maturing yellow, equal, elliptic, 11-20 x 7-13 mm, outer side densely covered with appressed hairs. Stamens ca. 2 mm, connective shield papillate. Carpels 12-20. Monocarps 4-20, green, maturing black, 12-23 x 8-14 mm, ellipsoid to ovoid, sparsely covered with appressed hairs to glabrous, apex rounded, stipes absent or up to 2 x 2 mm. Seed 12-15 x 8 x 5-6 mm, ellipsoid to ovoid, pitted and striate. *Forest. P (Maas & al. 9554, U)*. 350-1000 m. (Endemic).

Gutteria sessilicarpa is typical by its almost sessile monocarps, combined with coriaceous, rather densely verrucose leaves.

21. *Gutteria slateri* Standl., *Publ. Field Columbian Mus., Bot. Ser.* 4(8): 206 (1929). Holotype: Panama: *Cooper & Slater 177* (F).

Trees 4-30 m. Young twigs often zigzagging, rather densely covered with appressed, brown hairs, soon glabrous. Leaves 7-24 x 2.5-8.5 cm, narrowly elliptic to



Top: *Guatteria rotundata* Maas & Setten (McPherson 8475, U).

Bottom: *Guatteria sessilicarpa* Maas & Setten (Maas 9554, U).

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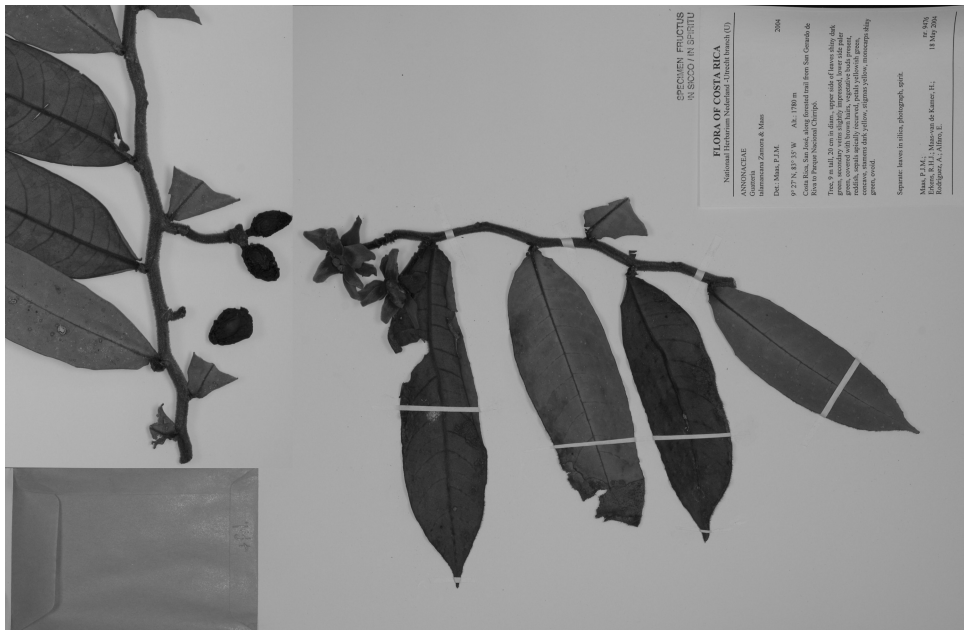
narrowly obovate, chartaceous to coriaceous, not verrucose, glabrous above, sparsely covered with appressed, brown hairs to glabrous below; base acute to attenuate; apex acuminate (acumen 5-15 mm long); midrib slightly raised to flat above, often keeled below; secondary veins distinct, 8-15(-20) per side, prominent above. Petioles 4-20 x 1-3 mm, decurrent as slightly prominent ridges in young twigs. Flowers solitary, rarely in pairs; pedicels 15-32(-42) mm, rather densely to sparsely covered with appressed hairs. Sepals 3-6 x 3-7 mm, deltate to shallowly ovate-triangular, apically reflexed or appressed, outer side sparsely covered with appressed hairs to glabrous. Petals green, maturing yellow, equal, ovate, obovate, or rhombic, 8-16 x 5-11 mm, outer side sparsely to densely covered with appressed hairs. Stamens 1.5-2 mm, connective shield densely papillate to densely hairy. Carpels 50-75. Monocarps 20-60, green, maturing red, to finally black, 8-10 x 5-8 mm, ellipsoid, sparsely covered with appressed hairs, soon glabrous, apex apiculate, sometimes rounded, stipes 3-10 x 1-2 mm. Seed 7-10 x 5-7 mm, ellipsoid, brainlike. *Forest. P* (Maas & al. 9513, U). (0-)600-2100 m. (Endemic).

Guatteria slateri is a species mostly found at high elevations, although the type has been collected at sea level. It has many features in common with *G. costaricensis*, the main differences being the shorter stipes (3-6 vs. 8-14 mm), longer petioles (4-20 vs. 3-7 mm), and longer pedicels (15-32 vs. 10-20 mm). Another difference is found in the upper leaf side (glabrous in *G. slateri*, whereas the midrib is covered with hairs in *G. costaricensis*). Ripe monocarps are rarely found in this species, except for Maas & al. 9513, with monocarps (measured from spirit material!) of 10-13 mm long and stipes 7-8 mm long, thus somewhat longer as shown in our description, based on herbarium collections.

22. *Guatteria talamancana* N. Zamora & Maas, *Bot. Jahrb. Syst.* 122: 241. f. 1, 2 (2000). Holotype: Costa Rica, Aguilar & Morales 4453 (INB).

Trees 2.5-20 m. Young twigs very densely covered with long-persisting, erect, brown hairs to 2 mm long. Leaves 13-23 x 3.5-8 cm, narrowly oblong-elliptic, sometimes narrowly obovate, coriaceous, very densely verrucose above, glabrous above, but primary vein densely covered with erect, brown hairs, densely covered with erect, brown hairs below; base obtuse, basal margins often revolute; apex shortly acuminate (acumen 5-15 mm long); midrib flat to slightly raised above; secondary veins distinct, 7-17 per side, flat to slightly prominent above. Petioles 2-5 x 3-4 mm. Flowers solitary; bracts 1-2, leafy, 25-30 mm long, upper side densely covered with erect, brown hairs; pedicels 25-55 mm, densely covered with erect, brown hairs. Sepals 15-20 x 10-15 mm, triangular, appressed, outer and inner side densely covered with erect, brown hairs. Petals yellow to cream, equal, ovate-oblong, 15-25 x 10-12 mm, outer and inner side densely covered with appressed, brown hairs. Stamens ca. 1.5 mm, connective shield densely hairy. Carpels ca. 50. Monocarps 10-15, black, 20-30 x 18-20 mm, ellipsoid to ovoid, glabrous, apex rounded, stipes 2-3 x 2-3 mm. Seed 8-11 x 5-6 mm, ellipsoid, brain-like. *Cloud forest. CR* (Maas & al. 9476, U); *P* (Correa A. & al. 2712, U). 1000-2000 m. (Endemic).

Guatteria talamancana, a species occurring at high elevations up to 2000 m (!), is unique among Central American species of *Guatteria* by its indument of long-persisting, very long, erect, brown hairs on most of its parts. It has been confused with the Colombian species *G. elegantissima* (known from Chocó), from which it differs by its much larger sepals (15-20 versus 6-8 mm) and monocarps (20-30 versus 8-9 mm), different leaf shape and size, and its occurrence at higher elevations (1000-2000 m versus sea level).



Top: *Guatteria slateri* Standl. (D'Arcy 11114, U).

Bottom: *Guatteria talamancana* N. Zamora & Maas (Maas 9476, U).

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23. *Guatteria tomentosa* Rusby, *Bull. New York Bot. Gard.* 6: 504 (1910). Holotype: Bolivia, R.S. Williams 453 (NY).

G. rigidipes R.E. Fr.; *G. dolichopoda* not of Donn. Sm.: Schatz, *Fl. Nicaragua* (85)1: 103 (2001); Zamora, *Arb. Costa Rica* 2: 227 (2000).

Trees 3-10(-25) m. Young twigs densely covered with erect, brown, rough, long-persisting hairs to 2 mm long. Leaves 13-23 x 4-6 cm, narrowly elliptic, sometimes narrowly obovate, chartaceous, not verrucose, densely to sparsely covered with erect, brown, rough, long-persisting hairs above, densely so below; base acute to obtuse; apex long-acuminate (acumen 10-35 mm long); midrib impressed above; secondary veins distinct, 8-14 per side, flat to slightly impressed above. Petioles 2-5 x 1-2 mm. Flowers solitary; pedicels 25-50 mm, densely covered with erect, brown, rough, long-persisting hairs. Bracts sometimes present on young pedicels, leafy, narrowly elliptic, 6-20 x 2-5 mm, densely covered with erect, brown, rough, long-persisting hairs. Sepals 10-13 x 7-10 mm, ovate-triangular, appressed, finally becoming patent, outer side densely covered with erect, brown, rough, long-persisting hairs. Petals green to greenish yellow, equal, narrowly ovate, 20-30 x 6-13 mm, outer side densely covered with appressed and erect, brown hairs. Stamens 1.5-2 mm, connective shield papillate. Carpels 75-100. Monocarps 20-50, green, maturing purple-black, 7-9 x 4-5 mm, ellipsoid, sparsely covered with appressed hairs, particularly near the apex, apex apiculate, stipes 7-17 x 1 mm. Seed c. 8 x 4 mm, ellipsoid, pitted. *Forest*. H (*Brant & Zúñiga* 2814, U); N (*Moreno* 26097, U); CR (*Hammel* 17561, U); P (*Maas & al.* 9521, MO). 0-1400 m. (Mesoamerica, pacific coast of Colombia, Peru, Brazil, Bolivia).

We have tentatively named this species *Guatteria tomentosa*, a species which is widespread over Central America and Western South America. It is a highly variable and complex species, including closely related species like *G. trichoclonia* Diels, which needs an intensive taxonomic study. It is easily recognizable by a hirsute indument of long-persisting, erect, brown hairs up to 2 mm long on most of its vegetative and flower parts like sepals and pedicels.

It is different from *G. dolichopoda* by its much denser indument, its longer sepals (10-13 versus 5-7 mm), and by the regular presence of leafy bracts.

Several collections from the region of the Fortuna Dam, Chiriquí, Panama (a.o. *McPherson* 9123 (PMA)) are deviating by having narrower leaves (2-3 cm).

24. *Guatteria* aff. *tomentosa* Rusby, *Bull. New York Bot. Gard.* 6: 504 (1910). Holotype: Bolivia, R.S. Williams 453 (NY).

Trees 3-8 m. Young twigs densely covered with erect, brown, rough, long-persisting hairs to 2 mm long. Leaves 9-15 x 3-8 cm, convex, narrowly ovate to obovate, sometimes elliptic, chartaceous, not verrucose, rather densely to densely covered with erect hairs above, densely so below; base cordate, oblique, basal margins often strongly folded inwards; apex acuminate (acumen 5-15 mm long), rarely acute, obtuse, or even emarginate; midrib impressed above; secondary veins distinct, 7-12 per side, flat to slightly raised above. Petioles 2-4 x 1-2 mm. Flowers solitary; pedicels 20-40 mm, densely covered with erect, brown hairs. Bract present on young pedicels, leafy, very broadly ovate, 4-5 x 4-5 mm, densely covered with erect, brown, hairs. Sepals 5-8 x 5-6 mm, very broadly ovate-triangular, appressed, outer side densely covered with erect, brown hairs. Petals green, maturing yellow, slightly unequal, outer ones narrowly ovate-triangular, 15-30 x 6-10 mm, acute, the inner ones ovate, 14-17 by 6-10 mm, obtuse, outer side densely covered with



Top: *Guatteria tomentosa* Rusby (Maas 9521, U).

Bottom: *Guatteria* aff. *tomentosa* Rusby (Maas 9555, U).

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erect, brown hairs. Stamens 1-2 mm, connective shield papillate. Carpels 40-50. Monocarps 10-15, green, maturing purple to black, c. 10 x 4-5 mm, ellipsoid, sparsely covered with appressed hairs, particularly near the apex, apex apiculate, stipes 4-6 x 1 mm. Seed c. 9 x 4 mm, ellipsoid, pitted. *Forest. P (Maas & al. 9555, U). 300-900 m. (Endemic).*

This species, restricted to the Cerro Jefe region in Panama, is unique by its oblique and cordate leaf base, combined by a long-persisting, hirsute indument of the leafy twigs. It belongs to a complex group of species like *G. trichoclonia* and *G. tomentosa*. As the circumscription of the species within this group is still very problematical we have refrained from naming it.

25. *Guatteria verrucosa* R. E. Fr., *Acta Horti Berg.* 12(3): 519-521, f. 35a (1939). Holotipo: Costa Rica, *Brenes 4058 (F!)*.

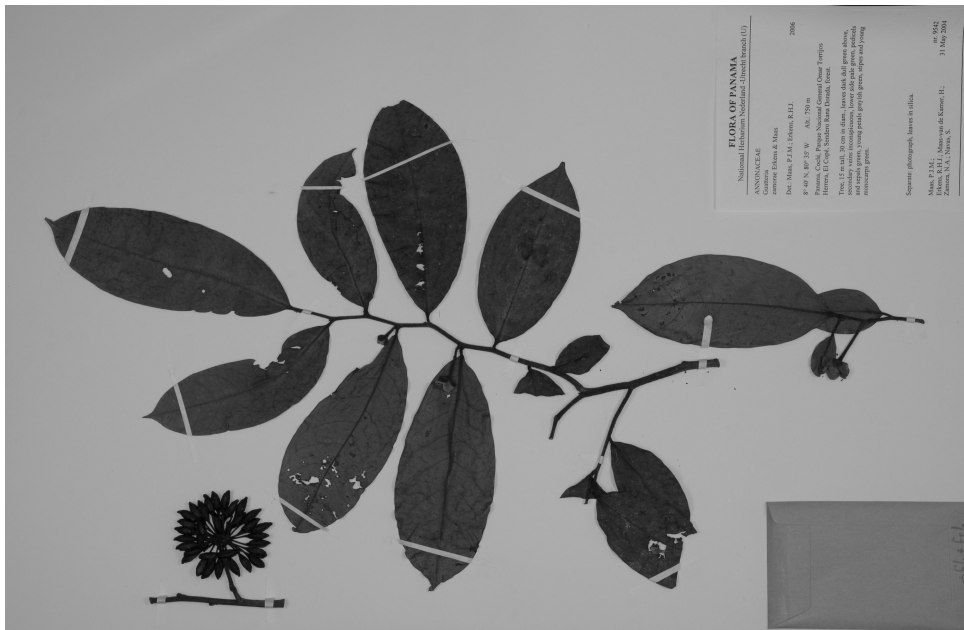
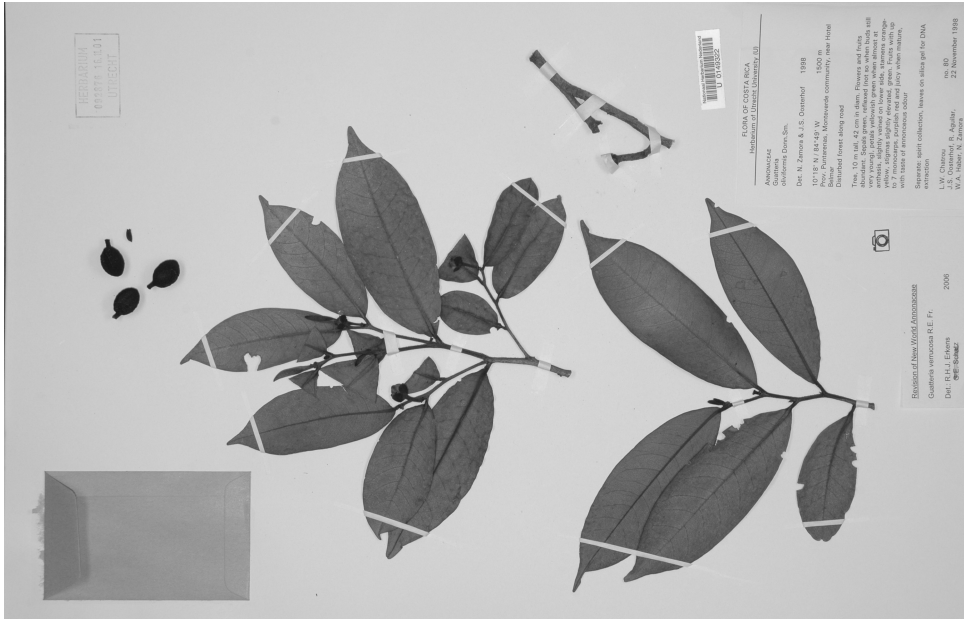
Trees 3-28 m. Young twigs rather densely covered with appressed hairs, to glabrous. Leaves 7-17 x 2.5-5 cm, narrowly elliptic to elliptic, chartaceous, verrucose above and below, dull, glabrous above, sparsely covered with minute appressed hairs below; base acute to attenuate, decurrent along the petiole; apex acuminate (acumen 5-15 mm long); midrib flat to slightly raised above, sparsely covered with erect hairs along the midrib above, sparsely covered with appressed hairs below; secondary veins distinct, 8-16 per side, prominent above. Petioles 3-5(-8) x 1-2 mm. Flowers solitary; pedicels 14-25 mm, rather densely to sparsely covered with appressed hairs, often bearing ca. 4 soon falling bracts. Sepals 3-4 x 5-6 mm, broadly ovate, reflexed, outer side rather densely to sparsely covered with appressed hairs. Petals creamish or yellowish green to cream or light yellow, subequal, ovate, 8-15 x 6-9 mm, rather densely to sparsely covered with appressed hairs. Stamens 1.5-2 mm, connective shield papillate. Carpels 20-25. Monocarps 15-25, green, red, to finally purplish black, 10-17 x 9-13 mm, ellipsoid to ovoid or broadly so, somewhat wrinkled, glabrous, apex rounded, stipes 2-5 x 1-3 mm. Seed 9-13 x 6-11 mm, ellipsoid, strongly wrinkled. *Forest. CR (Haber & Bello 3948, MO). 1100-1600 m. (Endemic).*

This species is easily confused with *G. oliviformis*. However, it can be recognized by its typical combination of young twigs densely covered with appressed hairs, leaves that are verrucose on both sides and the shortly stipitate, almost ovoid monocarps. Furthermore, this species is only known from the Monteverde region (Puntarenas) and the mountains of La Palma de San Ramón (Alajuela) in Costa Rica. It looks as somewhat intermediate between *G. oliviformis* and *G. costaricensis*, but is distinct from both.

The pedicels of this species are often woody below the articulation.

26. *Guatteria zamorae* Erkens & Maas, *Blumea* 51(2): 213. t. 3 & f. 6 (2006). Holotype: Panama, *Maas & al. 9531 (U)*.

Trees 11-15 m. Young twigs densely covered with erect, brown hairs, finally glabrous. Leaves 10-17 x 3-5 cm, narrowly obovate to narrowly elliptic, chartaceous, densely verrucose above, yellowish brown when dry, glabrous above, except for the densely hairy primary and secondary veins, densely covered with erect, brown hairs below; base acute; apex acuminate (acumen 5-10 mm long); midrib flat to slightly raised above; secondary veins distinct, 10-15 per side, prominent above. Petioles 3-9 x 1-2 mm. Flowers solitary; pedicels 25-35 mm, densely covered with erect hairs. Sepals 4 x 4-5 mm, very broadly ovate-triangular, patent, extreme apex rolled inwards, outer side rather densely to densely covered with appressed and erect hairs. Petals green to greyish green,



Top: *Guatteria verrucosa* R.E. Fr. (Chatrou 80, U).

Bottom: *Guatteria zamorae* Erkens & Maas (Maas 9542, U).

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subequal, ovate to ovate-oblong, 10-12 x 5-7 mm, outer side densely covered with appressed and erect hairs. Stamens 1.5-2 mm, connective shield densely papillate. Carpels 50-60. Monocarps 30-50, green, maturing dark wine-red, 9-12 x 4-5 mm, ellipsoid, glabrous, except for some scattered hairs near the apex, apex apiculate, stipes 6-10 x 1 mm. Seed 8-10 x 3-4 mm, narrowly ellipsoid, tuberculate. *Forest. P (Maas & al. 9542, U). 0-750 m. (Endemic).* *Guatteria zamorae* can be keyed out from the other Central American species of *Guatteria* with an indument of erect hairs on the young leafy twigs and verrucose leaves by the yellowish brown leaf colour after drying, by having very small petals (10-12 mm long!) and small leaves (10-17 x 3-5 cm) and by its apiculate monocarps. Phylogenetic analysis (chapter 5) suggests that this species belongs to a group comprising three Central American species, namely *G. talamancana*, *G. oliviformis*, and *G. allenii*. Two triangular bracts were seen around the flower buds. This is interesting because *G. talamancana* is known for its very large bracts on the pedicel. The latter, however, has a thick brown indument all over the leaf, while *G. zamorae* only has densely hairy primary and secondary veins.

27. *Guatteria* sp. 1

Trees 15-16 m. Young twigs densely covered with appressed hairs, soon glabrous. Leaves 7-14 x 3-5.5 cm, narrowly elliptic to narrowly obovate, chartaceous, not verrucose, glabrous above, sparsely covered with appressed hairs, soon glabrous below; base acute to obtuse; apex acuminate (acumen 5-10 mm long); midrib slightly raised above; secondary veins distinct, 10-14 per side, prominent above. Petioles 10-18 x 1-2 mm. Flowers solitary; pedicels 10-18 mm, sparsely covered with appressed hairs. Sepals ca. 4 x 5 mm, deltate, reflexed, outer side rather densely covered with appressed hairs. Petals green, equal, ovate, 8-10 x 4-7 mm, outer side densely covered with appressed hairs. Stamens ca. 1 mm, connective shield papillate. Carpels not yet studied. Monocarps 10-15, green, maturing purplish red, 20-25 mm in diam., globose, glabrous, wall to ca. 6 mm thick, apex rounded, stipes 1.5-2 x 2.5-3 mm. Seed ca. 9 x 3 mm, narrowly ellipsoid, surface brainlike. *Forest. CR (Herrera 5227, INB). ca. 1300 m. (Endemic).*

This species is very aberrant from any other species of *Guatteria* by its very thick monocarp wall (up to 6 mm thick) and also by its very short and thick stipes. The thick fruit wall of this species looks a little bit too much inflated and we wonder if this maybe a galled fruit. However, it is known from two different (nearby) localities in Limón, Costa Rica (*Aguilar 1121* and *Herrera 5227*) and on both localities this aberrant fruit type has been found. Another typical feature of this species is its long-attenuate leaves and long petioles (up to 18 mm).

28. *Guatteria* sp. 2

Trees or shrubs 3-16 m. Young twigs rather densely covered with appressed hairs, soon glabrous. Leaves 9-22 x 3-7 cm, narrowly elliptic to narrowly obovate, chartaceous, not verrucose, glabrous above, sparsely covered with appressed hairs to glabrous below; base acute to attenuate; apex acuminate (acumen 5-15 mm long); midrib impressed above, keeled below; secondary veins distinct, 9-15 per side, impressed above, distinctly raised below. Petioles 3-9 x 1-2 mm. Flowers solitary; pedicels 30-55(-65) mm, rather densely covered with appressed (and some erect) hairs. Sepals 4-5 x 4-5 mm, deltate, reflexed, outer side densely covered with appressed hairs. Petals color, equal, ovate to narrowly ovate, 10-18 x 5-9 mm, outer side densely to rather densely covered with appressed hairs. Stamens



Top: *Guatteria* sp. 1 (Herrera 5227, INB).

Bottom: *Guatteria* sp. 2 (Herrera 716,U).

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1.5-2 mm, connective shield densely papillate to hairy. Carpels 75-100. Monocarps 30-60, green, maturing pink to red and finally black, 6-10 x 4-8 mm, ellipsoid, sparsely covered with appressed hairs, soon glabrous, apex apiculate, stipes 7-13(-20) x 1 mm. Seed 8-9 x 6-7 mm, ellipsoid, slightly pitted. *Forest. P (Herrera 716, U)*. (150-)500-1200 m. (Panama, pacific coast of Colombia).

This species is known from the Darién region in Panama and the adjacent Chocó province in Colombia. It can be distinguished by a combination of long-pedicellate flowers, a keeled midrib, and an indument of appressed hairs on its young leafy twigs. As these characters are not very convincing we have refrained from naming it yet.

INSUFFICIENTLY KNOWN SPECIES

1. *Gutteria grandiflora* Donn. Smith, *Bot. Gaz.* 14: 25. 1889. Syntypes: *Donnell Smith 1235* (B, GH, K, P, US).

Only very little and poor material of this species could be investigated (*Steyermark 49140; Holdridge 2330; Donnell Smith 1235*). Probably this species should be united with *Gutteria anomala*. However, there are some slight differences noticeable when comparing this material with the latter species. The studied material of *G. grandiflora* seemingly has one terminal flower, has a more elliptic leaf shape (instead of more obovate) and is verrucose at the lower side of the leaf. These characters differ from the ones seen in *G. anomala* (which has a many-flowered terminal inflorescence, more narrowly obovate leaves and is not verrucose). Because these differences could be seen in all three examined specimens of *G. grandiflora*, it has not yet been sunk into *G. anomala*.

A drawing of *G. granfiflora* of Donn. Sm. shows a multi-flowered terminal inflorescence. However, this drawing might refer to a part of *G. grandiflora* that has been synonymized with *G. anomala* (see appendix 2).

2. *Gutteria macrantha* C. Presl, *Reliq. haenk.* 2(1): 78. 1831.

This species has been described by Presl as having stellate hairs and inflorescences opposite the leaves. Therefore it is unlikely that this species belongs to *Gutteria*. Furthermore, the monocarps are unknown and the locality is uncertain ("habitat in Mexico?"). Because the type was not seen, it is impossible to determine the genus this species belongs to. [modified from Fries (1939)]

3. *Gutteria panamensis* (R.E. Fr.) R.E. Fr., *Ark. Bot., n.s.*, 1(6): 335 (1950). Holotype: Panama, *Cooper 382* (F).

Gutteria costaricensis R.E. Fr. var. *panamensis* R.E. Fr.

Trees 6-13 m. Young twigs rather densely to densely covered with appressed hairs. Leaves 13-21 x 5.5-12 cm, narrowly obovate, chartaceous, not verrucose, dull, glabrous above, rather densely covered with appressed hairs below; base acute; apex acuminate (acumen 5-10 mm long); midrib flat above; secondary veins distinct to indistinct, 15-18 per side, flat to slightly prominent above. Petioles 3-5 x 1.5-2 mm. Flowers solitary; pedicels 20-40 x 1-2 mm, rather densely covered with appressed hairs. Sepals 3-4 x 4-6 mm, depressed ovate, appressed?, outer side densely covered with appressed hairs. Petals yellowish green to deep yellow, equal, broadly elliptic, 6-8 x 7-8 mm, outer side densely covered with appressed hairs. Stamens 1-2 mm, connective shield densely hairy along the edges. Carpels 30-40. Monocarps 30-40, colour unknown, 7-10 x 3-4 mm immature,



Top: *Guatteria grandiflora* Donn. Sm. (Steiermark 49140, F).

Bottom: *Guatteria panamensis* (R.E. Fr.) R.E. Fr. (Aizprúa B4240, F).

10 TAXONOMIC TREATMENT OF CENTRAL AMERICAN GUATTERIA SPECIES

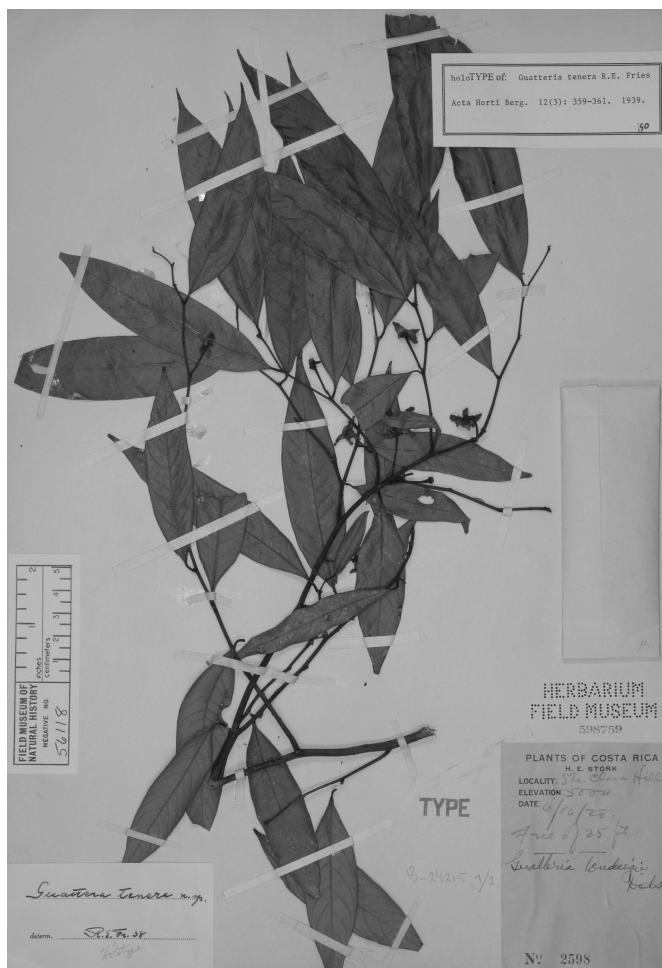
ellipsoid, sparsely covered with appressed hairs, apex apiculate, stipes 6-10 x 1 mm. Seed 8-9 x 3-4 mm, ellipsoid, rough. *Forest. P (von Wedel 1965, MO)*. 0-700 m. (Endemic).

This species is little known and resembles *Guatteria aeruginosa* with which it occurs sympatrically in Panama. However, the latter has verrucose leaves and erect hairs on the midrib on the upper side and on the lower side of the leaf. Fries identified *von Wedel 1965* (Panama, Bocas del Toro) as this species. A recent collection (*Aizprúa B4240*) from Bocas del Toro resembles this collection quite well and is the only recent collection that possibly belongs to this species.

4. *Guatteria tenera* R.E. Fr., *Acta Horti Berg.* 12(3): 359. f. 8c-d (1939). Holotype: Costa Rica, *Stork 2598* (F).

Tree c. 8 m. Young twigs sparsely covered with appressed hairs, soon glabrous. Leaves 8-12 x 2-3 cm, narrowly elliptic, chartaceous, sparsely verrucose on both sides, shiny above, glabrous above, sparsely covered with appressed hairs below; base acute; apex acuminate (acumen 5-6 mm long); midrib impressed above; secondary veins distinct, 13-15 per side, impressed to flat above. Petioles 3-5 x 0.5 mm. Flowers solitary; pedicels 10-20 mm, sparsely covered with appressed hairs. Sepals 3-4 x 3-4 mm, deltate, reflexed, outer side densely covered with appressed hairs. Petals colour unknown, equal, narrowly ovate, 8-12 x 3-4 mm, outer side densely covered with appressed hairs. Stamens 1-1.5 mm, connective shield papillate. Carpels c. 100. Monocarps and seed unknown. *Forest. CR. 1500* m. (Endemic).

This species, only known from the type collection (right) could not be placed. It is characterized by very narrow leaves with the veins impressed on the upper side. *Guatteria lucens* looks somewhat similar because of its slightly shiny, attenuate leaves.



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Espejo, A. 1488 (amp)
Espinosa, A. 720 (sp2); 1287 (sp.); 1377 (amp)
Espinoza, R. 185, 228 (dol); 534 (amp); 687, 748 (dol); 797 (chi); 819 (aer); 1455 (dol)
Espinoza, S. 512 (rec); 1170 (aer)
Estrada, A. 826 (chi); 2832 (amp)
Evans, R. 1063, 1623 (amp)

Fendler, A. 3 (amp, Type)
Fernández, A. 54 (aer); 556, 1224 (amp)
Fernández N., R. 1051, 1408 (amp)
Fletes, E. 490 (luc?); 634 (ros)
FLORPAN 1036 (amp); 1320 (all); 1611 (jef); 2497, 2662 (luc); 2909 (all); 2962, 3311, 3413 (sp2); 3621, 3657 (amp); 4556, 4564, 4606 (sp2)
Folsom, J.P. 1298 (amp); 1832 (cos); 1847 (jef); 1923 (sp.); 1970 (tom aff); 2011, 2502, 2510 (jef); 3560 (ses); 3852 (jef); 4878 (cos); 5856 (amp); 6629 (sp.); 6731 (sp.); 9928 (aer); 10142 (amp)
Förther, H. 11055 (amp)
Foster, R.B. 1306 (luc); 1393 (amp); 1657 (luc); 1897 (jef); 14641 (aer); 14716, 14628 (amp); 15716 (luc)
Frankie, G.W. 28, 396 (amp)
Fuentes, Z. 276 (ver)
Funk, V.A. 10527 (amp)

Galdames, C. 1225, 1444 (amp); 2034, 2103, 2281 (rec); 2444 (amp); 2732 (rec); 3081 (sp2); 3121 (sp.); 3316 (amp); 3782 (ses); 4136 (sp2); 4160 (luc); 4167 (tom aff); 4278 (dol); 4473 (abe); 4630, 4659 (cos); 5268 (rec)
Gamboia, B. 47 (dol)
García, D. 65 (dol); 195 (aer)
García M., A. 1829 (amp)
Garwood, N. 709 (dol); 1087 (aer); 1504 (amp); 1560 (amp); 1749 (amp); 2717 (sp2)
Gentle, P.H. 2133, 3258, 3429, 4306, 7602 (amp)
Gentry, A.H. 1152 (rec); 1973, 2857 (luc); 2881 (tom aff); 3184 (luc); 3434 (tom aff); 4834 (amp); 4886A (ses); 6286 (amp); 6745 (rec); 6951, 7092 (tom); 8789, 13412 (amp); 16860 (sp2); 17844 (tom); 48492 (amp); 48743, 48782, 48840, 71545, 71636 (ver); 71733 (aer); 78540, 78583 (amp); 78593 (aer); 78735 (sp.); 84-348525 (luc)
Gentry Jr., J.L. 2693 (ver)
Gereau, R.E. 3471 (amp)
Gómez, L.D. 2227 (oli); 19100 (sp.); 19102, 19491 (amp); 20272 (oli); 23305 (luc); 23550 (tom)
Gómez-Laurito, J. 9805 (ver); 10219 (amp); 11346 (oli); 11864, 12203 (amp)
Gomez-Pompa, A. 1448 (amp); 3562 (rec)
González, J. 192 (luc); 522 (amp); 1002 (aer); 1065 (amp)
Gordon, B.L. 5, 39, 79c (aer); 93C (luc)
Gordon, I. 80 (sp)
Gough, A. 95 (sp2)
Gradstein, S.R. 8178 (amp)
Grayum, M.H. 1927, 2389, 3601 (aer); 3628, 3630, 4305 (amp); 5111 (ver); 5514 (chi); 5524 (cos); 5586, 6163 (amp); 6228 (dol); 6503 (aer); 6996 (amp); 7741 (oli); 9466 (dol); 10496 (dol)

Greenman, J.M. 5442 (oli)
Grijalva, A. 3466, 3734 (amp)
Guerra, C. 1085 (sp.)
Gustafson, C. 191 (amp)

Haber, W. 1993, 2281 (cos); 3692 (ver); 3893 (oli); 3948 (ver); 4331 (ver); 4497 (ver); 5085 (amp); 5089 (cos); 5104 (amp); 5224 (ver); 5271, 5450, 5500 (cos); 6232 (ver); 6358, 6485, 6557, 6959 (cos); 7025 (ver); 7684 (cos); 7727 (ver); 7834, 8060 (cos); 11548 (amp); 11630 (cos); 11671, 11697 (amp)
Hahn, W. 329 (amp)
Hamilton, C. 3260, 5131 (amp); 937 (dol)
Hammel, B.E. 1034, 2562, 3134 (amp); 3734 (jef); 5131 (amp); 6302 (jef, Type); 11605 (rec); 12837 (sp.); 14681 (tal); 15281 (amp); 16335 (sp2); 16893 (luc?); 16922 (pud); 16934 (amp); 16935 (pud); 16936 (luc); 16960 (ros); 17316 (rec); 17375 (aer); 17561 (tom); 17736 (chi); 17755 (dol); 17913, 18168 (amp); 18875 (dol); 19101 (pud); 20185 (amp); 20663 (aer)
Harmon, P. 90 (luc); 187, 333 (amp)
Hartman, R.L. 12023, 12509 (sp2)
Hartshorn, G.S. 901 (aer); 940 (amp); 969, 1008 (aer); 1052 (amp); 1349 (aer); 1461 (ver); 1462 (ver); 1537, 1542 (aer); 1562 (amp); 1777 (ver); 1799 (rec); 1877 (pud); 1883 (pud); 2154 (dol)
Hawkins, T. 796 (tom); 875 (amp)
Hazlett, D.L. 3126, 3127 (dol); 3333 (tom); 5061 (dol); 8065 (amp)
Hernández G., H. 1 (amp); 479 (ano); 636, 680, 701, 817, 956 (amp); 1104, 1206, 1235 (gal); 1441, 1633 (amp); 1695 (gal); 1717, 1732, 2090 (amp); 2104 (gal); 2464 (amp)
Herrera, A. 937 (sp.); 1440 (amp)
Herrera C., G. 253 (oli); 546 (sp.); 629 (dol); 3307 (oli)
Herrera, G. 253 (oli); 629 (dol); 977 (aer); 2177 (amp); 2560 (aer); 2701 (tal); 3021 (tom); 3228 (oli); 3307 (oli); 3329 (tom); 4026 (pud, Type); 4216, 4243 (pud); 4506, 4879 (amp); 4969 (rec); 5050, 5127 (amp); 5227 (sp1); 5249 (tal); 5762, 5958 (oli); 7066 (chi); 7664 (sp.)
Herrera, H. 514 (jef); 716 (sp2), 1136 (ros); 1171, 1248 (amp)
Hill, S.R. 17792 (oli)
Him, J.J. 107 (acr)
Holdridge, L.R. 2519, 6762 (amp); 6669 (oli)
Holland, D.L. 56 (sp.)
Holst, B.K. 4198, 4207, 4280, 5190, 5765 (amp)
Howell, J.H. 20 (abe); 234 (amp)
Hunter, R. 95 (amp)

Ibañez, A. 1031 (sp.)
Ingham, S. 1738 (ver)
Iremonger, S. 874 (amp)
Ishiki, M. 2193 (gal); 2194 (ano); 2302 (amp)

Jacobs, B. 2496 (amp)
Jiménez, Q. 448, 575 (amp); 633 (aer) ; 646 (ros); 801 (amp); 833 (sp.); 1130 (aer); 1158, 2227, 2292 (dol)
Jiménez L., O. s.n. (May 1961) (dol)
Jiménez M., A. 524 (sp.); 1901 (dol) ; 2339 (amp); 2371 (dol) ; 2904, 3594 (amp); 3625 (aer); 3696 (amp); 3719, 3817 (rec) ; 4106 (amp); 4137 (aer)
Jones, G.C. 3013, 3254 (amp)
Jurgensen, C. 718 (amp, Type)

Kappelle, M. 1338, 862 (sp.)
Kellerman, W.A. 7172 (amp)
Kennedy, H. 2192 (amp); 3226 (all)
Kernan, C. 278 (amp); 598 (luc) ; 916A (amp)

- Khan, T. 728 (amp); 1128 (cos); 1285 (oli)
 Kinloch, J.B. 63 (amp)
 Kirkbride, J.H. 581 (tom); 1037 (sp.); 1453 (sp2)
 Knapp, S. 1077 (all); 2049 (sla); 2556 (sp.); 3554 (jef); 4497 (dol); 4580 (jef); 4984 (cos); 5853 (amp)
 Knight, D. s.n. (amp)
 Koptur, S. 113 (ver)
 Kress, W.J. 94-4900 (dol)
 Kriebel, R. 183, 434 (amp)
- Laguna, A.** 141 (amp)
 Lankester, C.H. 138 (oli); 1925 (amp)
 Lao, E.A. 96 (aer); 570 (rec)
 Laskowski, C. 1299 (rec)
 Lawton, R.O. 1145 (ver)
 Lellinger, D.B. 1280 (ver)
 Lems, K. 5154 (oli); 5165 (rec)
 Lent, R.W. 1622 (oli); 2244 (amp); 2383 (sp.); 2527 (amp); 2619 (cos); 2902 (amp); 3000, 3032 (oli); 3145 (sp.); 3330 (amp); 3460, 3764 (oli)
 Léon, J. 792 (dol)
 Lewis, W.H. 1996 (tom)
 Lezama, D. 104 (amp)
 Liebmann, F.M. 12 (amp, Type); 14 (amp?); 143 (gal)
 Liesner, R.L. 700, 3171 (amp); 4380 (all); 14631 (amp); 14981 (cos); 15199, 15361 (amp); 15579 (ver); 26145 (amp)
 Little Jr., E.L. 25246 (amp)
 Lobo, M.G.A. 114 (amp)
 Long, L.E. 136 (amp)
 Lorener, D.H. 4061 (amp)
 Lot, A. 2230 (amp)
 Luque, D. 509, 566 (abe)
 Luteyn, J.L. 578, 583 (oli); 1230 (all)
- Maas, P.J.M.** 1127, 1590, 7805 (amp); 7817, 7822 (rec); 7869 (pud); 7926, 7964 (amp); 7966 (cos); 7973 (dol); 8001 (oli); 8492 (amp); 8496 (tom); 9392, 9399 (cos); 9417 (amp); 9418 (aer); 9419 (amp); 9427 (aer); 9432 (rec); 9448 (amp); 9462 (dol); 9464 (chi); 9465, 9466 (dol); 9469 (chi); 9471 (oli); 9476 (tal); 9479 (sp.); 9483 (rec); 9484 (tom); 9486, 9491, 9492 (luc); 9493 (ros); 9495, 9496 (pud); 9497 (ros); 9498 (amp); 9508, 9509 (dol); 9510 (oli); 9513 (sla); 9516 (tal); 9519 (luc); 9521 (tom); 9523 (luc); 9525 (sp.); 9528 (tom); 9531 (zam); 9533, 9534 (amp); 9538 (all); 9539 (amp); 9542 (zam); 9543 (all); 9545 (sp.); 9549 (amp); 9553 (jef); 9554 (ses); 9555 (tom aff); 9556, 9561 (sp.); 9562 (rec); 9564, 9570 (abe); 9574 (amp); 9581 (luc)
- Manriquez, G.I. 2346 (amp)
 Marin, J. 45 (ros); 236 (amp)
 Marshall, N.T. 336 (amp)
 Martén, S. 748 (amp); 1075 (aer)
 Martinez, M. 31 (amp)
 Martínez S., E.M. 17675, 18627 (ano); 23614 (amp); 25429 (amp)
 Matuda, E. 3685 (amp)
 McDade, L.A. 807 (amp)
 McDaniel, S. 10242 (sp.)
 McDowell, T. 777 (amp); 818 (aer); 1003 (amp)
 McPherson, G. 6805 (sla); 6879 (jef); 6958, 6959 (amp); 7116 (jef); 7204 (sla); 7466 (ses); 7485, 7595 (amp); 7705, 7816 (sla); 7844, 7870 (tal); 7992 (amp); 7995 (ala); 8027, 8028 (sla); 8114 (luc); 8295 (sla); 8463 (amp); 8475 (rot); 8497 (ses); 8676, 8722 (tom); 8781 (sla); 8851 (oli); 8866, 8944 (sla); 9123 (tom); 9138, 9583 (sla); 9944 (ses); 10177 (amp); 10187 (tom); 10230 (amp); 10317 (rec); 10354 (luc); 10398 (sp.); 10478 (dol); 10739 (sla); 10941 (rec); 11118 (sla); 11200, 11262 (all); 11287 (ses); 11313 (sla); 11481 (amp); 11596 (sp2); 11756, 11869, 11898 (amp); 12084 (sla); 12143 (all); 12222, 12227 (sp2); 12599 (ses); 12689 (sla); 12787, 12812 (sp2); 13646 (sla); 13658 (tom); 13675 (ala); 14075 (sp2); 15405 (rec)
- Meave, J. 1097, 1372 (amp)
 Méndez, P. Ton, A. 6051, 6511 (ano)
 Méndez, R. 114, 147 (sp2)
 Miller, J.S. 841, 944 (amp)
 Molina R., A. 1844, 1857 (amp); 2011 (rec); 13453, 17217 (amp); 17467 (dol); 18022, 18226, 18324 (rec); 25634 (dol)
 Monro, A.K. 2634, 4257 (amp); 4453, 4924 (sp.); 4925 (tal); 5051 (sp.)
 Montenegro, E. 1174 (sla); 1948 (tom aff)
 Mora, E. 577 (luc); 583, 668, 1146, 1748 (amp); 1924 (ver)
 Mora, G. 12, 276 (dol); 413 (oli)
 Moraga, C. 45 (aer); 719, 822 (amp)
 Moraga, M. 262 (amp)
 Morales, C. 24 (amp)
 Morales, J.F. 27 (dol); 367 (tal); 388 (oli); 480, 2024 (dol); 2456 (ver); 2726 (oli); 4237 (oli); 6426 (chi); 7567 (sp.); 7731 (amp)
 Moreno, A. 27 (amp); 70 (sp.)
 Moreno, P.P. 12011, 12015, 12169, 12210, 12319, 12471, 12616, 13035, 13038, 13166, 13178, 13260, 14578, 14752, 14779, 23084, 23875B, 23934, 24118, 24638, 24956, 25577 (amp); 26097 (tom); 26257, 29954 (amp)
 Mori, S.A. 2315 (luc); 2894 (ala); 2952, 2980 (all); 3046 (amp); 3319 (ses); 3324 (amp); 4246 (sp2); 4555 (amp); 4981 (ses); 5037 (ses, Type); 5283 (sp.); 5494 (tom); 5531 (rot); 6078 (jef); 6256 (dol)6410 (all); 6501 (jef); 6542 (tom aff); 6612 (all); 7978 (amp)
 Murray, N.A. 816 (rec); 1384 (amp); 1478 (all); 1483 (tom)
- Navarro V., E.** 263 (dol); 697 (dol)
 Nee, M. 7099, 7930, 8715, 9092 (amp); 9147 (sp.); 9290 (amp); 10999 (rot, Type); 11078 (amp); 11277 (tom); 18818, 19990, 22717, 22721 (gal); 24723, 25079 (amp); 29819, 29949 (gal)
 Neill, D. 2606, 4364, 5041 (amp)
 Nelson, C. 850, 2681, 3282; 4765 (amp)
 Nelson, E.B. 4189 (amp)
 Nevers, G. de 4055 (sp.); 4303 (rot); 4473, 4822 (amp); 4986 (sp.); 4993 (amp); 5258 (rot); 5387 (sp.); 5564, 6110, 6423, 6603 (amp); 6873 (rec); 6923, 6968 (amp); 7168 (abe); 7540 (abe); 7578 (sp.); 8388, 8425 (sp2)
 Nevling, L.I. 2598 (amp)
- Opler, P.A.** 424 (sp.); 807 (amp)
 Orozco, A.D.L. 332 (amp)
 Ørsted, A.S. 146 (cos, Type)
 Ortega O., R. 1173 (gal)
 Ortiz, B. 160 (gal)
 Ortiz, R.T. 2330, 2332 (amp)
 Ortiz C., D. 886 (gal)
- Paredes, R.** 790 (amp); 954 (sp.)
 Penneys, D. 406 (cos)
 Pennington, T.D. 9612 (ano); 11525 (aer)
 Pérez, R. 550 (amp); 863 (luc); 882 (abe); 1028 (ses)
 Perino, C.H. 3186 (gal)
 Peterson, P.M. 6612, 6758 (tom); 6814, 7195, 8665 (amp)
 Picado, A. 83 (dol)
 Pipoly, J.J. 7042 (jef)
 Pittier, H. 3915 (luc, Type); 10958 (dol, Type); 16015 (amp)
 Ponce C., F. 19 (gal)
 Poveda, L.J. 62 (dol); 698 (amp); 3911 (chi)
 Proctor, G.R. 27116 (rec)

Quesada, F. 48 (ros); 62 (amp); 137 (dol); 173 (amp); 544 (dol); 589 (amp)

Rainer, H. 151 (amp); 157 (chi); 158 (amp)

Ramírez, V. 73 (amp); 354 (amp)

Ríos, D.E. 169 (amp)

Ríos, P. 37, 85 (amp)

Riveira, N. 355 (acr); 948 (dol); 1390 (dol)

Rivera, G. 539 (dol); 1000 (amp); 1069 (cos); 1390 (dol); 1693 (sp.); 1727 (dol); 2041 (oli)

Rivière, R. 359 (amp)

Robinson, B.L. 50 (amp)

Robles, R. 1243, 1284, 1326, 1930 (amp); 2042, 2068 (rec); 2109 (amp); 2828 (aer)

Robleto, W. 645 (amp)

Robyns, A. 65-31 (amp)

Rodríguez, A. 687 (luc); 1080 (oli); 1408 (aer); 2194 (dol); 2213 (amp); 3581 (ver); 4322 (luc); 4567, 5189 (amp); 5195 (aer); 7083 (amp); 7185 (dol); 7254 (cos)

Rodríguez, G. 17 (cos)

Rojas, E. 89 (chi); 143 (amp)

Rueda, R. 1486, 1666, 2587, 2645, 3498, 4100, 4104, 4136 (amp); 4137, 4871 (aer); 4930 (tom); 5444 (amp); 5796 (aer); 8545, 8635 (amp); 8730 (aer); 9637, 9659 (amp); 9714 (aer); 9798, 9866, 9968 (amp); 10116, 10233 (aer)

Saborio, J.C. 79 (amp)

Sakai, S. 506 (luc)

San Emeterio, L. 395 (amp)

Sánchez, P. 501 (amp); 537 (cos)

Sandino, J.C. 1647, 3443, 4577, 4601, 4771, 5144 (amp)

Santamaría, D. 888 (sp.); 1022 (amp); 1109 (oli)

Saunders, J. 1192 (amp)

Shattuck, O.E. 634, 1095 (luc)

Schatz, G.E. 571, 650 (aer); 957 (rec); 991 (amp); 1097 (dol); 1212 (ros); 1214, 1216 (pud); 1217 (amp); 1218 (chi)

Schipp, W.A. 298, 406 (amp)

Schmalzel, R.J. 1593 (oli)

Schultes, R.E. 560 (gal)

Segura, M. 72 (chi); 155 (amp)

Sessé, M. de 2312, 2322 (amp)

Seymour, F.C. 3396, 3780 (amp)

Shank, P. 14167, 14168 (rec)

Shattuck, O.E. 406 (amp)

Skutch, A.F. 1800 (amp); 2553 (tom, Type); 2589 (rec); 3316, 3430 (oli); 4171 (tom); 4234 (rec, Type); 5078 (rec); 5323 (amp)

Smith, A. s.n. (July 15, 1937), 100, H221, H492, H883 (oli); F1824 (amp); P2532 (dol); 4230 (oli)

Smith, D. 343 (amp)

Solano, J. 6, 109 (amp)

Solís 4354 (amp)

Somoza, A. 111, 112 (sp.)

Soza, D. 5, 376 (amp)

Spellman, D. 187 (amp)

Sperry, J. 687 (amp)

Standley, P.C. 19354, 19973, 30272 (amp); 37132 (amp, Type); 52628, 54647, 73061 (amp)

Starry, D.E. 170, 325 (amp)

Steiner, K. 314 (amp)

Stern, W.L. 425, 527, 665 (sp2)

Stevens, W.D. 4875, 4946, 7576, 7633, 8851, 9003, 12476 (amp); 13348 (aer); 13500, 19785 (amp); 19831 (rec); 20078, 20657 (amp); 23641 (aer); 23801 (amp); 23899 (aer); 24084 (amp); 24906 (aer); 24510 (amp); 24542 (aer); 24783 (amp); 24812 (sp.); 24919, 24996, 25236, 25252 (amp)

Steyermark, J.A. 38691, 39813, 3988, 44220, 45115 (amp); 49410 (ano)

Stolze, R.G. 1557 (oli)

Stone, D.E. 3260 (oli); 2148 (amp)

Stork, H.E. 1048 (oli); 2598 (ten, Type)

Sucre, D. 4760 (amp)

Sullivan, G.A. 196 (tom aff); 210, 230 (jef)

Sytsma, K.J. 1476 (jef); 1953 (amp); 2692 (sp.); 2845 (jef); 2864, 3097, 4025 (amp); 4169 (rec); 4256, 4389 (amp); 4864 (sla)

Télez V., O. 8523 (amp)

Tenorio L., P. 5250 (amp)

Thien, L.B. s.n. (March 1973) (amp); 4290 (jef)

Thomsen, K. 17, 24 (amp); 121 (luc); 142, 447, 575 (amp); 742 (pud); 941 (pud); 1193 (amp); 1232 (rec); 1469 (aer)

Tonduz, A. 9166 (dol, Type); 12970 (dol); 17680 (dol, Type)

Torres C., R. 81, 4485, 11157 (amp)

Türkheim, H. von 1480, 7815 (amp)

Tyson, E.L. 3424, 3593, 4348 (jef)

Utley, J.F. 927 (oli); 1245 (amp); 2141 (oli); 2439 (ver); 2608, 2755 (oli); 2844 (sp.); 3044 (oli); 3255a (sp.); 4935 (chi); 4954 (rec)

Utley, K. 6052 (amp)

Valdespino, I.A. 112, 286 (amp); 674, 682, 685 (jef)

Valerio, M. 74 (amp); 1015 (oli); 1281 (dol); 1647 (oli)

Valerio R., J. 1396 (oli)

Valverde, O. 258 (cos); 1039 (sp.); 1219, 1275 (amp)

Vargas, O. 218 (aer)

Vera Caletti, P. 109, 161 (gal); 170 (ano); 225 (amp)

Villarreal, D. 984 (sp2)

Villegas H., A. 128 (amp)

Walker, J.W. 118 (amp); 119 (aer); 194 (amp); 197 (chi); 205 (rec); 356, 361, 362, 363, 367 (amp); 383, 398 (tom); 413, 419 (oli)

Warszewicz, J. von 4 (oli)

Weaver, R.E. 1576 (luc)

Webster, G.L. 22054 (luc)

Wedel, H. von 155, 490 (aer); 907 (tom); 1460, 1716, 1932 (amp); 1965 (pan); 2108 (amp); 2856 (aer)

Wendt, T. 2831 (amp); 3057, 3303 (gal); 3330 (ano); 3572 (gal); 3755, 4268, 5672, 5677, 5692 (amp)

Werff, H. van der 6198, 6933 (sp2); 6964 (jef)

Whitefoord, C. 9332, 9337, 9373 (amp)

Wilbur, R.L. 9857, 10172 (oli); 10226 (dol); 10846 (rec); 11005 (dol)

Williams, L.I. 9162, 9315 (amp)

Williams, L.O. 24244, 28718 (rec); 28737 (amp)

Williams-Linera, G. 145, 332 (amp);

Wilson, R.G. s.n. (28 Feb. 1964) (dol)

Yuncker, T.G. 6155 (ano)

Zamora, N. 774 (dol); 1253 (chi); 1320 (ver); 1461 (chi); 1468 (oli); 1655 (rec); 1735 (aer); 1811 (amp); 2100 (oli); 2268 (aer); 2270 (oli); 2313 (amp)

Zetek, J. 4629 (amp)

Zumbado, M. 76 (amp)

Zúñiga, R. 201, 528 (chi); 623 (dol)

LIST OF ABBREVIATIONS USED

Guatteria aberrans (abe)
Guatteria acrantha (acr)
Guatteria aeruginosa (aer)
Guatteria alata (ala)
Guatteria allenii (all)
Guatteria amplifolia (amp)
Guatteria anomala (ano)
Guatteria chiriquiensis (chi)
Guatteria costaricensis (cos)
Guatteria dolichopoda (dol)
Guatteria jefensis (jef)
Guatteria galeottiana (gal)
Guatteria grandiflora (gran)
Guatteria lucens (luc)
Guatteria oliviformis (oli)
Guatteria panamensis (pan)
Guatteria pudica (pud)
Guatteria recurvisepala (rec)
Guatteria reinaldii (rei)
Guatteria rostrata (ros)
Guatteria rotundata (rot)
Guatteria sessilicarpa (ses)
Guatteria slateri (sla)
Guatteria talamancana (tal)
Guatteria tenera (ten)
Guatteria tomentosa (tom)
Guatteria aff. *tomentosa* (tom. aff.)
Guatteria verrucosa (ver)
Guatteria zamorae (zam)
Guatteria sp. 1 (sp1)
Guatteria sp. 2 (sp2)
Guatteria sp. (sp.)