A taxonomic survey of *Guatteria* section *Mecocarpus* including the genera Guatteriopsis and Guatteriella p.p. (Annonaceae)

P.J.M. Maas¹, L.Y.Th. Westra¹

Key words

Annonaceae Guatteria Guatteria sect. Mecocarpus Guatteriella Guatteriopsis Neotropics

Abstract This paper deals with a group of species of the Neotropical genus Guatteria (Annonaceae) which are characterized by leaves with tiny warts (verruculae) on both surfaces and by elongate and short-stipitate monocarps (i.e., the length of the monocarp body surpassing the length of the stipe). These species were placed by Fries in Guatteria sect. Mecocarpus (Fries 1939) (the name derives from Ancient Greek μηκων = Poppy and καρπος = fruit: fruit resembling that of Papaver species). All occur in South America, none having been found elsewhere so far. Although there is much doubt nowadays about the taxonomic significance of Fries's sections, we maintain sect. Mecocarpus at present for convenience's sake. Additionally, the former genus Guatteriopsis, united with Guatteria a short time ago (Erkens & Maas 2008b), is now also included in sect. Mecocarpus. The same applies to one of the two species attributed to Guatteriella (also merged with Guatteria by Erkens & Maas 2008b), namely Guatteriella tomentosa R.E.Fr. (not Guatteria tomentosa Rusby) which is put into synonymy with Guatteria trichocarpa Erkens & Maas. One new species is described, namely Guatteria griseifolia Maas & Westra. The two species complexes of G. guianensis and G. decurrens are now treated each as a single polymorphic species. The present study falls within the framework of a planned monograph of the whole genus Guatteria.

Published on 14 July 2011

INTRODUCTION

Guatteria is the largest genus within the family of Annonaceae and one of the largest genera of Neotropical trees (Erkens et al. 2008). Current research focuses on various aspects, viz., molecular phylogeny (Erkens et al. 2007a, b), biogeography (Erkens et al. 2007b, 2009) and taxonomy. Taxonomic studies involve Guatteria in Central America (Erkens et al. 2006, Erkens 2007), the Guianas (Scharf et al. 2005, 2006a, b, 2008) and the Neotropics in general with emphasis on South America (Erkens et al. 2008, Maas & Westra 2010), the latter including generic delimitation (Erkens 2007, Erkens & Maas 2008).

In 1939 Robert Fries published the last revision of the genus Guatteria as a whole, as part of his large-scale project 'Revision der Arten einiger Annonaceen-Gattungen' covering the period 1930-1939 (followed in 1949 by a supplemental part on sect. Chasmantha). He divided the genus Guatteria into 30 sections, one of which was sect. Mecocarpus. That section was defined by him as having middle-sized to very large ('folia gigantea') leaves, which were characteristically 'verruculosapunctata', i.e. the surface of the leaves being covered with wart-like excrescences. Other features were the more or less distinct loops formed by the secondary veins in the lamina, thick petals and relatively large and mostly shortly stipitate monocarps. Fries distinguished 18 South American species in sect. Mecocarpus.

The first feature in his key to the species was the leaf size. On the base of that feature the section was divided by him into three groups: group 1 with middle-sized leaves less than 20 cm long and appressed sepals, and groups 2 and 3 with large to very large leaves, group 2 having appressed sepals, group 3 having reflexed sepals; some other features which were used by Fries in his key to the species were leaf shape and leaf base.

In his contribution to Die natürlichen Pflanzenfamilien (1959), Fries maintained the sect. *Mecocarpus*, recognizing the same species as in his 1939 treatment, but adding one more species, namely G. pastazae, described by him in 1947 (Fries 1947).

In later years Simpson (1975) added G. scalarinervia, a strictly cauliflorous species, to the sect. Mecocarpus and Scharf et al. (2005) described G. pakaraimae Scharf & Maas, a species occurring high up in the Pakaraima Mts of Guyana. The most recent novelties in sect. Mecocarpus are G. duodecima, G. grandipes, G. japurensis and G. venosa (Erkens et al. 2008).

Molecular phylogenetic work on the genus Guatteria has been conducted by Erkens et al. (2007a, b). According to him (Erkens et al. 2007a) sect. Mecocarpus is a monophyletic group, also including 2 species of sect. Stenocarpus, namely G. inundata and G. riparia and G. megalophylla from the monospecific sect. Megalophyllum. Among morphological features characterizing sect. Stenocarpus are shortly stipitate and almost fusiform monocarps and leaves with often a distinct marginal vein, while the lack of verruculae on the leaves distinguishes sect. Stenocarpus from sect. Mecocarpus. (It is worth noting that sect. Stenocarpus is almost completely restricted to temporarily inundated forests. This is a rather exceptional habitat for Guatteria.) We cannot agree for the time being with Erkens's et al. (2007a) conclusion from his molecular studies that sections Mecocarpus s.l. and Stenocarpus should be united, as our morphological research shows considerable differences between both sections in leaves (texture, marginal vein, leaf base, presence or absence of verruculae), length of pedicels, length of stipes of monocarps, etc. Another point made by Erkens was that species of sect. Mecocarpus as described by Fries (1939) are easily recognizable and that monophyly of all its species was therefore to be expected. However, two accessions of Guatteria brevicuspis were found to form a separate clade (Erkens

¹ Netherlands Centre for Biodiversity Naturalis (section NHN), Biosystematics Group, Herbarium Vadense, Wageningen University, Generaal Foulkesweg 37, 6703 BL Wageningen, The Netherlands; corresponding author e-mail: paul.maas@wur.nl.

et al. 2007a, b). Though still poorly supported, these appeared more closely related to some species of *Guatteriopsis* (*Guatteriopsis friesiana* and *G. kuhlmannii*, now *Guatteria friesiana* and *G. cryandra* (Erkens & Maas 2008)) than to the remainder of sect. *Mecocarpus* (Erkens et al. 2007a).

In this study the species of the former genus *Guatteriopsis* are included (but with the exclusion of *G. ramiflora* – see Erkens & Maas 2008: 404). It should be noted that the species of *Guatteriella*, which was also merged with *Guatteria* (Erkens & Maas 2008), along with *Guatteriopsis*, share many features of *Guatteria* sect. *Mecocarpus*, notably the flowers on short pedicels and monocarps with short stipes, but *G. campinensis* lacks verruculae in the leaves. For that reason it is left out of this treatment.

Erkens et al. (2007a) performed a molecular study on the genera Guatteriopsis and Guatteriella, studying Guatteriopsis blepharophylla, G. friesiana, G. hispida, G. kuhlmannii and Guatteriella tomentosa. According to them "the species of Guatteriopsis do not prove to be monophyletic, there are 3 lineages: 1. Guatteriopsis blepharophylla with G. hispida; 2. Guatteriopsis friesiana with G. kuhlmannii; and 3. G. ramiflora". In the same paper (Erkens et al. 2007a) it is concluded that all species of Guatteriopsis are nested within Guatteria and that generic status is unjustified. The merger was done, as mentioned above, in a subsequent paper (Erkens & Maas 2008). The present paper goes even further in bringing Guatteria brevicuspis under the synonymy of the type species of the former genus Guatteriopsis: Guatteria blepharophylla. As rightly stated by Erkens et al. (2007a), with only six out of 20 species of sect. Mecocarpus having been investigated, increased taxon sampling is needed to gain more insight in the phylogenetic relationships of the species of this almost monophyletic section.

In Erkens's et al. (2007a, b) phylogenetic trees, there is one group with, among others, *G. decurrens*, *G. multivenia* (now put in the synonymy of *G. guianensis*), *G. inundata*, *G. riparia* (now put in the synonymy of *G. inundata*), *G. excellens* (now in the synonymy of *G. guianensis*), *G. guianensis*, *G. cf. meliodora* (now synonymous with *G. decurrens*, this paper, based on *Maas 9231*; unfortunately we were unable to retrace that collection when preparing the present text) and *G. megalophylla*. Several of these species fit very well in sect. *Mecocarpus* like *G. decurrens*, *G. guianensis* and *G. meliodora*. As already mentioned above *G. inundata* does, on morphological grounds, not belong here. The same holds true for *G. megalophylla* which shares the large leaves and the large and shortly stipitate monocarps with sect. *Mecocarpus*, but which totally lacks the verruculae on the leaves.

A note on the warts — Fig. 1a-c

As said in the introduction, Fries (1939) when describing *Guatteria* sect. *Mecocarpus* assigned great value to the presence of

warty leaves ("feinwärzige Blätter"). Warty (verruculose) leaves were found in all 18 species he described in this section. Fries did not explain the nature of these warts any further and it is only in some recent publications that some anatomical aspects possibly related to these structures have been dealt with.

Van Setten & Koek-Noorman (1986) in their leafanatomical survey of Neotropical genera of Annonaceae observed sclereids occurring in the leaves of 50 % of the genera. They found three types of sclereids, namely brachysclereids (stone cells), osteosclereids (poorly branched sclereids with thick, multi-layered cell walls) and astrosclereids (branched to stellate sclereids, which are mostly longer and thinner than the osteosclereids and often connected with terminal veins). Among the genera investigated Guatteriella, Guatteriopsis and Guatteria were found to have osteosclereids as well as astrosclereids, with osteosclereids being dominant in Guatteriella and Guatteriopsis, while in Guatteria both types appeared to be common. It should be noted that these three (now united) genera include species with verruculose leaves and it is tempting to suspect a connection between warts and the presence of sclereids. Strong indications for this also come from two other genera with warty leaves, namely Pseudoxandra and Unonopsis.

In both genera Van Marle (2003, 2007) studied the leaf anatomy down to quite some detail. In *Pseudoxandra* Van Marle (2003) observed osteosclereids in most species, traversing the leaf blade from one side to the other and touching the epidermis both above and below. Shrinking could readily explain why warts are so well visible in dried leaves, but do not show in fresh or wetted leaves. In *Unonopsis* Van Marle (2007) could detect similar osteosclereids reaching from the adaxial to the abaxial side in part of the species. This further leads one to suspect the same type of sclereids to play a role in *Guatteria*, but anatomical proof for this has yet to be provided before a final conclusion can be drawn.

MATERIAL AND METHODS

Herbarium material was investigated from the following herbaria: AAU, B, BM, BR, BRG, COAH, COL, F, FHO, FI, G, INPA, K, L, LE, M, MAD, MO, NY, P, R, RB, S, U, US, W, WAG, WIS, WU. Measurements as a rule were made of dried material. Measurements of material in spirit are given between curly brackets {}. Colour indications and descriptions of surface structures are based on dried material, unless stated otherwise. We have indicated the density of hair cover by using the following gradations: densely, rather densely and sparsely. Seed surface is indicated as foveolate (pitted), rugose (wrinkled, looking like a miniature brain) according to Van Setten & Koek-Noorman (1992), or smooth. All black-and-white photographs were made by L.Y.Th. Westra.

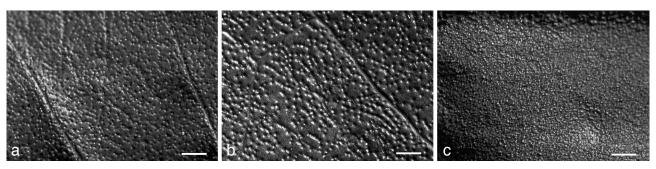


Fig. 1 Detail of upper leaf surface showing minute warts. a. Guatteria blepharophylla Mart. (Amaral et al. 1190); b. G. dura R.E.Fr. (Urrego G. et al. 1785), note arrangement in strings in several places; c. G. insculpta R.E.Fr. (Murillo & Rodriguez 544): very numerous tiny warts. — Scale bars = 1 mm.

1. Leaf base cordate; secondary veins indistinct. — Brazil

KEY TO THE SPECIES

1.	Leaf base acute, obtuse or attenuate; secondary veins mostly distinct
	Cauliflorous trees (but see note under <i>G. longicuspis</i>) . 3 Non-cauliflorous trees
3.	Petiole 15–20 mm long; stipes of monocarps 10–25 mm
3.	long; leaves not or sparsely verruculose. — Amazonian Ecuador and Peru, 200–350 m 19. <i>G. scalarinervia</i> Petiole 2–5 mm long; stipes of monocarps 5–12 mm long; leaves densely to sparsely verruculose 4
4.	Young twigs covered with appressed hairs; leaf base acute or obtuse; sepals 4–7 mm long; lower side of leaves sparsely covered with appressed hairs. — Amazonian Colombia, Venezuela, Ecuador, Peru and Brazil, 0–300 m
	Young twigs covered with erect hairs; leaf base long-attenuate; sepals 10–13 mm long; lower side of leaves densely to rather densely covered with appressed to erect hairs. — Colombia (Boyacá, Sur de Santander), 100–1100 m
5.	Young twigs covered with erect hairs 6 Young twigs covered with appressed hairs or glabrous. 12
	Young twigs covered with rough, erect hairs (hirsute) 7 Young twigs covered with soft, erect hairs (velutinous) 10
	Pedicels 70–90 mm long. — Amazonian Peru (Loreto), 20–140 m
	Marginal leaf vein absent; monocarps densely covered with erect, rough hairs. — Brazil (Amazonas), sea level
8.	Marginal leaf vein present; monocarps sparsely to rather densely covered with appressed or erect hairs 9
9.	Pedicels 12–40 mm long; stipes 5–15 mm long; monocarps sparsely to rather densely covered with appressed hairs; leaf base attenuate to acute. — Amazonian Colombia, Ecuador, Peru and Brazil, 100–500(–1300) m
9.	Pedicels c. 11 mm long; stipes c. 20 mm long; monocarps sparsely covered with erect hairs; leaf base obtuse. — Amazonian Colombia, 0–300 m 22. <i>Guatteria</i> sp. <i>B</i>
	Petiole 1–4 mm diam; monocarps densely covered with appressed hairs, wall 1–3 mm thick. — Amazonian Colombia and Brazil (Amazonas), sea level 20. <i>G. trichocarpa</i> Petiole 4–8 mm diam; monocarps sparsely to rather dense-
	ly covered with appressed to erect hairs, wall 0.5–1 mm thick
11.	Leaves with a marginal vein; leaf base attenuate; lower side of leaves rather densely to sparsely covered with erect to appressed hairs. — Colombia (Antioquia), French Guiana and Amazonian Ecuador, Peru and Brazil, 0–800 m
	Leaves mostly without a marginal vein; leaf base obtuse to rounded; lower side of leaves densely covered with erect hairs. — Amazonian Colombia, Venezuela and Brazil, 0–270 m
	Young twigs glabrous
13.	Leaves with 25–35 secondary veins; marginal vein distinct; pedicels 10–25 mm long. — Coastal Ecuador

13. Leaves with 8–18 secondary veins; marginal vein absent; 14. Leaves densely verruculose, with 8-10 secondary veins; monocarps 13-15 mm long, with stipes 1-2 mm long. — Guyana, 1135–1200 m 16. *G. pakaraimae* 14. Leaves sparsely or not verruculose, with 15–18 secondary veins; monocarps 17-20 mm long, with stipes 11-17 mm long. — Western Amazonian Brazil (Amazonas), c. 100 m12. G. japurensis 16. Leaves densely verruculose (the verrucae often forming strings of 2 or 3), apex shortly acuminate (acumen 5-10 mm long). — Amazonian Colombia, Venezuela, Peru, Bolivia and Brazil, 0–175 m 5. *G. dura* 16. Leaves sparsely verruculose (the verrucae never forming strings), apex often rounded and very shortly acuminate (acumen up to 5 mm long). — Amazonian Peru and Brazil and Guyana, 125-240 m 14. G. meliodora 17. Petiole 0.5-1 mm diam; sepals 2-4 mm long. — Amazonian Ecuador, Peru, Bolivia and Brazil (Acre), 150-2200 m 17. Petiole 1–3 mm diam; sepals 4–10 mm long 18 18. Leaf base acute, obtuse or rounded 20 19. Monocarps 11–15 mm long, longitudinally wrinkled, stipes 1-3 mm long, rarely up to 10 mm long; leaves with obscure secondary venation, primary vein slightly keeled below. — Amazonian Brazil, Ecuador and Peru, 0–1800 m 17. G. pastazae 19. Monocarps 17–25 mm long, not wrinkled, stipes 5–13 mm long; leaves with distinct secondary venation, primary vein rounded below. — Amazonian Venezuela, Ecuador, Peru, Bolivia, Brazil, French Guiana and Guyana, 0-800 m1. G. blepharophylla 20. Sepals 8-9 mm long; pedicels 20-30 mm long, up to 50 mm in fruit. — Amazonian Ecuador and Peru (San Martín), 900-2400 m 8. *G. griseifolia* 20. Sepals 4-6 mm long; pedicels 1-12 mm long, up to 15 21. Monocarps 16-24 mm long, stipes 5-8 mm long; petiole 5-10 by 1-3 mm. — Peru (Loreto), 125-580 m 21. Monocarps 10–12 mm long, stipes 1–3 mm long; petiole 2-5 by 1-2 mm. — Brazil (Amapá, Pará), 0-250 m 2. G. cryandra 1. Guatteria blepharophylla Mart. — Fig. 1a, 2, 3a; Plate 1a, b; Map 1 Guatteria blepharophylla Mart. (1841) 38. — Guatteriopsis blepharophylla

Guatteria blepharophylla Mart. (1841) 38. — Guatteriopsis blepharophylla (Mart.) R.E.Fr. (1934) 110, t. 6; Maas et al. (2007) 644. — Type: Von Martius s.n. (lecto M, selected by Erkens & Maas (2008)), Brazil, Amazonas, Rio Negro, Coarí, Nov. 1819.

Annona sessiliflora Benth. (1853) 8. — Guatteria sessiliflora (Benth.) Saff. (1914) 6. — Guatteriopsis sessiliflora (Benth.) R.E.Fr. (1934) 109. — Type: Spruce 1668 (holo K; iso B, BM, FI, LE, M, NY, W), Brazil, Amazonas, Rio Negro, towards confluence with Rio Solimões, May 1851.

Guatteria ucayaliana Diels (1924) 138, syn. nov. — Guatteria dielsiana R.E.Fr. (1938) 719. — Type: Tessmann 3212 (holo B; iso S), Peru, Loreto, Yarina Cocha, Middle Río Ucayali, 155 m, 24 Sept. 1923.

Guatteria brevicuspis R.E.Fr. (1939) 491, f. 28e, f, syn. nov. — Type: Krukoff 5589 (holo S; iso F, K, S, U), Brazil, Acre, Rio Purus, near mouth of Rio Macauhan (tributary of Rio Yaco), 21 Aug. 1933.

Guatteria cylindrocarpa R.E.Fr. (1957b) 601, t. 2, syn. nov. — Type: Schultes & López 8949 (holo US), Brazil, Amazonas, Rio Negro, Tapurucuara, 11 Sept. 1947.

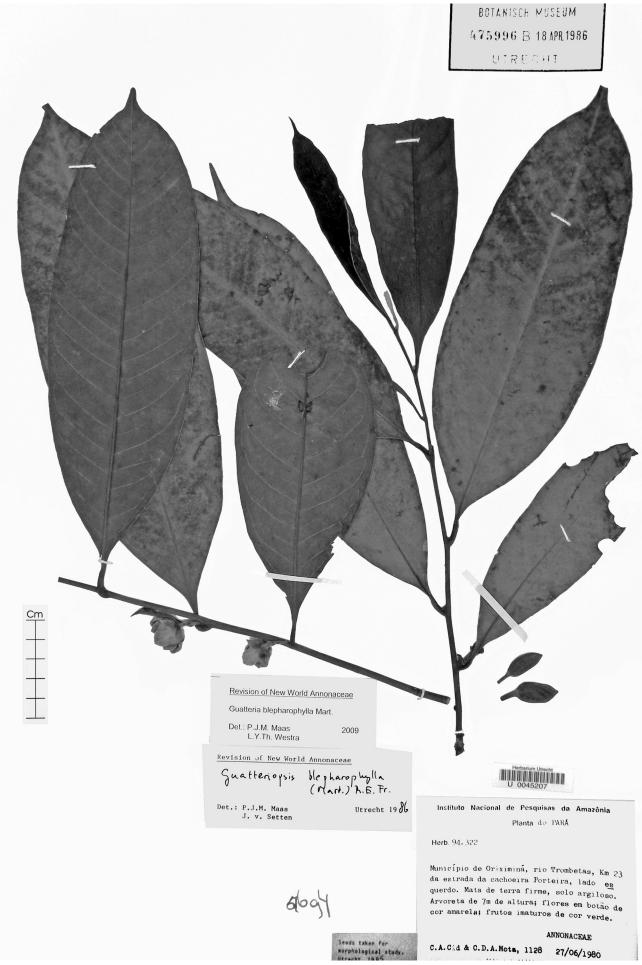


Fig. 2 Guatteria blepharophylla Mart. Flowering specimen and two loose monocarps (Cid et al. 1128, U).



Fig. 3 a. Guatteria blepharophylla R.E.Fr. Detail of flowers (Daly et al. 783, U). — b. Guatteria cryandra Erkens & Maas. Detail of flower (Rabelo et al. 2748, U). — c. Guatteria decurrens R.E.Fr. Detail of indument (Grández et al. 4203, U).

Shrub or tree 2-13 m tall, up to 10 cm diam; young twigs densely covered with appressed hairs, soon glabrous. Leaves: petiole 8-13 mm long, 2-3 mm diam; lamina narrowly obovate-oblong to narrowly ovate-oblong, rarely elliptic, 15-30 by 3.5-8.5 cm (leaf index 3.5-5.5), chartaceous, densely to rather densely verruculose, dull greenish brown to brown above, pale brown to brown below, glabrous above, densely to sparsely covered with appressed hairs up to c. 1 mm long below, base long-attenuate to attenuate, sometimes acute or obtuse, apex acuminate (acumen 10-30 mm long), primary vein impressed to flat above, secondary veins distinct, 16-22 on either side of primary vein, flat or slightly impressed above, smallest distance between loops and margin 2-3 mm. Flowers in 1-2-flowered inflorescences in axils of leaves; pedicels 4-10(-20) mm long, 1-3 mm diam, fruiting pedicels as the flowering pedicels or rarely up to 40 mm long, densely covered with appressed hairs, articulated at 0.2–0.5 from the base, bracts c. 5, soon falling; flower buds ovoid to broadly ovoid; sepals free or almost so, broadly ovate to broadly ovate-triangular, 4-9 by 3-7 mm, appressed, outer side densely covered with appressed hairs; petals greenish yellow, yellow-orange or cream in vivo, rhombic-ovate or elliptic, 8-20 by 5-10 mm, outer side densely covered with appressed, silvery hairs; stamens 1.5-2 mm long, connective shield papillate to glabrous. Monocarps 10-25, green, maturing red to black in vivo, brown to dark brown in sicco, narrowly ellipsoid, 17-25 by 7-9 mm, sparsely covered with appressed hairs, apex acute to apiculate (apiculum c. 0.5 mm long), wall 0.2-0.5 mm thick, stipes 5-13 by 1.5-2 mm. Seed narrowly ellipsoid, 18-22 by 6-9 mm, brown, rugose to rugose-pitted, with or without longitudinal furrows.

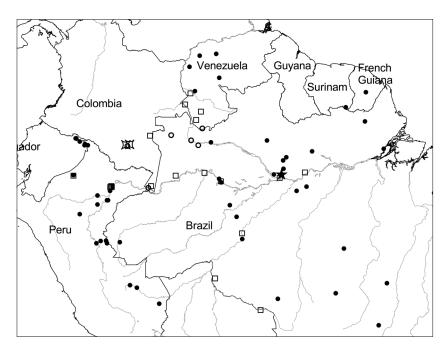
Distribution — Venezuela (Amazonas, Bolívar), Guyana, French Guiana, Ecuador (Sucumbios), Peru (Loreto, Madre de Dios, San Martín, Ucayali), Bolivia (Beni) and Brazil (Acre, Amapá, Amazonas, Mato Grosso, Pará, Rondônia, Roraima).

Habitat & Ecology — In non-inundated or inundated (restinga, tahuampa) forest, on clayey, rarely on sandy soil. At elevations of 0–800 m. Flowering and fruiting: throughout the year.

Vernacular names — Brazil: Envira preta (*H.C. Lima 2718*), Envireira (*Rodrigues 534*), Pindaíba preta (*Marimon 51*). Peru: Anonilla (*Freitas 7*), Hicoja negra (*Schunke V. 4294, 8674*), Huasca anonilla (*Vásquez 12285*), Huasca hicoja (*Schunke V. 7844*), Icoja (*Rimachi Y. 4175*). Venezuela: Kunguate (Yekuana) (*Aymard & Fernández 7324*), Kunwatö (Yekuana) (*Ang. Fernández 5266*).

Notes — Guatteria blepharophylla is recognizable by shortly pedicellate flowers (pedicels generally up to 10 mm long) and by petals which are densely covered with appressed, silvery hairs.

Characteristically, *G. blepharophylla* has long-attenuate, densely to rather densely verruculose leaves. It occurs in Brazil (Amazonas, Mato Grosso, Pará, Rondônia and Roraima) and Venezuela (Amazonas and Bolívar). In Ecuador and Peru the leaves tend to have a shortly attenuate, acute, or even obtuse base. Specimens from Jenaro Herrera, Loreto, Peru are very variable in leaf shape, particularly the leaf base which shows the whole variation range between long-attenuate and obtuse.



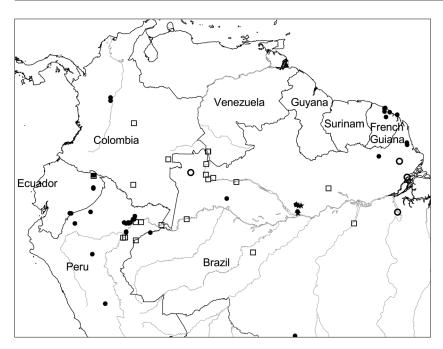
Map 1 Distribution of Guatteria blepharophylla Mart. (●), G. dura R.E.Fr. (□), G. hispida (R.E.Fr.) Erkens & Maas (★), G. insculpta R.E.Fr. (O), and G. sp. B (\mu).

2. Guatteria cryandra Erkens & Maas — Fig. 3b, 4; Map 2

Guatteria cryandra Erkens & Maas (2008) 404. — Guatteriopsis kuhlmannii R.E.Fr. (1937) 275, t. 8, not Guatteria kuhlmannii R.E.Fr. (1939). — Type: J.G. Kuhlmann RB24361 (holo S; iso RB), Brazil, Pará, Rio Tucuruí, affluent of Rio Xingu, Vitória, 17 Apr. 1924.

Tree 3–10 m tall, c. 10 cm diam; young twigs densely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–5 mm long, 1–2 mm diam; lamina narrowly elliptic to narrowly oblong-elliptic, 13–25 by 4–8 cm (leaf index 2.6–4.1), chartaceous, rather densely verruculose, pale greenish brown above, pale





Map 2 Distribution of *Guatteria cryandra* Erkens & Maas (O), *G. friesiana* (W.A. Rodrigues) Erkens & Maas (★), *G. guianensis* (Aubl.) R.E.Fr. (●), and *G. longicuspis* R.E.Fr. (□).

brown below, glabrous above, sparsely covered with appressed hairs below, the primary vein rather densely so, base obtuse to rounded, apex acuminate (acumen 15-25 mm long), primary vein flat to slightly raised above, secondary veins indistinct, 17-25 on either side of primary vein, slightly raised above, not or indistinctly loop-forming, smallest distance between loops and margin 1-4 mm. Flowers in 1-2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 1-5 mm long, 1-2 mm diam, fruiting pedicels up to 5 mm long and 3 mm diam, densely covered with appressed, brown hairs, articulated at c. 0.2 from the base, number of bracts not countable with certainty, one bract seen: broadly ovate-triangular, outer side densely covered with appressed, brown hairs; flower buds broadly ovoid; sepals basally connate, broadly ovate-triangular, 5-6 by 5-6 mm, appressed, outer side densely covered with appressed hairs; petals yellow to golden yellow in vivo, ovate, 10-15 by 8-10 mm, outer side densely covered with appressed, brown hairs; stamens c. 2 mm long, connective shield not seen. Monocarps 10-30, red to red-orange when ripe in vivo, blackish in sicco, ellipsoid, young ones 10-12 by 5-6 mm, sparsely covered with appressed hairs, apex apiculate (apiculum 0.5-1 mm long), wall not measurable, stipes 1-3 by 1 mm. Seed not seen.

Distribution — Brazil (Amapá, Pará).

Habitat & Ecology — In non-inundated forest, one specimen growing along river, often on clayey soil. At elevations of up to 250 m. Flowering: March, June, November; fruiting: August, September.

Vernacular names — None.

Other specimens examined. Brazil., Amapá, Rio Araguari, between camps 6 and 7, Pires et al. 50875 (FHO, U); Vila do Agua Branca, Upper Rio Cajari Mazagão, Rabelo & Cardoso 2748 (U). Pará, Rodovia Transamazonica, km 23 of road from Altamira to Itaituba, Bahia 58 (NY); Tucuruí, Rio Tocantins, km 20 of BR-422, Lisboa et al. 1413 (NY); Município Paragominas, Belém-Brasília Hwy (BR 010), 17 km S of Ligação do Pará, near kilometer marker 1509, 250 m, Plowman et al. 9413 (U); Mun. Altamirim, Monte Dourado, Estrada Perimetral, Santos 298 (NY).

Note — *Guatteria cryandra* is characterized by shortly petiolate leaves with a rounded to obtuse base, in combination with the stiffly appressed hairs on the leaves and the young branchlets, as well as with the shortly stipitate monocarps with stipes 1–3 mm long.

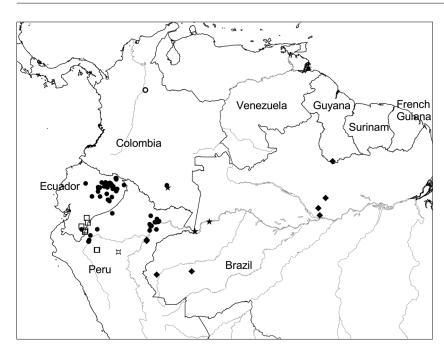
3. Guatteria decurrens R.E.Fr. — Fig. 3c, 5; Map 3

Guatteria decurrens R.E.Fr. (1938) 720. — Type: Killip & Smith 29585 (holo US; iso F), Peru, Loreto, Soledad, on Río Itaya, 110 m, 20–22 Sept. 1929. Guatteria rugosa R.E.Fr. (1939) 501, syn. nov. — Type: Krukoff 4664 (holo S; iso F, U), Brazil, Amazonas, Basin of Rio Juruá, near mouth of Rio Embira, tributary of Rio Tarauacá, 4 June 1933.

Tree 2.5-35 m tall, 2-40 cm diam; young twigs densely to rather densely covered with rough, brown, erect to half-appressed hairs up to 3 mm long, finally glabrous. Leaves: petioles 1-7 mm long, 2-3 mm diam; lamina narrowly elliptic-obovate or narrowly elliptic, rarely elliptic, 11-34 by 4-11 cm (leaf index 2.2-5.5), chartaceous, brownish green above, brownish green to light brown below, very densely to densely verruculose on both sides, glabrous above, densely to rather densely, sometimes sparsely covered with rough, erect to appressed hairs, up to 2 mm long below, base attenuate to acute, apex acuminate (acumen 10-40 mm long), primary vein impressed above, secondary veins 13–30 on each side, flat or slightly impressed above. forming a marginal vein at a shortest distance of 1.5-5 mm to the margin. Flowers in 1(-2)-flowered inflorescences in axils of leaves; pedicels 12-30 mm long, 1.5-2 mm diam, fruiting pedicels 25-40(-50) mm long, rather densely to sparsely covered with erect, half-appressed or sometimes appressed hairs up to 2 mm long, articulated at 0.1-0.3 from the base, bracts c. 5, soon falling; flower buds broadly ovoid or broadly ellipsoid; sepals free or basally connate, ovate to triangular to broadly so, 5-12 by 5-7 mm, appressed or at last reflexed, outer side densely to rather densely, sometimes sparsely covered with erect, half-appressed or sometimes appressed hairs up to 2 mm long; petals green, yellowish green, maturing yellow to creamy yellow, elliptic or ovate-elliptic or narrowly so, 15-25 by 6-13 mm, outer side densely (particularly the base) to rather densely covered with appressed pale brown hairs; stamens 1.5–2.5 mm long, connective shield papillate. Monocarps 15-60, green, maturing purplish black to black in vivo, brown in sicco, ellipsoid, 15-25 by 7-12 mm, sparsely to rather densely covered with rough, appressed hairs, apex rounded or apiculate (apiculum < 0.2 mm long), wall 0.3-1 (-1.5) mm thick, stipes 5-15 by 1-2 mm. Seed ellipsoid, 15-25 by 7-12 mm, dark brown to brown, shiny, slightly longitudinally and somewhat horizontally grooved.



Fig. 5 Guatteria decurrens R.E.Fr. Fruiting specimen (Palacios et al. 2929, U).



Map 3 Distribution of Guatteria decurrens R.E.Fr. (♠), G. griseifolia Maas & Westra (□), G. meliodora R.E.Fr. (♠), G. novogranatensis R.E.Fr. (♠), G. peruviana R.E.Fr. (♯), and G. trichocarpa Erkens & Maas (★).

Distribution — Colombia (Amazonas), Ecuador (Morona-Santiago, Napo, Pastaza, Sucumbios, Zamora-Chinchipe), Peru (Amazonas, Loreto, Oxapampa) and Brazil (Amazonas).

Habitat & Ecology — In primary, non-inundated, lowland or rarely premontane forest, sometimes in periodically inundated forest, on lateritic to clayey or rarely white sandy soil. At elevations of 100–500 m, rarely (in Ecuador) up to 1300 m. Flowering: August to April; fruiting: April to January.

Vernacular names — Ecuador: Caracaspi (*Alvarez et al.* 2407, *Zuleta 212*). Peru: Carahuasca (*Ellenberg 2852*), Espintana (*Ayala et al. 2546*), Yais (*Rojas et al. 36*).

Note — Guatteria decurrens can be confused with G. guianensis. For the differences see under that species.

4. Guatteria duodecima Maas & Westra

Guatteria duodecima Maas & Westra in Erkens et al. (2008) 483, f. 6. — Type: Zak & Espinoza 4811 (holo U; iso AAU, F, K, MO, WU), Ecuador, Pastaza, Cantón Pastaza, Pozo petrolero 'Ramirez', 20 km S of Curaray, 300 m. 21–28 Feb. 1990.

Guatteria sp. 12 Chatrou et al. (1997) 111.

Tree 5-40 m tall, up to 60 cm diam, one specimen reported with steep buttresses; young twigs densely to sparsely covered with appressed hairs, soon glabrous. Leaves: petiole 5-10 mm long, 0.5–1 mm diam; lamina narrowly elliptic to narrowly oblong-elliptic, 8-15 by 2-5 cm (leaf index 2.7-4.4), chartaceous, densely to rather densely verruculose, greyish to brown above, brown to greenish brown below, glabrous or sparsely covered with appressed hairs above, densely to rather densely covered with appressed, white, long hairs (sericeous) below, base attenuate, sometimes acute, apex acuminate (acumen 5-10 mm long), primary vein impressed to flat above, secondary veins distinct, 13–20 on either side of primary vein, raised above, smallest distance between loops and margin 1–3 mm. Flowers in 1–2-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 5-10 mm long, 0.5-1{-2} mm diam, fruiting pedicels up to 25 mm long, 2-3 mm diam, densely covered with appressed hairs, articulated at 0.2-0.7 from the base, bracts 3–5, soon falling, the upper bract 3–3.5 by 1.5-2 mm; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 2-4 by 2-4 mm, appressed, soon becoming reflexed, outer side densely covered with appressed, white hairs; petals green in vivo, maturing brownish yellow, narrowly oblong-elliptic to narrowly rhombic-ovate, 10–18 by 4–7 mm,

outer side densely covered with appressed, white hairs; stamens c. 1 mm long, connective shield papillate. *Monocarps* 10–40, green, maturing purple-black to black in vivo, brown to black in sicco, ellipsoid, 10–18 by 6–12 mm, rather densely covered with appressed hairs, apex rounded or bluntly apiculate (apiculum c. 0.5 mm long), wall 0.5–1 mm thick, stipes 2–10 by 1–2 mm. *Seed* ellipsoid, 10–13 by 5–6 mm, shiny brown, foveolate and longitudinally grooved.

Distribution — Ecuador (Orellana, Pastaza), Peru (Cuzco, Madre de Dios, Pasco, San Martín), Bolivia (La Paz) and Brazil (Acre).

Habitat & Ecology — In non-inundated forest (from lowland rainforest to premontane forest), sometimes in periodically inundated forest. At elevations of 150–2200 m. Flowering: throughout the year; fruiting: May to November.

Vernacular names — Bolivia: Piraquina, Oyshobo (Yuracare) (*Thomas & Agustin 2024*). Peru: Atzmiriqui.

Note — Guatteria duodecima can at first glance be distinguished by relatively narrow and verruculose leaves which are usually narrowed both toward the base and toward the apex and also are densely to rather densely covered with appressed, almost silvery hairs on the lower side. Other distinctive features of this species are found in the shortly pedicellate flowers and monocarps which are always longer than the stipes.

5. Guatteria dura R.E.Fr. — Fig. 1b, 6, 7; Map 1

Guatteria dura R.E.Fr. (1939) 499. — Type: Spruce 3354 (holo K; iso BM, BR, K, P), Venezuela, Amazonas, Río Pasimoni, Feb. 1852.

Guatteria kuhlmannii R.E.Fr. (1939) 498, syn. nov. — Type: *J.G. Kuhlmann* 460 = *RB24256* (holo S; iso RB), Brazil, Mato Grosso, Rio Ouro Preto, affluent of Rio Pacanova, 17 Sept. 1923.

Tree or shrub 2.5–30 m tall, 5–50 cm diam; young twigs densely covered with appressed to half-appressed hairs 1–2 mm long, soon glabrous. *Leaves*: petiole 5–10 mm long, 3–4 mm diam; lamina elliptic to obovate or narrowly so, 12–28 by 5–12 cm (leaf index 1.6–4), coriaceous, densely and coarsely verruculose (the verruculae often tending to form strings), dull above, brown on both sides, glabrous above, rather densely to sparsely covered with appressed to half-appressed hairs 1–2 mm long below, base acute and often slightly attenuate, apex shortly acuminate (acumen 5–10 mm long), primary vein impressed above, secondary veins distinct, 12–18 on either side of primary vein, flat to slightly impressed above, smallest

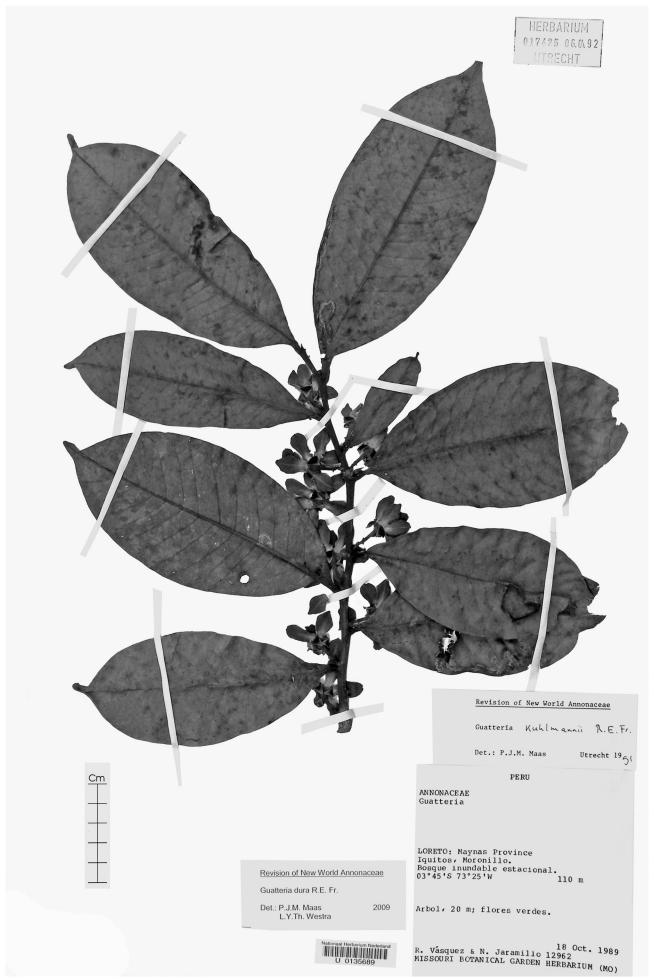


Fig. 6 Guatteria dura R.E.Fr. Flowering specimen (Vásquez et al. 12962, U).



Fig. 7 Guatteria dura R.E.Fr. a. Flowers; b. fruits; c. details of monocarp and seed (a: Steward et al. 276; b, c: Prance et al. 20620, all U).

distance between loops and margin 2-5 mm. Flowers in 1(-3)-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 5-20 mm long, 1-2 mm diam, fruiting pedicels up to 30 mm long, 3 mm diam, densely to sparsely covered with appressed hairs, articulated at 0.3-0.5 from the base, bracts 5-7, soon falling, basal bract depressed ovate, c. 2 mm long, the upper one broadly ovate, c. 4 mm long; flower buds depressed ovoid; sepals free, broadly triangular-ovate, 5-8 by 5-7 mm, reflexed, outer side densely covered with appressed hairs; petals green, maturing cream, white or yellow in vivo, narrowly elliptic to elliptic or obovate-elliptic, 15–40 by 5–17 mm, outer side sparsely covered with appressed hairs, the base and young petals densely so; stamens 1.5-2 mm long, connective shield papillate to almost glabrous. *Monocarps* 25–50, green, maturing purplish black in vivo, brown in sicco, ellipsoid, 18-19 by 7–11 mm, sparsely covered with appressed hairs, apex apiculate (apiculum < 0.5 mm long), wall 0.3-0.5 mm thick, stipes 5-10 by 1-1.5 mm. Seed ellipsoid, 15-18 by 6-8 mm, dark, shiny brown, rugulose and distinctly longitudinally ridged.

Distribution — Colombia (Amazonas), Venezuela (Amazonas), Peru (Loreto), Bolivia (Beni) and Brazil (Amazonas, Mato Grosso).

Habitat & Ecology — In periodically inundated or sometimes in non-inundated forest or in scrub savanna, often on clayey soil. At elevations of up to 175 m. Flowering: January, February, June, August to November; fruiting: March, April.

Vernacular names — Colombia: Jaacu (Muinane), Jaacuo (Muinane) (*Van Andel et al. 136*), Jakup (Muinane) (*Urrego et al. 1417*, 1572), Jimogu+ (Huitoto) (*Urrego et al. 1785*, 1979), Vara blanca (*Urrego et al. 293A*).

Notes — *Guatteria dura* is easily recognizable by densely and coarsely verruculose leaves, in which the large verrucae often form strings of 2 or 3.

Guatteria dura resembles G. meliodora in many aspects, among others by the thick leaves which completely lack the marginal vein so often found in this section; G. dura differs, however, by the densely verruculose lamina, the warts often forming strings of 2 or 3, vs the sparsely verruculose lamina with warts never

forming strings in *G. meliodora*. The distinction between both species requires further study.

There is quite some variation in petal size and shape in *G. dura*: in *Stergios et al.* 9935 the petals are obovate, measuring 20–30 by 15–17 mm, whereas in *Colella et al.* 2145 they are very large and narrow, namely 28–40 by 8–12 mm.

The only collection from Bolivia (*Guillén & Soliz 3833*) is aberrant by the upper side of the leaves being greyish green rather than brown.

Guatteria friesiana (W.A.Rodrigues) Erkens & Maas — Fig. 8a, 9; Plate 1c; Map 2

Guatteria friesiana (W.A.Rodrigues) Erkens & Maas (2008) 404. — Guatteriopsis friesiana W.A.Rodrigues (1981) 49, f. 1; Maas et al. (2007) 644. — Type: D. Coêlho INPA3609 (holo INPA), Brazil, Amazonas, Manaus, Igarapé do Passarinho, 14 Mar. 1956.

Tree 3–10 m tall, 4–10 cm diam; young twigs and petioles densely covered with a velutinous indument of erect, dark brown to blackish brown, long-persistent hairs up to 0.5 mm long. Leaves: petiole 2-8 mm long, 2-3 mm diam; lamina narrowly elliptic to narrowly obovate, 12-28 by 4-9 cm (leaf index 2.7-3.5), chartaceous to thinly coriaceous, very densely confluentverruculose, pale green to greyish green on both sides, glabrous above, sparsely covered with appressed brown hairs below, but rather densely to sparsely covered on primary vein, base cordate, apex acuminate (acumen 10-20 mm long), primary vein flat or almost so above, secondary veins indistinct, 10-24 on either side, flat or slightly impressed above, indistinctly loop-forming over most of the length or the entire length, shortest distance between loops and margin 2-5 mm. Flowers in 1-2-flowered inflorescences in axils of leaves; pedicels 5-10 mm long, 2-3 mm diam, densely covered with dark brown, appressed hairs, articulated at 0.3-0.5 from the base, bracts c. 5, soon falling, the upper bract broadly to depressed ovate, c. 5 mm long; flower buds ovoid to conical, acute; sepals free, triangular to ovate-triangular, 10–16 mm long, outer side densely covered with dark brown, appressed hairs; petals cream in vivo,



Fig. 8 a. Guatteria friesiana (W.A.Rodrigues) Erkens & Maas. Flower. — b, c. Guatteria griseifolia Maas & Westra. b. Detail of monocarps and seed; c. flower (a: Lepsch Cunha et al. 932; b: Palacios et al. 8401; c: Sánchez-Vega et al. 9971, all U).

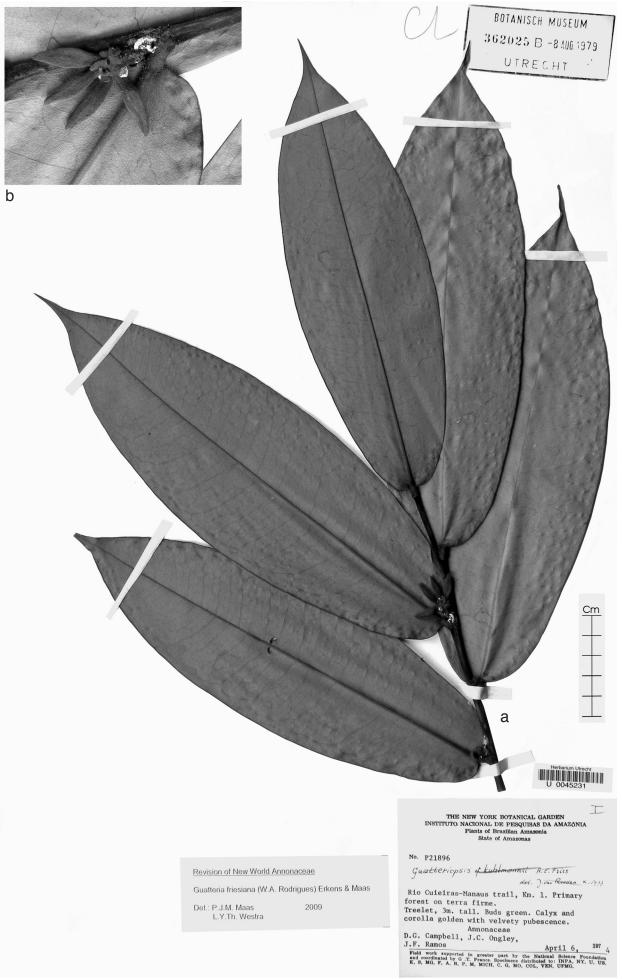


Fig. 9 Guatteria friesiana (W.A.Rodrigues) Erkens & Maas. a. Fruiting specimen; b. fruit (Campbell et al. P21896, U).



Plate 1 a, b. Guatteria blepharophylla Mart. a. Flowers; b. fruit. — c. Guatteria friesiana (W.A.Rodrigues) Erkens & Maas. Branch with flower and fruit. — d-f. Guatteria guianensis (Aubl.) R.E.Fr. d. Fruiting branch; e. inflorescence; f. mature flower. — g. Guatteria longicuspis R.E.Fr. Mature flower (left) and juvenile flower (a, b: from plant growing in Jardim Botânico do Rio de Janeiro; c: Brazil anno 1983, without further data; d: French Guiana, Piste de St. Elie, Prévost & Sabatier 3785; e: Brazil, Maas et al. 8051; f: Brazil, Maas et al. 8187; g: Brazil, Maas et al. 6835). — Photos: a, b. L.Y.Th. Westra; c. W. Morawetz; d. M.F. Prévost; e-g. P.J.M. Maas.



Fig. 10 Guatteria griseifolia Maas & Westra. Fruiting specimen (Palacios et al. 8401, MO).

narrowly ovate-triangular to narrowly oblong-ovate, outer petals 20-25 by 8-12 mm, inner ones 15-19 by 6-8 mm, outer side densely covered with dark brown, appressed hairs; stamens c. 2 mm long, connective shield hairy. *Monocarps* 7–10, green, maturing red in vivo, ellipsoid, 19-23 mm long, sparsely covered with appressed and erect hairs, apiculate (apiculum c. 2 mm long), stipes 1-3 mm long. *Seed* ellipsoid, 13-19 by 6-8 mm, dark, shiny brown, slightly sulcate at the base, slightly pointed at the apex.

Distribution — Brazil (Amazonas).

Habitat & Ecology — In non-inundated forest, on clayey to sandy soil. At elevations of 50–125 m. Flowering: February to May; fruiting: March to June.

Vernacular names — Brazil: Envireira (*Rodrigues & Loureiro* 5908).

Note — *Guatteria friesiana* can be recognized by its leaves with a cordate base, obscure secondary veins, a velutinous indument on young twigs and shortly pedicellate flowers.

7. Guatteria grandipes Maas & Westra

Guatteria grandipes Maas & Westra in Erkens et al. (2008) 497, f. 11. — Type: Stein et al. 4002 (holo MO; iso U), Peru, Loreto, Prov. Ramón Castilla, trail inland from Pucaurquillo, up Río Ampiyacu from Pebas, 140 m, 31 Jan. 1987.

Tree or shrub 4-6 m tall, diam not recorded; young twigs densely covered with erect, rough, brown hairs ('hirsute') 1.5-2.5 mm long. Leaves: petiole c. 5 mm long, 2-3 mm diam; lamina narrowly obovate to narrowly elliptic, 16-23 by 4-7 cm (leaf index 3.3-4), coriaceous, densely verruculose, dull, brown to greenish brown above, brown below, glabrous above, densely covered with erect, rough, brown hairs ('hirsute') 1.5-2.5 mm long below, base acute, apex acuminate (acumen 5-15 mm long), primary vein impressed above, secondary veins distinct, 15-25 on either side of primary vein, impressed to flat above, marginal vein present, smallest distance between marginal vein and margin 2-3 mm. Flowers solitary in leaf axils; pedicels 70-90 mm long, 1 mm diam, densely to rather densely covered with erect, rough, brown hairs ('hirsute') 1.5-2.5 mm long, articulated at ≤ 0.1 from the base, bracts not seen; flower buds subglobose; sepals free, ovate, 11-12 by 6 mm, appressed, outer side densely covered with appressed, white hairs; petals greenish cream in vivo, young ones ovate, c. 14 by 8 mm, outer side densely covered with appressed, white hairs; stamens c. 2 mm long, connective shield densely papillate. Monocarps c. 15, green in vivo, brown in sicco, ellipsoid, 15-16 by 7 mm, rather densely covered with erect hairs, apex apiculate (apiculum < 0.2 mm long), wall 0.2–0.3 mm thick, stipes 15–17 by 1 mm. Seed (young ones!) ellipsoid, c. 16 by 7 mm, pale brown, rugose.

Distribution — Peru (Loreto).

Habitat & Ecology — In forest (the type collection from 'swampy forest'), on lateritic soil. At elevations of 120–140 m. Flowering: August; fruiting: January.

Vernacular names — None.

Note — Guatteria grandipes belongs in Fries's sect. Mecocarpus because of its verruculose leaves, provided with a marginal vein. It differs from all species in this section by the extremely long pedicels up to 90 mm long!

Guatteria griseifolia Maas & Westra, sp. nov. — Fig. 8b, c, 10; Map 3

Ramulis saepe alatis, foliis griseo-viridibus apice rotundatis vel breviter acuminatis costa subtus saepe alata distincta. — Typus: *Gentry et al. 30941* (holo U, 2 sheets; iso MO), Ecuador, Morona-Santiago, Campamento La Playa, road construction camp 23 km SE of San Juan Bosco, 1050 m, 28 Jan. 1981.

Guatteria sp. 4 Chatrou et al. (1997) 110.

Tree 4–20 m tall, c. 10 cm diam; young twigs rather densely to sparsely covered with appressed hairs, soon glabrous, often with narrow wings, initiating below leaf insertion. Leaves: petiole 5–10 mm long, 4–5 mm diam; lamina narrowly obovate to narrowly elliptic, 18-35 by 6-13 cm (leaf index 2-3), chartaceous, sparsely verruculose, slightly to distinctly shiny, greyish green above, greenish brown below, glabrous above, sparsely covered with appressed hairs below, base acute, sometimes obtuse, apex obtuse to rounded or shortly acuminate (acumen up to 15 mm long), primary vein impressed above, often keeled below, secondary veins distinct, 12-17 on either side of primary vein, raised above, smallest distance between loops and margin 3–5 mm, tertiary veins reticulate, slightly raised above. *Flowers* in 1-2-flowered inflorescences in axils of leaves, to severalflowered on older branchlets; pedicels 20-30 mm long, 2-3 mm diam, fruiting pedicels 20-50 mm long, 2-3 mm diam, rather densely to sparsely covered with appressed hairs, articulated at 0.1–0.2 from the base, bracts 5–6, soon falling, the upper bract broadly elliptic, up to c. 7 mm long; flower buds broadly ovoid; sepals free, broadly ovate-triangular, 8-9 by 7-8 mm, appressed, outer side densely covered with appressed hairs; petals greenish yellow to brownish yellow in vivo, ovate, 13-20 by 10-12 mm, outer side densely covered with appressed hairs; stamens 2-2.5 mm long, connective shield papillate. Monocarps 50–100, white (mentioned on two labels) or green, maturing dark purple to black in vivo, black in sicco, ellipsoid, 10–17 by 5–6 mm, sparsely covered with appressed hairs to glabrous, apex apiculate (apiculum < 0.5 mm long), wall 0.1–0.2 mm thick, stipes 1-3 by 1 mm. Seed ellipsoid, 10-15 by 4-7 mm, shiny brown, pitted to brain-like.

Distribution — Ecuador (Morona-Santiago, Zamora-Chinchipe) and Peru (San Martín).

Habitat & Ecology — In non-inundated forest (cloud forest with abundant epiphytes, "bosque perennifolia", forest on limestone derived soil, locally with thick humus layer). At elevations of 900–2400 m. Flowering: January, July, November, December; fruiting: March, June, October to December.

Vernacular names — None.

Other specimens examined. Ecuador, Morona-Santiago, Gualaquiza, Cordillera del Cóndor, Valley of Río Quimi, 1300 m, 10 Dec. 2000, Neill et al. 12948 (U). Zamora-Chinchipe, Nangaritza, region of Cordillera del Cóndor, near 'Las Orquídeas', 890 m, 9 Nov. 2006, Kajekai 960 (MO, WAG); Cantón Nangaritza, Pachicutza, road to Hito, Cordillera del Cóndor, 1200—1300 m, 20 Oct. 1991, Palacios et al. 8401 (MO, U); Yacuambi, Parroquia La Paz, Centro Shuar Kiim, Reserva Tiwi Nunka, between Centro Shuar Kiim and Cordillera Chiichim Naint, 2400 m, 15 June 2006, Wisum et al. 584 (MO, WAG). — Peru, San Martín, Prov. Rioja, Distr. Pardo Miguel, Venceremo, Caserío El Afluente, 1440—1520 m, 14 Nov. 1996, Sánchez-Vega & Dillon 8682 (U); Prov. Rioja, Distr. Pardo Miguel, Caserío Jorge Chavez, km 398 of Carretera Marginal, 1400 m, 1 July 1999, Sánchez-Vega et al. 9971 (U); along road from Rioja to Pedro Ruiz, about bridge Serranoyacu, 1170 m, 5 Mar. 2001, Van der Werff et al. 16768 (U).

Note — Guatteria griseifolia is listed as "Guatteria sp. 4, sect. Mecocarpus, black leaf" in Chatrou et al. (1997). It occurs at quite high elevations in Ecuador and Peru and it can be distinguished by the often winged young twigs, greyish green leaves (hence the specific epithet), a leaf apex varying from obtuse, rounded, to shortly acuminate and an often keeled midrib.

Guatteria guianensis (Aubl.) R.E.Fr. — Fig. 11, 12; Plate 1d–f; Map 2

Guatteria guianensis (Aubl.) R.E.Fr. (1939) 505, f. 32a-c; Maas et al. (2007) 639. — Aberemoa guianensis Aubl. (1775) 610, t. 245. — Guatteria aberemoa Dunal (1817) 126, nom. illeg. — Type: Aublet s.n. (lecto BM), French Guiana, "in silvis remotis Sinemariensibus".

Guatteria aberemoa Dunal var. microcarpa DC. (1817) 502, syn. nov. — Type: not seen.

Guatteria multivenia Diels (1927) 171, syn. nov. — Type: Tessmann 5192 (holo B; iso G), Peru, Loreto, Lower Río Itaya, Soledad, 110 m, 13 June 1925.

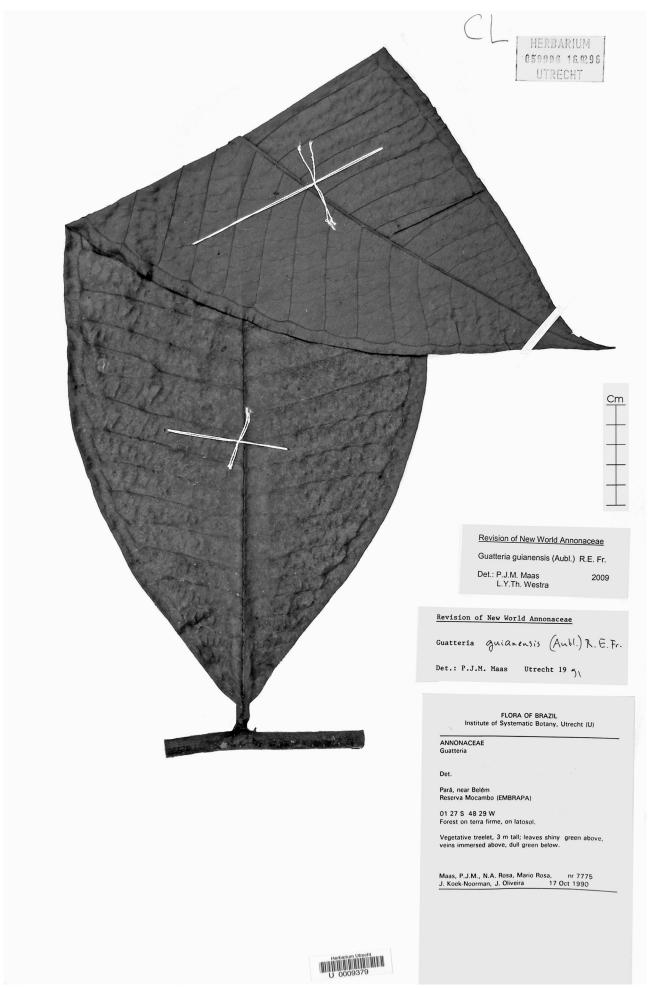


Fig. 11 Guatteria guianensis (Aubl.) R.E.Fr. A single large leaf (Maas et al. 7775, U).

Guatteria excellens R.E.Fr. (1938) 721, syn. nov. — Type: Klug 1273 (holo F; iso US), Peru, Loreto, Mishuyacu, near Iquitos, 100 m, Apr. 1930.

Guatteria calophylla R.E.Fr. (1939) 507, f. 32d–f, syn. nov. — Type: Krukoff 1534 (holo S; iso F, NY, U), Brazil, Mato Grosso, source of Rio Jatuarana, Machado River region, Dec. 1931.

Guatteria robusta R.E.Fr. (1957a) 328, syn. nov. — Type: Fróes 20788 (holo NY), Brazil, Amazonas, São Paulo de Olivença, Apr. 1945.

Tree 3-25 m tall, 4-25 cm diam; young twigs and petioles densely covered with a velutinous indument of erect, often curly, brown hairs up to 0.5 mm long, becoming glabrous in age. Leaves: petioles 0-10 mm long, 4-8 mm diam; lamina narrowly elliptic to narrowly elliptic-obovate, 20-63 by 6-21 cm (leaf index 2.6-4.5), chartaceous to thinly coriaceous, brown or greenish to greyish brown and often somewhat shiny above, brown below, densely to rather densely verruculose, glabrous above, rather densely to sparsely covered with erect to appressed hairs below, base attenuate, the extreme base a rounded lobule on each side, apex acuminate, (acumen 5–30 mm long and ending in a acute tip), primary vein impressed above, secondary veins 20-35 on each side, impressed above, forming a marginal vein at a shortest distance of 1–7 mm from the margin, tertiary veins percurrent, flat to prominulous above. Flowers in 1(-2)-flowered inflorescences in axils of leaves or on older branchlets; flower buds broadly ovoid, apex acute; pedicels 12-25 mm long, 2-3 mm diam, fruiting pedicels up to 35 mm long, 5 mm diam, densely covered with erect to appressed hairs, articulated at 0.3-0.5 from the base, bracts probably several, soon falling, the upper bract elliptic, 7–8 mm long; sepals almost free, broadly ovate-triangular to ovate-triangular, 7–12 by 8–11 mm, patent to reflexed, outer side densely covered with erect to appressed hairs; petals green, maturing cream, white or yellow in vivo, elliptic, 20-35 by 12-17 mm, outer side densely covered with erect to appressed brownish grey hairs; stamens 2-3 mm, connective shield papillate to glabrous. Monocarps 20-75, green, maturing reddish black to black in vivo, brown in sicco, ellipsoid, 13-25 by 8-15 mm, rather densely to sparsely covered with erect to appressed hairs, apex rounded, extreme apex apiculate (apiculum 0.5-1 mm long), wall 0.5-1 mm thick, stipe 4-10 by 1.5-2 mm. Seed ellipsoid, 15-25 by 6-9 mm, brown to reddish brown, rugose and with some more or less distinct longitudinal furrows.

Distribution — Colombia (Antioquia), French Guiana, Ecuador (Napo, Sucumbios), Peru (Amazonas, Loreto, Madre de Dios, Pasco, San Martín) and Brazil (Amapá, Amazonas, Pará, Rondônia)

Habitat & Ecology — In non-inundated forest, on clayey to sandy soil. At elevations of 0–800 m. Flowering: March to December; fruiting: throughout the year.

Vernacular names — Brazil: Envira da mata (*Fróes 20788*). Invira (*Krukoff 1534*, *Pires 51901*). Ecuador: Moncapatamo (*Aulestia & Bainca 3533*), Yaris (Shuar name) (*Morales et al. 1466*). French Guiana: Abéremou (Galibi), Mamanyaré, Pomme canelle. Peru: Carahuasca (*P. Díaz et al. 85*; *Vásquez et al. 5968*), Chu-

rum yeis (*Huashikat 832*, 1046), Wáshi yéis (*Huashikat 665*), Wasri yais (*Tunqui 857*), Wuáshi yais (*Leveau 250*).

Notes — *Guatteria guianensis* is easily recognizable by a combination of often very large, verruculose leaves with a quite distinct marginal vein and by young twigs covered with a velutinous indument of erect, mostly curly, brown hairs when young. It resembles *G. decurrens*, from which it differs by the indument of the young leafy twigs: erect, brown, soft, curly hairs up to 0.5 mm long in *G. guianensis* against erect to half-appressed, rough hairs up to 3 mm long in *G. decurrens*.

According to *Maas et al. 8186* (U) from Peru the ripe fruit has a sweet, edible pulp.

Guatteria hispida (R.E.Fr.) Erkens & Maas — Fig. 13; Map 1

Guatteria hispida (R.E.Fr.) Erkens & Maas (2008) 404. — Guatteriopsis hispida R.E.Fr. (1934) 111, t. 7, 8; Maas et al. (2007) 645. — Type: Ducke RB23903 (holo S; iso K, RB, US), Brazil, Amazonas, Manaus, Estrada do Aleixo, km 12, 9 Dec. 1932.

Tree or shrub 2.5–6 m tall, c. 5 cm diam; young twigs densely covered with brown, rough, erect, long-persistent hairs ('hispid') up to 3 mm long. Leaves: petiole 3-5 mm long, 1-1.5 mm diam; lamina narrowly oblong-elliptic, 10-27 by 3-6 cm (leaf index 3.2-4.5), chartaceous, densely verruculose, dull, greyish green to brownish green above, brown below, glabrous above, rather densely to sparsely covered with brown, rough, erect hairs below, base acute to obtuse, apex a abruptly and longacuminate (acumen 10-25 mm long), primary vein impressed above, secondary veins distinct, 10-15 on either side of primary vein, slightly raised above, smallest distance between loops and margin 3-7 mm. Flowers in 1-flowered inflorescences in axils of leaves; pedicels 5–8 mm long, 3–5 mm diam, fruiting pedicels up to 4 mm diam, densely to finally sparsely covered with erect, brown hairs, articulated at c. 0.8 from the base, bracts soon falling, the upper bract up to c. 7 mm long; flower buds subglobose; sepals free, broadly ovate-triangular, 8–10 by 8–10 mm, appressed, outer side densely covered with appressed, brown, long hairs; petals yellow in vivo, ovate-triangular, 15-20 by 8-14 mm, outer side densely covered with appressed, brown, long hairs; stamens c. 2 mm long, connective shield densely hairy. Monocarps 10-50, maturing greenish red to wine-red in vivo, brown in sicco, narrowly ellipsoid and fusiform, 20-35 by 7–8 mm, densely covered with erect, rough, brown hairs, apex distinctly and bluntly apiculate (apiculum up to 2 mm long), wall 0.5-0.7 mm thick, stipes 5-10 by 1-1.5 mm. Seed narrowly ellipsoid, 17-20 by 6-7 mm, apex pointed, brown, deeply longitudinally ridged.

Distribution — Brazil (Amazonas).

Habitat & Ecology — Mostly in campinarana forest, on sandy soil. At elevations below 200 m. Flowering: February, December; fruiting: June, July.

Vernacular names — Brazil: Envireira.



Fig. 12 Guatteria guianensis (Aubl.) R.E.Fr. a. Flower; b. fruit and loose monocarps; c. detail of indument (a: WWF Plot 2206-1818 s.n.; b: Vásquez et al. 13538; c: Ribeiro et al. 955, all U).



Fig. 13 Guatteria hispida (R.E.Fr.) Erkens & Maas. a. Fruiting specimen; b. detail of indument; c. detail of monocarps and seed (Ribeiro et al. 845, U).

Note — *Guatteria hispida* is one of the very few species in sect. *Mecocarpus* with a long-persistent indument of erect, rough, brown hairs on the leafy twigs, leaves and also on the monocarps!

11. Guatteria insculpta R.E.Fr. — Fig. 1c, 14, 15; Map 1

Guatteria insculpta R.E.Fr. (1939) 504, f. 28a, b; Murillo A. & Restrepo (2000) 95, f. 25. — Type: Spruce 2896 (holo K, 2 sheets; iso BM, P), Brazil, Amazonas, Ipanoré ('Panuré'), Rio Vaupés, Mar. 1853.

Tree or shrub 5-25 m tall, 5-30 cm diam; young twigs densely covered with a velutinous indument of erect, red-brown hairs, finally glabrous. Leaves: petiole 5-10 mm long, 4-7 mm diam; lamina narrowly elliptic to narrowly obovate, 20-50 by 5-16 cm (leaf index 2.3-4.4), chartaceous, very densely and minutely verruculose, dull, greyish green above, brown below, glabrous above, densely covered with erect, red-brown hairs below, base acute, the extreme base obtuse, apex acuminate (acumen 5-15 mm long), primary vein impressed above, secondary veins distinct, 20-35 on either side of primary vein, impressed above, sometimes with a more or less distinct marginal vein, smallest distance between loops and margin 3-4 mm. Flowers in 1-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 18-40 mm long, 2-4 mm diam, fruiting pedicels up to 50 mm long, 5 mm diam, densely covered with erect, red-brown hairs, articulated at c. 0.2 from the base, bracts soon falling, the upper bract up to c. 7 mm long; flower buds not seen; sepals free, triangular, 10-12 by 7-8 mm, reflexed, outer side densely covered with erect, red-brown hairs; petals green in vivo, obovate to elliptic, 16-20 by 8-12 mm, outer side sparsely covered with appressed, white hairs, the base densely so; stamens 1.5-2 mm long, connective shield papillate. Monocarps 10-50, green in vivo, maturing brown, pale brown in sicco, ellipsoid, 10-18 by 5-12 mm, sparsely covered with appressed hairs, apex rounded or apiculate (apiculum < 0.5 mm long), wall 0.5-1 mm thick, stipes 5-10 by 1-2 mm. Seed ellipsoid, 12-19 by 6-8 mm, shiny brown, longitudinally and transversely ribbed and wrinkled.

Distribution — Colombia (Amazonas, Caquetá), Venezuela (Amazonas) and Brazil (Amazonas).

Habitat & Ecology — In non-inundated, often caatinga forest, on sandy soil. At elevations of up to 270 m. Flowering: March, April, July, October; fruiting: January, February, April, October, November.

Vernacular names — Colombia: Jakuo (Muinane) (*Murillo A. & Rodríguez A. 544*), Jimokai (Huitoto), Palo de perfume.

Note — Guatteria insculpta can be recognized by very densely and minutely verruculose leaves and by young twigs covered with a velutinous indument of erect red-brown hairs. Furthermore, this species stands out by the dense cover of erect brown hairs on the lower side of the leaves.

12. Guatteria japurensis Maas & Westra

Guatteria japurensis Maas & Westra in Erkens et al. (2008) 497, f. 12. — Type: Amaral et al. 518 (holo U; iso NY, RB), Brazil, Amazonas, right bank of Rio Japurá, Vila Bittencourt, Serrinha, 100 m, 16 Nov. 1982.

Small tree c. 6.5 m tall, diam not recorded; twigs (no growth tip seen) glabrous. Leaves: petiole c. 10 mm long, 3-4 mm diam; lamina narrowly elliptic-ovate, 16-27 by 5-8.5 cm (leaf index 3-4), chartaceous to thinly coriaceous, rugulose above, not or sparsely verruculose along primary vein only, slightly shiny and brownish green above, dull brownish green below, glabrous on both sides, base shortly attenuate, apex acuminate (acumen c. 10 mm long), primary vein flat above, secondary veins indistinct, 15-18 on either side of primary vein, raised above, smallest distance between loops and margin 1–2 mm. Flowers in 1-several-flowered inflorescences in axils of leaves or on older branchlets, only seen in fruiting stage: fruiting pedicels 50-60 mm long, 1-1.5 mm diam, sparsely covered with appressed hairs to glabrous, articulated at c. 0.1 from the base; flower buds, sepals, petals and stamens not seen. Monocarps 10-15, immature, blackish brown in sicco, ellipsoid to narrowly ellipsoid, 17-20 by 7-8 mm, glabrous, apex apiculate (apiculum 0.2–0.4 mm long), wall c. 0.2 mm thick, stipes 11–17 by 1–1.5 mm. Seed narrowly ellipsoid, c. 18 by 7 mm, brown, shiny, slightly rugose.

Distribution — Western Amazonian Brazil (Amazonas).

Habitat & Ecology — In non-inundated forest, on stony soil covered with lichens and mosses. At an elevation of c. 100 m. Flowering: unknown; fruiting: November.

Vernacular names — None.

Note — *Guatteria japurensis* is most distinctive by the long and slender fruiting pedicels, which are very uncommon in *Guatteria*. Another noteworthy feature are the leaves with indistinct venation and which are rugulose on the upper surface.

Guatteria longicuspis R.E.Fr. — Fig. 16; Plate 1g; Map 2

Guatteria longicuspis R.E.Fr. (1900) 18, t. 2, f. 3–5. — Duguetia leptocarpa Benth. ex R.E.Fr. (1900) 18. — Type: Spruce s.n. (holo B; iso BM, K, P), Brazil, Amazonas, São Gabriel da Cachoeira, Jan.–Aug. 1852.

Guatteria amazonica R.E.Fr. (1938) 720, syn. nov. — Type: *J.G. Kuhlmann RB24260* (holo S; iso RB), Peru, Loreto, Río Amazonas, Chimbote, 3 Mar. 1924.

Guatteria microcalyx R.E.Fr. (1939) 497, f. 29c, d, syn. nov. — Type: Krukoff 1033 (holo S; iso BM, G, K, NY, S, U), Brazil, Pará, Fordlandia, Tapajos River region, Sept. 1931.

Guatteria sp. 2 Chatrou et al. (1997) 109.

A mostly cauliflorous tree 3–13 m tall, 4–15 cm diam; young twigs densely to sparsely covered with appressed hairs, soon glabrous. *Leaves*: petiole 2–5 mm long, 2–4 mm diam; lamina narrowly oblong-elliptic to narrowly obovate, 20–35 by 4–10 cm (leaf index 2.8–6), chartaceous, rather densely to sparsely, sometimes densely verruculose, greyish to brownish above, brown below, glabrous above, sparsely covered with appressed



Fig. 14 Guatteria insculpta R.E.Fr. a. Flower; b. fruits; c. detail of monocarps and seed (a: Nascimento et al. 647; b, c: Nee et al. 31051, all U).



Fig. 15 Guatteria insculpta R.E.Fr. Fruiting specimen (Stevenson et al. 946, U).

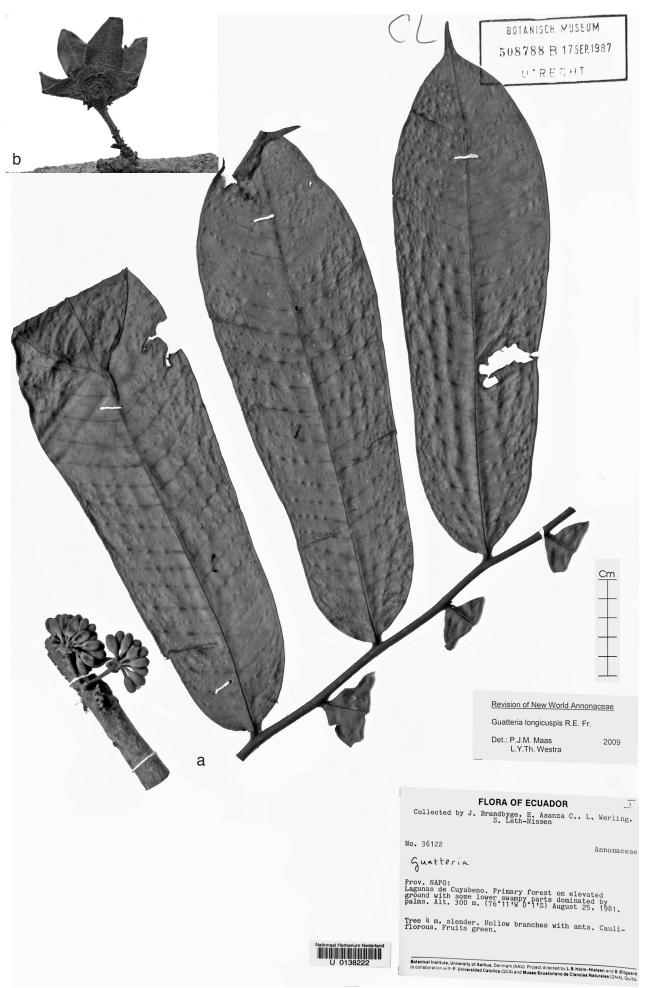


Fig. 16 Guatteria longicuspis R.E.Fr. a. Fruiting specimen; b. flower (a: Brandbyge et al. 36122; b: Balslev et al. 97092, all U).

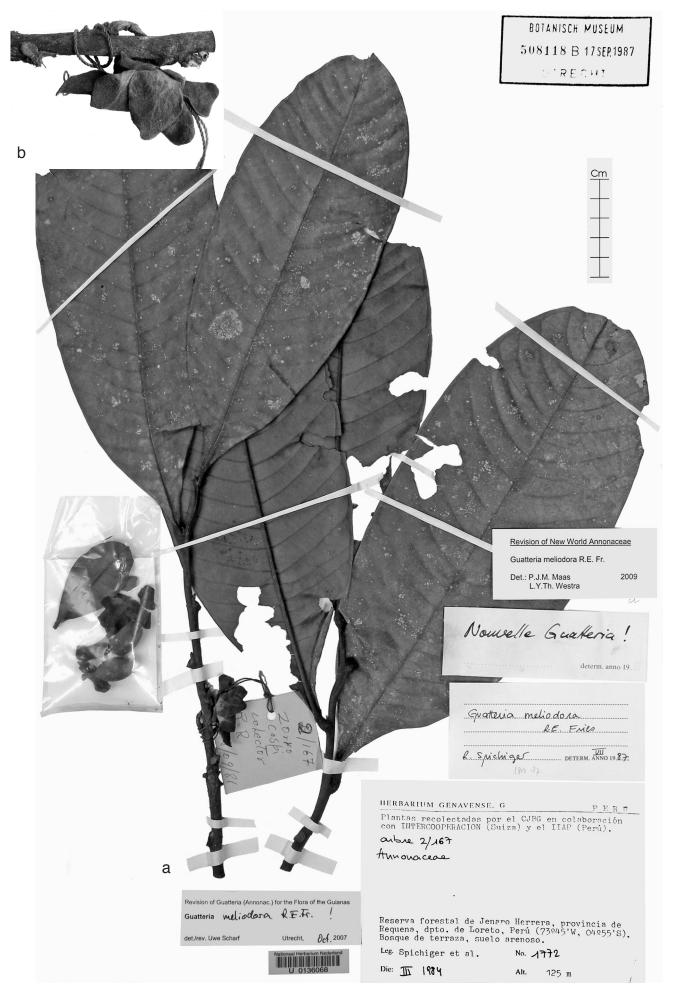


Fig. 17 Guatteria meliodora R.E.Fr. a. Flowering specimen; b. flower (all: Spichiger et al.1772, U).

hairs up to 1 mm long below, base acute or obtuse, often oblique, apex acuminate (acumen 10-20 mm long), primary vein impressed above, secondary veins distinct, 15-30 on either side of primary vein, impressed above, often with a distinct marginal vein, smallest distance between loops and margin 2-3 mm. Flowers mostly in 1-flowered inflorescences, on densely branched compact clusters, on the trunk, sometimes on large leafless branchlets, rarely axillary; pedicels 15-30 mm long, 1–2 mm diam, fruiting pedicels up to 35 mm long, 3–4 mm diam, densely covered with appressed hairs, articulated at 0.2-0.4 from the base, bracts 4–6, soon falling; flower buds not seen; sepals free, broadly ovate-triangular, 4-7 by 4-6 mm, appressed to reflexed, outer side densely covered with appressed hairs; petals yellow to greenish yellow in vivo, elliptic to obovate, 15-22 by 7-12 mm, outer side densely covered with appressed hairs; stamens 1.5-2 mm long, connective shield densely papillate. Monocarps 25-40, green, maturing dark brown in vivo, brown in sicco, ellipsoid, 17-23 by 4-11{-13} mm, rather densely covered with appressed hairs, soon subglabrous, apex rounded, wall 0.4-0.5 mm thick, stipes 5-10 by 1 mm. Seed ellipsoid, 13-17 by 7-10 mm, dark brown, rugose.

Distribution — Colombia (Amazonas, Caquetá, Vaupés), Venezuela (Amazonas), Ecuador (Napo, Sucumbios), Peru (Loreto) and Brazil (Amazonas, Pará).

Habitat & Ecology — In non-inundated or periodically inundated forest (várzea, igapó), on clayey soil. At elevations of up to 300 m. Flowering: April, May, July, August, October; fruiting: June to February.

Vernacular names — Colombia: Buutruchicu (Muinane) (*Murillo A. et al. 518*), Ñaatraje dujeku (Muinane) (*Murillo A. 619*). Peru: Bara (*Rimachi Y. 3593*).

Note — The majority of *G. longicuspis* plants studied is cauliflorous. The leaves are frequently oblong-elliptic in shape. The number of minute warts on the lamina varies greatly, the leaves ranging from densely to sparsely verruculose. The equally cauliflorous *G. novogranatensis* from Colombia (Boyacá and Sur de Santander) differs from *G. longicuspis* by much larger sepals (10–13 mm long and 5–7 mm long, respectively). A third cauliflorous species, *G. scalarinervia*, is easily distinguished from *G. longicuspis* by the long petioles (15–20 mm long and 2–5 mm long, respectively). It should be kept in mind, though, that the position of *G. scalarinervia* within this group is questionable. For further details, see under that species. The young monocarps of *G. longicuspis* are often pointed (hence Fries's epithet), but the ripe ones are rounded.

14. Guatteria meliodora R.E.Fr. — Fig. 17; Map 3

Guatteria meliodora R.E.Fr. (1939) 500; Spichiger et al. (1989) 124, f. 58; Maas et al. (2007) 640. — Type: Krukoff 5050 (holo S; iso BM, F, K, MO, NY, U, US), Brazil, Amazonas, Basin of Rio Juruá, near mouth of Rio Embira, tributary of Rio Tarauacá, 28 June 1933.

Tree 18–35 m tall, 10–20 cm diam, bark deeply fissured; young twigs rather densely covered with appressed hairs, very soon glabrous. *Leaves*: petiole 5–10 mm long, 3–5 mm diam; lamina narrowly obovate to narrowly elliptic, 22–35 by 8–12 cm (leaf index 2.4–3.2), coriaceous, sparsely verruculose, often shiny above, greyish green to brown above, brown below, glabrous above, sparsely covered with appressed hairs to almost glabrous below, base acute, slightly attenuate, apex often rounded and bluntly and very shortly acuminate (acumen up to c. 5 mm long), primary vein impressed above, distinctly keeled to rounded below, secondary veins distinct, 18–20 on either side of primary vein, raised above, smallest distance between loops and margin 3–4 mm. *Flowers* in 1-flowered inflorescences in axils of leaves or on leafless branchlets; pedicels 10–20 mm long, c. 2 mm diam, fruiting pedicels to 25 mm long, c. 3

mm diam, rather densely to sparsely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling, the basal bract (only 1 seen) depressed ovate, c. 2 mm long, the upper one broadly ovate, c. 3 mm long; flower buds depressed ovoid; sepals free, broadly ovate-triangular, 7–10 by 7–10 mm, reflexed, outer side densely to rather densely covered with appressed hairs; petals green, maturing yellow in vivo, ovate to obovate, 20–25 by 12–15 mm, outer side densely to rather densely covered with appressed, white hairs; stamens 1.5–2 mm long, connective shield papillate. *Monocarps* 50–100, green, maturing black in vivo, brown in sicco, ellipsoid, 18–22 by 10–13 mm, sparsely covered with appressed hairs to glabrous, apex rounded to apiculate (apiculum < 0.5 mm long), wall c. 1 mm thick, stipes 5–7 by 1–2 mm. *Seed* not seen, abortive.

Distribution — Guyana, Peru (Loreto) and Brazil (Acre, Amazonas).

Habitat & Ecology — In non-inundated (terra firme) forest, sometimes campinarana forest or campina forest, on sandy soil. The collection from Guyana (*Clarke et al. 7132*) is found in seasonally flooded forest on grey sand with *Eperua*, *Clusia* and *Oenocarpus*. At elevations of 125–240 m. Flowering: March, May, June, August, September; fruiting: August, December.

Vernacular names — Brazil: Envira. Peru: Carahuasca (*Vásquez 10436*), Zorro caspi (*Spichiger 1772*).

Notes — The label of the type collection of *G. meliodora* mentions that the yellow flowers have a strong odour resembling honey (hence the specific name).

Guatteria meliodora is well distinct from other species of sect. Mecocarpus by its thick, sparsely verruculose and often shortly acuminate and shiny leaves. It is noteworthy that the primary vein is keeled below in part of the material. For differences with G. dura see under the latter.

Pereira INPA/WWF 2303.6161 (U) from Brazil, Amazonas, Fazenda Dimona, 90 km N of Manaus, may belong here, but this sterile collection is aberrant in having a strongly attenuate leaf base.

15. Guatteria novogranatensis R.E.Fr. — Fig. 18; Map 3

Guatteria novogranatensis R.E.Fr. (1939) 496, f. 29a, b. — Type: Lawrance 552 (holo S; iso BM, MO, U), Colombia, Boyacá, El Umbo Region, 130 miles NW of Bogotá, 1100 m ('3500 ft.'), 27 Oct. 1932.

Cauliflorous tree 20-30 m tall, 50-120 cm diam; young twigs densely covered with erect hairs, soon glabrous. Leaves: petiole 4-5 mm long, 3-5 mm diam; lamina narrowly obovate to narrowly elliptic, 25-50 by 8-16 cm (leaf index 2.8-3.2), chartaceous, densely verruculose, pale brownish green above, brown below, glabrous above, densely covered with appressed to erect hairs on large veins, otherwise rather densely covered with appressed hairs below, base long-attenuate, apex acuminate (acumen 15–20 mm long), primary vein impressed above, more or less keeled below, secondary veins distinct, 25-30 on either side of primary vein, impressed above, with a more or less distinct marginal vein, smallest distance between loops and margin 4-7 mm. Flowers on densely branched compact clusters, on the trunk; pedicels 35-40 mm long, 2.5-3 mm diam, fruiting pedicels 40-60 mm long, densely covered with appressed hairs, articulated at c. 0.2 from the base, bracts not seen; flower buds not seen; sepals free, broadly ovate-triangular, 10-13 by 6-10 mm, appressed, outer side densely covered with appressed hairs; petals pale green to yellow in vivo, ovateoblong, 15-20 by 8-12 mm, outer side densely covered with appressed hairs; stamens 2-2.5 mm long, connective shield papillate. Monocarps 20-40, colour in vivo unknown, blackish brown in sicco, ellipsoid, 18-20 by 7-8 mm, glabrous, apex



Fig. 18 Guatteria novogranatensis R.E.Fr. Specimen with old inflorescence (Lawrance 635, MO).

apiculate (apiculum to 1 mm long), wall c. 0.2 mm thick, stipes 8–12 by 1 mm. *Seed* ellipsoid, 18–20 by 7 mm, dark, shiny brown, longitudinally and transversely striate.

Distribution — Colombia (Boyacá, Sur de Santander). Habitat & Ecology — In non-inundated forest. At elevations of 100–1100 m. Flowering: January, February; fruiting: October. Vernacular names — None.

Other specimens examined. Colombia, Boyacá, El Umbo Region, 130 miles NW of Bogotá, 1100 m ('3500 ft.'), 23 Feb. 1933, Lawrance 635 (MO, US, U). Sur de Santander, near Barranca Bermeja, Magdalena Valley, between Río Sogamoso and Río Colorado, Camp Mesa, 100–500 m, 1 Jan. 1935, Haught 1485 (S, not seen).

Note — Guatteria novogranatensis was collected from a very large tree 30 m tall and with a diameter of 1.2 m! It looks quite similar to the Amazonian species G. longicuspis, both being cauliflorous and sharing most leaf characters. G. novogranatensis differs by a dense indument on large leaf veins below (vs mostly sparsely so) and by larger sepals (10–13 mm long vs 5–7 mm long). It should not be ruled out that future research will prove the two taxa to be conspecific.

16. Guatteria pakaraimae Scharf & Maas

Guatteria pakaraimae Scharf & Maas (in Scharf et al. 2005) 568, f. 3. — Type: Henkel et al. 4279 (holo NY; iso BRG, U, US), Guyana, Pakaraima Mts, W slope on subplateau near head of Mo-toy-baru Creek, 1150–1200 m, 11 Nov. 1993.

Tree 12–13 m tall, diam not recorded; young twigs glabrous. Leaves: petiole 4-9 mm long, c. 2 mm diam; lamina elliptic to narrowly elliptic, 9-20 by 4-6 cm (leaf index 2.7-3.3), coriaceous, rather densely verruculose, somewhat shiny, greyish cream above, rusty brown below, glabrous above, covered with some scattered, appressed hairs below, base acute, apex shortly acuminate (acumen 5-15 mm long), primary vein impressed above, secondary veins indistinct, 8-10 on either side of primary vein, raised above, smallest distance between loops and margin 3-4 mm; tertiary veins reticulate, slightly raised above. Flowers solitary in axils of leaves; pedicels 50-60 mm long, c. 1 mm diam, finely longitudinally grooved, fruiting pedicels c. 70 mm long, c. 1.5 mm diam, glabrous, articulated at c. 0.1 from the base, bracts c. 5, soon falling, not seen; flower buds not seen; sepals broadly ovate-triangular, c. 3 by 3-4 mm, appressed, outer side subglabrous; petals green in vivo, ovate-oblong, 10-12 by 5 mm, outer base side densely covered with appressed, wavy hairs, towards the apex sparsely covered with very short, curly hairs; stamens c. 2 mm long, connective shield densely hairy. Monocarps c. 10, green in vivo, shiny black in sicco, ellipsoid to obovoid, 13-15 by 6-7 mm, glabrous, apex often apiculate (apiculum < 0.5 mm long), wall 0.2-0.3 mm thick, stipes 1-2 by 2 mm. Seed ellipsoid, 12-13 by 6-7 mm, shiny, reddish brown, strongly grooved and tuberculate ('rugulose').

Distribution — Guyana (Pakaraima Mts).

Habitat & Ecology — In cloud forest on sandstone, sand or grey sandy clay with thick layer of organic matter and peat (together with various woody plants including *Annonaceae*, *Araliaceae*, *Arecaceae*, *Clusia*, *Euterpe*, *Melastomatacae*, *Moronobea*). At elevations of 1135–1200 m. Flowering: November; fruiting: July.

Vernacular names — None.

Other specimen examined. Guyana, Potaro-Siparuni Region, Mt Wokomung, 1135 m, Clarke et al. 10861 (U, US).

Note — Guatteria pakaraimae is a striking species by its very long and small pedicels up to 70 mm long in fruit, an indistinct secondary leaf venation and shortly stipitate monocarps with stipes only 1–2 mm long.

17. Guatteria pastazae R.E.Fr.

Guatteria pastazae R.E.Fr. (1947) 5, t. 2; Erkens et al. (2008) 505, f. 16, pl. 1.

— Type: Lugo R. 191 (holo S; iso US), Ecuador, Pastaza, Mera, c. 600 m, 4 Apr. 1940.

Tree 4-28 m tall, 8-20 cm diam; young twigs densely to sparsely covered with appressed hairs, soon glabrous. Leaves: petiole 3–12 mm long, 2–3 mm diam; lamina narrowly oblongelliptic to narrowly oblong-obovate or narrowly ovate, 10-27 by 3–8 cm (leaf index 2.5–4.6), coriaceous to chartaceous, rather densely to sparsely verruculose, greyish green, greyish brown or brown above, pale to dark brown below, glabrous above except for some scattered hairs along primary and secondary veins above, sparsely covered with appressed hairs below, base attenuate, basal margins often somewhat rolled inwards, apex acuminate (acumen 10-15 mm long), primary vein impressed to flat above, slightly keeled below, secondary veins rather indistinct, 12–17 on either side of primary vein, slightly raised above, smallest distance between loops and margin 1-5 mm. Flowers in 1- (or 3-)flowered inflorescences mostly in axils of leaves or on branchlets after leaf shedding; pedicels 3-15 mm long, 1-2.5 mm diam, fruiting pedicels up to 25 mm long, up to 3 mm diam, densely to rather densely covered with appressed, brown hairs, articulated at 0.2–0.3 from the base, bracts 5-6, soon falling and leaving prominent scars on lower pedicel, c. 7 by 3 mm (only 1 seen); flower buds ovoid; sepals basally connate to free, broadly elliptic-ovate, 4-10 by 5-8 mm, appressed, but soon becoming patent to finally reflexed, outer side densely covered with appressed, brown hairs; petals green to greenish yellow and slightly tinged with red in vivo, elliptic-oblong to elliptic-obovate, the outer ones 12–15{–25} by 6-7 mm, the inner ones 18-20{-28} by 6-12 mm, outer side densely covered with appressed hairs; stamens 1.5-2 mm long, connective shield finely papillate-hairy. *Monocarps* 10-30, green, maturing purple in vivo, black in sicco, ellipsoid, 11–15{–20} by 7–9{–15} mm, longitudinally wrinkled in sicco, sparsely covered with appressed hairs to glabrous, apex acute to apiculate (apiculum < 0.5 mm long), wall 0.5–1{–4} mm thick, stipes 1-3(-10) by 1.5-2 mm. Seed ellipsoid, 10-15 by 6-8 mm, pale brown, slightly to strongly rugose (in sicco) to slightly foveolate (in vivo).

Distribution — Ecuador (Morona-Santiago, Pastaza, Zamora-Chinchipe), Peru (Cajamarca, San Martín) and Brazil (Amazonas).

Habitat & Ecology — In premontane and montane forest, rarely in lowland rainforest, on soils derived from sandstone substrate or on red clay. At elevations of 0–1800(–2200) m. Flowering: November to May, August; fruiting: July to March.

Vernacular names — Peru: Palo yais, Wampu yais (*Ancuash* 469), Yais (*Rojas et al.* 150).

Additional specimen examined. BRAZIL, **Amazonas**, Reserva Florestal Ducke, km 26 of Manaus-Itacoatiara Road, 8 Aug. 1995, *Sothers et al. 540* (INPA, U).

Notes — *Guatteria pastazae* can be recognized by having verruculose leaves with obscure venation and by an attenuate leaf base, combined with shortly pedicellate flowers and shortly stipitate monocarps.

Guatteria pastazae shows some features of *G. modesta* Diels but it differs by its much shorter stipes (stipes shorter than to almost equalling monocarp length) vs stipes longer than monocarp.

After the publication of Erkens et al. (2008) the present authors investigated a specimen collected a long distance from Ecuador and Peru, namely *Sothers et al. 540* from the lowlands of Amazonian Brazil, near Manaus. As that collection nicely fitted in all essential features (inconspicuous leaf venation, wrinkled fruits, etc.) with *G. pastazae* we have placed it there.

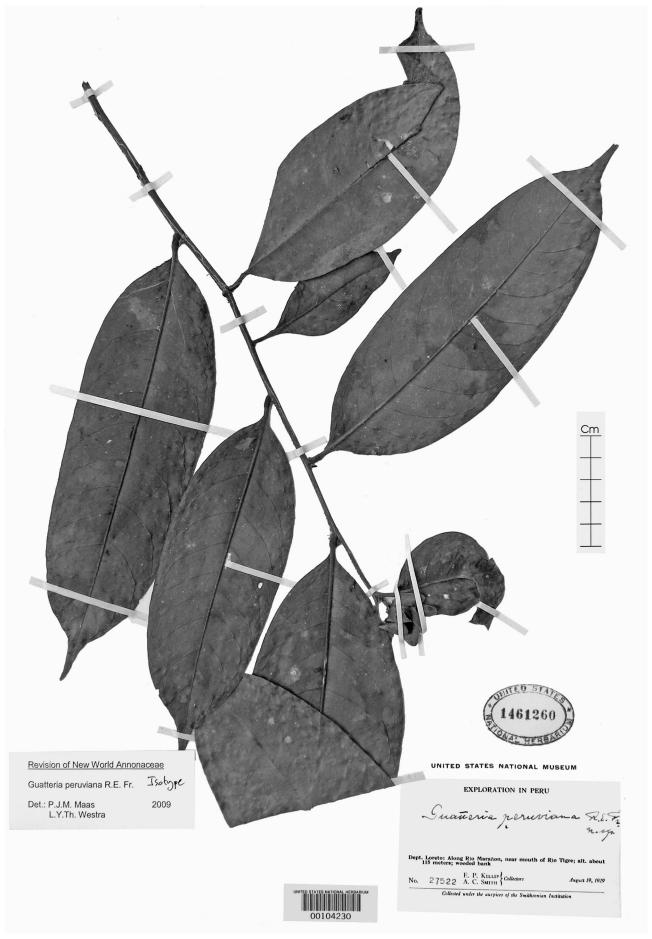


Fig. 19 Guatteria peruviana R.E.Fr. Flowering specimen (Killip & Smith 27522, iso US).

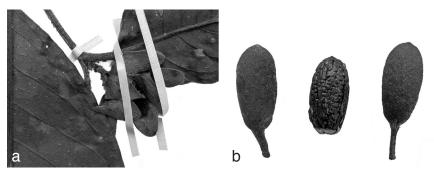


Fig. 20 Guatteria peruviana R.E.Fr. a. Flower, detail of fig. 19; b. detail of monocarps and seed (all: Killip & Smith 27522, iso US).

18. Guatteria peruviana R.E.Fr. — Fig. 19, 20; Map 3

Guatteria peruviana R.E.Fr. (1938) 720. — Type: Killip & Smith 27522 (holo F; iso B, US (2 sheets)), Peru, Loreto, Rio Marañon, near mouth of Río Tigre, 115 m, 19 Aug. 1929.

Guatteria macrocarpa R.E.Fr. (1938) 719, syn. nov. — Type: Killip & Smith 28965 (holo US; iso B), Peru, Loreto, Santa Rosa, lower Río Huallaga, below Yurimaguas, 135 m, 1–5 Sept. 1929.

Tree 6-15 m tall, diam not recorded; young twigs densely to rather densely covered with appressed and some erect hairs, soon glabrous. Leaves: petiole 5-10 mm long, 1-3 mm diam; lamina narrowly elliptic, 15-20 by 5-8 cm (leaf index 2.5-3), chartaceous, rather densely verruculose, greenish brown to brown on both sides, glabrous above, rather densely to sparsely covered with appressed hairs below, particularly along primary vein, base acute to obtuse, apex acuminate (acumen 5-20 mm long), primary vein flat to slightly impressed above, secondary veins distinct, 12–17 on either side of primary vein, flat above, smallest distance between loops and margin 1–3 mm. Flowers in 1-flowered inflorescences in axils of leaves; pedicels 7–12 mm long, 1-1.5 mm diam, fruiting pedicels up to 15 mm long, 2-3 mm diam, densely to sparsely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts 5–6, soon falling; flower buds not seen; sepals free, broadly ovate-triangular, 4-5 by 4-5 mm, reflexed, outer side densely covered with appressed hairs; petals pale salmon pink, elliptic, 15-20 by 5-6 mm, outer side densely covered with appressed hairs; stamens c. 2 mm long, connective shield glabrous. Monocarps c. 25, brown in sicco, ellipsoid, 16-24 by 8-10 mm, sparsely covered with appressed hairs, apex apiculate (apiculum c. 0.5 mm long), wall c. 0.5 mm thick, stipes 5-8 by 1-2 mm. Seed ellipsoid, c. 16 by 7 mm, dark brown, strongly longitudinally and transversely ridged.

Distribution — Peru (Loreto).

Habitat & Ecology — In non-inundated forest and along river banks. At elevations of 125–580 m. Flowering: August; fruiting: September.

Vernacular names — None.

Other specimen examined. Peru, San Martín, trail across valley from km 35 to km 20 on Tarapoto-Yurimaguas road, 7 Dec. 2003, 580 m, *Pirie et al.* 169 (U, sterile collection).

Note — *Guatteria peruviana* is united here with *G. macro-carpa*, since the features given by Fries (number of secondary veins and leaf base) are highly variable in the genus *Guatteria* and can therefore hardly be used for specific distinction.

19. Guatteria scalarinervia D.R.Simpson

Guatteria scalarinervia D.R.Simpson (1975) 306; Erkens et al. (2008) 507, f. 17, pl. 3. — Type: Reyna R. 40 (holo F; iso F, K, MAD, NY, P, WIS), Peru, Loreto, Prov. Maynas, Distr. Santa María, Río Nanay, 150 m, 15 Dec. 1967. Guatteria sp. 3 Chatrou et al. (1997) 109.

Cauliflorous tree 6–25 m tall, 5–25 cm diam; young twigs rather densely covered with appressed hairs, soon glabrous. *Leaves*:

petiole 15-20 mm long, 2-3 mm diam; lamina narrowly elliptic, 13-18 by 3.5-5 cm (leaf index 2.7-4), chartaceous, not verruculose or sometimes sparsely verruculose at least on parts of the leaves, dull above, dark greenish brown above, pale brown below, glabrous above, rather densely covered with appressed hairs below, base acute to abruptly attenuate, apex acuminate (acumen 5-20 mm long), primary vein impressed above, secondary veins distinct, 10–15 on either side of primary vein, impressed above, smallest distance between loops and margin 2-4 mm. Flowers in up to many-flowered clusters on the trunk; pedicels 20-35 mm long, 1-1.5 mm diam, fruiting pedicels up to 40 mm long, to 2{-3} mm diam, densely to sparsely covered with appressed hairs, articulated at 0.2-0.5 from the base, bracts 5-6, soon falling, the basal bracts broadly ovate, c. 1 mm long, the upper ones narrowly obtrullate to narrowly obovate-elliptic, 10-12 by 4-5 mm; flower buds broadly ovoid; sepals free, broadly ovate, 4-7 by 4-7 mm, appressed, outer side rather densely to densely covered with appressed hairs; petals green, maturing yellow to cream in vivo, ovate, elliptic, to oblong-obovate, 12-14 by 7-10 mm, outer side densely covered with appressed hairs; stamens c. 1.5 mm long, connective shield glabrous. Monocarps 25-50, green, maturing bluish black to black in vivo, brownish in sicco, ellipsoid, 15-21 by 7–11 mm, rather densely to sparsely covered with appressed hairs, apex apiculate (apiculum up to 1 mm long), wall 0.1–1 mm thick, stipes 10-25 by 1 mm. Seed ellipsoid, 15-18 by 7-9 mm, dark brown, rugose.

Distribution — Ecuador (Orellana, Sucumbíos) and Peru (Loreto).

Habitat & Ecology — In non-inundated forest (one collection from periodically inundated tahuampa forest), on red, clayey to lateritic soil. At elevations of 200–350 m. Flowering: April to June, October; fruiting: January, May, August to November.

Vernacular names — Ecuador: Dimonkawe (Huaorani), Nagewe (Huaorani) (*Naranjo & Freire 474*), Pungaracaspi, Pungaramuyo (*Palacios & Neill 1120*), Uñitawe (Huaorani) (*Freire & Naranjo 481*).

Note — Guatteria scalarinervia is easily recognized by being cauliflorous and having relatively long petioles and stipes. Unlike other species in sect. *Mecocarpus*, verruculae are not always evident on leaves in some collections or are clearly visible only in part of the leaves in a specimen. This deserves further attention.

Guatteria trichocarpa Erkens & Maas — Fig. 21, 22; Map 3

Guatteria trichocarpa Erkens & Maas (2008) 404. — Guatteriella tomentosa R.E.Fr. (1939) 541, f. 39; Murillo A. & Restrepo (2000) 124, f. 38. — Type: Ducke RB3916 (holo S; iso RB), Brazil, Amazonas, São Paulo de Olivença, Rio Solimões, 25 Feb. 1932; not Guatteria tomentosa Rusby (1910).

Tree or shrub 3–20 m tall, 12–80 cm diam; young twigs densely covered with a velutinous indument of erect and appressed

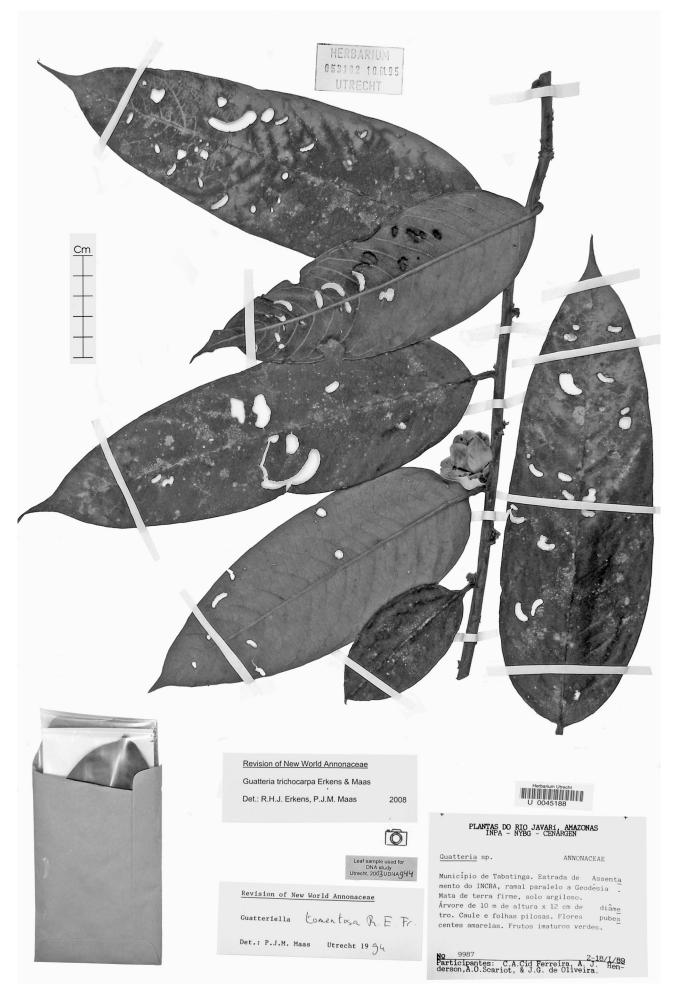


Fig. 21 Guatteria trichocarpa Erkens & Maas. Flowering specimen (Cid et al. 9987, U).

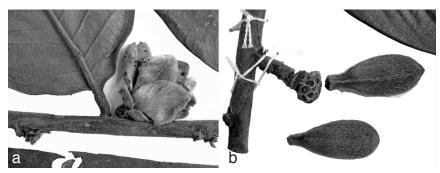


Fig. 22 Guatteria trichocarpa Erkens & Maas. a. Flower, detail of fig. 21; b. detail of fruiting pedicel and two monocarps (a: Cid et al. 9987; b: Cid et al. 8547, all U).

long-persistent hairs. Leaves: petiole 5-10 mm long, 1-4 mm diam; lamina narrowly oblong-ovate, 18-30 by 4-8 cm (leaf index 2.6–4.5), chartaceous, rather densely to sparsely verruculose, greyish to blackish brown above, brown below, glabrous above, but hairy primary vein densely covered with erect, brown hairs, densely covered with appressed and erect, brown hairs 3-4 mm long below, base obtuse to rounded, apex acuminate (acumen 15-30 mm long), primary vein impressed above, secondary veins distinct, 15-30 on either side of primary vein, raised above, smallest distance between loops and margin 1-3 mm. Flowers solitary in axils of leaves; pedicels 5-12 mm long, 2 mm diam, fruiting pedicels 12-20 mm long, 4-5 mm diam, densely covered with appressed, brown hairs, articulated at 0.5-0.8 from the base, bracts c. 6, very broadly ovate, to c. 4 mm long; flower buds ovoid; sepals free, broadly ovate-triangular, 7-10 by 6-8 mm, appressed, outer side densely covered with appressed, brown hairs; petals greenish yellow to yellow in vivo, ovate to oblong-ovate, 15-27 by 10-15 mm, outer side densely covered with appressed, brown hairs; stamens 1.5-2 mm long, connective shield densely covered with erect hairs. Monocarps 15-25, green in vivo, brown in sicco, ellipsoid, 19-30 by 10-15 mm, densely covered with appressed, brown hairs, apex rounded, wall 1-3 mm thick, stipes 3-8 by 3-5 mm. Seed ellipsoid, 16-20 by 8-9 mm, dark brown, longitudinally and transversely striate.

Distribution — Colombia and Brazil (both Amazonas).

Habitat & Ecology — In non-inundated forest, on clayey to sandy soil, one collection from caatinga on white, sandy soil. At elevations below 200 m. Flowering: December, January; fruiting: November.

Vernacular names — Colombia: Butruchicu (Muinane) (*Mu-rillo A. & Rodríguez A. 538*), K+y+meko (Miraña).

Other specimens examined. Brazil, Amazonas, Upper Rio Solimões, Mun. São Paulo de Olivença, road to Bom Fim, Cid et al. 8547 (U); Mun. Tabatinga, Estrada do INCRA, branch parallel to Geodésia, Cid et al. 9987 (U); Tabatinga, Estrada do INCRA, 6 km NE of Avenida Internacional, Daly et al. 4494 (U); São Paulo de Olivença, Creek Belém, Krukoff 8765 (NY). — Colombia, Amazonas, Peña Roja, Río Caquetá, Murillo A. & Rodríguez 538 (COAH, COL, U); Puerto Santander, trocha hacia Ciudad Perdida por Monochoa, Murillo A. et al. 699 (COAH, COL); trocha a La Chorrera, Murillo A. et al. 753, 760 (COAH. COL); Villazul, Río Caquetá, Murillo A. et al. 872 (COAH, COL).

Note — *Guatteria trichocarpa* can be recognized by a dense indument of appressed to erect, brown hairs on most parts of the plant. Furthermore, it is characterized by large, thick-walled monocarps, with short stipes up to 5 mm diam. The elongation of the fruiting pedicel is caused by growth of the part below the articulation, rather than growth of the upper part as is most commonly seen in *Guatteria*.

21. Guatteria venosa Erkens & Maas

Guatteria venosa Erkens & Maas in Erkens et al. (2008) 509, f. 18. — Type: T.D. Pennington et al. 15607 (holo U; iso K), Ecuador, Pichincha, Cantón Pedro Vicente Maldonado, Reserva Río Silanche, 600–700 m, Nov. 1996. Guatteria sp. 7 Chatrou et al. (1997) 110.

Tree (6–)10–24 m tall, 6–80 cm diam, with buttresses; young twigs glabrous, smooth or rather densely verruculose. Leaves: petiole 10–25 mm long, 3–5 mm diam; lamina narrowly elliptic to narrowly obovate, 16-40 by 6-15 cm (leaf index 2.6-3.6), coriaceous, not verruculose or sparsely to rather densely verruculose toward the base, shiny above, greyish white above, pale brown below, glabrous above, sparsely covered with appressed hairs to glabrous below, base attenuate, apex acuminate (acumen 5–10 mm long), primary vein impressed above, rather densely to densely verruculose below toward the base, becoming sparsely verruculose to smooth toward the apex, secondary veins distinct, 25–35 on either side of primary vein, strongly impressed above, marginal vein present, smallest distance between marginal vein and margin 2-5 mm. Flowers in 2-several-flowered inflorescences or single (at least in fruit) mostly on older branchlets or in axils of fallen leaves; pedicels 10-20 mm long, 1.5-2 mm diam, fruiting pedicels to 25 mm long, 5 mm diam, densely covered with appressed hairs, articulated at 0.2–0.3 from the base, bracts c. 5, soon falling; flower buds depressed ellipsoid to depressed ovoid; sepals basally connate to free, broadly ovate, 5-6 by 5-6 mm, appressed to patent, outer side densely covered with appressed hairs; petals green, greenish cream, tannish to yellow in vivo, broadly ovate to broadly ovate-triangular, c. 10 by 10 mm, outer side densely covered with appressed hairs; stamens c. 2 mm long, connective shield finely papillate-hairy to subglabrous. Monocarps 10-30, green, maturing black in vivo, black in sicco, ellipsoid, 11–14 by 5–6 mm, glabrous, except for some hairs at the apex, apex apiculate (apiculum c. 0.5 mm long), wall 0.5-0.8 mm thick, stipes 5-9 by 1.5-2 mm. Seed ellipsoid, 10-13 by 5-6 mm, pale to dark brown, rugose.

Distribution — Western Ecuador (Carchi, Esmeraldas, Pichincha).

Habitat & Ecology — In premontane wet forest. At elevations of 250–1000 m. Flowering: May, June, September to November; fruiting: February to June.

Vernacular names — Ecuador: Cargadera negra (*Méndez et al. 284*), Degteiug, Tilalde (Awapit) (*Aulestia & Grijalva 1187*).

Note — *Guatteria venosa* belongs to Fries's sect. *Mecocarpus* by its distinct marginal vein, the presence of verruculi on the leaves and by the short stipes. It is distinguished from other species of sect. *Mecocarpus* by an unusually high number of secondary veins (hence the specific name) and by the few verruculi on the leaves compared to other species in the section.

22. Guatteria sp. B — Fig. 23; Map 1

Guatteria sp. B Murillo A. & Restrepo (2000) 119, f. 36.

Tree (5–)13–16 m tall, diam not recorded; young twigs densely to rather densely covered with long-persistent, erect, rough



Fig. 23 Guatteria sp. B. a. Sterile specimen; b. indument, detail of a; c. young flower (a, b: Duque & Posada 4189; c: Murillo A. et al. 510, all U).

hairs up to 3 mm long. Leaves: petiole 3-5 mm long, 2-4 mm diam; lamina narrowly elliptic to narrowly obovate, 15-26 by 4-7 cm (leaf index 3-5), chartaceous, very densely verruculose, dull, brown to greyish brown above, brown below, sparsely covered with erect hairs, mainly along primary vein above, densely covered with erect, rough hairs to 3 mm long below, base obtuse, apex long-acuminate (acumen 10-20 mm long), primary vein impressed above, secondary veins distinct, 16-22 on either side of primary vein, impressed above, forming a distinct marginal vein, smallest distance between marginal vein and margin 2-4 mm. Flowers in 1-flowered inflorescences in axils of leaves; pedicels (3-)11 mm long, 1-2 mm diam, densely covered with long-persistent, erect, rough hairs up to 3 mm long, articulated at c. 1 mm from the base (fide Murillo A. & Restrepo 2000), bracts 5-11 by 4-6 mm; flower buds ovoid; sepals free, ovate to broadly ovate, 8-10 by 5-8 mm, appressed, apex acuminate, outer side densely covered with erect, brown hairs; petals green to white in vivo, oblong-ovate to elliptic, 8-15 by 4-7 mm, outer side densely covered with erect, woolly hairs; stamens 1.5-2 mm long, connective shield papillate. Monocarps purplish black in vivo, ellipsoid, c. 16 by 9 mm, sparsely covered with erect hairs, apex apiculate, stipes c. 20 by 1 mm (fide Murillo A. & Restrepo 2000). Seed not seen.

Distribution — Amazonian Colombia (Amazonas, Caquetá). Habitat & Ecology — In non-inundated forest, on clayey to sandy soil. At elevations of up to 300 m. Flowering: July, November; fruiting: January.

Vernacular names — Colombia: Buruchicu (Muinane) (*Van Andel et al. 161*), Carguero (Muinane), Duj+ku (Uitoto), J+d+ra (Uitoto) (*Cárdenas et al. 4064*), Ñaajeku (Muinane) (*Murillo A. et al. 510*).

Other specimens examined. Colombia, Amazonas, Villa Azul, Río Caquetá, Van Andel et al. 161 (U); Puerto Santander, Monochoa, Cárdenas et al. 4064 (COAH, U); Río Caquetá, Leticia, Villa Azul, 200–270 m, Duque & Posada 4189 (U); right margin of Río Caquetá, Quebrada Bocaduche, Murillo A. et al. 510 (COAH, COL, U). Caquetá, Municipio Solano, Río Mesay, raudal Masaca, 300 m, Cárdenas et al. 6772 (COAH, U).

Notes — This as yet undescribed species looks similar to *G. hispida* as to the leaf shape and the dense indument of stiff, erect hairs. It differs from the latter by the presence of a distinct marginal leaf vein, while in *G. hispida* the leaves do not show a marginal vein. There is scanty flowering material, only representing flowers in young stage. Murillo A. & Restrepo described fruiting material as well, but we did not see that. Altogether, it seems wisest at the moment not to formally publish a new species.

Murillo A. & Restrepo (2000) attribute the collection *Stein et al.* 4002 (MO, U) from Loreto, Peru, to this as yet undescribed species as well. Actually, it is the type collection of *G. grandipes*.

Acknowledgements Many thanks are due to Roy Erkens (Institute of Environmental Biology, Utrecht University) for critically reading the manuscript and making valuable additions to the introductory chapter and also for his help in preparing the distribution maps. We thank Lars Chatrou (WAG), Michael Pirie (Stellenbosch, South Africa), Jürgen Homeier (GOET), Marleen Botermans and Robin van Velzen (WAG) for making their photographs available for our study. Furthermore we thank the curators of all herbaria for sending us material on loan.

REFERENCES

- Aublet F. 1775. Histoire des plantes de la Guiane françoise 1: 610. Pierre-François Didot jeune, Paris, London.
- Bentham G. 1853. Notes on the American species of Myristica. Hooker's Journal of Botany and Kew Garden Miscellany 5: 8–9.
- Chatrou LW, Maas PJM, Repetur CP, Rainer H. 1997. Preliminary list of Ecuadorean Annonaceae. In: Valencia R, Balslev H (eds), Estudios sobre diversidad y ecología de plantas: 106–112. (Memorias del II Congreso

- Ecuatoriano de Botánica ... 1995). Pontificia Universidad Catolica del Ecuador, Quito / Universidad de Aarhus, Aarhus.
- De Candolle AP. 1817. Regni vegetabilis systema naturale 1: 502. Treuttel & Würtz, Paris.
- Diels L. 1924. Anonaceae. In: Mildbraed J, Plantae Tessmannianae peruvianae 1. Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 9: 137–141.
- Diels L. 1927. Anonaceae II. In: Mildbraed J, Plantae Tessmannianae peruvianae VI. Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem 10: 169–177.
- Dunal MF. 1817. Monographie de la famille des Anonacées: 126. Treuttel & Würtz. Paris.
- Erkens RHJ. 2007. From morphological nightmare to molecular conundrum. Phylogenetic, evolutionary and taxonomic studies on Guatteria (Annonaceae). PhD-thesis, Utrecht University, Utrecht, The Netherlands (electronically available at: http://igitur-archive.library.uu.nl/dissertations/2007-0227-200317/UUindex.html).
- Erkens RHJ, Chatrou LW, Koek-Noorman J, Maas JW, Maas PJM. 2007a. Classification of a large and widespread genus of neotropical trees, Guatteria (Annonaceae) and its three satellite genera Guatteriella, Guatteriopsis and Heteropetalum. Taxon 56: 757–774.
- Erkens RHJ, Chatrou LW, Maas JW, Van der Niet T, Savolainen V. 2007b. A rapid diversification of rainforest trees (Guatteria; Annonaceae) following dispersal from Central into South America. Molecular Phylogenetics and Evolution 44: 399–411.
- Erkens RHJ, Maas JW, Couvreur TLP. 2009. From Africa via Europe to South America: migrational route of a species rich genus of neotropical lowland rainforest trees (Guatteria; Annonaceae). Journal of Biogeography 36: 2338–2352.
- Erkens RHJ, Maas PJM. 2008. The Guatteria group disentangled: sinking Guatteriopsis, Guatteriella and Heteropetalum into Guatteria. Rodriguésia 59: 401–406.
- Erkens RHJ, Maas PJM, Chatrou LW, Schatz GE, Zamora N. 2006. Seven taxonomic discoveries in Annonaceae from South-Eastern Central America. Blumea 51: 199–220.
- Erkens RHJ, Westra LYT, Maas PJM. 2008. Increasing diversity in the species-rich genus Guatteria (Annonaceae). Blumea 53: 467–514.
- Fries RE. 1900. Beiträge zur Kenntnis der Süd-Amerikanischen Anonaceen. Kongl. Svenska Vetenskaps Academiens Handlingar, n.s., 34, 5: 18.
- Fries RE. 1934. Revision der Arten einiger Anonaceen-Gattungen III. Acta Horti Bergiani 12: 110–111.
- Fries RE. 1937. Revision der Arten einiger Anonaceen-Gattungen IV. Acta Horti Bergiani 12: 275.
- Fries RE. 1938. Annonaceae. In: Macbride JF, Flora of Peru. Field Museum of Natural History, Botanical series, 13, 2: 719–721.
- Fries RE. 1939. Revision der Arten einiger Annonaceen-Gattungen V. Acta Horti Bergiani 12: 289–577.
- Fries RE. 1947. Die Annonaceen der vierten Regnellschen Expedition. Arkiv för Botanik 33A: 5.
- Fries RE. 1949. Contributions to the knowledge of the Annonaceae in northern South America. Arkiv för Botanik n.s. 1: 338–340.
- Fries RE. 1957a. Annonaceae. In: Maguire B et al., The botany of the Guyana Highlands, Part II. Memoirs of the New York Botanical Garden 9.
- Fries RE. 1957b. New species of Annonaceae from the Upper Amazon Basin. Arkiv för Botanik n.s. 3: 601.
- Fries RE. 1959. Annonaceae. In: Melchior H (ed), Die Natürlichen Pflanzenfamilien ... begründet von A. Engler und K. Prantl, ed. 2, Band 17a II: 1–171. Duncker & Humblot, Berlin.
- Maas PJM, Maas H, Miralha JMS, Junikka L. 2007. Flora da Reserva Ducke, Amazonas, Brasil: Annonaceae. Rodriguésia 58: 644–645.
- Maas PJM, Westra LYT. 2010. New species of Annonaceae from the Neotropics and miscellaneous notes. Blumea 55: 259–275.
- Murillo A. J, Restrepo L. 2000. Las anonáceas de la región de Araracuara (Estudios en la Amazonia colombiana XX): 95, 119, 124. Tropenbos Colombia.
- Rodrigues WA. 1981. Guatteriopsis friesiana W. Rodrigues, nova espécie de Annonaceae para a Amazônia. Acta Amazonica 11: 49–51.
- Rusby HH. 1910. New species from Bolivia, collected by R.S. Williams I. Bulletin of the New York Botanical Garden 6: 504–505.
- Safford WE. 1914. Classification of the genus Annona with descriptions of new and imperfectly known species. Contributions from the United States National Herbarium 18: 6.
- Scharf U, Maas PJM, Morawetz W. 2005. Five new species of Guatteria (Annonaceae) from the Pakaraima Mountains, Guyana. Blumea 50: 563–573
- Scharf U, Maas PJM, Morawetz W. 2006a. Five new species of Guatteria (Annonaceae) from French Guiana, Guyana and Suriname. Blumea 51: 117–130.

Scharf U, Maas PJM, Morawetz W. 2006b. Guatteria richardii (Annonaceae) rediscovered along with two new species from French Guiana. Blumea 51: 541–552

Scharf U, Maas PJM, Prévost MF. 2008. An unusual new species of Guatteria (Annonaceae) from French Guiana and adjacent Brazil (Amapá). Blumea 53: 515–523.

Simpson DR. 1975. New species from South America II. Phytologia 30: 306. Spichiger R, Méroz J, Loizeau PA, Stutz de Ortega V. 1989. Contribución a la flora de la Amazonia Peruana. Los árboles del Arborétum Jenaro Herrera. I Moraceae a Leguminosae. Boissiera 43: 124.

Van Marle EJ. 2003. Leaf anatomy of Pseudoxandra. In: Maas PJM, Westra LYT, Revision of the Neotropical genus Pseudoxandra. Blumea 48: 206–211.

Van Marle EJ. 2007. Leaf anatomy of Bocageopsis, Onychopetalum and Unonopsis. In: Maas PJM, Westra LYT, Vermeer M, Revision of the Neotropical genera Bocageopsis, Onychopetalum and Unonopsis. Blumea 52: 419–425.

Van Setten AK, Koek-Noorman J. 1986. Studies in Annonaceae VI. A leafanatomical survey of genera of Annonaceae in the Neotropics. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 108: 17–50.

Van Setten AK, Koek-Noorman J. 1992. Fruits and seeds of Annonaceae. Morphology and its significance for classification and identification. Studies in Annonaceae XVII. Bibliotheca Botanica 142: 12. 52–54. pl. 22–23.

Von Martius CFP. 1841. Anonaceae. In: Von Martius CFP (ed), Flora brasiliensis 13, 1: 38. Frid. Fleischer in comm., München, Leipzig.

IDENTIFICATION LIST

The abbreviations behind the collector numbers refer to the following names:

Acevedo R. et al. 6076: ble; 7355: sca; 7408: dec – Almeida INPA783: fri – Alvarez et al. 2407: dec – Amaral et al. 518: jap; 674, 1190: ble – Ancuash 469: pas – Assunção 313: his – Aublet s.n.: gui – Aulestia et al. 288: dec; 693: ven; 957: dec; 1187, 1358: ven; 2472, 2595, 2663: sca; 3533: gui – Ayala 2546: dec; 2969: gui – Aymard C. et al. 6179, 7324: ble.

Bahia 58: cry – Baker et al. 5516: dec; 5716: pas – Balslev et al. 97092: lon; 97498: dec; 97500: gui – Berg & Palacios 1560: lon – Betancur et al. 2903: lon – Bloch & Valencia 67548: dec; 67887: gui; 67916: sca – Bonifaz & Cornejo 3832: ven – Boom & Weitzman 5264, 5382, 5586: ins – Bordenave 422: gui – Brandbyge et al. 33790: dec; 33854, 33979: ble; 36122: lon – Breteler 4759: ble.

Callejas et al. 4152, 8522: gui – Campbell et al. 8817: duo; P21887: ble; P21986: fri – Campos et al. 480: his; 3414, 3557: pas – Cárdenas et al. 4064, 6772: spB – Castillo et al. 641: duo – Castro et al. 101: duo – M. Cerón & Coello 3247: dec – Chatrou et al. 22, 25: duo; 174: sca; 196: dec; 245: ble; 392, 441, 442, 463: duo – Choo 217: lon – Cid et al. 543: ble; 775: dur; 979, 1128, 1843: ble; 3196: dur; 3642: sp.indet.; 4081, 4274, 6495, 6937: ble; 7008: mel; 7722: lon; 7727: ble; 8375: dur; 8547: tri; 9095: ble; 9987: tri; 10040: gui; 10591: ble – Clark et al. 3180: pas; 3194: dec – Clarke et al. 7132: mel; 10861: pak – D. Coêlho et al. INPA3609: fri: INPA4220: gui; INPA 92460: fri – L. Coêlho 3524: ble – Colella et al. 1804, 2145: dur – Cornejo et al. 26, 178: duo – Croat 18535, 18575: gui; 19402: dec; 20013: dur; 20759: dec.

Daly et al. 783: ble; 3997: gui; 4028: ble; 4494: tri; 9059: mel – Davidson 5330: dec; 5729: gui – Delprete et al. 7920: ble – Deward 76: gui – Díaz et al. 85, 426: gui; 785: ble; 1172: dec; 1543: gui; 1584: dec; 7888, 10260: pas – Dick et al. 5, 79: fri – Dik 705: sca – Dodson et al. 14807: ven – Ducke RB3916: tri; RB23903: his – Duque & Posada 453: dec; 4119: ins; 4189: spB.

Ellenberg 2852: dec – Espinoza et al. 268: dec; 535: sp.indet.

Ang. Fernández et al. 4985, 5266, 5794, 5916: ble – Ant. Fernández 2312: lon – Ferreira 9905: gui; 57-122: mel – Foster et al. 3751: gui; 5676, 7221: ble; 9525: gui; 11666: ble – Freire et al. 474, 481, 707: sca; 3610: dec – Freitas 7: ble – Fróes 20788: gui; 22108: ble; 26198: gui.

Gentry et al. 20430: sca; 20959: gui; 29344, 29763: dec; 30941: gri; 39057: gui; 39607: sca; 42254: dec; 43283: ble; 45155, 45732, 45841: duo; 47000: ins; 52230: ble; 54632: dec; 56359: ble; 57113: dur; 57593, 57667: duo; 61959, 61960: dec; 64984: sca; 65787: gui; 69284: fri; 70116: ven; 72309: dec; 77361: sca; 78417, 80686: duo — Gottsberger & Döring 11-28186: lon — Grández et al. 796, 921: dec; 1529: ble; 1855, 2094: gui; 2915: lon; 4193: gui — Grijalva et al. 369, 642: dec — Guánchez 379: ble — Gudiño 302: dec — Guillén & Soliz 3833: dur.

Hahn 3656: ble – Harling & Andersson 23337: ven – Haught 1485: nov – Haxaire et al. 2948, 3742, 3949: duo – Henkel et al. 4279: pak – Holm-Nielsen et al. 21626: ble – Homeier et al. 1570, 2098: pas; 2495, 2538: dec; 3819: pas – Hoyos & Hernández 807: gui – Huashikat 665, 832, 1046: gui – Hurtado et al. 14, 873, 2330, 2400, 2431: dec.

N. Jaramillo et al. 1201, 1269: pas.

Kajekai 960: gri; 1184: pas – Killip & Smith 27522, 28965: per; 29585: dec – Klug 1273: gui – Krukoff 1033: lon; 1534: gui; 4664: dec; 5050: mel; 5589: ble; 8500: lon; 8765: tri – Kubitzki et al. 79-245: lon? – Kuhlmann 460 = RB24256: dur; RB24260: lon; RB24361: cry – Kvist 1135, 1306: ble.

jap = G. japurensis = G. peruviana per Ion = G. longicuspis G. scalarinervia sca = mel = G. meliodora tri G. trichocarpa nov = G. novogranatensis = G. venosa ven pak = G. pakaraimae sp.indet. = G. sp. Bpas = G. pastazae

Lawrance 552, 635: nov – Lepsch Cunha et al. 422: ble; 932: fri – Leveau 250: gui – H.C. Lima et al. 2718: ble – J. Lima & Zimmerman 505: fri – Lisboa et al. 1413: cry – Lleras et al. P17021, P17337: lon – Lopes et al. 99: dur – Loubrie 263: gui – Loureiro 5908: fri – Lugo S. 181, 191, 227: pas.

Maas et al. 6206: ble; 6268: gui; 6700: ble; 6765, 6835: lon; 7775, 8186, 8187: gui; 8209: lon; 8228: ble; 8233, 8244, 8260: dec; 8269: sca; 8314: dec; 8357: ble; 8358: gui; 8365: ble; 8593: duo; 8611: dec; 9691: gui – Maceda 345: gui – Madison et al. 6323: ins – Maguire et al. 41745: dur; 56670: gui – Marimon 51, 67: ble – Méndez et al. 284: ven – Meyer 136: ble – Miralha et al. 270: ble; 283, 284: fri – Monteagudo et al. 5757, 6163: duo – Monteiro 1263: his – Morales at al. 1466: gui; 1885: pas – Mori & Gracie 21782: ble – Murillo A. et al. 510: spB; 518: lon; 529: sp.indet.; 538: tri; 544, 604: ins; 619: lon; 642: dec; 699, 753, 760, 872: tri.

Naranjo & Freire 180, 370, 474: sca – Nascimento 647: ins – Nee 31051: ins; 31691: duo – Neill et al. 5805, 6009: pas; 6304, 6350, 6819: dec; 7326: duo; 7954: sca; 8106: duo; 8961: dec; 9452: duo; 9976, 10173, 10317: dec; 12948: gri; 14269: pas – Nuñez et al. 11448: duo.

Oldeman 1895, B-1928: gui – Øllgaard et al. 57186: duo – Ortiz et al. 85: dec.

Palacios et al. 591, 1044, 1065: dec; 1120: sca; 1146, 2298, 2929, 2932, 3481: dec; 4654: duo; 5118, 5539, 5617, 7075: gen; 7769: ble; 7791: dec; 8006: ble; 8085: sca; 8401: gri; 8474: pas; 9048: ble; 9353: gui; 9411: lon; 9413: ble; 12213: ven; 13218: pas – R.D. Pennington et al. 124: duo – T.D. Pennington et al. 15607, 15384: ven; P22652: ble – Perea et al. 259: duo – Pereira INPA/WWF 2303.6161: mel – Pipoly et al. 12208: dec – Pires et al. 50875: cry; 51901, 52613: gui – Pirie et al. 81, 112, 126: dec; 131, 138: pas; 169: per; 172: pas – Pitman et al. 1794, 5181: dec; 6104: sca – Plowman et al. 8088: gui; 9413: cry; 12233: gui – Prance et al. 1799: gui; 2277: dur; 3889, 11415, 16328: ble; 20620: dur; 20958, 23543: ble; 24125: lon; 24942, 25063: ble; 58873: gui; 59392: ble – Prévost et al. 3364, 3495, 3785, 4269: gui.

Quizhpe et al. 1171: pas.

Rabelo et al. 2366: ble; 2748: cry; 2970: gui; 3132: ble – Rainer et al. 256: gui; 259: dur – Ramírez C. 79, 124: dur – Ramos 2827, 2844, P19680: ble – Renner 69066: sca – Revilla et al. 2188: sca – Reyna R. 40: sca – Ribeiro et al. 208: fri; 845: his; 955: gui; 1014: his; 1030: ble; 1034: his; 1571, 1646: gui; 1710: mel – Riera 478: gui – Y. Rimachi 3593: lon; 4175: ble – Rodrigues et al. 534: ble; 578: gen; 5384, 5827: ble; 5908: fri; 6745: gui – Rodriguez R. & Cruz A. 2053: pas – Rojas et al. 36: dec; 150: pas; 4090, 4660, 4663: duo – Romoleroux et al. 1966, 2184, 2317, 2933: sca – Rosa 1019: gui – Rubio et al. 42, 2392: dec – J. Ruiz & Jaramillo 1080: dec – M. Ruiz et al. 8018, 8137: ble.

Sabatier et al. 2388, 4042: gui — Sánchez-Vega et al. 8682, 9971: gri — Santos 298: cry — Schultes et al. 3937, 8939: lon; 8949: ble; 26118: mel — Schunke V. et al. 4294: ble?; 7844, 8674, 10555, 15266: ble — A.S.L. Silva et al. 381: gui — N.T. Silva & C. Rosário 5090: ble — Smith 5290: duo — Sothers et al. 540: pas — J.A. Souza 192: mel — M.A.D. Souza & Silva 37: ble — Spichiger 1772: mel — Spruce 1668: ble; 2896: ins; 3354: dur; s.n.: lon — Stein et al. 4002: gra — Stergios et al. 4216, 9763: lon; 9935: dur; 13121: lon — Stevenson et al. 946: ins — Steward et al. 276: dur; 376: lon; P19680: ble — Steyermark et al. 103043: ble; 129768: ins.

Teixeira et al. 164: ble; 1294: dur – Tessmann 3212: ble; 5192: gui – Thomas et al. 2024: duo; 3822: ble; 6787: dec – Tipaz et al. 1119, 1336: ven – Tirado 1884: dec – Toasa 5096: pas – Tunqui 857: gui.

Urrego et al. 293A, 1417, 1572, 1785, 1979: dur.

Valencia et al. 67738: gui – Valenzuela & Huamantupa 978: ble – Van Andel et al. 136: dur; 161: spB – Van der Werff et al. 10060: ble; 12046: ven; 16768: gri; 19221: pas – Vargas et al. 683, 920, 927: gen – Vásquez et al. 242: lon; 840: dur; 1017: mel; 1328, 1434: gui; 1895: ble; 1939: gui; 2304: ble; 2348: sca; 2600, 2865, 2928: gui; 4322, 4984: ble; 5109: gui; 5636: sca; 5961(?): ble; 5968: gui; 6642: ble; 6858: gui; 8357: ble; 8619, 8661: gui; 9255: per?; 10436: mel; 11052: dec; 12285: ble; 12289: ble; 12543,

12962: dur; 13013: dec; 13319: duo; 13538, 13811, 13814: gui; 14331, 14336: dec; 14341: gui; 14527, 16622: dec; 17500: gui; 19220, 19305, 25525, 25592, 25626, 25609: duo; 32940: duo – Vicentini & Assunção 1181: ble – Vieira et al. 720: gui; 745, 939, 1025: ble – Villa et al. 1226: dec – Von Martius s.n.: ble.

Wallnöfer 12-9788: per, aff. – Webber et al. 1276: dur – Wisum et al. 584: gri; 726: pas – Woytkowski 6107: ble – WWF Plot 2206-1818 s.n.: gui.

Yanez 187: dur.

Zak & Espinoza 4484: dec; 4811, 5016, 5057: duo – Zaruma 553: sca – Zuleta 212: dec.

INDEX TO SCIENTIFIC NAMES

Accepted taxa are in roman type, new taxa in **bold** and synonyms in *italics*. Numbers refer to the species number as used in this article.

Aberemoa guianensis Aubl. 9
Annona sessiliflora Benth. 1
Duguetia leptocarpa Benth. ex R.E.Fr. 13
Guatteria
aberemoa Dunal 9
var. microcarpa DC. 9
amazonica R.E.Fr. 13
blepharophylla Mart. 1
brevicuspis R.E.Fr. 1
calophylla R.E.Fr. 9
cryandra Erkens & Maas 2

calophylla R.E.Fr. 9 cryandra Erkens & Maas 2 cylindrocarpa R.E.Fr. 1 decurrens R.E.Fr. 3 dielsiana R.E.Fr. 1

duodecima Maas & Westra 4

dura R.E.Fr. 5 excellens R.E.Fr. 9

friesiana (W.A.Rodrigues) Erkens & Maas 6

Guatteria (cont.)

grandipes Maas & Westra 7
griseifolia Maas & Westra 8
guianensis (Aubl.) R.E.Fr. 9
hispida (R.E.Fr.) Erkens & Maas 10
insculpta R.E.Fr. 11
japurensis Maas & Westra 12
kuhlmannii R.E.Fr. 5
longicuspis R.E.Fr. 13
macrocarpa R.E.Fr. 18
meliodora R.E.Fr. 14
microcalyx R.E.Fr. 13
multivenia Diels 9
novogranatensis R.E.Fr. 15

pakaraimae Scharf & Maas 16

pastazae R.E.Fr. 17 peruviana R.E.Fr. 18 robusta R.E.Fr. 9 Guatteria (cont.)

robusta R.E.Fr. 9 scalarinervia D.R.Simpson 19 sessiliflora (Benth.) Saff. 1 sp. 2 Chatrou et al. 13

sp. 3 Chatrou et al. 19 sp. 4 Chatrou et al. 8

sp. 12 Chatrou et al. 4

sp. *B* 22

trichocarpa Erkens & Maas 20 *ucayaliana* Diels 1

venosa Erkens & Maas 21 Guatteriella tomentosa R.E.Fr. 20

Guatteriopsis

blepharophylla (Mart.) R.E.Fr. 1 friesiana W.A.Rodrigues 6 hispida R.E.Fr. 10 kuhlmannii R.E.Fr. 2 sessiliflora (Benth.) R.E.Fr. 1